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Conceptual shifts in animal systematics as reflected in the taxonomic history of a common aquatic snail species (*Lymnaea stagnalis*)

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Abstract

Lymnaea stagnalis (L., 1758) is among the most widespread and well-studied species of freshwater Mollusca of the northern hemisphere. It is also notoriously known for its huge conchological variability. The history of scientific exploration of this species may be traced back to the end of the 16th century (Ulisse Aldrovandi in Renaissance Italy) and, thus, *L. stagnalis* has been chosen as a proper model taxon to demonstrate how changes in theoretical foundations and methodology of animal taxonomy have been reflected in the practice of classification of a particular taxon, especially on the intraspecific level. In this paper, I depict the long story of recognition of *L. stagnalis* by naturalists and biologists since the 16th century up to the present day. It is shown that different taxonomic philosophies (essentialism, population thinking, tree thinking) led to different views on the species' internal structure and its systematic position itself. The problem of how to deal with intraspecific variability in the taxonomic arrangement of *L. stagnalis* has been a central problem that made systematists change their opinion following conceptual shifts in taxonomic theory.

Introduction

The development of science as a whole, as well as the progress of a particular scientific discipline, is a complicated and diverse process with many separate aspects (Hull 1988) that permit several distinct ways to represent the history of science. In my opinion, at least three approaches are imaginable in this case. Firstly, any history is a *story* telling us about a temporal sequence of events. It means that a narrative approach, which is merely an account of persons and their discoveries, is inevitable. Secondly, one may focus on conceptual shifts in scientists' minds that reflect the theoretical rather than temporal development of science. This approach presupposes a study of continuous changes in scientific concepts and ideas as well as in the methodological foundations of the art of doing science. It may well be a non-linear process since the development of theories does not always run parallel with the progressive sequence of events. Lastly, any description of the practical aftermath of these conceptual shifts may be considered as the third approach to the history of science. It encompasses the "external" manifestations of scientific activity, including modes of representing of knowledge, scientists' social interactions, university curricula, working classifications of studied objects, and so on.

Biological systematics is, probably, the oldest of the branches of life sciences. Its roots may be traced back to the pre-scientific epoch, since so-called "ethnotaxonomy" was just the first attempt to capture biological diversity by using more or less implicit categories and vernacular names (Atran 1990). The picture of the development of biological systematics is usually drawn following either a strictly narrative or conceptual (a history of ideas) approach (Stevens 1994; Wilkins 2009; Pavlinov and Lyubarskiy 2011), but this process has other inter-

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esting sides. It includes also the histories of the scientific exploration of particular taxa and their appreciation by practicing systematists. Some of these taxa are so spectacular and valuable practically that the history of their taxonomic treatment is as long as the history of systematics itself. Other species are less important, especially for folktaxonomists, and their taxonomic study started later in the epoch of the early systematics of the sixteenth and seventeenth centuries. To reconstruct the taxonomic history of an individual taxon is an important challenge allowing one to understand deeply the historical development of biological classifications and their practical issues (Schmidtler 2011).

The aim of this paper is to outline the taxonomic history of a widespread and commonly known invertebrate species in Europe and North America – the great pond snail, *Lymnaea stagnalis* (Linnaeus, 1758). The material for the study was obtained during my work with malacological collections of the Zoological Institute, Russian Academy of Sciences (Sankt-Petersburg; ZIN hereafter), Göteborgs Naturhistoriska Muséet (GNM hereafter), Vienna Museum of Natural History, Austria (NHMW hereafter), Naturhistoriska riksmuseet, Stockholm (Sweden), and Zoological Museum of the Copenhagen University, Denmark (ZMUC hereafter). These collections contain a large number of samples of *L. stagnalis* collected and identified by prominent malacologists of the end of the 18th – the first half of the 20th centuries, and examination of these materials helped me to understand how the taxonomists' views changed with time and to trace these changes by analysis of the information available from museum labels. The extensive search through old taxonomic literature has been carried out as well. I used the books kept in ZIN and NHMW libraries and utilized those fantastic facilities provided by electronic archives such as Biodiversity Heritage Library (http://www.biodiversitylibrary.org/).

It is a freshwater pulmonate snail (Fig. 1) using atmospheric air for breathing that allows it to migrate over long distances and to gain a foothold in waterbodies of different types. *L. stagnalis* is characterized also by extreme ecological plasticity and enormous variation in its shell size and proportions (Kobelt 1871; Hubendick 1951; Arthur 1982; Vinarski 2014a). Being, very likely, the largest species of freshwater snails in Europe, the great pond snail had attracted the attention of naturalists long before Linnaeus. The first scientific description of this species appeared nearly 400 years ago (see below). The taxonomic history of *L. stagnalis* will serve here as a mirror to reflect shifts in taxonomical practice driven by conceptual changes in animal taxonomy which occurred between the 16th and 21st centuries.

Figure 1. A great pond snail in its natural environment. 12.08.2014. Russia, Western Siberia, "Malaya Sos'va" Nature Reserve, Kopanoye Lake (photo: M. Vinarski).

Lymnaea stagnalis in pre-Linnaean zoology

Though the accepted scientific name of this snail should be credited to Linnaeus (1758), it had been repeatedly described under different names by predecessors of the great Swede. It seems a bit strange that such a large and abundant snail was utterly overlooked by the Ancient naturalists. Though, as Eduard von Martens (1860) noted in due time, the Greeks and Romans had very little interest in continental mollusks, both aquatic and terrestrial. The Ancient naturalists generally neglected them, and neither Aristotle nor Pliny the Elder nor any of the secondary Ancient authors described continental mollusks in detail. Aristotle, in his influential *Historia animalium* (HA) mentions only a certain kind of "lake oysters" (*limnostrea*, see HA IV, 40, 67) as well as some obscure "land ostracoderms" not divided into species (? helicid snails; see HA IV, 38).

The only (and rather curious) alleged mention of the pond snail in Antiquity belongs not to a naturalist but to an anonymous poet who was the author of the mock poem *Batrachomyomachia* ("Battle of Frogs and Mice") intended to mimic the Homer's masterpiece *The Iliad*. The poet describes the armour of the Frogs preparing to battle with the Mice:

"…their bucklers were
Good thick-leaved cabbage, proof ' gainst any spear;
Their spears sharp bulrushes, of which were all
Fitted with long ones; their parts capital
They hid in subtle cockleshells from blows"
(Chapman 1888: 10).

The German malacologist Menke (quoted after Jeffreys 1862) tried to determine the identity of these *subtle cockleshells* mentioned by Pseudo-Homer. He supposed it may have belonged to *Lymnaea stagnalis*. This hypothesis was criticized by Jeffreys (1862), who said that it is quite impossible to judge conclusively on this subject. The Greek text is so concise that it gives no chance to choose among large species of aquatic snails inhabiting Greece and to decide which of them provided the Frogs with their helmets. As Jeffreys (1862: 113) stated, "it

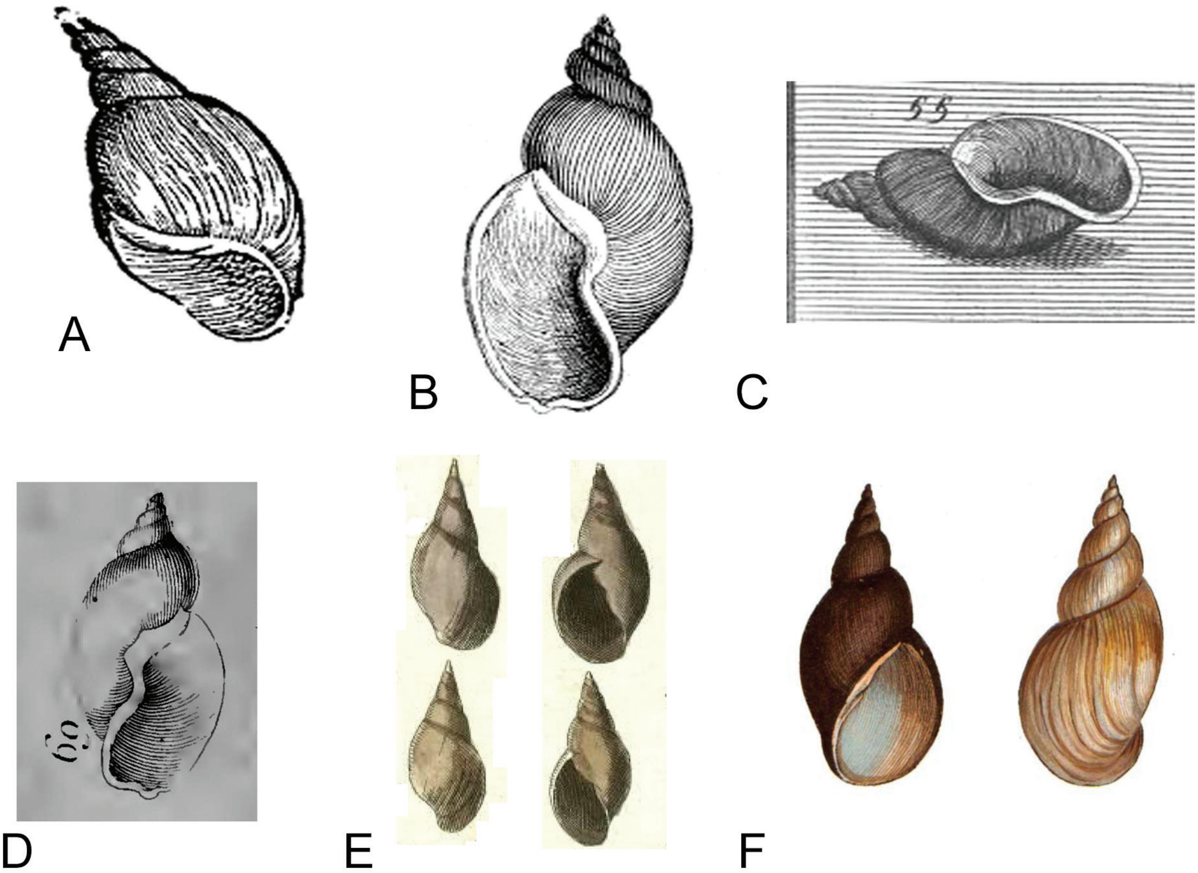

Figure 2. Evolution of accuracy in illustrations of *L. stagnalis* shell through two centuries. Sources of images: **A**. Aldrovandi 1606. **B**. Lister 1678. **C**. Bonanni 1681. **D**. Klein 1753. **E**. Seba 1758. **F**. Schröter 1779.

is not likely that Homer was a conchologist, or distinguished one shell from another for poetical purposes. The kind of shells in question must have made cumbersome helmets for the valiant Frogs".

Medieval descriptive zoology, being deeply dependant on the works of Aristotle and other Ancient naturalists, overlooked *L. stagnalis* as well. One need only envisage the image of this snail in the very crude drawings of aquatic snails which appeared at the end of the fifteenth century (see Allmon 2007, fig. 2). It is impossible, though, to judge on their true taxonomic identity with any certainty.

The first naturalists of early Modern Europe interested in aquatic animals, namely Pierre Belon (1517–1564), Guillaume Rondelet (1507–1566), and Konrad Gessner (1526–1565), did not mention the great pond snail either. Though these authors were not slavish commentators of the Greek and Roman texts and added their own observations on aquatic creatures, they were more interested in marine mollusks than in freshwater ones.

The first record of the great pond snail in the European scientific literature I managed to find is that by Ulisse Aldrovandi (1522–1605), a junior contemporary of Belon and Gessner. His posthumous treatise *De reliquis animalibus* (Aldrovandi 1606) contains a mention of this species that opens a long list of *L. stagnalis* recordings in early animal systematics. Aldrovandi's book also contained the first "scientific" illustration of the *L. stagnalis* shell (Fig. 2A) that allows us to ascertain its taxonomic identity definitely. It does not matter that the shell in this picture is sinistral (pond snails have normally dextral, or right-coiled, shells). Though sinistral mutant individuals are sometimes found in *L. stagnalis* populations (Vinarski 2007), I believe that Aldrovandi or his engraver had a normal (i.e. dextral) shell of this snail in their hands. The usual technique of engraving in the sixteenth and seventeenth centuries demanded that the plate must be a mirror image of the object to be illustrated. The printers usually were "not preparing a reversed engraving (on wood or copper), but carving the image [of a shell] as it appeared, which would produce a reversed image when printed" (Allmon 2007: 175). The biological mechanism of inversions in shell coiling in snails was not known and thus remained irrelevant for authors which permitted them to present their shells in "wrong" mirror appearance. The picture of *L. stagnalis* shells with right coiling direction did not appear in a printed book until 1681 (see Fig. 2C).

Aldrovandi (1606) gave no formal description of the great pond snail. More precisely, the Latin name of the snail ("Turbo laevis item in stagnis degens"; Aldrovandi 1606: 358) served as its proper description at this time. The early taxonomists were far from using binomial nomenclature consistently, and the species' names produced by them were *polynomials*. Each polynomial should contain several words whose quantity corresponded to the number of *es-*

Table 1. Polynomial taxonomic names proposed for the great pond snail in the 17th and 18th centuries.

Author	Latin name	English translation
Aldrovandi 1606: 358–359	Turbo levis item in stagnis degens	*Turbo* with smooth shell, living in stagnant waters
Lister 1678: 137	Buccinum longum 6 spirarum, omnium & maximum & productius, subflavum, pellucidum, in tenue acumen ex amplissima basi mucronatum	*Buccinum* with long [shell] having six whorls, whole, large, oblong, yellowish coloured, transparent, [apex] sharp and narrow, [shell] basis very ample
Bonanni 1709: 453	Longior antecedenti Turbo, levissimus, colore atro cum nitore	*Turbo* longer than the antecedent [species], smoothest, [shell] dark colored, glossy
Gualtieri 1742: [34]	Buccinum fluviatile, testa tenuissima, & fragillissima, prima spira notabiliter ventricosa, & elongata, in mucronem aculeatum statim definens, subflavum, pellucidum	*Buccinum* riverine, shell very narrow and fragile, the first whorl notably inflated and oblong, [shell] ends with sharp apex, yellowish, transparent
Linnaeus 1746: 374	Cochlea testa producta cuminata opaca, anfractibus senis subangularis, apertura ovata	*Cochlea* with elongated dark coloured shell having six subangulate whorls and ovale aperture
Seba 1758: 119	Cochlea fluviatilis, indigena, ex oblongo acuminata, lineolis veluti taeniata	*Cochlea* riverine, native [= European], with oblong and pointed shell, covered by thin lines
Klein 1755: 54–55	Auricula stagnorum – subflava, pellucida, in tenue acumen ex amplissima basi mucronata	*Auricula stagnorum* – [shell] yellowish and transparent, with pointed apex and very wide [shell] basis
Schlotterbeccius 1762: 283	Turbo fluviatilis major, corpore oblongo ampullaceo definente in mucronem acutissimum & limacem continente fuscum	*Turbo* riverine, large, body [= shell] oblong, inflated [in its base] and ending by a sharpest apex; it contains soft body of contunuosly dark coloration.
Geoffroy 1767: 72	Buccinum testa oblonga, fusca, anfractibus senis	*Buccinum* with oblong shell of brownish black colour, having six whorls
Favart d'Herbigny 1775: 139	Buccinum fluviatile, testa tenui et fragili, forma oblonga, ventricosa; sex spiris exertis parum convexis in apice acuto definentibus compositum; colore corneo, pellucido, apertura spatiosa, elongata, integra, et labio expanso distinctum	*Buccinum* riverine, its shell is narrow and fragile, oblong and inflated; it consists of six slightly convex whorls ending with a sharp apex; [shell] horny-coloured, transparent, aperture ample, elongated, whole, differs by a wide lip
Chemnitz 1786: 166	Helix <...> testa albida, pellucida, superne turrita, inferne ventricosa, apertura effusa seu ampliata, columella sinuosa	*Helix* <...> [with] whitish pellucid shell, in its upper part it is turreted; the lower part is inflated. Aperture ample or wide; columella folded

sential characters needed to be revealed in order to express what the species *is* and how to distinguish it from its congeners. The more species there were in a genus, the longer the species' names had to be produced (Pavlinov 2013). A polynomial is a name bearing the diagnosis of the taxon itself and it is very far from the Linnaean binomen, which is merely a useful verbal label serving to be remembered quickly (Vinarski 2013). The Linnaean name of the species under discussion, *Helix stagnalis*, contains no information about the *essence* of this species since it highlights the ecological preference of the great pond snail to live in stagnant waters. Certainly, this characteristic may be applied to numerous other species of European aquatic snails.

The essence of a taxon was an Aristotelian category not seen directly by the eyes, but being a mental construction based on the subjective weighting of animal characters aimed to distinguish between essential and secondary (accidental) ones. A modern scientist would say the essential diagnosis is a hypothesis since different authors may come to different views on which characters are essential and which are accidental. Therefore there was no commonly accepted scientific name for the great pond snail before Linnaeus' (1758) work. I collected a series of different polynomial names proposed from 1606 to 1786 for the designation of this species (it is by no means complete), and it is easy to see that no two authors had the same definition of its "essence" (Table 1).

The next step in the study of the great pond snail was undertaken almost 70 years later, in England. Martin Lister (1639–1712) was an English physician and naturalist, and vice-president of the Royal Society. He contributed extensively to many branches of science, including arachnology (Roos 2011) and chemistry (Roos 2008). Lister was a devoted conchologist and became the author of the first European treatises on mollusks (*Historiae Conchyliorum*, 1685; *Conchyliorum Bivalvium*, 1696). O.F. Müller (1774: xiii) called him "Conchyliologorum princeps" (head of conchologists) proposing a clear analogy with Linnaeus' informal title "Princeps botanicorum". Lister made numerous observations of mollusks' morphology (both external and internal), feeding, ecology, and distribution. His conchological works also included a description of the fossil species of shells.

In Lister's *Historiae animalium Angliae tres tractatus* (Lister 1678), one may find a detailed account of *L. stagnalis* that follows much higher standards of zoological descriptions compared with Aldrovandi's. This text contains not only the polynomial name (= short diagnosis) for this species but also a relatively long two-page sketch of the great pond snail's bionomics. Lister provides a lengthy general description of the animal's external morphology (including the pattern of mantle pigmentation), the shape of its excrements, the mode of copulation, the structure of egg-masses alongside a list of aquatic plants being its food. Some localities of *L. stagnalis* in England were also mentioned. Lister's species' account was almost 100 years ahead of its time. This high standard of publication of malacological data was not established un-

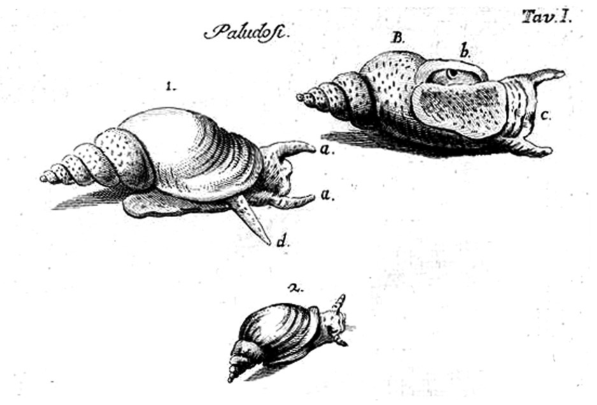

Figure 3. Illustrations of living *L. stagnalis* by Ginanni (1757).

til the end of the 18th / early 19th centuries when comparable works of European naturalists appeared (Müller 1774; Draparnaud 1805).

The picture of the great pond snail shell given by Lister (1678) is more informative than that by Aldrovandi though it is still rather crude and depicts a sinistral shell (see Fig. 2B).

Later on, Lister (1695) published a very detailed account of the *L. stagnalis* internal structure accompanied by engravings. Trained as a *medicus*, Lister was a brilliant anatomist aiming to dissect mollusks belonging to different taxa, both terrestrial and aquatic. He even estimated his own purely medical works as being of lower importance than his studies of molluscan anatomy (Heppel 1995). Another perfect anatomist of the age, Jan Swammerdam (1637–1680), was also interested in freshwater mollusks, and his study of the *L. stagnalis* anatomy was published posthumously in the author's prominent book *Bybel der natuure* (Swammerdam 1738). However, in both cases the advance of anatomical research did not enhance the progress in taxonomy. Systematists of the 17th and 18th centuries typically did not use anatomical information in their works, and the classification of mollusks long remained purely conchological (Vinarski 2014b). The use of anatomical data in lymnaeid taxonomy did not start until the first half of the 20th century (Baker 1911; Roszkowski 1914).

Most subsequent authors, whose works were published between the works of Lister and Linnaeus, were mere collectors of deposited shells of *L. stagnalis* and other freshwater species in their private museums and shell "cabinets". This form of hobby was extremely popular among European noblemen and the educated part of the middle class in the 17th and 18th centuries (Dance 1966). Some of these proud collectors published voluminous books targeted to present their treasures to a wide audience. Sometimes such books contained high quality hand-colored illustrations and therefore were extremely expensive (Dance 1966). Typically, their authors did not give lengthy accounts on species' morphology and bionomics and restricted themselves to the simplest scheme of exposition: a short diagnosis (i.e. polynomial name) of a species plus a picture of its shell. This scheme was used, among others, by Bonanni (1709), Gualtieri (1742), and Seba (1758). The quality and accuracy of shell images greatly increased through the 17th and 18th centuries, with the most accurate illustrations appearing in the 1770s (Fig. 2). Sometimes, rather realistic portraits of living snails appeared; for example, those of crawling pond snails in Ginanni's (1757) posthumous book. Ginanni's image is morphologically correct and depicts some important details such as the shape of tentacles and the respiratory opening of the animal (Fig. 3 compare with Fig. 1).

Klein (1753) was the first author to separate lymnaeid snails into a taxon of their own – the genus *Auricula* with three species included. Before Linnaeus' seminal work (Linnaeus 1758), Klein already used binomial nomenclature and introduced the first two-part name for the great pond snail – *Auricula stagnorum*. This name has a formal priority before the Linnaeus' *Helix stagnalis* but, being published before 1758, it was not available for taxonomical and nomenclatorial purposes.

Post-Linnaeus taxonomy: discovery of an intraspecific variation

Carolus Linnaeus, the Swede, was a great botanist and reformist of biological taxonomy, but his malacological (or, more correctly, conchological) works received rather low esteem among next authors. For example, Maton and Rackett (1804: 175) stated that "there has been a very general belief that less attention was devoted by Linnaeus to the history and arrangement of the Testacea than to any other order of the animal kingdom, and that he even thought their external coverings, or shells, scarcely worthy of becoming subjects of scientific distribution". Donovan (1807) expressed his disgust with the Linnaean conchological works in stronger phrases: "an opinion is pretty generally prevalent that less attention was devoted by Linnaeus to the history and arrangement of the testacea, than any other order of nature; and that he even thought them unworthy of becoming objects of scientific arrangement. These points have been contested. The truth however dill appears to be, that Linnaeus had not really bestowed much critical attention on this subject <…> When therefore the completion of the Systema required that some attention should be paid to testaceology, he was unprepared, and referring to the authorities of others, comprised this department in the smallest compass possible, more with the view of filling up a chasm, which the omission of a tribe so generally admired would occasion, than from any idea of elucidating the subject <…> It is time we should lay aside the trammels of servile adherence, and speak decidedly: – those early attempts of this celebrated writer, we do not scruple to say, if examined with candour, will be found only *a slight and ill conceived compendium* of what has been handed down to us by antecedent writers" (italics added by me).

The examination of several descriptions of *L. stagnalis* found in Linnaeus works (Linnaeus 1746, 1758, 1761,

1767) allows one to agree with the abovequoted words. Linnaeus did not move forward as compared with his predecessors (except for Lister). In 1746 he still used polynomials as the means of species designation (see Table 1). Since 1758, his species descriptions became two-part: the short binomial name proposed for the sake of utility accompanied by more detailed diagnosis being, in essence, nothing other than a traditional polynomial name (Pavlinov 2013). Thus, the great pond snail was christened in 1758 as *Helix stagnalis* and provided with a short diagnosis "*H*[*elix*] testa imperforata ovato-subulata subangulata, apertura ovata" (Linnaeus 1758: 774). Subsequent editions of "Systema Naturae" brought no new information on the great pond snail (Linnaeus 1767; Gmelin 1791).

Linnaeus and his immediate follower Johann Friedrich Gmelin (1791) did not recognize any variation within the species *Helix stagnalis*. The diagnosis of this taxon was presented as a list of essential conchological traits as if all snails were completely identical in their shell appearance. Though Linnaeus himself paid much attention to the problem of intraspecific variation in his theoretical works (i.e. in *Philosophy of Botany*; Linnaeus 1751), he was interested mainly in variations in plants. In the zoological part of *Systema Naturae* only a few animal species were mentioned as having varieties in their structure (notably, *Homo sapiens* Linnaeus, 1758 was among these species).

As a rule, animal taxonomists of the second half of the seventeenth century were still not aware of the existence of intraspecific variation (Vinarski 2013), though the most gifted observers among them knew well that there is some degree of phenotypical heterogeneity within common and widespread species. Possibly, the Danish naturalist Otto Frederick Müller (1730–1784) was the first student of non-marine mollusks to make an attempt to reflect this heterogeneity in a taxonomic work. Müller's opus magnum *Vermium terrestrium et fluviatilium* (Müller, 1774) became the most influential monograph on terrestrial and freshwater mollusks published between *Systema Naturae* and the dawn of the nineteenth century. Müller was a really great naturalist with a special interest in aquatic creatures, including infusorians, rotifers, crustaceans, and mollusks. He was the first naturalist to use a dredge for sampling benthic animals of inland waterbodies (Anderson and Rice 2006). Müller's species descriptions were rather lengthy and informative though *Vermium terrestrium et fluviatilium* did not contain illustrations of any described objects. The Dane established a new standard of arrangement of intraspecific variation in malacological treatises. His approach presupposed the enumeration of as many intraspecific varieties as was possible, each given a polynomial name serving as the diagnosis. The Greek alphabet letters were used for formal designation of these varieties. In some species of mollusks, especially of terrestrial ones, a number of such varieties could be rather high. For instance, Müller (1774) could distinguish 27 varieties of the common European garden snail, *Cepaea nemoralis* (L., 1758), designated by combinations of Greek letters, α to δδ. In aquatic snails, Müller (1774) identified far fewer varieties, and no intraspecific group was described within *L. stagnalis* at all. Nevertheless, this approach was accepted by subsequent students of freshwater mollusks (Draparnaud 1805; Pfeiffer 1821; Nilsson 1822).

At the end of the 19th century, the practice of recognition of varieties in *L. stagnalis* reached its summit in the works of S. Clessin (1884, 1887) and C. A. Westerlund (1885, 1897). Westerlund was, perhaps, the most prolific maker of varieties. He was able to determine as many as 19 varieties of the great pond snail in the Scandinavian region alone (Westerlund 1897), though he did not give a key for their exact categorisation. The users of his taxonomic catalogues were provided with only German or Latin diagnoses of the varieties with no chance to know the characters to distinguish among them precisely. The readers of Clessin's books (1884, 1887) were in a slightly more favourable position since the author illustrated shells of most varieties. This simple scheme of „species and its varieties" was applied in several influential malacological works of the 20th century; for instance, in those by Ehrmann (1933) and Zhadin (1952).

Having searched through the old malacological literature, I compiled a synonymy of *L. stagnalis* s. lato that contains nearly 80 varieties of this species described between the 1820s and 1920s (Electronic Appendix 1) A closer examination of this „zoo" reveals a plethora of causes serving as grounds for establishing new varieties. I had an opportunity to examine many of these varieties using samples of *L. stagnalis* identified by malacologists of the 19th century (Fig. 4) and now kept in the Europe's scientific institutions. It gave me a possibility to outline a rough classification of the varieties depending on the basis of their recognition. At least seven large groups of varieties may be separated:

1. Those reflecting variation in shell size. Example: *L. stagnalis* var. *major* Moquin-Tandon, 1855. Sometimes, shells of knowingly juvenile individuals were described as a distinct variety (*L. stagnalis* var. *junior* Nilsson, 1822).
2. Sinistral mutants: *L. stagnalis* var. *sinistrorsa* Jeffreys, 1862.
3. Variants of the shell surface colouration: *L. stagnalis* var. *bicolor* Hartmann, 1840; *L. stagnalis* var. *roseolabiata* Beck, 1837; *L. stagnalis* var. *fasciata* Merkel, 1908.
4. Varieties based on shell proportions: *L. stagnalis* var. *ampliata* Clessin, 1876; *L. stagnalis* var. *producta* Colbeau, 1859.
5. Varieties based on peculiarities of shell structure, including structure of aperture and umbilicus, whorls' shape: *L. stagnalis* var. *umbilicata* Hutton, 1905.
6. Varieties based on ecological preferences: *L. stagnalis* var. *lacustris* Studer, 1820; *L. stagnalis* var. *alpicola* Gredler, 1859
7. Geographical races: *L. stagnalis* var. *bottnica* Westerlund, 1884; *L. stagnalis* var. *gallica* Bourguignat, 1864.
8. Varieties based on conchological similarity with other lymnaeid taxa: *L. stagnalis* var. *palustriformis* Kobelt, 1870.

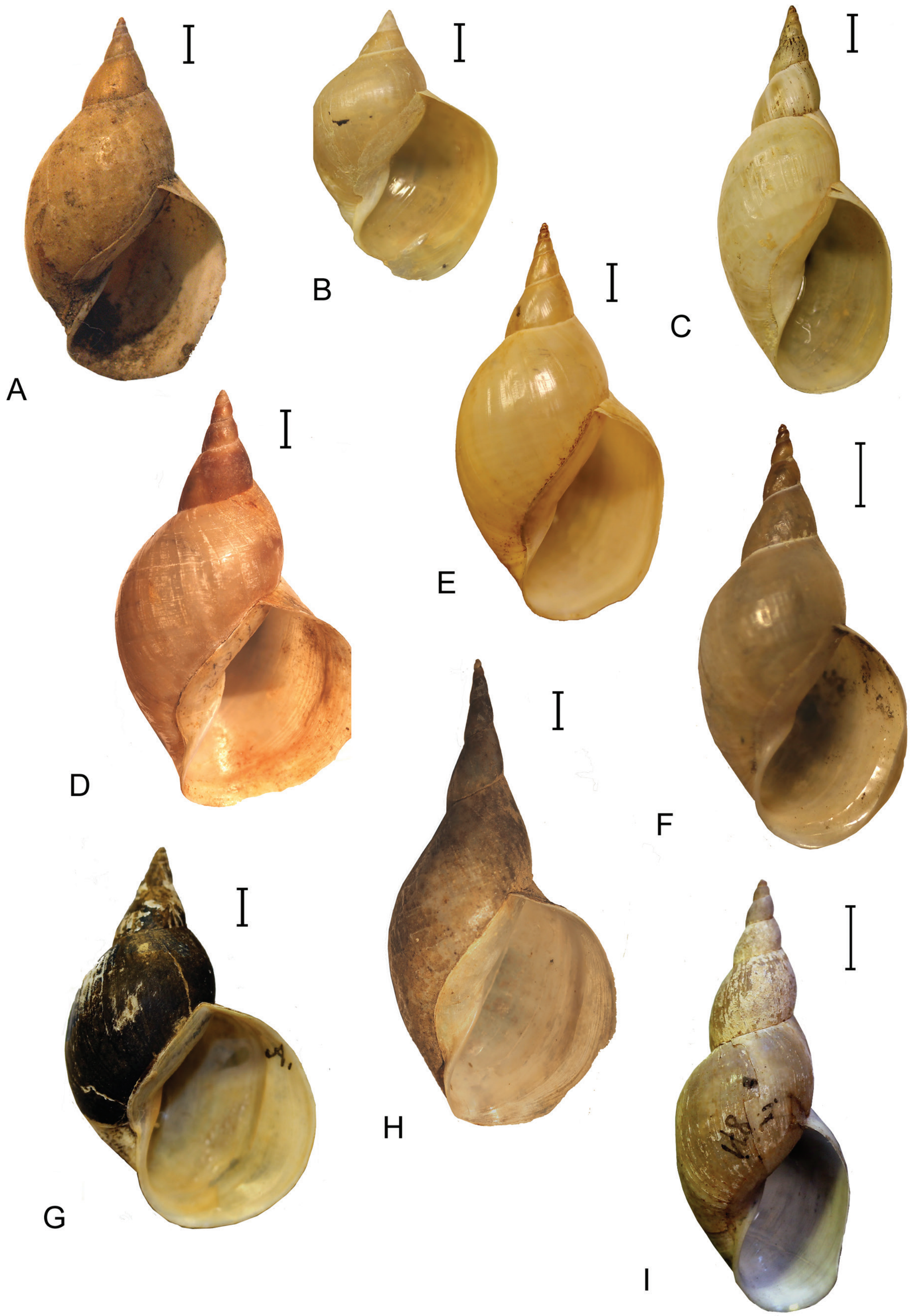

Figure 4. Varieties of *L. stagnalis* as they were identified by malacologists of the 19th century. **A**. *L. stagnalis* var. *typica* (det. S. Clessin; ZIN). **B**. *L. stagnalis* var. *media* (det. C.A. Westerlund; GNM). **C**. *L. stagnalis* var. *producta* (det. C.A. Westerlund; GNM). **D**. *L. stagnalis* var. *rosea* (identified by a unknown person; ZMUC). **E**. *L. stagnalis* var. *colpodia* (det. C.A. Westerlund; GNM). **F**. *L. stagnalis* var. *variegata* (det. C.A. Westerlund; GNM). **G**. *L. stagnalis* var. *turgida* (det. C.A. Westerlund; GNM). **H**. *L. stagnalis* var. *raphidia* (det. C.A. Westerlund; GNM). **I**. *L. stagnalis* var. *palustriformis* (det. A. Fuchs, NHMW). Scale bars 5 mm.

This short review shows how vague and indeterminate was this common practice of the discrimination of varieties. Zhadin (1952; 166) rightly advised the readers / users of his key that „we do not recommend to fit each collected shell to some variety; in most cases it is enough to give the shell measurements and only very divergent shells should be illustrated by drawings or photographs".

Some authors attempted to reduce this vagueness by making demand that only those varieties that are found to have a hereditary basis are real. For instance, Chaster (1907: 28) proposed a new definition of variety in malacology: „a variety is a group of individuals that differs from the typical or normal form in more or less distinct characters which are transmissible to the offspring".

Nevertheless, the most peculiar approach to the systematization of pond snails was realized by a group of French malacologists of the second half of the nineteenth century known under the name "Nouvelle École" (Dance 1970). The followers of it believed that a new species should be established if an individual is found to differ from all others by three characters or more (Davies 2004). Such a method led them to accept a huge number of nominal taxa of species' rank on the basis of very slight differences, usually in shell shape and proportions. Thus Locard (1893) was able to recognize no less than 22 "species" corresponding to *L. stagnalis* s. lato in the fauna of France alone (see Electronic Appendix 2). Most of these taxa were plain varieties raised to the rank of species. The unreliability of this approach was obvious, and no malacologist outside France could accept it.

A seemingly more productive approach to the *L. stagnalis* group taxonomy was proposed in Germany by Wilhelm Kobelt (1840–1916), a prominent zoologist who was also a strong critic of the "Nouvelle École" methods. Kobelt (1871) supposed that the shell variation in great pond snails has essentially ecological character, and their shell shape and proportions are moulded environmentally. Kobelt considered *L. stagnalis* as a Formenkreis ("circle of forms"), i.e. as a polymorphic species consisting of a series of ecological races that, in turn, embrace a plethora of varieties described prior to 1871. He distinguished at least four ecological forms (races) denoted by vernacular German names:

1. "Normalform" (a typical morph, see Fig. 4A).
2. "Hungerform" (a starvation morph) – dwarf phenotype of *L. stagnalis* arising allegedly as a result of food shortage.
3. "Seeform" – a phenotype of large lakes.
4. "Kanalform" – a phenotype produced in canals.

Kobelt's idea helped to reduce the mammoth number of varieties to a few comprehensible entities with relatively clear content. Its influence may be traced in the works of David Geyer (1927) in Germany and Vladimir Zhadin (1933, 1952) in USSR, who used the Formenkreis concept to outline a circle of varieties within widespread species of freshwater snails, including *L. stagnalis*, *Radix auricularia* (L., 1758), *Planorbarius corneus* (L., 1758) and others. In this context, Hans Modell's (1922) attempt to build a taxonomic framework for freshwater unionid mussels (very variable like lymnaeids) on the basis of the recognition of intraspecific ecological morphs is of high interest as another realization of Kobelt's idea.

Population thinking and its consequences: twentienth century systematics

The advent of population genetics in the 1910–1920s brought to malacologists a new way of thinking capable of explaining the great pond snail variation. The futility of establishing an endless number of obscure varieties was demonstrated by Mozley (1937), who insisted that it is almost senseless to use standard shell measurements and their ratios for the exact determination of *L. stagnalis* varieties. The cause was that the overall conchological variation in a particular waterbody is sometimes so wide that "it may approach the range of variation which is to be found over the whole of the geographical range of the species" (Mozley 1937: 185). Instead, Mozley proposed to use the "local race" concept, according to which each more or less isolated habitat, pond or lake, has its own recognizable race of *L. stagnalis*. Mozley himself observed such a situation in Finland, where these races are common and, more importantly, "do *not* appear to be specially adapted to the local conditions under which they live" (Mozley 1937: 186). Thus the local races are not identical to ecological races according to Kobelt (1871). The main factor of their origin is the spatial separateness of waterbodies preventing the gene flow among populations.

This idea was a consequence of a quite novel form of biological thought known under the label "population thinking" (Mayr 1982). This population thinking shifted biologists from the study of single (or few) individuals to the examination of representative samples of animals by means of the rigorous statistical methods developed by biometrics. Most students agreed that character variation in natural populations is a norm rather than an annoying exception (Vinarski 2013), and the biometric studies revealed the continuous characters of shell variation not comparable with the concept of many distinct varieties within a species.

Further progress in biometric studies and conchometry based on measurements of large samples for drawing statistical inferences led to the complete renunciation of the local race concept in "freshwater" malacology. Eventually it became a trivial fact that any well isolated population of a given species should differ phenotypically from other populations of the same species. A total number of local races of *L. stagnalis* would be positively immense, so that makes the concept itself impracticable. Another cause of neglect of local races and similar intraspecific entities were anatomical studies focused mainly on the reproductive morphology of lymnaeids. Though the first information on *L. stagnalis* anatomy was obtained as ear-

Table 2. Taxonomy of the *Lymnaea stagnalis* species complex according to Kruglov and Starobogatov (1993).

Subgenus	Section	Species
Lymnaea	*Lymnaea* s.str.	1. *L. doriana* (Bourguignat, 1862) 2. *L. fragilis* (L., 1758) – *L. fragilis fragilis* – *L. f. producta* (Colbeau, 1859) 3. *L. stagnalis* (L., 1758) – *L. stagnalis stagnalis* – *L. s. turgida* (Hartmann, 1840)
	Kobeltilymnaea Kruglov & Starobogatov, 1993	4. *L. araratensis* Kruglov & Starobogatov, 1985
	Stagnaliana Servain, 1881	5. *L. media* (Kobelt, 1877) 6. *L. bodamica* (Miller, 1873)

ly as the 17th century (M. Lister, J. Swammerdam), its taxonomic relevance was not acknowledged until the 1910s (Baker 1911; Roszkowski 1914). Pioneering work with broad taxonomic use of data on lymnaeid anatomy was published by Frank C. Baker (1911), a prominent American malacologists, who tried to construct a system of Lymnaeidae on the joint conchological-anatomical basis. Bengt Hubendick, the Swedish malacologist, put anatomy as the only cornerstone of his worldwide system of the family (Hubendick 1951). He failed to find any qualitative anatomical differences among conchologically distinct morphs and varieties of *L. stagnalis*. Hubendick (1951) identified all these intraspecific entities as mere conchological variants of the same biological species, having no real taxonomic significance. Anatomical features of lymnaeid snails were thought to be of much higher taxonomic value compared to the conchological ones. After Hubendick, most authors viewed *L. stagnalis* as a conchologically heterogenous but anatomically uniform species with no intraspecific taxa in its structure (Piechocki 1979; Jackiewicz 1998; Glöer 2002).

In the twenthienth century, the Synthetic Theory of Evolution (STE) absolutely dominated over biologists' minds. One of the most influential STE constituents was the so called 'biological species concept' (BSC) that is universally known and needs no detailed exposition here. I wish only to remind that BSC sees species as isolated gene pools able to keep their integrity due to complete or almost complete absence of gene flow among them (Mayr 1982; Wilkins 2009). Hubendick (1951) acknowledged the theoretical significance of BSC but refuted its practical application to the systematization of lymnaeids. He stated that a realization of BSC guidelines "offers considerable difficulties. A strictly practical application involves the conducting of crossing experiments between individuals from different populations. To carry out such a noteworthy degree with the Lymnaeids <…> is impossible in practice" (Hubendick 1951: 35).

The first attempt to apply BSC in lymnaeid systematics was undertaken in the USSR in the 1970s and 1980s by N.D. Kruglov and Ya.I. Starobogatov. They adopted two main methods of systematization: artificial crossing experiments (Kruglov 1975; Kruglov and Starobogatov 1985) and the so called "comparatorial (or comparatory) method" invented by Logvinenko and Starobogatov (1971). The latter is based on an analysis of the subtle differences in shell growth patterns of closely allied species of snails and bivalves (Kruglov and Starobogatov 1985; Shikov and Zatravkin 1991; Graf 2007). Starobogatov and his numerous disciples applied this method in order to revise all families of freshwater mollusks of the former USSR. Though Graf (2007) considers the comparatorial method as a peculiar "species concept", his statement is not fully correct since Starobogatov himself was a follower of BSC and published several papers on its application to the systematics of freshwater mollusks (Starobogatov 1968, 1977).

As a consequence, Kruglov and Starobogatov (1985, 1993) proposed a new taxonomic structure of the *L. stagnalis* complex drastically dissimilar to the Hubendick (1951) system. The great pond snail was thought to represent at least six independent species distributed among three sections of the genus *Lymnaea* (Table 2). I have to note, however, that only two species out of the six (*L. stagnalis* s.str., *L. fragilis* L., 1758) were really involved in the artificial breeding experiments conducted by the authors. The species status of the remaining taxa was proposed for the reason of lack of morphological intermediates between them under condition of syntopy. According to Starobogatov (1968, 1977), the absence of such intermediate specimens could serve as an indirect proof of the reproductive isolation between studied taxa and might be taken into account by taxonomists even if this alleged isolation was not tested experimentally. In particular, differences in geometric patterns of shell coiling between two forms revealed by means of the comparatorial method was regarded by some Russian workers as a solid proof of their belonging to different species (Shikov and Zatravkin 1991).

The fate of Kruglov and Starobogatov's (1985) crossing experiments is remarkable. Though their results appeared in an international malacological journal and the language of the publication was English, not Russian, a serious discussion on the subject did not started. Only Meier-Brook (1993) briefly discussed these experiments in his article devoted to the species problem in "freshwater" malacology: "If the criteria for the assessment of the descendants are convincingly as described in their paper, we have to admit logically that Kruglov & Starobogatov are right to consider distinct species in this case" ("Wenn die Kriterien für die Beurteilung der Nachkommenherkunft so überzeugend sind, wie in ihrer Publikation beschrieben, wird man konsequenterweise zugestehen müssen, daß Kruglov & Starobogatov Recht haben, hier von getrennten Arten auszugehen"' Meier-Brook 1993: 136). Other malacologists were not so loyal and either avoided any discussion or restricted themselves to general phrases with no sympathy for the "Russian" system ("opinions of Russian malacologists on the lymnaeid taxonomy <…> raised great doubts and <…> have not been taken into consideration"; Jackiewicz 1998: 3).

I think this question could not be resolved in principle before the modern "revolution" in taxonomy that was triggered by introduction of the molecular genetic techniques in the 1980s.

The great pond snail in the brave new world

The 'brave new world' of animal taxonomy relies heavily on inferences based on molecular studies and the quasi-cladistic way of bringing up and testing phylogenetic hypotheses (Mooi and Gill 2010). Though molecules are not the panacea for all puzzles systematists seek to solve, genetic methods provide us with an independent set of characters giving an opportunity to test hypotheses based on classical morphological studies. This has brought new possibilities and launched a new cycle of taxonomic studies on biological species, including the most well-studied ones such as *L. stagnalis*.

Already the first attempts to examine the internal diversity of *L. stagnalis* by molecular methods (Remigio and Blair 1997; Remigio 2002) revealed that its populations from different countries (Italy, Germany) and continents (Europe, North America) are separated by rather great genetic distances comparable with those separating distinct species of Lymnaeidae or even slightly exceeding them. Remigio (2002: 691) suggested that these populations "probably deserve at least subspecies status". The number of studied specimens/populations of *L. stagnalis* and the geographical scope in these early works were, however, not enough for making sound conclusions.

In 2008, a group of Ukrainian malacologists (Mezhzherin et al. 2008) submitted the two alleged species of the Kruglov and Starobogatov (1985) system, *L. stagnalis* s.str. and *L. fragilis*, to allozyme electrophoresis. They demonstrated that there are no significant genetic differences between these two taxa and they should be synonymized. Their reproductive isolation has also been questioned by Mezhzherin et al. (2008). An interesting pattern of congruence between genetic diversity and geography in the great pond snail was found: in the Ukraine, populations of *L. stagnalis* s. l. form two genetically distinct groups, "western" and "eastern", with the boundary between them lying somewhere in the central part of the country. Mezhzherin et al. (2008) proposed to treat the two groups as allospecies (sensu Amadon 1966) within the superspecies *L. stagnalis* s. l.

Having used the DNA sequencing technique and four gene markers (two nuclear and two mitochondrial), Vinarski et al. (2012) obtained results similar to those of Mezhzherin et al. (2008). In their study, two large genetically distinct groups whose distribution is clearly correlated with geography (geogroups) were found to exist within Palearctic *L. stagnalis* s. l. One of them is of mainly western distribution being found throughout Europe (except for the eastern parts of Ukraine and European Russia), and the second is widely distributed in Asia, from Transcaucasia eastwards to Mongolia, Tajikistan, and Lake Baikal. Most probably, these geogroups correspond to the two allospecies discovered by Mezhzherin et al. (2008) and therefore the use of the superspecies concept (Amadon 1966) is justified in this case. The phylogeographic pattern of the great pond snail, with separation of the species into two large divisions with eastern and western Palearctic distribution, resembles a number of similar examples found in different animal taxa, including freshwater amphipods (Vainio and Väinölä 2003), amphibians (Borkin et al. 2004), fish (Makhrov and Bolotov 2006) and mammals (Marmi et al. 2006). The usual explanation for such phylogeographic patterns is that of invoking Pleistocene glacial events, including the long isolation of groups of populations in refugia and the following recovery of the former range with the formation of zones of secondary intergradation.

However, a thorough analysis of morphological variation in *L. stagnalis* s. l. shows that the internal structure of the species cannot be restricted to molecularly defined groups. Though numerous morphs and varieties of the great pond snail lack the genetic support, the reality of some morphologically distinct entities within it has been proved by statistical methods (Vinarski 2014a). Four or five conchologically defined "morphotypes" can be delineated within *L. stagnalis* in Palearctic, with two of them, *L. stagnalis* (f. typica) and *L. fragilis* sensu Kruglov and Starobogatov being the most widely distributed (Vinarski 2014a). From the phylogenetic point of view, however, these morphotypes do not constitute separate clades and may arise in both geogroups in parallel. Their spatial distribution is apparently not governed by ecological or physical geographical factors (Vinarski et al. 2012; Vinarski 2014a).

These results represent a clear example of drastic incongruence between molecular and morphological data. Though the validity of "minor" species of the great pond snails accepted by Kruglov and Starobogatov (1985, 1993) was not corroborated genetically, the question of a possible existence of "cryptic" species (or other taxonomically significant entities of lower rank) within *L. stagnalis* s. lato remains opened. In my opinion, both "dimensions" of the species, genetic and morphological, are worthy of study since provide us with additional evidence and as such may be used in an integrative taxonomic approach. The geogroups teach us something of the history of the species' range and alleged Plestocene refugia. The morphotypes reflect another, functional aspect of biodiversity additional to the taxonomic one that may be measured at the infraspecific level (Albert et al. 2012). It has been assumed that conchological differences between the morphotypes may be of some adaptive value (Vinarski 2014a).

Nevertheless, this brave new view on *L. stagnalis* will, possibly, change in the nearest future since new, more powerful methods of molecular study (next generation sequencing, transcriptomics) are coming. The application of these methods may bring essentially new results concerning the great pond snail – this long studied but still not completely understood species.

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