
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 east 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 Gorbit-

za 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. *mongolicus* [Zhadin, 1952]. Haas [1969] considered *Unio mongolicus* a subspecies of the European *Unio crassus* (Philippson in Retzius, 1788), i.e. *Unio crassus mongolicus*.

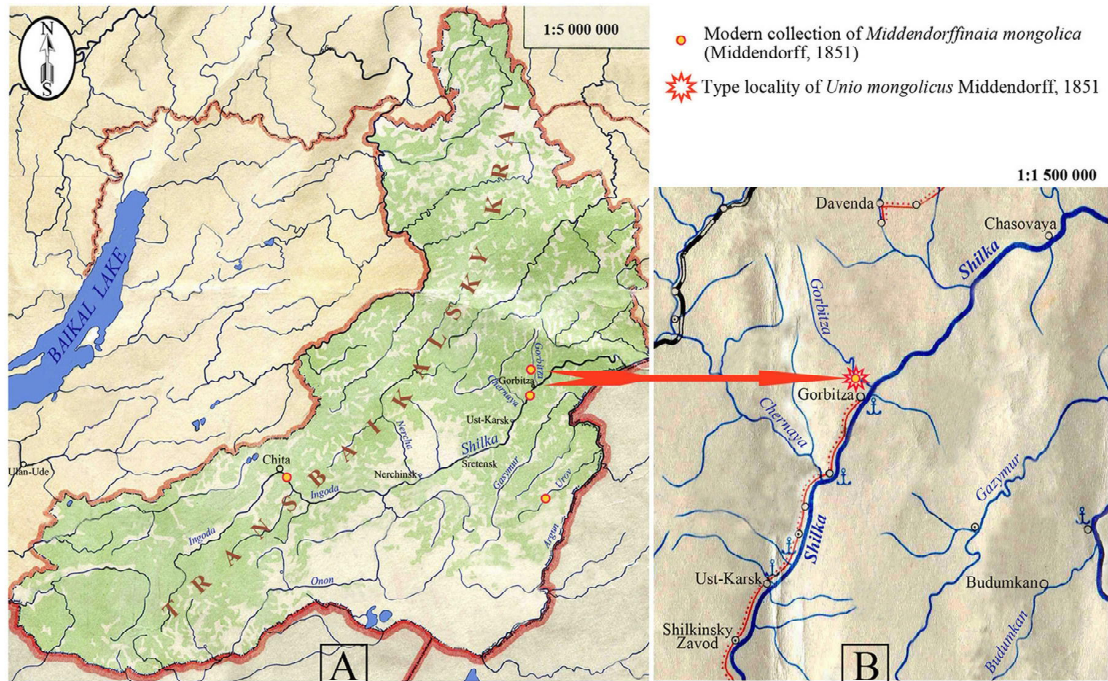


FIG. 1. Map of the collections of *Middendorffinaia mongolica*. **A.** Collection sites of *M. mongolica* in Gorbitza stream and rivers of the Upper Amur River basin. **B.** Type locality of *Unio mongolicus* in Gorbitza mountain stream.

РИС. 1. Карта сборов *Middendorffinaia mongolica*. **A.** Точки сбора *M. mongolica* в руч. Горбица и реках бассейна Верхнего Амура. **B.** Типовое местонахождение *Unio mongolicus* в горном ручье Горбица.

Later, this name was listed in a summary of Palearctic 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 (Khabarovsk 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 *U. mongolicus*. This species was included in the genus *Middendorffinaia* and listed in the identification guides to the bivalve mussels of the Far East of Russia [Zatravkin, Bogatov, 1987; Starobogatov *et al.*, 2004; Bogatov, 2012] and in the catalogues of molluscs of Russia and adjacent countries [Kantor, Sysoev, 2005; Vinarski, Kantor, 2016].

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] all Comparatory 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*.

Table 1. List of specimen samples sequenced (CO1) and GenBank accession numbers. *Unpublished

Табл. 1. Перечень секвенированных образцов (CO1) и инвентарные номера в ГенБанке. *Неопубликованные

Species	Locality	GenBank	Source
<i>Nodularia douglasiae</i> (Griffith et Pidgeon, 1833)	China	KT984763	He, Liu*
<i>Nodularia douglasiae</i>	China	KT984764	He, Liu*
<i>Nodularia douglasiae</i>	China	KT984765	He, Liu*
<i>Nodularia douglasiae</i>	China	KT984766	He, Liu*
<i>Nodularia douglasiae</i>	China	KX822653	Lopes-Lima <i>et al.</i> , 2017
<i>Nodularia douglasiae</i>	China	KJ434520	Uyang <i>et al.</i> *
<i>Nodularia douglasiae</i>	China	KJ434521	Uyang <i>et al.</i> *
<i>Nodularia douglasiae</i>	China	KJ434522	Uyang <i>et al.</i> *
<i>Nodularia douglasiae</i>	China	NC_026111	Wang <i>et al.</i> , 2015
<i>Nodularia douglasiae</i>	South Korea	GQ451862	Park <i>et al.</i> *
<i>Nodularia douglasiae</i>	South Korea	GQ451863	Park <i>et al.</i> *
<i>Nodularia cf. sinuolata</i> ?	South Korea	GQ451864	Park <i>et al.</i> *
<i>Nodularia douglasiae</i>	Amur River, Russia	MF975692	Klishko <i>et al.</i> , 2017
<i>Nodularia douglasiae</i>	Onon River, Russia	MF975693	Klishko <i>et al.</i> , 2017
<i>Nodularia douglasiae</i>	Onon River, Russia	MF975694	Klishko <i>et al.</i> , 2017
<i>Middendorffinaia mongolica</i> (Middendorff, 1851)	Shilka River, Russia	MH974547	This Study
<i>Middendorffinaia mongolica</i>	Gladkaya River Russia	MH974548	This Study
<i>Middendorffinaia mongolica</i>	Gladkaya River Russia	MH974549	This Study
<i>Middendorffinaia mongolica</i>	Gladkaya River Russia	MH974550	This Study
<i>Middendorffinaia mongolica</i>	Komarovka River Russia	MH974551	This Study
<i>Unio crassus</i> Retzius, 1788	Poland	AF514296	Soroka, 2010
<i>Unio pictorum</i> (Linnaeus, 1758)	Poland	HM014131	Soroka, Burzinsky, 2010
<i>Unio gibbus</i> Spengler, 1793	Morocco	KX822671	Lopes-Lima <i>et al.</i> , 2017
<i>Unio tumidus</i> Retzius, 1788	Ukraine	KX822672	Lopes-Lima <i>et al.</i> , 2017
<i>Anodonta anatina</i> (Linnaeus, 1758)	Ukraine	MH062766	Klishko <i>et al.</i> , 2018
<i>Anodonta cygnea</i> (Linnaeus, 1758)	Italy	MF414422	Froufe <i>et al.</i> , 2017
<i>Margaritifera dahurica</i> (Middendorff, 1850)	China	NC_023942	Yang <i>et al.</i> , 2015

Material and methods

We examined extensive material of *Middendorffinaia mongolica* from different localities in eastern Russia including Transbaikalia 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 Transbaikalia 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 fourth 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

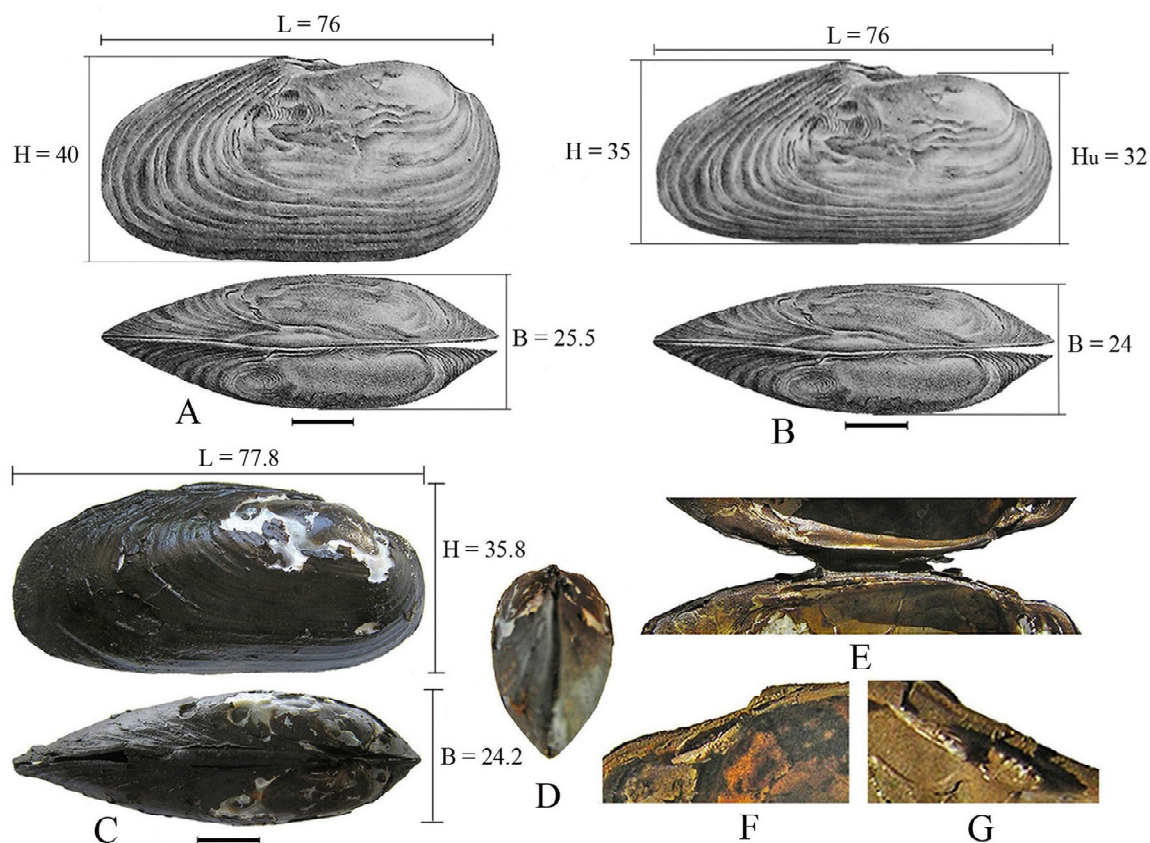


FIG. 2. Outside view and dorsal view of the shells from Gorbitza stream. **A.** *Unio mongolicus* – Middendorff, 1851: 277–278, Taf. XXVII, Figs 7, 8. **B.** The same *U. mongolicus* according to the shell dimensions by Middendorff, 1851: 278. **C-G.** *Middendorffinaia mongolica*. **D.** Frontal contour of shell. **E.** Lateral teeth. **F-G.** Pseudocardinal teeth of the right and the left valve (not scaled). Scale bars for A-D = 1 cm.

РИС. 2. Внешний вид и вид сверху раковин из руч. Горбица. **A.** *Unio mongolicus* – Middendorff, 1851: 277–278, Taf. XXVII, figs. 7, 8. **B.** Тот же *U. mongolicus* согласно размерам раковины по Миддендорфу, 1851: 278. **C-G.** *Middendorffinaia mongolica*. **D.** Фронтальный контур раковины. **E.** Латеральные зубы. **F-G.** Псевдокардинальные зубы правой и левой створки (не масштабировано). Масштаб для A-D = 1 см.

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 $\lambda = 0$ and its absence at $\lambda = 1$. 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. ussuriensis* 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 COI 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-

elTest 2.1.4 [Darriba *et al.*, 2012]. Model GTR+I+G was chosen and used in the phylogenetic analyses. Phylogenetic BI was performed using MrBayes version 3.2.6 [Ronquist *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.

Morphological data: am – anterior adductor muscle, exa – excurrent aperture, f – foot, fs – foot strip, ia – incurrent aperture, ig – inner gills, k – knobs, lp – labial palps, m – mantle, MCVS – maximal convexity of shell valve; og – outer gills, pg – pigment coating, pexa – papillae of the excurrent aperture, pia – papillae of the incurrent aperture.

Results

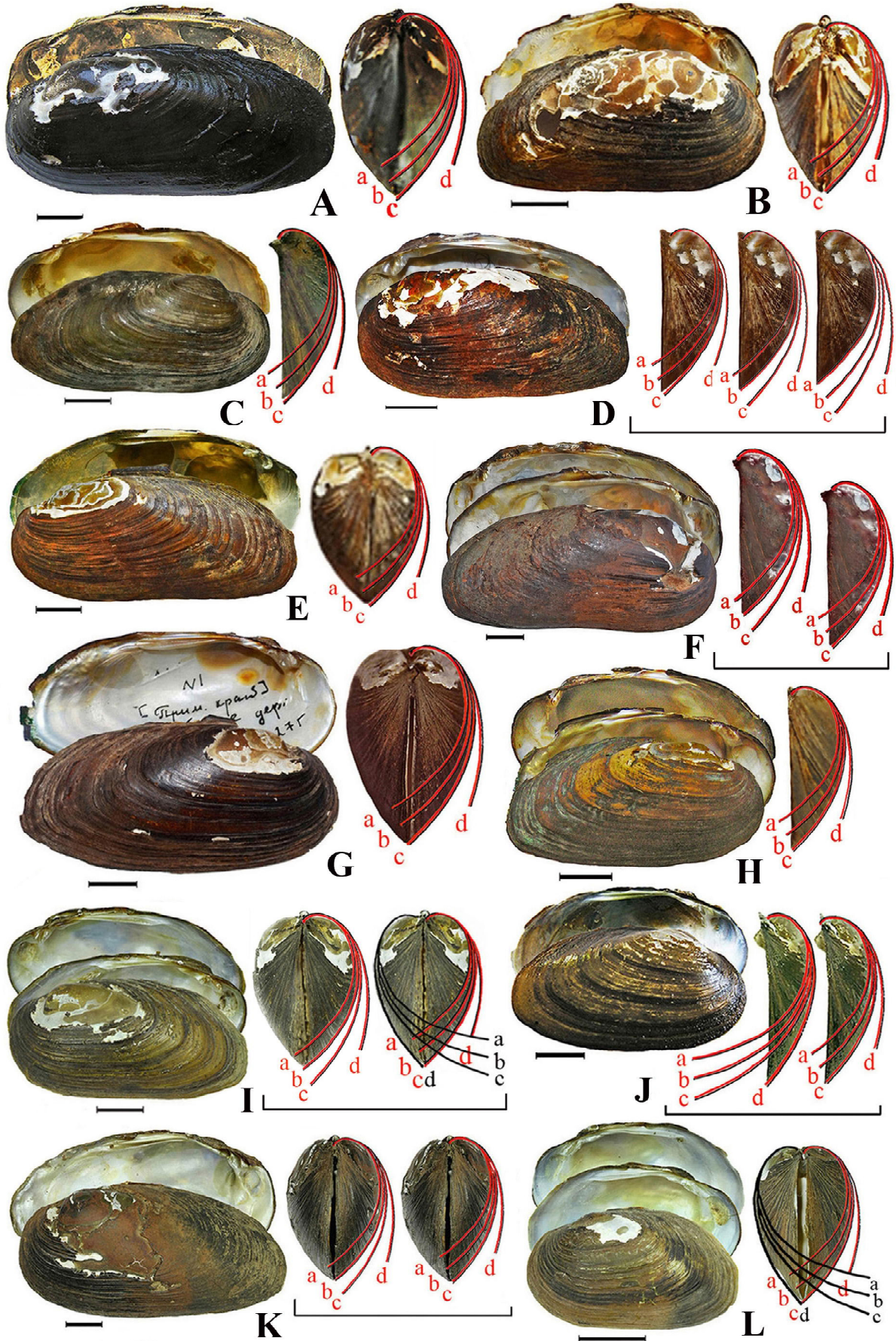
Unio mongolicus from the Gorbitza stream found by Middendorff in 1851 is shown in Fig. 2A. It has shell dimensions: length (76 mm), height at the ligament (35 mm), height at the umbo (32 mm) and width (24 mm) according to Middendorff [1851: 278]. But, a shell represented by Middendorff [Middendorff 1851: 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. mon-*

golica 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 «d» 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. Comparative 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 Comparative Species *Crassiana crassa* (Philipsson in Retzius, 1788), and *C. fuscula* (Rossmassler, 1836) (curves «5, 7») can also correspond to curve «4» – *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).



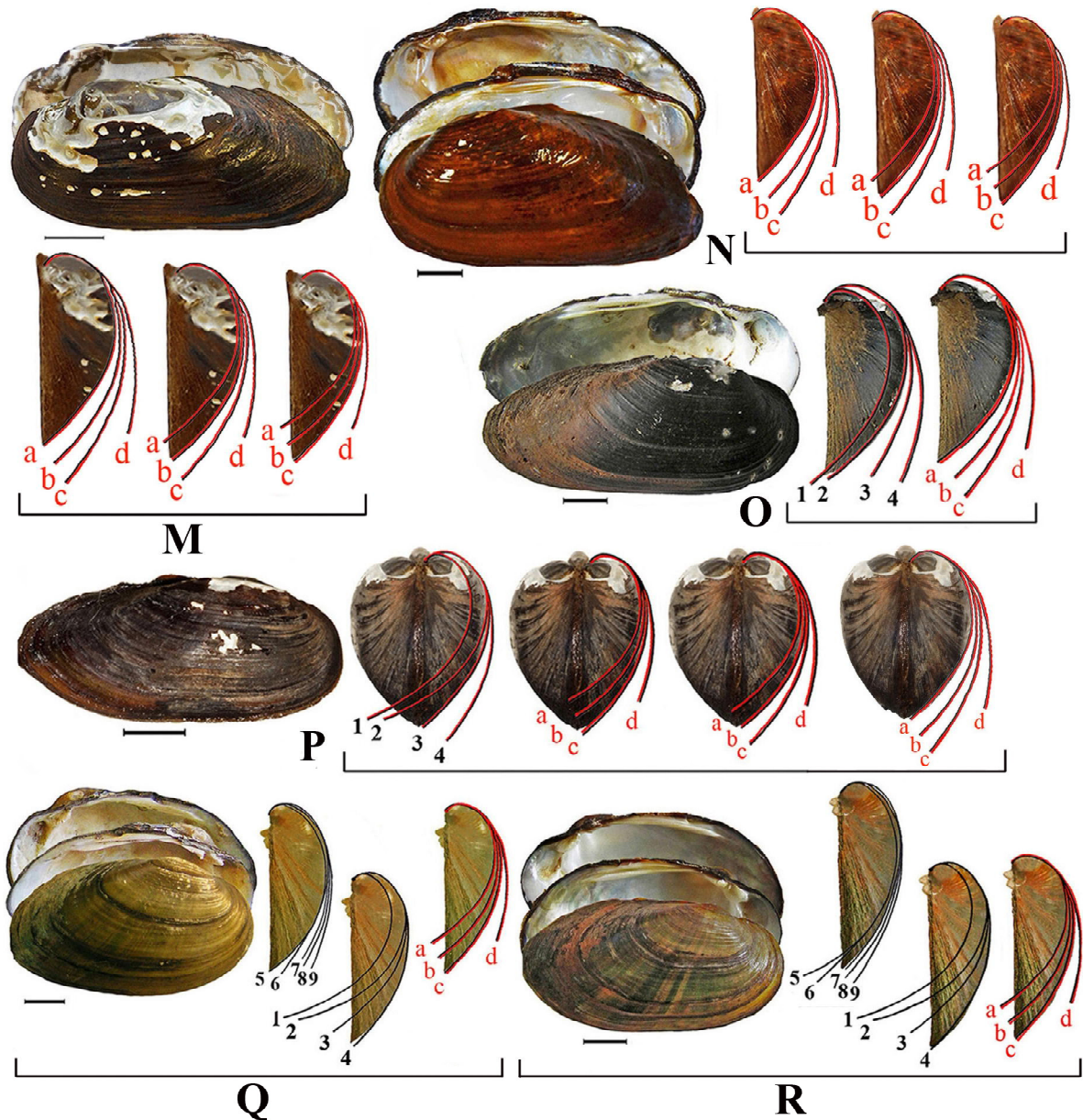


FIG. 3. Shell shape and contour section of MCVS. **A.** *Middendorffinaia mongolica* from Gorbitza stream. **B.** *M. mongolica* from Ingoda River. **C.** *M. ussuriensis* from Bolshaya Ussurka River (ZISP). **D.** *M. ussuriensis* from Ussury River (ZISP). **E.** *M. mongolica* from Ussury River (ZISP). **F.** *M. mongolica* from Ussury River (ZISP). **G.** *M. mongolica* from Daubikhe River (ZISP). **H.** *M. mongolica* from Arga River (ZISP). **I.** *M. mongolica* from Komarovka River. **J.** *M. alimovi* from Shilka River. **K, L.** *M. mongolica* and *M. alimovi* from Gladkaya River. **M.** *M. ochotica* (*M. arsenievi*) from Pashina River (ZISP). **N.** *M. mongolica* from Sungacha River (ZISP). **O.** *Nodularia douglasiae* from Amur River. **P.** *N. douglasiae* from Ussury River Basin. **Q, R.** *U. crassus* from Desna River, Ukraine (after Klishko *et al.* [2017]). Curves of MCVS for *Middendorffinaia*: **a.** *M. ochotica*, **b.** *M. ussuriensis*, **c.** *M. mongolica*, **d.** *M. alimovi*; for *Nodularia*: **1.** *N. flavoviridis* Haas, 1910, **2.** *N. amurensis*, **3.** *N. shrenskii*, **4.** *N. middendorffi* (after Bogatov [2012]); for *Unio crassus*: **5-9.** Comparative species of *Crassiana* (*Bataviana*) (after Starobogatov *et al.* [2004]). Scale bars = 1 cm.

РИС. 3. Форма раковины и контур сечения MCVS. **A.** *Middendorffinaia mongolica* из руч. Горбица. **B.** *M. mongolica* из р. Ингода. **C.** *M. ussuriensis* from р. Большая Уссурка (ZISP). **D.** *M. ussuriensis* из р. Чирка (ZISP). **E.** *M. mongolica* из р. Усури (ZISP). **F.** *M. mongolica* из р. Усури (ZISP). **G.** *M. mongolica* из р. Даубихе (ZISP). **H.** *M. mongolica* из р. Арга (ZISP). **I.** *M. mongolica* из р. Комаровка. **J.** *M. alimovi* из р. Шилка. **K, L.** *M. mongolica* и *M. alimovi* из р. Гладкая. **M.** *M. arsenievi* (*M. ochotica*) из р. Пашина (ZISP). **N.** *N. douglasiae* из р. Сунгача (ZISP). Амур. **O, P.** *N. douglasiae* из р. Амур и Лучегорского водохранилища, бассейн р. Усури. **Q, R.** *U. crassus* из р. Десна, Украина (данные Klishko *et al.* [2017]). Кривые MCVS для *Middendorffinaia*: **a.** *M. ochotica*, **b.** *M. ussuriensis*, **c.** *M. mongolica*, **d.** *M. alimovi*; для *Nodularia*: **1.** *N. flavoviridis* Хаас, 1910, **2.** *N. amurensis*, **3.** *N. shrenskii*, **4.** *N. middendorffi* (данные Bogatov [2012]); для *Unio crassus*: **5-9.** Компаративные виды *Crassiana* (*Bataviana*) (данные Starobogatov *et al.* [2004]). Масштаб = 1 см.

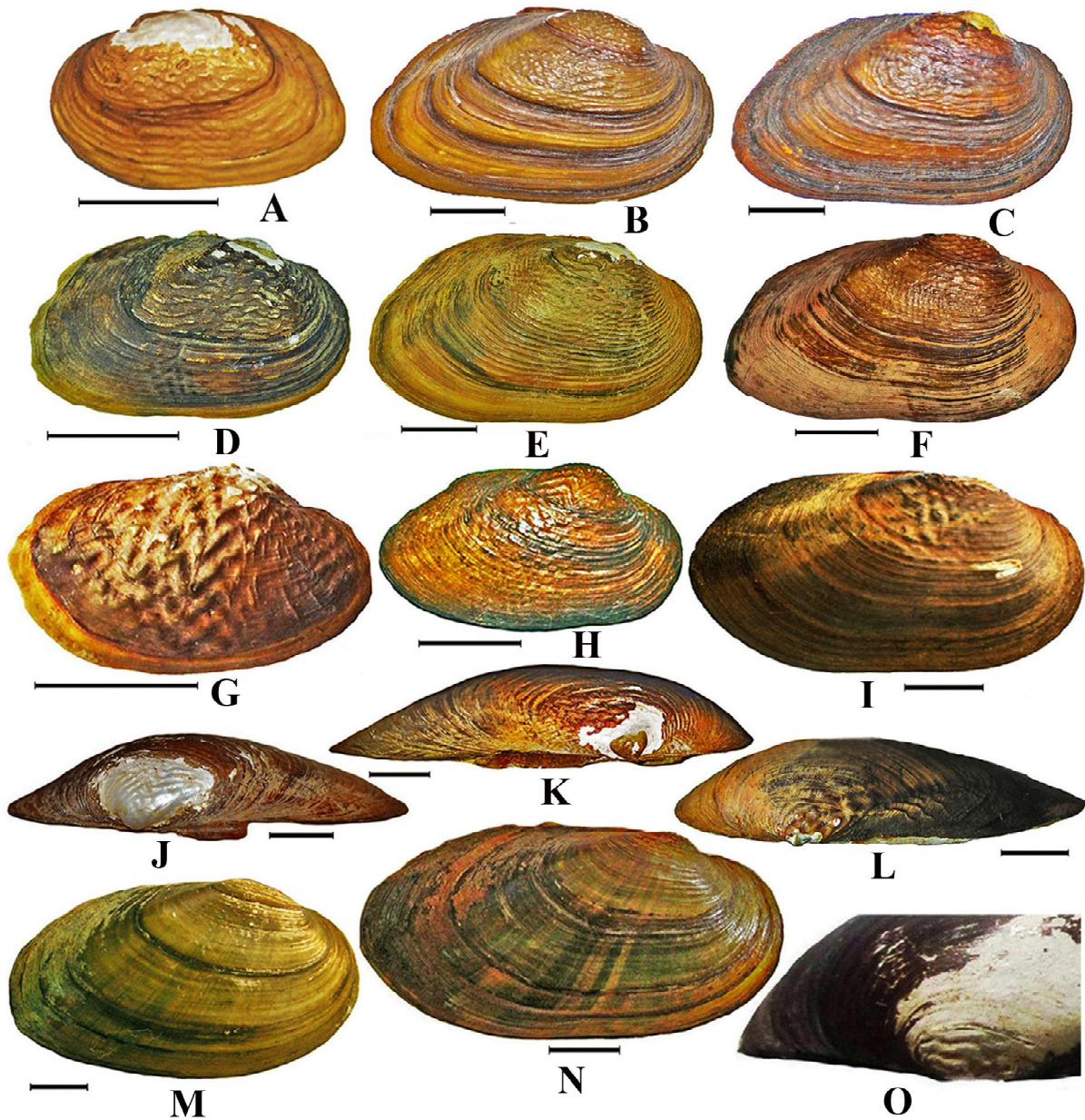


FIG. 4. Sculpture of umbo and shell. A-F. *Middendorffinaia* specimens. G-L. *Nodularia douglasiae*. M-O. *Unio crassus*. Scale bars = 1 cm.

РИС. 4. Скульптура макушки и раковины. A-F. Образцы *Middendorffinaia*. G-L. *Nodularia douglasiae*. M-O. *Unio crassus*. Масштаб = 1 см.

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

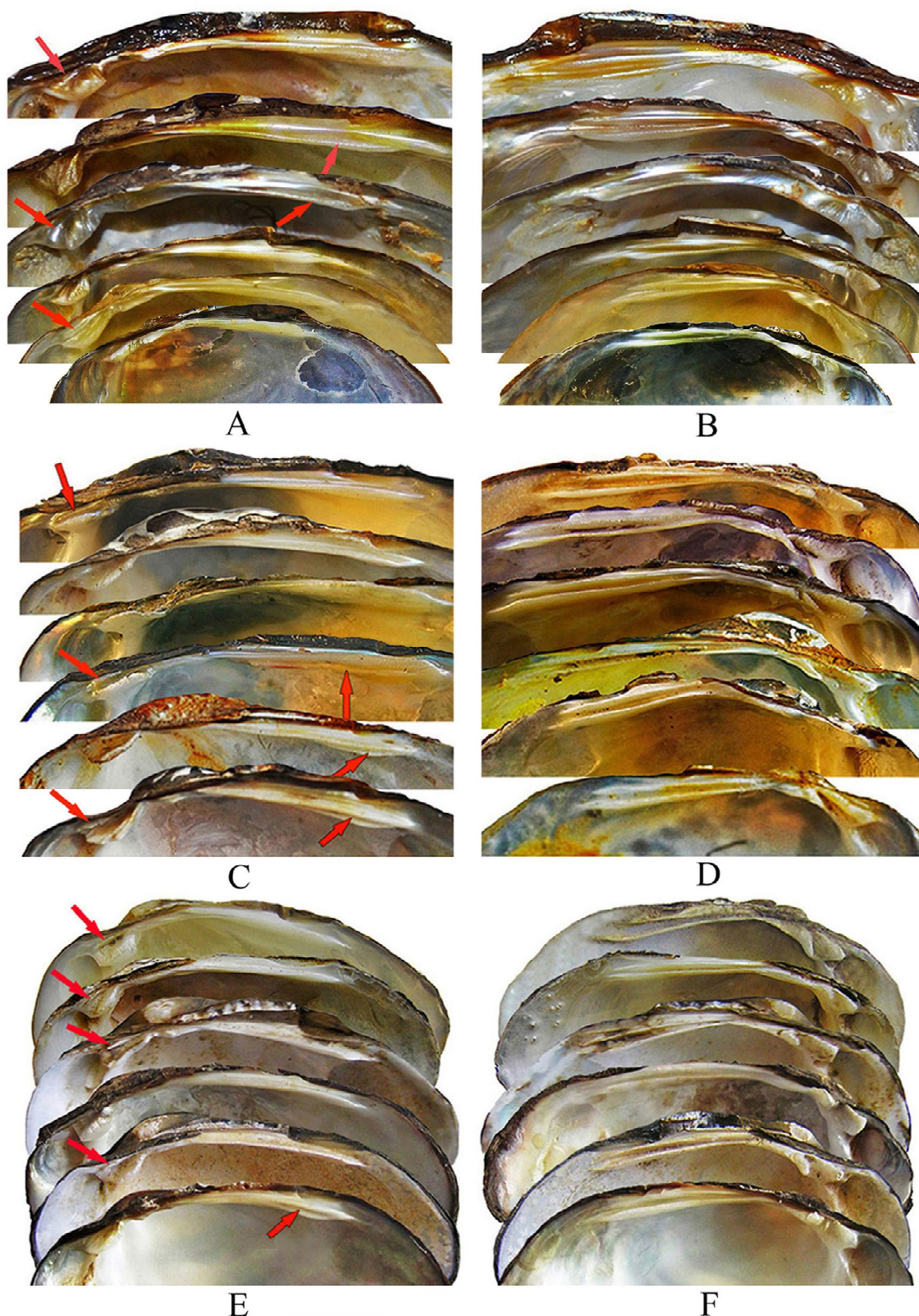


FIG. 5. Morphology of pseudocardinal and lateral teeth. **A, B.** Right and left valves of *Middendorffinaia mongolica*. **C, D.** The same of *Nodularia douglasiae* and **E, F.** *Unio crassus*. (Not scaled). Pointer descending indicates presence of a supplementary rudimentary tooth above pseudocardinal 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. **A, B.** Правая и левая створки *Middendorffinaia mongolica*. **C, D.** То же *Nodularia douglasiae* и **E, F.** *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.

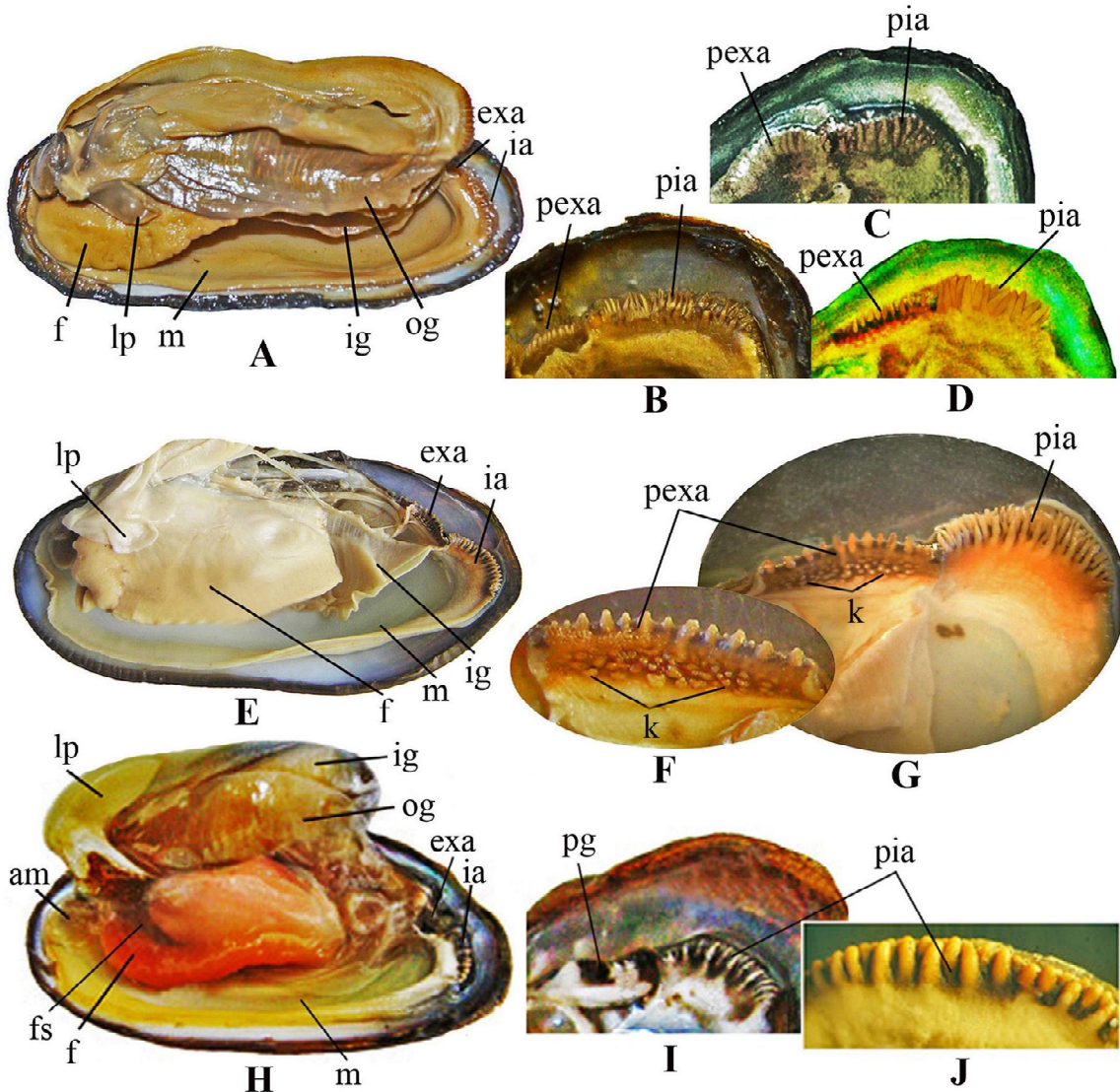


FIG. 6. General view and features of soft body. **A-D.** *Middendorffinaia mongolica*. **E-G.** *Nodularia douglasiae*. **H-J.** *Unio crassus*. Papillae of incurrent and excurrent apertures. **B.** *M. mongolica*. **C.** *M. ussuriensis*. **D.** *M. alimovi*; **F, G.** *N. douglasiae*. **I, J.** *U. crassus*. Figure symbols see Material and Methods.

РИС. 6. Общий вид и особенности мягкого тела. **A-D.** *Middendorffinaia mongolica*. **E-G.** *Nodularia douglasiae*. **H-J.** *Unio crassus*. Папиллы вводного и выводного отверстий. **B.** *M. mongolica*. **C.** *M. ussuriensis*. **D.** *M. alimovi*. **F, G.** *N. douglasiae*. **I, J.** *U. crassus*. Обозначения см. Материал и методы.

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, speci-

mens 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*

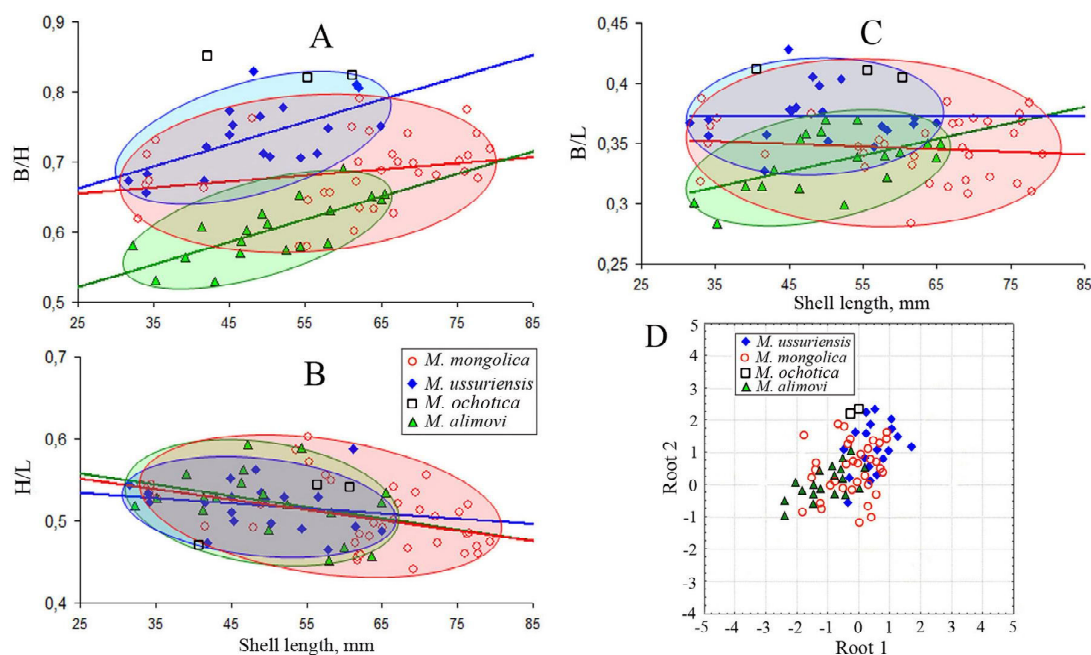


FIG. 7. Variation and trends of morphometric shell characters. A-C. Shell indexes B/H, H/L and B/L in *Middendorffinaia* (s. s.) in relation to shell length. D. Disposition in space of the first two roots of the discriminant analysis of comparative *Middendorffinaia* species.

РИС. 7. Варьирование и тренды морфометрических характеристик раковины. А-С. Индексы раковины B/H, H/L and B/L у *Middendorffinaia* (s. s.) относительно длины раковины. D. Расположение компаративных видов *Middendorffinaia* в пространстве первых двух корней дискриминантного анализа.

(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 λ (Wilk's lambda) show reliable absence of morphological discreteness among all Comparative Species of *Middendorffinaia* (s.s.) ($\lambda = 0.776$, $n = 73$, $F = 70.2$, $p < 0.0005$).

The same pattern was shown with nine Comparative 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. 8 B, 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. *sinuolata* (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

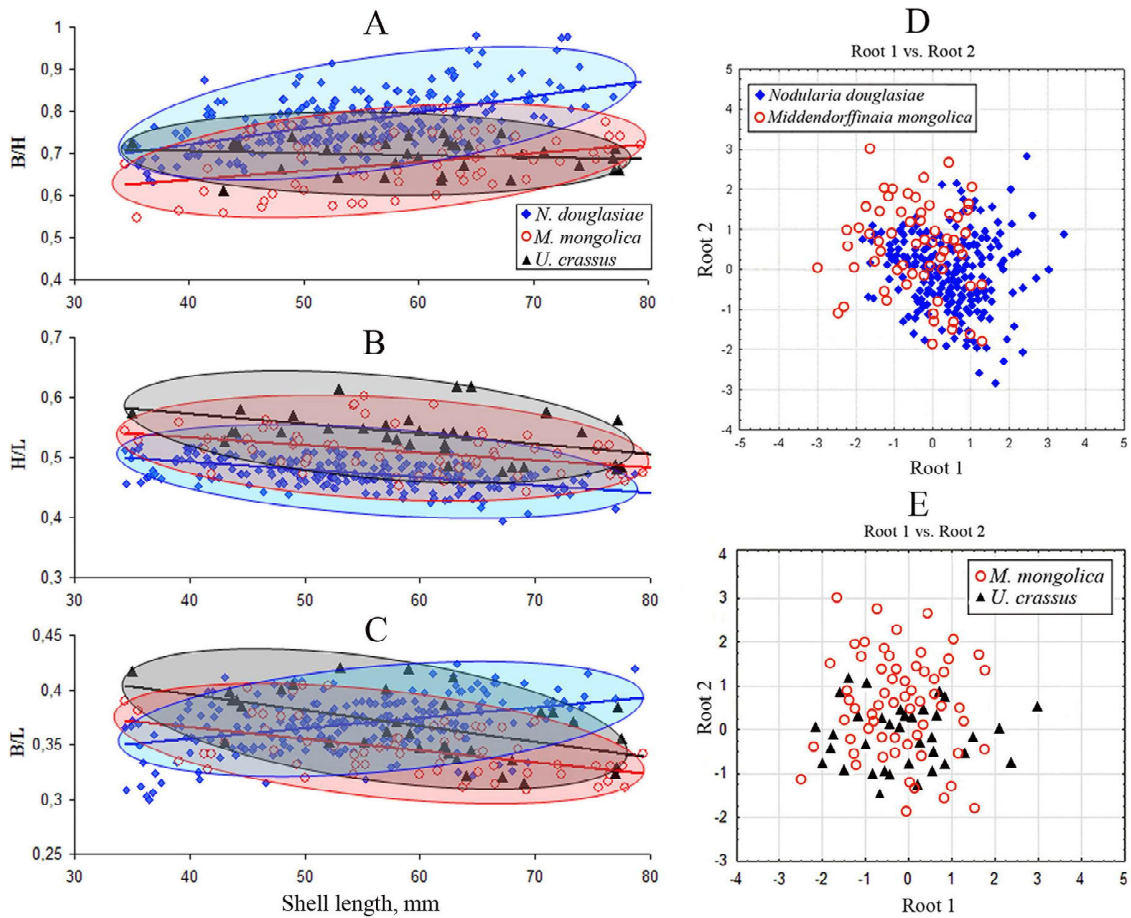


FIG. 8. Variation and trends of morphometric characters. A-C. Shell indexes B/H, H/L and B/L in samples of polymorphic species *N. douglasiae*, *M. mongolica* and *U. crassus*. D-E. Distribution of these patterns in space of the first two roots of the discriminant analysis.

РИС. 8. Варьирование и тренды морфометрических характеристик. А-С. Индексы раковины В/Н, Н/Л и В/Л в выборках полиморфных видов *N. douglasiae*, *M. mongolica* и *U. crassus*. D-E. Расположение этих выборок в пространстве первых двух корней дискриминантного анализа.

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).

Табл. 2. Матрица генетических различий (некорректированная *p*-дистанция) между видами *Nodularia* и *M. mongolica* (см. Рис. 9), рассчитанных по фрагменту гена COI. СЛЕВА: средняя внутривидовая генетическая дистанция (первый столбец) и стандартное отклонение этого показателя (второй столбец). СПРАВА: средняя межвидовая генетическая дистанция (ниже диагонали) и стандартное отклонение этого показателя (выше диагонали).

Within species			Among species			
Species			<i>N. douglasiae</i>	<i>N. cf. sinuolata</i>	<i>Nodularia</i> sp.	<i>M. mongolica</i>
<i>N. douglasiae</i>	0.017	0.003		0.012	0.010	0.013
<i>N. cf. sinuolata</i>	-	-	0.087		0.011	0.013
<i>Nodularia</i> sp.	-	-	0.076	0.080		0.013
<i>M. mongolica</i>	0.004	0.001	0.109	0.107	0.108	

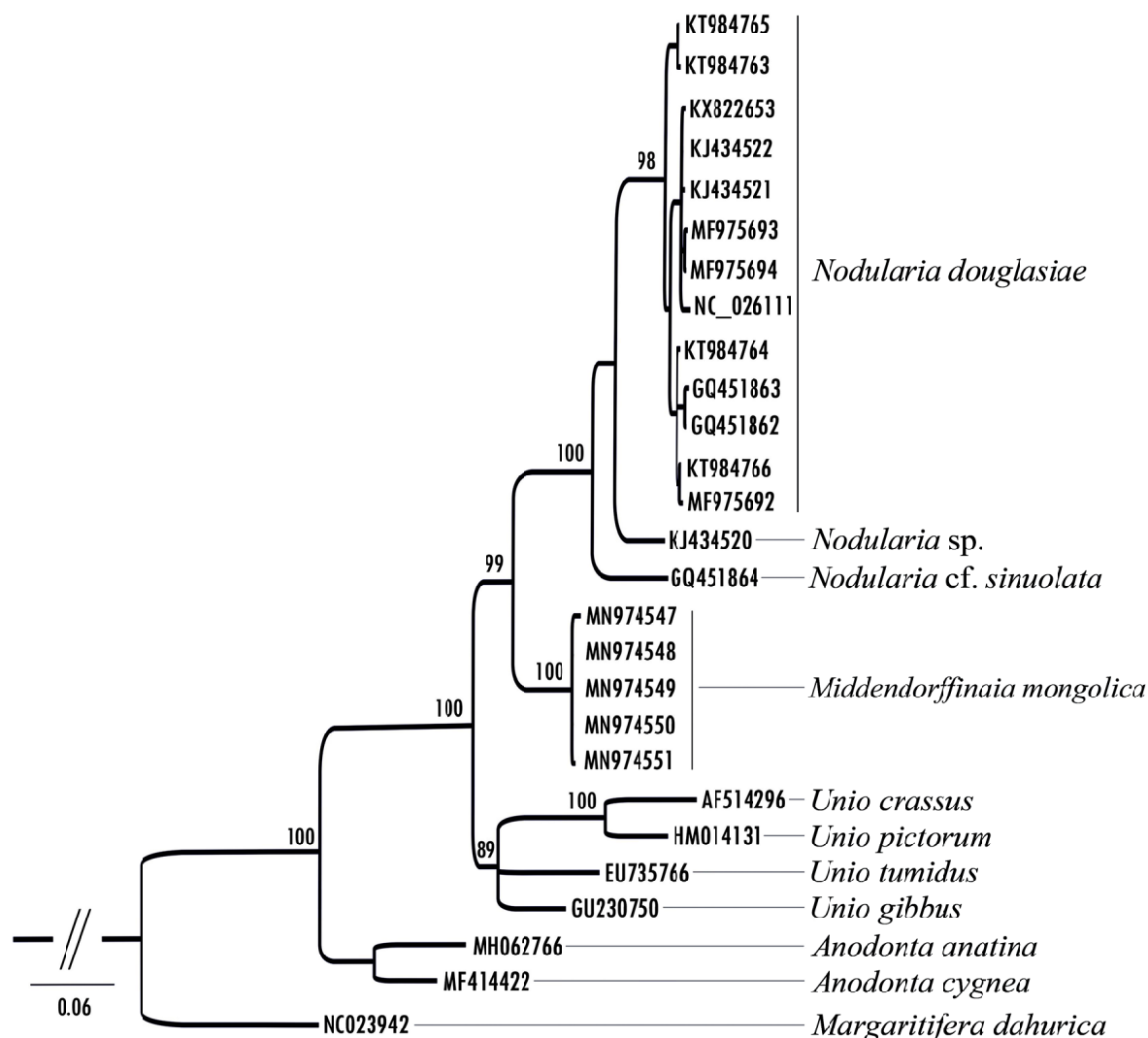


FIG. 9. Phylogenetic tree obtained by Bayesian Inference analysis, using mtDNA fragments (COI). Support values are given as Bayesian posterior probability above nodes, except for those within below 60 and within species clades, which have been omitted for clarity. Available sequences downloaded from GenBank and new sequences codes refer to Table 1.

РИС. 9. Филогенетическое дерево, рассчитанное методом Байесовского анализа на основе фрагментов митохондриального гена COI. Байесовские постериорные вероятности показаны над узлами (вероятности ниже 60% для межвидовых узлов и все значения вероятностей для внутривидовых узлов исключены для более четкого отображения модели). Коды сиквенсов, полученных из Генбанка, а также новых сиквенсов, представлены в Табл. 1.

specimens sequenced for the present study (Fig. 9). All species are supported by its high level of genetic divergence (mean COI uncorrected p -distance > 0.8) (Table 2).

According to the molecular analysis, all specimens of Comparative 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.

Margaritana mongolica – Zhadin, 1938: 115.
Unio douglasiae var. *mongolicus* – Zhadin, 1952: 298.
Unio crassus mongolicus – Haas, 1969: 59; Graf, 2007: 85.
Nodularia mongolica – Graf, Cummings: <http://mussel-project.uwsp.edu/2016>. [Accessed on April 2018].
Middendorffinaia (M.) arsenievi 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-z*).
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 Khabarovsk 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. amurensis*, *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 middendorffi* (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, pseudo-cardinal 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 Palaearctic 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 (Bivalvia: Unionidae) из типового местонахождения в Забайкалье и история его таксономии

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РЕЗЮМЕ. Представление о родовой принадлежности вида *Unio mongolicus* (Bivalvia: Unionidae), опи-

санного Миддендорфом в 1851 г из руч. Горбица 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 мтДНК 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* подтвердила 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*.

Таксономические 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.**

