
One, two, or several? How many lymnaeid genera are there?

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ABSTRACT. The problem of generic classification of the basommatophoran family Lymnaeidae Rafinesque, 1815 is reviewed as well as recent theoretical approaches to genus delineation in the zoological systematics. Two main versions of the generic system of lymnaeid snails are: 1) bigeneric approach where all diversity of lymnaeid species is split between two genera; and 2) polygeneric approach suggesting that there are several (about twenty) genera in the family. The first version is presented in systems developed by Kruglov and Starobogatov [1993] and Jackiewicz [1993, 1998]. The second one is most commonly accepted in current Western European and Northern American literature [Burch, 1989; Falkner *et al.*, 2001; Glöer, 2002]. However, there are no grounds to delimit lymnaeid genera *objectively* as the solution critically depends on what taxonomic methodology (cladistic or 'evolutionary' taxonomy) is followed by a particular author. The 'evolutionary' taxonomic methodology (*sensu* Mayr) is favorable to the bigeneric approach, whereas the cladistic (Hennigian) methodology leads to the separation of a series of taxa of generic rank within Lymnaeidae. It is impossible to prefer one approach to another ultimately since the problem of acceptability of paraphyletic taxa is still not resolved. The co-existence of two different generic systems of the same family is therefore inevitable. Different criteria of generic rank were critically discussed in perspective of their applicability to lymnaeid taxonomy. The morphological and ecological criteria as well as the criterion of hybridizability proved to be controversial and their use gives no key to select one of these approaches. The fourth criterion, that of monophyly, is more usable now, when the data of molecular phylogenetics are available. The recent advances in molecular taxonomy of pond snails have been reviewed briefly. It seems very reliable that the family consists of two large monophyletic clades of deep origin that differ from each other by chromosome number albeit there are no morphological characters to distinguish surely between representatives of these clades. It is impracticable to assign the generic rank for these clades due to their huge internal heterogeneity (morphological and ecological). The most reliable cladistic solution is to regard the two deep lymnaeid clades as separate subfamilies each containing a set of genera that are internally homogeneous enough to comply with most of criteria of the genus rank. The scheme of lymnaeid classification proposed here includes the nominotypical subfamily

Lymnaeinae (type genus *Lymnaea* Lamarck, 1799) with haploid chromosome number equal to 18 (rarely 19), and the new one **Radicinae** subfam.n. (type genus *Radix* Montfort, 1810). The latter taxon embraces genera and species of Lymnaeidae characterized by 16 or (most often) 17 chromosome pairs. **Radicinae** is, most probably, derived clade as compared to Lymnaeinae, however, there are no morphological synapomorphies to support it. The bigeneric system is, however, still acceptable for those who uses generic criteria proposed by "evolutionary systematics" such as "principle of the same degree of difference" [Golikov, Starobogatov, 1988] and others.

Introduction

The basommatophoran family Lymnaeidae Rafinesque, 1815 is a very diverse and almost globally distributed group of freshwater snails. The global species diversity of this family is estimated from nearly 100 [Strong *et al.*, 2008] to not less than 250 [Kruglov, 2005] extant species. There is, however, no agreement among today's systematists on how many species and higher taxa (genera, subgenera) should be recognized within the family, and several alternative systems were proposed in the second half of the 20th century, i.e. before the ongoing molecular revolution in the zoological systematics. The systems are those of Hubendick [1951], Kruglov and Starobogatov [1993a, b; Kruglov, 2005], and Jackiewicz [1993, 1998]. In many aspects these systems do not correspond to each other and even are contradictory in some regards. In particular, the question of how many lymnaeid genera should be accepted has not been answered unambiguously. Some researchers accept only two genera and a plethora of subgenera within a large cosmopolitan genus *Lymnaea* Lamarck, 1799 [Jackiewicz, 1998; Kruglov, Starobogatov, 1993a, b; Kruglov, 2005]. Other workers prefer to treat these subgenera (including *Lymnaea* s.str.) as distinct genera [Ponder, Waterhouse, 1997; Falkner *et al.*, 2001; Glöer, 2002]. As a result, we have as many as three different systems on the generic level even for the very thoroughly studied lymnaeids of Europe

Table 1. Comparison of the three most recent generic systems of the European Lymnaeidae.

Таблица 1. Сопоставление трех наиболее современных систем европейских Lymnaeidae.

Kruglov, Starobogatov, 1993a, b		Glöer, 2002 (genera only)	Jackiewicz, 1998 (genera only)
Genus	Subgenus		
<i>Aenigmomphiscola</i> Kruglov et Starobogatov, 1981	–	–	–
<i>Lymnaea</i> Lamarck, 1799	<i>Galba</i> Schrank, 1803	<i>Galba</i>	<i>Lymnaea</i>
	<i>Lymnaea</i> s.str.	<i>Lymnaea</i> s.str.	
	<i>Myxas</i> Sowerby, 1822	<i>Myxas</i>	
	<i>Stagnicola</i> Leach in Jeffreys, 1830	<i>Stagnicola</i>	
	<i>Corvusiana</i> Servain, 1881		
	<i>Radix</i> Montfort, 1810	<i>Radix</i>	
	<i>Peregriana</i> Servain, 1881		
<i>Omphiscola</i> Rafinesque, 1819	<i>Omphiscola</i>	<i>Omphiscola</i>	

(Table 1). The absence of a commonly accepted concept of genus in “freshwater” molluscan taxonomy has been mentioned repeatedly [Meier-Brook, 1993; Strong *et al.*, 2008], and certain authors have tried to develop some “operational” rules for assigning generic rank to freshwater gastropods [Skarlato, Starobogatov, 1974; Radoman, 1983]. None of these rules has become generally adopted.

The genera and their names are of high importance for zoological systematics and related fields of life sciences where the Latin binominal names of species are used since the name of a genus is inserted in each binomen and users of taxonomical information are interested in stability of generic names [Dubois, 1988; Tsvelev, 1991]. For example, in paleobiology, genera rather than species are used in quantitative analyses of mass extinctions, large-scale biogeographic or evolutionary changes or demonstration of adaptive radiations [Allmon, 1992]. From the practical point of view, it would be most preferable to reach a universal and stable generic system for the Lymnaeidae.

This article is intended to discuss two important points related to the problem described above:

1. Is it theoretically possible to delimit genera in the family Lymnaeidae unambiguously?

2. Are data from recent studies of lymnaeid molecular phylogenetics and taxonomy helpful for objective delimitation of higher taxa in this family? Are these congruent with the morphology-based versions of the system?

A history of the generic classification of Lymnaeidae

Since 1815, when the family Lymnaeidae was established by Rafinesque [1815], many authors

have attempted to arrange numerous species of these snails in a series of higher taxa, including sections, subgenera, and genera. Briefly, all these approaches could be divided into two categories:

1. Most lymnaeid species are placed in a large genus *Lymnaea* (usually subdivided into a series of subgenera) and a smaller one including morphologically distinct species. This approach is designated here as “bigeneric”.

2. The family is split into a plethora of genera (mainly on the basis of conchological traits). This approach is designated here as “polygeneric”.

In the nineteenth century, most systems of the Lymnaeidae were bigeneric. For example, Nilsson [1823] divided all lymnaeids into two genera: *Lymnaea* and *Amphipeplea* Nilsson, 1823 (= *Myxas* G.B. Sowerby I, 1822), and a single species, *Buccinum glutinosum* O.F. Müller, 1774, was included in the latter genus. Separation of *B. glutinosum* into an independent genus was grounded on its specific morphological peculiarities (almost transparent round shell, mantle covering the shell from outside when the animal is in motion). This opinion was followed by Beck [1837], Herrmannsen [1846-1847], Küster [1862], Clessin [1884, 1887], Locard [1893], and, in the twentieth century, by Kennard and Woodward [1926], Germain [1931], and Zhadin [1933]. Some malacologists, however, united all lymnaeid species in a single genus *Limnaea*, or *Limnaeus* (both names are incorrect subsequent spellings of *Lymnaea*), without subdividing it to subgenera [e.g. Turton, 1831; Forbes and Hanley, 1852-1853; Jeffreys, 1862]. This archaic version of the system may be designated as “monogeneric”.

Possibly, Beck [1837] was the first author who proposed the subgeneric classification of the genus *Lymnaea* (*Limnaea* in Beck’s spelling). He distin-

Table 2. The system of the family Lymnaeidae s.lato proposed by W. Dybowski [1903].

Таблица 2. Система семейства Lymnaeidae s. lato, предложенная В. Дыбовским [1903].

Family	Genus	Subgenus
Amphipeplidae	<i>Amphipeplea</i>	–
Limnaeidae	<i>Limnaea</i> s. str.	<i>Limnus</i> Montfort, 1810
	<i>Gulnaria</i> Leach in Turton, 1831	<i>Omphalolymnus</i> W. Dybowski, 1903
Limnophysidae	<i>Limnophysa</i> Fitzinger, 1833	–
	<i>Leptolymnaea</i> Swainson, 1840	–
	<i>Fossaria</i> Westerlund, 1885	–

guished four subgenera of *Limnaea*: *Limnaea* s.str., *Gulnaria* Leach in Turton, 1831; *Limnophysa* Fitzinger, 1833, and *Omphiscola* Rafinesque, 1819. This approach was adopted in North America by Haldeman [1841-1842] and Dall [1905]. In France, Moquin-Tandon [1855] followed Beck albeit accepting only three superspecific groups of unclear rank in the genus *Limnaea*: *Amphipeplea*, *Gulnaria*, and *Limnaea* s.str.

The classification scheme proposed by Beck [1837], in which only two genera were distinguished within Lymnaeidae (large genus *Lymnaea* subdivided into subgenera or groups of species, and a monotypic genus *Amphipeplea*), became the most influential in the European malacological literature of the second half of the 19th and first half of the 20th centuries, especially among German [Kreglinger, 1870; Clessin, 1884, 1887-1890; Goldfuss, 1900] and Scandinavian [Mörch, 1864; Westerlund, 1873, 1885] malacologists.

The first version of a polygeneric system of the family was developed by F.C. Baker [1911; see also Baker, 1915], who also was the first to widely exploit anatomical characters for generic classification of Lymnaeidae. Baker [1911] divided the family into two subfamilies (Amphipepleinae “Dybowski, 1903”¹, Lymnaeinae) and recognized six distinct genera in the subfamily Lymnaeinae (*Lymnaea*, *Pseudosuccinea* Baker, 1908, *Radix*, *Bulimnea* Haldeman, 1841, *Acella* Haldeman, 1841, and *Galba* Schrank, 1803). He believed that these genera differed from each other in the anatomical structure of their reproductive organs, but subsequent authors have shown that there are no significant qualitative distinctions among the reproductive structures of Baker’s genera [Colton, 1915; Hubendick, 1951; Kruglov, 2005], and that most lymnaeid species possess same reproductive system *Bauplan*. In spite of this, Baker’s polygeneric system has become standard for North American malacology, and, much modified, remains in use [Burch, 1989; Brown, 2001]. Moreover, some influential Europe-

an malacologists of the first third of the 20th century soon adopted Baker’s approach and accepted five [Ehrmann, 1933] or six [Geyer, 1927] genera in the lymnaeid fauna of Europe. Possibly, it reflects the fact that Baker’s [1911] generic arrangement was carried out not on the base of anatomical traits only, and the characters of shell and radula were taken into account [Baker, 1915]. Thus, this system proved to be attractive for malacologists accustomed to study shell features of snails. Also, it is suitable for paleontologists, who cannot use other characters except of the conchological ones.

The most radical revision of higher taxa in Lymnaeidae was undertaken by Władysław Dybowski [1903], who splitted the family into three smaller ones, namely Amphipeplidae, Limnophysidae Dybowski, 1903, and Limnaeidae s. str., each including from one to three genera (Table 2). The Dybowski’s system was so radical that no contemporary malacologist, including Benedykt Dybowski, brother of Władysław, would adopt it.

The next anatomy-based generic system of the family Lymnaeidae was developed by a prominent Swedish malacologist Bengt Hubendick [1951]. Contrary to the Baker’s [1911, 1915] opinion, he accepted that conchological differences are of lesser importance for lymnaeid taxonomy, and only qualitative structural distinctions in the reproductive anatomy would constitute a good basis for generic classification. During his extensive anatomical work, Hubendick [1951] could recognize only two structural types of reproductive organs within Lymnaeidae, and therefore referred all lymnaeids to two genera: *Lymnaea* and *Lanx* Clessin, 1882. The latter genus is North American and includes lymnaeids with limpet-like shells and very peculiar anatomy [Baker, 1925]. The internal structure of *Lanx* is so unusual as compared to the rest of Lymnaeidae that this genus has often been placed in a separate family Lancidae Hannibal, 1914 [Baker 1925; Taylor, Sohl, 1962; Harry 1964; Starobogatov, 1967; Taylor, 1981]. All other species of lymnaeids from all continents proved to be too uniform in their anatomical structure even to distinguish subgenera within the genus *Lymnaea* [Hubendick, 1951].

¹ Bouchet and Rocroi [2005] ascribe the authorship of this subfamily to Pini [1877].

In the recent (1980–2000s) malacological literature three more or less distinct approaches to generic arrangement of lymnaeid snails were developed.

1. Polygeneric system accepted by most of European [Gittenberger *et al.*, 1998; Falkner *et al.*, 2001; Glöer, 2002; Anderson, 2005; Bank, 2011], North American [Burch, 1989; Brown, 2001], and Australian [Ponder, Waterhouse, 1997; Puslednik *et al.*, 2009] researchers, including those working on cytotaxonomy [Inaba, 1969; Patterson, Burch, 1978], and molecular genetics [Remigio, Blair, 1997; Bargues *et al.*, 2003, 2006; Puslednik *et al.*, 2009; and many others]. Remigio [2002] considered that molecular data (16S gene sequences) support a polygeneric system since genetic distances allow distinguishing good genera.

2. Bigeneric system proposed by Jackiewicz [1993, 1998] for European lymnaeids. Most species are placed in the genus *Lymnaea* (with five subgenera), and the only species, *Omphiscola glabra* (O.F. Müller, 1774), constitutes a genus of its own (see Table 1). According to Jackiewicz [1998], a set of five morphological apomorphies determines the independent generic status of *O. glabra*. This hypothesis, however, has no support from the most recent research [Vinarski *et al.*, 2011].

3. Bigeneric system proposed by Kruglov and Starobogatov [1981, 1993a, b] to include the genus *Lymnaea* (with 26 extant subgenera) and the small genus *Aenigmomphiscola* Kruglov et Starobogatov, 1981 containing only three species. The latter taxon was erected on the basis of a unique structure of the copulatory apparatus [Kruglov, Starobogatov, 1981; see also Vinarski *et al.*, 2011].

Generic concepts and current lymnaeid taxonomy

The “genus problem” attracts much less attention from taxonomists than the notorious “species problem” that has been discussed in hundreds and thousands of articles and monographs. The number of publications specially devoted to the theoretical aspects of the genus concept is not very high [see, for instance, Sherff, 1940; Cain, 1956; Inger, 1958; Legendre, 1971; Clayton, 1972, 1983; Leman, Freeman, 1984; Dubois, 1988; Maggenti, 1989; Allmon, 1992; Kafanov, Sukhanov, 1995]. In most cases, the problem of genera delineation is discussed with reference to a particular taxon or a group of taxa. For example, there are papers dealing with the genus concept in various groups of animals [Shaposhnikov, 1974; Martens, 2007; Verzi, 2008], fungi [Djakov, 1986; Vellinga, 2004], and plants [Tsvelev, 1991; Muthama Muasya *et al.*, 2009]. However, taxonomic clustering of species into genera is not the same in diverse groups of organisms.

Thus, an “average” taxon of generic rank in birds (mammals, insects, molluscs) is not equivalent to an “average” genus in, say higher plants, and so on [Mayr, 1969].

There are almost 30 different “species concepts” now [Wilkins, 2009], but what about the genus concepts?

Genera have been used in biological taxonomy since the pre-Linnaean epoch [Bartlett, 1940]. Linnaeus himself regarded genera as natural groups of species “between which there were definite discontinuities of attributes” [Cain, 1956: 98]. Several definitions of what a genus *is* are available in the modern taxonomic literature (Table 3), but there is still no objective (nonarbitrary) definition of the genus category [Mayr, 1982]. Dubois [1988], who is the author of a special monograph devoted to the genus concept in zoology, could distinguish as many as four distinct working concepts of genera [see also Allmon, 1992]. All of these represent a sort of a scientific theory that is intended to give a definition of a genus and (optionally) to propose a set of operational criteria for generic delineation. The four generic concepts and criteria for generic delimitation associated with these concepts are listed below.

1. **Empirical concept.** This postulates that a genus is merely a creation of the human mind, a practical convention developed for the sake of usability. There are no real genera in nature. Thus, generic delimitation is the subject of some practically oriented rules (or conventions).

2. **Phenetic concept.** Generic delineation is based on the quantitative estimation or measurement of phenotypic similarities between groups of species. It is assumed that phenotypic similarity arises as a reflection of the genotypic one. Phenetic concept views genera as clustered in multidimensional character space, separated from other such groups by many differences [Allmon, 1992]. Neither phylogenetic nor ecological information is needed to delimit genera.

3. **Cladistic, or phylogenetic, concept.** This concept was developed by the school of “phylogenetic systematics” founded by Hennig [1966]. For cladists, classification must only be a transcription, as exact as possible, of the phylogenetic tree or cladogram on another level [Dubois, 1988]. Some practical rules have been invented in order to realize such transcription, for example, the rule of equal taxonomic rank for sister taxa. The cladistic definition of a genus may be as follows: “A genus is a group of species that are more closely related to one another than they are to any species assigned to another genus” [Wood, Collard, 1999; see Table 2]. Another relevant definition determines a genus as “a monophyletic group of species, a clade, distinguishable on the basis of at least one derived char-

Table 3. A small collection of definitions of the genus category in zoological systematics.

Таблица 3. Небольшая подборка определений категории рода в зоологической систематике.

Definition	Author
"I consider that the two essential criteria of a genus are that it should be a natural assemblage of related species and that it should be clearly delimitable from other genera... not necessarily or even preferably by a single character, but by some combination of characters"	Edwards, 1953
"...the essential property of genera is morphological distinctness (usually correlated with the occupation of distinctly different ecological niches)"	Mayr et al., 1953
"A genus is a taxonomic category containing a single species, or a monophyletic group of species, which is separated from other taxa of the same rank (other genera) by a decided [morphological] gap"	Mayr, 1969
A genus is a combination of all species "able to give birth to viable adult hybrids, be these fertile or not"	Dubois, 1988
"A genus ... is what competent workers in particular groups say it is"	Allmon, 1992
A genus is "a monophyletic group of species, a clade, distinguishable on the basis of at least one derived character shared among them"	Allmon, 1992
Genus is "a species, or monophylum, whose members occupy a single adaptive zone"	Wood, Collard, 1999
"A genus is a group of species that are more closely related to one another than they are to any species assigned to another genus"	Wood, Collard, 1999

acter shared among them" [Allmon, 1992]. Only holophyletic (i.e. monophyletic s. str.) genera are permissible, whereas paraphyletic and polyphyletic ones should be re-arranged to achieve their monophyly. A true monophyletic genus should include all descendants of a last common ancestor despite a large amount of morphological divergence that would separate them [Dubois, 1988; de Queiroz, Gauthier, 1992]. Thus, the cladistic concept makes no stipulations about morphological distinctiveness [Skarlato, Starobogatov, 1974; Wood, Lonergan, 2008], i.e. branching points of clades are all important in a classification, but degree of similarity of the branches is not considered [Mayr, 1998].

4. Synthetic concept. Dubois [1988] denotes as 'synthetic' the generic concept developed by proponents of so-called "evolutionary systematics". As described in the Ernst Mayr's [1969] influential monograph, this concept treats a genus as a monophyletic (not in cladistic sense!) taxonomic category containing a single species, or a group of species, which is separated from other taxa of the same rank by a morphological discontinuity (see Mayr's definition in Table 3). Paraphyletic taxa, i.e. those including some (but not all) descendants of a common ancestor, are fully acceptable in this approach since these allow capturing of morphological divergence (amount of change) between descendants by standard means of taxonomic work, i.e. by placing them into separate taxa of different rank. In contrast to the cladistic concept, this approach uses morphological distinctiveness as one of the criteria of genera delimitation [Dubois, 1988]. Thus, morphological similarity and phylogeny are the two main criteria of "evolutionary" classification [Mayr, 1998], and the third, ecological, criteri-

on is commonly added for better identification of genera: a genus must occupy its own adaptive zone in the ecological space [Mayr, 1969; Maggenti, 1989; Cela-Conde, Ayala, 2003]², therefore each generic name corresponds to a distinct mode of life [Inger, 1958]. Addition of the ecological dimension to the definition of genus [Mayr, 1969] was caused by the fact that Mayr's definition of a genus (see Table 3) taken literally is applicable to almost all higher taxa of every rank (not only genus). Using the criterion of the adaptive zone, one may distinguish genera from taxa of higher rank (for example, from families) that also could be defined on the basis of similarity and monophyly but are rarely restricted to a single adaptive zone. Thus, genera under the synthetic concept are regarded as phylogenetic, morphological, and ecological units [Dubois, 1988]. Dubois [1988] added one more, fourth, criterion for a genus, that of hybridization. He proposed to unite into a genus all species "liable to give birth to viable hybrids" (see Table 3). According to this author, the very possibility of two species hybridizing and generating viable adult hybrids (be these fertile or not) indicates that they "possess very close functional genetic characterization and must therefore be grouped together in a same genus" [Dubois, 1988: 77].

Additionally, some operational "rules" for generic delineation have been proposed by proponents of the "synthetic" approach [see Clayton, 1983 for review]. For instance, Mayr [1969] recommended

²"Adaptive zone" occupied by a genus should not be confused with "ecological niche" occupied by a certain species [Cela-Conde, Ayala, 2003]

that a genus must be of “optimal size” and it should not exhibit internal morphological heterogeneity.

The two latter concepts dominate in the current practice of zoological systematics [Wood, Loneragan, 2008], and the cladistic methodology seems to be even prevailing (“we are all cladists now”, as Cameron *et al.* [2006: 228] state). But none of the concepts outlined above is free from shortcomings. None of the criteria proposed to delimit genera is suitable for all possible cases of practical taxonomy [Dubois, 1988; Martens, 2007]. For example, the cladistic principle to assign the same rank to sister taxa is faced with the fact that number of nodes and branches of a typical phylogenetic tree generated by computational algorithms is usually too high to give for each pair of sister branches a certain rank. The number of ranks in the Linnaean hierarchy is simply not enough to accomplish this task [Skarlato, Starobogatov, 1974; Wood, Collard, 1999]. Another difficulty of the cladistic approach is that it is necessary to distinguish, *a priori*, between primitive and derived character states, that is to determine their polarity [Clayton, 1983]. Furthermore, in many cases the exact phylogeny of a concrete group is unknowable because of scarcity of the fossil record and other causes. Thus we get a classification that reflects merely our best estimate of phylogeny [Stevens, 1985].

The “synthetic” criteria for assigning generic rank are often criticized for their subjectivity. For example, the procedures of “character weighting” [Simpson, 1961] or definition of what size should be that “decided gap” between two taxa to acknowledge their generic status [Mayr, 1969] depend on personal qualification of a taxonomist. The “principle of the same degree of difference”³ is based on subjective decisions of a given scholar how to determine the proper level of distinctiveness. The genera in some groups of freshwater molluscs (Hydrobioidea) may share the same adaptive zone [Radoman, 1983] thus violating the ecological criterion of a genus proposed by Mayr [1969]. Inger [1958] presented more instances from non-molluscan groups to show that this criterion may be misleading if it is not accompanied by morphological data.

In this situation, some authors use compromise approaches by synthesizing, to a certain extent, criteria for genera delimitation proposed by rival concepts. For example, Wood and Collard [1999] defined genera on the basis of a principle of strict (Hennigian) monophyly united with a principle of

ecological cohesiveness (a genus occupies its own adaptive zone). This pragmatic approach does not require the adaptive zone to be unique. It just requires the adaptive zone to be “consistent and coherent across the species taxa in the putative genus” [Wood, Collard, 2001: 67]. It seems to be more attractive for practicing taxonomists than the strict adherence to a single concept in generic circumscription.

The problem with having several different concepts of genus is that these concepts are not wholly compatible. Therefore the same set of species can be arranged into genera in several different ways depending on which generic concept is used [Wood, Collard, 1999]. Lymnaeid taxonomy presents one good example of this kind. The classification of Kruglov and Starobogatov [1993a, b] includes two genera: *Aenigmomphiscola* and *Lymnaea* (see above). The generic distinctness of the three species of *Aenigmomphiscola* is defensible because these snails possess a very unusual copulatory organ, and the taxonomic “weight” of this structure is considered to be very high [Kruglov, Starobogatov, 1981]. From the “synthetic” point of view, the amount of morphological difference that separates the two taxa is thus large enough to treat them as two genera. But from the cladistic standpoint, the genus *Lymnaea* s. lato becomes paraphyletic in both morphology-based [Kruglov, 2005, Fig. 294] and molecular-based [Vinarski *et al.*, 2011] phylogenetic hypotheses. A similar situation has arisen with the Tasmanian lymnaeid genus *Kutikina* Ponder et Waterhouse, 1997. The authors of this taxon indicated a set of anatomical apomorphies to separate it from other lymnaeids [Ponder, Waterhouse, 1997], but a recent phylogenetic study has revealed that *Kutikina* should be synonymized with the genus *Austropeplea* Cotton, 1942 and does not constitute a separate clade [Puslednik *et al.*, 2009].

Due to incompatibility between “synthetic” and cladistic approaches to monophyly, it is hardly possible to reach an “objective” generic delimitation of lymnaeid snails since the solution of the problem how many lymnaeid genera are there depends on which taxonomic philosophy is adopted [Vinarski *et al.*, 2011]. If one accepts paraphyletic taxa [see a useful discussion in Hörandl, 2006, 2010; Hörandl, Stuessy, 2010; Schmidt-Lebuhn, 2012], the bigeneric system by Kruglov and Starobogatov is adequate. If we decide that paraphyletic taxa are not appropriate, we need to split *Lymnaea* s. lato into a series of genera as is accepted in European and North American taxonomy [Burch, 1989; Glöer, 2002].

It should be stressed here that the two approaches to definition of monophyly and the two taxonomic schools based on these different definitions are logically equivalent therefore at least two

³ It demands that the taxa of the same rank should be separated by the equal level of distinctiveness [Skarlato, Starobogatov, 1974; Mayr, 1969; Golikov, Starobogatov, 1988].

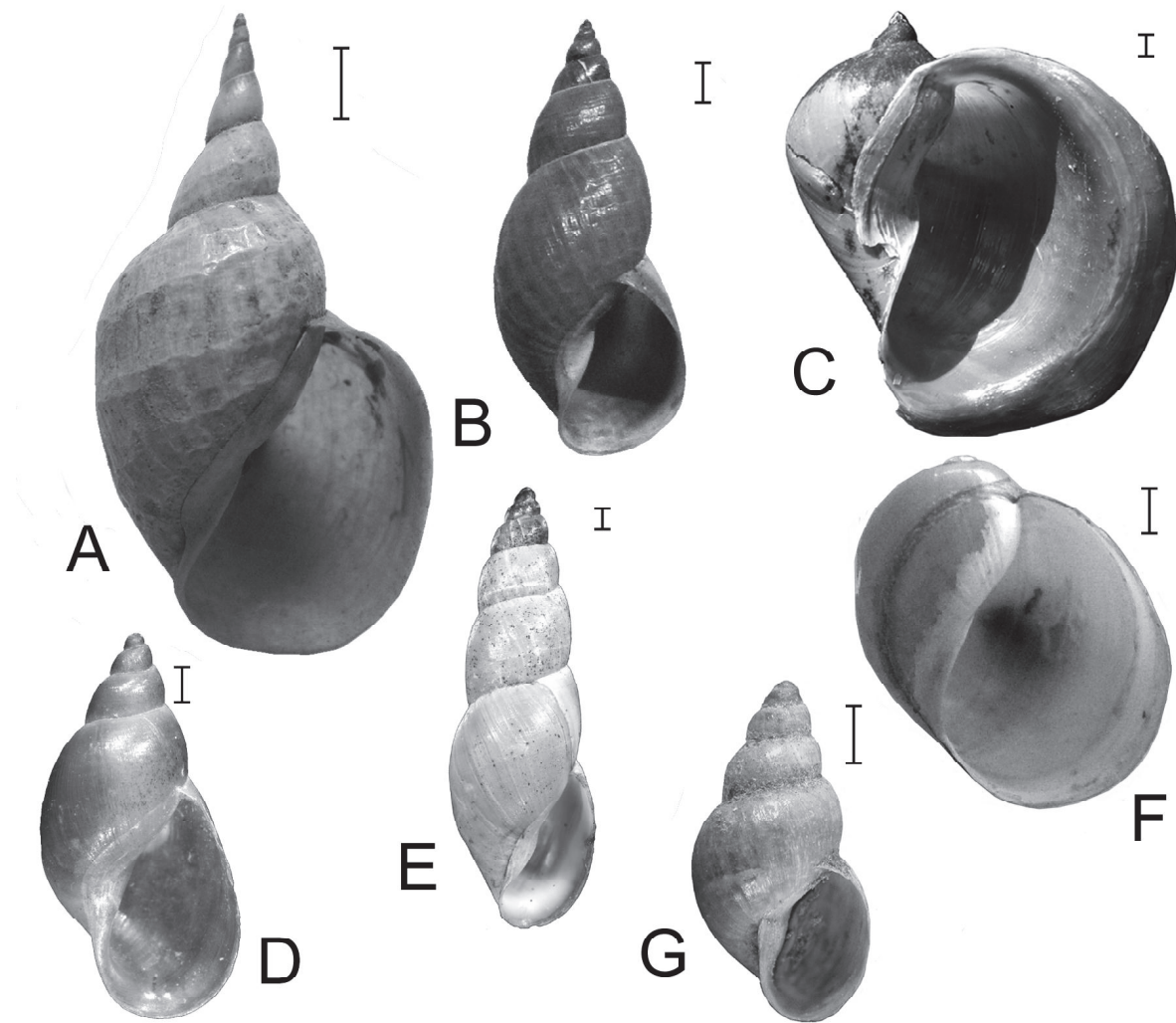


FIG. 1. Diversity of shell shape in Palaearctic representatives of the genus *Lymnaea*. **A.** *Lymnaea (Lymnaea) fragilis* (L., 1758). **B.** *L. (Stagnicola) saridalensis* Mozley, 1934. **C.** *L. (Radix) auricularia* (L., 1758). **D.** *L. (Peregriana) ulaganica* Kruglov et Starobogatov, 1983. **E.** *Lymnaea (Omphiscola) glabra* (O.F. Müller, 1774). **F.** *L. (Myxas) glutinosa* (O.F. Müller, 1774). **G.** *L. (Galba) truncatula* (O.F. Müller, 1774). The species names are given according to Kruglov [2005]. Scale bars: 1 mm (C-G), 2 mm (B), 5 mm (A).

РИС. 1. Разнообразие формы раковины у палеарктических представителей рода *Lymnaea*. **A.** *Lymnaea (Lymnaea) fragilis* (L., 1758). **B.** *L. (Stagnicola) saridalensis* Mozley, 1934. **C.** *L. (Radix) auricularia* (L., 1758). **D.** *L. (Peregriana) ulaganica* Kruglov et Starobogatov, 1983. **E.** *Lymnaea (Omphiscola) glabra* (O.F. Müller, 1774). **F.** *L. (Myxas) glutinosa* (O.F. Müller, 1774). **G.** *L. (Galba) truncatula* (O.F. Müller, 1774). Названия видов приведены в соответствии с Кругловым [2005]. Масштаб: 1 мм (C-G), 2 мм (B), 5 мм (A).

alternative generic systems of Lymnaeidae would co-exist. There are no theoretical objections to forbid such a co-existence as well as no grounds to prefer one of these exclusively [Pavlinov, 2003].

Let us compare the bigeneric and polygeneric systems by using different generic criteria listed above.

1. Morphological distinctness. Conchologically, lymnaeid snails are extremely diverse both in the size and shape of their shells. The polygeneric system reflects this heterogeneity more aptly than the bigeneric one. In the latter, species included in the genus *Lymnaea* demonstrate huge variability in their conchological characters (Fig. 1), whereas the

three species of *Aenigmomphiscola* are uniform in this respect. Moreover, shells of *Aenigmomphiscola* are utterly indistinguishable from those of the subgenus *Lymnaea (Omphiscola)* [Kruglov, Starobogatov, 1981; Vinarski *et al.*, 2011]. In contrast, the genera of the polygeneric system are characterized by more or less pronounced conchological homogeneity among species. For instance, all representatives of the genus *Galba* [= *Fossaria* Westerlund, 1885] possess minute shells (up to 10-13 mm height) of ovate-conical, high-conical or almost turriculate shape [Burch, 1989; Ponder, Waterhouse, 1997]. At the first glance, this is a good argument to prefer the polygeneric system, but we must remember that conchological similarity may

well be of homoplastic origin. Cases of striking conchological similarity between phylogenetically distant species are not rare among Lymnaeidae [Burch *et al.*, 1971; Patterson, Burch, 1978; Kruglov, Starobogatov, 1987]. Therefore anatomical features are usually regarded as being much weightier for taxonomy than conchological ones. The radular characteristics of most lymnaeid species are very similar and seem to be of low importance for taxonomy [Kruglov, 2005]. Phylogenetic uniqueness of some taxa with radular apomorphies (*Kutikina*) has been not corroborated by recent studies (see above). The reproductive system of almost all Lymnaeidae is of the same *Bauplan*, a strong argument against splitting the family into a large amount of genera [Hubendick, 1951; Kruglov, Starobogatov, 1981; Jackiewicz, 1998].

2. Ecological distinctness. Do all members of a lymnaeid genus share the same adaptive zone? In the bigeneric system this criterion is not followed as members of the genus *Lymnaea* s. lato are ecologically heterogeneous. Given that differences in lymnaeid shell shape may reflect their distinct adaptive strategies [Starobogatov, 1967], conchological heterogeneity of *Lymnaea* sensu Kruglov and Starobogatov reflects ecological heterogeneity. For example, *Lymnaea (Galba) truncatula* (O.F. Müller, 1774) typically dwells in spray-moistened habitats such as riversides as well as in small temporary pools [Beriozkina, Starobogatov, 1988; Kruglov, 2005], whereas *L. (Radix) auricularia* (L., 1758) is an oxiphilous snail that occurs in large permanent waterbodies [Jackiewicz, 1998; Kruglov, 2005]. Despite these differences, the species are placed in the same genus by followers of the bigeneric approach [Kruglov, Starobogatov, 1993a, b; Jackiewicz, 1998]. The genus *Aenigmomphiscola* has no ecological diagnosis since it shares an adaptive zone with representatives of *Lymnaea (Omphiscola)*. Thus the genus *Lymnaea* s. lato does not possess any ecological distinctness.

The genera accepted by proponents of the polygeneric system [Burch, 1989; Falkner *et al.*, 2001; Glöer, 2002] seem to reflect ecological distinctness better because at least some of these genera (*Galba* is the most outstanding example) can be characterized by their own adaptive zone. Hence, the polygeneric approach follows one of the empirical recommendations for generic delineation: «When a genus contains a large number of species and that is possible to recognize within it natural groups by whatever means, it is desirable to split it in several genera» [Laurent, 1956].

3. Hybridizability. The applicability of this criterion proposed by Dubois [1988] to lymnaeid systematics is limited. First, all pulmonate snails are hermaphrodites and some species reproduce by

almost obligate self-fertilization [Städtler *et al.*, 1993; Trouve *et al.*, 2005]. It is difficult to perform crossing experiments without a phenotypic marker that differentiates self- and cross-fertilization [Kruglov, Starobogatov, 1985a; Meier-Brook, 1993]. Therefore we still lack data on hybridizability of most species of the family. Second, all crossing experiments are carried out in the artificial laboratory conditions, which may lead to disruption of interspecific reproductive barriers that prevent hybridization between species in nature [Dubois, 1988; Jennings, Etges, 2009]. Third, it has been shown that some closely allied species of Lymnaeidae, namely, *Lymnaea fragilis* (L., 1758) and *L. stagnalis* (L., 1758) cannot produce viable hybrids [Kruglov, Starobogatov, 1985a], and, thus, should be placed in different genera following the Dubois [1988] criterion. However, no malacologist would accept this since the two species are very close in all other respects.

This short overview has demonstrated that the proposed generic criteria do not give us sound foundations to prefer a bigeneric to a polygeneric system or vice versa. The fourth (and, perhaps, the most important) generic criterion, that of monophyly, is discussed in the next section.

Recent advances in lymnaeid molecular phylogeny

Until recently, phylogenetic relationships among genera and subgenera in the Lymnaeidae have been investigated predominantly by means of morphological studies [Walter, 1968; 1969; Jackiewicz, 1998; Kruglov, 2005] though immunological and cytotoxic data were also available [Inaba, 1969; Burch *et al.*, 1971; Garbar *et al.*, 2004]. The determination of derived and primitive morphological character states is a difficult task [Stevens, 1985], so many contradictions among studies have been arisen. For example, Starobogatov [1976] considered the subgenus *Corvusiana* Servain, 1881 to be the most primitive extant lymnaeid group, whereas Inaba [1969] regarded *Austropeplea* and *Radix* to be the most archaic taxa. On the other hand, Jackiewicz [1993] believed that the most primitive group within the genus *Lymnaea* is *Galba*. As a result of these discrepancies, several incompatible phylogenetic hypotheses were proposed between 1960 and the 2000s [Inaba, 1969; Patterson, Burch, 1978; Jackiewicz, 1993, 1998; Kruglov, 2005] but none of them has been generally accepted.

Molecular phylogenetic methods have been used effectively for resolving phylogenetic relationships within Lymnaeidae since the late 1990s [Remigio, Blair, 1997; Bargues, Mas-Coma, 1997]. The molecular studies revealed that some “traditional” lymnaeid genera, such as *Stagnicola*, are polyphyletic

Table 4. Genetic distances of the cyt-b gene fragment (about 370 bp) between lymnaeid species belonging to different clades (17 chromosomes vs. 18 chromosomes). Calculated from data of Schniebs *et al.* [2011], and Vinarski *et al.* [2011].

Таблица 4. Генетические расстояния между видами лимнейд, принадлежащими разным кладам (17- и 18-ти хромосомной), рассчитанные на основе фрагмента гена cyt-b (длиной приблизительно 370 нуклеотидных пар). По данным Schniebs *et al.* [2011], Vinarski *et al.* [2011].

Group compared (in brackets – number of species pairs analyzed)	Min–max	Mean±σ
Distance between species of the 17-chromosome clade (10)	0.09–0.192	0.140±0.04
Distance between species of the 18-chromosome clade (15)	0.09–0.283	0.213±0.05
Distance between species belonging to different clades (11)	0.166–0.280	0.230±0.03

and should be split into several taxa [Meier-Brook, Bargues, 2002], though most of the morphology based lymnaeid genera seem to be congruent with terminal clusters of species on molecular trees [but see Correa *et al.*, 2010]. Some genera (*Kutikina*) proved to be synonyms of previously described taxa [Puslednik *et al.*, 2009]. The position of certain morphologically advanced genera (*Aenigmomphiscola*, *Omphiscola*) has been defined more exactly [Vinarski *et al.*, 2011]. The group of lymnaeid taxa with 18 chromosome pairs (including *Lymnaea* s.str., *Galba*, *Stagnicola*, and many others) proved to be of archaic origin whereas (sub-)genera having 16-17 pairs of chromosomes form a derived group of taxa [Remigio, Blair, 1997; Remigio, 2002; Correa *et al.*, 2010]. This result was confirmed by cytotaxonomic studies [Garbar *et al.*, 2004], though contrary to earlier cytotaxonomic results [Inaba, 1969; Patterson, Burch, 1978].

The most comprehensive molecular phylogenetic study of Lymnaeidae published to date is that of Correa *et al.* [2010], who used a representative range of species and three molecular markers to build a phylogenetic tree by means of a supermatrix approach. This tree has two deep branches (Fig. 2), of which the first includes the taxa with 16-17 pairs of chromosomes (*Austropeplea*, *Bullastra*, *Radix*). The second branch includes all lymnaeid groups with 18-19 pairs of chromosomes⁴. This dichotomy has a full bootstrap support (see Fig. 2).

Similar dichotomous branching pattern was obtained by Bargues *et al.* [2003], with all Holarctic lymnaeids divided into two big clades, one for *Radix* species and another for all other species. The same dichotomy of clades is evident in some trees of Palearctic lymnaeids [Artigas *et al.*, 2011, Fig. 2; Vinarski *et al.*, 2011, Fig. 2, A, C]. Among numerous trees generated by using the same set of Palearctic species of lymnaeids [Vinarski *et al.*, 2012], a

tree supporting the dichotomous branching pattern (*Lymnaea* clade vs. *Radix* clade) gets almost full bootstrap support (Fig. 3), whereas trees with different topology of branches have low or very low bootstrap values (51 to 71%). Repeatability of clades in separate phylogenetic analyses is considered as a good evidence for their reliability [Chen *et al.*, 2003].

According to our data [Schniebs *et al.*, 2011; Vinarski *et al.*, 2011], the genetic distances between species of the same clade are lower than those between species in different clades (Table 4). It is especially obvious when the mean distance between species of 17-chromosome clade is compared with the mean distance separating species from different clades. The genetic distances between species in different families of freshwater pulmonates (lymnaeids vs. physids, lymnaeids vs. planorbids) calculated from the data of the same authors lie between 0.260 and 0.331 (the mean distance is 0.288±0.02), i.e. typically a little higher than the distance between large lymnaeid clades.

From the morphological standpoint, however, there are no synapomorphies in shell and anatomical structures to determine the derived branch as is required by morphological cladistic methodology [Mooi, Gill, 2010]. The only character distinguishing the clades rigorously is the chromosome number. The primitive branch is that with 18-19 chromosome pairs. The ancestral state in Lymnaeidae seems to be n=18 [Correa *et al.*, 2010], and representatives of the family Chiliniidae Dall, 1870 (which is considered to be the ancestor of Lymnaeidae) have the same chromosome number [Garbar *et al.*, 2004]. The other, advanced, clade unites taxa with reduced chromosome number (16-17 pairs) which may be a synapomorphic state. Starobogatov [1985] suggested that these taxa arose by means of macromutational speciation (i.e. via chromosome reduction).

Though the results of molecular taxonomic studies are not free from errors and misinterpretations [Buhay, 2009; Mooi, Gill, 2010; Groenenberg *et al.*, 2011], difference in chromosome numbers between the two deep lymnaeid clades discussed above pro-

⁴ *Fossaria rustica* (Lea, 1841), a Nearctic species of Lymnaeidae, has 19 pairs of chromosomes, apparently the highest chromosome number among lymnaeids [Inaba, 1969; Garbar *et al.*, 2004].

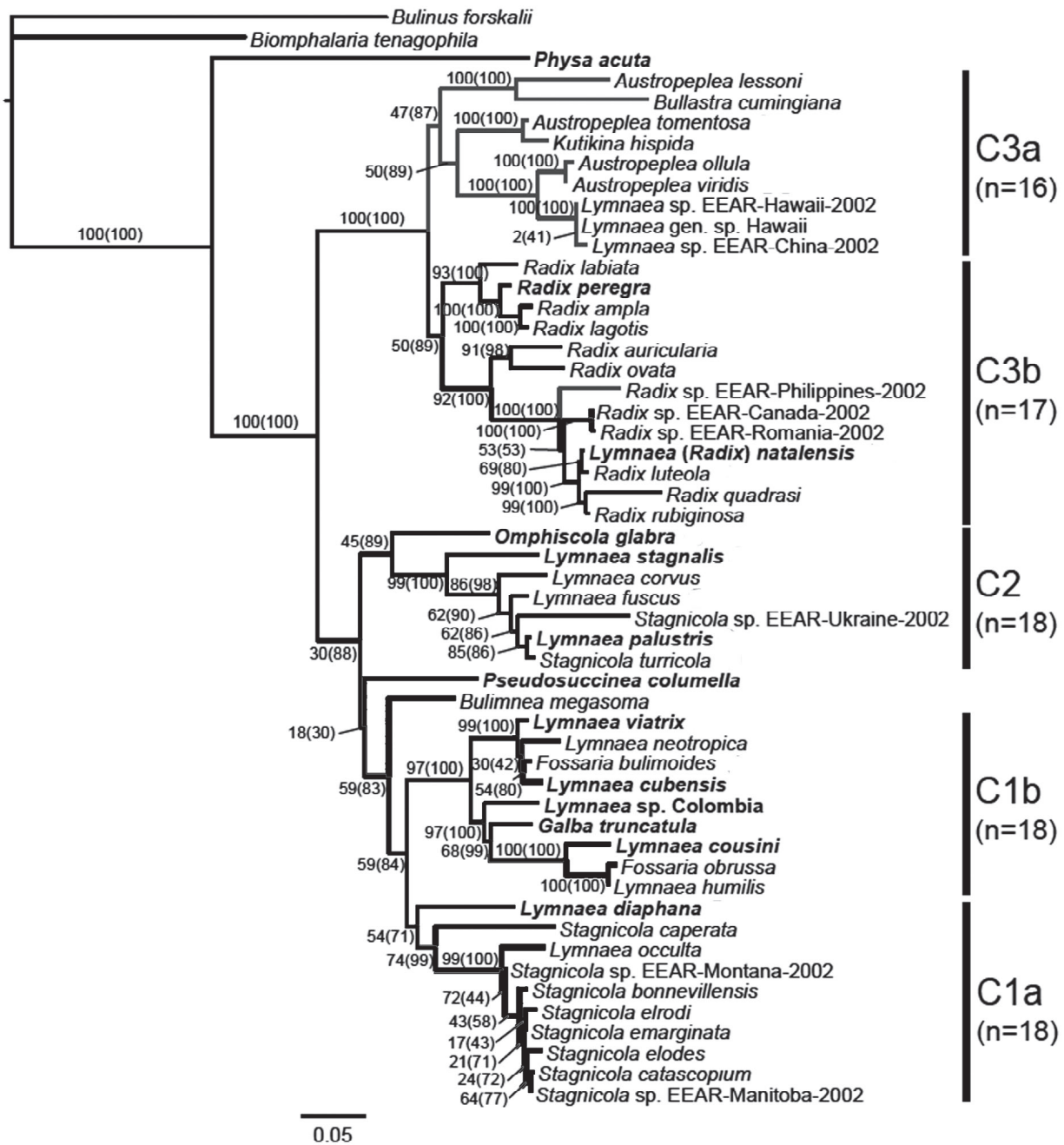


FIG. 2. The phylogeny of Lymnaeidae according Correa *et al.* [2010], simplified. The chromosome numbers are given in parentheses. Values on nodes represent bootstrap percentages (BP) and posterior probabilities (PP; given within parentheses).

РИС. 2. Филогения Лымнаеиде по Correa *et al.* [2010], упрощено. Число хромосом приведено в скобках. Значения на узлах соответствуют бутстрефу (BP) и апостериорной вероятности (PP; приведено в скобках).

vides a good support for this phylogenetic hypothesis. Hence, it seems likely that the family Lymnaeidae consists of two large monophyletic groups, and this conclusion is supported by statistical methods (bootstrap analysis, analysis of posterior probability [Correa *et al.*, 2010]) as well as by karyological data [Garbar *et al.*, 2004]. Kruglov [2005, fig. 294], in his phylogenetic hypothesis based on morphological and cytotoxic data, also placed all species with 16-17 chromosome pairs into a large clade distinct from those containing taxa with 18 pairs.

Most biologists now agree that classification should reflect phylogeny [Seberg, Petersen, 2009; but see Borgmeier, 1957; Skarlato, Starobogatov, 1974]. Therefore we need to assign taxonomic ranks for the two deep monophyletic clades. There are several possibilities. First, one can consider them as genera. In this case, we would have two very heterogeneous taxonomic entities each including a huge number of species that differ from each other both morphologically and ecologically. The internal heterogeneity of such genera would be, of course, taxonomically reflected by introducing sub-

generic taxa, but most of the recent generic criteria (see above) do not support this classification scheme.

A more appropriate cladistic solution is to regard the two deep lymnaeid clades as separate subfamilies within Lymnaeidae, each containing a set of genera that are internally homogeneous enough to comply with most of generic criteria. Each genus will unite a group of species exhibiting resemblance in shell appearance as well as in genital morphology and ecological traits.

Thus the polygeneric approach seems to be more preferable in the light of the recent advances in lymnaeid molecular phylogenetics. In this case, the taxonomic structure of the family should be as follows:

Family Lymnaeidae Rafinesque, 1815

Subfamily Lymnaeinae Rafinesque, 1815 (type genus *Lymnaea* Lamarck, 1799)

Diagnosis: shell of variable size (up to 70 mm in height) and shape (from subulate or turriculate to ovate conical or even auriculate). Prostate with one or many (5-10) internal folds or unfolded. Haploid chromosome number 18-19.

The subfamily includes a range of genera phylogenetically clustered with *Lymnaea* s.str. [see phylogenetic studies by Kruglov, 2005; Bargues *et al.*, 2003; Correa *et al.*, 2010; Vinarski *et al.*, 2011]. It corresponds to C1 and C2 clades of the phylogenetic tree presented by Correa *et al.* [2010].

Subfamily **Radicinae subfam. n.**

urn:lsid:zoobank.org:act:DE0E15F5-B1E7-4998-872C-63F167389AF6

(type genus *Radix* Montfort, 1810)⁵

Diagnosis: shell of medium size (up to 35 mm in height), spheroid, ovate, ovate-conical, or ear-shaped. Prostate with a single internal fold. Haploid chromosome number 16-17.

[**Диагноз.** Раковина среднего размера (до 35 мм в высоту), сферическая, овальная, овально-коническая или уховидная. Простата с единственной внутренней складкой. Гаплоидное число хромосом 16-17.]

This subfamily includes a range of advanced lymnaeid genera (possibly, of South Asian origin) that constitute the C3 clade of Correa *et al.* [2010]. It corresponds to the informal “radicine” group of species morphologically defined by Walter [1969].

⁵ Taylor [1981] used the name Radicinae for a group containing *Radix auricularia* (L.), however, he did not provide a diagnosis of Radicinae so this name is not available nomenclaturally [see International Commission. . . , 1999, article 13.1]. Radicinae was not listed by Bouchet and Rocroi [2005] in their comprehensive list of gastropod family-group names.

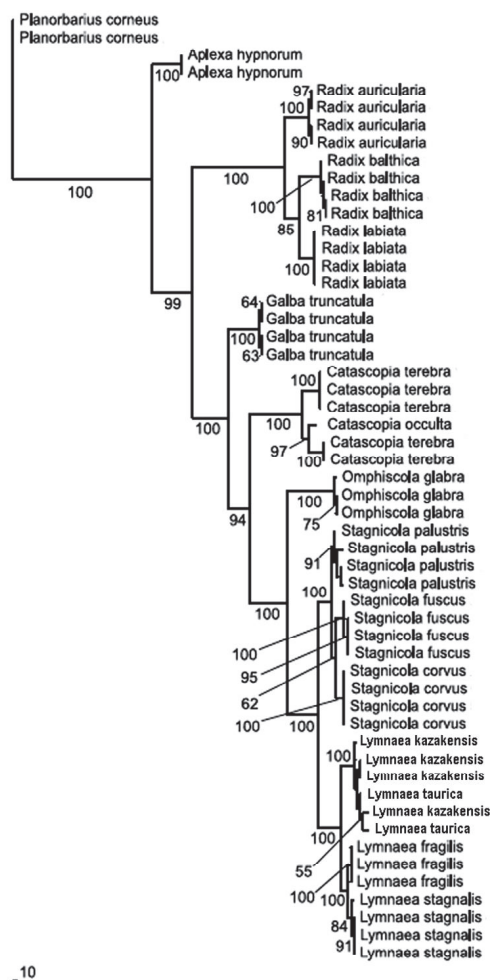


FIG. 3. The maximum-parsimony tree of Palearctic Lymnaeidae based on one of the 54 best maximum-parsimony trees of the nuclear marker ITS-2 (modified from Vinarski *et al.*, 2012).

РИС. 3. Максимально парсимонное дерево палеарктических Lymnaeidae, основанное на одном из 54 лучших максимально парсимонных деревьев, построенных по ядерному маркеру ITS-2 (модифицировано по Vinarski *et al.*, 2012).

An annotated list of recent genera and subgenera of lymnaeid snails arranged into subfamilies is given in Appendix. It presents a kind of provisional system of the family that will inevitably be updated and changed in future research. The list includes 26 taxa of the genus rank but I suggest that some of these genera should be considered as subgenera or even as synonyms of other genera.

I have to stress that studies used different sets of taxa and different sets of molecular markers to resolve the phylogeny of the family. Some groups of lymnaeids are not yet characterized molecularly. Therefore the phylogenetic hypothesis outlined above will, surely, be improved or, possibly, even rejected in future. The most intriguing problem is concerned with the phylogenetic affinity of the genus *Lanx* (see above) that has not been studied by molecular

methods. Future studies will show whether *Lanx* constitutes a separate clade sister to all other lymnaeids and, hence, whether it merits classification as a distinct (sub-)family. Interestingly, some morphologists [Walter, 1969] believe that *Lanx* is so closely related to “other” lymnaeids that even the generic status of this group is not justified.

The generic classification of the family Lymnaeidae proposed here is cladistic since the paraphyletic taxon *Lymnaea* sensu Kruglov and Starobogatov, 1993 is split into a series of monophyletic (in the strict sense) subfamilies and genera. I would like to emphasize again that the morphology based bigeneric system developed by Kruglov and Starobogatov [1993] is still acceptable for those taxonomists, who regard the degree of morphological divergence as the most important basis for classification in spite of probable contradictions with current phylogenetic hypotheses. Given the fact that any scientific hypothesis is not absolute and may be changed (or rejected) in future, there are no ground to hold either of these version of the lymnaeid systems to be ultimate and solely acceptable.

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APPENDIX

A provisional supraspecific system of recent Lymnaeidae

The list below includes all recent genera and subgenera of lymnaeid snails arranged provisionally into subfamilies. It is based mainly on works by Kruglov and Starobogatov [1993a, b] and Ponder and Waterhouse [1997] and updated by using results of the most recent molecular phylogenetic studies. Type species of genera and subgenera are indicated in parentheses as well as information on the method of their fixation (M – by monotypy; OD – by original designation; SD – by subsequent designation; SM – by subsequent monotypy). Main synonyms, taxonomic and nomenclatorial remarks and references are also provided. The order of taxa does not reflect any hypothesis of their phylogenetic relationships. The genus *Lanx* and its taxonomic position are not considered.

* – taxa studied by means of molecular phylogenetic methods

† – data on chromosome numbers are not available

‡ – rank of a taxon is not clear (genus or subgenus)

Family Lymnaeidae Rafinesque, 1815 Subfamily Lymnaeinae Rafinesque, 1815

- 1. Genus *Lymnaea*** Lamarck, 1799
(*Helix stagnalis* Linnaeus, 1758, M)*
subgenus *Lymnaea* s.str.*
subgenus *Kazakhlymnaea* Kruglov et Starobogatov, 1984 (*Lymnaea palustris kazakensis* Mozley, 1934, OD)* †
References: Vinarski *et al.*, 2012.
- 2. Genus *Corvusiana*** Servain, 1881
(*Helix corvus* Gmelin, 1791, SD) * ‡
subgenus *Corvusiana* s.str.*
subgenus *Kuesterilymnaea* Vinarski, 2003 (*Limnaea vulnerata* Küster, 1862 sensu Jackiewicz, 1988 non Kruglov, Starobogatov, 1986 = *Stagnicola fusca* sensu Glöer, 2002, OD)*
Remark: probably, *Corvusiana* s.str. and *Kuesterilymnaea* should be regarded as subgenera of *Stagnicola*.
References: Kruglov, Starobogatov, 1984; Vinarski, 2003; Vinarski *et al.*, 2012.
- 3. Genus *Stagnicola*** Leach in Jeffreys, 1830
(*Buccinum palustre* O.F. Müller, 1774, M)*
[= *Galba* Schrank, 1803, partim; = *Limnophysa* Fitzinger, 1833; = *Leptolymnaea* Swainson, 1840, partim; = *Fossaria* Westerlund, 1885, partim; = *Microlimnaea* W. Dybowski, 1908, partim; = *Palustria* W. Dybowski, 1908, partim; = *Turrimlymnaea* W. Dybowski, 1908, partim; = *Costolimnaea* B. Dybowski, 1913, partim]
References: Kruglov, Starobogatov, 1986; Meier-Brook, Barges, 2002; Barges *et al.*, 2003, 2006; Vinarski (in press).
- 4. Genus *Ladislavella*** B. Dybowski, 1913
(*Ladislavella sorensis* B. Dybowski, 1913 = *Limnaea palustris* var. *terebra* Westerlund, 1885, OD)*
[= *Polyrhytis* sensu Kruglov, Starobogatov, 1993a, partim; = *Walterilymnaea* Starobogatov et Budnikova, 1976; = *Catascopia* Meier-Brook et Barges, 2002]
References: Vinarski (in press).
- 5. Genus *Omphiscola*** Rafinesque, 1819
(*Buccinum glaber* O.F. Müller, 1774, SM)*
[= *Leptolymnaea* Swainson, 1840, partim]
References: Kruglov, Starobogatov, 1981; Vinarski *et al.*, 2011.
- 6. Genus *Aenigmomphiscola***
Kruglov et Starobogatov, 1981
(*Aenigmomphiscola europaea* Kruglov et Starobogatov, 1981, OD)* †
References: Kruglov, Starobogatov, 1981; Vinarski *et al.*, 2011.
- 7. Genus *Pseudosuccinea*** F.C. Baker, 1908
(*Lymnaea columella* Say, 1817, OD)*
References: Kruglov, Starobogatov, 1993b; Ponder, Waterhouse, 1997.

- 8. Genus *Hinkleyia*** F.C. Baker, 1928
(*Lymnaeus caperatus* Say, 1829, OD)*
[= *Pseudogalba* sensu Kruglov, Starobogatov, 1993b]
References: Taylor *et al.*, 1963; Kruglov, Starobogatov, 1985b, Burch, 1989; Ponder, Waterhouse, 1997.
- 9. Genus *Walterigalba***
Kruglov et Starobogatov, 1985
(*Galba montanensis* F.C. Baker, 1913, OD) ‡
Remark: probably, *Walterigalba* should be considered as a subgenus of *Hinkleyia*.
References: Kruglov, Starobogatov, 1985b; Ponder, Waterhouse, 1997.
- 10. Genus *Walhiana*** Servain, 1881
(*Lymnaea walhii* Möller, 1842 = *Lymnaea vahlii* Möller, 1842) † ‡
Remark: Baker [1911] included species of *Walhiana* in the *Stagnicola* group and, probably, *Walhiana* should be considered as a subgenus of the latter genus. However, Ponder and Waterhouse [1997] treat *Walhiana* as a synonym (or subgenus) of the genus *Radix*.
References: Kruglov, Starobogatov, 1993b; Ponder, Waterhouse, 1997.
- 11. Genus *Galba*** Schrank, 1803
(*Galba pusillum* Schrank, 1803 = *Buccinum truncatulum* O.F. Müller, 1774, M)*
[= *Fossaria* Westerlund, 1885; = *Pseudogalba* Baker, 1911, partim]
subgenus *Galba* s.str.*
subgenus *Bakerilymnaea* Weyrauch, 1964 (*Limnaea cubensis* Pfeiffer, 1839, OD)* ‡
subgenus *Sibirigalba* Kruglov et Starobogatov, 1985 (*Limnaea truncatula* var. *sibirica* Westerlund, 1885, OD)* †
Remark: *Sibirigalba* is considered here as a subgenus of *Galba* on the basis of molecular phylogenetic study of *Lymnaea sibirica* (K. Schniebs, M. Vinarski, unpublished).
References: Kruglov, Starobogatov, 1985b; Burch, 1989; Ponder, Waterhouse, 1997.
- 12. Genus *Sphaerogalba***
Kruglov et Starobogatov, 1985
(*Lymnaea bulimoides* Lea, 1841, OD)* ‡
Remark: Possibly, *Sphaerogalba* is a junior synonym of *Bakerilymnaea*.
References: Kruglov, Starobogatov, 1985b; Ponder, Waterhouse, 1997.
- 13. Genus *Bulimnea*** Haldeman, 1841
(*Lymnaeus megasomus* Say, 1824, M)*
References: Burch, 1989; Ponder, Waterhouse, 1997.
- 14. Genus *Acella*** Haldeman, 1841
(*Lymnaea gracilis* Jay, 1839 non Zieten, 1832 = *Limnaea haldemani* Binney, 1867, M)*
References: Burch, 1989; Ponder, Waterhouse, 1997.

- 15. Genus *Erinna*** H. Adams et A. Adams, 1855
(*Erinna newcombi* H. Adams et A. Adams, 1855, OD) †
References: Kruglov, Starobogatov, 1993b; Ponder, Waterhouse, 1997.
- 16. Genus *Pseudoisidora*** Thiele, 1931
(*Lymnaea rubella* Lea, 1841, OD) †
subgenus *Pseudoisidora* s.str.
subgenus *Pseudobulinus* Kruglov et Starobogatov, 1993 (*Physa reticulata* Gould, 1847, OD) †
References: Ponder, Waterhouse, 1997.

Subfamily **Radicinae** subfam. n.

- 17. Genus *Radix*** Montfort, 1810
(*Radix auriculatus* Montfort, 1810 = *Helix auricularia* Linnaeus, 1758, OD)*
[= *Gulnaria* Turton, 1831, partim]
subgenus *Radix* s.str.*
subgenus *Peregriana* Servain, 1881 (*Buccinum peregrum* O.F. Müller, 1774, SD)*
Remark: subgeneric rank of *Peregriana* is based on molecular phylogenetic studies by Pfenninger *et al.* [2006], Schniebs *et al.* [2011].
References: Kruglov, Starobogatov, 1993b; Ponder, Waterhouse, 1997.
- 18. Genus *Myxas*** Sowerby, 1822
(*Buccinum glutinosum* O.F. Müller, 1774, M)*
[= *Amphipeplea* Nilsson, 1822; = *Lutea* Gray, 1840; = *Cyclolymnaea* Dall, 1905]
Remark: The data of Pfenninger *et al.* [2006] show that *Myxas* forms a clade sister to *Radix* s.lato. Our own results [Schniebs, Vinarski, unpublished] confirm it though anatomically species of *Myxas* and *Radix* are virtually identical.
References: Kruglov, Starobogatov, 1993; Ponder, Waterhouse, 1997.
- 19. Genus *Pacifimyxas***
Kruglov et Starobogatov, 1985
(*Lymnaea magadanensis* Kruglov et Starobogatov, 1985, OD) † ‡
Remark: Possibly, *Pacifimyxas* should be ranked as a subgenus of *Myxas*.
References: Kruglov, Starobogatov, 1985c.
- 20. Genus *Cerasina*** Kobelt, 1880
(= *Limnaea bulla* Kobelt, 1880, OD) † ‡
Remark: Perhaps, *Limnaea bulla* Kobelt, 1880 is synonymical with *Radix rubiginosa* Michelin, 1831 [Hubendick, 1951; Ponder, Waterhouse, 1997]. In this case, *Cerasina* becomes a junior objective synonym of *Radix*.
References: Kruglov, Starobogatov, 1993b; Ponder, Waterhouse, 1997.
- 21. Genus *Pectinidens*** Pilsbry, 1911
(*Limnaea diaphana* King et Broderip, 1830, OD)

References: Kruglov, Starobogatov, 1993b; Ponder, Waterhouse, 1997.

22. Genus *Limnobulla*

Kruglov et Starobogatov, 1985

(*Lymnaea peculiaris* Hubendick, 1951, OD) †‡

Remark: Anatomy of the type species is unknown [Kruglov, Starobogatov, 1985c]. Its conchological traits [Hubendick, 1951] indicate it may be presumed placed in *Radicinae*.

References: Kruglov, Starobogatov, 1985c; Ponder, Waterhouse, 1997.

23. Genus *Orientogalba*

Kruglov et Starobogatov, 1985

(*Lymnaea heptapotamica* Lazareva, 1967 = *Lymnaea hookeri* Reeve, 1850, OD)*

References: Kruglov, Starobogatov, 1985b; Ponder, Waterhouse, 1997.

24. Genus *Austropeplea* Cotton, 1942

(*Lymnaea aruntalis* Cotton et Godfrey, 1938 = *Succinea tomentosa* L. Pfeiffer, 1855, OD)*

[= *Kutikina* Ponder et Waterhouse, 1997]

References: Kruglov, Starobogatov, 1985c; Ponder, Waterhouse, 1997; Puslednik *et al.*, 2009.

25. Genus *Bullastra* Bergh, 1901

(*Bullastra velutinoides* Bergh, 1901 = *Amphipeplea cumingiana* L. Pfeiffer, 1855, M)*

References: Kruglov, Starobogatov, 1985c; Ponder, Waterhouse, 1997; Puslednik *et al.*, 2009.

26. Genus *Lantzia* Jousseaume, 1872

(*Lantzia carinata* Jousseaume, 1872, OD) *‡

References: Brown, 1994; Ponder, Waterhouse, 1997.



Один, два или несколько? Сколько родов лимнеид следует выделять?

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РЕЗЮМЕ. Рассмотрены проблема построения системы семейства *Lymnaeidae* Rafinesque, 1815 на уровне рода, а также современные теоретические подходы к выделению родов в зоологической систематике. Существуют два основных подхода к выделению родов в семействе *Lymnaeidae*: 1) двухродовой подход, при котором все многообразие видов семейства подразделяется на два рода и 2) многогородовой подход, предполагающий, что в семействе следует выделять большое число (около двадцати) родов. Первый подход представлен системами, предложенными Н.Д. Кругловым и Я.И. Старобогатовым

[Kruglov & Starobogatov, 1993] и М. Яцкевич [Jackiewicz, 1993, 1998]. Второй подход в настоящее время практически общепринят в западноевропейской и североамериканской литературе [Burch, 1989; Falkner *et al.*, 2001; Glöer, 2002]. Однако решить проблему выбора между ними объективно невозможно, поскольку решение зависит от той таксономической методологии, которой придерживается конкретный исследователь. Так, методология «эволюционной систематики» (в смысле Майра) ведет к принятию двухродового подхода, а кладистическая (хеннигова) систематика благоприятствует подразделению семейства на серию таксонов родового ранга. Ввиду того, что конкурирующие методологии расходятся в вопросе о допустимости парафилетических таксонов, и этот вопрос вряд ли может быть решен окончательно, нельзя однозначно предпочесть кладистическую систему «эволюционной» или наоборот. Поэтому невозможно избежать сосуществования двух различных систем семейства, построенных на разных методологических основаниях. Рассмотрены различные критерии родового ранга в плане их применимости к таксономии лимнеид. Использование морфологического и экологического критериев рода, так же как и критерия гибридизируемости, ведет к противоречиям и не дает оснований однозначно предпочесть какой-либо из двух подходов к построению системы. Четвертый критерий (критерий монофилии) представляется более эффективным ввиду доступности данных по молекулярной филогенетике *Lymnaeidae*. Краткий обзор данных молекулярной систематики показывает, что вероятнее всего семейство включает две крупных монофилетических клады древнего происхождения, которые отличаются меж собой по числу хромосом, но не могут быть охарактеризованы четкими морфологическими различиями. Присваивать ранг рода каждой из этих клад непрактично ввиду их высокой внутренней гетерогенности, как морфологической, так и экологической. Представляется наиболее приемлемым рассматривать данные клады в ранге подсемейств, каждое из которых включает некоторое число родов, достаточно однородных, чтобы соответствовать большинству критериев родового ранга. Предложена новая классификационная система *Lymnaeidae*, в соответствии с которой семейство включает два подсемейства: номинативное *Lymnaeinae* (типовой род *Lymnaea* Lamarck, 1799) с гаплоидным числом хромосом равным 18 (редко 19) и вновь выделяемое *Radicinae* subfam.n. (типовой род *Radix* Montfort, 1810). Последнее включает роды и виды прудовиков, характеризующиеся 16 или 17 парами хромосом. *Radicinae*, скорее всего, это эволюционно продвинутый таксон в сравнении с *Lymnaeinae*, однако невозможно указать морфологические синапоморфии для его характеристики. При этом двухродовая система остается вполне приемлемой для тех исследователей, которые используют критерии родового ранга, предлагаемые «эволюционной систематикой», такие как «принцип единого уровня таксономической обособленности» [Голиков, Старобогатов, 1988] и тому подобные.