

THE SPECIES QUESTION IN FRESHWATER MALACOLOGY: FROM LINNAEUS TO THE PRESENT DAY¹

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ABSTRACT: The history of the species problem as applied to freshwater molluscs, from the beginning of scientific taxonomy to the present day, is outlined. Three main approaches to delineation of species boundaries (intuitive, conceptual, and operational) are discussed, with remarks on their practical usage in freshwater malacology. The central topic of the article is how malacologists changed their views on the essence of species category and the impact of these changes on the taxonomic practice. The opinions of some prominent and prolific workers in the field (Bourguignat, Kobelt, Hubendick, Starobogatov) are analysed as well as the debates around the theoretical foundations and practical results of the ‘Nouvelle École’ of the 19th century and the ‘comparatory’ systematics of the 20th century. It is shown that the operational approach to species delineation is the most popular in current systematic malacology, with strong inclination of practitioners to use reductionist methods.

KEYWORDS: species definitions, species concept(s), freshwater snails, freshwater bivalves

INTRODUCTION

Since the time of Linnaeus, species as a taxonomic unit has been fundamental in biological classification. Since the time of Darwin, species have been viewed as fundamental units of the evolutionary process. Every branch of modern biology uses the Latin binomial names invented for designation of species of living organisms. Various applications of biological knowledge, such as nature conservation or pest management, are critically dependent on species taxonomy. Species and their names are widely used in folk taxonomies and everyday communication among people. Paradoxically, though, no rank of the Linnaean taxonomic hierarchy generates so much debate and controversy as species does. Any comprehensive taxonomic monograph contains long lists of synonyms: binomial names independently proposed to designate the same species, and practicing systematists invest their time and energy to discuss problems related to species naming and delineation.

The discussion on the theoretical and methodological aspects of the species problem has been too long to be reviewed here, even briefly. I can only refer to some monographs dealing with the problem, including its historical facets (MAYR 1963, ZAVADSKY 1968, ERESHEFSKY 1992, STAMOS 2003, WILKINS 2009a, b, ZACHOS 2016).

While some theorists dream of the ‘unified’, or ‘general’ species concept applicable to all or almost all living creatures (DE QUEIROZ 2005, HEY 2006, HAUSDORF 2011, SEIFERT 2014, but see DUBOIS 2011), from archaea to mammals, the practicing taxonomists realise that the very meaning of the term ‘species’ may change depending on the group of organisms discussed. For example, the bacterial species definition (KONSTANTINIDIS et al. 2006, FRASER et al. 2009) is hardly applicable to higher dioecious eukaryotes with obligate allogamy. It makes sense to develop ‘parochial’ species concepts applicable within large taxa only.

Historically, the study of molluscs has been divided into three main domains corresponding to

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the three domains of the biosphere occupied by the Mollusca – marine, freshwater and terrestrial. The aim of this paper is to review the history and the present state of the species question in freshwater malacology. Earlier publications on this subject include HUBENDICK (1954), STAROBOGATOV (1968,

1977, 1996a), BOETERS (1979, 1982), GIUSTI & MANGANELLI (1992), MEIER-BROOK (1993), DAVIS (2004), GRAF (2007), and VINARSKI & ANDREEVA (2007). A useful collection of species definitions proposed by naturalists of the 19th century can be found in WESTERLUND (1892).

THE FOUR MAIN APPROACHES TO THE SPECIES PROBLEM

All approaches to species delimitation in zoology, including those used in the past, can be distributed among four large classes outlined below.

THE NAÏVE APPROACH

This approach was used by ‘primitive’ people and is often termed ‘folk (or folkbiological) taxonomy’. It constitutes the basis of the so-called “ethnobotany” and “ethnozoology” which are extensively studied now (see e.g. BERLIN 1973, LÓPEZ et al. 1997, ATRAN & MEDIN 2008). Not scientific at all, this approach reflects human demand for practical knowledge of plants and animals as well as the need of their proper distinguishing, naming and classifying. This approach is not discussed further in this article since folk taxonomies usually do not embrace freshwater molluscs, except a very limited number of practically important taxa.

THE INTUITIVE APPROACH

The intuitive taxonomist delimits species by means of his/her own subjective evaluation of similarities and differences among objects under classification. Being the matter of personal judgement, this procedure usually cannot be formalised as a set of strict guidelines, therefore the taxonomists rarely can explain how exactly they do their work. As H. A. Pilsbry formulated it (quoted after SOLEM 1978), it is ‘...an accurate *feeling* for subtle affinities for which no good reason can be given in words’. Such an approach almost inevitably leads to the so-called ‘cynic’s species concept’ (KITCHER 1984), first formulated by REGAN (1926: 75): ‘a species is a community, or a number of communities, whose distinctive morphological characters are, *in the opinion of a competent systematist*, sufficiently definite to entitle it, or them, to a specific name’ (italics added by me). The systematists-intuitivists often declare that they do not need any scientific theory to delimit species since they apprehend them as morphologically discrete and visibly recognisable groups of individuals. The aim of this activity is merely a working classification of a given taxon, not a causative *explanation* in a scientific sense (PAVLINOV & LYUBARSKIY 2011).

THE CONCEPTUAL APPROACH

The ‘species concept’ is a kind of biological theory defining the ‘essence’ of the species category, or, in other words, explaining ‘what is a species, and what is not’ (MAYR 1996). As HEY et al. (2003) state, this approach was introduced by MAYR (1942), who first distinguished not less than three distinct ‘species concepts’, while all preceding authors discussed only the ‘species concept’ (in singular). Every concept proposes its own definition of species, for example, “a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent” (WILKINS 2009b: 197), and, sometimes but not necessarily, gives us some criteria for species delineation (HAUSDORF 2011). Somewhat more than 30 different species concepts have been proposed up to now (ZACHOS 2016) but their proliferation has not brought agreement among systematists. Besides, it has caused some unpleasant outcomes for taxonomy, macroecology, and conservation biology, such as the so-called ‘taxonomic inflation’ (ISAAC et al. 2004, PADIAL & DE LA RIVA 2006, DUBOIS 2008). The apparent failure of theorists to reach consensus led some workers to the idea of total renunciation of species rank itself. As MISHLER (1999: 312) insists, ‘we must end the endless bickering over how this rank should be applied, and instead get rid of the rank itself’. Another proposition is to return to a certain common concept of species that should be based on some fundamental traits of natural species generally accepted by most biologists (HEY 2006). For example, one of such metaconceptual definitions is as follows: any species is a ‘closed, or, protected, gene pool’ (DUBOIS 1988: 18).

OPERATIONAL APPROACH

The operational approach seeks clear and unequivocal guidelines, possibly even conventional, for assigning species rank. This approach intends to clarify such widespread concepts as ‘similarity’ or ‘interbreeding’ and formalises them in order to reach communicability between scientists (HAILMAN 1995). It should not be confused with the intuitive approach since the operational criteria are explicitly based on the basic properties of biological species discerned by



the evolutionary theory. Each of these criteria follows some species concept. For example, the criterion of reproductive isolation (inability to produce fertile offspring) is based on the Mayrian biological species concept (BSC). The criterion of molecular evidence (or evolutionary distance) is based on the molecular clock hypothesis rooted in the phylogenetic species concept and similar concepts exploiting tree-based approach to species delineation (SITES & MARSHALL 2004) and so on. In other words, the operational criteria cannot tell us what species is but are able to

teach us how to discern species. There is a plethora of operational criteria for species delineation exploiting various data sources, including DNA sequences, ecological data (GIS-based), molecular markers etc. (see reviews by SITES & CRANDALL 1997, SITES & MARSHALL 2004, WIENS 2007, TOBIAS et al. 2010, ZAPATA & JIMÉNEZ 2012). The popularity of such criteria in current taxonomy is easily explained by their repeatability, formalised character and assumed objectivity of their use compared to the use of the *intuitive* approach.

SPECIES QUESTION IN FRESHWATER MALACOLOGY: THE 19TH CENTURY

Three naturalists can be regarded as the ‘fathers’ of freshwater malacology: Carl Linnaeus (1707–1778), Otto-Friedrich Müller (1730–1784), and Jacques Philippe Raymond Draparnaud (1772–1804). Their works laid a basis for the subsequent taxonomic description of non-marine gastropods and bivalves of Europe and other continents. However, none of the three did explicitly formulate his views on how to recognise species of Mollusca. For example, Linnaeus described more than 800 species belonging to his taxon Testacea (BORKIN 2009), but one cannot find in his opus magnum (*Systema Naturae*) any practical rules for assigning the species rank. Treatises on continental Mollusca published by Müller and Draparnaud also contain almost no such information. Though DRAPARNAUD (1801) explained that he delimited species taking into consideration several shell characters (shape, colouration, transparency of shell walls), he failed to mention how exactly he did it. In his influential monograph on the French continental malacofauna, Draparnaud even refused to discuss the difference between ‘good’ species and varieties, stating that “it does not matter whatever name we give to an assemblage of individuals linked by relations of resemblance and whether we call it ‘species’ or ‘variety’” [“D’ailleurs peu importe quel soit le nom que l’on donne à une réunion d’individus liés par des rapports de ressemblance, et qu’on l’appelle ‘espèce’ or ‘variété’”] (DRAPARNAUD 1805: VII).

All that we know about classification practice of these early students of continental molluscs is that they did not use anatomical data for species delineation, and their systems remained purely conchological (VINARSKI 2014a). The intuitive mode of species delimitation used by Linnaeus and his followers is obvious.

The neglect of the species question in works of practicing conchologists lasted a long time after Linnaeus. Between 1800 and 1850 many manuals and handbooks of systematic conchology, more or less comprehensive, were published in English, German, and French, but their authors, as a rule, did not dis-

cuss what a species was. They often avoided even a formal definition of the species rank. For instance, G. B. Sowerby’s *Conchological Manual* of 1839 (fourth edition – 1852), contained such chapters as Body whorl, Columella, Measurement, and Suture, but not Genus, or Species (SOWERBY 1839). The only definition of the term ‘species’ I could find among these numerous manuals belonged to William Turton, the British conchologist. TURTON (1819: XXIV) referred to species as ‘the individual of a family or genus, and distinguished from all others of its tribe by permanent marks, called specific characters’. Apparently, this definition is too generalised and vague to serve as a guideline for species delineation.

Perhaps, conchologists of that time saw species as something self-evident, not needing verbal expression. As far as I can judge, the absence of morphologically intermediate forms between groups of individuals (= hiatus) served as the most important sign of their appurtenance to two distinct species. At least some conchologists of the 19th century were obsessed by the search for hiatuses and became furious when intermediate specimens were found. WILKINS (2009a: 119) quotes an anecdote about William Stimpson (1832–1872), the American conchologist who, upon finding intermediate forms of a mollusc, could not place them in one species or another, ‘after he had studied it for a long time, put his heel upon it and grind[ing] it to powder, remarking “That’s the proper way to serve a damned transitional form”’.

Later, the procedure of mollusc species discrimination by means of hiatuses was explicitly described in the first volume of Jeffreys’ manual on the British Mollusca (JEFFREYS 1862). This author stated that species were ‘[...] more or less extensive groups of individuals, which resemble each other as well as their parents and offspring [...]. These groups, to deserve the name of species, must be distinct from others’ (JEFFREYS 1862: XVII). According to Jeffreys, there was a ‘well-established rule’ of species delimitation: all groups of organisms ‘living together and having a common feeding-ground, and which are not

connected or blended with each other by insensible gradations, are [...] entitled to the rank of species' (JEFFREYS 1862: XIX). If two or more groups are connected by morphologically intermediate forms, they should be ranked as 'races' of a single species (JEFFREYS 1862). Essentially the same rule was proposed by COUTAGNE (1895).

This procedure has gained much popularity among malacologists because of its clarity and easiness. A similar way of recognising species boundaries may be found even in relatively recent sources (RADOMAN 1983, SHILEYKO 1984). For ex-

ample, SHILEYKO (1984) recommends regarding two groups of snails inhabiting the same microhabitat as two good species if there is a clear phenetic gap between them.

Of course, a modern taxonomist knows that the absence of intermediate forms in itself is not only a diagnostic tool. It serves as a proxy for the likelihood of reproductive isolation between two groups of animals and indicates that there are two separate gene pools (DUBOIS 1988). I think that this 'gap rule' is the oldest of all operational criteria for species delineation used by malacologists.

THE NOUVELLE ÉCOLE AND ITS TAXONOMIC PHILOSOPHY

Probably, the members of the circle of conchologists known as the 'New School' ('Nouvelle École' in French) were the first workers to develop clear quantitative guidelines for assigning species rank in continental molluscs. DANCE (1970) provided an excellent story of the Nouvelle École and its activity. This school, led by Jules René Bourguignat (1829–1892), gained a bad reputation among contemporary zoologists. The 'Bourguignatians' are notoriously known as horrendous species splitters, whose scientific production consisted mostly in the description of tens and hundreds of new species of snails and bivalves. The genera and subgenera introduced by them were also quite numerous (GRAF 2010). To give an illustration, let us compare the numbers of species in some families of freshwater molluscs accepted by LOCARD (1893), one of the disciples of Bourguignat, and by the modern authors (Table 1). These numbers pertain to the French malacofauna only, but the drastic difference between the two estimates speaks for itself. Almost each freshwater mollusc species accepted in the conchological literature of the first half of the 19th century was split by the Bourguignatians into a series of separate species, though the differences among these minor taxa were barely discernible (KOBELT 1881a). For example, LOCARD (1893) recognised 12 species within his 'groupe du *Limnaea stagnalis*', six species of pearl mussels (corresponding to *Margaritifera margaritifera* s. lato) and so on.

Though this bizarre practice may seem to represent a version of the intuitive approach to classifi-

cation, the Nouvelle École had its own operational criteria of species delineation. DANCE (1970: 83) summarised these criteria as follows: 'Any form with less than three constant characters was a variety; any form with three or more was a species and merited a name'. CHASTER (1907) ascribed the invention of this artificial system to Edward Forbes (1815–1854), but unfortunately he did not cite any publication of the latter.

It is very important to stress that for Bourguignat and his followers species were not more than abstractions. The practitioners of the Nouvelle École believed that there were no real entities in nature that would correspond to the taxonomist's species. LOCARD (1893: 136) insisted that 'the malacological species is a purely arbitrary notion demanded by naturalists for the sake of knowledge and classification of [living] beings' ['L'espèce malacologique est une notion purement arbitraire, indispensable aux naturalistes pour le besoin de la connaissance et de la classification des êtres']. In his earlier publication, entirely devoted to the question of species, LOCARD (1884: 18) characterised the species as 'a purely conventional thing that everyone understands, but cannot exactly define' ['une chose purement conventionnelle, que tout le monde comprend, mais ne peut exactement définir'].

This belief may have induced Bourguignat and his adherents to adopt such formalised and narrow criteria for recognising mollusc species.

Most contemporaries of the Nouvelle École, both in France and beyond, disliked Bourguignat and his taxonomic philosophy (DANCE 1970). Among the strongest critics were the German Wilhelm Kobelt (1840–1916) and the American Charles Simpson (1846–1932). Kobelt expressed his extreme disgust with the Nouvelle École industry of creation of new species and refused to include many of these taxa into his catalogue of the European continental molluscs (KOBELT 1881a; see also KOBELT 1886). SIMPSON (1889) published a short critical note

Table 1. Comparison of two estimates of freshwater mollusc species richness in the fauna of France

Family	LOCARD (1893)	FALKNER et al. (2001)
Unionidae	≈ 500(!)	9
Lymnaeidae	≈ 130 (!)	11
Planorbidae	51	22
Valvatidae	25	3
Physidae	24	4
Viviparidae	11	3



against Bourguignat's principles of classification and later, in 1900, concluded that 'life is too short and valuable to be wasted in any attempt at deciphering such nonsense' as the system proposed by the Bourguignatians (SIMPSON 1900: 513).

However, the methods advocated by the critics were not as operational as the Bourguignatian ones. For example, KOBELT (1881b: 67; quoted after GIUSTI & MANGANELLI 1992) explicitly claimed his adherence to a truly intuitive and subjective manner of delineation of species boundaries: 'I obey a simple, practical rule, no matter how unscientific it may be. I call a good species what I can diagnose without long and careful comparisons and measurements. That which I can distinguish only by precise measurements I call a variety' ['Ich halte mich dabei an einen vielleicht nicht wissenschaftlichen, aber praktischen Character: was ich jederzeit ohne lange und sorgsame Vergleichung und Messung erkennen kann, das nenne ich eine gute Art; was ich aber nur durch eine genaue Messung unterscheiden kann, betrachte ich einstweilen als Varietät'].

Besides, it seems that Kobelt himself, like Bourguignat and Locard, denied the objective existence of species in nature. At least, in one of his publications, Kobelt declared that, for him, the species 'is not a concrete, but an abstract that the collector makes out to find his way through the chaos of forms, and which he therefore completely embrac-

es according to his needs' ['Die „Art“ ist für mich kein Concretum, sondern ein Abstractum, das der Sammler sich macht, um sich in dem Formenchaos zurecht zu finden und das er deshalb ganz seinen Bedürfnissen gemäss umgränzt'] (KOBELT 1886: 1).

At the same time, other malacologists promoted more advanced views on classification of molluscan species. This progress was, at least partly, stimulated by the reception of Darwin's evolutionary theory. Having discussed shell variation in land and freshwater snails from the point of view of the 'struggle for existence' theory, CLESSIN (1876) concluded that the shell characters were of small significance for species delimitation and that 'good' species of molluscs should be based on soft body characters.

In North America, TRYON (1882) proposed a new notion of species category that may be called a 'phylogenetic' one. Though the definition of species given by the author (TRYON 1882: 250) is very generalised, it contains an important specification: species is constituted by 'all the specimens or individuals, which are so much alike that we may reasonably believe them *to have descended from a common stock*' (italics added by me). However, he proposed no operational criteria for species delineation.

All these attempts to clarify the evolutionary aspect of species category are of great interest since they foresee the theoretical developments made in the 20th century.

SPECIES QUESTION IN FRESHWATER MALACOLOGY: THE 20TH CENTURY

The 20th century saw drastic changes in biologists' attitude toward species. During the first decades of the century, the evolutionary theory became universally accepted, and new branches of life sciences (population genetics, biometry) arose (BOWLER 2009). Quantitative methods of research started to spread slowly among taxonomists. The so-called 'population thinking' in biology shifted the emphasis from the study of individuals to the study of representative samples of conspecific animals inhabiting the same habitat and constituting a reproductively coherent entity (population) (MAYR 1982). The 'biological' definition of species (MAYR 1942, 1963, 1982) used by proponents of the BSC was the most popular one in the middle of the 20th century, including the community of malacologists (HUBENDICK 1951, 1954, STAROBOGATOV 1968).

The direct test of genetic incompatibility which is required by BSC to demonstrate that there is no gene flow between two species was possible by means of breeding experiments. It was repeatedly stressed by various authors (HUBENDICK 1951, STAROBOGATOV 1968, 1996a, MEIER-BROOK 1993) that the practicability of this method in studies on freshwater

molluscs is rather limited. Generally, crossing experiments were seldom carried out by 'freshwater' malacologists, though I would cite here several case studies of this kind (KRUGLOV & STAROBOGATOV 1985, KATOH & RIBI 1996, DILLON et al. 2002, 2011).

There was hope to ensure objective recognition of natural species of animals by means of a thorough study of their morphological variation. In freshwater malacology, this high hope was expressed by HUBENDICK (1954: 9), who thought that 'in practice species discrimination among limnic snails means, in the first place, study of morphological variation, definition of its limits and isolation of the distinguishing characters'. Much earlier, COUTAGNE (1895: 23) stated that 'it is [...] possible by purely morphological study of a large number of individuals, to arrive indirectly at the rational delimitation of specific groups' ['on peut néanmoins, par l'étude purement morphologique d'un grand nombre d'individus, arriver indirectement à la délimitation rationnelle des groupes spécifiques'].

Continental molluscs, and especially their shells, were among the most popular objects of early biometrical studies, starting from works of WELDON



(1901, 1904), one of the first biometricians. For example, in Russia alone, between 1923 and 1928 no less than six large papers devoted to studying of conchological variation of a single freshwater species, the great pond snail (*Lymnaea stagnalis*), appeared (ZHADIN 1923, 1928, TERENTIEV 1927, RUMIANTSEV 1928, SHVANSKY 1928, ZAKHVATKIN 1928). One of these publications was co-authored by Theodosius Dobzhansky, who later became one of the most influential geneticist of the 20th century (DOBZHANSKY & KOSSAKOWSKY 1925).

One of the first attempts to utilise measurements and their ratios for species discrimination was undertaken by Bourguignat, who invented his own scheme of measuring mussel shells (DANCE 1970). He apparently tried to gain some quantitative support for the 'minor' species that he could discern, but, again, such practice was strongly criticised by KOBELT (1886) who saw it as a means for uncontrollable species splitting. As KOBELT (1886) said, Servain (one of Bourguignat's pupils) created new 'species' of unionid mussels with a ruler in his hands and did not realise that some of these 'species' represented merely age classes.

The rise of biometrical techniques in the first three decades of the last century meant that the study of animal variation became a truly exact science. As a result of thorough works on intraspecific variation of continental molluscs, the number of recognised species and varieties declined dramatically (especially in comparison with the mammoth numbers of taxa accepted by the Nouvelle École practitioners). One of the most often cited examples of this drastic decline in the numbers of accepted species is HUBENDICK'S (1951) monograph. During his taxonomic study on the recent Lymnaeidae HUBENDICK (1951) reduced the huge number of 1,150 species and varieties of pond snails introduced prior to 1951 to a total of slightly under 40 species.

The biometrical approach to species delineation in freshwater molluscs was promoted by Ya. I. Starobogatov in the USSR (STAROBOGATOV 1968, 1977); he described a simple and operational procedure of assigning species rank based on the well-known Student's t-test. Theoretically, this procedure was based on the BSC. STAROBOGATOV (1968) acknowledged that it was rather difficult to perform crossing experiments with many species of freshwater snails and bivalves due to their hermaphroditism. Therefore no direct test of genetic incompatibility between a pair of alleged species was possible, and STAROBOGATOV (1968, 1977) proposed to use the criterion of statistical significance of a difference between two samples as a proxy for the existence of reproductive barrier separating them. One must only compare the mean values of a certain quantitative character in two syntopic samples by means

of Student's t-test to reveal whether the two belong to different statistical populations (= biological species). It was even stated that the existence of significant differences in a single conchological feature (e.g. shell width/height ratio) between two syntopic samples meant that they belonged to different populations i.e. were not conspecific (LAZAREVA 1967, STAROBOGATOV 1968, 1977).

Later, more powerful techniques for species discrimination, based on multivariate statistics, were introduced into the systematics of freshwater molluscs (MEHLHOP & CIFELLI 1997).

A quite different approach to species delimitation used in the 20th century zoological systematics was the biochemical one (THROCKMORTON 1968). In the 1960–1980s, three basic types of experimental biochemical taxonomy techniques were applied to freshwater Mollusca: chromatography, electrophoresis, and immunology (serology). DAVIS (1978) and MEIER-BROOK (1993) published reviews of these as applied to aquatic snails, with many examples of their practical use for recognising species. All these methods were aimed at identification of genotypic characters, including amino acid analysis of proteins, allowing thereby to characterise populations, species, or higher taxa of molluscs, and to assess relationships among them (DAVIS 1978). Allozyme electrophoresis was the most popular. DAVIS (1994: 3) praised it as 'an ideal tool for population genetics as applied to delineating species'. In today's malacological practice, all these techniques have been almost totally replaced with more effective methods of DNA taxonomy since the middle 1990s (WINNEPENNICKX et al. 1994, BARGUES & MAS-COMA 1997).

Cytotaxonomy also attracted many practitioners in the malacological systematics of the last century (PATTERSON & BURCH 1978, MEIER-BROOK 1993) and was still in some use at the dawn of the new millennium (GARBAR & KORNIUSHIN 2002, 2003, PERSHKO 2011). The significance of karyotype as a tool for delineation of species and higher taxa of Mollusca proved to be relatively small (MINICHEV 1974, PATTERSON & BURCH 1978). Haploid numbers within many large taxa of freshwater molluscs are very conservative. For example, such a morphologically diverse family as Lymnaeidae shows a narrow range of variation in haploid numbers ($n = 16-19$); in the vast majority of species of the subfamily Planorbinae the haploid number is $n = 18$, etc. (PATTERSON & BURCH 1978). There are few known cases among freshwater molluscs when closely allied species differ from each other in their chromosome numbers. Perhaps, the most prominent example of this kind was found among the African representatives of the pulmonate genus *Bulinus* O. F. Müller, 1781, with the chromosome numbers $2n = 36, 72, 108$ and 144 forming a series of polyploid species

(BROWN & WRIGHT 1972, PATTERSON & BURCH 1978, BROWN 1994).

However, there is ample evidence that closely related mollusc species can be distinguished by fine details of their chromosome morphology, not by their haploid numbers. For example, four species of the genus *Theodoxus* Montfort, 1810 (Neritidae) from

Spain differ from each other in the chromosome lengths and the centromere indices of chromosome pairs (BARŠIENE et al. 2000b). Interspecific differences in the chromosome morphology have been revealed in other families of freshwater snails, including Lymnaeidae (GARBAR & KORNIUSHIN 2003) and Viviparidae (BARŠIENE et al. 2000a).

THE 'COMPARATORY' SYSTEMATICS OF FRESHWATER MOLLUSCA AND THE DEBATES AROUND IT

Perhaps, the most controversial and peculiar approach to the species problem in freshwater malacology within the last fifty years was the so-called 'comparatory' systematics widely practiced in the former USSR during the 1970s–2000s. Its history started in 1971 when a short article on the taxonomic significance of the frontal section contour of the bivalve shell valve appeared (LOGVINENKO & STAROBOGATOV 1971). LOGVINENKO & STAROBOGATOV (1971) hypothesised that this character was species-specific and thus might be useful both for taxonomic recognising of valid species and for their subsequent identification by practitioners.

The authors were practicing malacologists well known for their revision of the Caspian Sea gastropods (LOGVINENKO & STAROBOGATOV 1968). Later, Starobogatov became one of the most influential Russian zoologists of the 20th century who eruditely contributed not only to freshwater molluscs systematics but also to a wide array of topics, from theoretical biology to evolutionary ecology. He had many disciples who worked across the former USSR and was an informal leader of the Soviet freshwater malacology of the second half of the last century (NESIS 1992). Starobogatov popularised the 'comparatory' method and attempted to apply it to the taxonomic revision of almost all families of aquatic snails and bivalves inhabiting the former USSR territory (except Dreissenidae). There was also one, rather unsuccessful, attempt to construct a 'comparatory' system of a single taxon of terrestrial snails (genus *Cochlicopa*) (STAROBOGATOV 1996b). According to Starobogatov (SHIKOV & ZATRAVKIN 1991), the 'comparatory' method was a practical application of the well-known RAUP (1966) geometrical model of shell coiling to taxonomy. The procedure was, in essence, visual comparison (hence the name of the method) of Raup's parameters of the studied shell with a stencil drawn from another object of known identity (for example, holotype) (Fig. 1). It is most suitable for snails with turbospiral shells where one can see all the whorls simultaneously (STAROBOGATOV, after SHIKOV & ZATRAVKIN 1991). Since the methodology of the 'comparatory' approach was repeated-

ly reviewed in English (SHIKOV & ZATRAVKIN 1991, KAFANOV 1998, KORNIUSHIN 1998, GRAF 2007), I can omit here all other technical details and proceed to the discussion of the practical consequences of the 'comparatory' taxonomy. These consequences are very contradictory and have generated a series of polemic articles, the most recent of which are those by GRAF (2007), BOLOTOV et al. (2013), and BOGATOV (2009, 2013, 2014).

The most disputed outcome of the 'comparatory' systematics is the extreme taxa splitting, at the genus and species levels, practiced by its adherents. The system of freshwater Mollusca developed by STAROBOGATOV and his co-workers is drastically different from what is common in Western Europe (KORNIUSHIN 1998, GRAF 2007, VINARSKI & ANDREEVA 2007, VINARSKI & KRAMARENKO 2015). VINARSKI & KANTOR (2016), in their catalogue of the

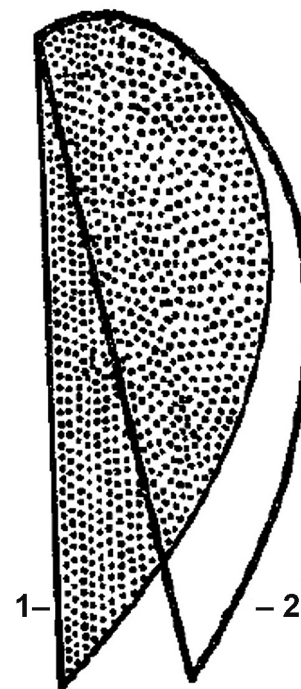


Fig. 1. Procedure of comparison of a shell contour (1) with a drawn stencil (2), within the framework of 'comparatory' method. After SHIKOV & ZATRAVKIN (1991)

ex-USSR freshwater Mollusca, published tables with a detailed comparison of these two systems. The number of species accepted as valid by the followers of the ‘comparatory’ method was 3–5 (in some taxa up to 10) times higher than the corresponding values in publications of their Western European counterparts. This result was strongly criticised by malacologists working beyond the former USSR (MEIER-BROOK 1993, BANK et al. 2006, GRAF 2007). REISCHÜTZ (1994), in a brief polemic note, even equated it with the revival of the Nouvelle École (‘Bourguignatisme’).

Though STAROBOGATOV himself insisted that the contour specificity as such was not the ultimate proof of species validity (SHIKOV & ZATRAVKIN 1991, see also BOGATOV 2014), some of his followers adopted the hypothesis of LOGVINENKO & STAROBOGATOV (1971) as a working tool for producing new species of Mollusca. For example, TIMM (1976: 37) insisted that the frontal section contour ‘is invariable within the limits of a species [...]. Even in the case of very similar species, the curves are entirely different’. ZATRAVKIN (in SHIKOV & ZATRAVKIN 1991: 157) expressed his belief that only by using this method ‘one can determine almost all species of freshwater Bivalvia’. A Pandora’s box was opened.

There was a lengthy discussion about the geometric foundations of the ‘comparatory’ method (KAFANOV 1975, 1998, BOGATOV 2014), however, whether or not the method was mathematically correct, the validity of the ‘comparatory’ species had to be checked by independent methods. The first attempts to test it were based on cytotaxonomy (PERSHKO 2011) and multivariate statistical analyses (SERGEEVA et al. 2008, KLISHKO 2014, VINARSKI 2014b). However, the DNA taxonomy is the most powerful and convincing tool to do it. Since 2010, a series of works of different authors dealing with molecular revisions of various ‘comparatory’ taxa has appeared. The family most intensively studied in this respect are the Unionidae (BOLOTOV et al. 2015, KLISHKO et al. 2014, 2016, 2017; and some

others). Besides, the validity of several ‘comparatory’ species of the family Lymnaeidae (BOLOTOV et al. 2014, AKSENOVA et al. 2016, 2017, VINARSKI et al. 2016), and Pisidiidae (VOODE 2017) has been checked.

In most of the above works, the hypothesis that the ‘comparatory’ species represented truly ‘biological’ entities was rejected after a thorough analysis of genetic data. For example, KLISHKO et al. (2017) confirmed the traditional classification of the genus *Unio* Retzius, 1788 (FALKNER et al. 2001), and rejected the validity of a series of ‘comparatory’ species recognised within this genus by STAROBOGATOV et al. (2004). In another publication (BOLOTOV et al. 2015), the authors showed that there were only three valid species in the family Margaritiferidae Henderson, 1929 in the Russian Far East, instead of the 11 species accepted in the ‘comparatory’ system.

On the other hand, some species of freshwater snails and bivalves recognised by STAROBOGATOV et al. (2004) sustained the molecular test. These were two species of the lymnaeid genus *Radix* Montfort, 1810 of Asiatic Russia: *R. (Peregriana) dolgini* (Gundrizer et Starobogatov, 1979) and *R. (P.) kamtschatica* (Middendorff, 1851) (AKSENOVA et al. 2016, VINARSKI et al. 2016), as well as two species of the unionid genus *Sinanodonta* Modell, 1945 (SAENKO et al. 2017, BESPALAYA et al. 2018). There is little doubt that, after a proper examination, a few of the remaining ‘comparatory’ species will turn out to represent biologically sound taxa. Therefore I cannot agree with GRAF (2007: 78), who proposed to reject all the ‘comparatory’ species a priori as lacking ‘an evolutionary or biological basis’. GRAF (2007) sees the ‘comparatory systematics’ as a revival of the hopelessly archaic typological approach to species delineation. In my turn, I would consider it as an early attempt to use the shell shape as a whole as a taxonomic character, the task that is today fulfilled by a sophisticated computer technique known as geometric morphometry.

THE CHANGING FACE OF THE SPECIES PROBLEM IN FRESHWATER MALACOLOGY (INSTEAD OF CONCLUSIONS)

One who is reviewing current publications on the taxonomy of freshwater snails and bivalves may discern two clear and almost opposite trends. First, the operational approach to recognising species dominates over the conceptual one. In other words, most taxonomists avoid theoretical debates upon species concepts and strive to use more or less formalised criteria, especially those based on sophisticated analyses of genetic data. To cite a few recent studies, I

would mention papers of ARAUJO et al. (2017) and VINARSKI et al. (2017), in which two different statistical approaches to define species boundaries were applied: the generalised mixed Yule coalescence model, and the Poisson tree process (PTP) model. Both approaches use haplotypic data sets and as such do not deal with morphology of animals at all. To put it simply, the problem of species delineation, ceasing to be a task of biology, becomes a purely statistical



enterprise. Species are no longer groups of living organisms made of flesh and blood; there is a tendency to see them as mathematical constructs. In my opinion, it is a sad tendency, despite all its operational value and 'objectivity'. I should note, however, that taxonomists are not bound to use statistical and molecular methods for species delineation; even today many new species and genera of freshwater molluscs are described without any molecular support (PÁLL-GERGELY 2017) and, sometimes, even on a purely conchological basis (see e.g. GREGO et al. 2017).

A different trend of current taxonomy is a tendency to build a system on the 'integrative' foundation. Integrative approach is popular among today's malacologists, and a number of recently published papers on the taxonomy of freshwater snails and bivalves contains the word 'integrative' in their titles (see e.g. HAASE et al. 2007, KONOPLEVA et al. 2017, PÁLL-GERGELY et al. 2017).

According to GOULDING & DAYRAT (2016), integrative taxonomy is very young, 10–12 years old only. Actually, an integrative (or integrated) approach to systematics and species delineation was proposed in malacology 40 years ago, when DAVIS (1978) used this term explicitly. This author stated that 'the limits of species and genera, the establishment of a classification, and the awesome task of reconstructing

phylogenies depends on utilizing all available data including information on morphology, ecological requirements and biogeography' (DAVIS 1978: 161). In those times, the allozyme analysis was the main source of genetic information for integrative taxonomy; now it has been replaced by DNA sequencing (GOULDING & DAYRAT 2016).

It is my personal conviction that the truly integrative approach, with its emphasis on synthesis of all available sources of data, may smooth the extremities of the molecular and statistical reductionisms.

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