Solution of taxonomic status of *Unio mongolicus* Middendorff, 1851 (Bivalvia: Unionidae) from the type locality in Transbaikalia and history of its taxonomy

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ABSTRACT. *Unio mongolicus* Middendorff, 1851 (Bivalvia: Unionidae) was described from Gorbitza mountain stream (in the eastern area of Trans-Baikal Territory, Russia) and the taxonomy has changed over the past century and a half. A specimen of *Middendorffinaia mongolica* from the Gorbitza stream collected 160 years later is a match with the type illustration of *Unio mongolicus* from the type locality. Comparison of the shell morphology of the type specimen of *U. mongolicus* with the modern specimen collected from this location, combined with our analyses of molecular, anatomical and conchological data of *M. cf. mongolica* species from rivers of the Upper Amur River Basin and the far eastern Russia, revealed that these taxa all belong to a single polymorphic species. The molecular analysis of the COI gene fragment of mtDNA of examined Comparative Species assigned to *Middendorffinaia* Moskvicheva et Starobogatov, 1973 confirmed they are only intraspecific forms of *M. mongolica*. Morphological and genetic distances between *M. mongolica* and *Nodularia douglasiae* (Griffith et Pidgeon, 1833) confirmed their assignment to two independent genera. Based on conchological characteristics and anatomical features, the differences between morphologically similar species *M. mongolica*, *N. douglasiae* and *Unio crassus* Retzius, 1788 were determined. History of the taxonomic changes for *Unio mongolicus* is discussed.

Introduction

*Unio mongolicus* Middendorff, 1851 (Bivalvia: Unionidae) was originally described from a Gorbitza mountain stream near Gorbitza village in Dauria (in the eastern area of Trans-Baikal Territory of Russia) [Middendorff, 1851: 277-278, pl. XXVII, figs 7–8], and has been an enigma for taxonomists. Middendorff [1851] noted that he only found a single specimen of *Unio mongolicus*, thus a holotype by monotypy. The holotype has been presumed lost, and this species has not been found or collected until recently. With only a rough description and the shell figure provided by Middendorff (showing an elongate oval shell with an extensively eroded umbo, pronounced pseudocardinal and lateral teeth) it was difficult for taxonomists to recognize *U. mongolicus* as a true species and to establish its generic placement. For that reason, its taxonomic placement has changed considerably over the last 150 years. Zhadin [1938] suggested that *U. mongolicus* represented a very rare species of freshwater pearl mussel, and in his monographic summary of large bivalves of the USSR, placed *U. mongolicus* within *Margaritana* (=*Margaritifera*) Schumacher, 1817 as *Margaritana mongolica* (Middendorff, 1851). A few years later, the same author after considering the well-developed lateral teeth which are characteristic of *Unio*, changed his mind moving the species back into *Unio Retzius, 1788*, as a subspecies of *Unio douglasiae* Griffith et Pidgeon, 1833, i.e. *Unio douglasiae var. mongolica* [Zhadin, 1952]. Haas [1969] considered *Unio mongolicus* a subspecies of the European *Unio crassus* (Philipsson in Retzius, 1788), i.e. *Unio crassus mongolicus*. 
Later, this name was listed in a summary of Palaearctic freshwater mussels, in which all species of the subgenus *Middendorffinaia* (s.s.) Moskvicheva et Starobogatov, 1973 (i.e., *M. mongolica*, *M. ussuriensis* and *M. arsenievi* Moskvicheva et Starobogatov, 1973, and *M. ochotica* Bogatov, 2000) were treated as synonyms of *Unio crassus mongolicus* [Graf, 2007].

Whereas the genus *Unio* did not occur in far eastern Russia, the new genus *Middendorffinaia* Moskvicheva et Starobogatov, 1973 was proposed with *Unio mongolicus* as the type species. One shell of *M. mongolica* collected by Levanidova in 1949 from the Khor River (Khabarovsky Territory) and specimens from the Razdolnaya and Sungacha rivers (collection of Sokolov, 1927 and of the expedition of Far East Branch of the Academy of Sciences, 1933) were surprisingly similar to the original description of *Unio crassus mongolicus* [Graf, 2007].

In Russian taxonomical system of freshwater *Unionidae*, the so called «Comparatory Method» (CM) is used today for species identification. The CM uses frontal contour of shell or the curves of maximal convexity of shell valve (MCVS) as main diagnostic character for species delimitation [Bogatov, Starobogatov, 1992; Bogatov, 2012]. It is believed CM alone is sufficient for determination of almost all species of freshwater mussels, since each curve of MCVS is species-specific and represents a “stencil” for species identification. Term “Comparatory species” i.e. species identified by CM, first was used by D. Graf with critical review of both CM and Comparatory species [Graf, 2007].

Recently, Sayenko [2015] noted the similarity of *Nodularia* and *Middendorffinaia* (s.s.) based on larval (glochidia) morphological analyses. According to Graf and Cummings [2018] allComparatory Species of *Middendorffinaia* (s.s.) belong to a single species under *Nodularia*, i.e. *Nodularia mongolica* (Middendorff, 1851), and all species names within this subgenus are synonyms of *N. mongolica*.

The aim of the present study is to verify the validity of Graf and Cummings’s [2018] opinion, based on morphological, anatomical and genetic analyses using our collections and museum specimens. In summary, the present study aims 1) to confirm that all Comparatory Species of *Middendorffinaia* (s.s.) belong to a single species, *M. mongolica*, 2) to clarify the generic position of *Unio mongolicus* and 3) to test if *Middendorffinaia* should be recognized as a valid genus or synonymized with *Nodularia*.
Material and methods

We examined extensive material of *Middendorffinaia mongolica* from different localities in eastern Russia including Transbaikal and Primorye Territories. Collections of *M. mongolica* near the type locality of *Unio mongolicus* and adjacent territory of Transbaikalia received special attention. Four specimens of *M. mongolica* were collected from rivers of the Upper Amur River Basin in the Transbaikal Territory (Fig. 1A). First, a poorly preserved shell was collected on June 06, 2014 from the Urov River (Argun River Basin) near the Argunsk village (50.4028°N, 118.1131°E). A second specimen of *M. mongolica* was collected on July 12, 2015 from a Gorbitza stream (53.1389°N, 119.263°E) near the type locality of *Unio mongolicus* (Fig. 1B). At the same time, one living specimen of *M. alimovi* Bogatov, 2012 was collected from the Shilka River (53.1048°N, 119.2202°E) near the Gorbitza village and was used for comparative anatomical and molecular analyses. The forth specimen of *M. mongolica* (dry shell) was collected on August 19, 2015 from Ingoda River (51.5372°N, 112.9083°E) near Chita City. All specimens were preserved and stored at the INREC SB RAS.

In addition, 14 specimens of *Middendorffinaia* (s.s.) from southern Primorsky Territory were collected by research workers of FRCISA RAS in summer of 2017 and used for comparative morphological and molecular genetic analyses. Additional museum specimens (six alcohol preserved specimens and 36 dry shells) of the three Comparative Species (*M. mongolica*, *M. ussuriensis* and *M. arsenievi*, ZISP), were selected for anatomical and morphological analyses. On each specimen, a detailed anatomical analysis was performed, tissues sampled for the genetic analysis, the shell dimensions, length (L), height (H) and width (B) were measured and its ratios (B/H, H/L, B/L) were calculated. In addition, 13 measured shells of the same species of the *Middendorffinaia* (s.s.) from Far East Russia from Zatravkin et Bogatov [1987] also were used for statistical analyses. A total of 73 specimens of *Middendorffinaia*, 245 of *Nodularia douglasiae* from far eastern Russia [Klishko et al., 2017] and 35 of *Unio crassus* from European Russia and Ukraine [Klishko et al., 2018a] were used for
comparative morphological and statistical analyses. The reliability of morphological discreteness between species and genera was assessed by λ (Wilk’s lambda), which values vary from 0 to 1 and indicates ideal discreteness at λ = 0 and its absence at λ = 1. Statistical analyses were performed using Microsoft Excel 2010 and discriminant analysis using STATISTICA v.6.1 software.

Molecular analyses were performed on specimens of Middendorffinaia (s.s.): M. mongolica, M. ussurensis and M. alimovi from Transbaikalia and Primorsky territories. For the genetic analyses, snips of mussel foot tissue of the examined species were preserved in 96% ethanol for molecular sequencing of CO1 mtDNA. Genomic DNA was extracted from tissue samples using a standard high-salt protocol [Sambrook et al., 1989]. The F-type CO1 gene (ca. 700 bp fragment) was amplified applying LCO_22me and HCO_700dy primers [Walker et al., 2006], annealing temperature of 50 °C and other polymerase chain reaction (PCR) conditions as described in Froufe et al. [2016]. Forward and reverse sequences were edited and assembled using ChromasPro 1.7.4 (Technelysium, Tewantin, Australia).

The alignment for the genetic analyses included the sequenced samples and selected Nodularia spp. CO1 sequences available in GenBank (n=12) (Table 1). For this alignment, the selected outgroups included sequences from one Margaritifera dahurica Middendorff, 1850, one Anodonta anatina (Linnaeus, 1758), one Anodonta cygnea (Linnaeus, 1758) and one representative of each of the main lineages of the genus Unio (i.e., Unio crassus Retzius, 1788, Unio pictorum Linnaeus, 1758, Unio gibbus Spengler, 1793 and Unio tumidus Retzius, 1788) (Table 1). The final data set was then analyzed using Bayesian inference (BI). The best-fit model of nucleotide substitution evolution under corrected Akaike Information Criterion was estimated using JMod-
of sequence divergence (uncorrected using Tracer 1.6 [Rambaut et al., 2012]. Two independent runs of 1 million generations were sampled at intervals of 100 generations producing a total of 10,000 trees. Burning was determined upon convergence of log likelihood and parameter estimation values using Tracer 1.6 [Rambaut et al., 2007]. Estimates of sequence divergence (uncorrected p-distances) were assessed using MEGA 6 software [Tamura et al., 2013].

Abbreviations used: Institutions: INREC SB RAS – Institute of Natural Resources, Ecology and Cryology, Siberian Branch of Russian Academy of Sciences, Chita; FRCISA RAS – Federal Research Center of Integrated Study of Arctic, Russian Academy of Sciences, Arkhangelsk; ZISP – Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia.


Results
Unio mongolicus from the Gorbitza stream found by Middendorff in 1851 is shown in Fig. 2A. It has shell dimensions: length (76 mm), height at the ligament (35 mm), height at the umbo (32 mm) and width (24 mm) according to Middendorff [1851: 278]. But, a shell represented by Middendorff [Middendorff 1851: Taf. XXVII, fig. 7, 8], with the same length, really has height at the ligament 40 mm and width 25.5 mm. The original picture has been digitally corrected according to the measurements of Middendorff and is shown on Fig. 2B. A specimen of Middendorffinaia mongolica from the Gorbitza stream (Fig. 2C), collected from near the type locality of U. mongolicus, has similar dimensions: length (77.8 mm), height at ligament (35.8 mm), height at umbo (32.1 mm), and width (24.2 mm) and looks identical to U. mongolicus presented on Fig. 2B. The shell shape and tooth morphology of the recently collected M. mongolica (Fig. 2E-G) also corresponds to the original description of U. mongolicus [Middendorff, 1851]. The facts show that both the recently recovered specimens of M. mongolica and the original U. mongolicus from the same location are possibly conspecific.

There is obvious similarity of the U. mongolicus type specimen and the recent specimens of M. mongolica collected from the Gorbitza stream and morphological characters are analogous to M. mongolicus from other rivers of the Trans-Baikal Territory and far eastern Russia. Middendorffinaia mongolica specimens examined have elongated oval or elongated quadrangular, rarely short oval, moderately convex shell. Posterior shell margin is always situated below a straight line relative to middle of shell height, nearer to the ventral shell margin which is straight or slightly concave (Fig. 3 A-N). The umbo is wide, not projecting above the dorsal shell margin, frequently eroded, is situated posterior to the anterior shell margin in 0.21-0.25% of shell length and usually is lower than the ligament. Periostracum colour varies from olive-green and brown to black. In contrast, to Nodularia douglasiae and Unio crassus, the position of the posterior shell margin is situated on a straight line relative to middle of shell height, ventral shell margin is straight or slightly convex (Fig. 3 O-P). The umbo of the shell in Nodularia is wide, projecting above the dorsal shell margin, and is situated away from the anterior shell margin in 0.25-0.33% of shell length and is usually above the ligament.

Species identification of Middendorffinaia (s.s.) specimens from Transbaikalia Territory and far eastern Russia have been performed with the Comparative Method, using the standard curves of the MCVS according to Bogatov [2012]. This method shows that examined specimens correspond with curves «c» or «b» thereby may be identified as M. mongolica and as M. ussuriensis. In addition, M. alimovi from Shilka, Komarovka and Gladkaya rivers which corresponds to curve «b» can be identified also as M. mongolica or M. ussuriensis by curve «c, b» (Fig. 3 I-J, L) though it differs from other examined Middendorffinaia (s.s.) by shorter oval and flattened shell. Comparatory Species of genus Nodularia, N. amurensis (Mousson, 1887) and N. shrencki (Westerlund, 1897) correspond to curves «2, 3», but can also correspond to curves «a, b, c» i.e. M. ochotica, M. ussuriensis, M. mongolica (Fig. 3 O-P). Unio crassus from the European part of Russia and Ukraine as Comparatory Species Crassiana crassa (Philipsson in Retzius, 1788), and C. fuscula (Rosmaessler, 1836) (curves «5, 7») can also correspond to curve «4b» – N. middendorffi (Westerlund, 1890) and «c» – M. mongolica (Fig. 3 Q-R).

Sculpture of the umbo and shell in Middendorffinaia species is represented by short or elongated wavy elevations and or small knobs, clearly visible in small specimens (Fig. 4 A-F) and weakly present or eroded in large shells. Shell sculpture of Nodularia specimens presents W-shaped discrete ribs or large chevrons (Fig. 4 G-L), strongly pronounced in small specimens and weakly visible or invisible in adult specimens. Unio crassus umbo sculpture is short or elongated wavy elevations, frequently absent or eroded (Fig. 4 M-O).
Morphology of hinge teeth of *Middendorffinaia* (s.s.) species are in general similar with *Nodularia douglasiae* and *Unio crassus*, but pseudocardinal and lateral teeth of *Middendorffinaia* are relatively more thickened, massive, indented (Fig. 5 A, B), with pseudocardinal teeth in the left valve united (Fig. 5B). Pseudocardinal and lateral teeth in *N. douglasiae* and *U. crassus* in comparison with *Middendorffinaia* are thin, lamellar, pseudocardinal teeth of left valve are separated (Fig. 5 C-D and E-F). In all examined specimens, the pseudocardinal teeth of the right valve may or may not a supplementary rudimentary tooth, the lateral tooth has or lacks a long or short protuberance on the ventral side (Fig. 5 A, C, E: shown by arrow).

The general soft body anatomy in *Middendorffinaia* and *Nodularia* specimens is quite like *Unio*, namely *U. crassus* (Fig. 6 A, E, H). However, there are some anatomical differences between the three genera. With the same shell size, form and evenly coloured body (cream or white) the outer and the inner gills, the mantle, foot and labial palps in *Middendorffinaia* and *Nodularia* (Fig. 6 A, E: og, ig, m, f, lp), the labial palps of *U. crassus* are different.
FIG. 5. Morphology of pseudocardinal and lateral teeth. A, B. Right and left valves of *Middendorffinaia mongolica*. C, D. The same of *Nodularia douglasiae* and E, F. *Unio crassus*. (Not scaled). Pointer descending indicates presence of a supplementary rudimentary tooth above pseudocardinal tooth in the right valve, up arrow – lateral tooth with a long or short protuberance on the ventral side.

РИС. 5. Морфология псевдокардинальных и латеральных зубов. А, Б. Правая и левая створки *Middendorffinaia mongolica*. 

С, Д. То же *Nodularia douglasiae* и Е, Ф. *Unio crassus*. (Не масштабировано). Стрелки направленные вниз, указывают на дополнительный рудиментарный зуб над псевдокардинальным зубом в правой створке, стрелка направленная вверх – латеральный зуб с длинным или коротким выступом на вентральной стороне.
in having a larger size and shape (Fig. 6H: lp). In *Middendorffinaia* and *Nodularia* papillae are present on both incurrent and excurrent apertures. The papillae of the incurrent aperture in both genera are well-developed, elongated, spindle-shaped, arranged in two-three tight rows (Fig. 6 B-D and F-G: pia). Papillae of the excurrent aperture of *N. douglasiae* are weakly-developed, short-conic, and arranged sparsely in a single row (Fig. 6 F, G: pexa). In addition in *Nodularia*, on the inner surface of the excurrent aperture, at the base of the papillae, there are specific knobs or raised bumps which stand out against dark pigmented background (Fig. 6 F, G: k). These knobs are missing from both *Unio* and *Middendorffinaia* excurrent apertures. In contrast, specimens of *Unio crassus* have orange feet with dark spot or stripe along its central part (Fig. 6H: f, fs), short-cylindrical papillae are present only in the incurrent aperture, arranged in a two row (Fig. 6 I, J: pia), the mantle surface of the excurrent aperture has only a pigment coating without papillae (Fig. 6 I: pg).

Morphometrical shell characters (B/H, H/L and B/L) of Comparative Species of *Middendorffinaia (s.s.)* have a wide range of variation in specimens of the same shell length from different localities and different trends with increasing shell length, significant overlap without a clear separation into independent species groups (Fig. 7 A-C). Values of B/H, H/L and B/L of *M. mongolica* have the largest range of variation and overlap in all *Middendorffinaia*
Taxonomic status *Unio mongolicus* Middendorff, 1851 (s.s.) species, from the more convex *M. ochotica* and *M. ussuriensis* to the flattened *M. alimovi*, indicating that they are intraspecific forms of *M. mongolica*. Discriminant analyses on the complex morphometric indexes (B/H, H/L and B/L) confirmed that all *Middendorffinaia* (s.s.) species belong to one polymorphic species, *M. mongolica*. Reliability of discrimination estimated by $\lambda$ (Wilk’s lambda) show reliable absence of morphological discreteness among all Comparatory Species of *Middendorffinaia* (s.s.) ($\lambda = 0.776$, n = 73, F = 70.2, $p<0.0005$).

The same pattern was shown with nine Comparatory Species of the genus *Nodularia* from eastern Russia and six species of genus *Crassiana* (subgenera *Crassiana* s.s. and *Bataviana*) Servain, 1882 from the European part of Russia and Ukraine, which belong to polymorphic species of the former *N. douglasiae* and the second *Unio crassus* [Klishko et al., 2017; 2018a]. In this study, *N. douglasiae*, *U. crassus* and *M. mongolica* specimens with shell length in range 30-80 mm were selected for morphometric comparative analysis. Morphometric shell index B/H of *N. douglasiae* by comparison with *M. mongolica* and *Unio crassus* have the greater range of variation and significant overlapping between all samples (Fig. 8A). Values of shell index H/L and B/L vary little, but also show significant overlapping (Fig. 8B, C). Extensive overlap of values of these indexes form a common cluster according to its disposition in space of the first two roots of the discriminant analysis, with no clear differentiation into discrete groups of species (Fig. 8 D, E). Weak morphological discreteness was found between *N. douglasiae* and *M. mongolica* ($\lambda = 0.579$, n = 308, F = 87, $p<0.00001$), and between *M. mongolica* and *U. crassus* ($\lambda = 0.567$, n = 98, F = 42, $p<0.001$). It indicates that *M. mongolica*, *N. douglasiae* and *U. crassus* are rather similar in morphometric shell indexes.

Aligned CO1 sequences had a total length of 588 bp, with 137 polymorphic and 102 parsimony informative sites. No indels and no unexpected stop codons were observed after translating all sequences to amino acids. The phylogenetic tree presents the three main clades within the ingroup, one for the *Unio* spp., one for *Nodularia* spp. and *Middendorffinaia mongolica* (Fig. 9). Inside the well supported *Nodularia* clade, three species can be determined: 1) *Nodularia douglasiae* which clusters specimens from China, South Korea, and the Russia, 2) *Nodularia cf. simulata* (Küster, 1833) a single specimen from South Korea, 3) an unnamed *Nodularia* sp., a single specimen from China, which is sister to a separate clade for *Nodularia douglasiae*, and 4) *Middendorffinaia mongolica*, corresponding to the
FIG. 8. Variation and trends of morphometric characters. A-C. Shell indexes B/H, H/L and B/L in samples of polymorphic species N. douglasiae, M. mongolica and U. crassus. D-E. Distribution of these patterns in space of the first two roots of the discriminant analysis.

Table 2. Pairwise genetic COI gene fragment distance matrix (unc. p-distance) of Nodularia species and M. mongolica (see Fig. 9). LEFT: (unc. p-distance) within species on the first column and respective standard deviation on the second. RIGHT: (unc. p-distance) among species (below the diagonal) and respective standard deviation (above the diagonal).

<table>
<thead>
<tr>
<th>Within species</th>
<th>N. douglasiae</th>
<th>N. cf. sinuolata</th>
<th>Nodularia sp.</th>
<th>M. mongolica</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. douglasiae</td>
<td>0.017</td>
<td>0.012</td>
<td>0.010</td>
<td>0.013</td>
</tr>
<tr>
<td>N. cf. sinuolata</td>
<td>-</td>
<td>0.087</td>
<td>0.011</td>
<td>0.013</td>
</tr>
<tr>
<td>Nodularia sp.</td>
<td>-</td>
<td>0.076</td>
<td>0.080</td>
<td>0.013</td>
</tr>
<tr>
<td>M. mongolica</td>
<td>0.004</td>
<td>0.109</td>
<td>0.107</td>
<td>0.108</td>
</tr>
</tbody>
</table>
Taxonomic status *Unio mongolicus* Middendorff, 1851

According to the molecular analysis, all specimens of Comparatory Species of *Middendorffinaia* (s.s.) belong to one polymorphic species, *M. mongolica* in a distinct genus *Middendorffinaia*. *Middendorffinaia mongolica* is a valid species confirmed by the molecular analysis of the COI gene (ca. 700 bp fragment) mtDNA (Table 2 and Fig. 9). We conclude that the taxon, *Unio mongolicus* Middendorff, 1851, represents a distinct genus and species *Middendorffinaia mongolica* which does not belong to *Unio crassus* or the genus *Nodularia*.

Current systematics

**Family Unionidae Rafinesque, 1820**

**Genus Middendorffinaia** Moskvicheva et Starobogatov, 1973

Type species (original designation): *Middendorffinaia mongolica* (Middendorff, 1851)

Synonymy:

*Unio mongolicus* Middendorff, 1851: 277-278, plate XX-VII, figs. 7-8.
Middendorffinaia (M.) arsenievki Moskvicheva, Starobogatov, 1973: 27, fig. 3 m-o. Middendorffinaia (M.) ussuriensis Moskvicheva, Starobogatov, 1973: 28-29, fig. 3 u-m.
Middendorffinaia (M.) ochotica Bogatov, 2000: 861-862, fig. in text (a-c).
Middendorffinaia (M.) alimovi Bogatov, 2012: 400, fig. 4; fig. 5: 1, 7z.

Geographical distribution. This species is widespread in eastern Russia from the Upper and Middle Amur River Basin (Transbaikalia and Khabarovsky Krai) to Ussury River Basin (Primorsky Krai) and the Kuchtuy River Basin (Okhotsk Region).

Discussion

The comparison of shell shape and dimensions of the type of Unio mongolicus Middendorff, 1851 with specimens subsequently identified as M. mongolica from the same location in the Gorbitza stream, Trans-Baikal Territory, show that they are conspecific (Fig. 2), and revealed their similarity with Comparatory Species assigned to Middendorffinaia (s.s.) from Far Eastern Russia (Fig. 3). The species identification using the curves of MCVO by Comparatory Method, according to Bogatov [2012] makes it possible to separate the intraspecific forms of each examined subgenus. However, the same specimen can correspond to curves of MCVO for the examined genus or other genera. For example, M. mongolica curve «c» can also correspond to curves «d» and «a, b», i.e. intraspecific forms M. alimovi and M. ussuriensis, M. ochotica (Fig. 3 D, F, I-L, M-N), also Nodularia douglasiae can correspond to curves 2, 3 (N. amurenensis, N. shrencki) and «a, b, c», i.e. intraspecific forms M. ochotica, M. ussuriensis, M. mongolica (Fig. 3 O-P). In addition, Unio crassus can correspond to curves of MCVO for Nodularia middendorphi (Westerlund, 1890) and Middendorffinaia mongolica (Fig. 3 Q-R). Therefore, the curves of MCVO are not species-specific and useless for species identification in the examined genera. No wonder Unio mongolicus was placed in Nodularia as N. mongolica or in the genus Unio as Unio crassus mongolicus [Graf, 2007; Graf, Cummings, 2018] since some of its conchological characteristics are so similar. However, there are specified differences of shell shape of three genera. The posterior shell margin of Nodularia douglasiae and Unio crassus is situated on a straight line relative to middle of shell height (Fig. 3 O-R) in contrast Middendorffinaia mongolica in which the posterior shell margin is situated always below a straight line relative to middle of shell height, near to ventral shell margin (Fig. 3 A-N). In addition there are a certain differences of hinge teeth, namely pseudocardinal and lateral teeth in N. douglasiae and U. crassus in comparison with Middendorffinaia specimens are thin, lamellar, pseudocardinal teeth of left valve are separated (Fig. 5 D, F). The pseudocardinal teeth of left valve of M. mongolica are united (Fig. 5B). Umbo and shell sculpture and also features of soft body anatomy of Nodularia and Unio differ considerably from Middendorffinaia (Fig. 4, 6).

Why Unio mongolicus was transferred to Margaritana by Zhadin [1938] becomes clear when the shell shape of U. mongolicus and Margaritifera dahurica (Middendorff, 1850) are compared. There is a surprising shell shape similarity among U. mongolicus and M. dahurica which is a good example of shell convergence between unrelated taxa. Unio mongolicus lacks the mantle attachment scars typical of the family Margaritiferidae. This shell similarity deceived Zhadin [1938: 115] who placed U. mongolicus under Margaritana (= Margaritifera). Later Unio mongolicus was moved to Unio douglasiae var. mongolica [Zhadin, 1952] which might be more appropriate for U. mongolicus than Unio crassus var. mongolicus [Haas, 1969] since Unio crassus Retzius, 1788 is a western Palaeartic species.

According to the data presented in this study, there are certain conchological characters and anatomical features in adult specimens that can be used to separate Middendorffinaia and Nodularia, and support Middendorffinaia as a separate genus. The Comparatory Species M. ussuriensis, M. ochotica and M. alimovi are intraspecific forms of M. mongolica (Fig. 7) which should also be synonymized with M. mongolica (Fig. 8, Table 2 and Fig. 9). The distinction between the specimens of M. mongolica and N. douglasiae under the different clades (Middendorffinaia and Nodularia) was confirmed by the molecular analysis (Fig. 9).

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Решение вопроса о таксономическом статусе вида *Unio mongolicus* Middendorff, 1851 (Бивалвия: Unioiidae) из типового местонахождения в Забайкалье и история его таксономии

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РЕЗЮМЕ. Представление о родовой принадлежности вида *Unio mongolicus* (Бивалвия: Unioiidae), опи-савенного Миддендорфом в 1851 г из руч. Горбича на востоке Забайкальского края России, изменялось в течение полутора веков. Экземпляр *Middendorffinaia mongolica* (Middendorff, 1851), обнаруженный 160 лет спустя в районе типового местонахождения, оказался идентичным с типовым. Сравнительный анализ *M. mongolica* из этого местонахождения и компараторных видов *M. cf. mongolica* из рек бассейна Амура и Дальнего Востока России выявил, что все эти таксоны принадлежат одному полиморфному виду. Молекулярный анализ фрагмента гена COI mtДНК исследуемых компараторных видов *Middendorffinaia* (s.s.) подтвердил, что все они принадлежат *M. mongolica* и представляют его внутривидовые формы. Морфологическая и генетическая дискретность между видами *M. mongolica* и *Nodularia douglasiae* подтверждена их положение в разных родах. Принимая во внимание конхологические признаки и анатомические особенности, выявлены различия морфологически сходных видов *M. mongolica, N. douglasiae* и *Unio crassus*. Обсуждается история таксономических изменений названия *Unio mongolicus*. Таксonomicкие решения, принятые в статье:

* Middendorffinaia (M.) ussuriensis = Middendorffinaia mongolica, syn. nov.
* Middendorffinaia (M.) arsenievi = Middendorffinaia mongolica, syn. nov.
* Middendorffinaia (M.) ochotica = Middendorffinaia mongolica, syn. nov.
* Middendorffinaia (M.) alimovi = Middendorffinaia mongolica, syn. nov.