



A new species of Ectinosomatidae Sars (Copepoda, Harpacticoida) associated with *Pseudoikedella achaeta* (Zenkevitch, 1958) (Echiura, Bonelliida)

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ABSTRACT

Adult stages of both sexes of a new Echiuran infesting copepod, *Parahalectinosoma maiorovae* gen. et sp. nov., are described from the abyss of the north-western Pacific Ocean. The new species, obtained from the coelom of *Pseudoikedella achaeta* Zenkevitch, 1958, shows derived characters of its appendages compared to other representatives of the Ectinosomatidae in which it is placed by general similar body shape and swimming legs P1–P4 and by reflecting the three following ectinosomatid autapomorphies: an absent naupliar eye, a longitudinally divided telson and the presence of a pseudopericulum. Morphological peculiarities mainly of the appendages of the new species do not fit a current generic concept within the Ectinosomatidae, thus the new genus *Parahalectinosoma* is established. *Parahalectinosoma maiorovae* gen. et sp. nov. appears to be a common host-specific species in the studied area. Species' density within the individual host can be high, but its intensity shows strong variation. Due to the absence of ovigerous females and nauplii an infecting event at a copepodid stage is assumed.

1. Introduction

Within the framework of a marine biodiversity study of the north-western Pacific Ocean, the Russian-German deep-sea expedition SokhoBio (Sea of Okhotsk Biodiversity Studies) was conducted during July and August 2015 to examine the benthos of the deepest part of the Sea of Okhotsk. Like during the successful precursors SoJaBio (Malyutina and Brandt, 2013) and KuramBio (Brandt and Malyutina, 2015) a broad set of abiotic and biotic data were obtained with the attempt to correlate them with previously obtained information and to test, whether there is a biogeographic link between the semi-isolated Sea of Japan and the Sea of Okhotsk to the open Pacific Ocean. Moreover, the abyssal parts of the Sea of Japan and the Sea of Okhotsk are not connected, and their connection to the abyssal plain areas of the NW Pacific is interrupted by the hadal Kuril-Kamchatka Trench. While studying part of the invertebrate fauna of the SokhoBio expedition, various copepod-invertebrate associations were observed. Among the selected organisms were also several echiurans. These unsegmented derived polychaetes (e.g. Bleidorn et al., 2003) are as almost all other marine invertebrates (Ho, 2001), well-known habitats for symbiotic copepods (e.g. Illg, 1975; Anker et al., 2005; Ijichi et al., 2017).

Surprisingly low is the number of copepods that are known from echiuran hosts. Only six species of the cyclopoidean genera *Echiuricopus* Kim, 2016, *Echiurophilus* Delamare Deboutteville & Nunes-Ruivo, 1955, *Goidelia* Embleton, 1901, *Hemicyclops* Boeck, 1872 are encountered as mainly obligate commensals (Anker et al., 2005), although their life cycle is hardly known (Ijichi et al., 2017). This reduced number surely results from a sampling bias, as yet five shallow water echiurians serve as associates. Of these one species is unidentified, the remaining belong to the order Echiuroidea.

Huys (2016) reviewed the symbiotic associations of harpacticoid Copepoda. With respect to polychaete hosts, six reports have been documented until today (Table 1). Whilst the associated six harpacticoid species distribute over six families, the hosts constitute three species only, belonging to two polychaete families.

With more than 235 species (324 species according to Walter and Boxshall, 2019) in 22 genera, Ectinosomatidae Sars, 1903 forms a very speciose taxon (Wells, 2007; Kihara and Huys, 2009; Sciberras et al., 2018), which systematic status remains the subject of controversial discussion. However, although an urgent need of systematic revision within that family is demanded at times and even recently (e.g. Boxshall and Halsey, 2004; Wells, 2007; Kihara and Huys, 2009), the

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Table 1
List of harpacticoid species associated with polychaetes (cf. Huys, 2016).

No.	Harpacticoid species	Polychaete host	Reference
1	<i>Tegastes falcatus</i> (Norman, 1869) (Tegastidae)	<i>Filograna implexa</i> Berkeley, 1835 (Sedentaria: Serpulidae)	Brady (1880)
2	<i>Amenophia peltata</i> Boeck, 1865 (Thalestridae)	<i>Filograna implexa</i>	Scott and Scott (1893)
3	<i>Mesocletodes monensis</i> Thompson, 1893 (Argestidae)	<i>Filograna implexa</i>	Scott and Scott (1893)
4	<i>Pseudocletodes vararensis</i> T. & A. Scott, 1893 (Normanellidae)	<i>Filograna implexa</i>	Scott and Scott (1893)
5	<i>Bulbamphiascus imus</i> (Brady, 1872) (Miraciidae)	<i>Capitella capitata</i> (Fabricius, 1780) (Sedentaria: Capitellidae)	Moore and O'Reilly (1993)
6	Ectinosomatidae sp.? (Ectinosomatidae)	<i>Hydroides norvegica</i> Gunnerus, 1768 (Sedentaria: Serpulidae)	O'Reilly (1995)
7	<i>Parahalectinosoma maiorovae</i> gen. et sp. nov. (Ectinosomatidae)	<i>Pseudoikedella achaeta</i> (Zenkevitch, 1958) (Echiura: Bonelliidae)	Present contribution

monophyletic status of Ectinosomatidae as proved by Seifried (2003) is not questioned. The high number of ectinosomatid species comes along with a likewise variety of habitat utilization and life ways. Ectinosomatidae are known mostly from marine but also from freshwater habitats; they occur from the marine littoral down to the deep sea; they include herbivore, carnivore and detritivore feeding types, and there are even a few species known living associated with other organisms (Boxshall and Halsey, 2004). As summarized by Huys (2016), preferred hosts for planktonic species (i.e. *Microsetella* Brady, 1880) seem to be chaetognaths, whilst benthic ectinosomatids apparently favour certain Bryozoa and serpulid Polychaeta. The present contribution documents the first association between a here described scientifically new species of Ectinosomatidae and an echiuran, namely the abyssal bonelliidean *Pseudoikedella achaeta* (Zenkevitch, 1958). The bathyal-abyssal host species is bi-hemisphere distributed in the Pacific and Atlantic Oceans (Zenkevitch, 1966; Murina, 1978; Maiorova and Adrianov, 2018). In the Kuril Basin of the study area (Sea of Okhotsk) the species is among the surface deposit feeders very dominant and occurs in high abundances in the benthos (Kharlamenko et al., 2018).

2. Material and methods

Dr Anastassya Maiorova (National Scientific Center of Marine Biology, Far Eastern Branch of Russian Academy of Sciences, Vladivostok, Russia), responsible for the worm-like invertebrates during SokhoBio, provided seven randomly selected specimens of *Pseudoikedella achaeta* from Agassiz Trawl (AGT) samples (frame of 350 cm × 70 cm [width × height] and a mesh size of 10 mm). The material on which the species description is based was collected from five host individuals (here labelled “a–e”, see Table 2) from station 6–8 on July 21st, 2015, from 48°00.161'N/150°00.464'E to 48°02.528'N/150°00.098'E (calculated trawled distance: 1278 m) at a depth range between 3347–3351 m (Fig. 1).

Station numbering indicates the sampling area (here: sampling area 6), whilst the hinder number refers to individual hauls, meaning that a broad set of gears was used in each sampling area, allowing us to plot the following abiotic conditions gained from data of the camera-epibenthic sledge (C-EBS) and box corer (BC) of the relevant area: temperature 1.9 °C, salinity 34.6, oxygen 81.4 μM/l (± 0.03), oxygen saturation 24.5% (± 0.009), pressure 3367.8 dB (± 0.026) [all from C-EBS]; sediment consists of fine, soft, nearly liquid, brown clay on surface (to 11 cm), in the deep friable greenish clay [from BC] (data extracted from Maljutina et al., 2015).

Table 2

Number of found individuals of *Parahalectinosoma maiorovae* gen. et sp. nov. in its host species *Pseudoikedella achaeta* from the type locality station 6–8. HT = Holotype; PT1–16 = Paratypes 1–16; CI, CIII, CV = copepodid stages I, III, V.

<i>Pseudoikedella achaeta</i>	<i>Parahalectinosoma maiorovae</i> gen. et sp. nov.	Total
St. 6–8	a	7 females, 1 male and 1 CV
	b	2 males
	c	1 male
	d	1 CIII
	e	2 males, 1 CI and 1 CIII

After the successful deployment of the AGT, organisms were hand-picked from sediment and immediately transferred to pre-cooled (−20 °C) 96% ethanol. The herein treated host specimens were put to our disposal by Stefan Eiler (Bavarian State collection of Zoology, München, Germany) for further investigation. After a careful examination of the body surfaces, the individual host specimens were opened longitudinally in lengths axis following the instructions of Stephen and Edmonds (1972) for anatomical studies on echiurans. The coelom was carefully flushed with 96% ethanol without damaging of the alimentary canal. Once the associated copepods were isolated, the alimentary canal was opened for cross-checking the digested sediment for copepods, but the latter step always yielded no copepods. The herein discussed copepod specimens thus come exclusively from the coelom. Evidence for host damaging was observable neither on tissue nor on any organs.

For species identification the keys provided by Lang (1948), Huys et al. (1996), Wells (2007) as well as original descriptions were used. Drawings were made with the use of a camera lucida on a Leica DMR compound microscope equipped with differential interference contrast. General terminology follows Lang (1948), Huys and Boxshall (1991), and Huys et al. (1996). The terms “telson” and “furca” are adopted from Schminke (1976).

Abbreviations used in the text: A1 = antennule, A2 = antenna, aes = aesthetasc, benp = baseopod, cpth = cephalothorax, enp = endopod, enp-1–enp-3 = endopodal segments 1–3, exp = exopod, exp-1–exp-3 = exopodal segments 1–3, FR = furcal rami, GDS = genital double somite, GF = genital field, n = number of specimens, P1–P6 = swimming legs 1–6, R = rostrum, T = telson.

3. Results

Subclass: Copepoda Milne-Edwards, 1840

Order: Harpacticoida Sars, 1903

Family: Ectinosomatidae Sars, 1903

Genus: *Parahalectinosoma* gen. nov.

Generic diagnosis: It is identical with the description of the here described *Parahalectinosoma maiorovae* gen. et sp. nov.

Etymology: The generic name points to the general similarity with the genus *Halectinosoma* Vervoort, 1962.

Type species: *Parahalectinosoma maiorovae* gen. et sp. nov. (present contribution).

Locus typicus: Russia, Sea of Okhotsk, Kuril Basin, SokhoBio Station

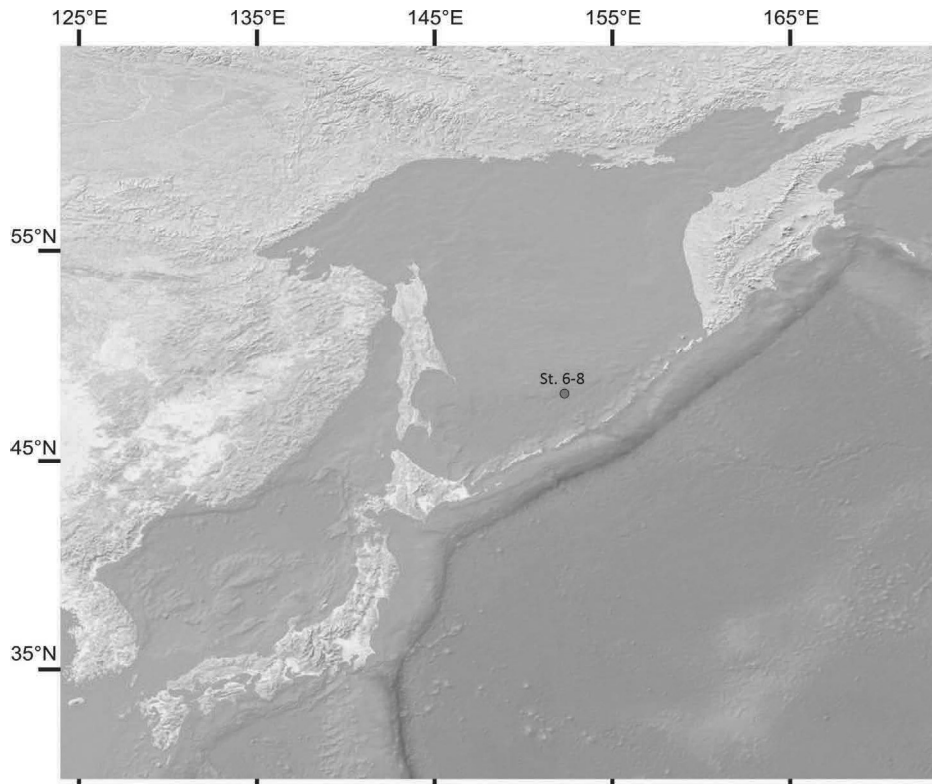


Fig. 1. Map of the Sea of Okhotsk, showing the type locality of *Parahalectinosoma maiorovae* gen. et sp. nov. (program downloaded from: www.diva-gis.org).

6–8: 48°00.161'N 150°00.464'E to 48°02.528'N 150°00.098'E, 3347–3351 m, coelom of *Pseudoikedella achaeta*.

Type material: The type material consists of 17 individuals, i.e. 7 females, 6 males, 1 CI, 2 CIII, and 1 CV copepodids. All type specimens were collected from the type locality but from five individual host specimens (see Table 2). The holotype and paratypes 1–3 and 6–16 are deposited in the collection of the Senckenberg Museum für Naturkunde, Frankfurt, Germany; paratypes 4 and 5 are stored at the Bavarian State collection of Zoology, Munich, Germany (Department Arthropoda).

Holotype: female, embedded with glycerol on 1 slide, collection number SMF 37183/1.

Paratypes: Paratype 1 (allotype): 1 male, embedded with glycerol on 1 slide, collection number SMF 37184/1; paratype 2: female, embedded with glycerol on 1 slide, collection number SMF 37185/1; paratype 3: female, embedded with glycerol and distributed on 10 slides, collection number SMF 37186/1–10; paratype 4: female, embedded with glycerol on 1 slide, collection number ZSMA20190001/1; paratype 5: male, embedded with glycerol on 1 slide, collection number ZSMA20190002/1; paratype 6: male, embedded with glycerol on 1 slide, collection number SMF 37187/1; paratype 7: CIII copepodid, embedded with glycerol on 1 slide, collection number SMF 37188/1; paratypes 8–12: 3 females, 1 male and 1 CV copepodid, preserved in a glass vial with 76% denaturated ethanol, collection number SMF 37189/1; paratypes 13–16: 2 males, 1 CI and 1 CIII copepodid, preserved in a glass vial with 76% denaturated ethanol, collection number SMF 37190/1.

Etymology: The species name honours Dr Anastassya Maiorova, an expert on worm-like deep-sea organisms and donator of the present host samples.

Description of the female:

Habitus (Fig. 2A and B) slender, fusiform, body length from rostrum to end of FR between 800 and 873 μ m (average: 822 μ m; $n = 6$). Rostrum fused to cphth, short. Cphth and body somites except penultimate

one with long sensilla; last thoracic and first abdominal somite fused to GDS; cphth, thoracic somites and GDS dorsally with finely serrated hyaline frills; P2–P4-bearing somites ventrolaterally cuspidate (Fig. 2A); GDS and following abdominal somites ventrally with row of fine spinules. Penultimate abdominal somite dorsally extended forming a pseudopericulum; telson smallest body somite, dorsally with pair of sensilla and paired row of fine setules running ventral towards anal opening.

FR (Fig. 2A–C) small, trapezoid in lateral shape, carrying 6 setae: I and II arising close together from outer distal margin, III lost, IV, V, and VI inserting apically, V being the longest seta, VII arising dorsally, triarticulate.

A1 (Fig. 4A) 4-segmented, small. First segment trapezoid, with few spinules and 1 bare seta on anterior apical margin. Second segment as long as first, carrying 11 bare setae; additionally with 1 aes accompanied by 1 long unipinnate seta. Third segment smallest, broader than long, with 1 unipinnate seta. Fourth segment about two times longer than third one, trapezoid in shape, with 4 setae, one of which bipinnate, and apically with trithec consisting of 2 bare setae and 1 aes.

Setal formula: 1-1; 2-12 + aes; 3-1; 4-6 + aes.

A2 (Fig. 3A–C) with basis, 1-segmented exp, and 2-segmented enp. Basis with row of long spinules along anterior margin. Exp small and slender, laterally with 1 multipinnate seta, apically with crest of spinules, 1 multipinnate and 1 biplumose seta. Enp-1 as long as basis, without setae and spinules. Enp-2 shorter than enp-1, with each 1 row of long spinules medially on its surface, on its anterior margin, and apically. Subapically with 2 strong spines with rounded tips and several long outer spinules, giving a brush- respectively comb-like aspect. Apically with 6 setae, 4 of which geniculated, the longest unipinnate.

Labrum (Figs. 2A and 3A, B) large and strongly sclerotized, in ventral view broad and with 2 sharp-edged notches apically; anteriorly extended into a prominent, hook-like, backwardly directed spike.

Mouthparts very small, atrophied. Thus, both the mx1 and mx could not be discerned clearly and were not drawn.

Md (Fig. 4B) with slender multicuspitate gnathobase that lacks any

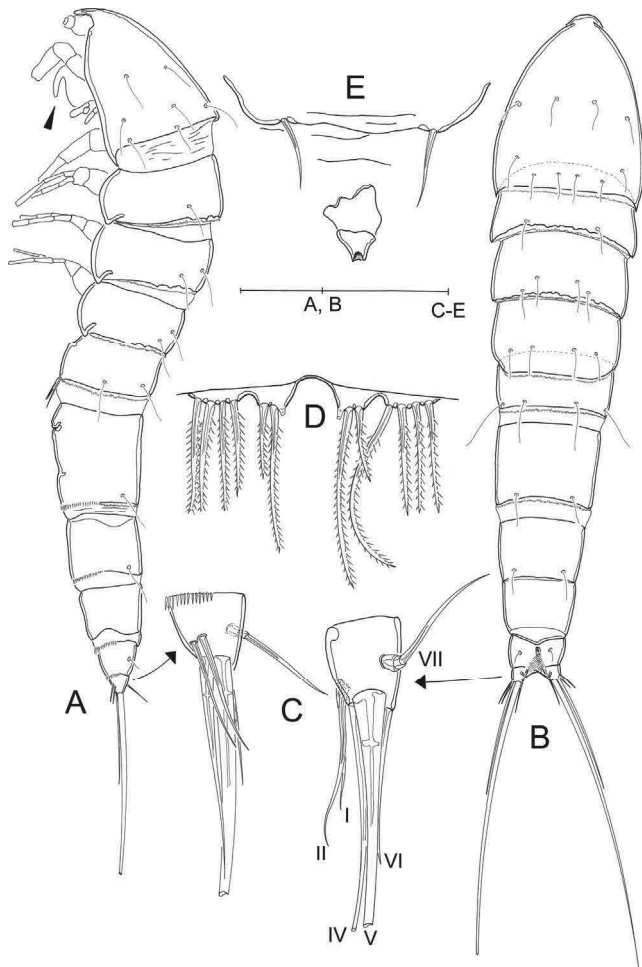


Fig. 2. *Parahalectinosoma maiorovae* gen. et sp. nov., female. (A) Holotype, habitus, lateral view. Arrowhead showing the prominent labrum, (B) Paratype 2, habitus, dorsal view, (C) FR, left: lateral view of A, right: dorsal view of B; Roman numerals naming the furcal setae, (D) Paratype 4, P5, (E) Paratype 4, P6 and genital field. Scales: A, B: 100 μm , C–E: 50 μm .

setae. Palpus composed of basis and 1-segmented enp and exp. Basis with 1 abexopodal bare seta. Enp as long as basis, with 2 apical setae, the outermost being bipinnate; additionally with 1 outer seta arising subapically, and with 1 inner seta staying close to the basis. Exp half as long as enp, with 1 inner and 2 apical bare setae.

Mxp (Fig. 3A) stenopodial, small, 2-segmented. Syncoxa(?) without seta, basis and enp fused(?), with 4 setae, the inner- and outermost being bipinnate.

P1 (Fig. 4C) coxa larger than basis; intercoxal sclerite small, rectangular but with triangular emargination of posterior margin. Basis with three rows of spinules on its surface, and with 1 outer multipinnate and 1 unipinnate inner seta. Exp and enp 3-segmented, of almost same length; all outer exopodal spines unipinnate on distal half, all inner and apical setae biplumose. Exp-1 with 1 outer spine and 3 overlapping rows of spinules; no inner seta. Exp-2 with row of spinules running from outer to apical margin; with 1 outer spine and 1 inner seta. Exp-3 with 2 uniplumose outer spines, and with 2 apical and 1 inner biplumose setae. All endopodal setae biplumose. Enp-1 with 2 rows of spinules and with 1 inner seta. Enp-2 apically with 1 row of spinules and 1 inner seta. Enp-3 without spinules, with 2 apical and 2 inner setae.

P2–P4 (Fig. 5B–D). General shape as in P1, with 3-segmented exopods and endopods, and with coxa being larger than basis. Basis with outer multipinnate seta, furthermore with rows of spinules at the bases of the exopodal and endopodal limbs. Additionally with tuft of long spinules on inner margin (not discernible in P2). Exopodal segments 1

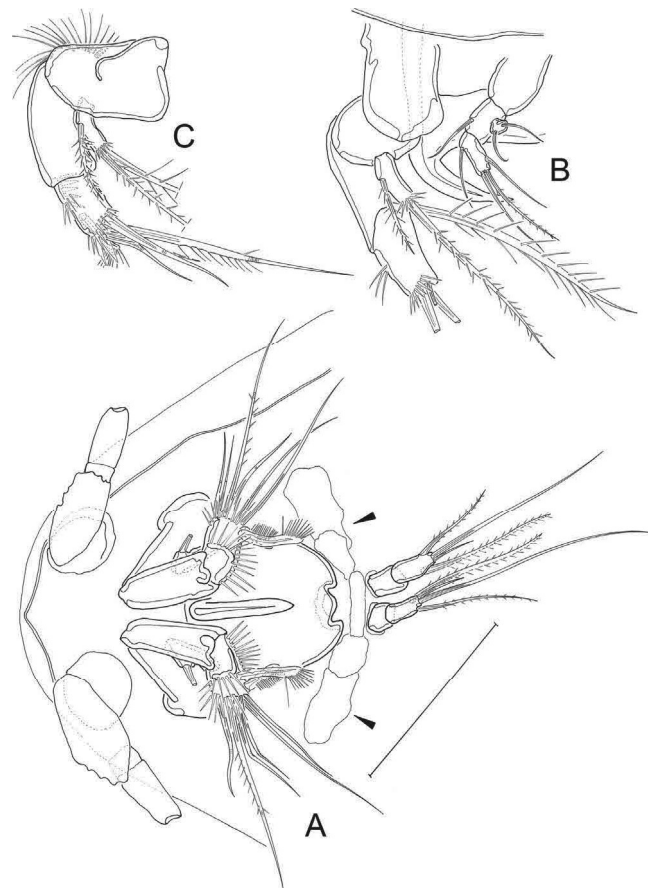


Fig. 3. *Parahalectinosoma maiorovae* gen. et sp. nov., female. (A) Paratype 4, cphth, ventral view showing in detail the A2, labrum, and mxp; remaining mouthparts only indicated (triangular arrowheads), (B) Holotype, A2, labrum and md palpus in lateral view, (C) Paratype 3, A2. Scale: 50 μm .

and 2 each with outer row of spinules and 1 outer unipinnate spine. In P2, exp-2 lacks an inner seta, whilst in P3 and P4 1 inner biplumose seta is present. Exopodal segment 3 carries 2 unipinnate outer spines, 2 apical and 2 inner biplumose setae. Endopod as long as exopod; endopodal segment 1 equipped with 1 inner seta surpassing the endopod's length. P2 and P3 enp-2 with, P4 enp-2 without inner seta. Exopodal segment 3 with 2 apical and 2 inner biplumose setae.

The setal formula of P1–P4 is given in Table 3.

P5 (Fig. 2D) very small, both the endopodal and exopodal lobes fused, strongly reduced and hardly pronounced. Benp carrying 2 bipinnate setae apically, the inner one 2–3 times longer than the outer one; additionally with 1 short tube pore on inner apical margin. Exp broader but shorter than benp, with 4 bipinnate setae of more or less same (but varying) length.

GF and P6 (Fig. 2E) small, gonopore sclerotized; P6 dislocated anteriorly, forming single plate that bears 2 bare setae.

Description of male:

The male of *Parahalectinosoma maiorovae* gen. et sp. nov. strongly resembles the female, particularly concerning the A2, the mouthparts, and the swimming legs. It differs, however, from the female in the following features:

Habitus (Fig. 6A). Smaller than female, reaching a total body length (rostrum to end of FR) between 609 μm and 726 μm (average: 670 μm , $n = 6$). Arrangement and number of sensilla on the body somites differ from that of female. Contrary to the female, the male exhibits a finely serrated hyaline frill also on the dorsal posterior margin of the second

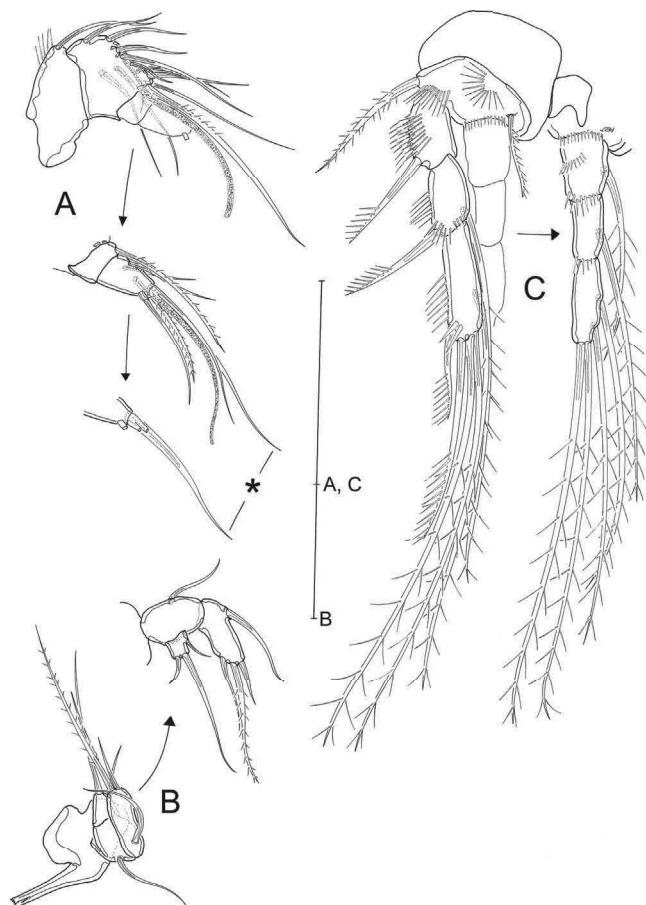


Fig. 4. *Parahaelectinosoma maiorovae* gen. et sp. nov. (A) Paratype 3, female A1, arrows pointing to detailed illustration of segments 3 and 4; asterisk* indicating same seta, (B) Paratype 3, female md, arrow pointing to turned mandibular palpus, (C). Allotype, male P1, coxa and intercoxal sclerite indicated. Scales: 50 μ m.

abdominal somite.

A1 (Fig. 6B) sexually dimorphic, 5-segmented and weakly sub-chirocer, geniculation between third and fourth segment. First segment with 1 bare seta, without spinules. Second segment equipped with 11 bare setae. Third segment marginally longer than second one, slightly swollen, distal part strongly sclerotized; aes arising medially from posterior margin without accompanying seta(e); anterior margin with 7 bare setae. Fourth segment as long as second segment, without setae. Fifth segment smallest, longer than broad, apically with trithec consisting of 2 bare setae and 1 aes.

Setal formula: 1–1; 2–11; 3–7 + aes; 4–0; 5–2 + aes.

P5 (Fig. C) almost identical with that of female, but the endopodal part slightly longer than that of female P5, whilst the exopodal part is a little bit more reduced.

P6 absent.

4. Discussion

4.1. Allocation of *Parahaelectinosoma maiorovae* gen. et sp. nov. to Ectinosomatidae

The here presented hypothesis of *Parahaelectinosoma maiorovae* gen. et sp. nov. as belonging to Ectinosomatidae is based on three autapomorphies of the latter as listed by Seifried (2003) [plesiomorphic condition always in square brackets]:

1. Nauplius eye absent [nauplius eye present];

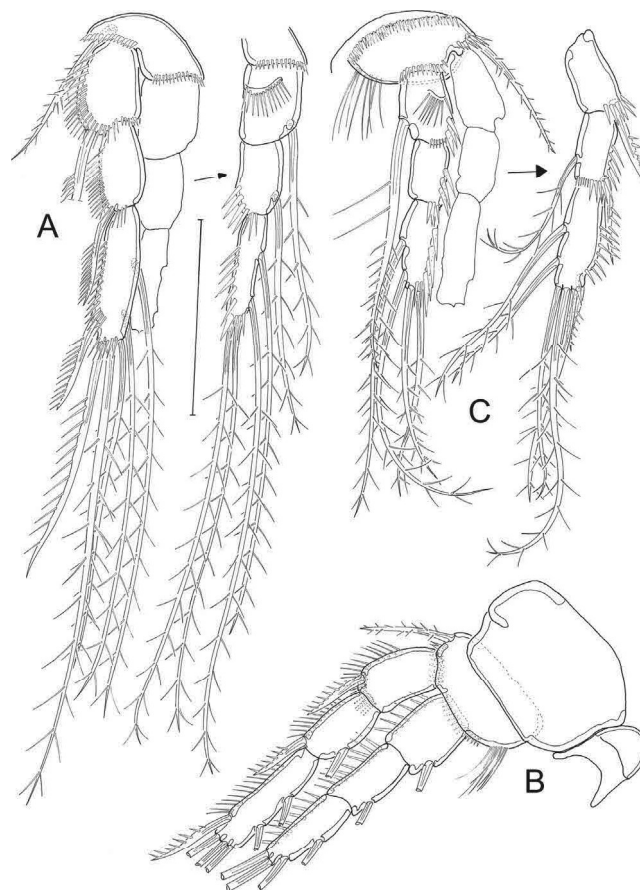


Fig. 5. *Parahaelectinosoma maiorovae* gen. et sp. nov., Paratype 3, female. (A) P2, (B) P3 with intercoxal sclerite, (C) P4. Scale: 50 μ m.

Table 3

Parahaelectinosoma maiorovae gen. et sp. nov., setal formula of P1–P4 (Roman numbers meaning outer setae/spines).

	Coxa	Basis	Exopod	Endopod
P1	0-0	I-1	I-0; I-1; II,2,1	0-1; 0-1; 0,2,2
P2	0-0	I-0	I-0; I-0; II,2,2	0-1; 0-1; 0,2,2
P3	0-0	I-0	I-0; I-1; II,2,2	0-1; 0-1; 0,2,2
P4 ♀	0-0	I-0	I-0; I-1; II,2,2	0-1; 0-0; 0,2,2

2. Telson divided longitudinally [telson not divided longitudinally];
3. Pseudopericulum present [pseudopericulum absent].

Whilst in their groundpattern both Podogenononta Lang, 1944 and Exanechentera Lang, 1944 present a nauplius eye (character 1), this became lost in Chappuisidae Chappuis, 1940 and Ectinosomatidae (Seifried, 2003), being also absent in *Parahaelectinosoma maiorovae* gen. et sp. nov. However, both Chappuisidae and Ectinosomatidae are characterized each by a series of further autapomorphies (Seifried, 2003), leading to the conclusion that the loss of the naupliar eye is due to convergence rather than constituting a synapomorphy of Chappuisidae and Ectinosomatidae, especially because the latter are well-justified as being the sistergroup of Exanechentera (Seifried, 2003, p. 171).

Whereas *Parahaelectinosoma maiorovae* gen. et sp. nov. does not share any of the further chappuisid autapomorphies, the new species presents above listed ectinosomatid apomorphies 2 and 3. Moreover, the shape of body and swimming legs P1–P4 fits that of (fusiform) Ectinosomatidae. On the other hand it results difficult to detect more ectinosomatid autapomorphies in *Parahaelectinosoma maiorovae* gen. et sp. nov. because of the remarkable secondary deviation of the

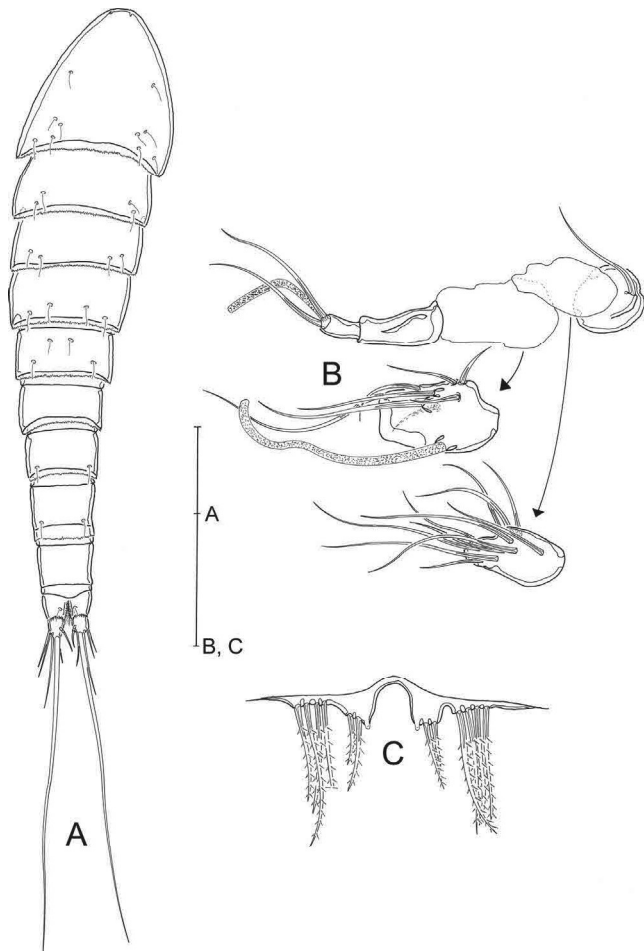


Fig. 6. *Parahalectinosoma maiorovae* gen. et sp. nov., male. (A) Paratype 5, habitus, dorsal view, (B) Paratype 5, A1. arrows pointing to detailed illustration of segments 2 and 3, (C) Allotype, P5. Scales: A: 100 μ m, B, C: 50 μ m.

respective appendages in that species. For instance, the shape of both the mx (character 4, see below) and the P5 (characters 5–7, see below), which are autapomorphies of Ectinosomatidae (Seifried, 2003) if compared with remaining Harpacticoida, cannot be confirmed for *Parahalectinosoma maiorovae* gen. et sp. nov., because in that species the mx is strongly atrophied (secondary deviation), and also the P5 in both the female and the male is strongly reduced and transformed in shape (secondary deviation). Same applies for e.g. the autapomorphic displacement of the seta on A2 enp-1 to the proximal margin (character 8, see below) or for the distal displacement of 1 seta on the cutting edge of the mandibular gnathobase (character 9, see below; cf. Seifried, 2003); in *Parahalectinosoma maiorovae* gen. et sp. nov., these setae are completely lost (secondary deviation). Finally, the new species presents several features that are more derived than the conditions described for the ectinosomatid groundpattern (characters 10–19):

4. Mx strongly atrophied [mx compound by syncoxa, allobasis, and 3-segmented enp, well developed];
5. P5 both legs fused medially [legs distinct];
6. P5 benp and exp fused [separated];
7. P5 exp very small, not extending basendopodal lobe [exp surpassing length of benp];
8. A2 enp-1 lacking proximal seta [proximal seta present];
9. Cutting edge of mandibular gnathobase lacking setae [with 2 setae, one at distal, one at proximal corner];
10. Female A1 4-segmented [female A1 5–7-segmented];
11. A2 exp 1-segmented [A2 exp 3-segmented];

12. Labrum enlarged, forming a broad plate with sharp-edged notches apically [labrum rather small, without apical notches];
13. Labrum anteriorly extended into a prominent, hook-like, backwardly directed spike [spike absent or minute in size];
14. Mandibular gnathobase slender, tiny [gnathobase broad, of regular size];
15. Basis of mandibular palp with 1 seta [with at least 3 setae];
16. Md enp with 4 setae [md enp with > 4 setae, exception: *Ectinosomella nitidula* Sars, 1910];
17. Mxl strongly atrophied [mxl compound by praecoxa, coxa, basis, enp and exp, well developed];
18. Mxp 2-segmented [mxp 3-segmented];
19. P2–P4 exp-3 with 2 outer spines [with 3 outer spines];

Summarizing the above made thread, *Parahalectinosoma maiorovae* gen. et sp. nov. is assigned to Ectinosomatidae basing on three familiar autapomorphies 1–3 as well on the general aspect of the fusiform body and of P1–P4. Such supposition may sound rather vague and unsatisfactory, in particular because the unambiguous ectinosomatid autapomorphies (mx, P5) are not found in the new species; however, as *Parahalectinosoma maiorovae* gen. et sp. nov. presents even more derived stages in the respective characters (possibly owed to the specialised life way), the above mentioned concordant characters support our hypothesis. Moreover it can be stated that many characters are indeed present in other Ectinosomatidae, although in a quite heterogeneous distribution over different species (listed examples restricted to the fusiform type only):

- A 4-segmented female A1 (character 10) has been described for *Pseudobradya hirsuta* (Scott and Scott, 1894) (Wells, 1967);
- A 1-segmented A2 exp (character 11) is present in *Bradyellopsis* Brian, 1924 [part.] (e.g. Brian, 1924; Steuer, 1941; Watkins, 1987);
- A large labrum with backwardly pointed hook-like spike (characters 12, 13) is formed in many representatives of *Halectinosoma* Lang, 1944, though in quite variable expression (e.g. Giesbrecht, 1882; Scott and Scott, 1894, Sars, 1904, 1919; Kunz, 1949; Clément and Moore, 1995, Sciberras et al., 2018), also in some species of *Ectinosoma* Boeck, 1865 (e.g. Sars, 1904; Borutzky, 1952; Noodt, 1958; Chislenko, 1967; Seifried, 1997; Seifried and Dürbaum, 2000), and even two species of *Pseudobradya* Sars, 1904, *P. barroisi* (Richard, 1893) and *P. beduina* Monard, 1935, developed a labrum bearing a small spike (Richard, 1863; Monard, 1935; Kunz, 1983);
- A P2–P4 exp-3 carrying 2 instead of 3 outer spines (character complex 19) is comparatively widespread among the different ectinosomatid genera, e.g. in *Bradyellopsis foliatus* Watkins, 1987, *Halectinosoma* (div. spp.), *Ectinosoma* (div. spp.), *Klieosoma* Hicks & Schriever, 1985 (div. spp.), *Pseudectinosoma* Kunz, 1935, and *Sigmatidium* Giesbrecht, 1881;
- Last but not least, also a P5 resembling that of *Parahalectinosoma maiorovae* gen. et sp. nov. (characters 5–7) is found in other ectinosomatid representatives like *Halectinosoma japonicum* (Miura, 1964) (only male), *Bradya* (*Parabradya*) (surface seta present), *Ectinosoma soyeri* Apostolov, 1975 (surface seta present), *Pseudectinosoma* (even more reduced; exp lacking setae), *Rangabradya indica* Karanovic & Pesce, 2001 (benp and exp fused together, but legs not fused medially), *Sigmatidium* [part.].

Therefore, apart from sharing the ectinosomatid autapomorphies 1–3 as well as the general shape of a fusiform body and the swimming legs, *Parahalectinosoma maiorovae* gen. et sp. nov. collates many characters that are distributed over Ectinosomatidae, most of them shared by the new species and *Halectinosoma*. In addition, some characteristics present in the new species are unique and must be regarded as specific autapomorphies; apart from perhaps minor deviations like e.g. the loss of setae in the antennular segments, the mandibular gnathobase, and the swimming legs particularly (i) the strong atrophy of the mouthparts,

especially of the mandibular gnathobase, the mxl and the mx; (ii) massive enlargement of the labrum including the development of a prominent, backwardly directed spike; (iii) diminishment of the mxp by loss of one segment. Although any phylogenetic analysis would be premature at the time, an establishment of the here described new species as *Parahalectinosoma maiorovae* gen. et sp. nov. seems therefore justified.

Speculating, one might assume that the overall reduction of the original mouthparts was a result from specific adaptation of *Parahalectinosoma maiorovae* gen. et sp. nov. to a mode of life that is linked to its co-housing with *Pseudoikedella achaeta* (Zenkevitch, 1958) (see below). A hint may be the size and shape of the A2 and its position with respect to the labrum and its spike (see Fig. 3A and B). In all observed individuals the A2 is backwardly directed, with its enp-1 staying close to the spike, whilst the enp-2 spreads outwardly. The latter is, furthermore, equipped with quite specific brush- respectively comb-like spines and several long spinules, whose function might be related to clipping/ingestion activity. In that context it might be of interest that the only appendage of a mouthpart that is not strongly atrophied, is the mandibular palp. As observable from Fig. 3B, the palp is positioned laterally beside the spike of the labrum and might therefore also be involved in any ingestion activity, together with the labrum and the A2.

4.2. Remarks concerning *Pseudoikedella achaeta* and *Parahalectinosoma maiorovae* gen. et sp. nov.

Out of seven randomly selected individuals of the deep-sea bonelliidean echiuran *Pseudoikedella achaeta*, we observed in five specimens a varying degree of utilization by the here described *Parahalectinosoma maiorovae* gen. et sp. nov.

The host species is in the study area one of the dominant benthic organisms and it is suggested that this is supported by an enhanced availability of organic matters at the deep-sea floor (e.g. Kharlamenko et al., 2018). Maiorova and Adrianov (2018) examined the echiuran diversity and abundance of the SokhoBio material and considered *P. achaeta* as one of the most abundant species. The authors encountered a total of 260 echiuran specimens of seven genera and species from eight of 11 SokhoBio sampling areas within a depth range of 1700–4700 m. The present host species contributes with a total of 150 specimens (~58%) to the investigated echiuran fauna, whereby 43 specimens (~29%) were recorded from the AGT station 6–8, the here designated type locality of *Parahalectinosoma maiorovae* gen. et sp. nov. (Fig. 1). According to Maiorova and Adrianov (2018) this station showed the highest abundance of *P. achaeta*, which co-occurs here with the two other bonelliid species *Alomasoma nordpacificum* Zenkevitch, 1958 (8 specimens) and *Bengalus* sp. (2 specimens).

Calculating the 43 collected specimens (including our data) to the trawled distance (see above), we get an approximate density of 9.6 specimens per 1000 m². Following here Bush et al. (1997) we found the prevalence of infected host specimens 5/7 (~71%). Taken into account the low number of host specimens we examined it may be assumed that *Parahalectinosoma maiorovae* gen. et sp. nov. is not uncommon in the studied area. However, the copepod intensity in their host seems to vary strongly (see Table 2). We found for example females in a single specimen only, males however were available in four of five specimens. Noteworthy, none of the examined females was ovigerous, nauplii and eggs were not found. As all copepods were exclusively found in the host's coelom their density in an individual host may be considerable high, here with a maximum of nine specimens per host. Whether a mean intensity of 3.4 is a realistic value, seems to be questionable, as the individual intensity of copepodids and sexes is too heterogeneous. Nothing is known about the life style of *Parahalectinosoma maiorovae* gen. et sp. nov. The complete lack of any developmental stages prior a copepodid leads us to assume that infection occurs at this stage earliest, but how the species enter its host, and releases the eggs or larvae

remains unclear. Damages on the host's tissues could not be observed and also the subsequent examination of the dissected alimentary canal yields no copepods. At the current stage we also may not discuss the host selection of the *Parahalectinosoma maiorovae* gen. et sp. nov. as we examined *Pseudoikedella achaeta* only.

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