# PONDSNAIL PROBLEMS: INVESTIGATING THE LYMNAEIDAE

**David Campbell,** Department of Natural Sciences, Gardner-Webb University, Box 7270, Boiling Springs NC 28017,
pleuronaia@gmail.com

## ABSTRACT

Although lymnaeid snails are common worldwide in Mesozoic to Recent freshwater settings and are important intermediate hosts of human and livestock parasites, their generic nomenclature is in chaos. Nearly 200 genera have been proposed. This reflects radical variation in classification philosophy, use of the family as a wastebasket for random freshwater snails, and genuine variability in a global, mid-Mesozoic to Recent taxon. Different authors currently recognize between 1 and about 50 genera and/or subgenera. The influential monograph of Hubendick (1951) argued for a single genus and only about 40 Recent species worldwide, but relied on misidentifications to "prove" extreme intraspecies variation. Conversely, Starobogatov, Kruglov, and colleagues, like the "Nouvelle École" a century before, recognize almost any variation as worthy of at least a species name. To sort this out, it has been necessary to review the entire family, including DNA sequencing of extant species, tracking down obscure literature, and morphological examination of fossils. Problematic fossil names include *Pitharella, Berellaia,* and *Scalaxis*, from the Paleocene of western Europe; *Zalophancylus* from the Neogene of the northwestern US.; *Zagrabica* from the Neogene of the Balkans; and *Zaptychius,* reportedly Carboniferous from western North America. Specimens of *Pitharella* in the Paleontological Research Institution enabled investigation, confirming that is not a lymnaeid but probably an acteonid instead. *Zalophancylus* is a fish vertebra impression; *Zaptychius* is a Cretaceous ellobiid; affinites of *Zagrabica*, *Berellaia,* and *Scalaxis* are less certain but *Zagrabica* is probably a large rissooidean. Problems exist among Recent names as well, such as *Bocourtia*, described as a southeast Asian lymnaeid with unspecified major anatomical differences from known species but actually a South American landsnail. The lymnaeids in the southeastern U.S. and Caribbean region are generally assignable to *Galba* (including *Bakerilymnea*), *Polyrhytis* (including North American "*Stagnicola*"), and *Pseudosuccinea*. .

## MYSTERY FOSSILS

The Lymnaeidae has a good fossil record from the mid-Mesozoic to the present. Many unusual fossil lymnaeids are well-known from the Paratethys region, but assorted other forms have been rather tenuously placed here. *Zalophancylus,* from the Neogene of the northwestern US, was initially identified as a lymnaeid limpet related to *Lanx*; however, Hanna (1925) reported it was merely an impression of a fish vertebra. Walcott (1883) reported the discovery of Carboniferous freshwater snails, including *Zaptychius, "Ampullaria?",* and *Physa.* These continue to be reported as the first occurrences for their groups *(e.g.*, The Fossil Record 2). However, MacNeil (1939) demonstrated that the locality was an isolated patch of Cretaceous age. reportedly Carboniferous from western North America.

*Pitharella*, *Berellaia,* and *Scalaxis* are Paleocene genera from western Europe. Of these, *Berellaia* and *Scalaxis* are poorly-understood, tall-spired, sinistral forms with rather tenuous connections to Lymnaeidae. Pilsbry (1909) created the genus *Scalaxis* in his index with no description, simply to exclude the species from the group he was studying. *Pitharella* was initially assigned to the Lymnaeidae in 1860, when the name was used to include multiple modern families of freshwater snails. The type is a large adult specimen, similar to one lot present in the Paleontological Research Institution collection (Figure 1A). The shell is sufficiently eroded to make its taxonomic affinities unclear, and the mixed freshwater/marine nature of the deposit does not help. However, the PRI collection includes additional lots. One is labeled "jeunes pour l'étude de la protoconque" (young for study of the protoconch) (Figure 1B). Regrettably, that label is on acidic cardboard, and the specimens had been degraded by Byne's disease (Figure 2A). A third lot, however, contained well-preserved juveniles, showing detail (Figures 2B, 3).

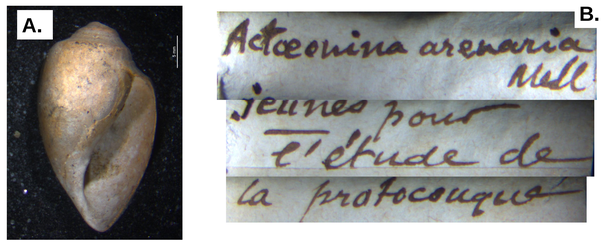


**Figure 1**. **A.** *Pitharella* adult, PRI collection. **B.** Label on stiff cardboard from a vial of juvenile *Pitharella arenaria.*

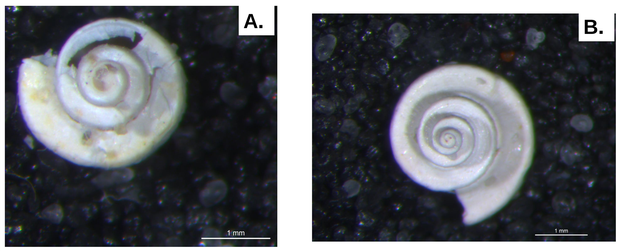


**Figure 2. A.** *Pitharella* with Byne's disease. **B.** Well-preserved *Pitharella* showing heterostrophic protoconch.


**Figure 3.** Well-preserved *Pitharella*, apertural view.

Both the heterostrophic protoconch and the angular shoulder are not normal for lymnaeids. Rather, *Pitharella* is a marine acteonoidean, probably Acteonidae.

Several unusual freshwater snails occur in the Neogene Paratethys of central to southeastern Europe. Among the lymnaeids, a trend towards wider apertures and more rapid whorl expansion culminated in large, limpet-shaped forms such as *Valenciennius* and *Delminiella. Adelina* has been assigned to Viviparidae and to Lymnaeidae, but the consensus favors lymnaeid affinities. It's also a junior homonym, replaced with *Adelinella.* Further confusion relates to the species. The original material of the type species, *Adelina elegans* Cantraine, 1841, was of uncertain origin but thought to be from Italy. Forbes (1847) reported finding the species in Turkey, but did not think it deserved a separate genus. Regrettably, instead of calling it *Lymnaea elegans*, he called it "Limneus Adelina", apparently demoting the genus to a species name and creating the appearance of naming a new species. Another puzzling genus from the Paratethys is *Zagrabica.* In shape, it suggests a rissooidean, but it is unusually large for that group. Overall, it seems more likely to be a rissoidean than a lymnaeid.

The Neogene of northwestern North America includes a remarkable fauna with some similarities to the Paratethys forms; however, these are believed to be convergent developments in similar large lakes. *Pliopholyx* was described in Lymnaeidae, but Taylor (1966) transferred this genus to Viviparoidea based on a viviparid-like color pattern, not known in Lymnaeidae. *Zalophancylus* was named by Hannibal as a patelliform lymnaeid similar to *Lanx*, but Hanna (1925) indicated that it was actually a mold of the end of a fish vertebra.

The identity of several Recent taxa assigned to Lymnaeidae have also been problematic. In the late 1800's to early 1900's, the "Nouvelle École", a group of primarily French workers headed by Bourguignat, saw at least a species if not a genus in almost every individual variation. They named over 20 new lymnaeid genera and suggested that over 200 extant species were present in Europe. Other workers of the time, though not as extreme, often named many variants. Reaction against this in the mid-1900's is exemplified by Hubendick's influential monograph of 1951. He assigned all living lymnaeids to *Lymnaea* or *Lanx* and recognized only about 40 species worldwide, with extensive intraspecific variation and all features dismissed as not significant at the genus level. However, Hubendick uncritically accepted misidentifications, taking them as evidence of intraspecific variability. Some of his comments on previously published names are also inaccurate, such as dismissing Iredale's genera as nude. Iredale's genera have brief, unsatisfactory descriptions, but they have descriptions and type species and so are not nude.

Similarly, Hubendick misrepresents Rochebrune with a misleading quotation about Rochebrune's genus *Bocourtia*: "..., il serait impossible de ne pas les considérer comme faisant partie du genre *Lymnaea* et dans le voisinage du *L. palustris*,..." (it would be impossible to not consider them as belonging to the genus *Lymnaea* and in the neighborhood of *L. palustris*), as the first ellipsis conceals the words "sans l'étude de l'animal" (without studying the animal). In fact, Rochebrune stated that Bocourtia was very different anatomically from *Lymnaea*. Unfortunately, he failed to say how. Ancey (1905) and Germain (1910) examined the specimens and identified them as land snails from Ecuador, not pondsnails from Bangkok as Rochebrune had thought.

Beginning in the 1970's, Starobogatov and colleagues returned to an extreme splitting approach, though with myriad subgenera and sections in Hubendick's broadly defined .

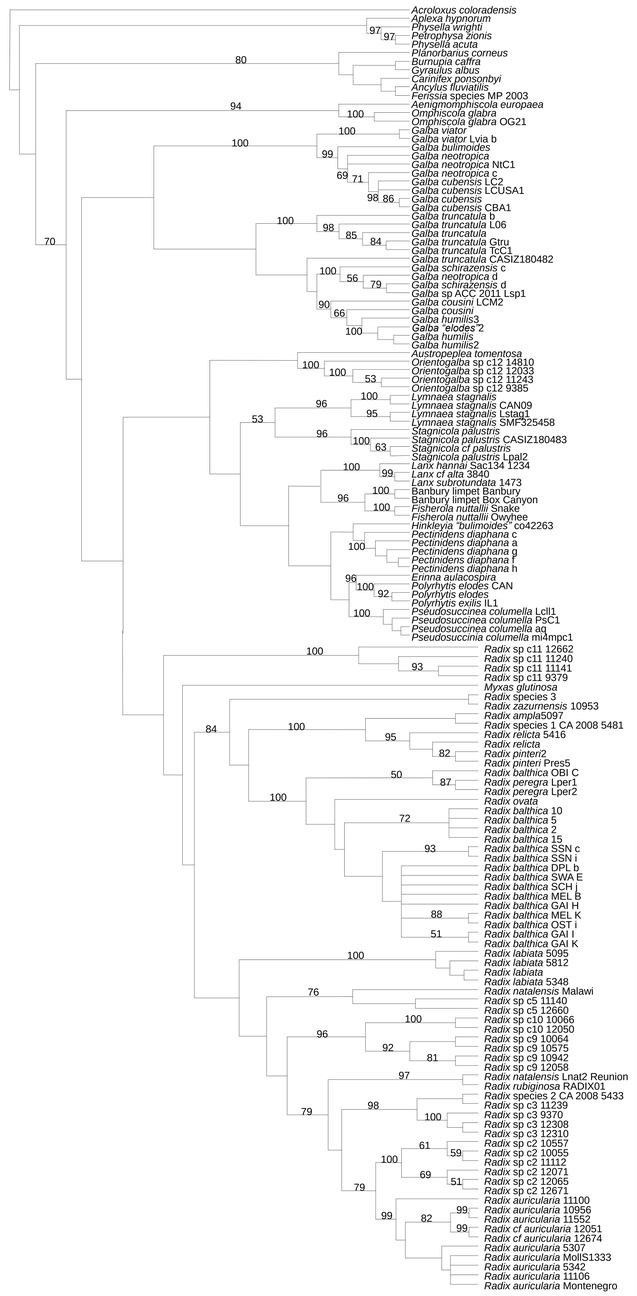


**Figure 5.** Parsimony analysis of *cox1* sequence data.
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**Figure 6.** *"Stagnicola" exilis*. From the shell, this specimen from Illinois is nearly identical to *Stagnicola palustris* from Europe. However, anatomical, radular, and molecular characters separate it.

Molecular data support anatomical-based division of Lymnaeidae into at least three major groups, though resolution of relationships between genus-level groupings are often poor, especially in mitochondrial data (Figure 5). The oldest genus name available for the small , somewhat tall-spired lymnaeids commonly called *Fossaria* or *Bakerilymnaea* is *Galba*. However, *Bakerilymnaea* seems to represent a valid group within these primarily New World snails. The group of larger, more rapidly expanding lymnaeids in northern North America and Asia to central Europe (Figure 6) is anatomically similar to *Galba*; *Polyrhytis* is the oldest name for this group. *Pseudosuccinea*, also a New World form (widely invasive) also belongs to this anatomical and genetic group.

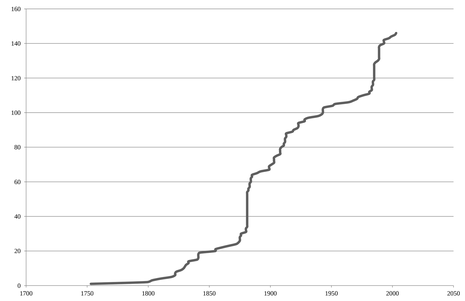


**Figure 7.** Cumulative genus names in Lymnaeidae by year.

## CONCLUSIONS

Over 150 genus names have been associated with the Lymnaeidae in its modern sense (Figure 7). Of these, 119 are legally proposed genus names for gastropods, including 14 non-lymnaeids. Only about 30 of the remaining 105 actually seem useful. Unjustified lumping and splitting have been common, leaving the nomenclature in a state of confusion. Genetic data support the recognition of several extant groups, in agreement with anatomical features and biogeographic patterns. Convergent shell form is common, posing a challenge for identifying fossils.

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