


Morphology of the cephalothorax integument of *Bryocamptus pygmaeus* (Copepoda: Harpacticoida: Canthocamptidae), based on a new research method

Морфология интегумента цефалоторакса *Bryocamptus pygmaeus* (Copepoda: Harpacticoida: Canthocamptidae) на основе нового метода исследований

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Abstract. The number and location of sensilla and pores of the cephalothorax integument of the species *Bryocamptus pygmaeus* (G.O. Sars, 1863) (Copepoda, Canthocamptidae) were studied for the first time on the material from several European regions: the southeastern part of the Bolshezemelskaya tundra (Nenets Autonomous District), the north of the Komi Republic, the Republic of Karelia, and the central part of European Russia (Udmurt Republic). In the samples examined, two groups of populations differing in the characters of cephalothorax integument were recognised. These differences were found to correlate with the variability of the endopod of fourth pair of female legs, which bears four setae in specimens of the eastern form, while a specimen examined from Karelia has five setae. Pore maps are composed for both groups of morphotypes. A statistical analysis was carried out based on a new technique using three-dimensional models of the cephalothorax. As a result of this analysis, a high similarity between individuals of the eastern form and differences of the latter from the Karelian specimen were revealed.

Резюме. Впервые изучены число и расположение интегументальных пор и сенсилл цефалоторакса вида *Bryocamptus pygmaeus* (G.O. Sars, 1863) (Copepoda, Canthocamptidae) из нескольких европейских регионов: юго-восточной части Большеземельской тундры (Ненецкий автономный округ), севера Республики Коми, Республики Карелия и центральной части европейской России (Республика Удмуртия). В исследованном материале выявлены две группы популяций, различающихся по признакам интегумента цефалоторакса. Установлено, что эти различия коррелируют с изменчивостью эндоподита четвертой пары ног самок, несущего четыре щетинки у особей восточной формы, и пять щетинок – у изученной особи из Карелии. Составлены карты пор для обеих групп морфотипов. Проведен статистический анализ по новой методике с использованием трехмерных моделей цефалоторакса. В результате этого анализа выявлено высокое сходство между особями восточной формы и отличие ее от карельского экземпляра.

Key words: integumental organs, copepods, freshwater harpacticoids, variability, Canthocamptidae

Ключевые слова: интегументальные органы, веслоногие раки, пресноводные гарпактициды, изменчивость, Canthocamptidae

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Introduction

The exoskeleton of copepods bears structures that are responsible for the interaction of the organism with the environment. The so-called integumental windows are involved in osmoregulation (Hosfeld & Schminke, 1997, 1999), whereas the sensilla and pores are necessary for the sensory reception (Fleminger, 1973) or secretion (Seifried & Dürbaum, 2000). In recent decades, the structure of the integument, namely the number and location of sensilla and pores, has been included in the taxonomic descriptions of copepods as species-specific characters (Fleminger, 1973; Karanovic & Lee, 2012).

The integumental structures may be useful in phylogenetic studies of the harpacticoid copepods (Karanovic & Kim, 2014). These organisms are known to possess high intraspecific and intrapopulation variability and cryptic speciation. In particular, such variability was observed in *Bryocamptus pygmaeus* (G.O. Sars, 1863) of the family Canthocamptidae (Lang, 1948). This species is widespread in the inland waterbodies of Europe, North America and North Africa, although records from North America require confirmation (Lang, 1948; Borutsky, 1952). The species is found in different types of waterbodies: from plumbing systems (Reid, 2001) and groundwater biotopes to large lakes and streams (Lang, 1948). Even in the very first works on the fauna and ecology of harpacticoids (Donner, 1928; Lang, 1948), authors drew attention to the variability of countable morphological features (at the anal operculum and thoracic legs) of *B. pygmaeus*, depending on the environmental conditions, as well as to the location and shape of three integumental windows of this species: on the cephalothorax and on the sides of the first and second thoracic somites. Much later, the cytological structure of these osmoregulatory organs of *B. pygmaeus* was studied (Hosfeld & Schminke, 1999). However, other structures of the integument of this species have not yet been investigated. We believe that additional data on countable features of *B. pygmaeus* would be useful for clarifying the taxonomic status of the species and increasing the accuracy of its identification, for example, when structures bearing diagnostically important features are damaged or only one specimen of any sex is available, etc.

The aim of this work was to test the significance of the fine armature of the cephalothorax integument in the taxonomy of harpacticoids on the example of *B. pygmaeus*. To accomplish this, it was necessary: (1) to determine the number and location of sensilla and pores on the cephalothorax, the shape and size of the integumental window of *B. pygmaeus*; (2) to analyse how stable and variable these features are within and between populations; and (3) to investigate sexual dimorphism in the structure of the cephalothorax integument of this species.

Material and methods

The work is based on specimens from formalin-preserved hydrobiological samples collected by us in 2018–2019 from the waterbodies of the Nenets Autonomous District (Okrug in Russian) (Pymvashor Stream), the Komi Republic (Adak Stream, Lake Bolshoy Kharbey) and the Udmurt Republic, Russia (Table 1, Fig. 1). We also used specimens from the collections of the Zoological Institute of the Russian Academy of Sciences, St Petersburg (collected by A.V. Zhuravsky from the Pymvashor Stream in 1905, No. 45-06) and the Zoological Museum of M.V. Lomonosov Moscow State University (collected by Z.I. Filimonova in Karelia: one sample from the village of Saynavolok and another without specifying a sampling locality). The waterbodies from which the specimens were collected varied widely in characteristics and are represented by surface waterbodies, groundwater, and hydrosulfuric brackish streams (Table 1). A total of 16 adult specimens of *Bryocamptus pygmaeus* and one female of *B. zschokkei komi* Borutzky, 1962 (from the Lake Bolshoy Kharbey) were examined (Table 1). For statistical analysis, we studied three females and one male from the Adak Stream, two females from the Pymvashor Stream, two females from Udmurtia, one female from Saynavolok, and one female from an unknown reservoir in Karelia (Table 1).

The identification of crustaceans and the study of their structure were carried out using a Leica DM 4000 B and a LOMO Micmed 2 microscopes. The species was identified according to Wells (2008) and Lang (1948).

To study the structure of the integument, the samples were prepared according to the following

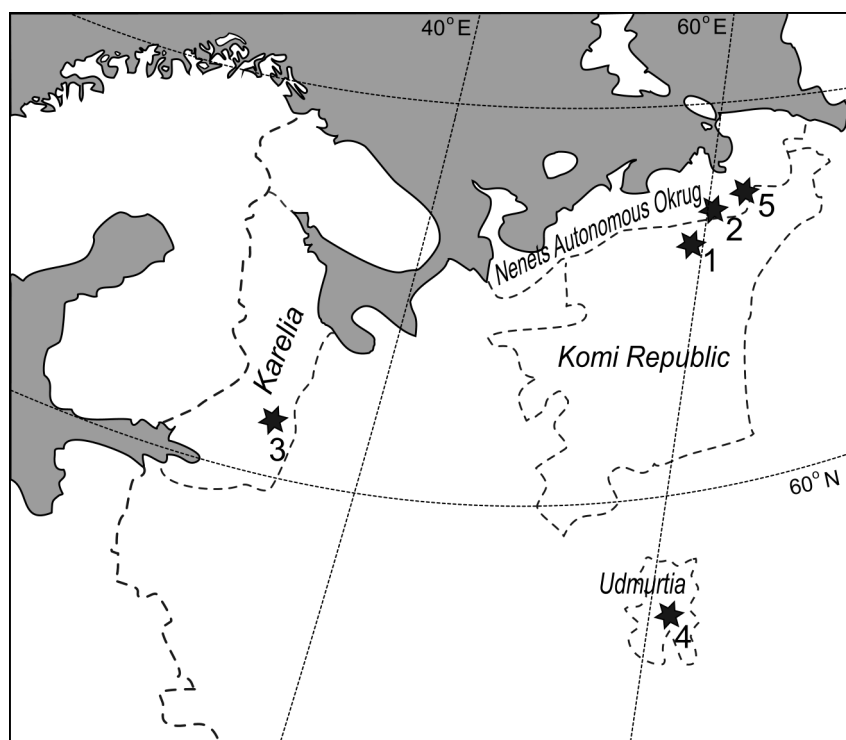
Table 1. Materials examined (1–4, *Bryocamptus pygmaeus*; 5, *B. zschokkei komi*).

No. in Fig. 1	Sampling region or locality	Locality coordinates	Sampling date	Type of water-body	Number of specimens	Specimens used in cluster analysis
1	Komi Republic, Adak Stream	66°28'N 59°34'E	22.VII.2018	hydrosulphuric brackish stream	3 females 2 males	3 females, 1 male: adak_f1, adak_f2, adak_f3, adak_m1
2	Nenets Autonomous Distr., Pymvashor Stream	67°09'N 60°51'E	24.VIII.2019	stream	3 females	1 female: pym_f1
		-	IX.1905	no data	1 female	1 female: pym_f1905
3	Karelia, Saynavolok Vill.	61°44'N 34°28'E	1976	no data	2 females	1 female: sajna_f1
	Karelia	no data	1976	no data	1 female	1 female: karel_f1
4	Udmurtia	56°51'N 52°12'E	17.VI.2018, 21.VII. 2019	pond and groundwater	3 females 1 male	2 females: udm_f1, udm_f2
5	Komi Republic, Bolshoy Kharbey	67°32'N 62°50'E	3.VIII.2012	lake	1 female	1 female: <i>B. zschokkei komi_f1</i>

method (Fig. 2). The cephalothoraxes were separated and placed into a 10% sodium hypochlorite solution for several minutes to remove soft tissues (Fig. 2A), then into distilled water for rinsing. The cleaned fragments of the exoskeleton were placed in glycerine on glass slides, and then each slide was covered with a cover slip with pieces of plasticine between the cover slip and the slide.

To compare the specimens examined, we used an original method. Drawings of each cephalothorax with pores and an integumental window were made in the dorsal and lateral projections from photographs (Fig. 2B). Based on these projections, a 3D model was created in Blender software. The projections of the pores of each specimen were plotted on one model also in Blender software (Figs 2C, 3A), which allowed them to be compared, reducing the effect of size variability. For convenience, we divided all the pores into groups and numbered them within the groups. The use of a 3D model significantly surpasses the classical methods of geometric morphometry in that our method does not depend on the position of the object under the glass.

To study the variability of the positions of the pores, we also created dorsal and lateral projections of each model. In CorelDraw software, each pore was superimposed with a scattered point. This made it possible for us to create

**Fig. 1.** Map of sampling localities of *Bryocamptus* spp. The numbers of localities are given in Table 1.

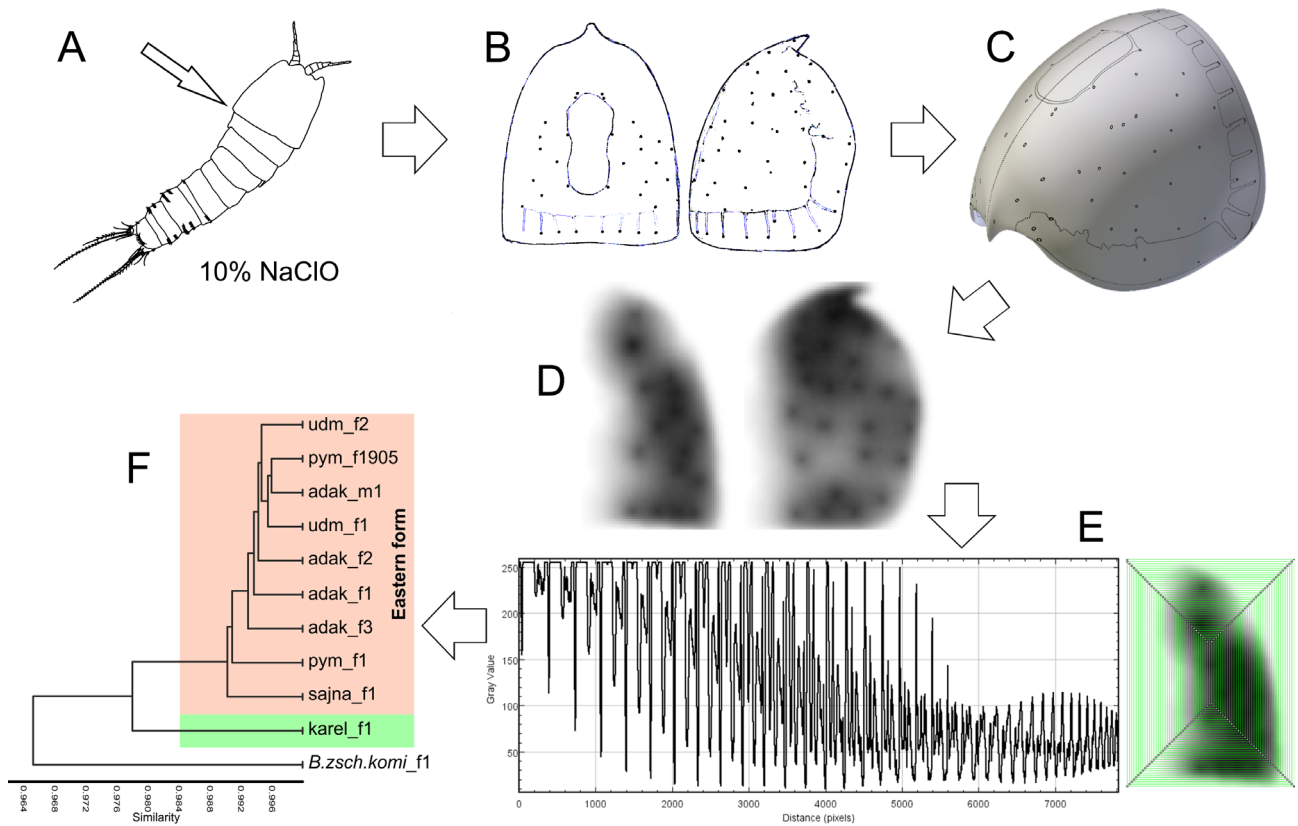


Fig. 2. Step-by-step methodology for comparing integumental sensilla and pores. **A**, dissection of specimens, dissolution of cephalothorax in sodium hypochlorite and preparation of slides with cephalothorax; **B**, cephalothorax in two projections; **C**, creation of 3D model of cephalothorax and application of pores and sensilla on it; **D**, creation of probabilistic maps of position of integumental pores and sensilla; **E**, per-pixel scan of lightness of probability map; **F**, analysis of data obtained.

probabilistic maps of the positions of the integumental pores (Fig 2D). All template maps had the same resolution. In ImageJ software (Abràmoff et al., 2004), we made a pixel-by-pixel spiral sweep of lightness using a macro developed by us (Figs 2E, 3B). The macro is represented as Electronic supplementary material 1 (see the section “Addenda”). Using the “Plot profile” tool of ImageJ, we obtained a series of data for each image (15,656 values for an image) (Fig. 2E; Electronic supplementary material 2, see the section “Addenda”). The obtained series of data were compared in PAST software (Hammer et al., 2001) using cluster analysis with the Single linkage algorithm and Euclidean similarity index (Fig. 2F). We included the data on ten specimens of *B. pygmaeus* and one specimen of *B. zschokkei* as an outgroup in the statistical analysis. The compared schemes are shown in Fig. 4.

Our method has certain advantages over the construction of the classical binary matrix of cla-

distics, in which each value in a cell indicates a certain state of the character. First, it is not necessary to search for homology between elements of different specimens and species, which makes it possible to avoid errors of individual perception. Second, this method allows us taking into account not only the number, but also the position of the pores, which makes it possible to indirectly compare the size of the dorsal window. It should be noted that the size of crustaceans is irrelevant here and their variability does not affect the results.

The following abbreviations are used below: A1 – antennule; A2 – antenna; P1–P5 – thoracic legs from first to fifth, respectively.

Results

The structure of A1, A2, P1–P4 exopod, P1–P3 endopod, P5, caudal rami and anal operculum of all the specimens of *Bryocamptus pygmaeus* (Fig. 5A)

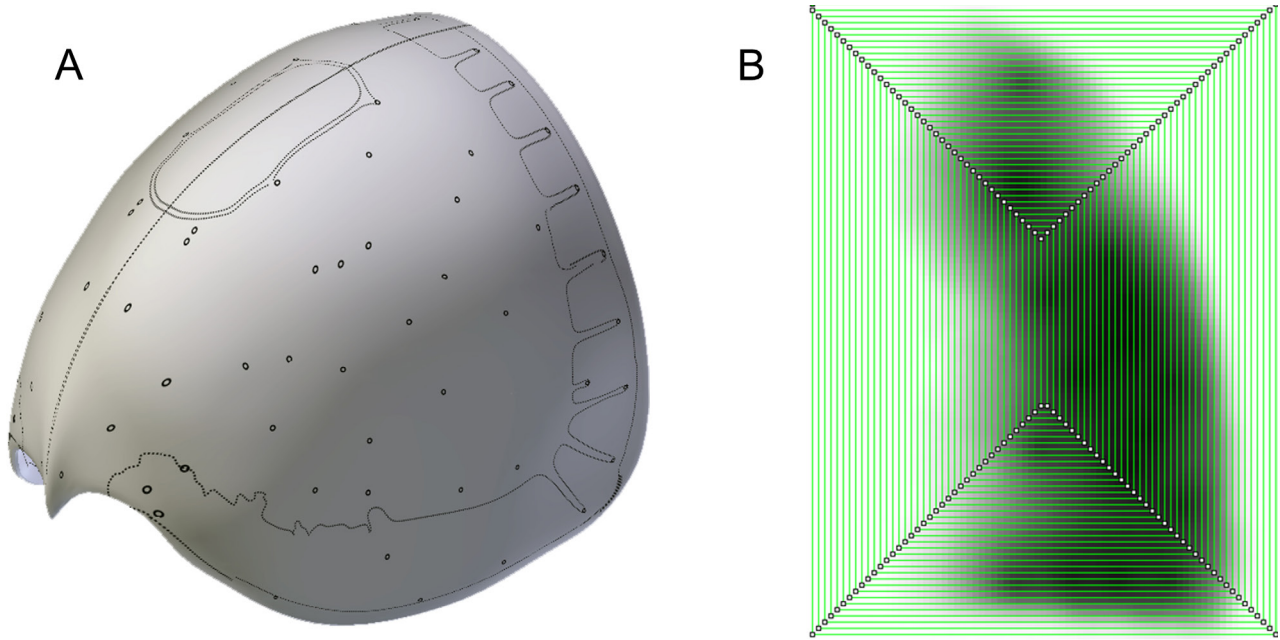


Fig. 3. Template of 3D model of cephalothorax (A) and per-pixel scan of probability map with lightness value of each pixel from 0 to 255 (B).

studied by us is typical for this species according to Lang (1948). However, variation within populations was found in the structure of the female P4 endopod (Fig. 5B, C). Specimens (conditionally named by us “eastern form”) from the Komi Republic, Nenets Autonomous District and Udmurtia have one seta at the inner side of the endopod and one shorter inner apical seta reaching the apex of the exopod and about 0.8 times as long as it (Fig. 5B). Both females from Saynavolok (Karelia) have the similar P4 endopod. The female from another Karelian sample have P4 as illustrated in Fig. 5C. Its endopod with two setae at the inner side and a long inner apical seta (the ratio of the length of inner apical seta to the length of exopod is 1.4).

The males and females from the Komi Republic, Nenets Autonomous District, Udmurtia and Saynavolok (eastern form) have the rounded cephalothorax of approximately equal length and width, the relatively small integumental window, and are generally similar in the number and position of the integumental pores and sensilla. The length of cephalothorax is $167.0 \pm 3.7 \mu\text{m}$ ($n = 6$). At the outer surface of the cephalothorax in the specimens of these populations, a total of 47 pairs of pores and sensilla were found. They were subdivided into the following groups according to their location (Fig. 6A): on the rostrum (sensilla R1),

on the anterodorsal part (group F with three pairs of sensilla and one pair of pores), on the anteroventral part (groups A, K and M, each with two pairs of sensilla), at the edge of integumental window (group W with three pairs of sensilla), on the posterior margin of cephalothorax (group P with nine pairs of pores), one accessory sensilla in front of the posterior group (Pp1), on the ventral margin of cephalothorax (group V with three pairs of pores), and on the lateral side of cephalothorax (group T with four pairs of sensilla; group L with three pairs of sensilla; groups B, C, H, each with two pairs of sensilla and one pair of pores; groups D, G, each with two pairs of sensilla). A total of five pairs of pores were found: B2, C2, F1, H1, and one pair not shown in the figure. The latter is located at the inner side of the cephalothorax in the area of the beginning of the antenna allobasis.

The individual examined from Karelia (kr_f1 in Table 1) differs from the eastern form. In this specimen, there are 45 or 46 pairs of pores and sensilla on the outer surface of the endopod (Fig. 6B). The size of cephalosome exceeds that of the individuals from the eastern population. The length of cephalothorax is $188.0 \mu\text{m}$ ($n = 1$); its height is slightly less than its width. The dorsal window is very large. Most groups of the pores and sensilla coincide with those of the eastern form in terms

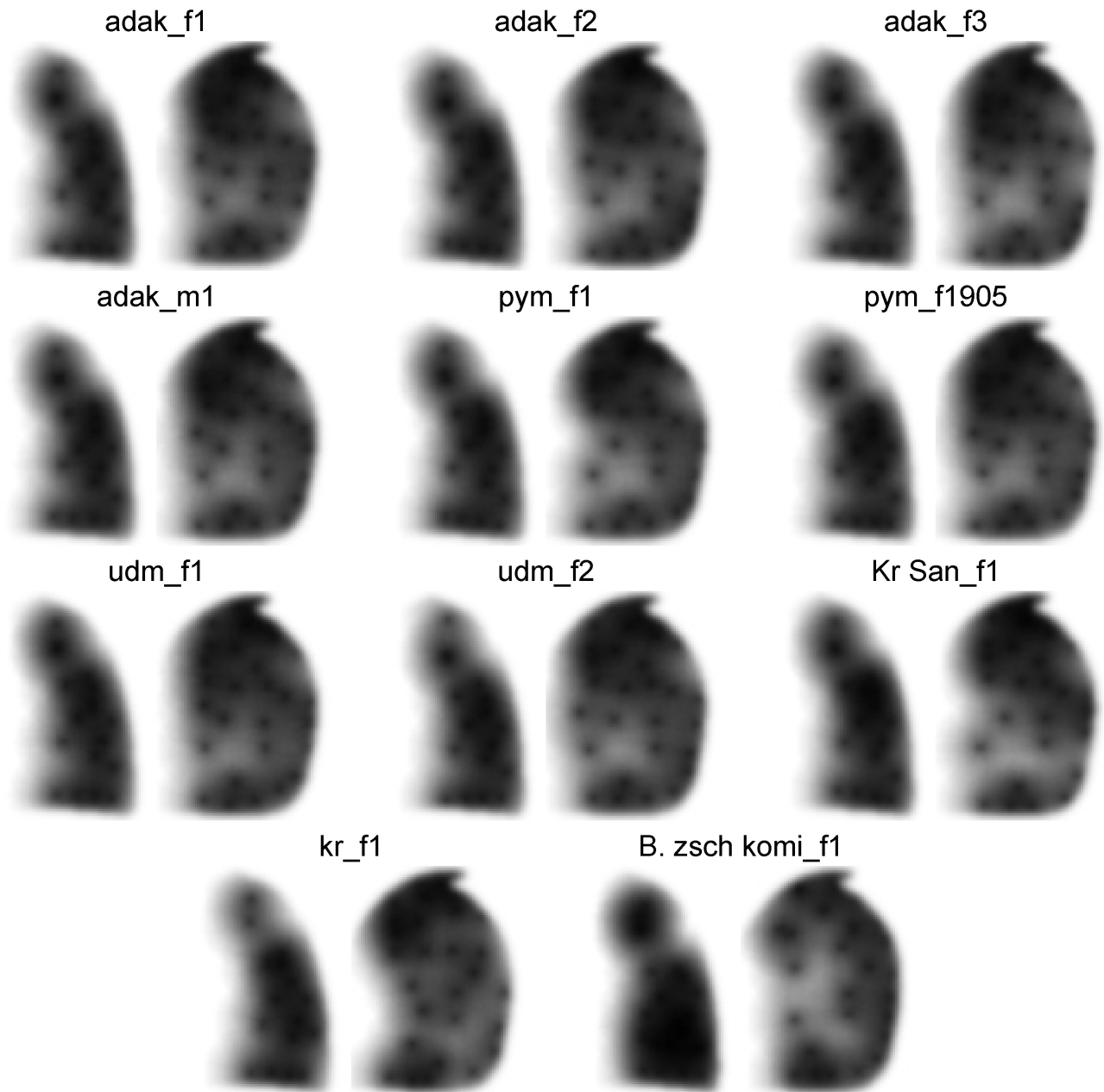


Fig. 4. Probability maps of pore and sensilla distribution in dorsal and lateral projections after applying a scattered point on each pore. Abbreviations are given in Table 1.

of the number of elements and configuration. The groups L and V differ significantly in configuration, so that their homology is ambiguous. The group H lacks H3 sensilla. One pore in the group F (F1) is apparently located on the thickened outer border of the integumental window, and therefore its presence in this group is questionable.

The individual of *B. zschokkei komi* was used for comparison with the specimens of *B. pygmaeus*. Its cephalothorax is flattened dorsoventrally, much

larger than in *B. pygmaeus*; the dorsal window is small, with wide borders. The length of the cephalothorax is 218.0 μm ($n = 1$). There are 49 pairs of pores and sensilla on the surface (Fig. 6C). In general, the integumental pattern is very different from that of both the eastern and typical forms of *B. pygmaeus*, and therefore, the homology of the sensilla of some groups may be questionable. The groups A, B, C, D, L, P, Pp, R, and W are rather similar in topology and number of the elements. The anteroventral groups

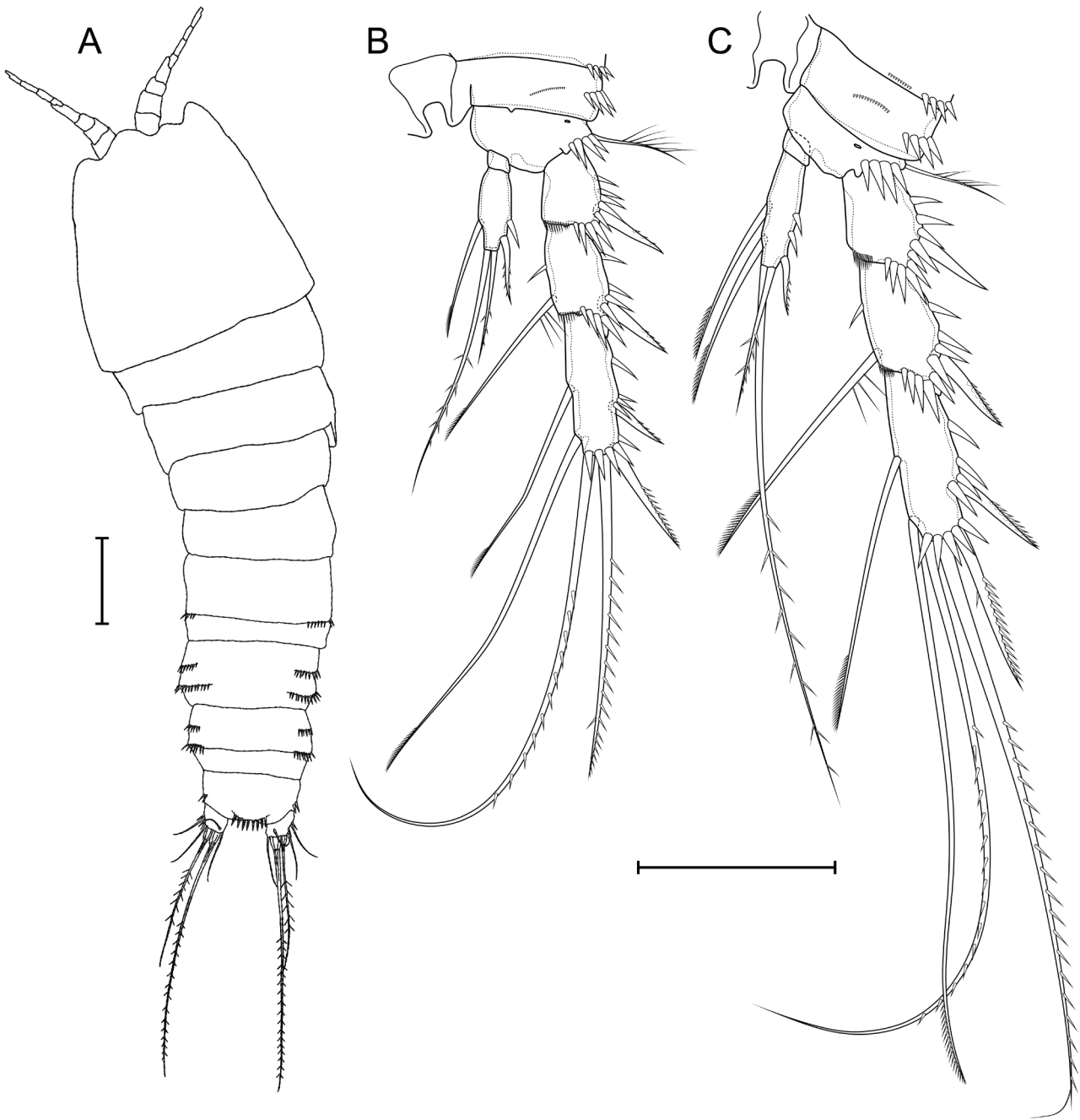


Fig. 5. *Bryocamptus pygmaeus* (G.O. Sars, 1863), female. **A**, habitus of eastern form (Adak Stream, Komi Republic); **B**, P4 endopod of eastern form (Adak Stream, Komi Republic); **C**, P4 endopod (Karelia). Scale bars: 50 μ m.

M, H and K are not similar to those of *B. pygmaeus*. The group F completely coincides in both species in the number of sensilla, but has additional pores F5 and F6 in *B. zschokkei komi*. In the posterior part of the cephalothorax of the latter species, there are pores that were the most difficult to classify. They were subdivided into a proximal group (Tp with three pairs of sensilla) and a distal group (Tt with two pairs of sensilla and one pair of pores).

Cluster analysis showed a high degree of similarity in the structure of the cephalothorax integument in the specimens from the eastern populations of *B. pygmaeus* and a female from the village of Saynavolok (kr San_f1) (Fig. 7B). It can also be seen that there are no noticeable subgroups among the specimens of the eastern form, which indicates the homogeneity of this cluster (Fig. 7B). The data on a single male from the Adak population (adak_m1)

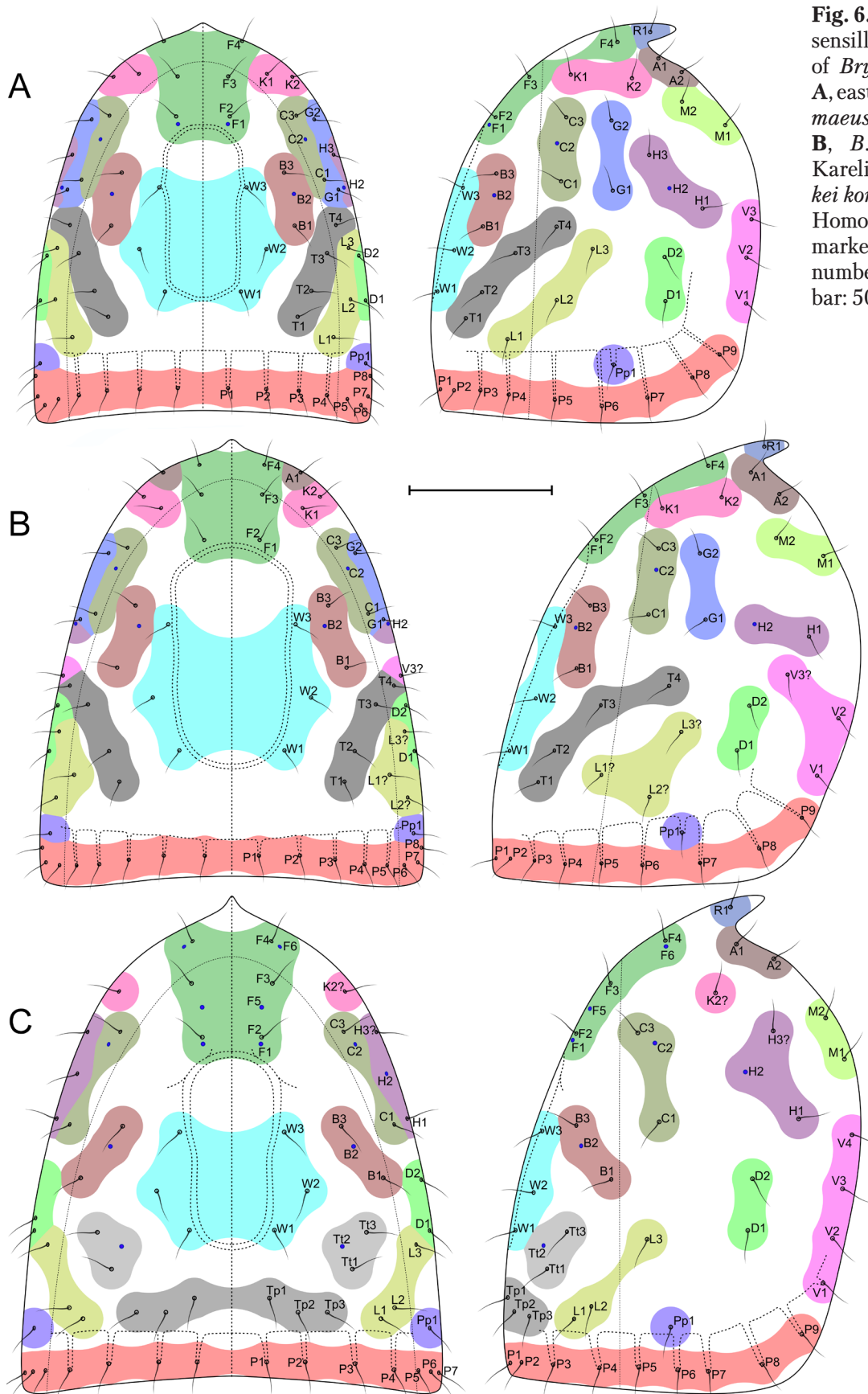


Fig. 6. Maps of pores and sensilla of cephalothorax of *Bryocamptus* species. **A**, eastern form of *B. pygmaeus* (G.O. Sars, 1863); **B**, *B. pygmaeus* from Karelia; **C**, *B. zschokkei komi* Borutzky, 1962. Homologous pores are marked with the same number and colour. Scale bar: 50 μ m.

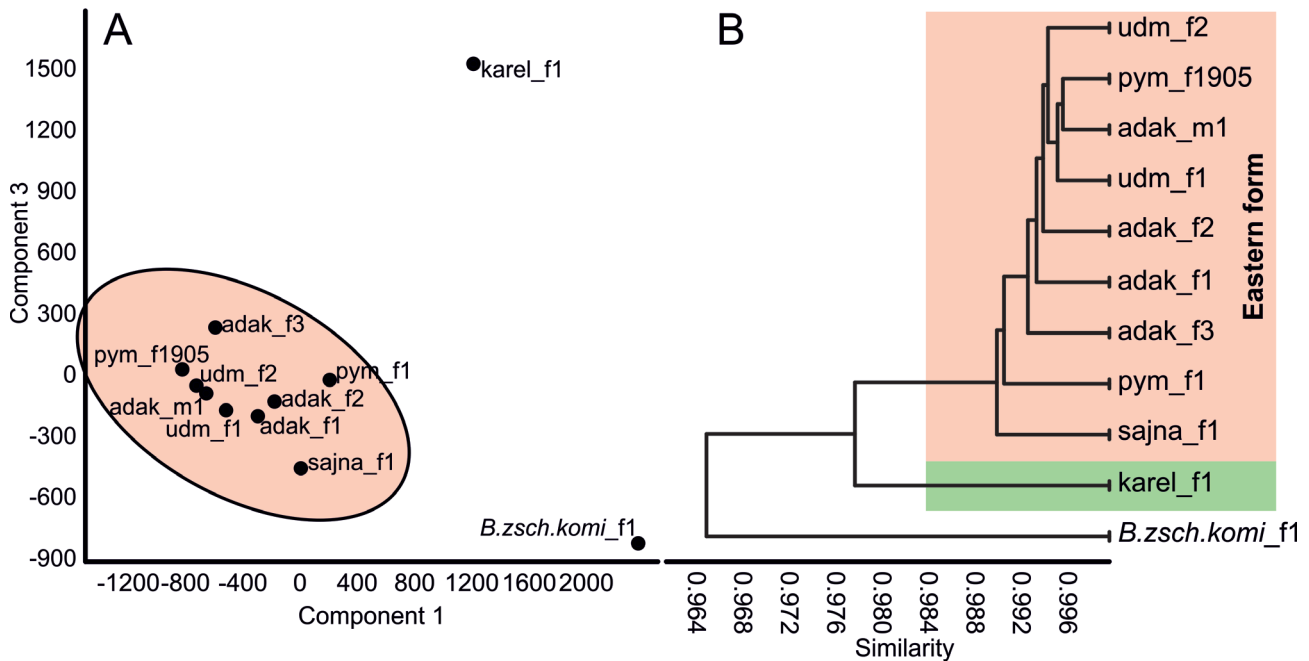


Fig. 7. Principal component analysis (PC1 – 31%, PC3 – 12%) (A) and cluster correlation analysis (B). Abbreviations are given in Table 1.

does not distinguish its features from the set of features of females in this comparative analysis. At the same time, the female of *B. pygmaeus* from Karelia, which differs in the P4 endopod structure (Fig. 5C) from the eastern form (kr_f1), formed a separate cluster in the analysis of the integumental structure (Fig. 7B).

Discussion

The females of *B. pygmaeus* examined from the Nenets Autonomous District, the Komi Republic, Udmurtia, and the village of Saynavolok are similar in the structure of P4 endopod with the specimens of this species from the Bolshoy El River of the Vychegda River basin and from the Uhta River of the Pechora River basin (Komi Republic) (Fefilova, 2015), as well as from the Jägala River (northern Estonia) (Fefilova, 2010). These data support the conclusion made as a result of this study that there exists a fairly stable eastern form of the species, which is widespread in the European Northeast from Estonia and Karelia to the western Urals. The pattern of the distribution of population sizes of the eastern form by the type of waterbodies suggests that the species prefers groundwater in this region. The largest concen-

trations (20–94 specimens per sample) of the eastern form were found in the Adak and Pymvashor streams in places of groundwater outflow: in hot and cold karst springs, including hydrosulphuric ones, where crustaceans formed single-species taxocoenoses (Loskutova et al., 2020). In the rivers of the Komi Republic, as well as in a pond in Udmurtia, single specimens of this species were found. In the tundra zone, where the outflow of groundwater into surface waterbodies are virtually absent, *B. pygmaeus* has not yet been recorded (Borutzky, 1952; Fefilova, 2015); the Pymvashor Stream located there is an exception in the type of water supply and is the only known location of the species in the tundra. We also found that the structure of the integument in the eastern form has a rather low variability.

The only female examined from Karelia, with a different structure of the P4 endopodite than in the eastern form, is similar in this feature to the specimens from Norway (Sars, 1907), from where the species was described (Sars, 1863), as well as to the specimens depicted by Gurney (1932) from different localities of Western Europe. The P4 endopod of this Karelian specimen has the same structure as that of the specimens from springs in Poland (Karpowicz, 2016, pers. comm., including

a photo). According to Karpowicz, the inner apical seta on the P4 endopod of females from Poland is 1.3–1.4 times as long as the P4 exopod; the P4 endopod has two setae at the inner side. *Bryocamptus pygmaeus* with such structure of the P4 endopod is widespread in Western Europe (Lang, 1948). The features of this form are not stable: the intraspecific variability was also observed in the armature of the thoracic legs (Donner, 1928) and the P4 endopod (Roy, 1935). For example, Roy (1935) observed that the number of internal setae on the endopods of *B. pygmaeus* varies, depending on the ecological conditions and habitat of the species in France in large waterbodies or karst springs. In the drawing of *B. pygmaeus* from Romania (Damian-Georgescu, 1970), the inner apical seta of the P4 endopod is 1.1 times as long as the P4 exopod, which makes the Romanian specimens closer to the eastern form in this feature. It would be interesting to ascertain whether the variability in the P4 endopod in Western European populations is consistent with the integument structure. Based on the data presented in this article, we can only assume that both features are interrelated.

The discovery of additional distinctive features supports an opinion about the heterogeneity of *B. pygmaeus*. It was previously shown (Kochanova et al., 2018; Kochanova & Gaviria, 2018; Kochanova et al., 2021) that a number of species of freshwater harpacticoid copepods are complex and include several genetically differentiated forms. Their distribution indicates the geographical variability of taxa. It was found (Kochanova & Gaviria, 2018; Kochanova et al., 2021), for example, that the typical form of *Attheyella crassa* (G.O. Sars, 1863) is distributed to the south and southeast from the type locality of this species (Sognsvann, Norway) and is genetically close to populations from Switzerland and the Volga River basin, while in the regions studied by us (Udmurtia, Komi Republic, and Nenets Autonomous District), another genetic form of *A. crassa* was found. Our data on the European species *B. pygmaeus* may supplement the still poor understanding of the biogeography of freshwater harpacticoids. This requires further studies of individuals from West Europe including the type locality (south of Norway), and an analysis of their molecular genetic variability relative to the eastern form. As a re-

sult of such studies, it would be possible to clarify the taxonomic status of this form of *B. pygmaeus*.

Addenda

Electronic supplementary material 1. Macro for a pixel-by-pixel spiral sweep of lightness in ImageJ software. File format: RAR.

Electronic supplementary material 2. Matrix of lightness values for each pixel on the maps of the probability of distribution of pores and sensilla in the examined individuals of *Bryocamptus*. The specimen codes are given in Table 1. Values range from 0 to 255. File format: XLSX.

All these materials are available from: <https://doi.org/10.31610/zsr/2021.30.2.320>

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