

Morphological and Genetic Identification of *Harpacticella inopinata* (Harpacticoida, Copepoda) from Lake Baikal and the Yenisei River (Russia)

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Abstract—The results of studies of the morphology and genetics of the Baikal subendemic (*Harpacticella inopinata* Sars, 1908 harpacticoid) are presented. The collections of 1969 and 2017–2022 from the southern part of Lake Baikal and the Yenisei River within the city of Krasnoyarsk are used as material. It is demonstrated that morphological variability within the species is most pronounced in the structure of the antenna exopodite and the number of pores and sensilla on the integument of thoracic somites. The genetic variability of the studied *H. inopinata* sample is described by three clades with an average distance between them of 0.24; genetic distances between individuals within the detected genetic groups do not exceed 0.005. It is found that *H. inopinata* from geographically distant habitats (Lake Baikal and the Yenisei River) form a single morphological and genetic group. The analysis of genetic diversity of *H. inopinata* confirms the relatively recent Baikal origin of the species in the Yenisei River, probably associated with an anthropogenic invasion.

Keywords: Baikal harpacticoids, morphological variability, species genetic heterogeneity, geographical distribution, genetic marker (COI), phylogenetic tree, haplotype network

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INTRODUCTION

Out of all harpacticoids indicated for Lake Baikal, most species belong to the family Canthocamptidae, and only one species (*Harpacticella inopinata* (Sars, 1908)) belongs to the family Harpacticidae (mainly marine). Purely freshwater Harpacticidae are limited by the genus narrowly distributed in East Asia (Lee et al., 2014). In Lake Baikal, *H. inopinata* (found along the entire perimeter of the lake and from the water edge to the depths of 20 m) is the most widespread representative of harpacticoids and crustaceans (Okuneva and Evstigneeva, 2001). In addition to Lake Baikal, *H. inopinata* was noted in the Angara and Yenisei rivers and Irkutsk and Bratsk reservoirs, where it also reaches a high abundance. Apparently, the high development of populations in all habitats of the species is associated with its biological peculiarities: a wide range of nutrition, eurythermy, habitation on different types of bottom grounds, and peculiarities of precopulatory behavior (Okuneva, 1989; Evstigneeva, 1993). The large significance of *H. inopinata* in the communities of Baikal meiofauna contributed to the fact that

the postembryonic development and population dynamics of the species and its ecology are well studied; a significant role of *H. inopinata* in the nutrition of Baikal fish larvae was revealed (Okuneva, 1989). In the course of these studies, an assumption was made (Evstigneeva and Sobakina, 2008) that several species of the genus *Harpacticella* inhabit the lake: differences between the crustaceans and the typical material collected in the western part of the lake were found (Peschanaya Bay, 52°15'28" N, 105°42'15" E). These differences were manifested in the armament of the antennae exopodite, first swimming limb, and caudal branches. To solve the problem of separating possible sister *Harpacticella* species, a detailed morphological study and molecular genetic analysis of *H. inopinata* from Lake Baikal and other water objects is topical.

The aim of the work was to give a morphological characteristic of *H. inopinata* from Lake Baikal and the Yenisei River for an analysis of species variability, as well as determine the level of genetic differences of the species in two water objects based on an analysis of

Table 1. Materials of morphological and genetic studies of *Harpacticella inopinata*

Collection point	Coordinates		Date of collection	<i>n</i> , specimen	
	N	E		morphol.	genet.
Lake Baikal, Utulik–Murino	51°33'14"	104°03'40"	June 18, 1969	10♀♀, 5♂♂	–
Lake Baikal, settl. Listvyanka	51°50'29"	104°53'06"	Oct. 10, 2017, May 18, 2022	10♀♀, 5♂♂	5♀♀
Lake Baikal, settl. Bol'shie Koty	51°54'01"	105°03'47"	June 3, 2018, June 4, 2018	10♀♀, 5♂♂	3♀♀
Yenisei River	55°59'24"	92°47'49"	June 9, 2021, July 31, 2021, May 19, 2022	12♀♀, 5♂♂	4♀♀

A dash indicates no sample; *n*, number of individuals.

sequences of a variable fragment of the cytochrome oxidase subunit I (COI) gene.

MATERIALS AND METHODS

Harpacticella inopinata individuals from Lake Baikal and the Yenisei River, as well as five samples of zoobenthos from the Lena River, were used as material for the study. The material from Lake Baikal included a harpacticoid from the collection of formalin samples of the Zoological Museum of Moscow State University collected in 1969 in the Utulik–Murino region (part of the water area along the southeastern coast from the settlement of Utulik to the Murino station) and collections of the authors from the vicinity of the settlements of Listvyanka and Bol'shie Koty (the southwestern part of Lake Baikal) in 2017–2022 (Table 1). All samples were collected from the shore by a net at a depth of 0.2–0.3 m or by a dredge (in Bol'shie Koty) from a depth 0.5–1 and 20 m. The material from the Yenisei River was taken within the city of Krasnoyarsk in 2021–2022; the samples from the Lena River were taken in the area of the settlement of Kachug (54°0'27" N, 105°47'4" E, 53°56'40" N, 105°53'0" E) on July 28, 2022.

For a morphological study, the crustaceans were fixed in 4% formalin; for a genetic study, they were fixed in 96% ethanol and stored in a freezer at a temperature of –20°C. In total, 30 females and 20 males from formalin samples and 12 females from alcohol samples were analyzed.

The keys and descriptions of Sars (Sars, 1908), Borutsky (1952), and Okuneva (1989) were used to identify the species. The morphology of crustaceans was studied using Leica DM 4000 B (Germany) and LOMO Mikmed 2 (Russia) microscopes.

When studying morphology, special attention was paid to the structure of antennae (A2) of the female, thoracic legs (P1–P5), and caudal branches of males and females of *H. inopinata* from alcohol and formalin samples, as well as to the structure of the integument of thoracic somites II–IV. The figures were made using a drawing device and processed in Adobe Photoshop CS3 Extendet and Xara Photo & Graphic Designer 6. The figures of thoracic somites were made

over photographs on a paper or in Inkscape program. The integument of thoracic somites was studied in three females: two from the Yenisei River and one from Lake Baikal (settl. Listvyanka).

To analyze the genetic diversity of harpacticoids, a fragment of mitochondrial DNA cytochrome oxidase subunit I (COI) gene was used. DNA isolation and the acquisition and processing of PCR products were carried out at the Molecular Biology Center for Collective Use of the Institute of Biology, Komi Science Center, Ural Branch, Russian Academy of Sciences, according to the protocol previously published in the work (Kochanova et al., 2018). DNA isolation was carried out in a single step by the incubation of the sample in a solution containing a Chelex 100 chelating agent and proteinase K. When isolating DNA, no mechanical destruction of the sample was carried out; therefore, the morphology of the exoskeleton of crustaceans preserved in the Chelex 100 solution was reexamined after a genetic study. To amplify the COI gene region, forward and reverse universal primers developed for invertebrate organisms were used: HCO 2198 (5' TAAACTTCAGGGTGACCAAAAAATCA 3') (Folmer et al., 1994) and LCO 1384 (5' GGTCATG-TAATCATAAAGATATTGG 3') (Machida et al., 2004). The product of PCR reaction was exposed to electrophoresis. Amplicons from the agarose gel were purified using a Cleanup S-Cap kit (Evrogen, Russia). The sequencing of DNA samples of most individuals (ten specimens) was carried out at the Genome Center for Collective Use of the Engelhardt Institute of Molecular Biology, Russian Academy of Sciences (Moscow), and, for two samples (from the Yenisei River), in the Laboratory of Molecular Systematics and Ecology of the Finnish Museum of Natural History (Helsinki, Finland).

The nucleotide sequences were aligned using a ClustalW algorithm and analyzed in Mega 11.0 software. A phylogenetic tree with the calculation of bootstrap supports of branch nodes (1000 replications) was constructed according to the UPGMA algorithm using a Tamura–Nei three-parameter model (Tamura and Nei, 1993).

RESULTS

In the samples from Lake Baikal and the Yenisei River, *H. inopinata* was found in masse. It was the only harpacticoid species in the samples from Lake Baikal; in July 2021, the members of the family Canthocampidae (*Maraenobiotus insignipes* (Lilljeborg, 1902) and *Moraria mrazeki* Scott, 1903) were found in a sample from the Yenisei River in addition to *H. inopinata*. No *H. inopinata* was found in the Lena River.

Morphological Description. The studied *H. inopinata* individuals from Lake Baikal and the Yenisei River had in general a similar structure according to all examined morphological traits. The sizes of crustaceans varied from 850 to 1100 μm . The body shape of females and males was characterized as of “cyclopoid type” (the cephalosome and thoracic somites were almost twice as wide as the abdominal somites (Fig. 1a). The antennules of females did not reach the middle of the cephalosome length; the rostrum was large, wide, and fused with the cephalosome. The legs P2–P4 were of the same structure in females and males, swimming type; P1 was of a well-pronounced grasping type (Figs. 1b, 1c) (terminal segments of the exopodite and endopodite carried sickle-curved spines). The anal operculum was absent. The caudal branches (Figs. 1a, 1k) were short and square; the middle apical caudal seta was long, of the same length as the whole body; the outer one was three times shorter than the inner one. A description of some of morphological structures of *H. inopinata* that we studied in more detail and comments on their variability are given below.

The exopodite A2 (Figs. 1e–1j) was two-segmented (Figs. 1e and 1h) or unclear two-segmented (Figs. 1f, 1g, 1i, 1j). The first segment is armed with a distally feathered spiny seta; the second segment is armed with an unfeathered thin seta in the middle of the inner edge and several short spinules and one longer seta at the end, as well as a feathered spine, the length of which exceeds the length of the apical seta by 2–2.5 times. The variability of A2 exopodite was manifested in the studied individuals in the number of short spinules on the terminal segment (from one to four). In addition, four females from Lake Baikal near settl. Listvyanka had additionally 4–6 thin long spinules in the middle of the first segment of the exopodite A2 (Fig. 1g). The portion of such females among all studied ones from Lake Baikal was 13% and, from Lake Baikal near settl. Listvyanka, 40%. The structure of the exopodite A2 in Baikal *H. inopinata* was in general more variable than in Yenisei ones (Figs. 1i, 1j). In females from the Yenisei River, this structure was unclear two-segmented without the additional spinules on the surface of the first (unclear segmented) segment.

The first pair of legs (Fig. 1b) was with three-segmented exopodite and endopodite. The endopodite is shorter than exopodite and carries a long seta on the

inner edge of the first segment and curved bare spine and seta apically on the distal (third) segment. The exopodite was with one short seta on the outer edge of the first segment and second segment. The inner distal end of the second exopodite segment carries a short thin seta. The terminal segment of the exopodite (Fig. 1c) was very short, unclear separated from the second segment and armed with four clawlike spines, out of which the inner is the longest and the outer is the shortest. The outer distal angle of the second segment of the exopodite P1 was drawn into a short, cylindrical outgrowth. In most individuals that we analyzed, this outgrowth is smooth; in one of the females (from Utulik–Murino), the outgrowth is equipped with very small spinules (Fig. 1d).

The fifth pair of female legs was two-segmented; the inner lobe of the basiendopodite was longer than the exopodite, trapezoidal, with five setae, out of which the second from the outer edge was the longest. The exopodite was oval, with five setae, out of which the first from the inner edge was the longest. The outer and inner edges of the exopodite and the lobes of the basiendopodite were covered with fine spinules. The basiendopod P5 of the male was strongly reduced; it is a very thin, medially fused plate, armed with one unfeathered lateral seta on each side. The exopodite P5 of the male was square, armed with three bare setae. The male P6 was in the form of a small lobe, carried three long setae, out of which the inner one was feathered. The structure of P5 was similar in all analyzed individuals, with the exception of one female from Lake Baikal (settl. Listvyanka), which had an additional armed seta on the outer edge of the lobe of the right P5.

All setae on the caudal branches of *H. inopinata* females and males were well developed. A variability in the structure of caudal branches was observed in the number of spines above the apical caudal setae (Fig. 1k). These spines were always present.

The study of the integument of thoracic somites in *H. inopinata* from Lake Baikal and the Yenisei River demonstrated the presence of up to 18 pairs of sensilla and 16 pairs of pores on the somite II, up to 17 pairs of sensilla and 10 pairs of pores on the somite III, and up to 12 pairs of sensilla and 7 pairs of pores on the somite IV (Fig. 2a). Out of them, 4–5 pairs of sensilla and 1–4 pairs of pores were larger and more visible; the rest were, smaller, barely distinguishable. Variability in the number of these structures was manifested between individuals from the same reservoir (Yenisei River) (Figs. 2b, 2c) and different ones (Lake Baikal and the Yenisei River) (Figs. 2b–2d). In all studied individuals, an asymmetry in the number of pores and sensilla and their location on the right and left sides of the somites was present. Based on the analysis of the integument of thoracic somites, a reconstruction of the maximum possible number of pores and sensilla on them in *H. inopinata* was constructed (Fig. 2a).

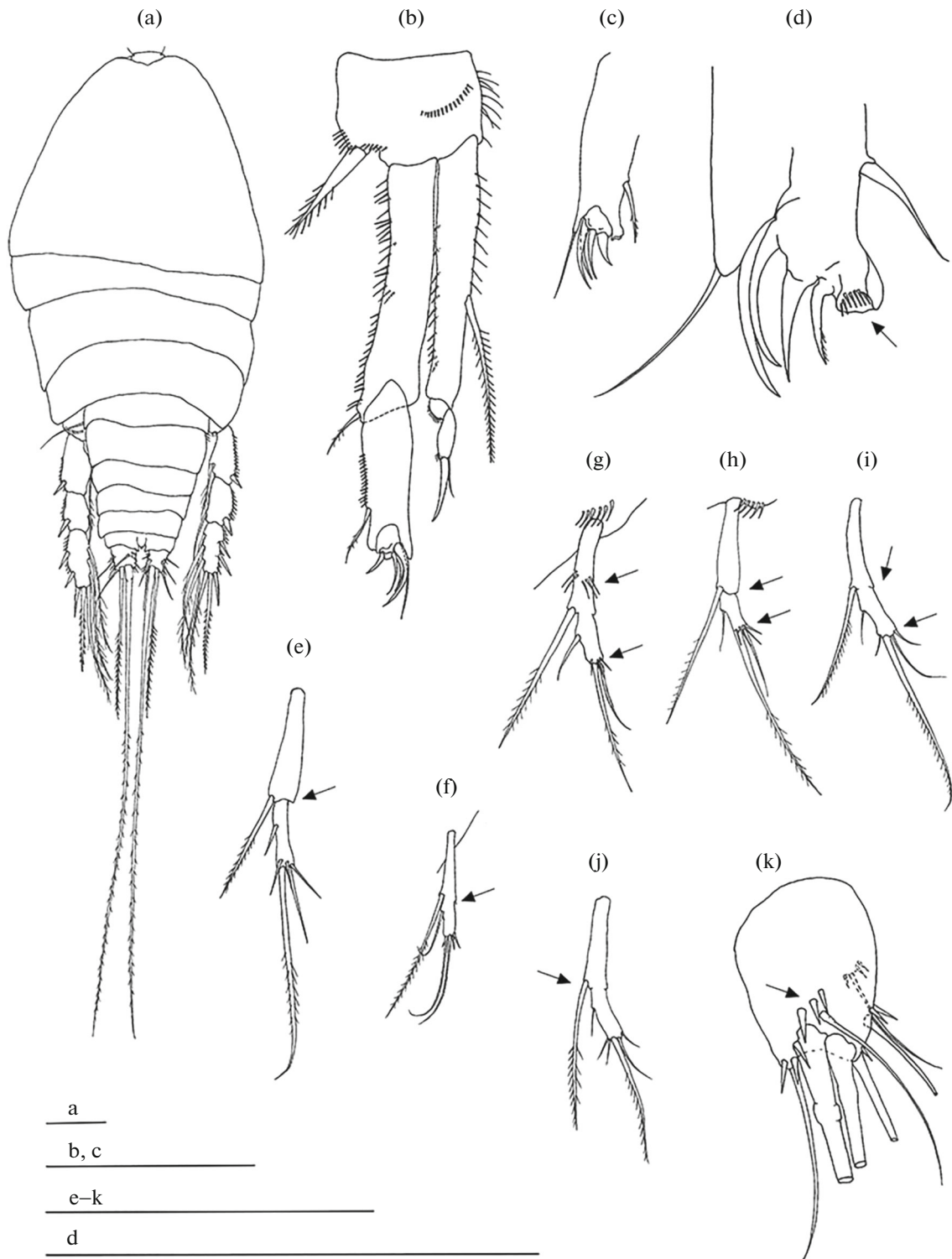


Fig. 1. Variable traits of *Harpacticella inopinata* female: (a), general view dorsally; (b), P1; (c, d), distal segment of P1 exopodite; (e–j), A2 exopodite; (k), caudal branch dorsally; (a–c, h), from Lake Baikal, Utulik–Murino; (d–g, k), Lake Baikal, settl. Listvyanka; and (i, j), Yenisei River. Variable traits are demonstrated by arrows. Scale: 100 μ m.

Genetic Distances. Sequencing of a variable fragment of the COI gene was carried out in eight *H. inopinata* individuals caught in Lake Baikal and four individuals from the Yenisei River within the city of Kras-

noyarsk. The sequences that we obtained were listed in GenBank under the numbers OP093570–OP093573 (Yenisei River) and OP413644, OP413645, OP413647–OP413654 (Lake Baikal). The analysis of sequences

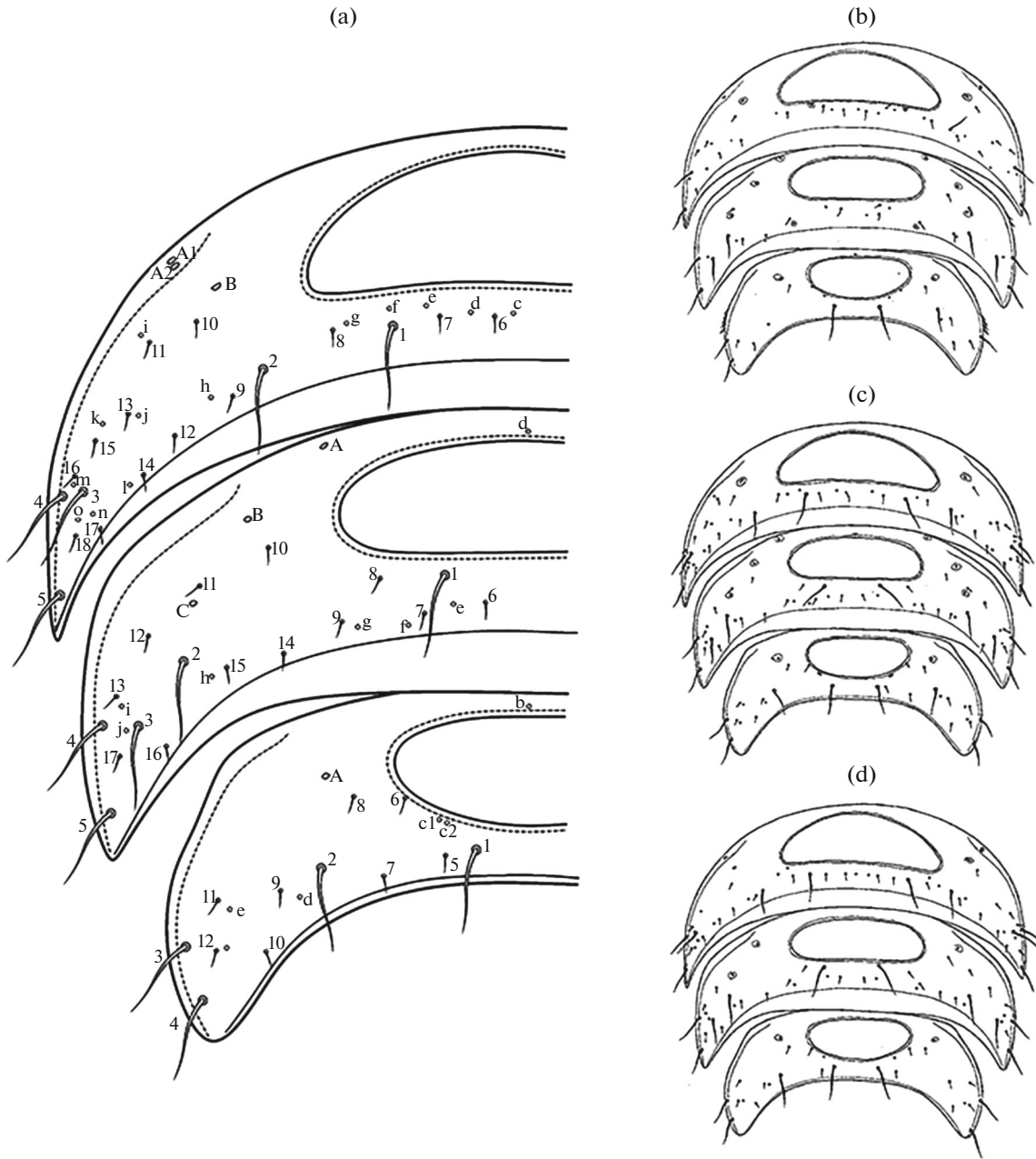


Fig. 2. Structure of integument II–IV of *Harpacticella inopinata* thoracic somites: (a) reconstruction of the maximum number of pores and sensilla; (b, c) from the Yenisei River and (d) Lake Baikal, settl. Listvyanka. Sensilla numbers are indicated by numbers and pore numbers by letters.

indicates a complex intraspecific genetic structure of *H. inopinata* in Lake Baikal. The samples were divided into three clades (Fig. 3), separated by a genetic distance 0.21–0.25 according to the Tamura–Nei model. At the same time, the genetic distances between individuals within the detected genetic groups did not exceed 0.005. The genetic groups are not divided in any way according to the place of material collection inside the lake. Thus, clades I and III are formed by individuals from settl. Listvyanka and Bol'shie Koty

and clade II by an individual from settl. Listvyanka and Yenisei River.

Four individuals from the Yenisei River were genetically similar to each other (a maximal distance was 0.01) and formed a single clade with one individual from Lake Baikal (the average genetic distance between one individual from Lake Baikal and all individuals from the Yenisei River was 0.015), which, apparently, represents a separate intraspecific genetic group of *H. inopinata* in Lake Baikal. The time of hap-

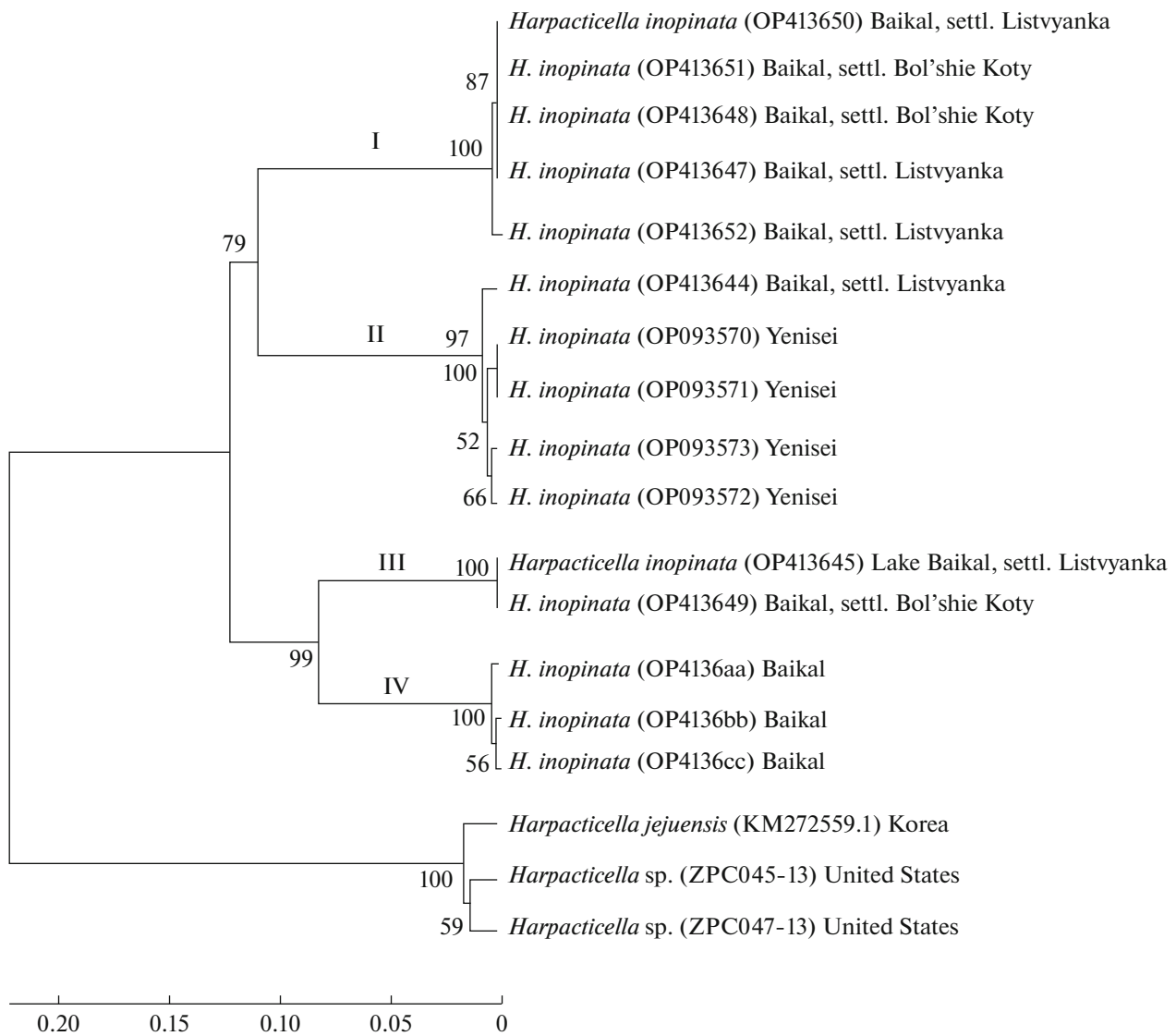


Fig. 3. Results of phylogenetic analysis of *Harpacticella inopinata* performed by the maximum likelihood method using the Tamura–Nei model based on the nucleotide sequence of the COI mitochondrial gene fragment. (I–III) Clade numbers. Registration numbers in GenBank are given in brackets. Data from GenBank on other representatives of the genus *Harpacticella* were used as an outer group.

lotype divergence within Lake Baikal determined by the number of mutations accumulated between them is illustrated on the haplotype network (Fig. 4). It was demonstrated that it significantly exceeds the time of differentiation of the Yenisei group from one of Baikal ones.

DISCUSSION

The studies of *H. inopinata* from Lake Baikal and the Yenisei River demonstrated its correspondence to the original description of the species (Sars, 1908) by most traits. The discrepancies between individuals that we analyzed and the original description were observed in the structure of the exopodite A2. Accord-

ing to Sars (1908), this is a two-segmented appendage that has three setae (one on the first segment and two on the second); according to Borutsky (1952), the exopodite A2 of *H. inopinata* (from Lake Baikal) carries three setae on the terminal segment; in the work (Okuneva, 1989), no armament of this limb was described. Thus, we supplemented the description of the species by clarifying the traits of the exopodite A2, and demonstrated a high variability of this structure in Lake Baikal. The variability that we observed in the number of segments of the exopodite A2 and in its armament can explain the inconsistencies between its early descriptions. It is possible that, in other parts of the *H. inopinata* area, there are individuals with a different structure of the exopodite A2, which supple-

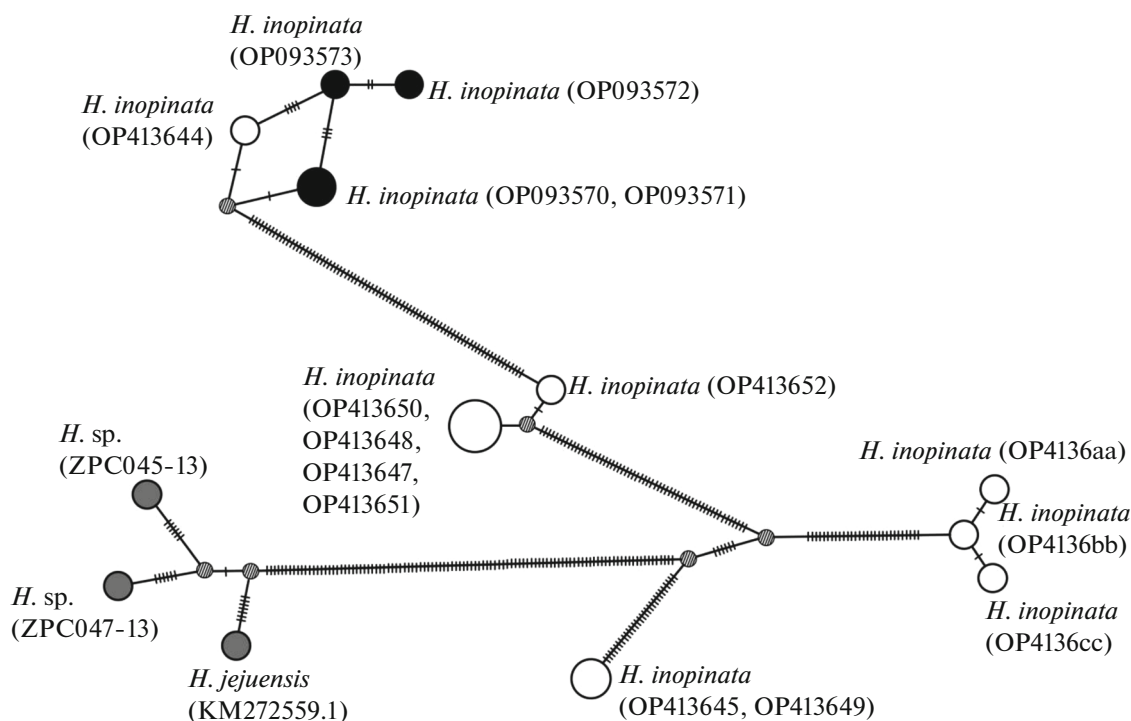


Fig. 4. Haplotype network of *Harpacticella inopinata* constructed based on the analysis of nucleotide sequence of the COI mitochondrial gene fragment. Registration numbers in GenBank are indicated in brackets. Black circles are haplotypes from the Yenisei River, white circles are haplotypes from Lake Baikal, and gray circles are the outer group. The number of mutations between haplotypes is indicated by dashes.

ments the pattern of species variability by this trait. In further analysis based on more material, taking into account differences in the A2 structure, can contribute to the clarification of the *H. inopinata* taxonomy.

The number and location of pores and sensilla on thoracic somites (that we studied for the first time) became other traits that supplement the morphological characteristics of *H. inopinata*. These traits of integument are species-specific in other representatives of Harpacticoida, and their analysis can serve for the identification of related taxa or morphological separation of ecological groups and be involved in phylogenetic constructions (Karanovic and Kim, 2014; Karanovic, 2017; Seifried and Dürbaum, 2000; Karanovic et al., 2018). However, such studies are not widely used due to methodological difficulties (the work on recognizing the pores and sensilla of the integument of such small organisms as harpacticoids requires a special level of microscopy). According to our data, there are relatively many pores and sensilla on the thoracic somites of *H. inopinata*; moreover, in addition to the elements comparable in size to those in the representatives of other families (Canthocamptidae (Novikov and Sharafutdinova, 2022), Heteropsyllidae (Novikov and Sharafutdinova, 2021), and Miraciidae (Karanovic and Cho, 2014)), most of them are very small. Along with a rather high variability in the structure of the integument (that we identified),

such a peculiarity hinders the use the associated traits for studying the intraspecific structure and morphological identification of the *H. inopinata* clades. However, they can be undoubtedly used for further similar studies of *Harpacticella*, for example, another genus of the family Harpacticidae (*Tigriopus*) (Karanovic et al., 2018). We found that the composition of the integumental elements of free thoracic somites is generally very similar in *H. inopinata* from the Yenisei River and Lake Baikal.

Thus, according to morphological traits, the Yenisei population of *H. inopinata* forms a common group of morphotypes of the species with Baikal ones. The genetic analysis also indicates that the Yenisei population is very close to one of Baikal haplotypes of *H. inopinata*. The genetic distances between them were lower than the distances between geographically separated genetic groups of some Palearctic species of harpacticoids from the family Canthocamptidae (Kochanova et al., 2021): *Canthocamptus staphylinus* Jurine (0.028–0.036) and *Attheyella crassa* (Sars) (0.013–0.065). A high level of polymorphism and genetic diversity of *H. inopinata* in the lake was demonstrated not only by us, but by other researchers (Kochanova et al., 2022). As for other Baikal invertebrates (Mayor et al., 2010; Karanovic and Sitnikova, 2017; Martin et al., 2019), high values of genetic distances according to the COI gene in *H. inopinata* can

indicate an antiquity of the species and/or an accelerated rate of its evolution. This can also be a confirmation of the Baikal origin of the species and its late settlement in the basin of the Yenisei River. If it is accepted that the settlement of *H. inopinata* in the Yenisei River originated from Lake Baikal, the mechanisms of entry of this harpacticide almost a thousand kilometers from its maternal population are interesting.

Previously, a “striking fact” was noted that “such an ecologically plastic species ... does not occur in the reservoirs adjacent to Baikal” (cited according to Okuneva and Evstigneeva, 2001, pp. 488–489). This meant numerous rivers flowing into the lake and isolated lakes along its coast, as well as the Lena River, the source of which is located just a few kilometers from Lake Baikal. Such peculiarities of the *H. inopinata* distribution distinguish this species among the Baikal harpacticoids, the vast majority of which (>80%) are endemic to the lake; the rest (living in quarrels (bays) and places where the rivers and streams flow into Lake Baikal) are most widely distributed in the Palearctic (Okuneva, 1989; Okuneva and Evstigneeva, 2001).

In our opinion, the peculiarities of *H. inopinata* distribution are associated with the following biological characteristics of the species. It was established (Okuneva, 1989) that crustaceans develop year-round without a diapause in Lake Baikal,¹ which apparently limits their ability to overcome land areas using the mechanism of settlement at latent stages by birds (Frisch et al., 2007) and fish (Bartholme et al., 2005) known for freshwater harpacticoids. At the same time, *H. inopinata* swims well, but its nauplii lead a benthic way of life, moving and feeding in the littoral of Lake Baikal on filamentous algae of the genera *Ulothrix*, *Didymosphenia*, and *Cladophora*, the survival rate of nauplii is low (Okuneva, 1989). Thus, the success of colonization of new habitats by the species can be associated with the survival of nauplii in them on a suitable plant substrate.

It was demonstrated (*Lake Baikal ...*, 1998; Shulepina et al., 2013; Porfiriev et al., 2021) that several dozen taxa of macroinvertebrates (worms, amphipods, amphibiotic insects, etc.), Baikal subendemics, have a distribution similar to *H. inopinata* (Lake Baikal and the south of the Yenisei basin) and are absent, for example, in the Lena River. However, the diversity of this faunal group consistently decreases with a distance from the lake, being the largest in the upper reaches of the Angara River and the lowest in the Yenisei River. As a result of special genetic studies for some Baikal subendemics, it was proven that their invasion into the basin of the Angara River came from Lake

Baikal, but not vice versa (Porfiriev et al., 2021). In our opinion, the settlement of these species and *H. inopinata* outside the lake was contributed by anthropogenic factors, namely, navigation, which has been and continues to be active in the south of the Yenisei basin for two centuries. The anthropogenic mechanism of invasion of *H. inopinata* into the region of Krasnoyarsk (located far upstream of the confluence of the Angara River into the Yenisei River) seems the most probable, since it best explains the successful passage of a large distance upstream of the main channel of the basin by the species.

CONCLUSIONS

Morphological and genetic studies confirmed the identity of the Yenisei *H. inopinata*, at least one of genetic groups of the species inhabiting Lake Baikal. According to our data, *H. inopinata* in the Yenisei River is of Baikal origin: morphological and genetic variability of the species in Lake Baikal is higher, which indirectly indicates its greater antiquity as compared with the Yenisei River. Since the anthropogenic mechanism of invasion of the species into the Yenisei River is most probable, this settlement occurred relatively recently. The analysis of morphological variability of *H. inopinata* demonstrated that the structure of the antenna exopodite and the integument of the second–fourth thoracic somites are the most variable traits. The studies of the antenna can be the most promising for further taxonomy of the species in Lake Baikal. The suitability of characteristics of the integument of the second–fourth thoracic somites for this purpose is doubtful due to a high individual variability of these structures. A genetic heterogeneity of *H. inopinata* in Lake Baikal was established: three geographically unseparated genetic groups of the species were identified only in the southern part of the lake, which indicates the need to revise its taxonomy (identification of new subspecies or species).

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

¹ For this reason, the role of the size and morphometry of individuals in the coordination of morphological traits and genetic clades is probably limited, since to a large extent these traits can depend on the nutritional conditions, growth rate, and maturation of individuals of different generations of *H. inopinata* (authors' comment).

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

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