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An unexpected record of *Moina* Baird, 1850 (Crustacea: Cladocera) in Pleistocene deposits of North-Eastern Eurasia

Неожиданная находка *Moina* Baird, 1850 (Crustacea: Cladocera) в плейстоценовых отложениях Северо-Восточной Евразии

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КЛЮЧЕВЫЕ СЛОВА: ветвистоусые ракообразные, мамонтовая фауна, Республика Саха, Якутия, Берингия, палеоэкология, зоогеография.

ABSTRACT. We found several ephippia belonging to the genus *Moina* Baird, 1850 (Branchiopoda: Cladocera: Moinidae) in two Pleistocene paleo-sites located in the northern portion of Sakha (Yakutia) Republic, Eastern Siberia, Russia. Based on morphological data, we identified all inspected ephippia as *Moina* cf. *macrocopa* (Straus, 1820) due to presence of a specific sculpture: flattened cells at the ephippium perimeter and fine meshes on the egg chambers. In the Asian part of Russia, Central Yakutia is the north-easternmost region where moinids were found to date, but we here demonstrate that, during the Pleistocene, they occurred in more northern and eastern territories. Together with some other branchiopods, most moinids can be considered as a group associated with the arid shallow water bodies. This type of water bodies is completely absent in the northern Yakutia now. Therefore, our records of fossil *Moina* in northern Yakutia fit well with the earlier proposed concept of the existence of none-analogous communities of branchiopod crustaceans in North-Eastern Eurasia during the Late Pleistocene.

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РЕЗЮМЕ. Мы обнаружили несколько эфиппиумов, принадлежащих роду *Moina* Baird, 1850 (Branchiopoda: Cladocera: Moinidae), в двух местонахождениях плейстоценового возраста, расположенных в северной части Республики Саха (Якутия), Восточная Сибирь, РФ. По морфологическим данным все изученные эфиппиумы определены нами как *Moina* cf. *macrocopa* (Straus, 1820) на основе специфической скульптуры: наличия уплощенных клеток по периметру эфиппиумов и рисунка в виде мелкой сеточки в зоне яйцевых камер. В азиатской части России самым северо-восточным регионом, где в настоящее время обнаружены моины, является центральная Якутия. Мы показали, что в плейстоцене они обитали в более

северных и более восточных регионах. Вместе с некоторыми другими бранхиоподами, большинство моин могут рассматриваться как группа, связанная со степными мелководными водоемами. В настоящее время этот тип водоемов полностью отсутствует на севере Якутии. Таким образом, наши находки ископаемых *Moina* в северной Якутии хорошо вписываются в концепцию существования безаналоговых сообществ жаброноших ракообразных в северо-восточной части Евразии в позднем плейстоцене.

Introduction

Nowadays, the global environmental change on Earth is one of the issues most widely discussed by scientists and the general public [Moss *et al.*, 2010; Garcia *et al.*, 2014]. Based on instrumental meteorological observations, we can obtain reliable data on climatic changes over the last 150–200 years [Brönnimann *et al.*, 2019]. However, even for such recent period of time, the instrumental meteorological data are incomplete or lacking for some areas, and information on other environmental factors several centuries ago is completely absent. In this situation, an analysis of plant and animal remains in lake bottom sediments in combination with some other methods allows to trace the environment (i.e. climate) changes during last two centuries quite accurately [Smol *et al.*, 2005; Smol, Douglas, 2007]. Paleoecology offers great opportunities for environmental reconstructions of more ancient periods. Paleo-soils and lake sediments, containing remains of terrestrial and aquatic biota, serve as an important source of information about composition and structure of ancient communities, which reflect the paleoenvironment.

In recent decades, many studies of the Late Pleistocene – Early Holocene terrestrial communities of Sakha (Yakutia) Republic (Eastern Siberia, Russia) have been carried out [Bocherens *et al.*, 1996; Kienast *et al.*, 2008; Ashastina *et al.*, 2018]. Zoological studies are mainly focused on the "Mammoth fauna" [Sher *et al.*, 2005; Boeskorov, 2020; Plotnikov, Mashchenko, 2020]. Significantly less attention was paid to invertebrates (except the insects), especially to the inhabitants of continental water bodies [Berman *et al.*, 2011; Kuzmina *et al.*, 2011; Frolova *et al.*, 2017]. Paleoecologists often overlook invertebrates due to their small size and poor preservation. However, some groups attract the attention of researchers, first of all, the water fleas (Crustacea: Branchiopoda: Cladocera). Cladoceran remains were found in the wool of mammoths [Kotov *et al.*, 2018], their feces [Kirillova *et al.*, 2016] and even in the intestine [Kosintsev *et al.*, 2010; Van Geel *et al.*, 2011] and extracted from many permafrost sections [Frolova *et al.*, 2017; Kotov *et al.*, 2020]. The family Daphniidae Straus, 1820 is the most abundant and relatively well studied group there [Frolova *et al.*, 2017; Kotov *et al.*, 2020; Neretina *et al.*, 2020a]. In contrast, the remains of Moinidae Goulden, 1968 are much rarer in Pleistocene sediments [Zharov *et al.*, 2020], although they were found in much older paleo-localities [Goulden, 1968; Van Damme, Kotov, 2016].

We found specimens belonging to the genus *Moina* Baird, 1850 in two samples from Pleistocene paleolocalities in the northern portion of the Republik of Sakha (Yakutia), namely, in Verkhoyansk and Abyiski districts. Since this genus does not occur in northeastern Russia nowadays and the distribution range of recent Moinidae is located further south [Andreeva *et al.*, 2023], our records are of the interest for reconstructions of non-analogous inland water communities existing in Beringia during the Late Pleistocene [Neretina *et al.*, 2020a]. The aim of this study is to describe Pleistocene moinid ephippia and discuss the conditions under which these cladocerans lived.

Materials and methods

The Batagay outcrop (67.578° N, 134.763° E) is located 10 km southeast of Batagay, the municipal center of the Verkhoyansk District (Fig. 1A). The site is located at a distance of 2.3 km from the left bank of the Batagay River, a tributary of the Yana River [Ashastina *et al.*, 2018]. Samples were taken by F. Kienast during field works in summer of 2014 [Ashastina *et al.*, 2018] and dried in the field directly after collection. The original samples are kept at the Senckenberg Research Institute and Natural History Museum. The whole Batagay section was described in several previous publications [Ashastina *et al.*, 2017, 2018; Opel *et al.*, 2019; Vasil'chuk, Vasil'chuk, 2019; Courtin *et al.*, 2022; Jongejans *et al.*, 2022; Kizyakov *et al.*, 2023]. According to absolute dating and stratigraphy, the Batagay permafrost sediments have been deposited since the late Middle Pleistocene and experienced erosional events during the Late Pleistocene and the Holocene [Ashastina *et al.*, 2018; Vasil'chuk, Vasil'chuk, 2019]. According to the recent data, meadow steppes occurred in the Yana Highlands from MIS 6 to MIS 2 and demonstrated a remarkable environmental stability. The proportion of meadow steppe vegetation merely shifted in response to the respectively prevailing climatic conditions. Their persistence indicates low precipitation and a relatively warm growing season throughout and beyond the late Pleistocene [Ashastina *et al.*, 2018]. The ephippia of *Moina* were found by F. Kienast in the samples 30.6/N/6/38.5 and 30.6/N/5/37.5 (see Table 1) in the Unit IIa according to Ashastina *et al.* [2018] belonging to MIS4 phase of the Late Pleistocene.

Another series of specimens was retrieved from the wool of a woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach, 1799). The carcass was found in August of 2020 by A. Savvin on the bank of the right tributary of the Terekhtyakh River (the Yana basin) in the Abyiski district (68.588° N, 147.120° E) (Fig. 1A). The carcass was buried in loess-like loam and vein ice at a depth of 3–4 meters on the slope of a ravine overgrown with bushes (Fig. 1B). The rhinoceros was found on the "adit" (artificial formation in the permafrost) top, after a collapse of the upper layers of soil (Fig. 1C). In the field, the carcass was cleaned from the surrounding soil by a water pumping. The subsequent photographing and detailed description of the carcass (Fig. 1D) was done in the laboratory. The carcass itself is kept at the Depositary of the Academy of Sciences of Sakha (Yakutia) Republic (city of Yakutsk). Details of this finding will be published in another paper.

The radiocarbon dating of the wool was carried out at the Center for Applied Isotope Studies, University of Georgia, USA: 36543–36938 years BP (UGAMS 65491); calibration was performed in CALIB REV8.2 packet [Stuiver, Reimer, 1993] using the calibration dataset of Reimer *et al.* [2020]. Therefore, the wooly rhyno carcass belongs to MIS3.

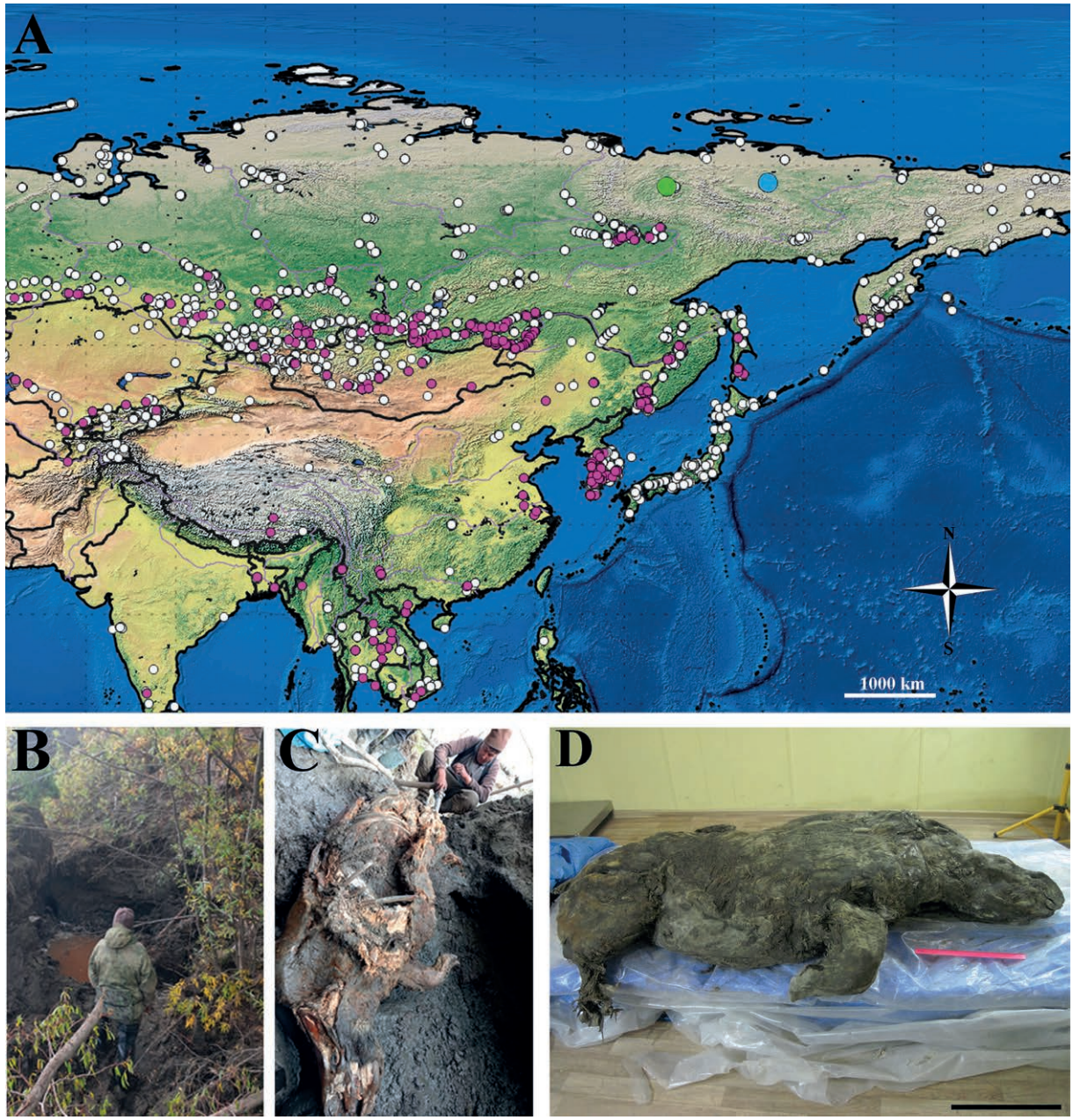

Fig. 1. Localities where recent or Pleistocene moinids were found. A — a map of Russia and some adjacent countries with recent localities studied by our group. The white circles illustrate samples in which moinids were not found; the pink circles show samples in which different recent species of *Moina* and fossil records of Moinidae were found; large green circle — Batagay outcrop; large blue circle — Terekhtyakh River. B — the locality where the carcass of woolly rhinoceros was found; C — carcass of the woolly rhinoceros in the field, immediately after extraction from the permafrost; D — carcass of the woolly rhinoceros in the laboratory (scale bar: 40 cm).

Рис. 1. Местонахождения, в которых были найдены современные и плейстоценовые моиниды. А — карта России и некоторых сопредельных стран с точками отбора современных проб. Белыми кружками показаны образцы, в которых моиниды не обнаружены; розовыми кружками показаны образцы, в которых были найдены различные виды *Moina*; большой зеленый кружок — обнажение Батагай; большой синий кружок — река Терехтях. В — место, где была найдена туша шерстистого носорога; С — туша шерстистого носорога в полевых условиях, сразу после извлечения из мерзлоты; D — туша шерстистого носорога в лаборатории (масштабная линейка: 40 см).

Frequently, remains in the wool of carcasses are younger than the mammals themselves [Kotov *et al.*, 2020], but the chance that such remains also belong to MIS3 is very high. Different bones were found in the same region of the Terekhtyakh River: woolly mammoth, Lena horse, wolf, brown bear, reindeer, steppe bison and several birds [Boeskorov *et al.*, 2021]. Several carcasses from the closest vicinity of the rhinoceros locality were previously dated, e.g. two lion cubs (43448±389 and 27962±109 years BP, see Chernova *et al.* [2020]) and a bird (42600±1100 years BP, see Boeskorov *et al.* [2021]) were found about 2 km from this locality; a wolf (28319±110 years BP, see Plotnikov *et al.* [2022]) was found at about 3 km from it. All these mammals are also of MIS3 age, and most sediments in the region belong to MIS3 phase of the Late Pleistocene.

Table 1. Information on fossil specimens investigated here.
Таблица 1. Информация об исследованных особях.

Original number of the sample in the expedition	Working number of samples	Number of ephippia, belonging to *Moina*	Link to the figure in this publication	Size (length / height), mm
30.6/N/6/38.5	AAK-2018-085	2	2A, B	0.59 / 0.39; 0.61 / 0.38
30.6/N/5/37.5	AAK-2018-085	2		
	AAK 2022-074	1		
	AAK 2022-077	1	2C	0.67 / 0.42
	AAK 2022-081	1	2D	0.62 / 0.43
	AAK 2022-082	1	2E	0.63 / 0.45
	AAK 2022-083	1	2F	0.58 / 0.38

Table 2. Remains of other crustaceans found together with *Moina* in the Batagay outcrop and wool of Abyiski rhinoceros.
Таблица 2. Остатки прочих ракообразных, найденные вместе с эфиппиумами *Moina* на обнажении Батагай и в шерсти Абыйского носорога.

Group	Batagay outcrop	Wool of Abyiski rhinoceros
Daphnia (Daphnia) (ephippia)	+	+
Eurycercus sp. (head shield)		+
Bosmina sp. (valves)		+
Ceriodaphnia sp. (ephippium)		+
Chydoridae gen. sp. (ephippia)		+
Simocephalus sp. (ephippia)		+
Ostracoda		+

Table 3. Information on ephippia of recent moinids investigated in the frame of current study.
Таблица 3. Информация о эфиппиумах современных моинид, исследованных в ходе выполнения данной работы.

Number of the sample in the personal collection of A.A. Kotov	Morphological identification	Locality	Comments
AAK-1999-030	*Moina macrocopa* (Straus, 1820)	A Pool near the forest road in vicinity of Maliy Utrish, Krasnodar region, European part of Russia, coll. 15.05.1995 by A.O. Bienkowski, M.J. Orlova-Bienkowskaja	Corresponds to *M. macrocopa* s.l. published by Montoliu-Elena *et al*. [2019]
AAK-M-1329	*Moina macrocopa* (Straus, 1820)	A pool near the road in the Avacha River delta (53.070° N, 158.536° E), Kamchatka, Asian part of Russia, coll. 11.08.2009 by A.A. Kotov	Corresponds to *M. macrocopa* s.l. according to genetic data (individuals from this sample were studied by Bekker *et al*. [2016]
AAK-M-3118	*Moina* cf. *macrocopa* (Straus, 1820)	Zun-Torey Lake (50.225° N, 115.642° E), Zabaikalsky Territory, Asian part of Russia, coll. 25.08.2015 by A.A. Kotov	Corresponds to genetic Clade L of *M. macrocopa* s.l. described by Bekker *et al*. [2016].
AAK-2017-016	*Moina kaszabi* Forró, 1988	Boor Nuur (45.404° N, 112.996° E), Sukhbaatar, Mongolia, coll. 31.08.2006 by M. Alonso	Near type locality of this species
NNS-2002-102	*Moina belli* Gurney, 1904	Mtubatuba (S 28.367°, E 32.193°), KwaZulu-Natal, the Republic of South Africa, coll. 25.10.1994 by K. Martens	Near type locality of this species

For analysis of the rhinoceros wool content, we selected wool at several body regions, dried and investigated it in the laboratory. The wool contained dispersed soil, detritus and different fossil remains. The content of wool was shaken out on a white piece of paper, and then all invertebrate fragments were picked from the bulk using a stereomicroscope Leica MZ75 (Leica Microsystems, Germany) using thin metal needles (see full list of investigated specimens in Table 1). Together with remains of *Moina*, we also recorded the presence of other crustaceans in the samples (Table 2).

All selected fossil ephippia of *Moina* were attached to stubs via conductive non-porous carbon tape, coated with gold in a S150A Sputter Coater (Edwards, UK), and studied under CamScan MV 2300 or MIRA 3 LMH scanning electron microscopes (SEM) (Tescan, Czech Republic).

For identification of fossil material, we also investigated ephippia of several recent *Moina* species under SEM (see Table 3). Recent material was prepared for SEM as described previously [Alonso *et al.*, 2019].

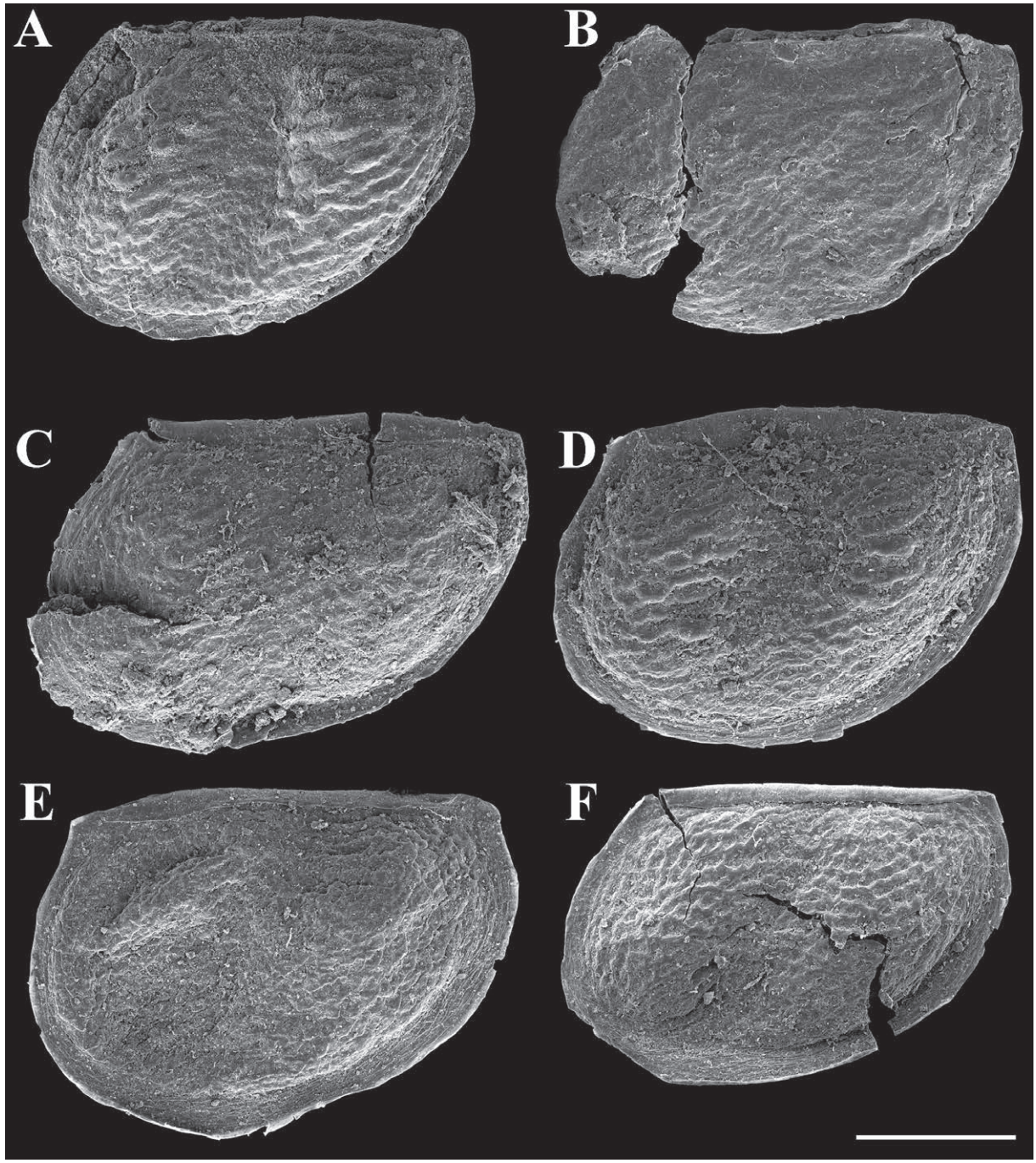

Fig. 2. Fossil ephippia of *Moina* from Sakha (Yakutia) Republic. A–B — general view of ephippia from the Batagay outcrop (AAK-2018-085); C–F — general view of ephippia from the wool of the Abyiski rhinoceros (AAK-2022-77, AAK-2022-81, AAK-2022-82, AAK-2022-83, respectively). Scale bar: 0.2 mm.

Рис. 2. Ископаемые эфиппиумы *Moina*, найденные в Республике Саха (Якутия). A–B — общий вид эфиппиума из обнажения Батагай (AAK-2018-085); C–F — общий вид эфиппиума из шерсти Абыйского носорога (AAK-2022-77, AAK-2022-81, AAK-2022-82, AAK-2022-83, соответственно). Масштабная линейка: 0,2 мм.

A single SEM stub with specimens from two localities is deposited at the Collection of Borissiak Palaeontological Institute of Russian Academy of Sciences, Moscow (accession number PIN 5918).

Analysis of distribution range of recent moinids and its comparison with fossil records of *Moina* in Verkhoyansk and Abyiski districts was carried out in QGIS for Windows 10 (x64) based on original data in the personal database of A.A. Kotov.

Abbreviations for collections in the text, tables and figures: AAK — Personal collection of A.A. Kotov; NNS — Personal collection of N.N. Smirnov. All collections are kept at A.N. Severtsov Institute of Ecology and Evolution now.

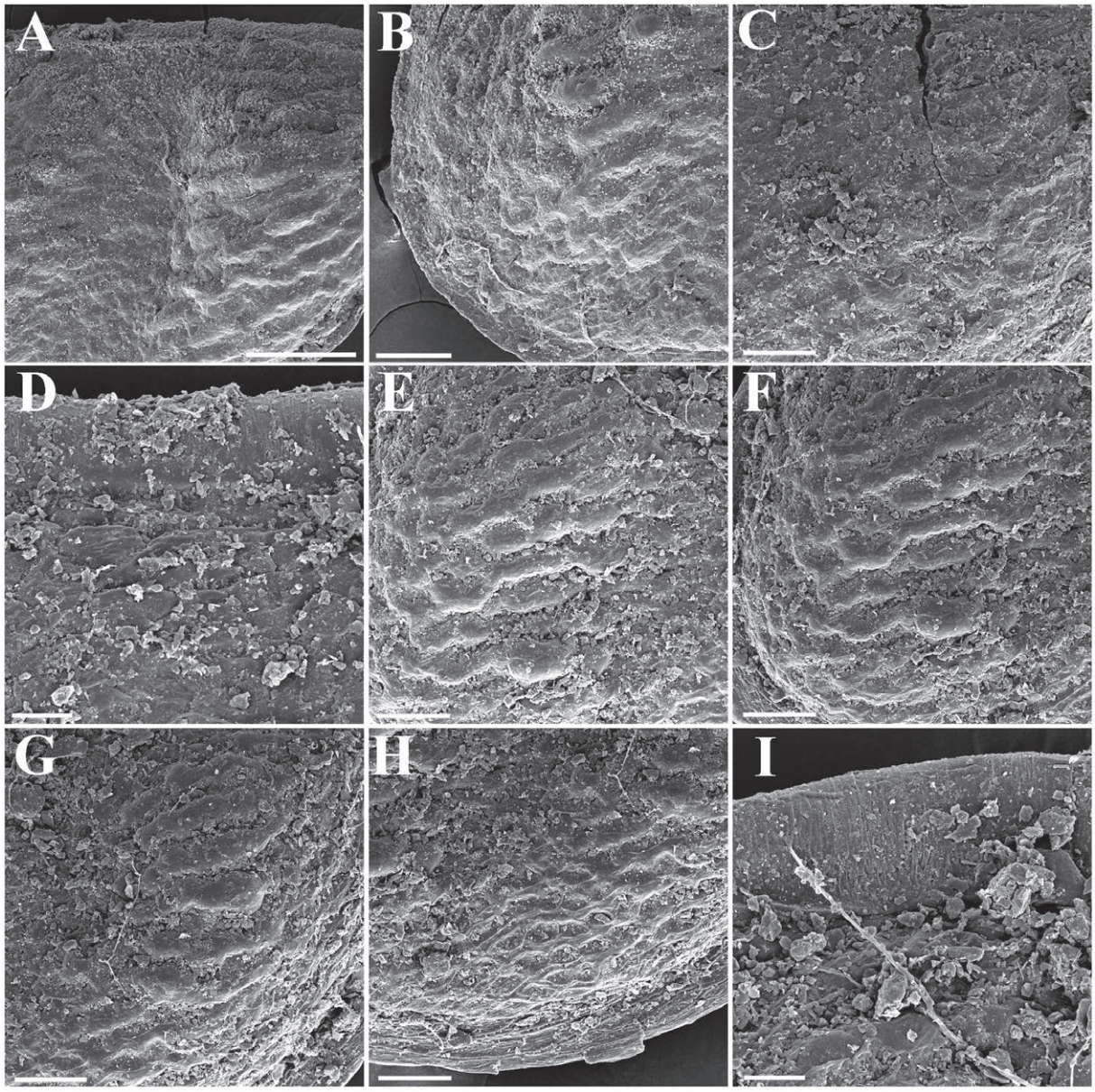

Fig. 3. Fragments of fossil *Moina* ephippia found in the Batagay outcrop (A–B) and from the wool of the Abyiski rhinoceros (C–I) under higher magnification. A–B — central and anterior portions of an ephippium from the sample AAK-2018-085; C–E — central, dorsal and anterior portions of an ephippium from AAK-2022-77; F–I — central, anterior, posteroventral and dorsal portions of an ephippium from AAK-2022-81. Scale bars: A — 0.1 mm; B–C, E–H — 0.05 mm; D, I — 0.02 mm.

Рис. 3. Детали ископаемых эфиппиумов *Moina*, найденных в обнажении Батагай (A–B) и в шерсти Абыйского носорога (C–I), при большом увеличении. A–B — центральная и передняя части эфиппиума из пробы AAK-2018-085; C–E — центральная, дорсальная и передняя части эфиппиума из AAK-2022-77; F–I — центральная, передняя, задне-вентральная и дорсальная части эфиппиума из AAK-2022-81. Масштабные линейки: A — 0,1 мм; B–C, E–H — 0,05 мм; D, I — 0,02 мм.

Results

Totally, we found nine well-preserved ephippia apparently belonging to the genus *Moina*. Eight of them were investigated under SEM. General views of six ephippia and fragments of their ornamentations are represented in Figs 2–4. All studied specimens from the Batagay outcrop and from the wool of the Abyiski rhinoceros have a relatively large size (up to 0.67 mm in length) (Table 1) and could be observed (as small brownish dots) even with the naked eye on white paper. All ephippia carry two eggs (Fig. 2A–F). Ornamentation of ephippia is relatively well preserved and represented by flattened hillocks or meshes and their combinations on the surface of egg chambers, anterior, ventral and posterior portions (Figs 3–4). The dorsal plate is covered by tiny wrinkles, perpendicular to the longitudinal axis of the ephippium. Despite the fact that each ephippium looks slightly different from others due to a different degree of ornamentation abrasion, we tend to believe that all the studied ephippia belonged to

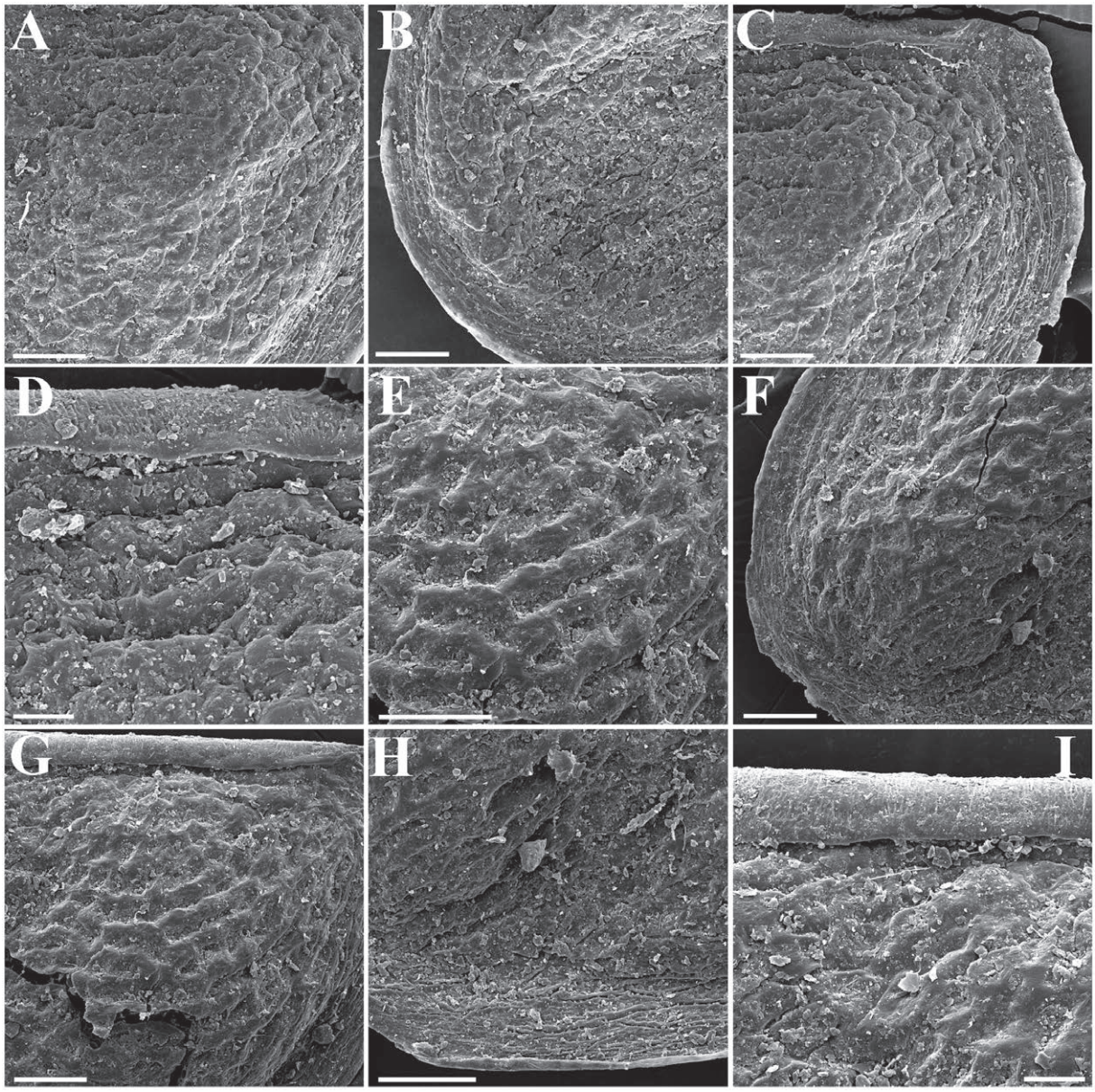

Fig. 4. Fragments of fossil *Moina* ephippia found in the wool of the Abyiski rhinoceros (A–I) under higher magnification. A–D — central, anterior, posterior and dorsal portions of an ephippium from AAK-2022-82; E–I — central, anterior, posterodorsal, ventral and dorsal portions of an ephippium from AAK-2022-83. Scale bars: A–C, E–H — 0.05 mm; D, I — 0.02 mm.

Рис. 4. Фрагменты ископаемых эфиппиумов *Moina*, найденных в шерсти Абыйского носорога (A-I), при большом увеличении. A–D — центральный, передний, задний и дорсальный фрагменты эфиппиума AAK-2022-82; E–I — центральный, передний, дорсо-постериорный, вентральный и дорсальный фрагменты эфиппия из образца AAK-2022-83. Масштабные линейки: A–C, E–H — 0,05 мм; D, I — 0,02 мм.

a single species. Studying ephippia of recent moinids (Table 2, Fig. 5), we came to the conclusion that fossil ephippia belong to the *Moina macrocopa* (Straus, 1820) species group. Visually, among investigated ephippia of recent species, *M.* cf. *macrocopa* from Zabaikalsky territory (Fig. 5C) is the taxon most similar to the fossil specimens. Its ephippium displays flattened cells at the perimeter and meshes on the egg chambers.

In addition to *Moina*, other crustaceans were found in two studied Pleistocene localities (Table 2). Most of them, including *Daphnia* (*Daphnia*), cannot be identified up to the species level. Some remains could have been brought from the surrounding rocks and recent water bodies in the process of natural erosion or during the initial cleaning of samples. However, this problem is not of paramount importance for this work, since all found taxa inhabit Beringia at the present time, while the distribution range of recent moinids is located much further south (Fig. 1A). Therefore, ephippia of *Moina* are autochthonous in both Pleistocene localities.

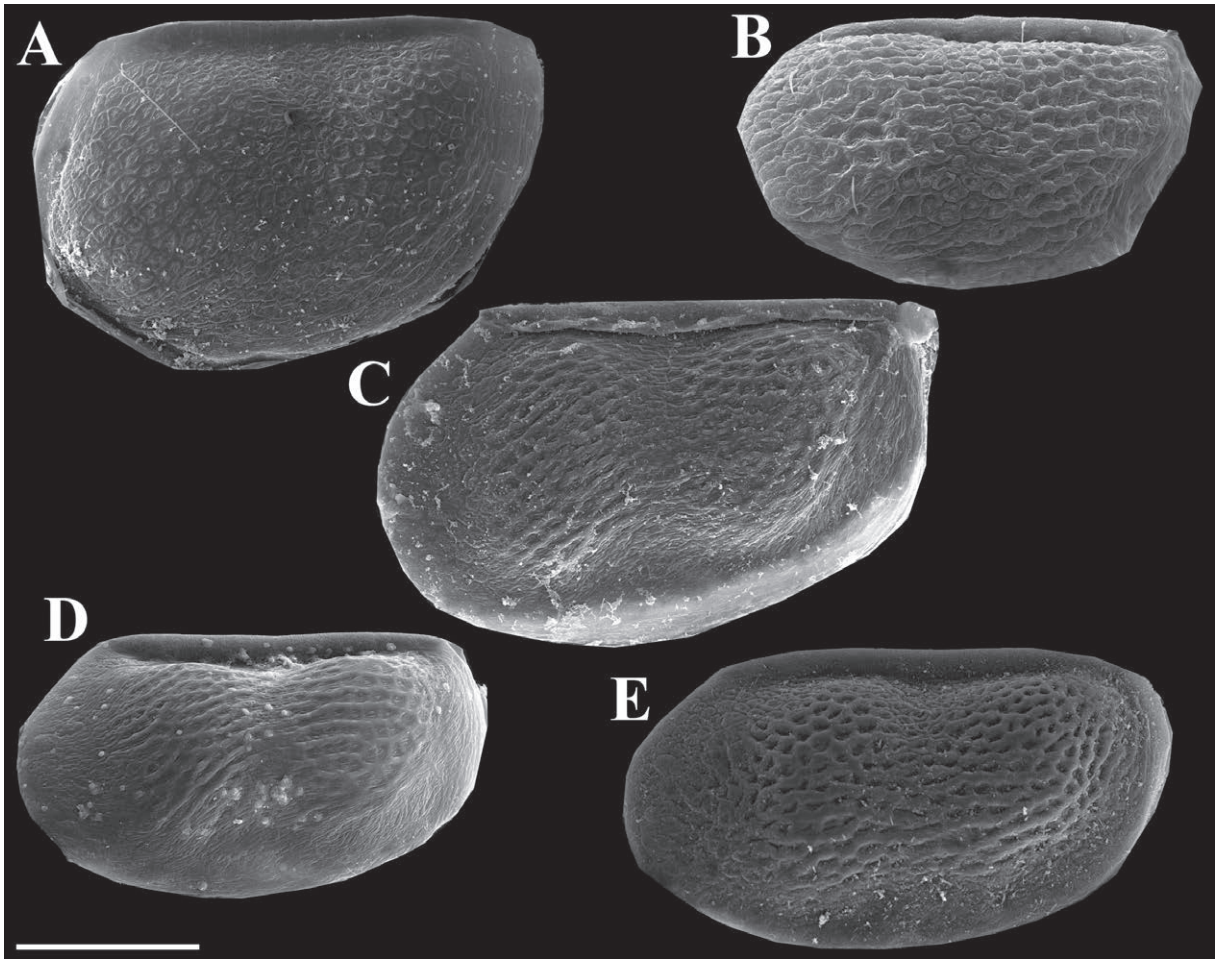

Fig. 5. Recent ephippia of *Moina* from different localities. A — *M. macrocopa* from Krasnodar region, European part of Russia; B — *M. macrocopa* from Kamchatka, Asian part of Russia; C — *Moina* cf. *macrocopa* from Zabaikalsky territory, Asian part of Russia; D — *M. kaszabi* from Sukhbaatar, Mongolia; E — *M. belli* from KwaZulu-Natal, the Republic of South Africa. Scale bar: 0.2 mm.

Рис. 5. Современные эфиппиумы *Moina* из различных местонахождений. A — *M. macrocopa* из Краснодарского края, европейская часть России; B — *M. macrocopa* с Камчатки, азиатская часть России; C — *Moina* cf. *macrocopa* из Забайкальского края, азиатская часть России; D — *M. kaszabi* из Сухэ-Батора, Монголия; E — *M. belli* из Квазулу-Натал, Южно-Африканская Республика. Масштабная линейка: 0,2 мм.

Discussion

Despite significant progress achieved in the investigations of Moinidae during the last ten years [Bekker *et al.*, 2016; Alonso *et al.*, 2019; Elías-Gutiérrez *et al.*, 2019; Montoliu-Elena *et al.*, 2019; Ni *et al.*, 2019; Makino *et al.*, 2020; Nam *et al.*, 2022], only few attempts have been made to study the ephippia of recent *Moina* under SEM. Data on variability of the ephippium shape and ornamentation are sporadic and not systematized. At the same time, the ephippium ornamentation could be an important feature for distinguishing species and species groups within Moinidae [Alonso *et al.*, 2019; Elías-Gutiérrez *et al.*, 2019; Montoliu-Elena *et al.*, 2019]. To date the species of *Moina* with a sole egg in the ephippium [Van Damme, Dumont, 2008; Alonso *et al.*, 2019; Elías-Gutiérrez *et al.*, 2019] are much better studied than taxa, producing ephippium with two eggs [Montoliu-Elena *et al.*, 2019; Neretina, Kirdyasheva, 2019; Neretina *et al.*, 2020b].

Within the large-bodied *Moina* inhabiting water bodies of the Old World, the most widespread pattern of ephippium ornamentation is a sculpture of flattened hillocks, or meshes, or their combinations [Goulden, 1968; Smirnov, 1976; Montoliu-Elena *et al.*, 2019; this study, Fig. 5], in contrast to the New World and Australia, where much more types of ornamentation are found [Goulden, 1968; Smirnov, 1976; Neretina, Kirdyasheva, 2019; Neretina *et al.*, 2020b]. According to the genetic data, *M.* cf. *macrocopa* is the most common species in the Palaearctic [Bekker *et al.*, 2016; Ni *et al.*, 2019]. We briefly compared populations of *M. macrocopa* from European and Asian parts of Russia (Fig. 5A–B) and did not find any differences between them based on ephippia morphology. Our data correspond to the data of Montoliu-Elena *et al.* [2019] on *M. macrocopa* s.l. from Europe. Investigated ephippia of *M.* cf. *macrocopa* are characterized by a prominent coarse ornamentation (Fig. 5A–B). At the same time, ornamentation in fossil specimens is finer and visually more similar to that in *M.* cf. *macrocopa*

from Zabaikalsky Territory. This population was marked by Bekker *et al.* [2016] as a separate genetic "clade L" of *M. macrocopa* s.l. (Table 3). Presumably, clade L has a more compact recent distribution, than the "clade M", including the largest number populations known from Palearctic region belonging to *M. macrocopa* s.str. [Bekker *et al.*, 2016]. At the same time, ephippia with similar fine ornamentation are found by us in populations of *M. kaszabi* Forró, 1988 and *M. belli* Gurney, 1904, in the samples taken closely to their type localities in Mongolia and the Republic of South Africa (Table 3, Fig. 5D–E). But these species have not yet been revised and studied genetically, and we have no opportunity to compare them with *M.* cf. *macrocopa* from clade L and other members of the *M. macrocopa* species group. But it should be noted that ephippia of *M. kaszabi* and *M. belli* differ from *M. macrocopa* s.l. by a more elongated shape.

It is interesting to note that *M. kaszabi*, *M. belli* and *M.* cf. *macrocopa* inhabit shallow water bodies in the arid steppe regions of the Old World and do not penetrate into the north farther then 51° N [Goulden, 1968; Smirnov, 1976; Bekker, 2016], whereas *M. macrocopa* occurs in eutrophic pools and ponds up to 61° N in the European part of Russia [Bekker *et al.*, 2016]. In the New World, *Moina* was found in Churchill (c.a. 59° N), Manitoba, Canada [Jeffery *et al.*, 2011].

Moinids are usual in the southern half of Asian Russia [Smirnov, 1976; Garibian *et al.*, 2020], but the northeasternmost region where they were found to date is Central Yakutia [Andreeva *et al.*, 2023], while they were not found to date in Northern Yakutia [Sobakina, 2013; Novichkova *et al.*, 2020; Chertoprud, Novichkova, 2021], Chukotka [Streletskaya, 2010; Novichkova, Chertoprud, 2015] and Alaska [Goulden, 1968; Reed, 1962; Tash, Armitage, 1967]. Our Pleistocene ephippia were found significantly further north of recent moinid distribution range (Fig. 1A). Moreover, we directly studied samples from several water bodies in the vicinity of the Batagay outcrop, and there were also no moinids found there. Nowadays, moinids predominantly inhabit ephemeral shallow water bodies. They are important primary consumers in water bodies located in arid regions. Some moinids occur in eutrophic waters and even in water bodies with a high salinity [Goulden, 1968; Smirnov, 1976]. In Transbaikalia, they were found both in recent [Bekker *et al.*, 2016] and Pleistocene samples [Zharov *et al.*, 2020]. Together with some species of Anostraca, Notostraca and some other Cladocera, moinids can be considered as a group associated with shallow arid water bodies. We think that the Pleistocene moinids occurred in small, slightly brackish ponds with fluctuating water level sometimes drying out under rather arid conditions. This type of water bodies is completely absent in northern Yakutia today. The numerous thermokarst lakes in the Northern coastal lowlands are an inappropriate habitat for the moinids. But in central Yakutia, a similar type of water bodies is found in so-called "alases" — flat-bottomed hollows of a thermokarst origin, at the bottom of which a lake has usually formed.

Our records of fossil *Moina* in northern Yakutia (roughly, with age of c.a. 70–30 Kya) fit well with the conception of the existence of non-analogous communities of branchiopod crustaceans in northeastern Eurasia during the Late Pleistocene [Neretina *et al.*, 2020a]. As a result of this study, we obtained new evidence of changes in the composition of the invertebrate fauna of small water bodies in Beringia at the Pleistocene/Holocene boundary, which allow us to assume that water bodies fundamentally different from recent types existed in Pleistocene Beringia carrying a specific branchiopod community not having recent analogues.

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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