One, two, or several? How many lymnaeaid 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 lymnaeaid 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.
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 [Skarlatoto, Starogobatov, 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 Amphipelea 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-
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”), Lymnaeidae 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-
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, et al., 2009] considers 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
How many lymnaeid genera are there?

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

<table>
<thead>
<tr>
<th>Definition</th>
<th>Author</th>
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<tr>
<td>“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”</td>
<td>Edwards, 1953</td>
</tr>
<tr>
<td>“…the essential property of genera is morphological distinctness (usually correlated with the occupation of distinctly different ecological niches)”</td>
<td>Mayr et al., 1953</td>
</tr>
<tr>
<td>“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”</td>
<td>Mayr, 1969</td>
</tr>
<tr>
<td>A genus is a combination of all species “able to give birth to viable adult hybrids, be these fertile or not”</td>
<td>Dubois, 1988</td>
</tr>
<tr>
<td>“A genus … is what competent workers in particular groups say it is”</td>
<td>Allmon, 1992</td>
</tr>
<tr>
<td>A genus is “a monophyletic group of species, a clade, distinguishable on the basis of at least one derived character shared among them”</td>
<td>Allmon, 1992</td>
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<tr>
<td>Genus is “a species, or monophylum, whose members occupy a single adaptive zone”</td>
<td>Wood, Collard, 1999</td>
</tr>
<tr>
<td>“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”</td>
<td>Wood, Collard, 1999</td>
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Character 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 [Skarlasto, 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, criterion 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], 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 systematic [Wood, Lonergan, 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: *Aenigmomphisiscola* and *Lymnaea* (see above). The generic distinctness of the three species of *Aenigmomphisiscola* 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 & 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 [Pusleink 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
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 [Beriozka, 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; Trouvé 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 cytotaxonomic 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 Austropelea 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.
Таблица 4. Генетические расстояния между видами лимнеид, 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].

| Группа сопоставления | Мин–макс | Среднее±о.
|----------------------|----------|------------
| Расстояние между видами 17-хромосомной клады (10) | 0.09–0.192 | 0.140±0.04 |
| Расстояние между видами 18-хромосомной клады (15) | 0.09–0.283 | 0.213±0.05 |
| Расстояние между видами разных клад (11) | 0.166–0.280 | 0.230±0.03 |

* 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].
provides 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 cytotaxonomic 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. (type genus Radix Montfort, 1810)

**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.

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].

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 *Lax* 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 *Lax* 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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Family Lymnaeidae Rafinesque, 1815
Subfamily Lymnaeinae Rafinesque, 1815

1. Genus Lymnaea Lamarck, 1799
(Helix stagnaLimnaea, 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 Kuster, 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; = Limnophyes Fitzinger, 1833; = Leptolympneae Swainson, 1840, partim; = Fossaria Westerlund, 1885, partim; = Microlymnaea W. Dybowski, 1908, partim; = Palustria W. Dybowski, 1908, partim; = Turritlymnaea W. Dybowski, 1908, partim; = Costolymnaea B. Dybowski, 1913, partim]
References: Kruglov, Starobogatov, 1986; Meier-Brook, Bargues, 2002; Bargues 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)*
[= Polybryta sensu Kruglov, Starobogatov, 1993a, partim; = Walterilymnaea Starobogatov et Budnikova, 1976; = Cacatopsia Meier-Brook et Bargues, 2002]
References: Vinarski (in press).

5. Genus Omphiscolla Rafinesque, 1819
(Buccinum glaber O.F. Müller, 1774, SM)*
[= Leptolympneae Swainson, 1840, partim]
References: Kruglov, Starobogatov, 1981; Vinarski et al., 2011.

6. Genus Aenigmophiscolla
Kruglov et Starobogatov, 1981
(Aenigmophiscolla europaea Kruglov et Starobogatov, 1981, OD)*†
References: Kruglov, Starobogatov, 1981; Vinarski et al., 2011.

7. Genus Pseudosuccinea F.C. Baker, 1908
(Lymnaea columnella Say, 1817, OD)*

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)

(*Lymnaeus caperatus* Say, 1829, OD)*

[= *Pseudogalba* sensu Kruglov, Starobogatov, 1993b]


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*.


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*.


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 (*Lymnaea cubensis* Pfeiffer, 1839, OD)* †

subgenus *Sibirigalba* Kruglov et Starobogatov, 1985 (*Lymnaea 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).


12. Genus *Sphaerogalba*

Kruglov et Starobogatov, 1985

(*Lymnaea bulimoides* Lea, 1841, OD)* †‡

Remark: Possibly, *Sphaerogalba* is a junior synonym of *Bakerilymnaea*.


13. Genus *Bulinnea* Haldeman, 1841

(*Lymnaeus megasomus* Say, 1824, M)*


14. Genus *Acella* Haldeman, 1841

(*Lymnaea gracilis* Jay, 1839 non Zieten, 1832 = *Limnaea haldemani* Binney, 1867, M)*


15. Genus *Erinna* H. Adams et A. Adams, 1855

(*Erinna newcombi* H. Adams et A. Adams, 1855, OD)* †


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) †


Subfamily *Radicinae* subfam. n.

17. Genus *Radix* Montfort, 1810

(*Radix auriculatus* Montfort, 1810 = *Helix auricularia* Linnaeus, 1758, OD)*

[= *Gnarnia* Turton, 1831, partim]

subgenus *Radix* s.str.*

subgenus *Peregrina* Servain, 1881 (*Buccinum pergrum* O.F. Müller, 1774, SD)*

Remark: subgeneric rank of *Peregrina* is based on molecular phylogenetic studies by Pfenninger et al. [2006], Schniebs et al. [2011].


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.


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

(= *Lymnaea bulla* Kobelt, 1880, OD) †

Remark: Perhaps, *Lymnaea bulla* Kobelt, 1880 is synonymous with *Radix rubiginosa* Michelin, 1831) [Hubendick, 1951; Ponder, Waterhouse, 1997]. In this case, *Cerasina* becomes a junior objective synonym of *Radix*.


21. Genus *Pectinidens* Pilbry, 1911

(*Lymnaea diaphana* King et Broderip, 1830, OD)

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 presumedly placed in Radicinae.

23. Genus Orientogalba
Kruglov et Starobogatov, 1985
(Lymnaea heptapotamica Lazareva, 1967 = Lymnaea hookeri Reeve, 1850, OD)*

24. Genus Austropeplea Cotton, 1942
(Lymnaea arunitalis Cotton et Godfrey, 1938 = Succinea tomentosa L. Pfeiffer, 1855, OD)*
References: Kruglov, Starobogatov, 1985c; Ponder, Waterhouse, 1997; Kruglov & Starobogatov, 1993b; Puslednik et al., 2009.

25. Genus Bullastra Bergh, 1901
(Bullastra velutinoides Bergh, 1901 = Amphipeplea cunningiana 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) **‡

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

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РЕЗЮМЕ. Рассмотрены проблемы 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) многородовой 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. Яцкович [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 (хенингова) систематика благоприятствует подразделению семейства на серию таксонов родового ранга. Ввиду того, что конкурирующие методологии расходятся в вопросе о допустимости параклетических 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 лимневид. Использование морфологического и экологического критериев рода, так же как и критерия гибридинируемости, ведет к противоречиям и не даёт оснований однозначно предпочесть какой-либо из двух подходов к построению системы. Четвертый критерий (критерий монофилетии) представляется более эффективным ввиду доступности данных по молекулярной филогенетике Lymnaeidae. Критический обзор данных молекулярной систематики показывает, что вероятнее всего семейство включает два крупных монофилетических клада древнего происхождения, которые отличаются меж собой по числу хромосом, но не могут быть охарактеризованы четкими морфологическими различиями. Присваивая 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 Lymnaeidae (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, характеризующихся 16 или 17 параметами хромосом. Radicinae, скорее всего, это эволюционно продвинутый таксон в сравнении с Lymnaeidae, 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 «инципи единого уровня таксономической обособленности» [Го- ликов, Старобогатов, 1988] и тому подобное.