

First data on crustacean remains (Crustacea: Branchiopoda) in the coastal sediments of Lake Pechevalavato (Yamal Peninsula, Russia)

Первые данные об остатках ракообразных (Crustacea: Branchiopoda) в береговых отложениях озера Печевалагато (полуостров Ямал, Россия)

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КЛЮЧЕВЫЕ СЛОВА: Cladocera, Notostraca, полуостров Ямал, Западная Сибирь, Голоцен, палеосреда, палеоэкология.

ABSTRACT. Here we present the first data on crustacean remains in Holocene sediments of Lake Pechevalavato (Yamal Peninsula, Western Siberia). An investigated outcrop was formed as a result of thermal abrasion of deposits located at the second marine terrace. From this outcrop, 48 samples were collected for paleolimnological analysis; crustacean remains were found in nine samples. In total, 34 ephippia, a fragment of thoracic limb filter plate and 45 mandibles were analyzed. Based on details of morphology, 20 ephippia were classified as belonging to *Daphnia pulex*-type, 14 ephippia — to *D. longispina*-type. A filter plate was found in the upper layer together with *Daphnia* ephippia and presumably belongs to this genus. Based on shape and size, all found mandibles belonged to notostracan *Lepidurus arcticus* (Pallas, 1793). According to our data, the outcrop point became to be a part of a lake (most probably, Lake Pechevalavato or a separate lake near it) c.a. 5.5–6 kya, before this time it was a terrestrial or swampy territory. Then the lake surface and depth were reduced for some reasons unknown to us. Fauna of this lake was poorer as compared to previously described Holocene water bodies of Yamal. We have demonstrated that different types of water bodies existed in the central part of Yamal Peninsula during the Holocene.

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РЕЗЮМЕ. В данной работе мы представляем первые данные по остаткам ракообразных в голоценовых отложениях озера Печевалагато (полуостров Ямал, Западная Сибирь). Обнажение, исследованное нами, образовалось в результате термоабразии отложений, расположенных на второй морской террасе. Из этого обнажения было отобрано 48 образцов для палеолимнологического анализа. Остатки ракообразных были найдены в девяти образцах. Всего нами было проанализировано 34 эфиппиума, фрагмент фильтративной пластинки торакальной конечности и 45 мандибул. По морфологическим данным, 20 эфиппиумов были отнесены нами к типу *Daphnia pulex*, 14 эфиппиумов — к типу *D. longispina*. Фильтративная пластинка была найдена в верхнем слое вместе с эфиппиумами *Daphnia* и предположительно принадлежит этому роду. По форме и размеру все обнаруженные мандибулы соответствуют щитню *Lepidurus arcticus* (Pallas, 1793). Согласно нашим данным, исследованная точка стала частью озера (скорее всего, палео-озера Печевалагато или отдельного озера рядом с ним) около 5500–6000 лет назад, до этого данная территория была сухой или заболоченной низиной. Затем поверхность и глубина озера сократились по некоторым причинам, неизвестным нам.

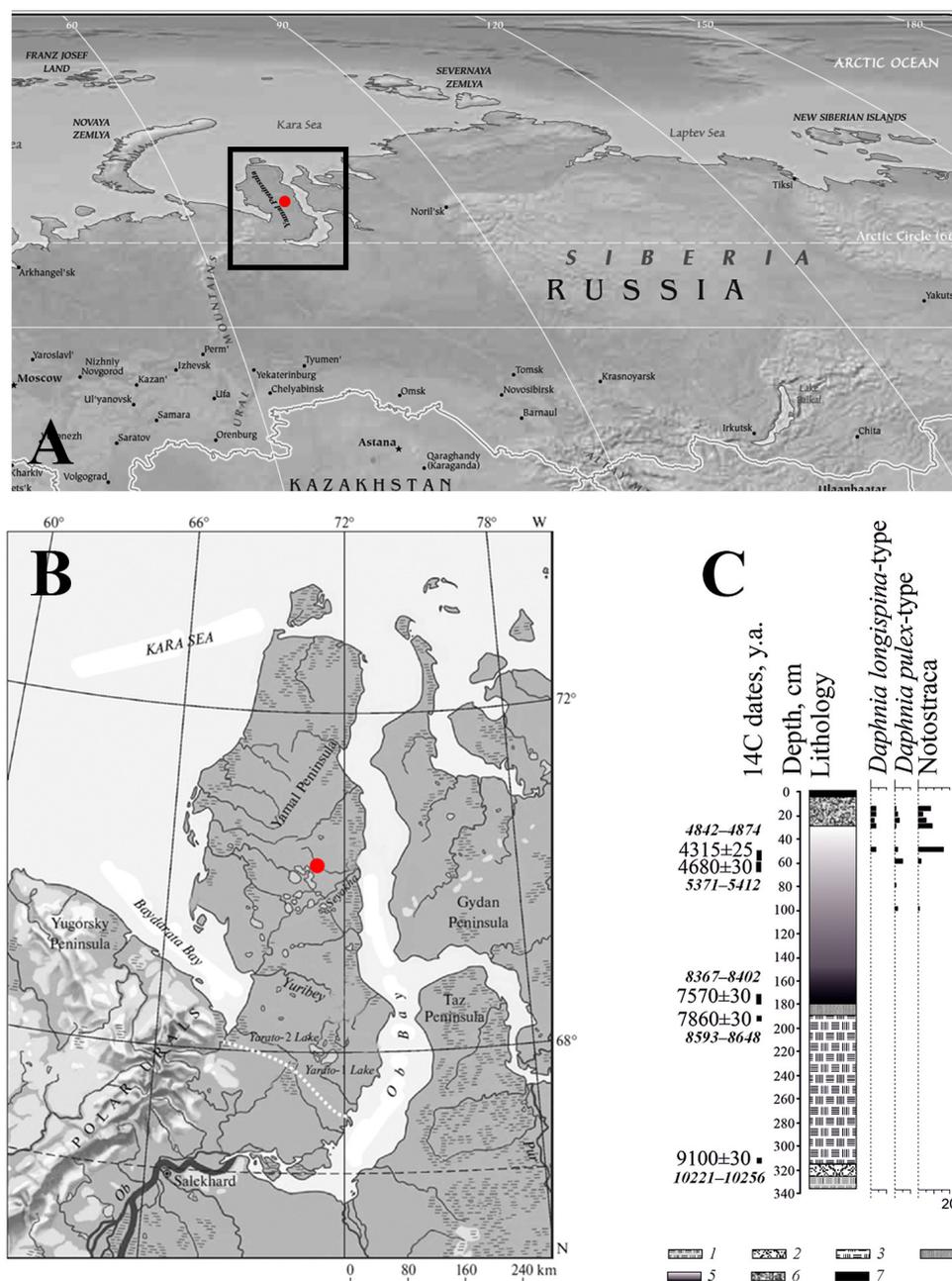


Fig. 1. Position of Lake Pechevalavato. A, in Northern Eurasia, map of Northern Eurasia from CIA public domain: <https://www.cia.gov/library/publications/resources/theworld-factbook/docs/refmaps.html>. B — in Yamal Peninsula, map from Lapteva *et al.* [2024], with modifications. Red circle marks Lake Pechevalavato. C — studied outcrop with results of the crustacean remain analysis. Lithological layers: 1 — peat; 2 — light grey sand; 3 — weakly decomposed peat with branches of shrubs and thin interlayers of sandy loams and siltstones; 4 — sand; 5 — sandy loam with peat; 6 — yellow-gray sandy loam; 7 — turf.

Рис. 1. Положение озера Печевалавато. (А) в Северной Евразии, карта на основе данных CIA public domain: <https://www.cia.gov/library/publications/resources/theworld-factbook/docs/refmaps.html>. В — на полуострове Ямал, карта из: Lapteva *et al.* [2024], с изменениями. Красным кружком отмечено озеро Печевалавато. С — схема изученного обнажения, с результатами анализа остатков ракообразных. Литологические слои: 1 — торф; 2 — песок светло-серый; 3 — торф слаборазложившийся с ветками кустарников и маломощными прослоями супеси и алевроитов; 4 — песок; 5 — супесь оторфованная; 6 — супесь желто-серая; 7 — дерн.

Фауна этого озера была обедненной по сравнению с ранее описанными голоценовыми водоемами Ямала. Таким образом, мы продемонстрировали, что в центральной части полуострова Ямал в течение голоцена существовали различные типы водоемов.

Introduction

Crustaceans (Arthropoda: Crustacea) represent an important component of inland water faunas in Arctic region [Bespalaya *et al.*, 2015; Novichkova, Azovsky,

2017]. Faunistic studies on this group in the Russian Arctic were started since the second half of the 19th century [Fischer, 1851; Sars, 1898; Voronkov, 1911]. Nowadays crustacean community changes are regarded as indicators both of climate warming consequences and anthropogenic impact, especially pollution from oil and gas deposit exploitation. During the last two decades, faunistic studies on the microscopic crustaceans in Arctic and Subarctic regions have intensified in response to increasing interest in the formation of regional faunas under hard climatic conditions and their transformation under pressure by natural and anthropogenic factors [Bespalaya *et al.*, 2015; Ermolaeva, 2016; Novichkova, Chertoprud, 2017; Loskutova, Ponomarev, 2019; Chertoprud *et al.*, 2022; 2023; Novikov *et al.*, 2023; Soromotin *et al.*, 2024]. However many areas remain poorly studied due to their remote position and short summer period.

Despite a long history of crustacean investigations in recent communities, Yamal Peninsula still belongs to such areas. Inventory of recent microscopic crustaceans in the inland waters of Yamal Peninsula was started at the beginning of the 20th century [Voronkov, 1911; Vereshchagin, 1913]. The most comprehensive report on recent aquatic fauna was published by Bogdanov *et al.* [2000], however their data are constantly updated until now (e.g. Bogdanova [2009]; Ermolaeva [2016]; Koporikov *et al.* [2022]). In general, widespread species of microcrustaceans make the greatest contribution to Arctic local faunas [Ermolaeva, 2016], although some such taxa require a comprehensive taxonomic revision [Korovchinsky *et al.*, 2021]. The highest species diversity was recorded in floodplain water bodies and in large lakes [Bogdanov *et al.*, 2000], while small water bodies were studied rarely investigated [Vekhov, 1976].

Holocene crustacean remains were episodically studied in sediments from lakes located in southern and central portions of the Yamal Peninsula [Ibragimova *et al.*, 2020; 2022; Nigmatullin *et al.*, 2022]. However, our knowledge of Holocene history of the crustaceans from Yamal is still poor as compared to that of both the European part of the Russian Arctic [Frolova *et al.*, 2017; Nigmatullin, Frolova, 2023] and Eastern Siberia (e.g. Kirillova *et al.* [2016]; Kotov *et al.* [2019]; Frolova *et al.* [2024]).

Here we present the first data on crustacean remains in Holocene coastal sediments of Lake Pechevalavato, located in NE Yamal.

Material and methods

Lake Pechevalavato is located in the north-eastern portion of the Yamal Peninsula, 25 kilometers northwest of the village of Seyakha (Yamalo-Nenets Autonomous Okrug, Tyumen Region, Subarctic Russia) (Fig. 1A–B). Recent climate of this region is basically Subarctic, with an average annual temperature of 8–10 °C below zero. Precipitation amount is about 400 mm/year.

Lake Pechevalavato is situated in the Seyakha River basin. The lake is located on the second marine terrace at 20 m a.s.l. and has a thermokarst origin. The material for an investigation was collected from an outcrop (70.217° N, 71.833° E) formed as the result of thermal abrasion of Holocene deposits of this terrace [Lapteva *et al.*, 2024]. The thickness of the organomin-

eral deposits at the sampling site reached 334 cm. A preliminary inspection revealed that the deposits include seven lithological layers typical of the Subarctic zone (Fig. 1C). In total, 48 samples with thickness of 5–10 cm were manually collected from this outcrop, as a result we had a whole core of 334 cm long. Each sample was individually packed to a zip-packet and kept at 5 °C until their examination. See further details in previous paper [Lapteva *et al.*, 2024]. Six samples were used for radiocarbon dating at the Joint Usage Center “Laboratory of radiocarbon Dating and Electron Microscopy” of the Institute of Geography of Russian Academy of Sciences. Calendar age of the oldest sample with plant remains was estimated as 9085–9141 ya [Lapteva *et al.*, 2024]. Plant remains were analyzed from all samples according to standard methods of pollen and carpological analysis [Lapteva *et al.*, 2024].

Crustacean remains (Supplementary Table 1) were found in nine samples during their carpological analysis following standard method of its performing [Nikitin, 1969]. They were picked individually from the samples under a stereomicroscope Leica MZ75 (Leica Microsystems, Germany) via thin needles. All remains were attached to the aluminum stubs via conductive non-porous carbon tape, coated with gold in a S150A Sputter Coater (Edwards, UK), and studied under MIRA 3 LMH scanning electron microscopes (Tescan, Czech Republic) and measured in the Gwyddion 2.69 software. For identification of the crustacean remains, we used both keys for recent taxa [Jaksch, 1992; Korovchinsky *et al.*, 2021] and previously published information on subfossils [Kirillova *et al.*, 2016; Kotov *et al.*, 2019; Neretina *et al.*, 2020; Zharov *et al.*, 2020; Rogers *et al.*, 2021]. Diagrams of the remain numbers were constructed using Tilia2.6.1 (<https://tilia-manual.readthedocs.io/en/latest/tools.html>).

Results

In toto, we found the following remains belonging to branchiopod crustaceans in 48 samples: 34 daphniid ephippia (Figs 2A–I, 3A–I), a fragment of the thoracic limb filter plate (Fig. 4A–C) and 45 notostracan mandibles (Figs 5A–K, 6A–C) (Supplementary Tables 1–2). Almost all crustacean remains were found in the upper outcrop portion, starting from the layer No. 36 (depth of 99–98 cm) corresponding to the time of c.a. 5.5–6 kya; however, any remains were absent in upper 9 cm of the outcrop.

Ephippia were partly destroyed or deformed at fossilization, they usually did not keep a natural shape. They contained two resting eggs with longitudinal axes directed almost perpendicularly to the ephippium dorsal margin and lacking a caudal needle. In most cases anterior, posterior, dorsal and ventral portions were distinguishable. All these ephippia belonged to the genus *Daphnia* O.F. Müller, 1785, namely, to two major groups within the subgenus *Daphnia* s.str.: *D. pulex* and *D. longispina*.

1. Ephippia of the *D. pulex*-type (Figs 2A–I, 7A). Length 0.89 to 1.65 mm, height 0.71 to 1.03. Ephippium subtriangular, relatively high (height/length ratio from 0.57 to 0.92), with an almost straight or convex dorsal margin (Fig. 2A, D, G), caudal needle missing. Dorsal plate with prominent spinules (Fig. 2B, E, H), most ephippium surface with a rectangular ornamentation (Fig. 2C, F, I). Resting egg axes almost perpendicular to dorsal margin (Fig. 2A, D, G).

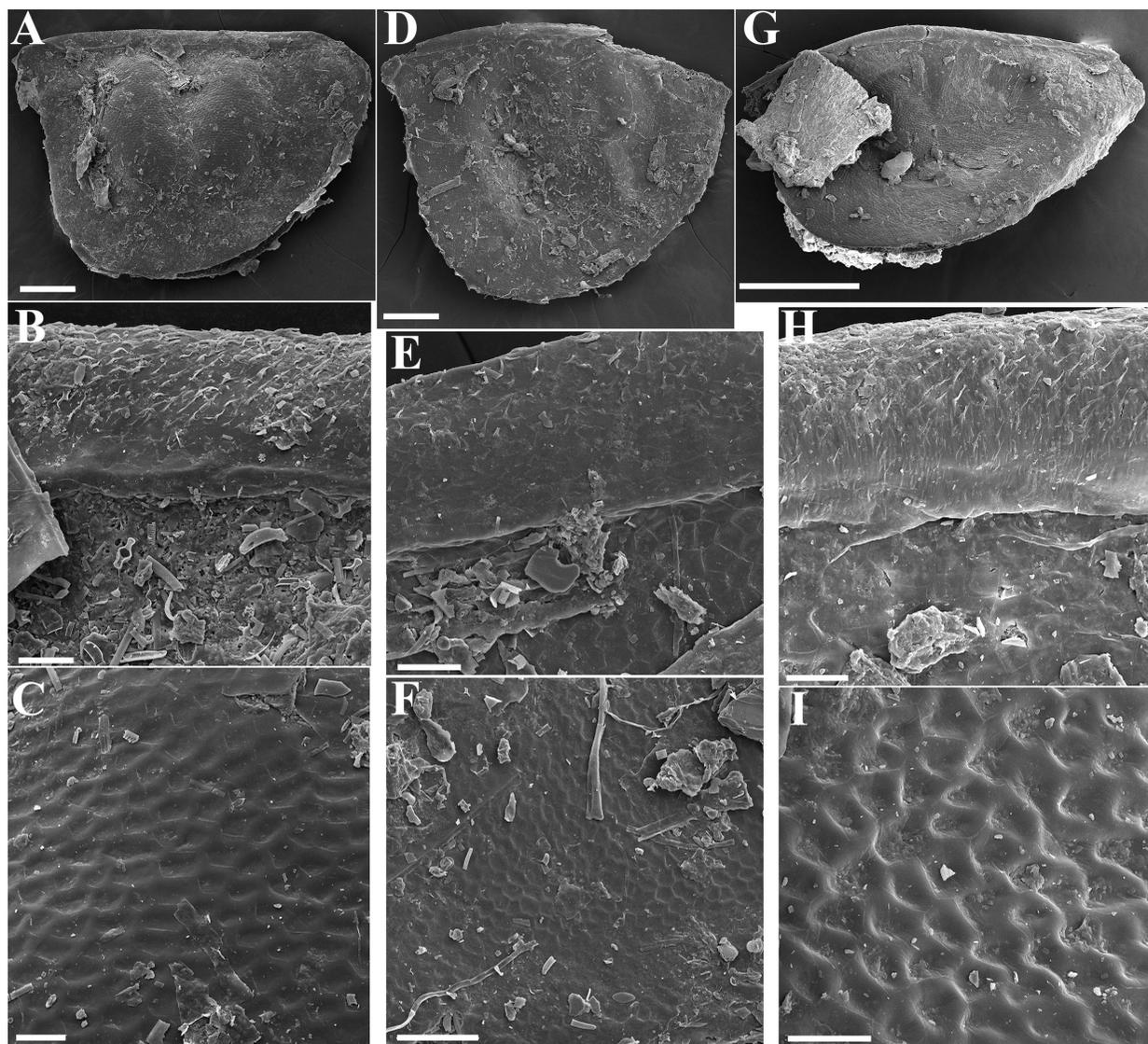


Fig. 2. Ephippia of the *Daphnia pulex* group. A–C — an ephippium from sample 36, its dorsal and central portions. D–F — an ephippium from sample 40, its dorsal and central portions. G–I — an ephippium from sample 44, its dorsal and central portions. Scale bars: G — 0.5 mm; A, D — 0.2 mm; F — 0.05 mm; B–C, E, H–I — 0.02 mm.

Рис. 2. Эфиппиумы группы видов *Daphnia pulex*. A–C — эфиппиум, его спинная и центральная части, образец 36. D–F — эфиппиум, его спинная и центральная части, образец 40. G–I — эфиппиум, его спинная и центральная части, образец 44. Масштабные отрезки: G — 0,5 мм; A, D — 0,2 мм; F — 0,05 мм; B–C, E, H–I — 0,02 мм.

Such ephippia were dominated in the outcrop samples with cladoceran remains.

2. Ephippia of the *D. longispina*-type (Figs 3A–I, 7A). Length 0.82 to 1.36 mm, height 0.69 to 1.03. Ephippia subtriangular, relatively high (height/length ratio from 0.59 to 0.91), with an almost straight dorsal margin (Fig. 3A, D, G); caudal needle missing. Dorsal plate smooth, without prominent spinules (Fig. 3B, E, H), most ephippium surface with rectangular ornamentation (Fig. 3C, F, I), in most cases less prominent than in the *pulex*-type. Resting egg axes almost perpendicular to dorsal margin (Fig. 3A, D, G).

Ephippia were rarer than those of the *pulex*-type.

3. A fragment of branchiopod thoracic limb filter plate (Fig. 4A–C). Length of setae remains about 0.1 mm,

their diameter around 0.003 mkm. All setae covered by densely located setulae (Fig. 4A–C).

A sole fragment was found in the sample 46 together with *Daphnia* ephippia. Presumably this fragment belongs to this genus.

4. Notostracan mandibles (Figs 5A–K, 6A–C, 7B). Shape of mandibles typical of the notostracans (Fig. 5A–K). Maximum width (near base of mandibular teeth) 0.25–1.49 mm. All mandibles were ranged based on this value to have information on size variability (Fig. 7B). Basal portion better preserved in smaller mandibles (Fig. 5I–K) and often destroyed in larger mandibles (Fig. 5A–H). Mandibular teeth with rounded tops (Fig. 6A–C). Bunches of bristles recognizable near bases of some teeth (Fig. 6B–C).

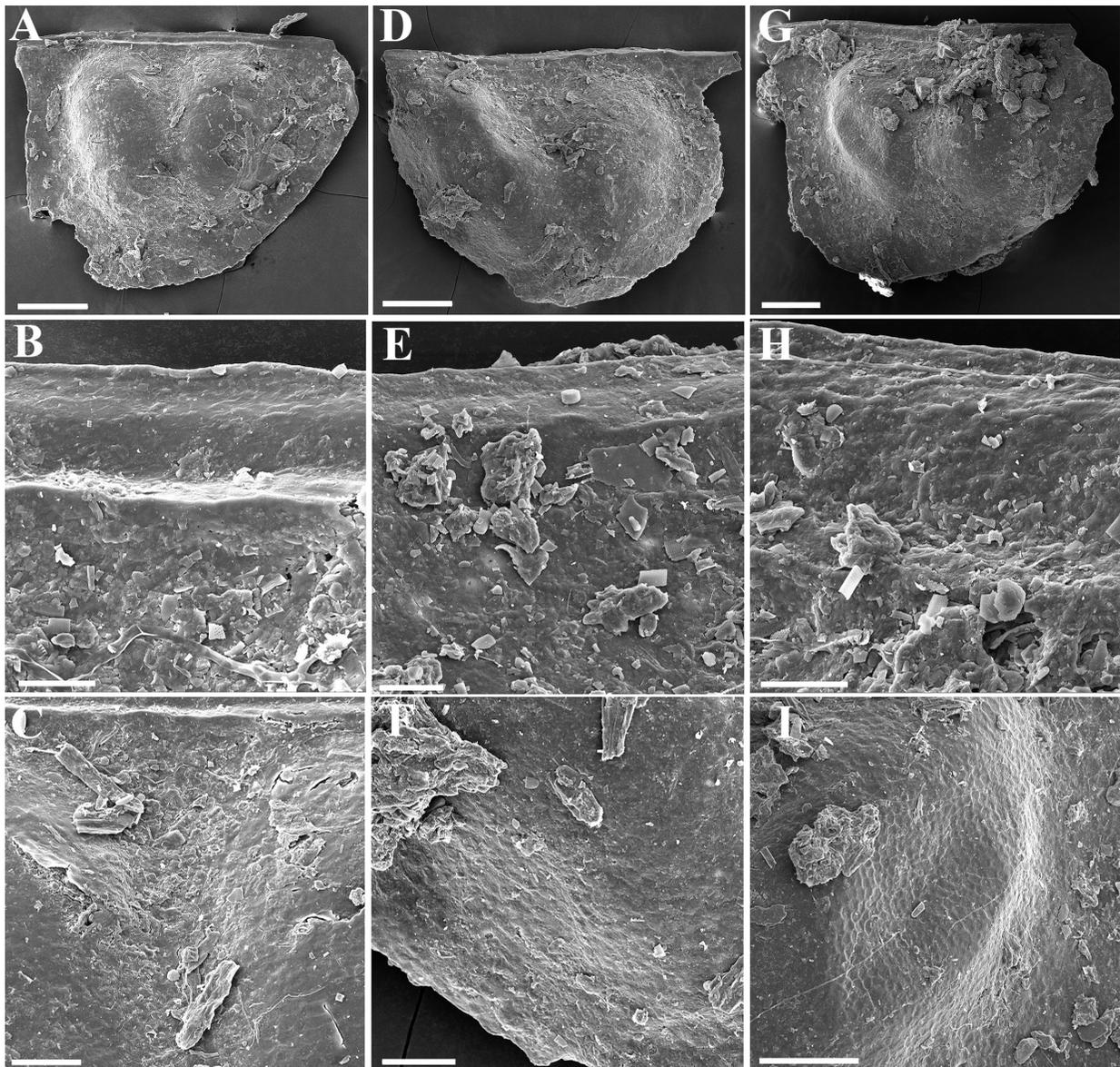


Fig. 3. Ephippia of the *Daphnia longispina* group. A–C — an ephippium from sample 41, its dorsal and central portions. D–F — an ephippium from sample 43, its dorsal and ventral portions. G–I — an ephippium from sample 45, its dorsal and central portions. Scale bars: A, D, G — 0.2 mm; I — 0.1 mm; C, F — 0.05 mm; B, E, H — 0.02 mm.

Рис. 3. Эфиппиумы группы видов *Daphnia longispina*. A–C — эфиппиум, его спинная и центральная части, образец 41. D–F — эфиппиум, его спинная и брюшная части, образец 43. G–I — эфиппиум, его спинная и центральная части, образец 45. Масштабные отрезки: A, D, G — 0,2 мм; I — 0,1 мм; C, F — 0,05 мм; B, E, H — 0,02 мм.

Characters of all mandibles match those of *Lepidurus arcticus* (Pallas, 1793), a notostracan species very usual in shallow ponds in the Arctic zone [Rogers, 2001].

Discussion

Branchiopod remains identification. Notable progress was achieved in the description of *Daphnia* ephippia during recent decades. However, fine data on the ephippial morphology in recent *Daphnia* species are still incomplete. Especially, it concerns the subgenus *Daphnia* s.str. [Kotov *et al.*, 2019]. The most comprehensive identification key was proposed previously by

Mergeay *et al.* [2005] for the taxa found in Africa, but it was a single such attempt except for Glagolev's [1983] paper where the conclusions on the possibility of species differentiation based on ephippia were very pessimistic. In contrast, morphology of ephippium works well for the identification of *Ceriodaphnia* species and species groups [Kotov *et al.*, 2018].

In Eurasia, morphology of recent ephippia was studied under a scanning electron microscope in some European populations [Glagolev, 1983; Jaksch, 1992; Juračka *et al.*, 2010]. Morphology of ephippia in recent taxa from the subgenus *Daphnia* s.str. from the Arctic and Subarctic regions is not studied in detail. Note that results

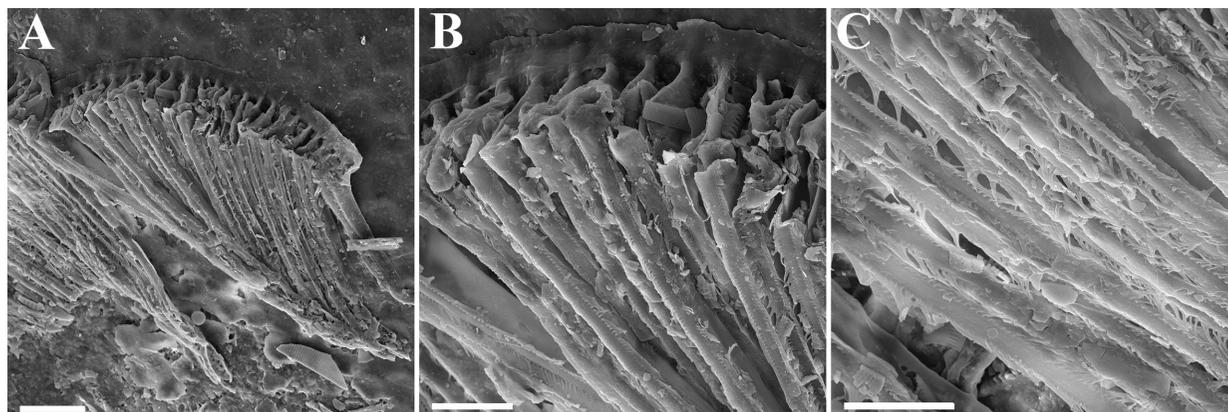


Fig. 4. Fragments of filter plates from sample 46 (A–C). Scale bars: A — 0.02 mm; B–C — 0.01 mm.

Рис. 4. Фрагменты фильтрационной пластинки из образца 46 (А–С). Масштабные отрезки: А — 0,02 мм; В–С — 0,01 мм.

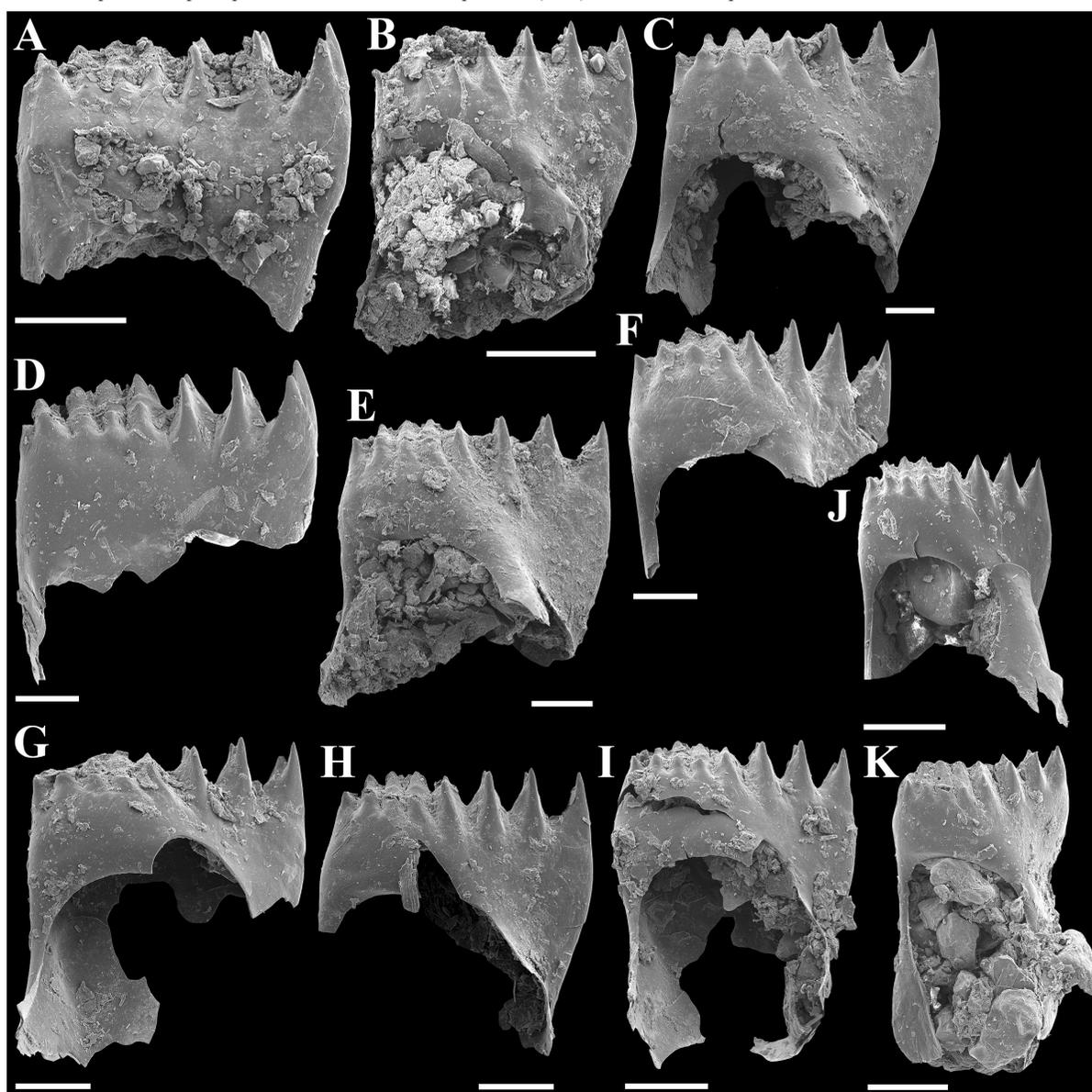


Fig. 5. Mandibles of Notostraca, general views, ranking in the size decrease (A–K). A, C, F, I — from sample 44. B, G, J — from sample 41. D–E — from sample 43. H, K — from sample 46. Scale bars: A–B — 0.5 mm; C–K — 0.2 mm.

Рис. 5. Мандибулы Notostraca, общие виды, расположенные в порядке убывания размера (А–К). А, С, F, I — образец 44. В, G, J — образец 41. D–E — образец 43. H, K — образец 46. Масштабные отрезки: А–В — 0,5 мм; С–К — 0,2 мм.

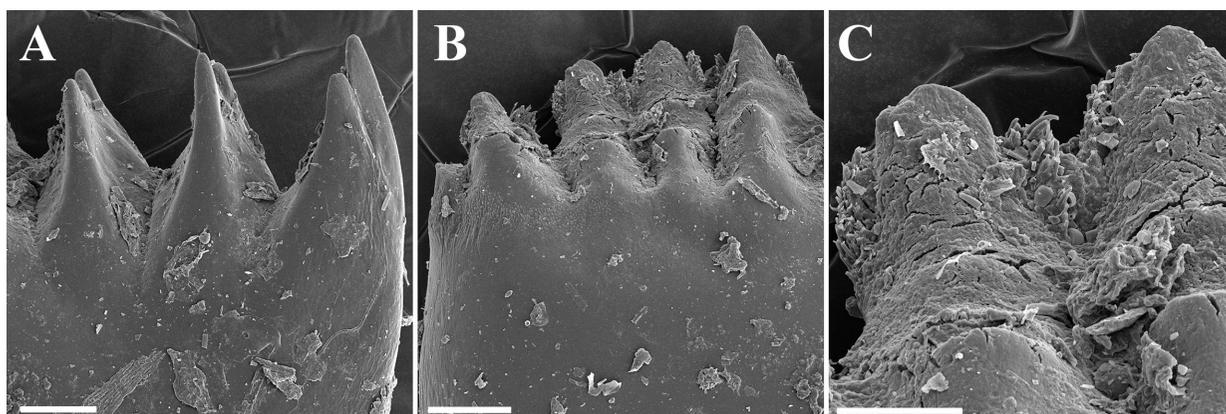


Fig. 6. Fragments of Notostraca mandible under higher magnification, sample 43. A–B — 0.1 mm; C — 0.05 mm.

Рис. 6. Фрагменты мандибулы Notostraca при большем увеличении, образец 43. А–В — 0,1 мм; С — 0,05 мм.

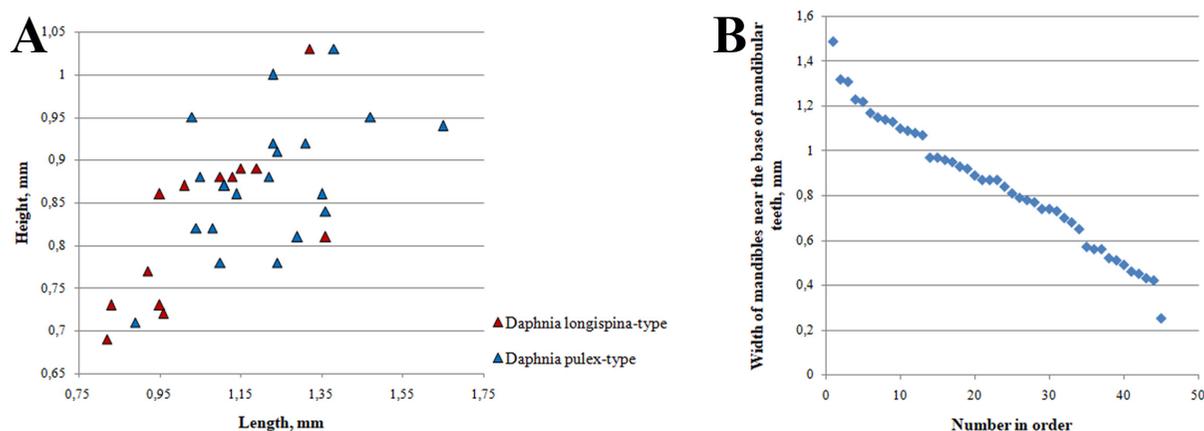


Fig. 7. Analysis of size for detected crustacean remains. A — height/length graph for ephippia of *Daphnia*. B — distribution of Notostraca mandibles ranking in the size decrease.

Рис. 7. Анализ размера найденных остатков ракообразных. А — зависимость высоты от длины эфиппиума для *Daphnia*. В — распределение мандибул Notostraca, расположенных в порядке убывания их размера.

of morphological identification of recent Arctic populations of *Daphnia* are questionable, even based on the morphological characters of the females [Korovchinsky *et al.*, 2021]. Moreover, the scattered morphological data on the diversity of *Daphnia* in the high latitudes are not coordinated with genetic clades [Colbourne *et al.*, 1998] instead of Mergeay *et al.* [2005].

Previous efforts to study fossil remains of the subgenus *Daphnia* were summarized by Kotov *et al.* [2019]. It is known that presence of relatively large spinules on the dorsal plate is a character of *D. pulex* species group in contrast to *D. longispina* group with almost smooth dorsal margin. However, “species discrimination within the latter two large groups using ephippia is very difficult...” [Kotov *et al.*, 2019: 187, figs 1a–c, 2a–f]. The value of ephippium ornamentation remains questionable and requires the investigations under the same magnification for reliable comparison [Glagolev, 1983; Jaksch, 1992; Kotov *et al.*, 2019]. In the frame of our study, we detected two morphological groups of the ephippia: those having dorsal plate covered by prominent spinules (*pulex*) and with almost smooth dorsal plate (*longispina*), although they are almost identical in size (Fig. 7A).

In the frame of our study, a single filter plate of *Daphnia* limb was found. Probably, the conditions of crustacean remain accumulation in this layer were optimal for preservation of delicate structures. Nowadays fragments of daphniid filter plates are under-counted by paleolimnologists due to a pre-treatment of the samples by concentrated alkali solutions. This method destroys delicate structures. Remains of filter plates might be more widespread in the Holocene deposits, but we need to use non-pre-treated samples [Zharov *et al.*, 2022]. The records of daphniid filter plates in the untreated material during our study confirm this statement, but, as we suppose, the conditions of fossilization are also important for preservation of thoracic limbs fragments. Fragments of the branchiopod filter plates also are known from older deposits, but such records are not numerous [Richter *et al.*, 2017; Kirillova *et al.*, 2016].

Ephippia of *Daphnia* co-occurred with mandibles of Notostraca, presumably belonging to *L. arcticus*. The latter inhabits recent shallow water bodies drying seasonally, and often co-existed with *Daphnia* species (e.g. Bespalaya *et al.* [2015]; Neretina *et al.* [2020]; Korovchinsky *et al.* [2021]).

Populations belonging to the *D. pulex* and *D. longispina* groups, as well as populations of *L. arcticus*, are known from some recent water bodies in Yamal Peninsula [Bogdanova, 2009; Ermolaeva, 2016; Movchan, Stogov, 2016]. We can hypothesize that similar communities existed here in the Late Holocene.

In the upper layers of the same core, were found only ephippia of the *D. pulex* group [Frolova *et al.*, 2017]. Remains of this group are known from some Late Pleistocene lake sediments [Frolova *et al.*, 2024] and from permafrost in East Siberia [Kotov *et al.*, 2019; Neretina *et al.*, 2020; Zharov *et al.*, 2020]. Presumably, the subgenus *Daphnia* appears more resistant to environment transformation at the late Holocene boundary, than ctenodaphniids whose distribution ranges had moved further south [Neretina *et al.*, 2020; Zharov *et al.*, 2020].

Water body property reconstruction. Lapteva *et al.* [2024] have made a detailed study of the vegetation dynamics in the vicinities of Lake Pechevalavato during the whole Holocene based on pollen (helpful for revealing of global changes) and carpological analysis (helpful for reconstruction of local vegetation structure). However, most found remains represented truly terrestrial, swamp and near-water vegetation instead of aquatic plants. Any reconstructions of the lake margin changes were not performed by Lapteva *et al.* [2024]. Above, we described the remains of truly aquatic organisms, and they give us such a chance. According to our data, the outcrop point became a part of a lake (most probably, Lake Pechevalavato or a separate lake near it) c.a. 5.5–6 kya. The layers, in which the remains of branchiopods are absent, can be associated with the periods, when the level of water was insufficient for the development of a stable crustacean community, or for successful remains fossilization. Therefore before 5.5–6 kya, it was a terrestrial or swampy territory. Note that only a single occasional ephippium was found in the bottom 2/3 of the core (the layer 8), it is apparently allochthonous in its origin.

Preservation of aquatic organism remains is associated with the layers formed by highly peaty sandy loam and yellow-grey sandy loam. Since 5.5–6 kya to, at least, the time represented by the layer 46 (depth of 14–9 cm) the sampling point belonged to a shallow bay of Lake Pechevalavato, or a smaller lake near it. Numerous remains of notostracans suggest that this water body was shallow and, most probably, fishless [Rogers *et al.*, 2021]. The version of a single large lake seems to be preferable for us as compared to a separate water body. Lake Pechevalavato had a larger surface relative to its recent state. Then its surface and depth were reduced for some reasons unknown to us: the uppermost layers are not accurately dated, we only know that it happened before 4 kya, and it is difficult to associate such an event with any global (climatic or other) or local environmental changes without exact dates.

Note that previously studied Lake Yambeto [Nigmatullin *et al.*, 2022], Lake Neito-Malto [Nigmatullin *et al.*, 2024] and a small unnamed lake [Ibragimova *et al.*, 2022], located in the southern and central parts of the Yamal Peninsula, had a significantly richer crustacean

fauna during the Holocene. The afore-mentioned authors marked predominance of cladocerans from the benthic-phytophilous complex typical of permanent lakes with a developed macrophyte zone. Fauna of our lake belonged to another type. Therefore there were different types of water bodies in the central part of the Yamal Peninsula during the Holocene.

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.

Supplementary data. The following Word-tables are available online.

Supplementary Table 1. Abundance of the main types of crustacean remains in the samples.

Supplementary Table 2. Morphometric data on the main types of crustacean remains found in the samples.

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