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DISCUSSION

Results of Testing the Comparatory Method: The Curvature of the Shell Valve Frontal Section Is Inappropriate as a Systematic Character for the Freshwater Pearl Mussel of the Genus *Margaritifera*

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Abstract—This paper continues a discussion on the number of pearl mussel species of the genus *Margaritifera* in northern Europe. A biometric study of 1711 pearl mussel *Margaritifera margaritifera* shells from 15 rivers in Russia and Latvia (basins of the White and Baltic seas) has been conducted. All the examined samples fall into two groups: the northern group (with the shells more flattened on average, f. *margaritifera*) and the southern one (with more convex shells, f. *elongata*); the boundary between these groups is at 63° N. Analysis of intrapopulation variation has shown that the samples contain individuals that correspond to f. *margaritifera*, f. *elongata*, and f. *borealis*. However, any hiatus between these forms is absent in all the samples, and individuals belonging to two intermediate forms are rather frequent. The hypothesis on the species specificity of the shell valve frontal section has not been confirmed based on examination of large shell samples. The pearl mussels inhabiting rivers of Northern Europe belong to a single species, *M. margaritifera*.

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A specific feature of Russian malacology is use of the so-called comparatory method, which is based on the assumption of taxonomic constancy of the angle of the logarithmic spiral describing the contour of the frontal section of the shell valve of bivalve mollusks. This method was proposed by Logvinenko and Starobogatov (1971, p. 7), who stated that "...these curves are identical in individuals of the same species independently of the part of the distribution area from which they are taken (of course, within reasonable limits) and coincide when juxtaposed." The authors referred to a large volume of analyzed specimens on many mollusk species but did not indicate the values of these "reasonable limits." Then, 20 years later, this method was positioned as the leading doctrine in Soviet malacology (Shikov and Zatravkin, 1991), although it was repeatedly and reasonably criticized (Kornyushin, 2002; Graf, 2007; Kafanov, 2007). Recently, even a follower of the comparatory method (Bogatov, 2010) has admitted that "...the disadvantages of comparatory method have led to unjustified description of new species, eventually discrediting the method itself" (however, the author immediately proposes a new modification of this method).

Actually, the comparatory method formed the basis of the Russian key for freshwater mollusks (Starobogatov et al., 2004). For some reason, this is not mentioned in the key itself; however, one of its authors (Bogatov, 2009, p. 497) explains that "...the ratios of the major shell measurements (length, height, and convexity), including B/H_m (the ratio of convexity to maximal valve height) as the simplest and most available diagnostic parameters are used by experts only for preliminary identification of bivalve mollusks, keeping in mind that such identifications will be further verified by a more laborious, comparatory, method." However, the founders of the comparatory method (Logvinenko and Starobogatov, 1971, p. 9), on the contrary, regarded the comparatory method as supple-

Table 1. Characterization of the pearl mussel *Margaritifera margaritifera* samples

No.	River	Basin	Morphometric parameters, mm						*n*
			length, L		maximal height, H_m		convexity, B		
			M ± *SE*	min–max	*M* ± *SE*	min–max	*M* ± *SE*	min–max	
1	Muna[1]	Umba (White Sea)	93.3 ± 1.2	74.4–109.8	42.0 ± 0.5	33.5–48.7	24.9 ± 0.3	19.5–30.8	43
2	Mutkaioki[2]	Paanajarvi Lake (White Sea)	111.2 ± 1.8	57.1–136.0	52.3 ± 0.8	29.2–65.0	30.5 ± 0.5	16.1–39.2	111
3	Keret’[1]	White Sea	89.6 ± 2.6	41.1–123.0	43.0 ± 1.1	21.0–57.2	23.3 ± 0.7	9.4–34.5	56
4	Gridina[1]	″	108.6 ± 1.8	76.2–149.6	49.3 ± 0.7	36.3–57.2	28.8 ± 0.6	19.6–34.8	42
5	Solza[3]	″	85.5 ± 1.9	10.8–114.5	42.7 ± 0.9	5.7–56.8	23.7 ± 0.5	3.4–33.7	93
6	Kazanka[3]	Solza (White Sea)	96.1 ± 1.1	49.5–136.3	44.5 ± 0.5	23.0–60.5	25.7 ± 0.3	12.5–37.1	198
7	Nimen’ga[4]	White Sea	113.0 ± 0.6	79.9–135.0	52.0 ± 0.3	37.9–62.5	30.5 ± 0.2	20.5–38.2	277
8	Yud’ma[5]	Nimen’ga (White Sea)	100.2 ± 0.9	69.0–134.2	47.1 ± 0.4	34.7–61.6	27.2 ± 0.2	18.4–35.0	178
9	Maloshuika[3]	White Sea	112.7 ± 0.9	45.0–142.9	52.3 ± 0.4	22.9–65.9	30.0 ± 0.3	12.0–39.4	226
10	Kozha[3]	Onega (White Sea)	93.8 ± 1.0	52.6–120.8	44.2 ± 0.4	26.2–55.5	26.9 ± 0.3	14.4–33.8	151
11	Shotkusa[1]	Neva (Baltic Sea)	121.7 ± 2.5	76.8–135.7	59.9 ± 1.1	41.3–67.6	35.4 ± 0.6	23.9–40.1	25
12	Bezymyannaya[2]	Baltic Sea	106.5 ± 1.2	76.0–130.8	48.5 ± 0.4	34.9–62.8	30.1 ± 0.4	20.1–40.7	156
13	Khorinka[1]	Neva (Baltic Sea)	77.6 ± 3.0	59.3–106.1	38.4 ± 1.3	29.6–50.0	23.5 ± 1.1	17.0–33.9	22
14	Rauza[6]	Gauya (Baltic Sea)	98.1 ± 1.6	61.0–125.5	47.9 ± 0.8	29.0–61.5	29.5 ± 0.5	17.0–38.0	91
15	Tumšupe[6]	Zapadnaya Dvina (Baltic Sea)	88.8 ± 1.3	67.5–105.0	42.7 ± 0.5	35.0–49.0	26.7 ± 0.5	20.5–32.0	42
Total sample			102.6 ± 1.4	10.8–149.6	48.0 ± 0.6	5.7–67.6	28.2 ± 0.4	3.4–40.7	1711

Note: *M* ± *SE*, mean value and standard error; min–max, variation limits for Tables 1, 2. Operators that measured shells: [1] A.A. Makhrov, [2] I.V. Vikhrev, [3] Yu.V. Bespalaya, [4] S.E. Sokolova, [5] Yu.S. Kolosova, and [6] M. Rudzīte.

mentary to conventional diagnostic characters: “...this method may be used, for example, for a preliminary identification of *Sphaerium* and *Pisidium* with further obligatory verification using conventional diagnostic characters.”

Thus, it is most topical to clarify to what degree the groups identified according to the curvature of shell valve frontal section are discrete, that is, to what degree use of the comparatory method is justified. We used the European pearl mussels of the genus *Margaritifera* as a model group. Traditionally, all the pearl mussels of the Russian northwest have been ascribed to the species *M. margaritifera* (Zyuganov et al., 1993; Nagel et al., 1998; Smith, 2001). However, examination of museum samples of pearl mussel shells using the comparatory method has identified two additional species of this genus for the examined region, namely, *M. elongata* and *M. borealis* (Bogatov et al., 2003; Starobogatov et al., 2004). A discussion on how many species of freshwater pearl mussels inhabit the Russian northwest was held in the journal *Biology Bulletin* (*Izvestiya Rossiiskoi Akademii Nauk*: *Seriya Biologicheskaya*). We demonstrated that only one freshwater pearl mussel species—*M. margaritifera*—is present in the north of Europe, Russia included (Sergeeva et al., 2008). Later, Bogatov (2009) in his paper criticized our work advocating the validity of the taxa *M. elongata* and *M. borealis*. This paper continues the discussion of this question.

The European pearl mussels represent an important component of the river ecosystems (Zyuganov et al., 1993). Their abundance is rapidly declining, and they are currently protected in all countries of Europe. Large pearl mussel populations have remained in some rivers; however, most populations need protection and remediation (Rudzīte, 2004; Bespalaya et al., 2007, 2012; Makhrov, 2010; Makhrov et al., 2011; Ostrovsky and Popov, 2011; Rudzīte and Rudzītis, 2011). Clarification of the species composition of pearl mussels is necessary for both development of adequate measures for their protection and identification of pearl mussel species that died because of violations of environmental regulations. However, a case is known (P.V. Kiyashko, personal communication) in which experienced taxonomists failed to identify pearl mussels that died of aquatic pollution using the key tables (Starobogatov et al., 2004).

MATERIALS AND METHODS

Samples of pearl mussel shells from 15 rivers of Russia and Latvia belonging to the basins of the White and Baltic seas (Table 1) were examined. Several papers (Zhadin, 1939; Zyuganov et al., 1993; Bespalaya et al., 2007; Makhrov, 2010; Makhrov et al., 2011; Ostrovsky and Popov, 2011; Rudzīte and Rudzītis, 2011; Bolotov et al., 2012) give biological characterization of pearl mussel populations and describe the hydrological conditions for many of these rivers. Almost all the samples were collected by the authors in 2005–2011 except for the shell samples collected by V.I. Zhadin in 1938 in the Muna River (basin of the Umba River, Kola Peninsula) and stored with the Zoological Institute, Russian Academy of Sciences (Sergeeva et al., 2008). Some of them are stored under the name *M. margaritifera* and the remaining ones are under *M. elongata.* Our samples from most of the rivers are composed of empty shells of dead mollusks. Biological diving was also used for some rivers: live mollusks were collected into net bags and conveyed to the bank for weighing and measuring. Then the mollusks were returned to the same river sites from which they were collected.

To characterize the shells, we measured their length (L), maximal height (H_m), and convexity (B) (Skarlato et al., 1990) with the help of calipers (with accuracy of 0.1 mm). The same operator made all measurements for the samples of one river. Then the following morphometric indices were calculated for each shell: B/H_m, B/L, and H_m/L. According to the available key tables (Bogatov et al., 2003), the first index allows for distinguishing between pearl mussel species: this ratio does not exceed 0.56 for *M. margaritifera*; is no less than 0.58 but does not exceed 0.62 for *M. elongata*; and is no less than 0.65 for *M. borealis.*

It was earlier demonstrated analytically that the ratio of shell valve convexity to its height (B/H_m) unambiguously determines the constant angle of the logarithmic spiral that describes the contours of the valve frontal section for bivalve mollusks (Kafanov, 1975). However, Bogatov (2009, p. 498) made the following critical remark to our previous paper (Sergeeva et al., 2008): "The authors of the discussed paper decided to simplify the problem and abolished the diagnostic value of the curvature of the shell frontal section based on the idea that the character in question can be determined only for a small percentage of individuals." Although this is an unexpected criticism, we decided to take it into account and examined several shells that we had at our disposal using the comparatory method (Logvinenko and Starobogatov, 1971; Skarlato et al., 1990).

The obtained empirical comparatory curves were grouped for each sample and compared to the reference curves for the three pearl mussel species (Bogatov et al., 2003). The new modification of the comparatory method proposed by Bogatov (2010) considerably differs from the old version of this method (Skarlato et al., 1990). In essence, this is another method; moreover, the three species of European pearl mussels of the genus *Margaritifera* were distinguished based on a classic variant of the comparatory method (Bogatov et al., 2003; Bogatov, 2009). Therefore, the paper gives the data obtained with the help of the traditional variant of the comparatory method.

Here as well as in our previous paper (Sergeeva et al., 2008), we consider the three pearl mussel species identified by Bogatov et al. (2003) as a single species, *M. margaritifera.* For the sake of convenience in discussion, we designate here the "comparatory-based taxa," regarded by the mentioned authors as separate species, as the morphological forms f. *margaritifera*, f. *elongata*, and f. *borealis* and also consider two forms displaying intermediate characteristics. We distinguished these forms based on the B/H_m value (Bogatov et al., 2003). Mel'nichenko et al. (2004) used the same approach when studying the set of morphotypes of the species *Unio crassus.*

Statistical analysis of the biometric data involved standard methods (Puzachenko, 2004). The hypothesis on sample distributions was verified by the Kolmogorov–Smirnov test. The statistical significance of the differences between several samples was assessed by one-way ANOVA; the test for means was used for comparing two samples. The samples were classified according to three morphometric indices using cluster analysis; the dendrogram was constructed by Ward's method. The Statistica v. 6.1 and Microsoft Excel v. 2000 software packages were used for computations.

RESULTS

The mean values of morphometric indices for the shells in the studied samples varied considerably (Fig. 1). One-way ANOVA has demonstrated that the differences between samples for each of the indices are statistically significant: for B/H_m $F = 33.2$, $d.f. = 14, 1696$, $p < 0.001$; for B/L, $F = 47.0$, $d.f. = 14, 1653$, $p < 0.001$; and for H_m/L $F = 46.6$; $d.f. = 14, 1652$, $p < 0.001$. The indices B/H_m and B/L are minimal for the samples from northern rivers and are considerably higher for the samples from southern regions, whereas H_m/L does not display such a distinct clinal variation. Here, the shells from the Solza and Keret' rivers with their relatively large height fail to fit the general trend, as well as the shells from the Bezymyannaya River, displaying relatively small H_m values. According to the mean B/H_m value, the samples from the Keret' and Solza rivers can be classified as f. *margaritifera*, and the samples from the Mutkaioki, Gridina, Nimen'ga, Shotkusa, Muna, Khorinka, Kozha, Rauza, and Bezymyannaya rivers can be classified as f. *elongata.* The samples for the remaining four rivers occupy an intermediate position, and their B/H_m values according to the availably key tables (Bogatov et al., 2003) fall to the hiatus zones between different morphological forms.

The composition of pearl mussel samples estimated according to the rates of different morphological forms distinguished according to the B/H_m value dis-

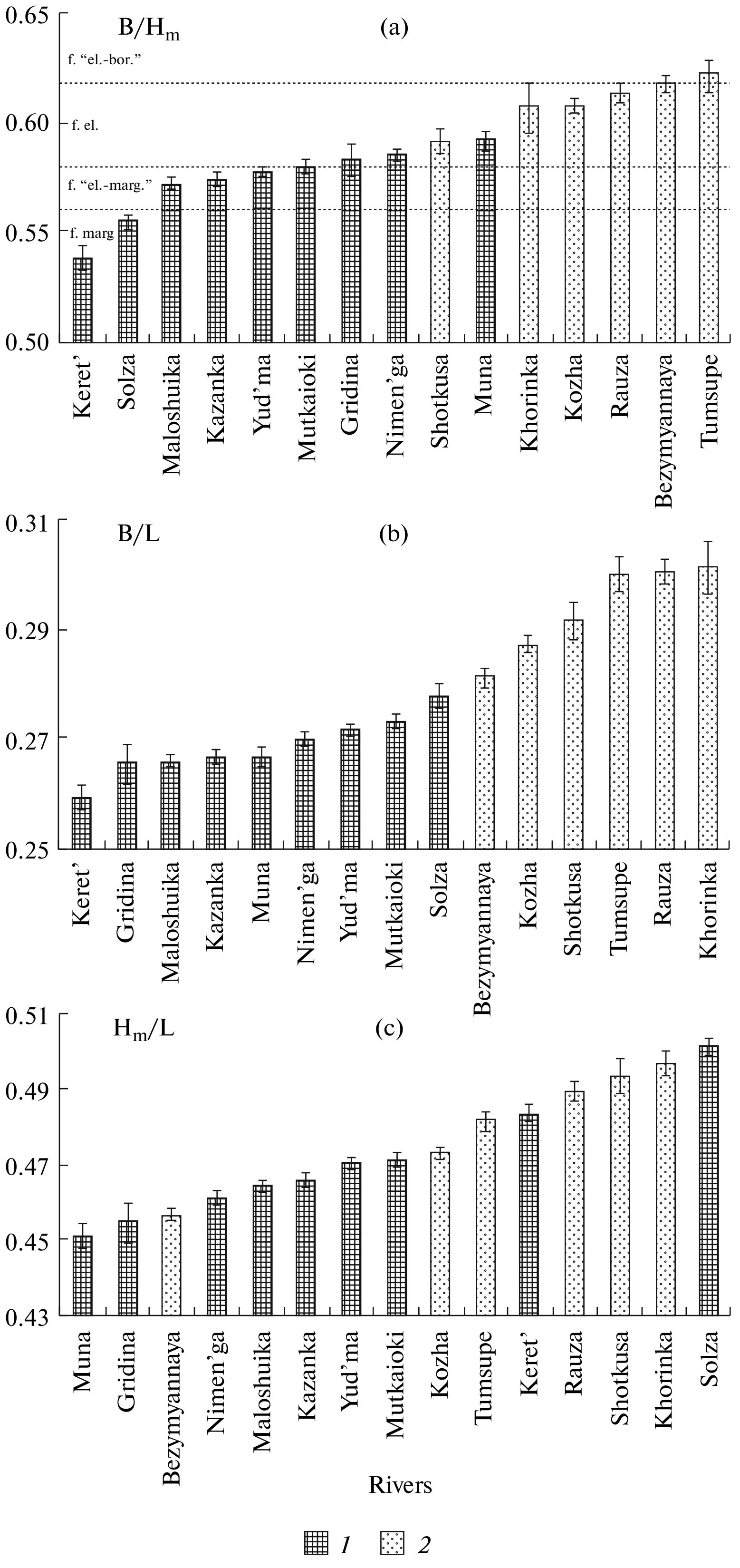

Fig. 1. Changes in the morphometric indices in the pearl mussel *Margaritifera margaritifera* samples from European rivers: (*1*) northern and (*2*) southern populations; f. "el.-bor.", intermediate form between f. *elongata* and f. *borealis*; f. el., f. *elongata*; f. marg., f. *margaritifera*; and f. "el.-marg.", intermediate form between f. *elongata* and f. *margaritifera*.

Table 2. The B/H_m index for the pearl mussel *Margaritifera margaritifera* samples grouped according to cluster analysis data*

Group of samples	$M \pm SE$	SD	min–max	n
Northern	0.575 ± 0.001	0.038	0.441–0.705	1224
Southern	0.614 ± 0.002	0.046	0.485–0.767	487

Note: *SD*, standard deviation.
* Samples follow a normal distribution (Kolmogorov–Smirnov test); differences between means are statistically significant ($p < 0.001$).

plays a noticeable spatial variation (Fig. 2). In the sample from Northern Europe, the individuals belonging according to this character to f. *margaritifera* or f. *elongata* (depending on the individual sample, either form may be predominant or both forms are present in approximately equal amounts) are more frequent. Southward, the percentage of individuals with a more convex shell (belonging to f. *borealis* according to B/H_m) increases. Individuals with the morphology intermediate between these three forms are also encountered at a high rate. Moreover, their spatial distribution follows a common trend: the rate of individuals with a more convex shell increases southward. Interestingly, the compositions of different forms differ in the main river and its tributary (for example, the Solza River with its tributary the Kazanka or the Nimen'ga River with the Yud'ma). Note that any hiatus between the forms is absent in all samples, so here we speak only about partition of continuous ordered series of B/H_m values, characterizing morphological variation of individuals in particular samples, into unequal intervals.

Cluster analysis of the samples according to the values of three morphometric indices has demonstrated that they all fall into two groups with a distinct geographic affiliation, northern and southern (Fig. 3). The boundary between these groups goes approximately along 63° N. These groups differ in the shell convexity index, B/H_m, in a statistically significant manner (Table 2). According to the centers of sample distributions, the northern samples are closer to f. *margaritifera* (more flattened shell), while the southern ones are closer to f. *elongata* (more convex shell).

Analysis of the intrapopulation variation of the shell frontal section curves for samples of two rivers (Mutkaioki and Bezymyannaya rivers) has shown that these curves vary in a wide range in each sample (Fig. 4). Note also that each of the samples contains individuals with a shell curvature coinciding with the reference curves for identification of different pearl mussel species (Bogatov et al., 2003; Starobogatov et al., 2004). On the other hand, each sample contains also a considerable number of individuals with intermediate variants of the comparatory curves. Thus, a continuous "fan" of curves is observed instead of the anticipated three discrete groups.

DISCUSSION

Two alternative approaches currently exist in the systematics of freshwater mollusks of the Northern Palearctic; these approaches have led to completely different systems at the specific and intraspecific levels (Vinarskii and Andreeva, 2007). While the foreign system is based on a relatively small number of polymorphic species, the system created by the school of Starobogatov (Starobogatov et al., 2004) is accepted in Russia as the basic one. From the latter standpoint, many of the species distinguished by European taxonomists are actually miscellaneous and represent complexes of independent taxa of various ranks. Revision of the Russian freshwater bivalve mollusks was based on the comparatory method. Application of this method partitioned the shell samples into groups discrete in the curvature of the shell valve frontal section, which was the basic concept for describing "comparatory" species, the term proposed by Graf (2007); that is, the hypothesis on the species specificity of the shell valve frontal section (Logvinenko and Starobogatov, 1971) was unambiguously accepted. Starobogatov (1968) believed that statistically significant differences between the syntopic samples even in one character indicated that they belonged to different species.

"Actually, these are not species but rather morphospecies, the status of which requires additional confirmation, for example, using supplementary characters of a certain independent group, such as anatomic, molecular, or others" (Vinarskii and Andreeva, 2007, p. 138). Note that many papers describing "comparatory" species also involve additional characteristics, including some auxiliary conchological characters (for example, the structure of the shell valve top), details in the structure of the mollusk's soft body, morphology of glochidia (including scanning electron microscopy data), and some others (Bogatov et al., 2002, 2003; Saenko et al., 2009). However, the data on intraspecific variation in these characters are not described and the estimates made are based on examination of very small samples, usually single individuals.

We have proved that the index B/H_m displays a high interpopulation variation, which has a pronounced latitudinal trend. The most significant boundary between our samples goes along approximately 63° N, which coincides with several other biogeographic boundaries (for example, between the north taiga and middle taiga subzones). It is known that the growth

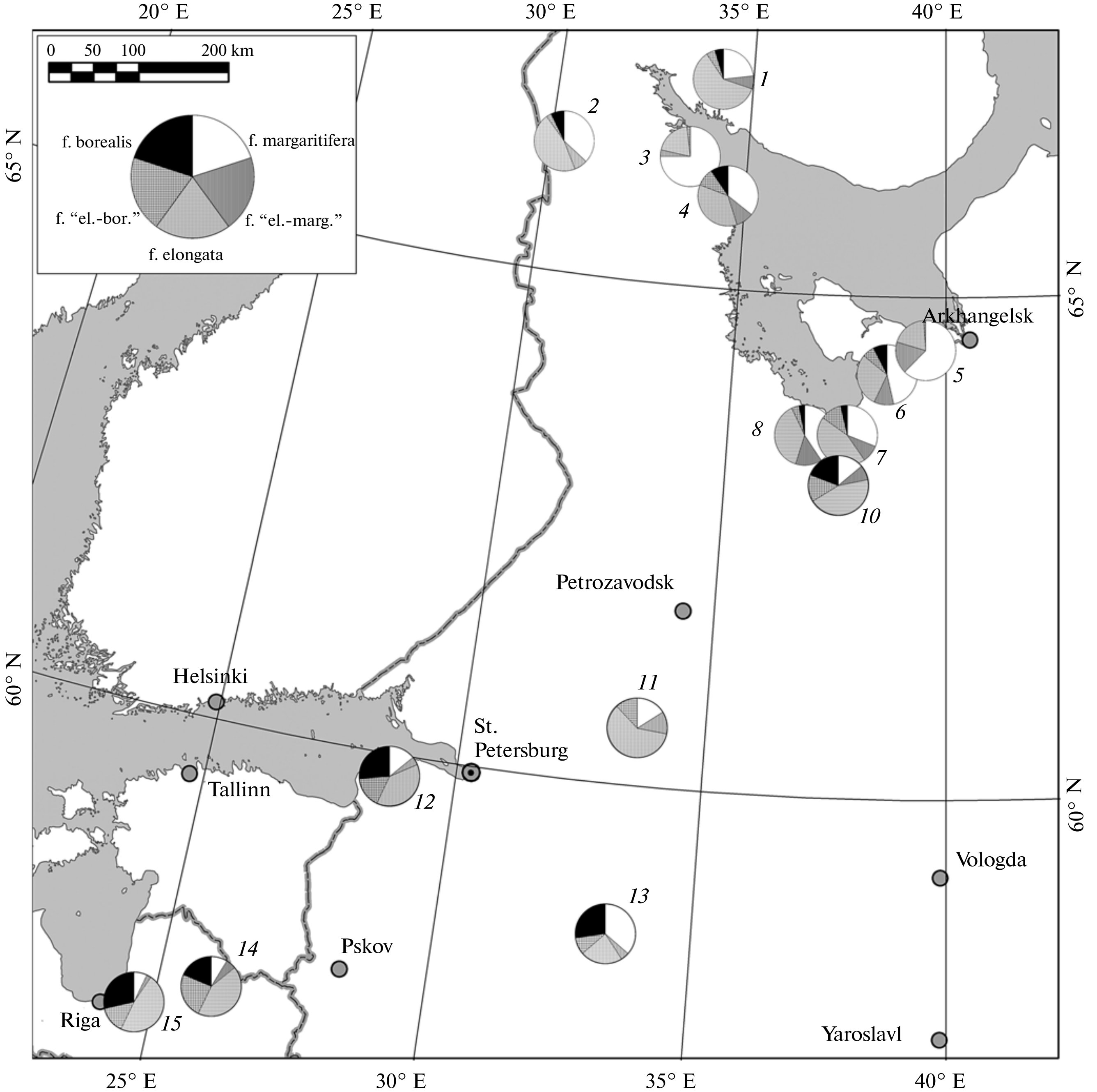

Fig. 2. Compositions of the *Margaritifera margaritifera* samples from European rivers (see Table 1 for designations of rivers and Fig. 2 for designations of intermediate pearl mussel forms).

and lifespan of pearl mussels are strictly associated with regional heat supply (Semenova at al., 1992; Akiyama and Iwakuma, 2009). The maximal lifespan of *M. margaritifera* in the rivers of Northwestern Europe ranges from 114 to approximately 200 years, and in the United Kingdom, it is 48–123 years versus 35–65 years in the south, for example, in Spain (Helama and Valovirta, 2008; Akiyama and Iwakuma, 2009). With the same shell length, the age of the mollusks from northern and southern rivers may differ two–threefold (Akiyama and Iwakuma, 2009). The rates of the increase in shell size change considerably depending on the latitude (Bauer, 1992; Semenova et al., 1992) as well as depending on the environmental conditions in individual years (Sinyavichene, 1982; Helama and Valovirta, 2007, 2008). It is well known that the sizes of the shells of the same age may vary considerably within the same river (Semenova et al., 1992; Hastie et al., 2000; Popov and Ostrovskii, 2010; Ostrovsky and Popov, 2011). Even these facts alone

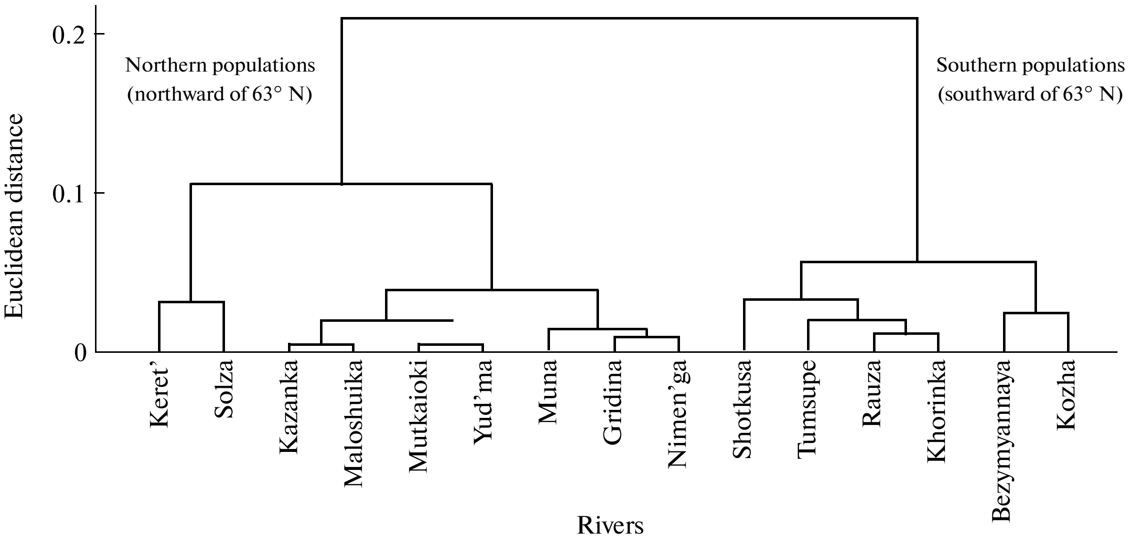

Fig. 3. Dendrogram of cluster analysis for the pearl mussel *Margaritifera margaritifera* samples according to mean values of the shell morphometric indices B/H_m, B/L, and H_m/L.

suggest that the morphological parameters of pearl mussels will display a pronounced clinal variation in the latitudinal gradient, which is confirmed by our data.

A high interpopulation variation in the shape of the pearl mussel shell valve contour has been observed in the rivers of Ireland (Preston et al., 2010). As has been shown, *M. margaritifera* has a plastic phenotype, and its shell shape is connected with the pH gradient. The morphological differences of the pearl mussels from the Nore River (Ireland) were the reason for regarding them as an independent species (*M. durrovensis*) or subspecies (*M. m. durrovensis*). However, molecular genetic analysis has proved that this is only a reflection of their ecological–phenotypic variation. Note that morphological forms of pearl mussels are referred to as ecophenotypes.

Analysis of intrapopulation variation has demonstrated that none of the analyzed morphometric indices allows any discrete groups to be distinguished in our samples. They all form continuous variation series with the distribution close to normal. Bogatov (2009, p. 498) believes that in one of the samples that we examined (Sergeeva at al., 2008), "...we actually have not a single distribution but rather at least two distributions or even a whole 'family' of distributions." This inference was made with the help of probability paper method without providing any details of the calculations. Our analysis demonstrates that the studied distribution displayed no statistically significant differences from the normal one.

Estimation of the frontal section curves for mass samples shows that any discrete groups here are also indistinguishable. Each studied sample contains both individuals with the shell valve curvature close to the reference curve of one of the three "comparatory" pearl mussel species and individuals with intermediate values of the character. Thus, the hypothesis on a species specificity of the shell valve frontal section is refuted based on examination of large samples of the mollusks belonging to the genus *Margaritifera*.

Moreover, it has been shown that the specimens from the collection of the Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia), distinguished as independent species *M. elongata* and *M. borealis* (Bogatov et al., 2003) based on morphological characters display no differences from *M. margaritifera* in the nucleotide sequence of the mtDNA *COI* gene and, consequently, belong to the same species (Bukhanova, 2011). Thus, only one pearl mussel species, *M. margaritifera*, lives in Northern and Middle Europe, which completely confirms the conclusion made earlier (Sergeeva et al., 2008).

Let us additionally consider the objections to our previous results (Sergeeva et al., 2008) made by Bogatov (2009). He writes: "Experts are aware that since the taxonomic keys after all use the ratios of the main shell measurements, such ratios characterize exclusively sexually mature mollusks, having, as a rule, average sizes. The results of measurements of young and old shells in this case are not taken into account" (Bogatov, 2009, p. 497). Then (p. 498), Bogatov specifies the size of the analyzed shells, 7 to 11 cm.

This statement is completely incorrect for the pearl mussels. Bauer (1987) in a study specially focused on the reproduction of *M. margaritifera* demonstrates that these mollusks reach their maturity at the age of about 20 years and continue to reproduce until death. Thus, any pearl mussels with a shell length of over 11 cm cannot be regarded as immature. Moreover, when characterizing both *M. margaritifera* and *M. borealis*, Westerlund (1871), who described the lat-

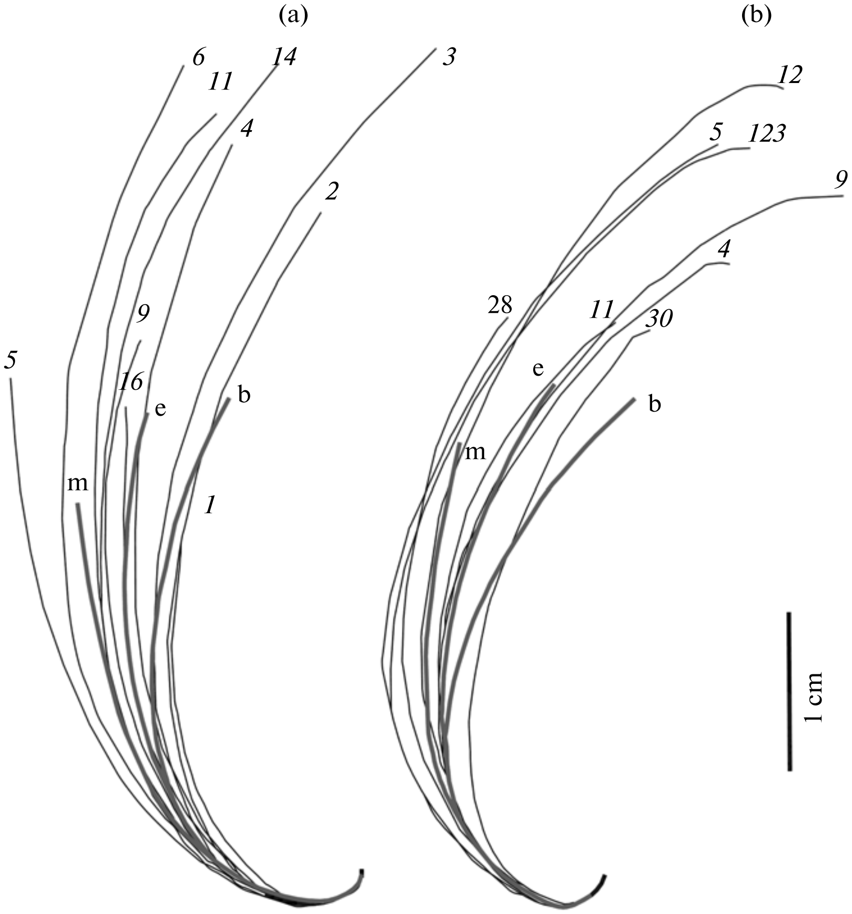

Fig. 4. Curves of the shell valve frontal section for samples from some pearl mussel *Margaritifera margaritifera* populations compared to the reference curves for the species (m) *M. margaritifera*, (e) *M. elongata*, and (bo) *M. borealis* (Bogatov et al., 2003): (a) Mutkaioki River and (b) Bezymyannaya River. Numbers of curves correspond to numbers of shells in samples.

ter form, used individuals with a length of over 12 cm. Bloomer (1927) reported measurements of the shell that Linnaeus most likely used for describing the species *M. margaritifera*; the length of this specimen was 12 cm. Thus, once we follow the recommendations by Bogatov (2009), we should exclude from consideration the holotype used for describing the corresponding species, thus violating the basic principles of systematics.

Bogatov also wrote (2009, pp. 497–498) that "...the taxonomic keys do not reflect all the values obtained for the shells of a middle age. Usually, the values of indices are given in the range of ±1 to ±2 standard deviations, which correspondingly covers 68 to 95% of a sample (except for the situations when a species is known as solitary specimens)." However, we have not found such rules in any taxonomic guidelines. In particular, they are absent in the manuscript by Pankhurst (1978), which comprehensively describes the procedure for creation of biological keys. Mayr in his monograph (1971, p. 316) distinctly specifies that the overlapping characters belong to characters inappropriate for any key.

The accuracy of the comparatory method is quite evident from a short communication by Bogatov (2010), suggesting that when a shell valve is placed under a microscope in a position somewhat differing from that recommended in the classical variant of the comparatory method, it appears that several specific and even supraspecific (!) taxa have been inaccurately identified. In particular, a large-scale revision of the Unioniformes inhabiting the Far East resulted in reduction of the genus *Nodularia* from three subgenera and 12 species to one subgenus and eight species, the genus *Middendorffinaia* from three subgenera and 11 species to two subgenera and eight species, and the genus *Sinanodonta* from three subgenera and nine species to one subgenus and seven species (Bogatov, 2010). Thus, 30% of the previously described "comparative" species and over 50% of the subgenera are regarded as inexistent only when the shell valve is looked at from a somewhat different angle of view. It remains unclear what the advantages of the new variant of the comparatory method are as compared with the previous one; presumably, the shell valve may be placed under a microscope in several other positions.

Evidently, a fundamentally new vision of the system for Unioniformes will correspond to each position.

Thus, based on analysis of large samples, we have proved that the curvature of the shell valve frontal section is inappropriate as a systematic character for the pearl mussels of the genus *Margaritifera* because of the high variation in this parameter; that is, it is impossible to determine the status of the species belonging to this group using the comparatory method. These data confirm the concept that the taxa specified with the help of the comparatory method are not valid from the standpoint of modern systematics and cannot be regarded as biological species (Kornyushin, 2002; Kafanov, 2007; Graf, 2007; Klishko, 2009). The pearl mussels inhabiting rivers of Northern and Middle Europe belong to a single species, *M. margaritifera*, which should be kept in mind when using the existing key tables (Bogatov et al., 2003; Starobogatov et al., 2004).

Actually, the partition of the European pearl mussels into three species is biologically invalid. The key role in the ecology and evolution of the naiads in general and pearl mussels in particular is played by adaptation of larvae to parasitizing various host fish species (Bauer and Wächtler, 2001). Each of the extant pearl mussel species is stringently associated with one or several, usually closely related, host fish species (Zyuganov et al., 1993).

In the case of the European pearl mussel *M. margaritifera*, these are two closely related salmon species of the genus *Salmo*, namely, the Atlantic salmon (*S. salar*) and brown trout (*S. trutta*). The particular host is yet unknown for the majority of the examined pearl mussel populations. However, it has been shown that there are no Atlantic salmon in the Mutkaioki River and that pearl mussel larvae in this river parasitize brown trout (Makhrov, 1995). However, this population displays no statistically significant differences in the B/H_m index from the population in the Gridina River, parasitizing brown trout (Makhrov et al., 2011). Thus, the morphological differences between the European pearl mussel populations are not associated with adaptation to different host species.

Therefore, it may be theoretically expected that two species could develop in a rather remote future based on *M. margaritifera* as the ancestral form, one of which will be stringently associated with the Atlantic salmon and the other, with the brown trout. Some pearl mussel populations adapted to parasitizing a specific host are known (Larsen, 2002; Oulasvirta, 2011). However, this is the very initial state of microevolutionary processes.

Shileiko (2009, p. 496) in the preface to the paper by Bogatov (2009) notes: "Actually, the dispute between V.V. Bogatov and I.S. Sergeeva et al. is largely of a theological character, because it reduces to the matter of credence: whether the comparatory method, proposed in their time by Logvinenko and Starobogatov (1971), is reliable when distinguishing between species." This most precisely captures the major specific feature of the "comparatory" systematics—in its essence, this is not a scientific approach but rather a theological doctrine based on belief in the verity of the hypothesis that the curvature of the shell valve front section is a species-specific characteristic. However, this hypothesis is readily testable in an experimental manner using particular systematic groups. Unlike science, any belief rests upon inerrability of the original postulate, which we actually observe in the considered situation. Evidently, this explains both the amazing autonomy of the Russian systematics of mollusks and its remoteness not only from the approaches used worldwide (Graf, 2007), but also from Russian field biology and ecology. We cannot but hope that the situation will change in the very near future and that the comparatory method (with modifications) will find its own place among the "scientific myths" of the 20th century. Then historians will try to answer the question why a mere belief was in Russia for over 40 years a "cornerstone" for one of the key sections in zoology.

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