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Cladoceran remains as a tool for reconstruction of past environmental conditions during the Late Pleistocene–Holocene in Central Karelia (NW Russia). Part I. Traditional quantitative analysis

Остатки ветвистоусых ракообразных как средство для реконструкции условий среды в позднем плейстоцене–голоцене в Центральной Карелии (Северо-Запад России). Часть I. Традиционный количественный анализ

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KEY WORDS: Holocene, paleolimnology, taphocenosis, subfossil, Cladocera.

КЛЮЧЕВЫЕ СЛОВА: голоцен, палеолимнология, тафоценоз, субфоссильный, Cladocera.

ABSTRACT. The bottom sediment core of 2.9 m. length was taken from Lake Torosjarvi (Central Karelia, NW Russia) from the ice in April 2016 using a Russian corer (diameter 0.5 cm, lehgth 1 m). Radiocarbon dating demonstrated that this core covers the Holocene, and even Late Pleistocene. To study the cladoceran remains, 33 sediment samples were collected in 6–8 cm intervals throughout the core. The remains of 42 cladoceran taxa were identified; *Bosmina* (*Eubosmina*) cf. *longispina*, *Biapertura affinis* and *Alona quadrangularis* were predominanted in the subfossil community (taphocenosis) of the lake. The cladoceran taphocenosis of Lake Torosjarvi included five faunistic zones, and the composition of predominants changed throughout the core. These changes were most probably associated with fluctuations in climatic conditions in NW Russia and variations in the water levels due to a separation of Lake Torosjarvi from a larger Lake Segozero. Analysis of the cladoceran remains demonstrated that Lake Torosjarvi was cold-water, oligotrophic, and rather deep during its history.

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РЕЗЮМЕ. Колонка донных отложений длиной 2,9 м была отобрана из озера Торосярви (Центральная Карелия, Северо-Запад России) со льда в апреле 2016 г. при помощи русского торфяного бура (диаметр желонки 0,5 см, длина 1 м). Радиоуглеродное датирование показало, что разрез донных отложений охватывает весь голоцен и даже позднеплейстоценовое время. Для изучения остатков ветвистоусых ракообразных (Cladocera) было отобрано 33 образца осадка с интервалом 6–8 см по всему керну. Были идентифицированы остатки 42 таксонов ветвистоусых ракообразных; *Bosmina* (*Eubosmina*) cf. *longispina*, *Biapertura affinis* и *Alona quadrangularis* были субдоминантами в сообществе ископаемых остатков (тафоценозе) озера. Тафоценоз кладоцер озера Торосярви включает пять фаунистических зон, и состав доминантов менялся на протяжении изученного интервала времени. Эти изменения, скорее всего, были связаны с колебаниями климатических условий на Северо-Западе России и изменением уровня воды в результате отделения озера Торосярви от более крупного озера Сегозеро. Анализ остатков кладоцер показал, что озеро Торосярви в течение всей его истории было холодноводным, олиготрофным и довольно глубоким.

Introduction

Every year new studies are performed around the world to investigate environment, including climate, changes [Dietz *et al.*, 2020; Abbass *et al.*, 2022]. At the beginning of the 21st century, attention to this topic was greatly increased, and the last two decades have demonstrated almost exponential growth of global studies [Klingelhöfer *et al.*, 2020]; large-scale transect studies were also started [Caddy-Retalic *et al.*, 2017; Subetto *et al.*, 2017; Griffiths *et al.*, 2024]. Simultaneously, there is also an expanding pool of regional publications [Belle *et al.*, 2022; Rudna *et al.*, 2023] e.g. dealing with multiproxy reconstructions of the past environment based on palaeoecological approach [Rudaya *et al.*, 2012; Nazarova *et al.*, 2020a; Wetterich *et al.*, 2021].

Biological indicator taxa, sensitive to ecological and climatic changes, have proven to be effective for paleoreconstructions of the environmental changes through the Holocene. The remains of aquatic invertebrates, such as Chironomidae [Luoto *et al.*, 2019; Syrykh *et al.*, 2017], Cladocera [Frolova *et al.*, 2017; Ibragimova *et al.*, 2024a; Tumskaya *et al.*, 2024], Ostracoda, testate amoebae [Li *et al.*, 2024; Sysoev *et al.*, 2024], and also plant spore, pollen [Nigamatzyanova *et al.*, 2019; Herzschuh *et al.*, 2023] and diatom algae [Hoff *et al.*, 2014; Ludikova *et al.*, 2023], well-preserved in lake bottom sediments, serve as long-term archives of natural data on past ecosystems and past environmental conditions [Subetto, 2009; Subetto *et al.*, 2017].

This study represents the results of our analysis of the cladoceran taphocenosis from Lake Torosjarvi (NE Russia) during the Late Ppleistocene-Holocene. This is the first study of cladoceran taphocenoses to be conducted in this lake, although the diatom flora in a short bottom sediment core [Shelekhova, Tikhonova, 2022] and grain size compositions of a Holocene core [Myasnikova, Potakhin, 2021] were published previously. The aim of the study was to confirm the ability to use Cladocera as a proxy for change in the lakes' environmental conditions during Neopleistocene-Holocene in Karelia and describe the changes in species structure of taphocenoses which reflected these changes.

Material and methods

The sediment core from Lake Torosjarvi (63.48° N, 33.23° E; area 0.58 km²; 120.4 m a.s.l., maximum depth: 8.9 m) was taken from the ice in April 2016. The lake is located in the Medvezhegorsky District in the West Karelian Upland, Central Karelia, NW Russia (Fig. 1). The climatic conditions in this region are typical of the northern taiga subzone of Karelia. The landscape is denudation-tectonic hilly-ridgy, characterised by complexes of glacial and water-glacial formations, with prevalence of a medium-swampy landscape with a predominance of pine forests [Gromtsev, 2003].

The bottom sediment core of Lake Torosjarvi was taken using a Russian corer with a 0.5 m overlap. The total length of the recovered sediment sequence was 2.9 m. The preliminary stratigraphical description of the sediment core were described in the field and photo-documented, the sediment cores were carefully packed and sent to the depository of the Northern Water Problems Institute of the Karelian Research Centre RAS, where the sediments were prepared for analysis of different biological indicators (spores and pollen, diatom algae, chironomids, Cladocera) and Loss on Ignition (LOI 550 C). A few additional samples from different core portions were selected for radiocarbon dating, which was conducted at the Laboratory of Radiocarbon Dating and Electron Microscopy at the Institute of Geography of the Russian Academy of Sciences and the Center for Applied Isotope Studies at the University of Georgia (USA). The data were calibrated using the IntCal20 curve [Reimer *et al.*, 2020]. An age model was constructed based on the obtained data (Table 1; Fig. 2).

To study the Cladocera remains in the bottom deposits of Lake Torosjarvi, 33 sediment samples were taken from the core at 6–8 cm intervals. The samples were treated according to Frey [1986] and Korhola & Rautio [2001]. In the laboratory, a wet sediment suspension was dissolved in a 10% KOH solution, heated to 75 °C for 30 minutes, stirred manually with a glass rod, and then filtered through a 50 µm mesh sieve. The filtered suspension was stained with a safranin-alcohol solution. Samples were examined under Axiostar Plus Carl Zeiss and Carl Zeiss Axio Lab A1 light stereomicroscopes at magnifications of x100–400. Remains were identified based on various chitinous structures of Cladocera, primarily carapaces and head shields, and less frequently based on morphological characters of the postabdomens, postabdominal claws, ephippia, mandibles, etc. When counting carapace remains, two valves (halves of the carapace) found in each sample were considered as belonging to a single specimen of Cladocera. At least 100 specimens of the cladoceran remains were identified in each sample; those with a minimal species density and, as a result, lower counts were excluded from our subsequent statistical analysis. Consequently, six samples at depths between 298 and 253 cm were not included in the data analysis.

The remains were identified according to modern keys for identification of the branchiopod crustaceans [Kotov *et al.*, 2010, 2016] and their subfossil remains from European water bodies [Szeroczyńska, Sarmaja-Korjonen, 2007], as well as based on

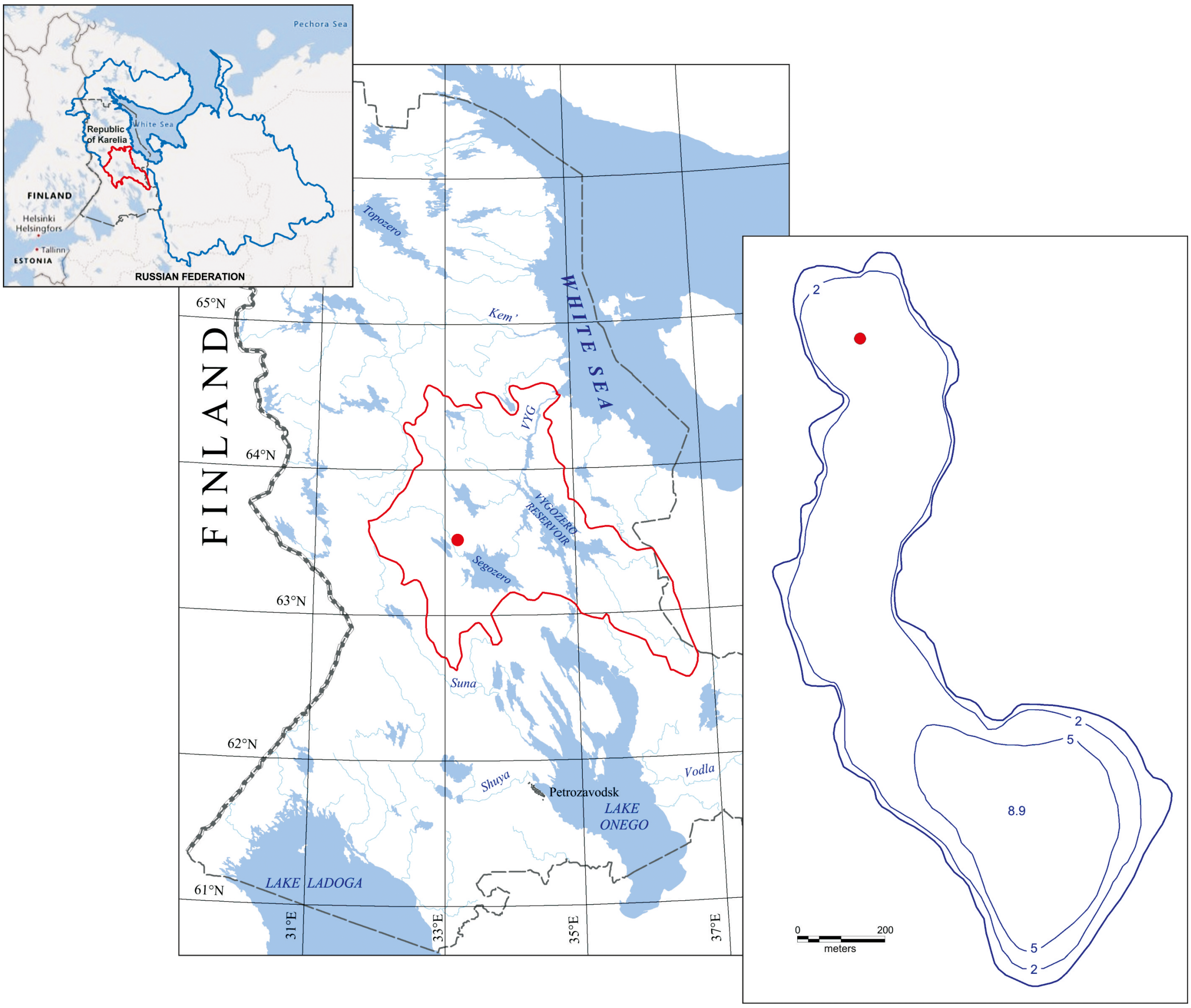

Fig. 1. Physical and geographical position, bathymetry of Lake Torosjarvi (West Karelian Upland, Central Karelia).
Рис. 1. Физико-географическое положение и батиметрия озера Торосярви (Западно-Карельская возвышенность, Центральная Карелия).

Table 1. Results of the radiocarbon dating of samples from the Lake Torosjarvi sediment core, and calibration of the obtained data using IntCal20 curve.
Таблица 1. Результаты радиоуглеродного датирования образцов колонки донных отложений озера Торосярви и калибровка полученных данных с использованием кривой IntCal20.

Lake	Sample ID	Composite depth (cm)	Radiocarbon age with error (a BP)	Calibrated median age (a cal BP)	Calibrated 2σ age range (a cal BP)	Sample type
Torosjarvi	IGAN-7469, No. 1 133 Torosjarvi (417–418 cm)	168	9565±25	11080	10886–11242	Bulk, TOC
Torosjarvi	IGAN-7470, No. 2 145 Torosjarvi (405–406 cm)	156	9540±25	10808	10674–11030	Bulk, TOC
Torosjarvi	IGAN-7471, No. 3 206 Torosjarvi (344–345 cm)	95	7535±25	8392	8240–8535	Bulk, TOC
Torosjarvi	IGAN-7472, No. 4 227 Torosjarvi (323–324 cm)	74	6530±20	7489	7352–7632	Bulk, TOC
Torosjarvi	IGAN-7473, No. 5 268 Torosjarvi (282–283 cm)	33	1235±20	1256	1105–1439	Bulk, TOC

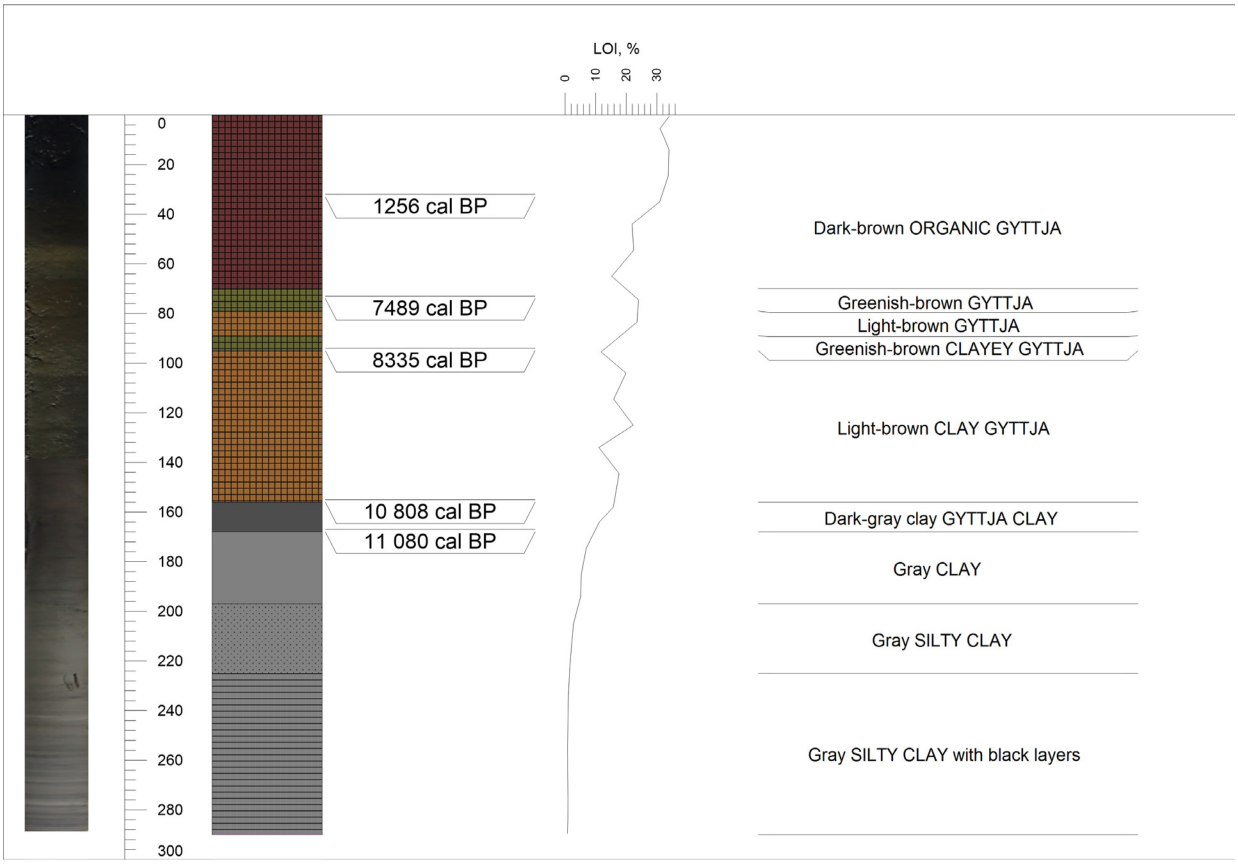

Fig. 2. Lithostratigraphic description of the Lake Torosjarvi sediment core.

Рис. 2. Литостратиграфическое описание колонки донных отложений озера Торосярви.

contemporary publications on the ecology and taxonomy of certain cladoceran groups [Korovchinsky, 2004; Kotov *et al.*, 2016; Van Damme, Nevalainen, 2019]. All detected remains of the Cladocera were classified to species level, species group, or (in cases where they belong to a taxonomically complex group) only to genus level. The ecological and faunistic traits of the identified cladoceran species were accepted based on literature data [Orlova-Bienkowskaja, 2001; Korovchinsky *et al.*, 2021], taxon name verification was made based on the FADA database [Kotov *et al.*, 2013]. The scheme of Blitt and Sernander, adapted by Mangerud *et al.* [1974], is used for the periodization of climate changes.

Statistical and stratigraphic analyses were performed using the C2 program [Juggins, 2007] and the PAST 3.26 [Hammer *et al.*, 2001]. Faunal zones were delineated using CONISS cluster analysis in TILIA 2.0.b.4 with Edwards & Cavalli-Sforza's chord distance [Grimm, 2004]. The initial data are demonstrated in Supplement Table 1. Figures and microphotographs were developed using graphic editors Adobe Illustrator CC 2017, Adobe Photoshop 7.0, ZEN (Carl Zeiss, Germany), and Helicon Focus 7.0.2 (2018). Visualization of the geographical location of the lake was done in MapInfo Professional 7.0 software.

Results

Lithostratigraphic analysis and LOI

Based on visual inspection and analyses, the sediment thickness was subdivided into clearly defined lithostratigraphic units (from bottom to top): 290–225 cm — gray silty clay with black layers; 225–197 cm — gray silty clay; 197–168 cm — gray clay; 168–156 cm — dark-gray clay silt; 156–95 cm — light-brown silt; 95–89 cm — greenish-brown silt; 89–79 cm — light-brown silt; 79–70 cm — greenish-brown silt; 70–0 cm — dark-brown silt (Fig. 3).

Bottom sediments are characterized by a low content of organic matter (Fig. 3). The LOI decreases from top to bottom: dark-brown silt (0–70 cm) contains less than 20–30%, dark-gray clay silt (156–168 cm) shows 7–12%, and gray silty clay with black layers (290–225 cm) has less than 1%.

Cladocera analysis

The remains of 42 Cladocera taxa (species and species groups) belonging to 31 genera, 12 subfamilies, and seven families (Chydoridae (72.84%), Bosminidae (24.36%), Sididae (2.18%), Macrothricidae (0.41%), Daphniidae (0.1%), Cercopagididae (0.07%), Polyphemidae (0.03%)) were identified in the sediment core. Representatives of the family Chydoridae were the most abundant in terms of species diversity in the sediment samples, which is common for the cladoceran taphocenoses [Frey, 1986; Hofmann, 1986; Hann, 1989]. Predominants of the subfossil Cladocera community were *Bosmina* (*Eubosmina*) cf. *longispina* (23.51%), *Biapertura affinis* (16.68%), *Alona quadrangularis* (16.14%). The stratigraphic dia-

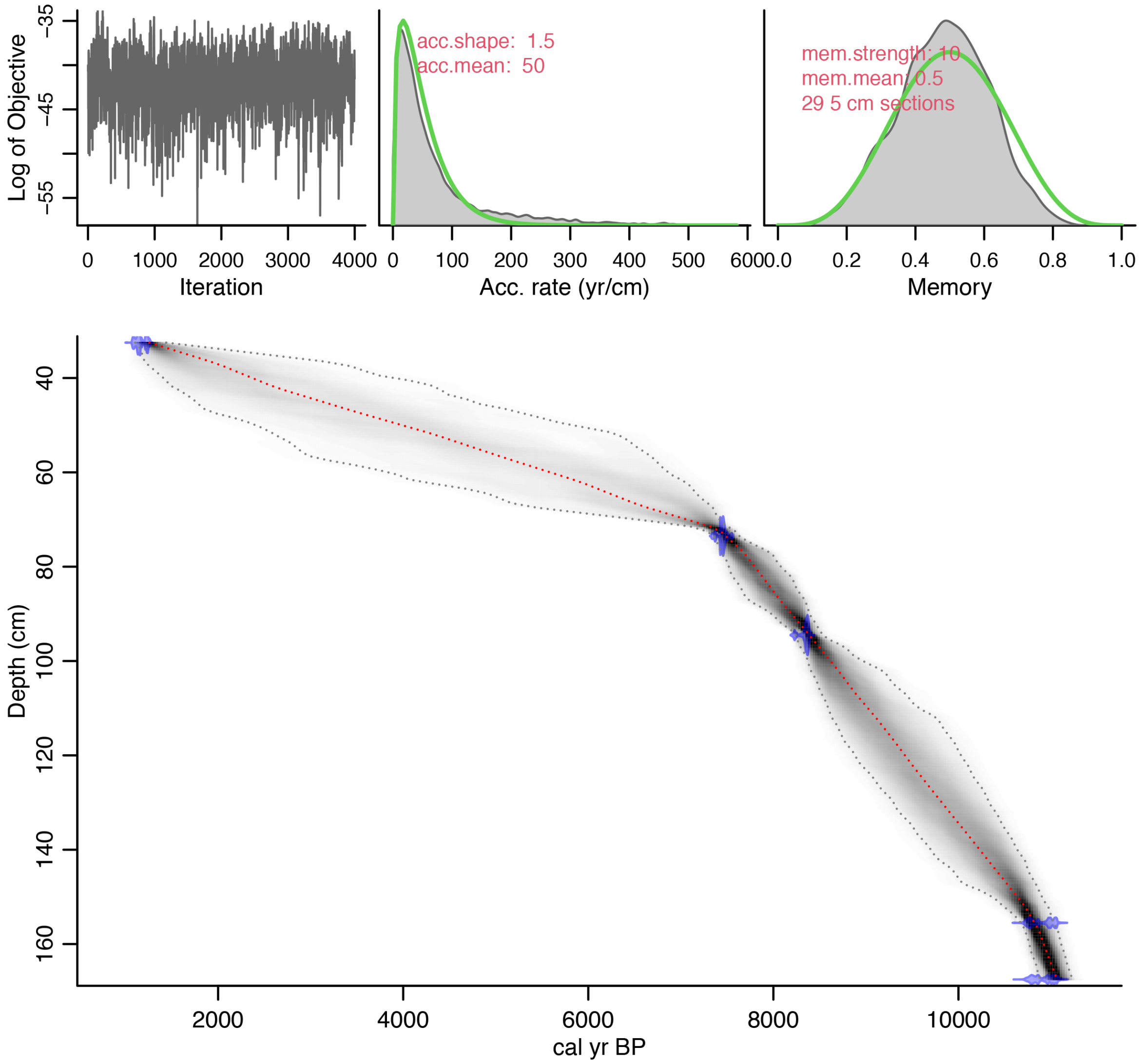

Fig. 3. Age model of the Lake Torosjarvi sediment core.

Рис. 3. Возрастная модель колонки донных отложений озера Торосярви.

gram of the cladoceran taphocenosis of Lake Torosjarvi was subdivided into five faunal zones (Fig. 4). To avoid confusion when describing the zones in the Part II, which includes statistical analysis of the qualitative data, it was decided to designate the zones as I, IIa, IIb, IIIa, IIIb. The dominant composition of Cladocera in each faunistic zone (I–IIIa) of the sediment cores from Lake Torosyarvi, indicating the depth of sample collection and the geological period to which they belong (Late Pleistocene (LP), Early Holocene (EH), Middle Holocene (MH), Late Holocene (LH)) is represented in the Table 2. Below we represent the main data on the changes within the communities of cladocerans in each designated faunistic zone.

Cladocera species structure from Late Pleiastocene till present days

Zone I: remains of 22 taxa of Cladocera were identified. Community was dominated by *Alonella nana* (29.03%) and *Chydorus* cf. *sphaericus* (20.84%) and subdominated by *B.* (*E.*) cf. *longispina* (10.92%), *Rhynchotalona falcata* (9.18%), *Paralona pigra* (6.7%) and *A. quadrangularis* (4.96%). *Bosmina longirostris* (2.73%) was noted here but the number of its remains decreased to the core top. Two head shields of *Rhynchotalona latens* were found in this zone and was not found in upper sediments of Lake Torosjarvi.

Zone IIa: remains of 24 Cladocera taxa were identified. Cladocera community was dominated by *A. quadrangularis* (27.19%) and *B.* (*E.*) cf. *longispina* (27.37%) and subdominated by *A. nana* (9.66%) and *C.* cf. *sphaericus* (4.8%) and *B. affinis* (8.05%). The relative abundance of *Rhynchotalona falcata* (2.32%) was decreased. The share of species occurring among submerged vegetation and their diversity increased — small *Alona* species, *Leydigia leydigi* (2.86%), *Acroperus harpae* (2.1%), *Eurycercus* sp. (0.54%), *Graptoleberis testudinaria* (0.36%),

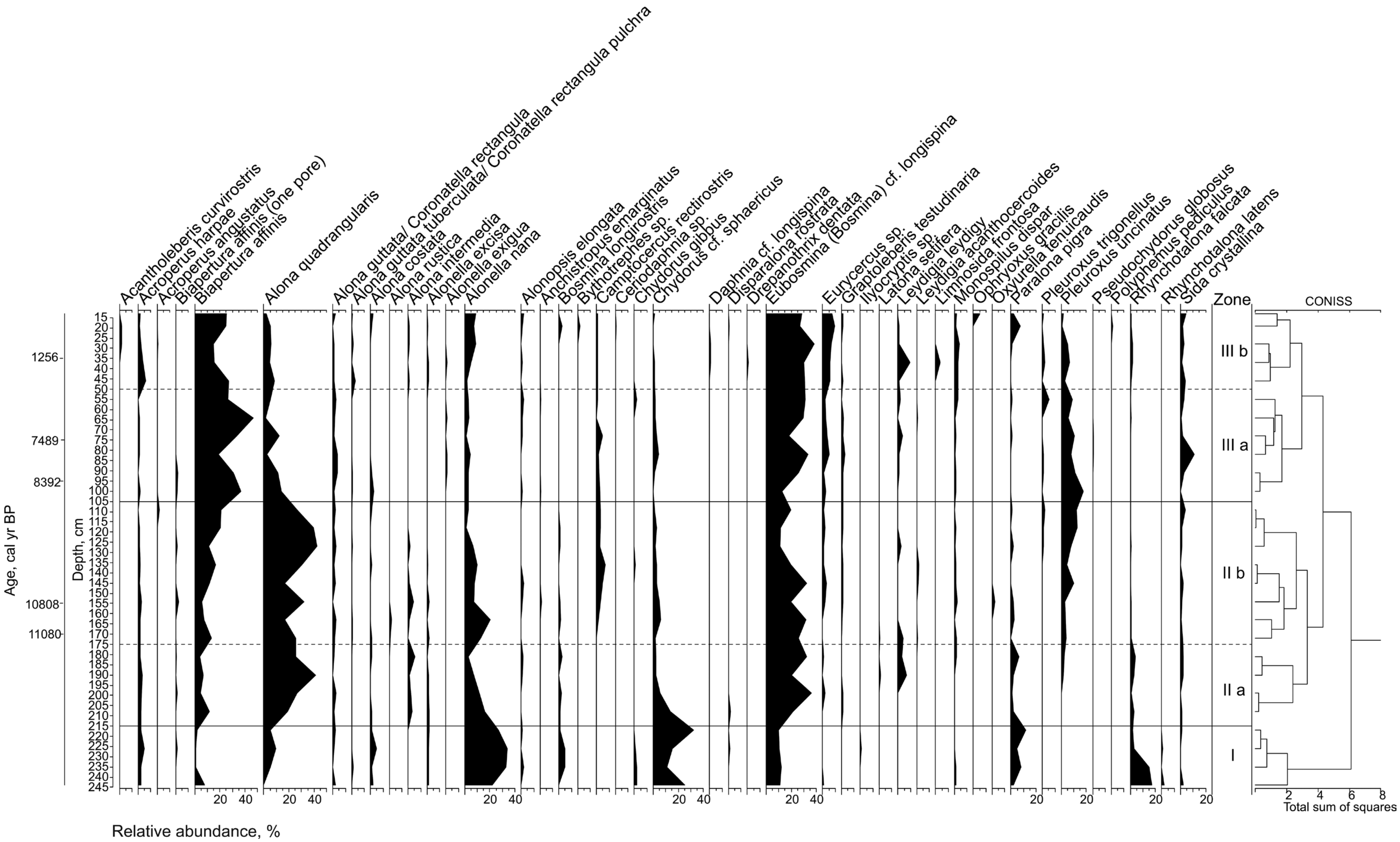

Fig. 4. Distribution of the cladoceran taxa in the sediment core from Lake Torosjarvi.
Рис. 4. Распределение таксонов Cladocera в колонке донных отложений озера Торосярви.

Table 2. Composition of predoninants and secondary species by faunal zones in the sediment core from Lake Torosjarvi.
Таблица 2. Состав субдоминантов и второстепенных видов в фаунистических зонах в колонки донных отложений озера Торосярви.

Zone	Depth (cm)	Period (cal. yr BP)	Predominants	Secondary species	Number of taxa
I	244–217	LP (12.9–11.6)	*A. nana* (29.03%), *C.* cf. *sphaericus* (20.84%)	*B.* (*E.*) cf. *longispina* (10.92%), *R. falcata* (9.18%), *A. quadrangularis* (4.96%), *P. pigra* (6.7%)	22
II a	217–181	EH (11.6–10.6)	*A. quadrangularis* (27.19%), *B.* (*E.*) cf. *longispina* (27.37%)	*A. nana* (9,66%) *u C.* cf. *sphaericus* (4.8%), *B. affinis* (8.05%)	24
II b	181– 118	MH (10.6–9.0)	*A. quadrangularis* (29.02%), *B.* (*E.*) cf. *longispina* (20.9%)	*B. affinis* (13.2%), *A. nana* (8.37%), *P. uncinatus* (7.32%)	31
III a	118–55	MH (9.0–5.8)	*B. affinis* (32.24%), *B.* (*E.*) cf. *longispina* (25.37%)	*A. quadrangularis* (7.61%), *P. uncinatus* (10.15%)	29
III b	55–13	LH (5.8–present days)	*B. affinis* (21.54%), *B.* (*E.*) cf. *longispina* (30.34%)	*A. quadrangularis* (5.24%), *A. nana* (6.37%), *Eurycercus* sp. (7.12%)	33

Zone IIb: remains of 31 Cladocera taxa were identified. Cladocera community was dominated by A. *quadrangularis* (29.02%) and *B*. (*E*.) cf. *longispina* (20.9%) and subdominated by *B. affinis* (13.2%), *A. nana* (8.37%), and *Pleuroxus uncinatus* (7.32%). Remains of *Camptocercus rectirostris* (3.53%), were found here for the first time.

Zone IIIa: subfossil remains of 29 taxa of Cladocera were identified. Cladocera taphocenosis was dominated by *B. affinis* (32.24%) and *B*. (*E*.) cf. *longispina* (25.37%) and subdominated by *A. quadrangularis* (7.61%) and *P. uncinatus* (10.15%). An increase of the portion of cladocerans associated with higher aquatic vegetation, e.g., *Eurycercus* sp. (2.83%) and *G. testudinaria* (1.19%) was observed. The share of *C. rectirostris* (1.94%) and *Sida crystallina* (3.28%) increased, while the share of *A. nana* (2.84%) and *Acroperus harpae* (0.75%) — decreased, remains of *Alona intermedia* completely disappeared.

Zone IIIb: remains of 33 Cladocera taxa were identified. Subfossil Cladocera community was dominated by *Biapertura affinis* (21.54%) and *B*. (*E*.) cf. *longispina* (30.34%); subdominated by *Alona quadrangularis* (5.24%), *A. nana* (6.37%), and *Eurycercus* sp. (7.12%). Representatives of *Daphnia* appeared, and the portion of *B*. (*E*.) cf. *longispina* increased. Remains of the predatory *Bythotrephes* sp. were found in this zone. An increase of the abundance of *A. nana* and *Ophryoxus gracilis* (1.12%) was noted, while the relative abundance of *C. rectirostris* (0.94%) and *Sida crystallina* (2.8%) decreased. Remains of *Limnosida frontosa* (0.75%) and *Drepanothrix dentata* (0.19%) were found in this zone.

Discussion

General notes

The taxonomic composition of the subfossil cladoceran community in the sediment core is typical of the study region [Ibragimova *et al*., 2016, 2017, 2918]. The most abundant species of the Cladocera community found in Lake Torosjarvi are also typical of the region [Smirnov, 2010; Ibragimova, 2021]. They inhabit different types of boreal water bodies, ranging from oligo-dystrophic to eutrophic [Chengalath *et al*., 1984; Flössner, 2000; Smirnov, 2010; Nevalainen *et al*., 2008, 2011; Ji *et al*., 2015] and tolerant to low organic matter and acidophilic environmental conditions [Mäemets, 1961; Flössner, 2000; Van Damme, 2008]. The change in the composition of Cladocera during the Late Pleistocene–Holocene occurred according to the standard scenario for the study region, as well as for other regions of boreal Europe: the early colonizers, represented by cold-water species inhabiting the open littoral in low organic matter conditions, were replaced by pelagic taxa and species that prefer more favorable environmental conditions [Smirnov, 2010; Milecka *et al*., 2011; Zawisza *et al*., 2016; Ibragimova *et al*., 2016, 2017, 2018; Ibragimova, 2021; Nazarova *et al*., 2020]. In general, the dominance of *C*. cf. *sphaericus* during the Late Pleistocene was common not only for the Kola-Karelia region, taphocenoses dominated by it are among the most common worldwide [Smirnov, 2010]. This group of species can successfully inhabit both the littoral and pelagic zones from eutrophic to oligotrophic water bodies, with the latter condition apparently being characteristic of the early stages of water body filling after the end of Last Glaciation [Fryer, 1968; Flössner, 2000; Kotov, 2016; Korovchinsky *et al*., 2021]. The further climate change and deepening of the lake, associated with the infilling of lake depression by glacial waters, led to an increase in the pelagic part of the water body and the development of new substrates, which, in turn, affected the structure of the Cladocera community. The lake was cold-water, oligotrophic, and rather deep, as confirmed also by the results of diatom analysis of a short core from Lake Torosjarvi [Shelekhova, Tikhonova, 2022]. The subfossil complex of Cladocera from Lake Torosjarvi was represented by 42 taxa, which exceeds the number previously identified in the regional taphocenoses: in individual lakes of the Kola-Karelian region maximum 40 taxa were previously identified [Ibragimova, 2021]. Either pelagic (*B*. (*E*.) cf. *longispina*) or littoral taxa (*C*. cf. *sphaericus*, *A*. *nana*, *A*. *quadrangularis*, *B*. *affinis*) were characterized by maximal abundance in communities depends on stages of the lake history (Table 2). However, in previous studies, *A. quadrangularis* was only subdominant in subfossil Cladocera communities and was not previously listed among the dominants [Smirnov, 2010; Ibragimova, 2021]. *A. quadrangularis* prefers silt and soft flocculent organic substrates, while *B. affinis* is found on various littoral substrates [Van Damme, Dumont, 2008; Smirnov, 2010].

Findings of remains of head shields with distinctive structural features (aberrations) is another feature of Cladocera community of the Lake Torosjarvi. Aberrations of the head shields of *Biapertura affinis* (Fig. 5E–F) were observed throughout the entire core of the bottom sediments of Lake Torosjarvi, starting from the bottom layers dated as belonging to the Late Pleistocene. The same aberrations were previously detected among subfossil remains from Lake Rubskoye [Ibragimova *et al.*, 2019] and reason of such aberration has not been found yet. Normal individuals of this species have a head shield with a triangular posterior portion and two connected major head pores [Szeroczyńska, Sarmaja-Korjonen, 2007; Sinev, Dadykin, 2022]. A significant number of head shields of this species, characterized by the presence of only a single pore, have been found by us in the lake Torosjarvi.

Our results demonstrate that the dominant complex in the cladoceran taphocenosis of Lake Torosjarvi has changed twice since its formation. Below are discussed the features of the formation of cladoceran taphocenosis in each period.

Cladocera species structure from LP till present

Zone I (Late Pleistocene). Late Pleistocene climate conditions of that period: the average annual temperature was 5–9° lower than present, (°C) in July it was 3–6° and in January 8–14° lower, with precipitation being 175–250 mm/year less [Filimonova, Lavrova, 2015]. The dominance of *A. nana* was also reported from some lakes in Finland [Sarmaja-Korjonen *et al.*, 2006; Smirnov, 2010] and West Karelian Upland [Nazarova *et al.*, 2020; Ibragimova, 2021; Subetto *et al.*, 2022]. Podzolic soils in Karelia were formed on coarse sandy and carbonate-free moraine sediments; they are acidic and poor in bases and humus [Kravchenko, 2007], which may explain the predominance of *A. nana*. *Paralona pigra*, which was unusually abundant among the cladocerans during the initial period of Lake Onega's formation [Smirnov, 1978], was also reported as one of the early colonizers of the Lake Torosjarvi and Lake Yujnoye Haugilampi [Ibragimova, 2021; Subetto *et al.*, 2022]. Findings of *Rhynchotalona latens* remains, considered to be sensitive to climate changes [Nevalainen *et al.*, 2019; Van Damme, Nevalainen, 2019], also confirm cold temperatures and oligotrophic conditions in Lake Torosjarvi in Late Pleistocene [Nevalainen *et al.*, 2019; Sinev, Dadykin, 2022; Ibragimova *et al.*, 2024a]. The proportion of pelagic species in this zone was negligible, they were represented by pelagic cold-water forms of the genus *Bosmina*. The greater development in the lake was achieved by *B*. (*E*.) cf. *longispina*, which is likely also related to the fact that it is more tolerant of low pH than *B. longirostris*. Thus, at the initial stage of its formation, the lake was cold-water, shallow, with some areas covered by aquatic vegetation and a well-represented zone of open littoral.

Zone IIa (Pre-boreal period). Changes in subfossil Cladocera community of that period corresponded to the climatic events and a major restructuring of the hydrographic network, occurring with the Fennoscandian Ice Sheet melting [Subetto, 2009; Stroeven *et al.*, 2016] lead to significant change in dominance species structure of taphocenoses. In the Early Holocene climate became suddenly warmer and more humid [Borzenkova *et al.*, 2015; Boyes *et al.*, 2024]: annual temperatures were 4 °C lower as compared to present, e.g. average July temperatures were 2 °C and January 6 °C lower than now; average annual precipitation was 150 mm less [Filimonova, Klimanov, 2005]. Conditions were still unfavorable for cladocerans, which is confirmed by presence of cold-water species: *Alona intermedia* and *Latona setifera* [Kotov *et al.*, 2010; Błędzki, Rybak, 2016]. Numerous small residual lakes formed as a result of the regression of large glacial reservoirs in that period, what may explain the increase in the proportion of pelagic *B*. (*E*.) cf. *longispina* [Flössner, 2000; Kotov, 2016]. The increase in abundane of this species in the early Holocene was synchronous across many lakes in NW Russia and in lakes in Europe — Germany, Poland, and Finland [Smirnov, 2010; Szeroczyńska, 2019; Korhola, Rautio, 2001], which were flooded by waters from glacial water bodies. The widespread accumulation of organogenic sediments began, although the inflow of mineral particles into water bodies remained significant. During this time, Lake Torosjarvi was separated from a larger body of water, marking a change in sedimentation patterns and an increase in organic matter (gray clay — dark-gray clay silt — light-brown silt, with an increase in LOI from 1 to 15%), which is confirmed by the increase in the share of *A. quadrangularis* [Van Damme, Dumont, 2008; Smirnov, 2010] and representatives of the genus *Leydigia* [Frolova, 2011]. It is important to note that we are not discussing separation of Lake Torosjarvi from the Onega Ice Lake, as the separation of the northern part of the latter (including large Segozero Lake) occurred earlier (around 13,200 cal. yr BP); instead, we discuss its separation from the Segozero glacial lake [Biské, 1959]. The development of higher aquatic vegetation is also shown by the occurrence of *G. testudinaria*, which lives on the leaves of submerged macrophytes [Fryer, 1968; Kotov *et al.*, 2010] (Fig. 5D). According to the results of our analysis, Lake Torosjarvi was characterised as an oligotrophic cold-water body with a developed littoral zone and macrophyte area, showing a tendency to increase in the proportion of organic matter and water content.

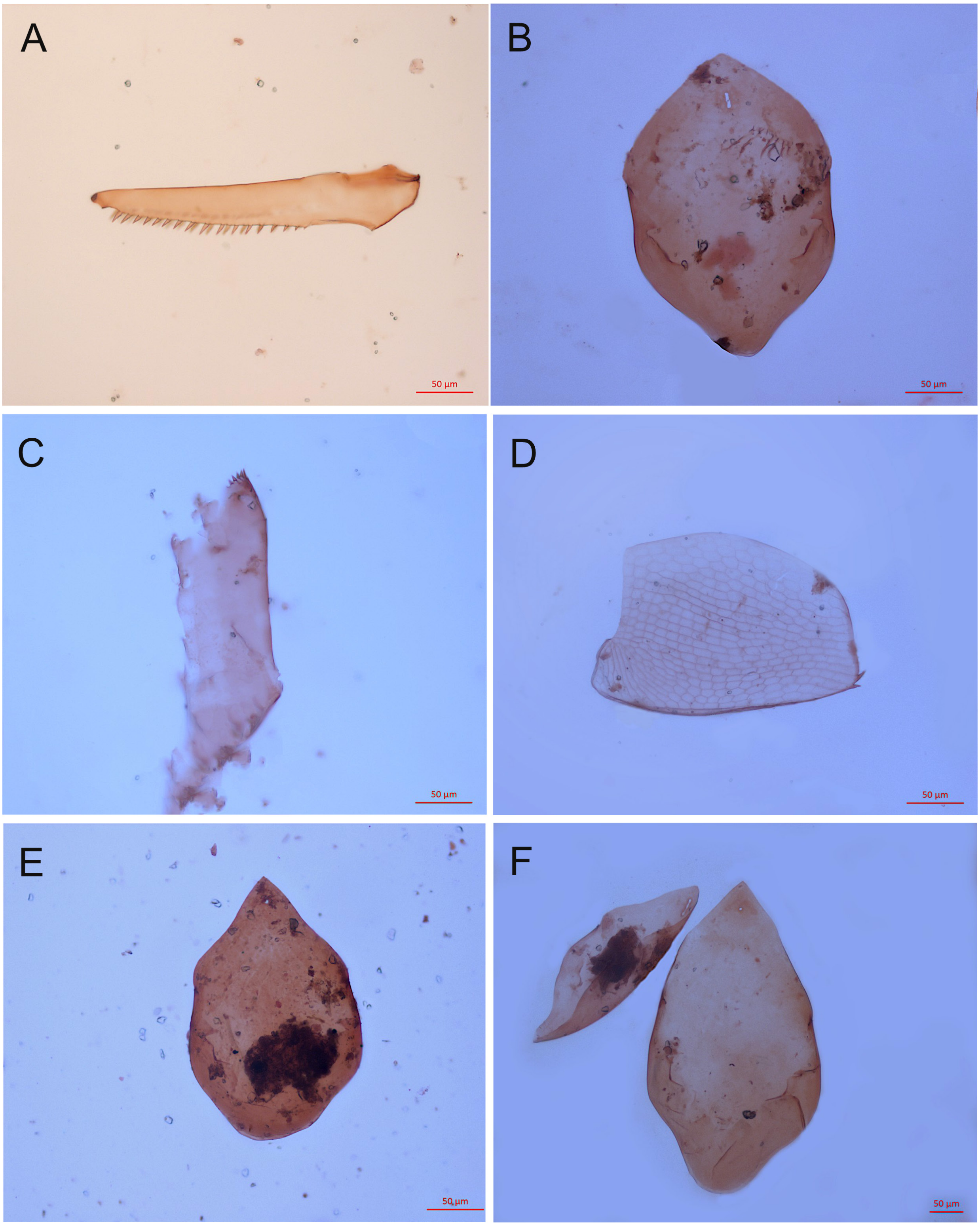

Fig. 5. Subfossil remains of some cladocerans found in the bottom sediments of Lake Torosjarvi: A — postabdomen of *Camptocercus rectirostris*; B — head shield of *Leydigia acanthocercoides*; C — 2nd segment of exopodite of *Sida crysyallina*; D — carapace of *Graptoleberis testudinaria*; E — head shield of *Biapertura affinis* with a single head pore; F — from left to right, head shield of *Alona quadrangularis*, head shield of *B. affinis* with a single head pore.

Рис. 5. Субфоссильные остатки некоторых видов Cladocera, обнаруженные в колонке донных отложений озера Торосярви: A — постабдомен *Camptocercus rectirostris*; B — головной щит *Leydigia acanthocercoides*; C — 2-й сегмент экзоподита *Sida crysyallina*; D — створка раковины *Graptoleberis testudinaria*; E — головной щит *Biapertura affinis* с одной головной порой; F — слева направо, головной щит *Alona quadrangularis*, головной щит *B. affinis* с одной головной порой.

Zone IIb (Boreal period). This zone covered the end of the Pre-boreal and the Boreal period with continually increase of temperature, annual average was 2.5 °C lower than present, in July it was 1.5 °C and in January 3.5°C lower than present, the precipitation was also decreased to 25 and 75 mm/year, respectively [Filimonova, Lavrova, 2015]. Changes in climate may explain appearance of *C. rectirostris* (Fig. 5A), which prefers heavily overgrown and low-productive lakes, ponds, and rivers; it thrives among detritus-rich macrophyte thickets and detritus over sandy soils [Flössner, 2000]. The increased proportion of *C. rectirostris* is generally attributed to milder environmental conditions and usually found in more southern regions [Flössner, 2000; Szeroczyńska, Zawisza, 2011; Milan *et al.*, 2017]. According to lithostratigraphic analysis of bottom sediments, this zone corresponded to the transition from clayey, organic-poor sediments to sapropels, confirming the change of conditions in the lake. Moreover, it has been observed that in the lakes of the Kola-Karelian region previously studied by us, *C. rectirostris* abundance increases when organic matter content rises [Ibragimova, 2021]. Thus, the taxon proves its indicator ability in terms of organic matter content and climate change. Relative abundance of *A. quadrangularis* and *Leydigia* (Fig. 5B) was also increased with organic content of the Lake Torosjarvi. The composition of Cladocera taphocenosis indicates a further development of the vegetation zone in the lake, an increase in trophic status, and climate warming in the study region.

Zone IIIa (Atlantic period). The climatic optimum of the Holocene, which was characterized by further increase in mean annual temperatures, in June it was by 1.0–2.5 °C and in January — by 1–4 °C higher than present-day temperatures, precipitation was 100–150 mm/year higher [Filimonova, Klimanov, 2005]. During this time, fine-detrital sapropels and diatoms, specifically light-brown silt (with LOI greater than 20%), intensively accumulated in the lakes, which confirms the change in environmental conditions in the study region and raise to change in dominant species structure of cladocerans and the ratio of pelagic to littoral species of the Lake Torosjarvi. Taphocenoses were characterised by the increase of phytophilous species abundances (e.g. *Eurycercus* sp. and *G. testudinaria*) confirmed the softening of climatic conditions in the study region. Thus, the proportion of warm-water species (*C. rectirostris*, *S. crystallina*) [Kudrin, 2016] increased, while the proportion of northern taxa (e.g. *A. nana*, *A. intermedia*) decreased. Observed decrease in share of *A. quadrangularis* observed in our study contradict with previous results [Ibragimova, 2021; Ibragimova *et al.*, 2024b] and we suggest that the use of this taxon as an indicator of organic matter content requires more detailed study of the prevailing environmental factors. Thus, this cladoceran taphocenosis indicated favorable climatic conditions, an increase in lake water levels, and the development of higher vegetation zone.

Zone IIIb (Subboreal and Subatlantic periods). The shift towards northern Cladocera species confirms sharp cooling and a decrease in hydration, which evidently was caused by a reduction in solar radiation during the summer months [Berger, Loutre, 1991]: mean annual temperatures became higher than present-day levels by 1.0–2.0 °C in Subboreal (1 °C lower and in January 2 °C lower than today in Subatlantic period), while precipitation decreased by 50 mm/year [Filimonova, Klimanov, 2005]. The levels of previously formed lakes have been lowered, and water mineralization and pH have decreased [Shelekhova, Lavrova, 2011], which is consistent with the increase of relative abundance of acidophilic species *A. nana*. The further overgrowth and swamping of lakes' shores [Subetto *et al.*, 2022] correlated with an increase of phytophilous *A. harpae* and appearance of *Ophryoxus gracilis* [Kotov *et al.*, 2010] in Cladocera community. A drop in organic content (from 24 to 15%) followed by its increase (up to 20 and 30%). The decrease in organic matter was correlated with reduction decrease in relative abundance of *C. rectirostris*. The proportion of pelagic species increased, likely related to the increase in deep-water areas of Lake Torosjarvi. The appearance of *Bythotrephes* sp. in water bodies was associated with a decrease in the number of planktivorous fish, which served as a food source, and/or an increase in the proportion of small planktonic animals that served as food for *Bythotrephes* [Fefilova *et al.*, 2014]. It is likely that the increase in large-sized cladoceran taxa (*B. affinis*, *C. rectirostris*, *Eurycercus* sp.) contributed to the rise in the share of *Bythotrephes* in the taphocenosis of Lake Torosjarvi. The rise in the share of *Bythotrephes* is also often attributed to a deterioration in habitat quality or warming [Fefilova *et al.*, 2014]. Notably, only in this zone we have found remains of *Limnosida frontosa* and *Drepanothrix dentata* — indicators of oligotrophic conditions [Kotov *et al.*, 2010; Błędzki, Rybak, 2016]. In Zone IIIb, changes in the distribution of cladoceran taphocenosis were associated with cooling and deepening of the lake, while areas of macrophytes remained well-developed.

Conclusion

The Cladoceran taphocenosis of the Lake Torosjarvi confirmed the synchronicity of changes in the community occurring in the Late Pleistocene–Holocene for the Kola-Karelia region and for other regions of boreal Europe. Similarities and differences in the formation of taphocenoses were identified. The early colonizers of Cladoceran taphocenosis of Lake Torosjarvi represented by cold-water species inhabiting the open littoral in low organic matter conditions, were replaced by pelagic taxa and species that prefer more favorable environmental conditions. Subsequently, an increase in species diversity was observed; a total of 42 Cladocera taxa (species and species groups) belonging to 31 genera, 12 subfamilies, and seven families have been identified in the lake taphocenosis. The structure of the subfossil community has undergone two changes in the predominant complex, which were associated with both changes in climatic conditions in the study region and fluctuations in the lake water levels due to its separation from a larger lake. The indicator capacity of Cladocera species regarding organic composition, water level and climate change was also confirmed. According to cladoceran analysis (as well as based on the diatom analysis), Lake Torosjarvi was cold-water, oligotrophic, and rather deep during its existence.

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 Excel-tables are available online.

Supplementary Table 1. Taxonomic structure and distribution of the cladoceran taxa in the sediment core from Lake Torosjarvi.

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