

***Bythotrephes* Leydig, 1860 (Crustacea: Cladocera: Onychopoda) of Lake Onega**

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ABSTRACT: Lake Onega is one of the largest reservoirs in Europe and in the world with oldest history of its studies. In particular, the zooplankton studies of large Russian reservoirs started here for the first time in the 1860s. The taxonomic composition of this community is now known relatively adequately, but at a fairly routine level. In Lake Onega, representatives of the genus *Bythotrephes* Leydig, 1860 (Crustacea: Cladocera) were described for the first time at the end of the 19th century. Their exact identification was changing several times over a long period of studies. In general, in different periods they were attributed to three species and two interspecific hybrid forms. A study based on investigation of old (museum) material and samples recently collected in the lake led us to the conclusion that the local population belongs to the interspecific hybrid form *B. brevimanus* x *B. cederstroemii*.

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KEY WORDS: *Bythotrephes*, Cladocera, Lake Onega, taxonomic status, interspecific hybrid form.

***Bythotrephes* Leydig, 1860 (Crustacea: Cladocera: Onychopoda) Онежского озера**

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РЕЗЮМЕ: Онежское озеро входит в число самых крупных и давно исследуемых водоемов Европы и мира. В частности, здесь впервые в России в 1860-х гг. началось исследование зоопланктона крупных водоемов, состав которого теперь известен относительно полно, но на достаточно рутинном уровне. Представители рода *Bythotrephes* были описаны в Онежском озере впервые в конце XIX века, за долгий период исследований их систематическое положение менялось. В целом в разные периоды их относили к трем разным видам и двум межвидовым гибридным формам. Исследование, проведенное с использованием старого музейного и нового коллекционного материала, привело к выводу о принадлежности местной популяции к межвидовой гибридной форме *B. brevimanus* x *B. cederstroemii*.

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КЛЮЧЕВЫЕ СЛОВА: *Bythotrephes*, Cladocera, Онежское озеро, таксономическое положение, межвидовые гибридные формы.

Introduction

Kessler (1868) was the first researcher who studied zooplankton of Lake Onega, the large lake where the plankton was investigated for the first time in Russia. At the same time, it is necessary to clarify that zooplankters obtained by him were recovered exclusively from fish stomachs rather than from water depth. Any specimens of *Bythotrephes* Leydig, 1860 (Crustacea: Cladocera) have not been recorded among them. Only thirty years later, Linko (1898) found this crustacean in the plankton samples from the lake and identified them as belonging to two species: *B. longimanus* Leydig, 1860 and *B. cederstroemii* Schödler, 1877. The latter species was recorded for the first time in Russia (Korovchinsky, 2015).

Several following researches recorded there either *B. longimanus* (or *B. l.* var. *connectens*) or *B. cederstroemii* (Veselov, Korovina, 1932; Smirnov, 1933; Gerd, 1946; Polivannaya, 1954) until Smirnova (1972) has revealed the presence of only one species, *B. longimanus*, based on approach of Mordukhai-Boltovskaya (1959) who regarded two aforementioned taxa as only forms of a single species, *B. longimanus*. Starting from the 19th century, no one figure of the morphological features of the local specimens of the genus has been presented.

The modern taxonomic revision of the genus *Bythotrephes* (Litvinchuk, 2002, 2007; Korovchinsky, 2015, 2018) has confirmed the validity of the two above mentioned species as well as the existence of interspecies hybrid forms (Litvinchuk, 2002, 2007; Litvinchuk, Litvinchuk, 2016; Korovchinsky, 2019) the presence of which misleads zooplanktonologists much. The hybrid form *B. brevimanus* x *B. cederstroemii* is especially common and widely distributed (Korovchinsky, 2019, 2020). Its representatives are morphologically variable and closely resemble those of *B. cederstroemii*, distinguishing from it only in minor features which are seen best in a sufficient set of

individuals rather than in single specimens what makes it possible to assess the morphological variability.

In the course of the aforementioned modern taxonomic revision, the specimens of the genus from Lake Onega have also been investigated but, however, with controversial results. Initially, they were attributed both to *B. cederstroemii* and the hybrid form *B. brevimanus* x *B. cederstroemii* based on morphological and biochemical (allozyme) data (Litvinchuk, 2002; Litvinchuk, Litvinchuk, 2016). Then, the reassessment of morphological diagnostic features has led to the conclusion of the presence of another hybrid form, *B. cederstroemii* x “*B. crassicaudus*”, in the lake (Korovchinsky, 2015). Soon, such approach was found to be incorrect and the specimens from Lake Onega have been attributed to *B. cederstroemii*, though the presence of hybrids in the lake was not excluded as well (Korovchinsky, 2018). In the following publications, the local representatives have been attributed either to the hybrid form *B. brevimanus* x *B. cederstroemii* (Korovchinsky, 2019) or to *B. cederstroemii* (Korovchinsky, 2020).

In the recent publications on zooplankton of Lake Onega, the representatives of the genus *Bythotrephes* are often excluded from the examination due to their comparative rarity (see Kulikova *et al.*, 1997; Lake Onega: Atlas, 2010; Syarki, Fomina, 2019a, b). Only in a single publication (Kuchko, Kuchko, 2010) they were identified as *B. brevimanus* (Lilljeborg, 1901).

Thus, by now, the representatives of *Bythotrephes* of Lake Onega have been attributed by different researchers to three different species, *B. longimanus*, *B. cederstroemii*, *B. brevimanus*, and two hybrid forms. The present investigation aims to describe the local *Bythotrephes* population and resolve its taxonomic status based on results of recent taxonomic revisions of the genus and morphological investigation of more abundant material.

Material and methods

LOCALITY. Lake Onega, which lies on the southeastern edge of the Baltic Shield, is a part of the terminal unit of the vast drainage system of North-west Europe. Its present state was formed about 2000 years ago. This lake, with an area of 9.69 thousand km², together with the even larger Lake Ladoga, is the largest lake in Europe and among the second dozen of the world's largest lakes.

The aquatic ecosystem of Lake Onega formed under cold-water conditions, low concentrations of mineral nutrients for autotrophic organisms, and abundant input of phyto-organic matter to the lake. The variability of temperatures, hydrochemical and hydrodynamic conditions, together with diverse river inflows along the lake perimeter, created special conditions for spatial variations among the developing biota. Subsequent human activities, which have intensified during recent decades, have increased the nutrient and toxic inflow to the lake. This has changed its ecological functions and transformed the aquatic communities. It has also increased the spatial differentiation of the ecosystem (Mandych *et al.*, 1995).

The lake habitats are very diverse in terms of thermal, hydrodynamic, and hydrochemical conditions. This is because of the rather indented shoreline, a great number of bays and inlets, varying depths of the limnic zone, and irregular river discharges along the shores. Seasonal and annual fluctuations of the climatic factors and river discharges cause considerable temporal variability among the zooplankton community, which comprises more than 200 species, including Rotatoria, Cladocera and Copepoda (Kulikova, 1990; Mandych *et al.*, 1995). The ecosystem of Lake Onega, including fish and zooplankton, had been studied since the 1860s and may be considered one of the longest surveyed lake biota in the world.

ABBREVIATIONS. Morphology: ad — adult parthenogenetic females; BL — body length; CPCL — length of proximal claws of caudal process; CPL — length of caudal process; gam — gamogenetic females; ICD — distance between postabdominal claws and proximal claws of caudal process (interclaw distance); ICTh — thickness of caudal process between postabdominal claws and proximal claws of caudal process (interclaw thickness); juv — juvenile females and males; PCL — length of postabdominal claws; TIL — length of the thoracic limb of first pair (tl I). Museums: MNB — Museum für Naturkunde (Berlin, Germany), ZIN — Zoological Institute of the Russian Academy of Sciences (St.-Petersburg, Russia)

MATERIAL: 1) Bottle (MNB) with a tube labeled "Onega Lake, Aug 1890..?", H. Linder, *Bythotrephes Cederströmii* Schödler", 5 ad, 4 males, 1

juv; 2) Two total mounts, 1898, ZIN, coll. A. Linko, 3 ad; 3) Bottle (ZIN, № 73-915) labeled "Collection by A.K. Linko" with 17 tubes, one of them with a label "Lake Onega" (probably all samples originate from this lake), in total, 87 ad and 27 juv (due to body deformation these specimens were not suitable for morphometric measurements); 4) specimens from Lake Onega collected in 1993–2010s by M.T. Syarki, 20 ad, 2 gam, 3 males, 4 juv.

METHODS. Specimens were examined using the dissecting microscope Lomo MBS-10 and a compound microscope, Olympus BX-41 with *camera lucida*. Body measurements were made according to the scheme by Korovchinsky (2015) on adult females. In total, the values of seven measurements were calculated and analyzed by application of statistical parameters (M, SD, CV).

Results

BRIEF DESCRIPTION OF THE STUDIED SPECIMENS. Data on body and body parts measurements of specimens from Lake Onega are presented in Table 1.

Female. *Body* is elongated and divided into four parts: head, thorax, abdomen, and postabdomen with a long caudal process. Its longitudinal axis is conspicuously incurved when the head is located at an almost right angle to the thorax. Also, the highly movable abdomen can be either in a straight line with the thorax or stay at different angles to it. The head is large with a rounded anterior part filled by an enormously developed compound eye and bears small antennules ventrally. The posterior part of the head bears long swimming antennae, mouth parts consist of mandibles, maxillules (mx I), and upper lip (labrum). Thorax with strongly developed muscular ventral side bearing four pairs of thoracic limbs of different size directed antero-ventrally. Dorsally, the thorax bears a sack-like carapace transformed into a brood pouch, sometimes reaching a large size. The abdomen (metasome) is elongated, cylindrical, inconspicuously three-segmented (see Korovchinsky, 2015) and flexible, connected with a small postabdomen, bearing ventrally a pair of claws and posteriorly a long caudal process with one or two pairs of claws proximally. The body length of females (without the caudal process) reaches 2.7 mm, while the length of caudal process may exceed the body length by 2.0–2.7 times (on average, about 2.4 times).

Swimming antennae are comparatively long, with an elongated cylindrical basipodite which has a thin dorsal feathered seta on its folded proximal part. Of the two antennal branches, the upper branch (exopodite) is four-segmented and the lower branch is three-segmented. The general formula of antennal

Table 1. Data on body and body parts measurements of the *Bythotrephes*' specimens collected in Lake Onega in 1993–2010s (in columns, from top to bottom: range, M, SD, CV) (n = 22) (other abbreviations see above)

Таблица 1. Данные промеров размеров тела и его частей у 22 особей *Bythotrephes*, собранных в Онежском озере в 1993–2010-х гг. (в каждой колонке сверху вниз: пределы изменчивости, среднее значение (M), среднее квадратичное отклонение (SD) и коэффициент вариации (CV)) (другие сокращения см. выше).

BL, mm	TIL : BL, %	CPL : BL, %	PCL : BL, %	CPCL : BL, %	ICD : BL, %	ICTh : BL, %
2.0–2.7	62.3–79.3	207–268	3.5–19.7	3.3–13.4	15.1– 50.7	3.4–6.0
2.3	71.9	237	8.6	7.4	28.7	4.4
	1.9	20.6	1.7	2.7	9.4	0.6
	2.7	8.7	19.9	36.4	32.9	13.2

setae: 0–1–2–5/1–1–5 (see Korovchinsky (2015) for more details).

Carapace resembles a bag-like structure, strongly modified into a closed brood pouch widely connected in its base with the dorsal surface of the thorax. It may often be well developed and massive, being filled by large embryos.

Four pairs of *thoracic limbs* which are strongly chitinized, stenopodous and directed antero-ventrally. All of them have complex and variously setaceous armament along their inner sides. Limbs of the three anterior pairs are five-segmented and those of the last, fourth pair are three-segmented. The first pair of limbs (tl I) are especially long and strong, their length is comparatively short (minimally 62%, on average 72% of body length). The first segment of the endopodite is long and bears a few lateral setae and distally a shorter anterior seta and long posterior seta (Fig. 1P). The second segment of the endopodite is conspicuously shorter and bears only two apical setae, similar to those on the end at the previous segment but usually shorter (Fig. 1Q).

“*Postabdomen*” actually consists of two parts: the last small abdominal segment and the postabdomen *per se* (see Korovchinsky, 2015), which is comparatively small, with the anal opening situated between the postabdominal claws. These claws are of very different sizes (3.5–19.7%, on average 8.6% of body length) (Table 1) and shape (Fig. 1A–K).

Caudal process is directly connected with the postabdomen and proceeds as a very long, proximally thicker spine-like structure, variable in its length (207–268%, on average 237% of body length), thus exceeding the body length by 2.0–2.7 times. Generally, the caudal process is strongly chitinized and its surface covered by numerous minute spinules. The caudal process may often be straight (in 66% of all specimens) or more rarely, bears a rather developed bend bearing small curved denticles (10%) (Fig. 1L,

M); in other cases, this bend may be slightly developed (10%) or only small denticles are present in its place (14%) (Fig. 1N, O). Basally, the caudal process bears one or two pairs of claws similar or not similar to those of the postabdomen but usually smaller (e.g., proximal claws reach 3.3–13.4% of body length) (Table 1). Pairs of claws sit either close or quite distant to each other (e.g., distance between postabdominal claws and proximal claws of caudal process (interclaw distance) constitutes 15.1–50.7%, on average 28.7% of body length). Between the latter, the thickness of the structure may be different: 3.4–6.0%, on average 4.4% of body length. Body length 2.0–2.7 mm.

Gamogenetic females differ from parthenogenetic ones only in the presence of two-four large yellow-brownish resting eggs (0.43–0.45 mm in diameter) in their brood pouches. Body length 2.4–2.6 mm.

Males have the comparatively shorter thoracic limbs of the first pair (tl I) as well as each segment of them, especially the distal one, which is slightly swollen proximally and bears on its inner side a small strongly chitinized clasping hook with two inner denticles, and a field of tiny prominences situated under it. The copulatory appendages are small and armed with numerous minute spinules terminally. The caudal process always bears one pair of claws. Body length 1.8–2.5 mm.

INTRAPOPULATIONAL VARIABILITY. All the measured parameters shown in Table 1 demonstrate the increased morphological variability of the studied specimens, which is especially characteristic of the shape and size of postabdominal and caudal process' claws as well as of interclaw distance (the highest values of CV = 32.9–36.4) (Table 1).

According to the shape of postabdomen and caudal process' claws, a number of specimens may be attributed either to “*B. cederstroemi*” (Fig. 1A,

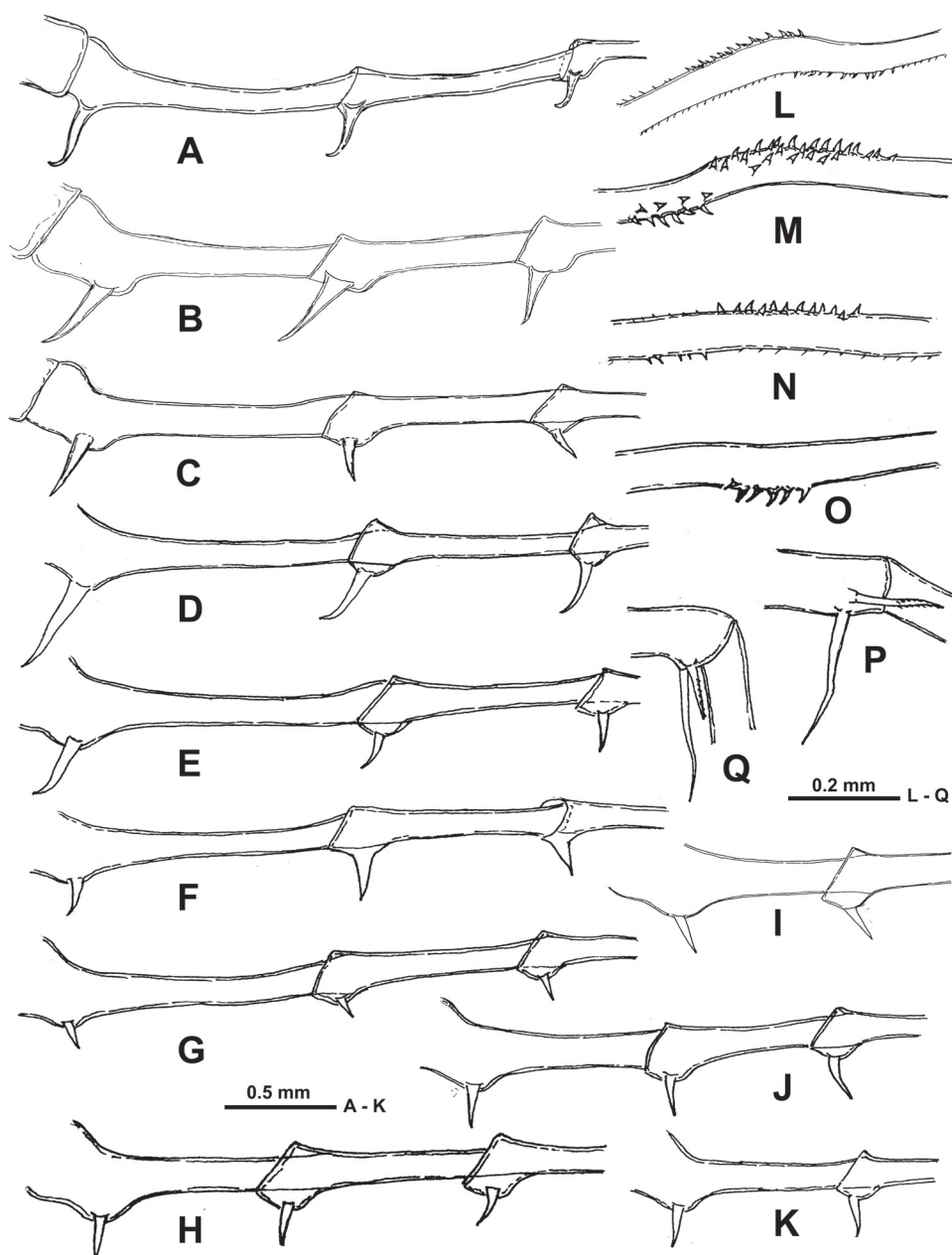


Fig. 1. Body parts of *Bythotrephes*' specimens from Lake Onega (A–C, L — specimens from the collection by A.K. Linko (1890s); D–K, M–Q — specimens collected in 1993–2010s. A–K — postabdominal and caudal claws; L–O — bend or its rudiment of caudal process; P, Q — setae of distal end of 1st and 2nd endopodite segments of the thoracic limb of 1st pair (tl I), respectively.

Рис. 1. Части тела особей *Bythotrephes* из Онежского озера (A–C, L — особи из коллекции А.К. Линко (1890-е гг.); D–K, M–Q — особи, собранные в 1993–2010-х гг. A–K — коготки постабдомена и каудального выроста; L–O — изгиб или его рудимент на каудальном выросте; P, Q — щетинки дистального конца 1-го и 2-го члеников эндоподита 1-й пары торакальных конечностей соответственно.

B, D, E) or to "*B. brevimanus*" (Fig. 1G, I, J, K). However, most of them possess a straight caudal process lacking a denticulated bend (66%) whereas in other specimens a process bears more or less developed bend or at least traces of its presence. A considerable number of specimens have a claw armament of intermediate appearance (Fig. 1C, F, H).

Discussion

Lake Onega is the first large Russian lake which was surveyed in respect of zooplankton. It is listed among few well studied lakes with respect to cladoceran species richness (Dumont, Segers, 1996). However, it was noted that all species identifications of its zooplankton are routine and, especially those of *Daphnia* and *Bosmina*, need further attention (Korovchinsky, 2000). The present study shows that this is also true for *Bythotrephes*, although these cladocerans are not listed among dominant zooplankters (see Kulikova *et al.*, 1997; Lake Onega: Atlas, 2010; Syarki, Fomina, 2019a, b).

First of all, this situation has developed due to the lack of a modern taxonomic revision of the representatives of the latter genus. Such revisions were initiated in the 2000s (Litvinchuk, 2002, 2007; Litvinchuk, Litvinchuk, 2016; Korovchinsky, 2015, 2018, 2019, 2020). They showed that the bythotrophes of Lake Onega do not belong to *B. longimanus* as it was considered initially (see, e.g., Linko, 1898; Smirnova, 1972) but rather to a set of forms close to *B. cederstroemii*. Fortunately, by that time, it became known about the presence of interspecific hybrids among the representatives of the genus (Litvinchuk, 2002, 2007) but their morphological features and morphological variability have not been described. Besides, the taxonomy of the genus has not been elaborated well enough. For these reasons, the initial reassessment of *Bythotrephes* from Lake Onega has led to the conclusion of the presence of a hybrid form *B. cederstroemii* x "*B. crassicaudus*" there (Korovchinsky, 2015). This was soon found to be incorrect and specimens from Lake Onega were attributed to *B. cederstroemii*, although the presence of hybrids in the lake was not excluded as well (Korovchinsky, 2018). In the following publications, the local representatives have been attributed either to the hybrid form *B. brevimanus* x *B. cederstroemii* (Korovchinsky, 2019)

or to *B. cederstroemii* (Korovchinsky, 2020). Mostly, these confusions were due to the lack of sufficient material from Lake Onega, which was represented only by old and usually deformed specimens from the museum's collections (materials by A.K. Linko collected in XIX century).

As is evident from the original and literature data (Korovchinsky, 2019), the specimens of hybrid populations are characterized by increased morphological variability and usually include both typical specimens quite similar to the parental species *B. cederstroemii* and *B. brevimanus* and specimens of different intermediate morphs. Because according to data by Litvinchuk (2002, 2007), there is no concordance between morphological and genetic (allozyme) traits of hybrid specimens which may have the parental appearance, it is not possible to discriminate morphologically the real hybrid and parental specimens which can co-occur. For this reason, so far, all specimens of such highly variable populations should be considered hybrids. For this reason, the highly variable *Bythotrephes* representatives from Lake Onega should be attributed to the widely distributed interspecies hybrid form *B. brevimanus* x *B. cederstroemii* presented here at least since the 19th century.

If hybrid specimens from Lake Onega are compared with those from other populations (see Korovchinsky, 2019: Table I), it is evident that in most traits they are more or less similar. However, the former ones differ from most others in smaller claws of postabdomen and caudal process and larger distance between them.

According to data by Litvinchuk & Litvinchuk (2016), these hybrids make up only 17% of the Lake Onega bythotrophes population, while most individuals are related to *B. cederstroemii*. Based on the morphological characteristics of the specimens studied from the lake, this statement seems incorrect because no individual with the typical set of species-specific diagnostic characteristics of *B. cederstroemii* (comparatively large body size, specific claws of postabdomen and caudal process with apical ends curved anteriorly, long caudal process with well or not well developed denticulate band) was found in the material studied. Further morphological and molecular-genetic studies are very needed to investigate the taxonomic status of *Bythotrephes* from Lake Onega in more detail.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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