Palearctic freshwater mussel (Mollusca: Bivalvia: Unionoida) diversity and the Comparatory Method as a species concept

Author: Graf, Daniel L.

Source: Proceedings of the Academy of Natural Sciences of Philadelphia, 156(1) : 71-88

Published By: The Academy of Natural Sciences of Philadelphia

URL: https://doi.org/10.1635/0097-3157(2007)156[71:PFMMBU]2.0.CO;2

PROCEEDINGS OF THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA 156: 71-88 JUNE 2007

Palearctic freshwater mussel (Mollusca: Bivalvia: Unionoida) diversity and the Comparatory Method as a species concept

DANIEL L. GRAF

The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia PA 19103 USA email: graf@ansp.org

ABSTRACT.—The current taxonomy of freshwater mussels (Mollusca: Bivalvia: Unionoida) in the Palearctic (western and northern Eurasia, from Western Europe to Eastern Russia, Korea and Japan) is confused by two competing species concepts: the Biological Species Concept (BSC) and the Comparatory Method (CM). The CM uses the "frontal contour" of the shell as the primary/sole character to delimit bivalve species. Based upon review of the literature, 45 Biological species in 16 genera are recognized in the Palearctic vs. 156 Comparatory species in 34 genera. I argue that the Comparatory Method is typological and that the "species" recognized have no evolutionary or biological basis. The traditional, Biological species are regarded as better representative of actual species diversity, but further revision is required. The problematic legacy of the *Nouvelle École* on Palearctic freshwater mollusk systematics is discussed.

INTRODUCTION

Freshwater mollusks are globally imperiled, freshwater mussels of the bivalve order Unionoida in particular (Lydeard *et al*., 2004). Freshwater mussels are worldwide in distribution (Graf and Cummings, 2006), and the widespread degradation of rivers and lakes suggests the potential for a significant decrease in the extant diversity (Bogan, 1993). Sooner rather than later, the malacological and conservation biology communities will need a correct understanding of the historical and contemporary processes impinging upon unionoid diversity in order to prioritize human efforts to intervene. Basic to such an understanding is an accounting of freshwater mussel species and their geographical distributions. For many areas of the world, an accurate tally is currently unavailable. For example, the freshwater mussel faunas of the tropical regions of southeastern Asia, South America, and Africa have yet to be completely described.

In contrast, understanding of the Unionoida of the Palearctic region of Eurasia and northern Africa suffers from *over* description, as well as two competing classes of hypotheses for describing biological diversity: the Biological Species Concept (BSC) and the Comparatory Method (CM). The BSC defines a species as "a group of interbreeding natural populations that is reproductively isolated from other such groups" (Mayr and Ashlock, 1991: 26). Subsequent authors have emphasized the cohesiveness of those populations (rather than isolation from others) or their "evolutionary identity," but the unifying theme is that the members of a species are linked together by genealogy (Wiley, 1981; Wheeler and Meier, 2000).

The eastern Russian disciples of Ya.I. Starobogatov and his "Comparatory" (or "Comparatorial") Method are describing something different when they use the term "species." The CM, as applied to the Bivalvia, derives from the simple assumption that a single character, the "frontal section contour" of the shell, can be treated as diagnostic of freshwater mussel species (Shikov and Zatravkin, 1991; Korniushin, 1998). The determination of species diversity in a sample of shells is achieved through qualitative comparisons of each specimen's frontal contour, and two specimens with non-identical curves cannot belong to the same species. Such an operation to delimit species, while seemingly objective and repeatable, is based upon assumptions inconsistent with the modern view of Biological (or Evolutionary or Phylogenetic) species. A number of Russian freshwater malacologists have dissented from Starobogatov's method (*e.g*., Ziuganov *et al*., 1994; Kornishin, 1998), but the CM is alive and well in the Russian literature (Kantor and Sysoev, 2005 and references cited therein).

Because the CM allows for no infra-specific variation and the BSC emphasizes it, estimates of species diversity stemming from the two systems differ significantly. For example, while Falkner *et al*. (2002) recognized nine native species for France (and western Europe in general), Starobogatov *et al*. (2004) reported about three times that number for roughly the same area. And, whereas Zatravkin and Bogatov (1987) listed some 56 species for the region of the Amur River in the Russian Far east, Simpson (1914), Zhadin (1938) and Haas (1969a) provided estimates around a fifth of that value. Given this disparity, one might expect a scientific literature full of lively debate over how best to meet our societal obligations as taxonomists. Instead, the two systems, Biological vs. Comparatory, have progressed in parallel with both schools only infrequently acknowledging the other. The objectives of this paper are to (1) explicitly reconcile these disparate systems for the freshwater mussels of the Palearctic Region and (2) address the shortcomings of the CM so that this regional fauna can be understood from a global perspective.

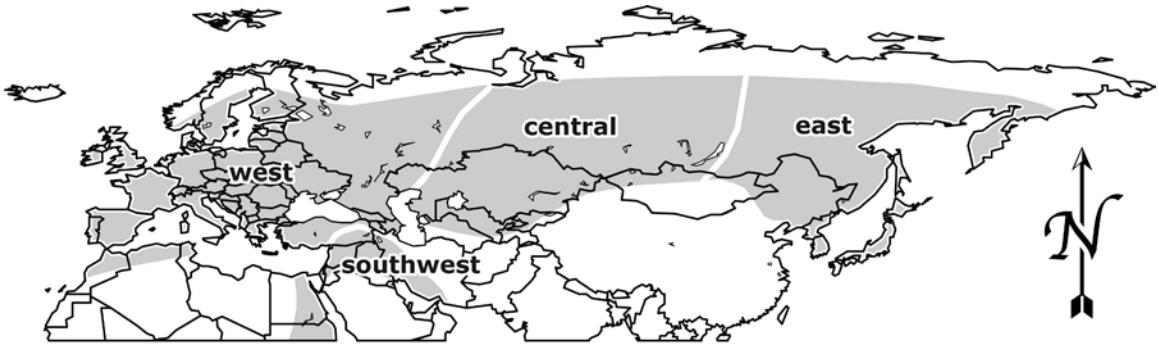

Figure 1. The Palearctic Region, showing the primary subregions of freshwater mussel endemism: Western, Southwestern, Central and Eastern. The northern boundary of the Palearctic Region is the boreal extent of suitable unionoid habitat (Banarescu, 1990: Fig. 4/1). The Western Subregion is bounded to the south by the Sahara Desert in Africa, the extent of the Black Sea Basin and the Caucasus Mountains to the southeast, and the Ural Mountains to the east. The Southwestern Subregion includes the Tigris-Euphrates Basin, west to the Orontes and Jordon. The Nile Basin in northeastern Africa could be considered to fall within the Southwestern Subregion as well, but except for one species (*Unio mancus*), the malacofauna of that river is endemic to Africa. The Central Subregion reaches from the Caspian Sea, across Central Asia, to Lake Baikal. The Eastern Subregion is composed of the Amur Basin east to Sakhalin Island, Japan and the Kurils, and north to Magadan and Kamchatka. The southern boundaries of the Central and Eastern subregions of the Palearctic are limited by a broad line of desert and mountains that extends from Turkmenistan and Iran to Mongolia. In China, the southern extent of the Palearctic Region, as here applied, is the northern limit of the diverse Indotropical unionoid assemblage (Haas, 1969a; Liu, 1979; Prozorova *et al*., 2005).

The Palearctic Region is one of six ecozones used to describe the biogeography of terrestrial/continental organisms: Nearctic (North America), Neotropical (Central and South America), Afrotropical (Sub-Saharan Africa), Indotropical (southeastern Asia), Australasian (Australia, New Zealand and New Guinea) and Palearctic (Eurasia) (Brown and Lomolino, 1998). As applied here to describe the distributions of freshwater mussels, the Palearctic stretches from the Atlantic Ocean, British and Irish Isles, Western Europe and North Africa to Siberia, Japan, Korea, Kamchatka and the Pacific. Based upon observed patterns of endemism, the Palearctic Region is further divided into four subregions: Western, Southwestern, Central and Eastern (Figure 1). In political terms, the Palearctic Region includes Europe, Morocco, the former Soviet Union, the Middle East, Korea, Japan and adjoining areas. Banarescu (1990) and Bába (2000) recently provided useful atlases of Palearctic unionoid distributions. However, the former study did not treat clades to the species level, and the latter suffered from an inconsistent taxonomy and did not treat the Middle East or Japan.

The current absence of a robust consensus on the diversity of Palearctic freshwater mussels is not solely the result of a contemporary, methodological disagreement. The peculiar history of the taxonomy of Palearctic freshwater mussels has made a relatively simple system extremely complicated, and since our customary algorithm for zoological nomenclature relies upon priority and precedence, a complicated past entails a complicated present. Based upon the data in Haas (1940, 1969a), ca. 250 species-group level nomina had been described for the Western Palearctic fauna by 1860. Given that these names, in his estimate, referred to roughly 14 species, that corresponded to a ratio of about 17 synonyms per species. On average the fauna was, by that time, over-described. Many of those described species, though, were illustrated in Rossmässler *et al*. (1835-1920) and Reeve and Sowerby (1864-1868; Sowerby, 1867-1870) and others, so later taxonomists had little trouble identifying and circumscribing them into valid taxa. Unfortunately, once the *Nouvelle École* — the French "New School" of malacology (Dance, 1970) — turned its attention to the Unionoida of Europe, maintaining taxonomic order became all but impossible. Instigated by Jules-René Bourguignat and most ardently followed by Arnould Locard, more than 1000 additional names were introduced in the period from 1860-1914 to describe this same freshwater mussel assemblage. Symbolically, the end of Locard's career as a supernominator coincided with the efforts of Charles T. Simpson (1900, 1914) to bring taxonomic relief and usher in a new era of freshwater malacology. Simpson synthesized the preceding 150 years of alpha-taxonomy, and his synopsis became the benchmark for 20th century systematic studies of the Unionoida.

Simpson's work, while comprehensive, was not exhaustive. He explicitly ignored the superfluous though nomenclaturally available names of the *Nouvelle École* (1900, p. 513),

> "I have endeavored to consider names applied before 1870 in my synonymy. I have made no effort to do this with those applied by authors to the forms of Europe since that time, as I do not believe that any new species of *Unio, Margaritana, Anodonta,* or *Leguminaia* have been found in the last thirty years . . . . In 1892 Arnould Locard, one of the great lights of the new school, stated that there were 208 species of Unios and 250 Anodontas in France alone. Life is too short and valuable to be wasted in any attempt at deciphering such nonsense, and I have not even cumbered the pages of this work with a list of these new species."

The task of deciphering that "nonsense" fell to Fritz Haas (1940, 1969a-b). Haas's mid-20th century arrangement was implicitly influenced by the BSC and the New Synthesis (Mayr, 1942, 1963; Huxley, 1942), and it remained relatively stable, at least among Western malacologists, for much of the remainder of the 20th century (*e.g.*, Nagel *et al*., 1998; Nagel and Badino, 2001; Falkner *et al*., 2001, 2002; Bank *et al*., 2001; Graf, 2002; but see also Zhadin, 1938, 1952, 1965; Bába, 2000). The description of freshwater mussel diversity derived from the CM, as recently articulated by Starobogatov *et al*. (2004), is a significant departure that needs to be acknowledged and appraised from a cosmopolitan perspective.

MATERIALS AND METHODS

This project to synthesize the available data on the Unionoida of the Palearctic was carried out as part of a larger effort to revise the global Unionoida, the MUSSEL Project (abbreviated MUSSELp). Toward that end, the MUSSEL Project Database (MUSSELpdb) was created to facilitate the integration and analysis of the copious amount of taxonomic data that has accumulated since before the 10th edition of *Systema Naturae* (Linnaeus, 1758). Kevin Cummings (Illinois Natural History Survey, Champaign) and I developed the MUSSELpdb in FileMaker Pro (FileMaker Inc., Santa Clara, California; http://www.filemaker.com/), and a schematic of our data model is available on the MUSSEL Project Web Site (http://www.mussel-project.net). Of particular utility for the problem of determining the correspondence between Biological and Comparatory taxa is the capacity of the MUSSELpdb to track and display both (1) the taxonomic history of nominal taxa and (2) the alignment among various circumscriptions of "valid" taxa under different authors' systems.

Taxonomic bibliographical data were digitized by manual data entry into the MUSSELpdb. The process began with the global syntheses of Simpson (1900, 1914) and Haas (1969a-b) and then proceeded through the major works relevant to the problem of Palearctic freshwater mussel diversity (cited below). For each work, the complete synonymy was captured by associating a "taxonomic opinion" with each nominal species. For each nomen then, there is a related set of taxonomic opinions indicating the author(s), date of publication, whether or not the nomen was considered valid, which nominal species was treated as the senior synonym (if invalid), and the combination of genus and species applied. When available, range data were also recorded in the original language, except for some Russian text, which was translated into English to make use of the Latin alphabet. Advances in software and operating systems over the course of this project have made incorporating Cyrillic easier. Each nominal species was assigned to a valid species (or labeled as a *nomen dubium*). Thus, in the MUSSELpdb, each valid species is related by synonymy to a comprehensive history of how the taxonomic components of that species had been variously treated by different authorities (Figure 2).

To facilitate analysis and discussion, the various systems of the Palearctic Unionoida were divided into two broad Schools of Malacology: those that apply a Biological Species Concept and those that apply the Comparatory Method. The distinction between these two camps is actually based upon whether or not taxa are treated as having an evolutionary basis (be they Biological, Evolutionary, Phylogenetic, *etc*. species). Unfortunately, Fritz Haas and the other authors of revisions of species considered here to be Biological species (cited below) were not particularly explicit about their concepts of what species are. Nevertheless, those workers have treated taxa reasonably consistently and implicitly aligned themselves according to the research tradition that includes the recognition of species as evolutionary entities. That they are "Biological" species (rather than some other modern species concept) is inferred from the history of those ideas (Mayr, 1942; Huxley, 1942) and the consistency of those taxa with the predictions of the BSC (Wheeler and Meier, 2000). Similarly, Starobogatov and the practitioners of the Comparatory Method aligned themselves according to a tradition of typology and the rejection of the taxonomies with an hypothesized evolutionary basis. On a practical level, these authors have created these groups by the references they cite and their descriptions of freshwater mussel diversity. While splitting the systematists of the Palearctic Unionoida into two groups based upon their philosophical leanings may be an oversimplification, it is instructive for recognizing the actual disparity in the estimates of species diversity among the various workers.

In addition to Simpson (1900, 1914) and Haas (1969a-b), key references to the Biological species and genera described from the Palearctic were Zhadin (1938, 1952, 1965), Haas (1940), Bába (2000), Nagel *et al*. (1998; Nagel and Badino, 2001), Falkner *et al*. (2001, 2002) and Bank *et al*.

valid species
Kunashiria haconensis (von Ihering, 1893)

synonyms
Anodonta haconensis von Ihering, 1893
Amuranodonta sihotealinica Zatravkin & Starobogatov, 1984
Kunashiria japonica boreosakhalinensis Labay & Shulga, 1999

nominal species
Anodonta haconensis
von Ihering, 1893, Abn. Senckenb. Naturf. Ges. 18: 153, fig. 4.

taxonomic opinions
Kunashiria haconensis (Ihering, 1893). Kantor & Sysoev, 2005: 338.
Kunashiria haconensis (Ihering, 1893). Starobogaatov et al., 2004: 43, pl. 31, figs. 3-4.
Kurashiria haconensis (Ihering, 1893). Zatravkin & Bogatov, 1987: 110, figs. 20, 26.
Kunashiria haconensis (Ihering, 1893). Zatravkin, 1893: 43.
+ Anodonta (Sinanodonta) woodiana (Lea, 1834). Habe, 1977: 120.
+ Anodonta (s.s.) woodiana japonica von Martens, 1874. Haas, 1969: 357.
+ Anodonta japonica von Martens, 1874. Simpson, 1914: 410.
+ Anodonta japonica von Martens, 1874. Simpson, 1900: 640.
N Anodonta haconensis von Ihering, 1893, 153, fig. 4.

Figure 2. Sample records from the Valid Species and Nominal Species tables of the MUSSELpdb. Each Valid Species record is linked to the Nominal Species records circumscribed under it and to their associated taxonomic histories. Taxonomic Opinion records indicate how a nomen was treated by various authors. Opinions marked with a plus sign (+) show when the nominal species was treated as a junior synonym, and those marked with an N indicate the reference in which the nomen was originally introduced.

(2001). Other references provided specialized information on subsets of the Palearctic diversity: Margaritiferidae (Ziuganov *et al*., 1994; Smith, 2001; Huff *et al*., 2004), anodontines (Modell, 1945), North Africa (Van Damme, 1984; Daget, 1998), the Far East (Habe, 1977, 1991; Kondo, 1982, 1997, 1998) and the Tigris-Euphrates Basin (Haas, 1952; Starmühlner and Edlauer, 1957; Biggs, 1971; Schütt, 1983, 1992; Falkner, 1994). The species and genera recognized by the CM in the former Soviet Union were listed by Zatravkin (1983) and summarized more recently for Russia (and adjacent areas) by Bogatov *et al*. (2003, 2005), Starobogatov *et al*. (2004) and Kantor and Sysoev (2005). Akromovski (1976), Stadnichenko (1984) and Zatravkin (1987) summarized the data for Eastern European and Transcaucasian species, Starobogatov and Izzatullaev (1984) for Central Asia, and the freshwater mussels of the Far East were reviewed by Moskvicheva (1973a-b), Zatravkin and Bogatov (1987) and Chernyshev (2004). For those Palearctic taxa beyond the geographical extent of recent Russian revisions, Comparatory species were inferred from Starobogatov's (1970) list of genera: if he used a genus as valid, it must contain at least one species. The complete data set is available at the MUSSEL Project Web Site (cited above).

More complete bibliographies of Old World freshwater mussel literature can be found in Starobogatov *et al*. (2004) and Kantor and Sysoev (2005). The CM was described in detail (in English) by Shikov and Zatravkin (1991), and Korniushin (1998) was the first (in English) to comprehensively address the correspondence between Biological and Comparatory Taxa.

To synthesize and summarize (see the Appendix), the arrangement of Biological genera and species employed here is largely that of Haas (1940, 1969a-b) as updated by Falkner (1994; Falkner *et al*., 2001, 2002), ignoring subspecies except to show correspondence with Comparatory genera and species. Comparatory taxa generally follow Starobogatov *et al*. (2004) and Kantor and Sysoev (2005), as augmented for the entire former Soviet Union by Zatravkin (1983). Correspondence between the Biological and Comparatory genera and species was determined by aligning the taxa via the nominal species shared between them. Following Korniushin (1998), it was assumed that the Comparatory taxa are simply more split than the lumped Biological species (*i.e*., that Biological species-group level taxa correspond to Comparatory genus-group level taxa). For example, *Anodonta haconensis* von Ihering, 1893 was considered by Haas (1969a) to be a synonym of *Anodonta woodiana japonica* (von Martens, 1874). Zatravkin (1983) and Zatravkin and Bogatov (1987) placed *A. haconensis* in its own genus, *Kunashiria* Starobogatov in Zatravkin, 1983. Thus, subsequent taxa derived from the CM and assigned

to *Kunashiria* can reasonably be assumed to be synonymous with Haas's (1969a) concept of *Anodonta woodiana japonica*. For each Comparatory taxon, this assumption was corroborated by examining published figures and by verifying that the reported range of the split taxon fell within that of the lumped Biological analogue. The correspondence between Biological and Comparatory genera and species applied in this article is provided in the Appendix.

In order to examine geographical patterns among the various taxa, species were assigned to one (or more) of the subregions of the Palearctic shown in Figure 1.

RESULTS

Forty-five Biological species of freshwater mussels inhabit the Palearctic, and they correspond to 156 Comparatory species in the same area (summarized in Table 1 and detailed in the Appendix). The Biological species are grouped into 16 genera, while there are 34 Comparatory genera (43 subgenera). The tally of nominal species that serve as the links between these two different taxonomic systems is 1779, but this value represents a rough estimate based upon the secondary works of Simpson (1900, 1914), Haas (1940, 1969a) and numerous others. It is likely that both (1) some unavailable nomina were treated as available and (2) other available names have been omitted — explicitly so, according to Simpson (quoted above). While this number is likely to be refined when the works of Rossmässler *et al*. (1835-1920), Westerlund (1890) and the primary literature are scrutinized, it seems unlikely to change significantly. The total number of species-group level nomina available for these 45 Biological species accounts for a third (1779/4967) of the available, non-fossil nomina in the MUSSELpdb for the entire order Unionoida (840 spp.; Graf and Cummings, 2006 and unpublished data).

While the European fauna (Western Subregion) constitutes only one third of the Palearctic diversity of Biological species (15/45; Table 1), those few taxa account for 86% of the nominal species described for the entire region (1521/1779). The two most over named lineages are the European anodontas (577 nomina) and *Unio crassus* (266). The European anodontas, in the recent literature (Falkner, 1994; Falkner *et al*., 2001, 2002), are *Anodonta cygnea, A. anatina* and *A. cyrea*. The last attempt at a complete synonymy for those taxa was Haas (1969a), but he lumped them as a single species. Thus, most nominal *Anodonta* spp. from Europe have not been circumscribed into a modern species. Just the European anodontas and *Unio crassus* account for more than half of the species names introduced for Europe (843/1521). Of the 1779 nominal species described for the Palearctic, 44% of the names were introduced by four *professeurs* of the *Nouvelle École*: Locard (347), Bourguignat (222), Drouët (154) and Servain (71). Of those described taxa, only 60 were ever treated as valid at the species- or subspecies-levels in any of the works examined (since 1940), and only 7 are considered valid Biological species (Table 1). In the Far East, 80 new Comparatory species have been described since 1970.

Determining correspondence between the Biological and Comparatory systems at the species and genus levels was trivial in most cases (Appendix). The overwhelming majority of available names and their placements in the two taxonomic arrangements were consistent with the assumptions that (1) the Comparatory system is simply more split than the lumped Biological system (Korniushin, 1998) and (2) recently described species in Comparatory genera could be assigned to Biological species by simply examining the assignment of previously described species to genera in the Comparatory system. However, for some Biological taxa, such as the species *Unio crassus* and the genera *Inversidens* and *Anodonta*, the alignment is imperfect, suggesting a genuine difference in how different systematists perceive the freshwater mussel diversity of the Palearctic region.

Figure 3 graphs the species diversity of freshwater mussels in the four subregions of the Palearctic according to both taxonomic systems. The most species-rich areas are the Western and Eastern subregions, while the Central subregion is relatively depauperate.

DISCUSSION

Having made explicit the disparity between the estimates of Palearctic freshwater mussel diversity derived from both the BSC and CM (Table 1; see also the Appendix), it is evident that the two systems are incompatible. Moreover, given the need among non-systematists for consistent taxonomies in order to communicate accurately about biological diversity across disciplines (*e.g*., conservation biology, ecology, physiology, paleontology), it is imperative that these discrepancies be rectified. Science is hypothesis-driven, and, unlike nomenclature, does not function on precedence, democracy or consensus. These two systems are not equivalent, and, from the perspective of serving the objectives of taxonomy, one of them must be better — and neither of them may be completely adequate.

What are the objectives of taxonomy? A detailed answer to this question is beyond the scope of this article, but the reader is referred to Mayr (1963; Mayr and Ashlock, 1991), Wiley (1981) and the references cited therein. In brief, the objectives of taxonomy are to describe and classify biological diversity. Modern systematists have also articulated their desire that named taxa should reflect evolutionary patterns, that taxa are genealogical lineages, not human constructs of convenience but objective, natural entities. At the

Table 1. Species-level freshwater mussel diversity of the Palearctic. Distributions and correspondence with Comparatory taxa are listed in the Appendix. Distributions refer to Palearctic Subregions in Figure 1. Abbreviations W Western, SW Southwestern, C Central and E Eastern. See text for discussion.

Palearctic species	distribution	Comparatory spp.	synonyms
1. *Unio pictorum* (Linnaeus, 1758)	W	4	147
2. *Unio tumidus* Philippson in Retzius, 1788	W	3	62
3. *Unio mancus* Lamarck, 1819	W, SW	1	202
4. *Unio terminalis* Bourguignat, 1852	SW	1	23
5. *Unio tigridis* Bourguignat, 1852	SW	1	25
6. *Unio crassus* Philippson in Retzius, 1788	W, SW, E	21	266
7. *Inversidens pantoensis* (Neumayr, 1899)	E	3	7
8. *Inversidens brandtii* (Kobelt, 1879)	E	1	2
9. *Inversidens japanensis* (Lea, 1859)	E	2	2
10. *Inversiunio reinianus* (Kobelt, 1879)	E	2	2
11. *Inversiunio jokohamensis* (von Ihering, 1893)	E	1	1
12. *Inversiunio yanagawensis* (Kondo, 1982)	E	1	1
13. *Nodularia douglasiae* (Griffith and Pigeon, 1834)	E	10	34
14. *Lanceolaria cylindrica* (Simpson, 1900)	E	4	5
15. *Lanceolaria acrorrhyncha* (von Martens, 1894)	E	1	1
16. *Lanceolaria oxyrhyncha* (von Martens, 1861)	E	1	2
17. *Anodonta cygnea* (Linneaus, 1758)	W	16	568
18. *Anodonta anatina* (Linnaeus, 1758)	W, C		
19. *Anodonta cyrea* Drouët, 1881	C	3	9
20. *Anodonta pseudodopsis* Locard, 1883	SW	1	3
21. *Anodonta vescoiana* Bourguignat, 1856	SW	1	4
22. *Anodonta woodiana* (Lea, 1834)	E	17	87
23. *Anodonta ogurae* (Kuroda and Habe, 1987)	E	1	1
24. *Anodonta beringiana* Middendorff, 1851	E	6	7
25. *Anodonta euscaphys* (Heude, 1879)	E	1	3
26. *Anodonta arcaeformis* (Heude, 1877)	E	16	23
27. *Pseudanodonta complanata* (Rossmässler, 1835)	W	5	68
28. *Cristaria plicata* (Leach, 1815)	E	2	17
29. *Cristaria discoidea* (Lea, 1834)	E	1	12
30. *Hyriopsis schlegelii* (von Martens, 1861)	E	1	1
31. *Lamprotula coreana* (von Martens, 1886)	E	1	1
32. *Lamprotula gottschei* (von Martens, 1894)	E	1	1
33. *Pseudodon omiensis* (von Heimburg, 1894)	E	1	2
34. *Potomida littoralis* (Cuvier, 1798)	W, SW	3	93
35. *Leguminaia wheatleyi* (Lea, 1862)	SW	1	9
36. *Leguminaia saulcyi* (Bourguignat, 1852)	SW	2	5
37. *Microcondylaea compressa* (Menke, 1830)	W	1	18
38. *Pseudodontopsis euphratica* (Bourguignat, 1852)	SW	1	6
39. *Margaritifera margaritifera* (Linneaus, 1858)	W	3	20
40. *Margaritifera dahurica* (Middendorff, 1850)	E	6	7
41. *Margaritifera laevis* (Haas, 1910)	E	3	8
42. *Margaritifera togakushiensis* Kondo and Kobayahi, 2005	E	1	1
43. *Margaritifera middendorffi* (Rosén, 1926)	E	2	3
44. *Margaritifera auricularia* (Spengler, 1793)	W	1	15
45. *Margaritifera homsensis* (Lea, 1864)	SW	1	5
TOTAL: 45 species		**156**	**1779**

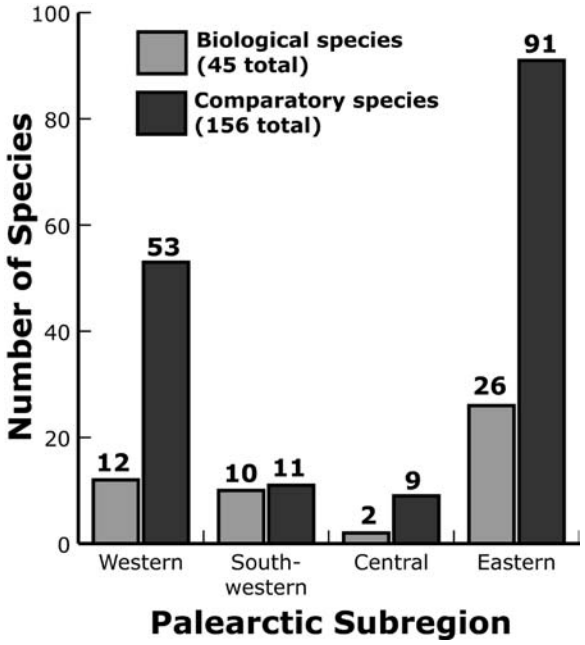

Figure 3. Geographical distribution of freshwater mussel diversity in the Palearctic. The graph illustrates the number of Biological and Comparatory species considered to occur in each subregion of the Palearctic (Figure 1).

species level, there is still considerable debate as to what species are and how to recognize them, but there is agreement that species are real things that can (and should) be delimited and described (Wheeler and Meier, 2000). While that theoretical debate smolders on among ecologists, evolutionary biologists and systematists, we can safely rule out the CM on the grounds that, while seemingly objective, it has little value for describing evolutionary patterns, at least as regards the freshwater mussels of the Palearctic.

Shikov and Zatravkin (1991) described the history, reasoning and operations behind the CM, and that was followed up by Korniushin (1998). The impetus for the CM was the apparent lack of diagnostic characters among freshwater mollusks, well known for extreme infra-specific variation of continuous, "shape" characters (*e.g.*, Ortmann, 1920; Graf, 1998). Logvinenko and Starobogatov (1971) claimed to have found such a diagnostic character for bivalves: the contour of the frontal section of the shell. The maximum curvature of the profile of a freshwater mussel valve is drawn with the aid of a camera lucida, and the resulting segment of a logarithmic spiral is used to qualitatively compare specimens (Figure 4). According to Shikov and Zatravkin (1991),

> "The resultant picture is traced with drawing ink and thus, a stencil is obtained which may be used with the same drawing tube and at the same magnification without fail . . . for comparison with other shell contours. . . . If the shell contour of another mollusc does not coincide with the stencil contour, a new stencil should be drawn. Thus, molluscs are divided into groups corresponding to one or another stencil." (p. 153)

And,

> "The popularity of the comparative method is explained by its simplicity. Using it only practically, everybody can divide into groups more than 100 any shells within an hour. It permits us also to compare real shells with photograph or precise drawing of the type-specimen when present in literature." (p. 156)

While E.V. Shikov (in a personal closing statement) expressed some doubts about the validity of the CM as he and M.N. Zatravkin described it, his co-author was enthusiastic.

> "I believe that only by using of the comparative method one can determine almost all species of freshwater Bivalvia. Only in complicated cases, for example, in corrosion of beaks, when curvatures of the frontal section of two species are very close etc., one should use other diagnostic features." (p. 157).

The frontal contours of these shells are not examined statistically "because of the complex measuring of the polar angle value" to quantify the logarithmic spiral (Shikov and Zatravkin, 1991: 150). As reviewed by Korniushin (1998), various statistical and phenetic studies of other morphological characters and allozymes have claimed support both for (*e.g.*, Starobogatov, 1977; Zatravkin and Lobanov, 1986; Sayenko *et al*., 2005) and against (*e.g.*, Kodolova and Logvinenko, 1973, 1974, 1988; Logvinenko and Kodolova, 1983) the CM. However, the apparently conflicting results of these empirical studies aside, the explanation of the underlying assumptions and application of this school of taxonomy demonstrates its short-comings and explains the disparity between diversity estimates based on the BSC and those derived from the CM.

The philosophical basis for the CM as a species concept is typology, the pre-Darwinian notion that species are simply different "kinds" and that taxonomists should separate individuals (*i.e.*, specimens) into species on the subjective basis of how different they are from each other. As argued by Starobogatov (1977), the BSC leads to "negation... of the significance of the difference of degree for the establishment of the species status." But, a typological concept of species denies (or at least ignores) the biological and evolutionary reality of species, treating them as human-cre-

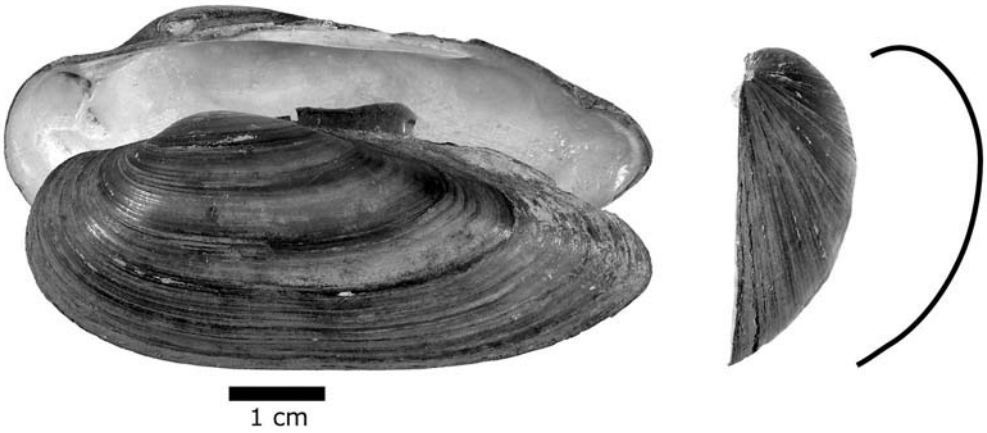

Figure 4. *Unio pictorum* and its frontal shell contour. The frontal shell contour was drawn in a plane perpendicular to the longitudinal axis of the left valve, viewed from the anterior end, per the instructions of Shikov and Zatravkin (1991).

ated categories of convenience. Though perhaps beginning as a search for diagnostic characters among highly variable freshwater mussel taxa, the leap from the observation that the frontal contour of the shell *doesn't* vary within species to the assumption that it *can't* started the practitioners of the CM down a slippery slope. By this logic (as quoted above and evidenced by recent works), freshwater mussels species are operationally reduced to mere curves (Figure 5).

While most species of freshwater mussels (and most other species on Earth!) are recognized solely on the basis of morphological characters, the determinations are hypotheses derived from predictions based upon the evolutionary or biological nature of species. Species recognized by the CM lack an evolutionary or biological basis, and speciation, rather than being an evolutionary process acting upon populations, is simply the development of a novel frontal shell contour in an individual freshwater mussel. The application of the CM results in repeated patterns of narrowly restricted generic endemism with numerous broadly sympatric species (see the Appendix). In an evolutionary context, this would raise questions about reproductive isolation and the historical processes that led to such diversification. But because the Comparatory School is not trying to describe biological diversity from an evolutionary perspective, the deviation of their method from modern evolutionary theory is irrelevant to its practitioners. The frontal shell contours described by the CM do not yield "species" equivalent to species as conceived by the Biological (or Evolutionary or Phylogenetic) Species Concept, and they do not merit validity in a classification intended to describe and explain freshwater mollusk diversity in an evolutionary context.

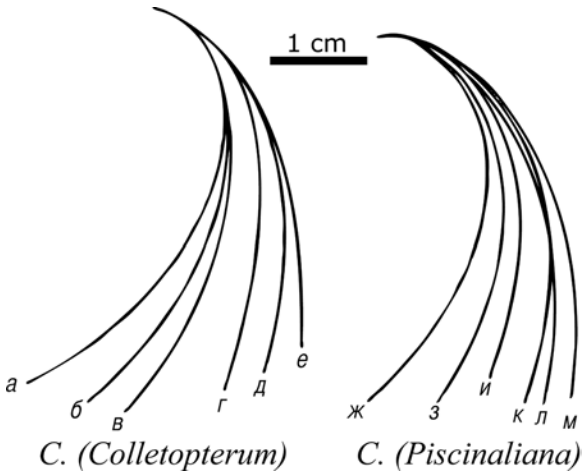

Figure 5. *Colletopterum* species in Russia and adjacent territories. Each curve represents a "stencil" for identifying Russian species of *C. (Colletopterum) and C. (Piscinaliana)*. Re-drawn from Bogatov *et al*. (2005).

Having argued against the logic of the CM and the excessive Palearctic freshwater mussel species proliferated over the last thirty years, it must also be emphasized that, while a better alternative, the BSC as it has been applied to freshwater mollusks is not the final answer. The BSC, championed by Ernst Mayr, has been widely criticized for overemphasizing reproductive isolation and lumping species diversity (Wiley, 1981; Wheeler and Meier, 2000). The tendency among systematists under this model has been to use sympatry as the test of reproductive isolation, and the result has been the recognition of widespread, "polymorphic" species composed of allopatric subspecies. At any one site, the BSC can correctly separate the sympatric species occurring there, but across geographical (or chronological) distances the tendency has been to assume that similar forms retain their potential to interbreed. As we have moved into an era of molecular phylogenetics, we have repeatedly run into the problem of over-lumped freshwater molluscan taxa and the need to refine our concepts (*e.g.*, Nagel *et al*., 1998; Nagel and Badino, 2001; Källersjö *et al*., 2005). The list of Palearctic freshwater mussel species listed in Table 1 is a good estimate of species diversity, but it isn't excellent.

Despite incompatibility in how the two schools describe and classify freshwater mussel diversity, the arrangement proposed by Haas (1940, 1969a-b) is largely congruent with that of Starobogatov *et al*. (2004) and Kantor and Sysoev (2005), except for the frame shift in taxonomic level (Korniushin, 1998). This is perhaps to be expected, since both groups are attempting to describe the same actual diversity, only with different assumptions about its nature and variation. The correspondence between the Biological and Comparatory taxa shown in the Appendix should not be taken as evidence of congruence between the two systems, since maximizing congruence was the primary assumption for aligning them. However, the areas of incongruence highlight areas in obvious need of reevaluation.

For example, *Unio crassus* as delineated by Haas (1940, 1969a) and Falkner (1994; Falkner *et al*., 2001, 2002) is a widespread, variable species with numerous subspecies. It is found from the Atlantic to the Ural Mountains in European Russia and the Tigris-Euprates in the Middle East, and eastward through the Amur Basin in eastern Russia. Haas (1940, 1969a) grouped all the nominal species described from eastern Black Sea drainages and the Caucasus into the subspecies *U. crassus gontieri*. Zatravkin (1983, 1987) treated some of those Transcaucasian species in the genus *Eolymnium*, suggesting a closer affinity to *U. terminalis* and *U. tigridis* in the Tigris-Euphrates than with *U. crassus* sensu stricto in Europe. Bába (2000) followed Zhadin (1952, 1965) in recognizing Haas's taxon as a number of distinct species: *Unio sieversi* Drouët, 1881, *U. stevenianus* Drouët, 1881 and *U. mingrelicus* Drouët, 1881. Further to the east, Haas (1940, 1969a) recognized a widely disjunct subspecies in the Amur, *U. crassus mongolicus*. Zhadin (1952, 1965) considered that same taxon to be a subspecies of *Nodularia douglasiae*. The Comparatory literature, however, treats that "subspecies" as the subgenus *Middendorffinaia (s.s.)*, with five currently recognized species, and *Middendorffinaia (Pseudopotomida)* and *Pronodularia* on the Comparatory side contend with *Inversidens* and *Inversiunio* to explain the diversity in Japan and the Russian Far East (Kondo, 1982, 1998; Chernyshev, 2004). At least three classes of hypotheses for the species-level diversity have been suggested for the highly variable, widespread "*Unio crassus* Complex" in recent years (*i.e.*, Haas, Zhadin/Bába, Comparatory), and none rests on a robust taxonomic footing.

Haas's (1940, 1969a) concept for the western species of *Anodonta* demonstrates the same type of conflict. Haas treated all anodontas from western Eurasia under the single species, *Anodonta cygnea*. More recently, Falkner (1994; Falkner *et al*., 2001, 2002), Nagel *et al*. (1998; Nagel and Badino, 2001) and others have recognized *A. anatina* and *A. cyrea* as separate species, although no study has thoroughly revised the 577 nominal species of European anodontas since Haas (1969a). These three Biological species correspond to 19 Comparatory species in two genera, *Anodonta* and *Colletopterum*. The Comparatory concept of *Anodonta* corresponds to the Biological species *A. cygnea*, and *Colletopterum* relates to *A. anatina* and *A. cyrea* (see the Appendix). *Anodonta*, as conceived in the Western literature, is the most widespread freshwater mussel genus on Earth, extending from the British and Irish Isles, through Asia, across the Bering Strait, and through North America to the Atlantic Ocean. This pattern is the result of systematists being thus far unable to find the diagnostic morphological characters to either split the genus into smaller units or to relate molecular phylogenetic results to species that have not yet been analyzed. As with *U. crassus*, the systematics of *Anodonta* is in need of revision.

Even with these caveats about the BSC and the continued need for systematic research on the Unionoida of the Palearctic, we can consider the evolutionary patterns of this geographical assemblage from a more cosmopolitan, global perspective. In terms of species diversity, the Palearctic is relatively species-poor, with only 45 species (Table 1). Compared to more diverse, much smaller areas like the Gulf Coastal Plain of North America (145 spp.) or Indochina (91), the apparent paucity of Palearctic freshwater mussel diversity is striking. Of the six ecozones listed in the Introduction, only Australasia has fewer species (33) (Graf and Cummings, 2006, and unpublished data). Above the species level, the only families to occur in the Palearctic region (Figure 1) are the Unionidae and Margaritiferidae (al-

though the Iridinidae is known from the Nile in northern Africa). The taxonomy of the Margaritiferidae has been recently revised by both Smith (2001) and Bogatov *et al*. (2003), although the molecular phylogenetic study by Huff *et al*. (2004) contradicted many of their generic conclusions (but see Walker *et al*., 2006). The taxonomy of the Unionidae is in a state of transition, as discussed by Graf (2002; also Graf and Cummings, 2006). The various traditional classifications of unionid genera (Modell, 1964; Haas, 1969a-b; Starobogatov, 1970) have been rejected by recent molecular phylogenetic work (Huang *et al*., 2002; Roe and Hoeh, 2003; Campbell *et al*., 2005; Walker et al., 2006), but, for many Old World lineages, taxon sampling has been insufficient to propose a robust alternative system. Recent, novel classifications have been suggested for the European genera (Nagel *et al*., 1998; Nagel and Badino, 2001) and await rigorous phylogenetic analyses.

Molecular phylogenetic/phylogeographic studies will only be one facet of the evidence necessary to properly describe, document and understand the biological diversity of Palearctic freshwater mussels. All biological disciplines rely upon taxonomists to discover and precisely describe the evolutionary context of organisms in order to confirm the general applicability of research results. A stable and accurate classification of the freshwater mussels of the Palearctic is of critical importance if we, as the stewards of biological diversity, are going to successfully stem the tide of extinction. The CM is not a reasonable solution to the problem of describing freshwater mussel evolution, but our traditional system is outmoded. Species-group level taxa in particular need to be reexamined across their entire ranges to assess their fit with various modern species concepts (Mishler and Donoghue, 1982), and type specimens will need to be reevaluated to provide a reliable nomenclature. Given the vigor with which the *Novelle École* muddied the waters, that is no mean feat.

It would seem that modern taxonomists of the European fauna have been unmotivated to thoroughly revise those mollusks. And who can blame us? The amount of new information to be directly gained from taking up this challenge will be small relative to the effort necessary to bring the numerous described species (and genera: Vokes, 1980: 79-81) into the light. But, the lack of a comprehensive and robust taxonomic infrastructure bogs down freshwater malacology and inhibits progress in other biological disciplines. There is still a great deal to be discovered about the biology of these mollusks (*e.g*., spurting behavior; Vicentini, 2005), but they may be gone before we can get our malacological house in order. In the name of preserving biological diversity, it might be necessary to take some drastic actions, among them formally suppressing the nomenclatural availability of at least some of the malacological works of Arnould Locard and others.

ACKNOWLEDGMENTS

This research was supported by an NSF-REVSYS grant (DEB-0316125). Kevin Cummings is a valued collaborator in all aspects of the MUSSEL Project. Jack Burch provided a copy of Starobogatov *et al*. (2004), and Yuri Kantor generously shared an invaluable electronic version of the relevant portions of Kantor and Sysoev (2005) in English. Paul Callomon lent his facility with Palearctic languages, and Dan Otte granted me access to his personal, doodled-upon library. This work was inspired by discussions with Ken Boss and Philippe Bouchet, Tim Pearce provided many useful insights, and drafts at various stages were read and critiqued by Mark Sabaj (C.M.), Jon Gelhaus, Nancy Shefferly, Gary Rosenberg and two other reviewers. Tim Hayes rendered the original map upon which Figure 1 is based, and Katie Vazquez contributed helpful research assistance. I am grateful for the contributions from all of the above to this article, but I alone am responsible for any errors of fact, omission, judgment or proofreading.

REFERENCES CITED

Akromovski, N.N. 1976. *Fauna Armyanskoi SSR: Mollyuski (Mollusca)*. Akademiya Nauk Armyanskoi SSR, Yerevan. 268 pp.

Bába, K. 2000. An area-analytical zoogeographical classification of Palearctic Unionaceae species. *Bollettino Malacologico* 36: 133-140.

Banarescu, P. 1990. Zoogeography of Fresh Waters: General Distribution and Dispersal of Freshwater Animals. AULA-Verlag, Wiesbaden. 511 pp.

Bank, R.A., P. Bouchet, G. Falkner, E. Gittenberger, B. Hausdorf, T. von Proschwitz and T.E.F. Ripken. 2001. CLECOM-PROJECT: Supraspecific classification of European non-marine Mollusca (CLECOM Sections I and II). *Heldia* 4: 77-128.

Biggs, H.E. 1971. Mollusca of the Iranian Plateau-III. *Journal of Conchology* 27: 211-220.

Bogan, A.E. 1993. Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. *American Zoologist* 33: 599-609.

Bogatov, V.V., L.A. Prozorova and Ya.I. Starobogatov. 2003. The family Margaritiferidae (Mollusca: Bivalvia) in Russia. *Ruthenica* 13: 41-52.

Bogatov, V.V., Ya.I. Starobogatov and L.A. Prozorova. 2005. Mollusks of the genus *Colletopterum* (Anodontinae, Bivalvia) from Russia and adjacent territories. *Zoologicheskii Zhurnal* 84: 1050-1063.

Brown, J.H. and M.V. Lomolino. 1998. *Biogeography*. 2nd edition. Sinauer Associates, Inc., Sunderland. 691 pp.

Campbell, D.C., J.M. Serb, J.E. Buhay, K.J. Roe, R.L. Minton and C. Lydeard. 2005. Phylogeny of North American amblemines (Bivalvia, Unionoida): prodigious polyphyly proves pervasive across genera. *Invertebrate Biology* 124: 131-164.

Chernyshev, A.V. 2004. The generic systematics of the najads

(Bivalvia, Unionida) of the Russian Far East. *Byulleten' Dal'nevostochnogo Malakologicheskogo Obshchestva* 8: 5-16.

Daget, J. 1998. *Catalogue Raisonné des Mollusques Bivalves d'Eau Douce Africains*. Backhuys Publishers/ORSTOM, Leiden/Paris. 329 pp.

Dance, S.P. 1970. "Le fanatisme du nobis": a study of J.-R. Bourguignat and the "Nouvelle Ecole." *Journal of Conchology* 27: 65-86.

Falkner, G. 1994. Systematik vorderorientalischer Najaden als Vorstudie zur Bearbeitung archäologischer Funde. *Forschungen und Berichte Zur Vor- und Frühgeschichte in Baden-Württemberg* 53: 135-162.

Falkner, G., R.A. Bank and T. von Proschwitz. 2001. CLECOM-PROJECT: Check-list of the non-marine Molluscan species-group taxa of the states of Northern, Atlantic and Central Europe (CLECOM I). *Heldia* 4: 1-76.

Falkner, G., T.E.J. Ripken and M. Falkner. 2002. *Mollusques Continentaux de France: Liste de Référence Annotée et Bibliographie*. *Patrimoines Naturels* 52. Muséum National d'Histoire Naturelle, Institut d'Ecologie et de Gestion de la Biodiversité, Paris. 350 pp.

Graf, D.L. 1998. Freshwater pearly mussels: pigtoes and Ortmann's Law. *American Conchologist* 26: 20-21.

Graf, D.L. 2002. Molecular phylogenetic analysis of two problematic freshwater mussel genera (*Unio* and *Gonidea*) and a re-evaluation of the classification of Nearctic Unionidae (Bivalvia: Palaeoheterodonta: Unionoida). *Journal of Mollusca Studies* 68: 65-71.

Graf, D.L. and K.S. Cummings. 2006. Palaeoheterodonta Diversity (Mollusca: Trigonioida + Unionoida): What we know and what we wish we knew about freshwater mussel evolution. *Zoological Journal of the Linnean Society* 148: 343-394.

Haas, F. 1940. A tentative classification of the Palearctic unionids. *Zoological Series of Field Museum of Natural History* 24: 115-141.

Haas, F. 1952. Shells collected by the Peabody Museum Expedition to the Near East, 1950. I. Mollusks from the Persian Gulf. *Nautilus* 65: 114-119.

Haas, F. 1969a. Superfamilia Unionacea. *Das Tierreich* 88. Walter de Gruyter and Co., Berlin. 663 pp.

Haas, F. 1969b. Superfamily Unionacea. pp. N411-470. [in] R.C. Moore, ed. *Treatise on Invertebrate Paleontology*. Part N, Vol. 1. Geological Society of America and the University of Kansas. 489 pp.

Habe, T. 1977. *Systematics of the Mollusca of Japan: Bivalvia and Scaphopoda*. Hokuryukan, Toyko. 372 pp.

Habe, T. 1991 [1990]. Catalogue of non-marine molluscs in Japan. *Hitachiobi* 56: 3-7.

Huang, Y.-Y., H.-Z. Liu, X.-P. Wu and S. Ouyang. 2002. Testing the relationships of Chinese freshwater Unionidae (Bivalvia) based on analysis of partial mitochondrial 16S rRNA sequences. *Journal of Molluscan Studies* 68: 359-363.

Huff, S.W., D. Campbell, D.L. Gustafson, C. Lydeard, C.R. Altaba and G. Giribet. 2004. Investigations into the phylogenetic relationships of freshwater pearl mussels (Bivalvia: Margaritiferidae) based on molecular data: implications for their taxonomy and biogeography. *Journal of Molluscan Studies* 70: 379-388.

Huxley, J. 1942. *Evolution: The Modern Synthesis*. Harper and Brothers Publishers, New York. 645 pp.

Källersjö, M., T. von Proschwitz, S. Lundberg, P. Eldenäs and C. Erséus. 2005. Evaluation of ITS rDNA as a complement to mitochondrial gene sequences for phylogenetic studies in freshwater mussels: an example using Unionidae from north-western Europe. *Zoologica Scripta* 34: 415-424.

Kantor Yu.I. and A.V. Sysoev. 2005. *Katalog Mollyuskov Rossii i Sopredel'nykh Stran*. KMK Scientific Press Ltd., Moscow. 627 pp.

Kodolova, O.P. and B.M. Logvinenko. 1973. Comparison of different populations of bivalves *Unio pictorum* and *U. tumidus* (Unionidae) by systems of myogens and shell morphology. *Zoologicheskii Zhurnal* 52: 988-999.

Kodolova, O.P. and B.M. Logvinenko. 1974. Comparison of different populations of bivalve molluscs of the genus *Anodonta* (Unionidae) by systems of myogens and shell morphology. *Zoologicheskii Zhurnal* 53: 531-545.

Kodolova, O.P. and B.M. Logvinenko. 1988. Disputable issues in the taxonomy of Amur-Khanka mollusks of the genus *Cristaria* (Bivalvia, Unionidae). *Zoologicheskii Zhurnal* 67: 506-510.

Kondo, T. 1982. Taxonomic revision of *Inversidens* (Bivalvia: Unionidae). *Venus* 41: 181-198.

Kondo, T. 1997. Taxonomic position and distribution of *Unio biwae* (Bivalvia: Unionidae). *Venus* 56: 41-47.

Kondo, T. 1998. Revision of the genus *Inversiunio* (Bivalvia: Unionidae). *Venus* 57: 85-93.

Korniushin, A.V. 1998. Review of the studies on freshwater mollusc systematics carried out by the Russian taxonomic school. *Bivalvia I. Malacological Review, Supplement* 7: 65-82.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae..., etc*. 10th edition. Holmiae, Impensis Direct. Laurentii Salvii. 823 pp.

Liu, Y.-Y. 1979. *Freshwater Mollusks. Economic Fauna of China*. Science Press, Beijing. 124 pp. [in Chinese]

Logvinenko, B.M. and O.P. Kodolova. 1983. On the level of similarity of the electrophoretic spectra of myogens between different species and genera of molluscs of the family Unionidae. *Zoologicheskii Zhurnal* 62: 447-451.

Logvinenko, B.M. and Ya.I. Starobogatov. 1971. Krivizna frontalnogo secheniya stvorki kak sistematicheskiy priznak u dvustvorchatykh molluskov. *Nauchnye Doklady Vysshey Shkoly, Biologicheskie Nauki* 5: 7-10. [not seen; as cited in Shikov and Zatravkin (1991) and Korniushin (1998)]

Lydeard, C., R.H. Cowie, W.F. Ponder, A.E. Bogan, P. Bouchet, S.A. Clark, K.S. Cummings, T.J. Frest, O. Gargominy, D.G. Herbert, R. Hershler, K.E. Perez, B. Roth, M. Seddon, E.E. Strong and F.G. Thompson. 2004. The global decline of non-marine mollusks. *Bioscience* 54: 321-330.

Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York. 334 pp.

Mayr, E. 1963. *Animal Species and Evolution*. The Belknap Press of Harvard University Press, Cambridge. 795 pp.

Mayr, E. and P.D. Ashlock. 1991. *Principles of Systematic Zoology*. 2nd edition. McGraw-Hill, New York. 475 pp.

Mishler, B.D. and M.J. Donoghue. 1982. Species concepts: a case for pluralism. *Systematic Zoology* 31: 491-503.

Modell, H. 1945. Die Anodontinae, Ortm. emend. (Najad., Mollusca). *Jenaische Zeitschrift für Naturwissenschaft* 78: 58-100.

Modell, H. 1964. Das natürliche System der Najaden. 3. *Archiv für Molluskenkunde* 93: 71-126.

Moskvicheva, I.M. 1973a. Molluscs of the subfamily Anodontinae (Bivalvia, Unionida) in the Amur and Marine Territory basin. *Zoologicheskii Zhurnal* 52: 822-834.

Moskvicheva, I.M. 1973b. Unionoidea (Bivalvia) of the Amur and the Marine Territory basin. *Zoologicheskii Zhurnal* 52: 1458-1471.

Nagel, K.-O. and G. Badino. 2001. Population genetics and systematics of European Unionoidea. pp. 51-80. [in] G. Bauer and K. Wächtler, eds. *Ecology and Evolution of the Freshwater Mussels Unionoida*. *Ecological Studies* 145. Springer-Verlag, Berlin. 394 pp.

Nagel, K.-O., G. Badino and G. Celebrano. 1998. Systematics of European naiades (Bivalvia: Margaritiferidae and Unionidae): A review and some new aspects. *Bivalvia I. Malacological Review, Supplement* 7: 83-104.

Ortmann, A.E. 1920. Correlation of shape and station in fresh-water mussels (Naiades). *Proceedings of the American Philosophical Society* 59: 269-312.

Prozorova, L.A., E.M. Sayenko, V.V. Bogatov, M. Wu and Y.-Y. Liu. 2005. Bivalves of the Yangtze River drainage. *Byulleten' Dal'nevostochnogo Malakologicheskogo Obshchestva* 9: 46-58.

Reeve, L.A. and G.B. Sowerby. 1864-1868. Genus *Unio*. *Conchologica Iconica* 16: pls. 1-96.

Roe, K.J. and W.R. Hoeh. 2003 .Systematics of freshwater mussels (Bivalvia: Unionoida). pp. 91-122. [in] C. Lydeard and D.R. Lindberg, eds. *Molecular Systematics and Phylogeography of Mollusks*. *Smithsonian Series in Comparative Biology*. Smithsonian Books, Washington. 312 pp.

Rossmässler, E.A., W. Kobelt *et al*. 1835-1920. *Iconographie der Land und Süsswasser Mollusken* etc. 30 Volumes.

Sayenko, E.M., T.A. Pearce and E.K. Shea. 2005. Glochidial morphology of selected species of the genera *Cristaria* Schumacher, 1817 and *Sinanodonta* Modell, 1945 (Bivalvia: Unionidae) from Far Eastern Russia. *American Malacological Bulletin* 20: 11-21.

Schütt, H. 1983. Die Molluskenfauna der Süßwässer im Einzugsgebiet des Orontes unter Berücksichtigung benachbarter Flußsysteme. *Archiv für Molluskenkunde* 113: 17-91.

Schütt, H. 1992. Die grossen süßwassermuscheln von Dalaman (Turkei) (Eulamellibranchiata: Unionacea). *Malakologische Abhandlungen* 16: 59-63.

Shikov, E.V. and M.N. Zatravkin. 1991. The comparative method of taxonomic study of Bivalvia used by Soviet malacologists. *Malakologische Abhandlungen* 15: 149-159.

Simpson, C.T. 1900. Synopsis of the Naiades, or pearly freshwater mussels. *Proceedings of the U.S. National Museum* 22: 501-1044.

Simpson, C.T. 1914. *A Descriptive Catalogue of the Naiades or Pearly Freshwater Mussels*. Published Privately by Bryant Walker, Detroit. 1540 pp.

Smith, D.G. 2001. Systematics and distribution of Recent Margaritiferidae. pp. 33-49. [in] G. Bauer and K. Wächtler, eds. *Ecology and Evolution of the Freshwater Mussels Unionoida*. *Ecological Studies* 145. Springer-Verlag, Berlin. 394 pp.

Sowerby, G.B. 1867-1870. Genus *Anodon*. *Conchologica Iconica* 17: pls. 1-37.

Stadnichenko, A.P. 1984. Molyuski (Perlivnitsevi, Kul'kovi). *Fauna Ukraini* 29. 382 pp.

Starmühlner, F. and A. Edlauer. 1957. Ergebnisse der Österreichischen Iran-Expedition 1949/50. *Sitzungsberichten der Österreichische Akadamie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 166: 435-494.

Starobogatov, Ya.I. 1970. *Fauna Mollyuskov i Zoogeograficheskoe Raionirovanie Kontinental'nykh Vodoemov Zemnogo Shara*. Akademiya Nauk SSSR, Leningrad. 371 pp.

Starobogatov, Ya.I. 1977. On relationships between biological and typological species concepts. *Zhurnal Obshchei Biologii* 38: 157-165.

Starobogatov, Ya.I. and Z.I. Izzatullaev. 1984. Bivalvian molluscs of the family Unionidae in the Soviet Central Asia. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 89: 74-81.

Starobogatov, Ya.I., L.A. Prozorova, V.V. Bogatov and E.M. Sayenko. 2004. Bivalvia. pp. 11-251. [in] S.J. Tsalolikhin, ed. *Opredelitel' Presnovodnykh Besnozvonochnykh Rossii i Sopredel'nykh Territorii* 6. Nauka, St. Petersburg.

Van Damme, D. 1984. *The Freshwater Mollusca of Northern Africa: Distribution, Biogeography and Palaeoecology. Developments in Hydobiology* 25. Dr. W. Junk Publishers, Dordrecht. 164 pp.

Vicentini, H. 2005. Unusual spurting behavior of the freshwater mussel *Unio crassus*. *Journal of Molluscan Studies* 71: 409-410.

Vokes, H.E. 1980. *Genera of the Bivalvia: A Systematic and Bibliographic Catalogue (Revise and Updated)*. Paleontological Research Institution, Ithaca. 307 pp.

Walker, J.M., J.P. Curole, D.E. Wade, E.G. Chapman, A.E. Bogan, G.T. Watters and W.R. Hoeh. 2006. Taxonomic distribution and phylogenetic utility of gender-associated mitochondrial genomes in the Unionoida (Bivalvia). *Malacologia* 48: 265-282.

Westerlund, C.A. 1890. Malacozoa Acephala. *Fauna der in der Paläarctischen Region Lebenden Binnenconchylien* 7. 319 pp.

Wheeler, Q.D. and R. Meier, eds. 2000. *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press, New York. 230 pp.

Wiley, E.O. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Wiley and Sons, Inc., New York. 439 pp.

Zatravkin, M.N. 1983. Unionidae in the fauna of the USSR and their role as intermediate hosts of Trematoda and as eliminators cercariae. pp. 40-44. [in] I.M. Likharev, ed. *Mollyuski:*

Sistematika, Ekologiya i Zakonomernosti Rasprostraneniya. Akademiya Nauk SSSR, Leningrad. 262 pp.

Zatravkin, M.N. 1987. Recent species of the subfamily Psilunioninae (Bivalvia, Unionidae) in the fauna of the USSR. *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 92: 46-59.

Zatravkin, M.N. and V.V. Bogatov. 1987. *Krupnye Dvustvorchatye Mollyuski Presnykn i Solonovatykh Vod Dal'nego Vostoka SSSR: Opredelitel'*. Akademiya Nauk SSSR, Vladivostok. 153 pp.

Zatravkin, M.N. and A.L. Lobanov. 1986. Morphometric characters of shells of *Nodularia* (Bivalvia, Unionidae) from USSR and possibility of using them for species identification. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* 148: 39-45.

Zhadin, V.I. 1938. Sem. Unionidae. *Fauna SSSR, Mollyuski* 4. Izdatel'stvo Akademii Nauk SSSR, Leningrad. 169 pp.

Zhadin, V.I. 1952. Mollyuski presnykh i solonovatykh von SSSR. *Opredeliteli po Fauna SSSR* 46. Izdatel'stvo Akademii Nauk SSSR, Leningrad. 376 pp.

Zhadin, V.I. 1965. *Mollusks of Fresh and Brackish Waters of the U.S.S.R*. Israel Program for Scientific Translations, Jerusalem. 368 pp. [English translation of Zhadin (1952) by A. Mecado]

Ziuganov, V., A. Zotin, L. Nezlin and V. Tretiakov. 1994. *The Freshwater Pearl Mussels and their Relationships with Salmonid Fish*. VNIRO Publishing House, Moscow. 104 pp.

APPENDIX

Species- and Genus-Level Correspondence Between Biological and Comparatory Freshwater Mussel Taxa of the Palearctic

In the following table, Biological and Comparatory species are numbered to maintain a running count of diversity estimates based upon the two systems; numbers correspond to those used in Table 1 for Biological species. Only species occurring in the Palearctic Region are numbered, but other taxa are included to show correspondence between the two systems. Each Biological species is assigned to one or more subregions of the Palearctic (Figure 1); each is also provided with a concise range statement as determined from the literature reviewed.

++ indicates a Comparatory species inferred from a valid genus in Starobogatov (1970).

* indicates a Comparatory species inferred from a corresponding Biological species.

Biological Genera and Species	**Comparatory Genera and Species**
Family UNIONIDAE	
Unio Philippson in Retzius, 1788	*Unio*
1. *U. pictorum* (Linnaeus, 1758). WESTERN: widespread in Europe from the Atlantic to the Volga and Black Sea.	1. *U. pictorum* 2. *U. limosus* (Nilsson, 1822) 3. *U. rostratus* Lamarck, 1819 4. *U. protractus* Lindholm, 1922
2. *U. tumidus* Philippson in Retzius, 1788. WESTERN: widespread in Europe from the Atlantic to the Volga and Black Sea.	*Tumidiana* Servain, 1882 5. *T. tumida* 6. *T. conus* (Spengler, 1793) 7. *T. muelleri* (Rossmässler, 1838)
3. *U. mancus* Lamarck, 1819. WESTERN and SOUTHWESTERN: discontinuous, circum-Mediterranean distribution, including the Nile, and east to the Tigris-Euphrates Basin	*Turtoniana* Locard, 1889 8. *T. manca* ++
4. *U. terminalis* Bourguignat, 1852. SOUTHWESTERN: Orontes and Jordon basins.	*Eolymnium (s.s.)* Prashad, 1919 9. *E. (E.) terminalis*
5. *U. tigridis* Bourguignat, 1852. SOUTHWESTERN: Orontes east to the Tigris-Euphrates Basin.	10. *E. (E.) tigridis*
6. *U. crassus gontieri* Bourguignat, 1856 WESTERN: Ukraine south to Transcaucasia.	*Eolymnium (Shadininaia)* Starobogatov in Zatravkin, 1983. 11. *E. (S.) byzantinium* (Drouët, 1879) 12. *E. (S.) araxenum* (Drouët, 1881) 13. *E. (S.) colchicum* (Drouët, 1881) 14. *E. (S.) raddei* (Drouët, 1881) 15. *E. (S.) koutaisianum* (Kobelt, 1886) *Crassiana* Servain, 1882 16. *C. irenjensis* (Kobelt, 1912) 17. *C. mingrelica* (Drouët, 1881) 18. *C. sobriewskii* (Rosen, 1925) 19, *C. stevenianiformis* (Zhadin, 1938) 20. *C. gregorii* (Kobelt, 1912)
U. crassus crassus Philippson in Retzius, 1788, and other European and southwestern Asian subspecies. WESTERN and SOUTHWESTERN: widespread in Europe, from the Atlantic to the Volga, and southeast through the Tigris-Euphrates Basin.	21. *C. crassa* 22. *C. musiva* (Spengler, 1793) 23. *C. nana* (Lamarck, 1819) 24. *C. fuscula* (Rossmässler, 1835) 25. *C. cyprinorum* (Locard, 1882) 26. *C. irgizlaica* (Lindholm, 1904)

U. crassus mongolicus Middendorff, 1851.
EASTERN: Amur Basin and Primorye, north to Magadan, eastern Russia.

Inversidens Haas, 1911

7. *I. pantoensis* (Neumayr, 1899).
EASTERN: widespread, from southern

8. *I. brandtii* (Kobelt, 1879).
EASTERN: Endemic to Japan.

9. *I. japanensis* (Lea, 1859).
EASTERN: Japan.

Inversiunio Habe, 1991

10. *I. reinianus* (Kobelt, 1879).
EASTERN: Japan.

11. *I. jokohamensis* (von Ihering, 1893).
EASTERN: Japan.

12. *I. yanagawensis* (Kondo, 1982).
EASTERN: Japan.

Nodularia Conrad, 1853

13. *N. douglasiae* (Griffith and Pidgeon, 1834).
EASTERN: widespread from China, Japan and Korea north through the Amur Basin and Sakhalin Island to Magadan.

Lanceolaria Conrad, 1853
L. grayana (Lea, 1834). [China]

14. *L. cylindrica* (Simpson, 1900).
EASTERN: the Lower Amur Basin, including the Ussuri, in eastern Russia, south into China.

15. *L. acrorrhyncha* (von Martens, 1894).
EASTERN: Korea.

16. *L. oxyrhyncha* (von Martens, 1861).
EASTERN: Japan.

Anodonta Lamarck, 1799

17. *A. cygnea* (Linnaeus, 1758).
WESTERN: from the Atlantic east through the Volga.

Middendorffinaia (s.s.) Moskvicheva and Starobogatov, 1973
27. *M. (M.) mongolica*
28. *M. (M.) arsenievi* Moskvicheva and Starobogatov, 1973
29. *M. (M.) ussuriensis* Moskvicheva and Starobogatov, 1973
30. *M. (M.) ochotica* Bogatov, 2000

Middendorffinaia (Pseudopotomida) Moskv.& Starobog., 1973
M. (P.) continentalis Haas, 1910
31. *M. (M.) dulkeitiana* Moskvicheva & Starobogatov, 1973
32. *M. (P.) shadini* Moskvicheva and Starobogatov, 1973
33. *M. (P.) suifunensis* Moskvicheva and Starobogatov, 1973
34. *M. (P.) weliczkowskii* Moskv. & Starobogatov, 1973

Inversidens
35. *I. brandtii* ++

Pronodularia Starobogatov, 1970
36. *P. japanensis*
37. *P. haconensis* (von Ihering, 1893)
38. *P. reiniana*
39. *P. hirasei* (Haas, 1911)
40. *P. jokohamensis*
41. *P. yanagawensis* *

Nodularia (s.s.)
N. (N.) douglasiae [China]
42. *N. (N.) amurensis* (Mousson, 1887)
43. *N. (N.) middendorffi* (Westerlund, 1890)
44. *N. (N.) schrencki* (Westerlund, 1897)
45. *N. (N.) abbreviata* (Westerlund, 1897)
46. *N. (N.) flavoviridis* Haas, 1910
47. *N. (N.) vladivostokensis* Moskvicheva, 1973
48. *N. (N.) moskvichevae* Bogatov and Starobogatov, 1992
49. *N. (N.) sakhalinensis* Bogatov, 2001

Nodularia (Amurunio) Zatravkin and Bogatov, 1987
50. *N. (A.) lebedevi* Zatravkin and Starobogatov, 1984

Nodularia (Magadaninaia) Martynov and Chernyshev, 1992
51. *N. (M.) extremalis* Martynov and Chernyshev, 1992

Lanceolaria (s.s.)
L. (L.) grayana

Lanceolaria (Pericylindrica) Tomlin, 1930
52. *L. (P.) maacki* Moskvicheva, 1973
53. *L. (P.) chankensis* Moskvicheva, 1973
54. *L. (P.) ussuriensis* Moskvicheva, 1973
55. *L. (P.) bogatovi* Zatravkin and Starobogatov, 1984
56. *L. (P.) acrorrhyncha* *
57. *L. (P.) oxyrhycha* *

Anodonta
58. *A. cygnea*
59. *A. zellensis* (Gmelin, 1791)
60. *A. stagnalis* (Gmelin, 1791)

18. *A. anatina* (Linnaeus, 1758).
WESTERN and CENTRAL: from Europe and northern Africa east to Lake Baikal.

Colletopterum (s.s.) Bourguignat, 1880
61. *C. (C.) subcirculare* (Clessin, 1873)
62. *C. (C.) ostiarium* (Drouët, 1881)
63. *C. (C.) convexum* (Drouët, 1888)
64. *C. (C.) apollonicum* (Bourguignat, 1880)
65. *C. (C.) milaschevichi* (Bogatov, Starob. & Proz. 2005)
66. *C. (C.) baeri* (Bogatov, Staro.& Prozorova, 2005)
Colletopterum (Piscinaliana) Bourguignat, 1881
67. *C. (P.) anatinum*
68. *C. (P.) piscinale* (Nilsson, 1823)
69. *C. (P.) ponderosum* (Pfeiffer, 1825)
70. *C. (P.) rostratum* (Rossmässler, 1836)
71. *C. (P.) depressum* (Bourguignat, 1881)
72. *C. (P.) sorensianum* (Dybowski, 1913)
73. *C. (P.) nilssonii* (Küster, 1842)

19. *A. cyrea* Drouët, 1881.
CENTRAL: Aral Sea and southern Caspian Sea drainages.

74. *C. (P.) cyreum* (Drouët, 1881)
75. *C. (P.) bactrianum* (Rolle, 1897)
76. *C. (P.) kokandicum* Starobogatov and Izzatullaev, 1984

20. *A. vescoiana* Bourguignat, 1856.
SOUTHWESTERN: Endemic to the Tigris-Euphrates Basin.

Euphrata Pallary, 1933
77. *E. vescoiana* ++

21. *A. pseudodopsis* Locard, 1883.
SOUTHWESTERN: Endemic to Lake Antioch, Syria.

Gabillotia Servain, 1890
78. *G. pseudodopsis* ++

22. *A. woodiana woodiana* (Lea, 1834).
EASTERN: widespread, from Indochina and China north to Korea, Japan, Primorye and the Amur Basin in eastern Russia.

Sinanodonta (s.s.) Modell, 1945
S. (S.) woodiana [SE Asia]
79. *S. (S.) fukudai* Modell, 1947
80. *S. (S.) amurensis* Moskvicheva, 1973
81. *S. (S.) schrencki* Moskvicheva, 1973
82. *S. (S.) likharevi* Moskvicheva, 1973
83. *S. (S.) crassitesta* Moskvicheva, 1973
84. *S. (S.) primorjensis* Bogatov and Zatravkin, 1988
S. (S.) puerorum (Heude, 1880) [introduced]
S. (S.) orbicularis (Heude, 1880) [introduced]
S. (S.) gibba (Benson, 1855) [introduced]
Sinanodonta (Ellipsanodon) Bogatov and Starobogatov, 1996
85. *S. (E.) manchurica* Bogatov and Starobogatov, 1996

A. woodiana japonica (von Martens in Clessin 1874)
EASTERN: Japan, Primorye, Sakhalin Island and the southern Kurils.

Kunashiria Starobogatov in Zatravkin, 1983
86. *K. japonica*
87. *K. haconensis* (von Ihering, 1893)
88. *K. iwakawai* (Suzuki, 1939)
89. *K. iturupica* Bogatov, Sayenko and Starobogatov, 1999
90. *K. sinanodontoides* Bogatov, Sayenko and Starobog., 1999
91. *K. taranetzi* (Zhadin, 1938)
92. *K. coptzevi* (Zatravkin and Bogatov, 1987)
93. *K. zimini* (Zatravkin and Bogatov, 1987)
94. *K. compressa* (Bogatov and Starobogatov, 1996)
95. *K. zarjaensis* (Bogatov and Zatravkin, 1988)

23. *A. ogurae* (Kuroda and Habe, 1987)
EASTERN: Japan.

Oguranodonta Kuroda and Habe, 1987.
96. *O. ogurae*

24. *A. beringiana* Middendorff, 1851.
EASTERN: widespread Beringian distribution, from Primorye, the Lower Amur and Sakhalin Island through the Kurils, Kamchatka and the Aleutians to Pacific North America.

Beringiana Starobogatov in Zatravkin, 1983
97. *B. beringiana*
98. *B. youkanensis* (Lea, 1867)
99. *B. kamchatica* Bogatov and Starobogatov, 2001
B. georginensis Bogatov and Starobogatov, 2001 [USA]

25. *A. euscaphys* (Heude, 1879).
EASTERN: China north to the Lower Amur, eastern Russia.

26. *A. arcaeformis* (Heude, 1877).
EASTERN: China, Japan and Korea north to the Lower Amur and Primorye, eastern Russia.

Pseudanodonta Bourguignat, 1877

27. *P. complanata* (Rossmässler, 1835).
WESTERN: Atlantic Europe east to the Volga, including the Danube and other tributaries of the Black Sea.

Cristaria Schumacher, 1817

28. *C. plicata* (Leach, 1815).
EASTERN: Indochina and China north to the Amur Basin, eastern Russia and Mongolia.

29. *C. discoidea* (Lea, 1834).
EASTERN: widespread in eastern Asia, from Japan south to Indochina.

Hyriopsis Conrad, 1853
H. bialatus Simpson, 1900 [Indochina]

30. *H. schlegelii* (von Martens, 1861).
EASTERN: Endemic to Japan.

Lamprotula Simpson, 1900
L. plumbea (Chemnitz, 1795) [SE Asia?]

31. *L. coreana* (von Martens, 1886).
EASTERN: Korea.

32. *L. gottschei* (von Martens, 1894).
EASTERN: Korea, south to the Yangtze; Japan?

Pseudodon Gould, 1844
P. inoscularis (Gould, 1844) [Indochina]

33. *P. omiensis* (von Heimburg, 1884)
EASTERN: Japan.

100. *B. compressa* Sayenko and Bogatov, 1998
101. *B. chereshnevi* Bogatov and Starobogatov, 2001
102. *B. derzhavini* Bogatov and Starobogatov, 2001

Anemina Haas, 1969
A. euscaphys [China]
103. *A. fuscoviridis* (Moskvicheva, 1973)
A. arcaeformis [China]
104. *A. buldowskii* (Moskvicheva, 1973)
105. *A. shadini* (Moskvicheva, 1973)

Buldowskia Moskvicheva, 1973
106. *B. suifunica* (Lindholm, 1925)
107. *B. suifunensis* (Zhadin, 1938)
108. *B. flavotincta* (von Martens, 1905)
109. *B. cylindrica* Moskvicheva, 1973
110. *B. starobogatovi* (Moskvicheva, 1973)
111. *B. suputinensis* Moskvicheva, 1973
112. *B. koreana* Bogatov and Starobogatov, 1996
113. *B. possietica* Bogatov and Starobogatov, 1996

Amuranodonta Moskvicheva, 1973
114. *A. kijaensis* Moskvicheva, 1973
115. *A. parva* Moskvicheva, 1973
116. *A. sitaensis* (Bogatov and Starobogatov, 1996)
117. *A. boloniensis* (Zatravkin and Bogatov, 1987)
118. *A. lomakini* (Zatravkin and Bogatov, 1987)
119. *A. pulchra* Bogatov and Starobogatov, 1996

Pseudanodota
120. *P. complanata*
121. *P. nordenskioldi* Bourguignat, 1880
122. *P. klettii* (Rossmässler, 1835)
124. *P. elongata* (Holandre, 1836)

Cristaria
C. plicata [China]
125. *C. tuberculata* Schumacher, 1817
126. *C. herculea* (Middendorff, 1848)

Plethholophus Simpson, 1900
127. *P. discoideus* ++

Hyriopsis
H. bialatus

Nipponihyria Starobogatov, 1970
128. *N. schlegelii* ++

Lamprotula
L. plumbea

129. *L. coreana* *

130. *L. gottschei* *

Pseudodon
P. inoscularis

Obovalis Simpson, 1900.
131. *O. omiensis* ++

Potomida Swainson, 1840	*Potomida*
34. *P. littoralis* (Cuvier, 1798). WESTERN and SOUTHWESTERN: widespread from western and southern Europe and northern Africa, east to Syria.	132.*P. littoralis* 133.*P. armeniacus* (Kobelt, 1912) 134. *P. komarowi* (Boettger, 1880)
Leguminaia Conrad, 1865	*Leguminaia (s.s.)*
35. *L. wheatleyi* (Lea, 1862). SOUTHWESTERN: Lake Antioch and the Orontes of Syria, east to the Tigris-Eurphrates in Iraq.	135. *L. (L.) wheatleyi*
36. *L. saulcyi* (Bourguignat, 1852) SOUTHWESTERN: Syria.	136. *L. (L.) saulcyi*. *Leguminaia (Pseudoleguminaia)* Germain, 1911 137. *L. (P.) chantrei* Locard, 1883 ++
Microcondylaea Vest, 1866	*Leguminaia (Microcondylaea)*
37. *M. compressa* (Menke, 1830). WESTERN: eastern Mediterranean Europe.	138. *L. (M.) compressa*
Pseudodontopsis Kobelt, 1913	*Pseudodontopsis*
38. *P. euphratica* (Bourguignat, 1852). SOUTHWESTERN: Tigris-Euphrates Basin, Iraq.	139. *P. euphratica*
Family MARGARITIFERIDAE	
Margaritifera Schumacher, 1816	*Margaritifera*
39. *M. margaritifera* (Linneaus, 1858). WESTERN: amphi-Atlantic distribution, northern Europe and the UK, west to eastern North America.	140. *M. margaritifera* 141. *M. elongata* (Lamarck, 1819) 142. *M. borealis* Westerlund, 1871
40. *M. dahurica* (Middendorff, 1850). EASTERN: the Amur Basin, Primorye and Sakhalin Island, eastern Russia.	*Dahurinaia* Starobogatov, 1970 143. *D. dahurica* (Middendorff, 1850) 144. *D. tiunovae* Bogatov and Zatravkin, 1988 145. *D. ussuriensis* Bogatov, Prozorova & Starob., 2003 146. *D. prozorovae* Bogatov and Starobog. in Bogatov *et al*., 2003 147. *D. sujfunensis* Moskvicheva, 1973 148. *D. komarovi* Bogatov, Prozorova and Starobogatov, 2003
41. *M. laevis* (Haas, 1910). EASTERN: Japan and north through Sakhalin Island and the southern Kurils.	*Kurilinaia* Bogatov and Zatravkin, 1988 149. *K. laevis* 150. *K. kurilensis* (Zatravkin and Starobogatov, 1984) 151. *K. zatravkini* Bogatov, Prozorova and Starob., 2003
42. *M. togakushiensis* Kondo and Kobayashi, 2005. EASTERN: Japan.	152. *K. togakushiensis* *
43. *M. middendorffi* (Rosén, 1926). EASTERN: southern Kamchatka, eastern Russia.	153. *K. middendorffi* 154. *K. kamchatica* Bogatov, Prozorova and Starob., 2003
44. *M. auricularia* (Spengler, 1793). WESTERN: Iberian Peninsula, western Europe, and northern Africa.	*Pseudunio* Haas, 1910 155. *P. auricularia* ++
45. *M. homsensis* (Lea, 1864). SOUTHWESTERN: Syria.	156. *P. homsensis* *