# A new minute ectosymbiotic harpacticoid copepod living on the sea cucumber *Eupentacta fraudatrix* in the East/Japan Sea

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**Abstract**

The ectosymbiotic copepod, *Vostoklaophonte eupenta* gen. & sp. nov. (Copepoda: Harpacticoida: Laophontidae), was found associated with the sea cucumber *Eupentacta fraudatrix* in the subtidal zone of Peter the Great Bay, East/Japan Sea. The new genus, *Vostoklaophonte*, is closely related to *Microchelonia* Brady, 1918 in the flattened body form, reduced mandible, maxillule and maxilla, but with well-developed prehensile maxilliped, and reduced segmentation and setation of legs 1-5. Most appendages of the new genus are more primitive than those of *Microchelonia*. The previous inclusion of the symbiotic genera *Vostoklaophonte* and *Microchelonia* in Laophontidae based on morphological observation is supported here by molecular data. This is the third record of harpacticoid copepods living in symbiosis with sea cucumbers from the Korean and Californian coasts.

## Introduction

Symbiotic harpacticoids that use holothurians as hosts are rarely reported compared to the orders Poecilostomatoida and Siphonostomatoida (Humes, 1980, Ho, 1982, Jangoux, 1990, Mahatma, Arbizu & Ivanenko, 2008). Among harpacticoids, one species of Tisbidae Stebbing, 1910 —*Sacodiscus humesi* Stock, 1960— and two species of Laophontidae T. Scott, 1905 —*Microchelonia californiensis* (Ho & Perkins, 1977) and *M. koreensis* (Kim, 1991)— have been found associated with sea cucumbers (Huys, 2016).

Stock (1960) found *S. humesi* Stock, 1960 in washings of *Holothuria tubulosa* Gmelin, 1791 collected in the Bay of Banyuls. *Microchelonia californiensis* (Ho & Perkins, 1977) was found associated with the holothurian *Apostichopus parvimensis* (Clark, 1913) at the Californian coast. *Microchelonia californiensis* was originally described as a new genus and species, *Namakosiramia californiensis* Ho & Perkins, 1977, and was designated by Ho & Perkins (1977) as the type of their newly established "siphonostome" cyclopoid family Namakosiramiidae. XXXX Huys (1988) re-examined the type material of *N. californiensis*, removed the family from the Siphonostomatoida and placed it in the Harpacticoida, and relegated it to a junior subjective synonym of the family Laophontidae (see also Huys (2009)). The second species, *M. koreensis* (Kim, 1991), was described from the holothurian

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*Apostichopus japonicus* (Selenka, 1867) kept in the aquarium of a fish market in Kangreung at the Korean east coast (Kim, 1991).

The symbiotic copepods of the genus *Microchelonia* represents the family Laophontidae including 325 valid species in 73 genera and two subfamilies (Walter & Boxshall, 2017). The family includes diverse living forms having cylindrical or dorsoventrally flattened body shape, as well as various reductions of the pedigerous legs (Gheerardyn et al. 2007).

During a survey of symbiotic copepods associated with invertebrates at Peter the Great Bay, East Sea (Japan Sea), a new harpacticoid copepod of the family Laophontidae, *Vostoklaophonte eupenta* gen. & sp. nov., was found and is described herein.

**Materials and methods**

Harpacticoid copepods living on the sea cucumber *Eupentacta fraudatrix* as well as *Microchelonia koreensis* living on the sea cucumber *Apostichopus japonicus* (Genbank Accession numbers: MG012752) were collected same day (October 17 2013) at the subtidal zone of the "Vostok" research station at Peter the Great Bay of the East Sea (Japan Sea). 23 specimens of sea cucumbers (17 specimens of *Eupentacta fraudatrix* and 5 specimens of *Apostichopus japonicas*) were collected by hand. The sea cucumbers were placed in plastic bags *in situ* and washed in 10% ethanol. The washings were sieved using a 60 µm sieve and copepods were sorted with a pipette under an Olympus SZX 7 dissecting microscope.

The specimens of *M. koreensis* used for molecular phylogenetic analyses were collected in the same location from the spiked sea cucumber *A. japonicus*.

Copepods were dissected in lactic acid, and the dissected parts were mounted on slides using lactophenol as mounting medium. Preparations were sealed with transparent nail varnish. All drawings were prepared using a camera lucida on an Olympus BX51 differential interference contrast microscope.

Specimens for SEM micrographs were dehydrated through graded ethanol series, critical point dried, mounted on stubs and sputter-coated with platinum. The material was photographed using a Hitachi S-4700 scanning electron microscope at Eulji University, Seoul, Korea. All the specimens were deposited in the collection of the National Institute of Biological Resources, Korea (NIBR) and in the Zoological Museum of Lomonosov Moscow State University.

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Huys, R. 2016. Harpacticoid copepods—their symbiotic associations and biogenic substrata: a review. Zootaxa 4174(1): 448-729.

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DNA was extracted from ethanol-preserved specimens using Diatom DNA Prep 100 kit (Isogene, Moscow, Russia). Nuclear 18S rDNA was amplificated using Encyclo Plus PCR kit (Evrogen) and universal primers Q5 and Q39 (Medlin et al, 1988). Following PCR conditions were used: 3 min at 95 'C, the 37 cycles of 94 'C for 20 s, annealing at 54 ’C for 30 s, 72 'C for 1m 30s and final elongation at 72 'C fo 5 m. PCR products were purified with preparative electrophoresis in 1% agarose gel. Bands of DNA of appropriate length were excised from gel and DNA was extracted using GelPrep spin-column kit (Cytokine). Extracted DNA was sequenced on ABI 3730 capillary sequencer from both ends.

The copepod taxa examined in this study are listed taxonomically in Table 1. Previously recorded sequences of nuclear 18S-rDNA from GenBank were aligned using the Muscle algorithm integrated in MEGA 6.0 (Edgar 2004). Consequently, we generated an alignment of 1929 bp for 43 taxa (listed in Table 1) for 18S-rDNA. Models of nucleotide evolution were estimated using ModelGenerator (Keane et al., 2006). GTR+G+I model (General Time-Reversible with gamma distribution of rates across sites and proportion of invariant sites) was found optimal. Neighbor-joining trees were built in MEGA 6.0 (Tamura et al., 2013) and Bayesian phylogenetic trees were built in PhyloBayes 3.3 (Lartillot, Lepage & Blanquart, 2009). Two MCMC chains were run in parallel and the analyses were stopped when maximum discrepancy of bipartitions between chains was below 0.1. 6000 tree generations were produced Burn-in was set at 1000 trees.

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1–P6, first to sixth legs; exp(enp)-1(2, 3) denotes the proximal (middle, distal) segment of the exopod(endopod). Scale bars in figures are in $\mu$m.

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:4FDE5EAE-24A0-4320-A06C-1FD8F983A0BE. The online

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## Systematics

**Order Harpacticoida Sars, 1903**
**Family Laophontidae T. Scott, 1905**
**Subfamily Laophontinae T. Scott, 1905**
***Vostoklaophonte* gen. nov.**
urn:lsid:zoobank.org:act:1988C43D-50A0-4785-83CC-A3BB870A1972

**Diagnosis.** Laophontidae. Body dorsoventrally flattened; female genital field with 2 setae on P6 and small copulatory pore located in median depression; anal operculum well-developed. Sexual dimorphism in antennules, P3–P6, and in genital segmentation. Rostrum large and rectangular, fused at base; antennule 6–segmented in female, and 7–segmented, subchirocer in male, aesthetasc on segment 4 and 6 in female, on segment 5 and 7 in male; mandibular palp with 4 elements; coxal endite of the maxillule small with 3 elements; coxa of maxilliped with 1 element. P1 exopod 2-segmented; P2 with 3-segmented exopod and 2-segmented endopod; P3 with 3-segmented exopod and 2-segmented endopod in the female, with 2-segmented exopod and 2-segmented endopod in the male; male P3 endopod without apophysis; P4 exopod 1–segmented in female, 2–segmented in male; P4 endopod 1-segmented in both sexes; P5 exopod separated from baseoendopod in both sexes.

**Etymology.** The generic name refers to the type locality, the Vostok research station. Gender: feminine.

**Type species.** *Vostoklaophonte eupenta* gen. & sp. nov., by monotypy.

***Vostoklaophonte eupenta*** gen. & sp. nov.
urn:lsid:zoobank.org:act:67348997-40CB-4C48-92F6-066BEBE90B67
**Figs. 1-8**

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**Type locality.** The subtidal zone at the Vostok research station (42°53'37.5"N 132°44'00.9"E), Peter the Great Bay, the East Sea (Japan Sea); 0.2-1m depth; October 17, 2013.

**Material examined.** 1♀ holotype (NIBRIV0000812797) dissected on one slide. 15 paratypes as follows: 1♂ (NIBRIV0000812897) dissected on one slide, 1♀ (NIBRIV0000812898) dissected on seven slides, 1♀ (NIBRIV0000812899) dissected on ten slides, 2♀♀ and 1♂ (NIBRIV0000812900) preserved in 70% alcohol, 2♀♀ and 3 copepodites (Me-1208) preserved in 70% alcohol. Four specimens (3♀♀ and 1♂) dried, mounted on stubs, and coated with gold for SEM (NIBRIV0000812901). All specimens are from the type locality.

**Etymology.** Specific name refers to the host of the new species, the holothurian *Eupentacta fraudatrix* (D'yakonov & Baranova in D'yakonov, Baranova & Savel'eva, 1958).

**DNA-barcode (18s rDNA).** Sequences were submitted to GenBank (Genbank Accession numbers: MG012753).

**Host.** Sea cucumber, *Eupentacta fraudatrix* (Echinodermata: Holothuroidea: Dendrochirotida). Information was checked from Worms (Paulay, 2010).

**Description of female.** Total body length from anterior margin of rostrum to posterior margin of caudal rami 583 ㎛ (n=3, mean=563 ㎛). Maximum width 336 ㎛ (n=3, mean=331 ㎛) measured at posterior margin of cephalothorax. Body (Fig. 1A) dorsoventrally flattened with 2 egg sacs. Rostrum (Fig. 1A) well developed, large and rectangular with 1 pair of anterior sensilla. Prosome (Fig. 1A) 4-segmented, comprising cephalothorax and three pedigerous somites; P1-bearing somite fused to cephalothorax. Length: width ratio of cephalothorax, 0.78, subrectangular, with denticles on dorsal surface and setules along lateral margin. Sensilla scattered on cephalothorax, rarely present on other somites. All pedigerous somites with denticles on dorsal surface, long setules along lateral and posterior margins (Figs. 1A). Urosome (Figs. 1A, 2C–D, 7B) 5-segmented, comprising P5-bearing somite, genital double-somite, and two free abdominal somites, and anal somite. Genital double-somite wide, with a row of long spinules arising from transverse surface ridge dorsally and laterally. Genital field (Figs. 2C) located ventrally near anterior margin of genital double-somite, with median genital pore (arrowed in Fig. 7B). P6 (Fig. 2C) a single plate, with well-developed opercula closing off paired genital apertures, each leg represented by 2 naked setae. Anal somite broader than wide, with well-

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developed smooth anal operculum, sensilla associated to the anal operculum not visible (Figs. 1A, 2D).

Caudal rami (Figs. 2C–D, 7C) parallel, widely separated; length: width ratio, 0.93 ventrally, 0.88 dorsally; dorsal surface smooth, with a short row of subdistal inner spinules ventrally; with well-developed tube pore at outer distal corner (arrowed in Fig. 7C); with 7 setae: seta I smallest; setae II and III well developed, naked; seta IV pinnate; seta V pinnate, well developed, longest; seta VI naked, arising at inner distal corner; seta VII naked, triarticulate at base.

Antennule (Fig. 2A) slender, 6–segmented; segment 1 with rows of spinules along anterior lateral margin, and along near articulation with succeeding segment; segments 2, and 3 with a row of spinules along posterior margin; segment 4 with 1 bare seta plus 1 slender seta fused basally with aesthetasc, the latter two elements issuing from sub–cylindrical process; segment 6 with six setae with articulated bases, with apical acrothek consisting of aesthetasc fused basally to 2 slender naked setae. Armature formula: 1–[1], 2–[8], 3–[7], 4–[1 + (1+ae)], 5–[1], 6–[3 + 6 articulated + acrothek].

Antenna (Fig. 3A) 3–segmented, comprising coxa, allobasis, and 1–segmented endopod. Coxa small, naked. Allobasis with 1 pinnate abexopodal seta located midway inner margin. Exopod 1–segmented with 4 pinnate setae. Endopod rectangular, slightly longer than allobasis, with proximal inner and subdistal outer spinules, lateral armature consisting of 3 strong and 1 pinnate spines, and 2 bare and 2 geniculate setae.

Mandible (Fig. 3B) small, with elongated gnathobase armed with several blunt teeth. Mandibular palp two-segmented (some specimen only with one-segmented with 4 elements, not figured); proximal segment with 1 short inner and 1 long outer naked setae; distal segment with 2 distal naked setae.

Maxillule (Fig. 3C). Praecoxa thin and elongated, without ornamentation. Arthrite of praecoxa armed with several sharp, narrow and tooth-like elements. Coxal endite fused to basis, endopod, and exopod, forming 1 reniform segment with 1 inner and 2 naked distal setae.

Maxilla (Figs. 3D). Syncoxa with a subdistal row of outer spinules, with 1 slender endite consisting of 2 fused spines. Allobasis produced into strong curved pinnate claw. Endopod incorporated into allobasis, represented by 2 naked setae.

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Maxilliped (Fig. 3E) 3-segmented. Syncoxa with 1 naked seta. Basis strong, ovoid, with a row of spinules near outer distal end. Endopod drawn out into smooth, strong claw, the latter with 1 accessory naked seta and 1 tube pore proximally.

P1 (Figs. 4A). Coxa without ornamentation. Basis armed with 1 outer and 1 inner naked seta. Exopod 2-segmented; exp-1 with 1 outer seta; exp-2 slightly longer than exp-1, with 5 setae/spines. Endopod large, 2–segmented; enp-1 2.4 times as long as exopod, without ornamentation; enp-2 with 1 small accessory seta and 1 large strong claw, ornamented with inner and outer spinules.

P2 (Fig. 4B). Praecoxa triangular. Coxa without surface ornamentation. Basis with 1 outer plumose seta, with a row of spinules at the base of the outer basal seta and between rami. Exopod 3-segmented, about 2 times as long as endopod; exp-1 with outer spinules and 1 stout outer spine; exp-2 with 1 stout outer spine, without additional ornamentation; exp-3 with 4 elements (2 stout outer spines, 1 distal long, and 1 inner, short, naked seta). Endopod 2-segmented; enp-1 larger than enp-2, with spinules as shown, without armature; enp-2 with some outer spinules and 1 distal plumose seta.

P3 (Figs. 4C, 7A). Coxa without ornamentation. Basis with spinules at based of outer seta. Exopod 3-segmented, each segment with outer spinules as shown; exp-1 with 1 long, pinnate, outer spine; exp-2 with 1 stout, short, outer spine; exp-3 with 2 pinnate, outer spines, (1 abnormal short inner seta was observed in paratype GIVE HERE THE ACCESSION NUMBER, as arrowed in Fig. 7A) and 2 pinnate setae (1 inner and 1 distal). Endopod 2-segmented; first segment with outer spinules; second segment with outer spinules and 2 inner spinules; enp-1 with 1 inner pinnate seta; enp-2 with 3 pinnate elements (1 inner and 1 distal seta, and 1 outer spine).

P4 (Fig. 4D). Coxa smooth, fused to somite. Basis with spinules at base of outer seta and between rami. Exopod 2.6 times as long as endopod. Exopod 1-segmented, rectangular, twice as long as wide, with 3 distal and 2 outer pinnate setae; with dense rows of spinules as figured; with 1 secretory pore near median distal margin. Endopod 1-segmented, cylindrical, with 1 pinnate distal seta, and a row of spinules along outer margin.

Armature formula as follows;

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P5 (Fig. 4E). Baseoendopod and exopod ornamented with spinules as shown. Baseoendopod with outer basal, naked seta. Endopodal lobe small, with 2 pinnate setae. Exopod rectangular, with 5 pinnate setae.

**Description of male.** Body (Fig. 5A) dorsoventrally flattened; total body length 366 ㎛ (n=2, mean=383 ㎛) measured from anterior margin of rostrum to posterior margin of caudal rami. Maximum width 232 ㎛ (n=2, mean=220 ㎛) measured at posterior margin of cephalothorax. General body shape and ornamentation as in female except for lack of sensilla on the cephalothorax. Sexual dimorphism expressed in A1, P3, P4, P5, P6 and genital field.

Antennule (Figs. 5B-D, 7D) 7-segmented, robust, subchirocer; segment-1 with row of inner spinules; segment 4 smallest, an incomplete sclerite with only 1 small seta; segment 5 swollen, largest, with 2 modified spines (1 compressed, 1 short and trifid); segments 5 and 7 with aesthetasc. Armature formula; 1-[1], 2-[9], 3-[6], 4-[1], 5-[9 + 2 modified + (1+ae)], 6-[1 + 2 processes], 7+[7 + acrothek]. Apical acrothek consisting of aesthetasc and 2 naked setae.

Antenna (Fig. 7E), mandible, maxillule, maxilla and maxilliped (not shown) as in female.

P1 (not shown) as in female.

P2 (Figs. 6A, 7F). Coxa with spinules close to joint with basis. Basis as in female, except for additional pore and lack of spinules between rami. Exopod as in female except for one spinular row only on exp-1, and for some spinules on exp-2 and -3. Endopod as in female, except for lack of spinules on enp-1.

P3 (Figs. 6B, 7F). Basis with some spinules at the base of outer seta. Exopod 2-segmented; outer spines more robust and shorter than in female; exp-1 with outer spinules, with 1 stout outer, pinnate spine; exp-2 with 1 inner, 1 distal, and 3 outer pinnate elements. Endopod 2-segmented, without apophysis; enp-1 ornamented with a row of outer spinules distally, without armature; enp-2 with some inner spinules midway inner margin, with 2 distal pinnate setae.

P4 (Fig. 6C). Coxa without ornamentation. Basis with some spinules at the base of outer seta. Exopod 2-segmented; exp-1 with 1 pinnate outer spine and a row of outer

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**Comment [R38]:** But then, it seems to me that P2 should be added to the list of sexual dimorphisms above.
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spinules; exp-2 with 1 inner and 2 distal elements, with 1 outer pinnate spine, and with outer and inner spinules. Endopod 1-segmented, trapezoid with 1 pinnate distal seta.

P5 (Fig. 6D) fused to somite. Baseoendopod with 1 pinnate outer basal seta, and endopodal lobe represented by 1 pinnate seta. Exopod small, rectangular, with 1 outer naked and 3 distal pinnate setae.

P6 (Fig 6E), asymmetrical, represented on both sides by small plate (only left one functional) and 1 spermatophore present as in Fig.5A; outer distal corner produced into cylindrical process with 1 outer pinnate seta, and several spinules.

**Phylogenetic position**

In the phylogenetic trees (figure 8) based on nuclear 18S rRNA gene all three members of the family Laophontidae representing genera *Paralaophonte*, *Microchelonia*, *Vostoklaophonte* are grouped together with high support (98% bootstrap support in NJ tree and 98% Bayesian posterior probability in Bayesian tree). The sister relationship of *Vostoklaophonte* and *Microchelonia* has100% support.

**Discussion**

The new genus, *Vostoklaophonte,* is attributed to the subfamily Laophontinae T. Scott, 1905 based on the following set of characters: (1) the female antennule is six-segmented, and seven-segmented subchirocer in the male, (2) one abexopodal seta on antennary endopod, and four setal elements on the one-segmented antennary exopod, (3) the syncoxa of maxilliped bearing only one seta, (4) P1 with large prehensile endopod and small exopod, (5) sexual dimorphism in antennules, genital segmentation and P5 and P6. All these characters correspond to the diagnosis of the family Laophontidae T. Scott, 1905 (see Boxshall and Halsey, 2004), and furthermore the diagnostic features of the subfamily Laophontinae (see Huys and Lee, 2000).

*Vostoklaophonte eupenta* has the following unique combination of characters: dorso-ventrally flattened body form, highly reduced mouth parts, except for well-developed maxillipeds, sexually dimorphic setation and segmentation of P2–P4. In addition, *V. eupenta* has two segments distal to geniculation in the male antennule, maxillipedal syncoxa with one seta, the first endopodal segment of P1 without inner seta, the second endopodal segment of P2 without outer spine, and the endopod P3 of male without proximal inner seta in the female endopod.

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**Comment [R39]:** Please move this somewhere in the beginning of the decription of the male.

**Comment [R40]:** Consider: "with one seta issuing from long setophore ornamented with some spinules."

**Comment [R41]:** At the end of the manuscript the authors wrote that the "….lack of molecular data for most genera of laophontids limits our analysis of the laophontid phylogenetic relationships." I'm not sure about this paragraph. Since a very limited set of molecular data is available for the subfamily Laophontinae (no molecular data is available for the subfamily Esolinae) it seems premature to suggest a sister group relationship between the new genus and Microchelonia. It is always good to have new molecular data like the one presented by the authors, but in this case, I think it would be better to present the phylogeny of the subfamily Laophontinae, and the position of the new genus based on morphological data.

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**Comment [R42]:** But the authors said that "The new genus, *Vostoklaophonte*, is attributed to the subfamily Laophontinae T. Scott, 1905 based on the following set of characters:…" Then, the list of characters above are not for the subfamily Laophontinae but for the family Laophontidae. Please make the necessary adjustments to this paragraph.

**Comment [R43]:** Also, the list of character states above does not correspond to the diagnosis of the subfamily as presented in Huys & Lee (2000: 104) [Basal resolution of laophontid phylogeny and the paraphyly of Esola Edwards]. Please make the necessary adjustments to this paragraph. I suggest mentioning first why the new genus is attributed to Laophontidae and then why it is attributed to Laophontinae.

**Comment [R44]:** Please add here why you think the genus Vostoklaophonte is unique among the other Laoph ... [22]

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**Comment [R45]:** Are these really unique to the new species? Is there any autapomorphy for the new species?

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**Comment [R46]:** All these correspond to the character states for the subfamily Laophontinae as diagnosed ... [23]

Brady (1918) established the new genus *Microchelonia* for *M. glacialis* Brady, 1918 found in washing of *Laminaria* from Macquarie Island in the southwest Pacific Ocean. The genus *Microchelonia* was unveiled after the listing as a *genus inquirendum* by Boxshall & Halsey (2004). Later, Huys (2009) regarded *Namakosiramia* as the junior synonym of *Microchelonia*. Later on, Huys (2016) proposed an identification key to two species of *Microchelonia* Brady, 1918, and redefined diagnosis of the genus within the family Laophontidae.

The new genus is close to the genera *Peltidiphonte* Gheerardyn & Fiers, 2006 and *Microchelonia* Brady, 1918 in having dorso-ventrally compressed body form, and the genera *Afrolaophonte* Chappuis, 1960 and *Aequinoctiella* Cottarelli, Bruno & Berera, 2008 in having reduced postmaxillipedal legs. *Vostoklaophonte* seems to be closely related to *Microchelonia* Brady, 1918 by the flattened body form, the reduced mandible, maxillule, and maxilla, but well-developed maxilliped, and by the reduced segmentation and setation of P1 - P4 (Kim, 1991; Huys, 2009). The new genus has less derived states of most appendages than those of *Microchelonia*. For example, the female antennule of the new genus is 6-segmented, but 4-segmented in *Microchelonia*, the male antennule is 7-segmented in *Vostoklaophonte*, but 6-segmented in *Microchelonia*, the antennary exopod has four setal elements in both genera, but the distal spine on the endopod is more developed in *Microchelonia*. Also, the mandible, maxillule, and maxilla of the new genus possess more setae than those of *Microchelonia*. For example, the mandibular palp of *Vostoklaophonte* possesses four elements (see Fig. 3B), instead of with two as in *Microchelonia* (compare Ho & Perkins, 1977: 370, Huys, 1988: 1519, and Kim, 1991: 431, and Fig. 2C, present study); the arthrite of the praecoxa of the maxillule of *Microchelonia* lacks ornamentation, and that the coxal endite/basis is completely missing (compare Ho & Perkins, 1977: 370, Huys, 1988: 1519, and Kim, 1991: 431, Fig. 2D), but the maxillule of *Vostoklaophonte* possesses a 1-segmented coxa with three elements (see Fig. 3C, present study); the maxilla is similar in both genera, except for the endopod represented by two setae in *Vostoklaophonte*, but represented by three setae in *Microchelonia koreensis* (compare Kim, 1991: 431, Fig. 2E, and Fig. 3D in this study); the maxilliped is well developed and stout in both genera, but the maxilliped of *Microchelonia* is ornamented with more dense spinular patches than in the new genus and species (compare *M. californiensis* in Ho & Perkins (1977: 369, Fig. 7), and in Huys (1988: 1523, Fig. 3F), and

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**Comment [R47]:** I do not understand this. Boxshall & Halsey (2004: 844) mentioned this genus in their list of "generic names – not in current use". It would be interesting to know at what point in history (and why) the genus Microchelonia was forgotten. It was Huys (2009, 2016) that gave the genus the status of "genus inquirendum" probably because, as Huys (2016: 615) wrote, the only species of Microchelonia known at the time of Boxshall & Halsey's (2004) book was M. glacialis that was inadequately described.

**Comment [R48]:** Well…. What Huys (2009: 4) wrote [note that the reference in the list of references in this ms is wrong] is that the genus Microchelonia belongs to the family Laophontidae and considered this genus a senior subjective synonym of Namakosiramia. Here, as far as I understand, Huys (2009) applied the Principle of Priority (ICZN, Art. 23)….but please double check. Huys (2009: 30) also wrote that Namakosiramia is the junior objective synonym of Microchelonia. Huys (2016) wrote that the family Namakosiramiidae is a junior synonym of the family Laophontidae. However, it was Huys (1988) who proposed that Namakosiramia should be placed in the Laophntidae: Laophontinae, and that Namakosiramiidae should be regarded as a synonym of Laophontidae.

**Comment [R49]:** In his key to the species of Microchelonia, Huys (2016) included only two species, M. californiensis and M. koreensis because "the description of M. glacialis is grossly inadequate and its host is as yet unknown".

**Deleted:** Consequently …ater on, Huys (2016) pro ... [25]

**Comment [R50]:** Where is the diagnosis of the genus? Huys (2016: 614-615) only gave an historical account around Microchelonia and Namakosiramia and gave some hints to identify the genus Microchelonia, but did not give a diagnosis of the genus. The diagnosis of Namakosi ... [26]

**Comment [R51]:** This term should be used cautiously. It could mean that the genera mentioned here are ... [27]

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**Comment [R52]:** I suggest to delete these references. It seems to me that these references support the idea t ... [29]

**Comment [R53]:** But the authors compared their new genus with one species of Microchelonia only, M. ... [30]

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**Comment [R54]:** Ornamentation? Spinules and setules? Or do the authors mean armature? Spines? Also, note t ... [33]

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**Comment [R55]:** I'm not sure here. The structure of the gnathobase looks different indeed, but Kim omitted ... [34]

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**Comment [R56]:** The maxilla looks different to me. Also, the authors were comparing their new genus and sp ... [36]

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*M. koreensis* in Kim (1991: 431, Fig. 2F), and the new genus and species, Fig. 3E, in the present study).

The exopod of P1 is one-segmented with five elements in *Microchelonia*, but two-segmented with a total of six elements in *Vostoklaophonte* (compare Ho & Perkins (1977: 369, Fig. 8), Huys (1988: 1524, Fig. 4A) and Kim (1991, Fig. 2G), and Fig. 4A in the present study). The endopod of P1 is two segmented and possesses a distal claw in the second segment in both genera, but spinules are present on the coxa and basis of *Microchelonia* only (compare Ho & Perkins (1977: 369, Fig. 8), Huys (1988: 1524, Fig. 4A) and Kim (1991, Fig. 2G), and Fig. 4A in the present study). Contrary to what has been observed in the new genus and species herein proposed, *Microchelonia* displays extreme reductions in P2-P4.

Sexual dimorphism of *Microchelonia* is expressed in the relative length of the setae on P2-P4 (Kim, 1991, Figs. 2H-J, 3C-D), and armature complement of P5 and P6 (Kim, 1991 Figs. 2K-L, 3F-G). Sexual dimorphism in the new genus and species *Vostoklaophonte* is expressed in P3 and P4 and no significant dimorphism was observed in P1 and P2. For example, the exopod of P3 is three-segmented in the female, but two-segmented in the male. Also, the endopod of P3 in both sexes is two segmented, but the male P3 endopod possesses a reduced number of setae on both segments. Based on the position of setae of segment, the exp-2 of male is homologous to the exp-2 and exp-3 articulating in female. The exopod of P4 is one-segmented in the female, but two-segmented in the male. The exopod of P4 possesses five setae in both sexes, but the homologous setae are difficult to define. The exopod of P5 is clearly separated from the baseoendopod and possesses the maximum number of setae observed for laophontids. P6 is armed with two setae in the female and one seta in the male, similar to the condition observed for *Microchelonia*, and also typical for other family members.

Besides *Microchelonia* and *Vostoklaophonte* the flatten body form is also present in *Peltidiphonte*. However, *Peltidiphonte* possesses well developed mouthparts and swimming legs. *Peltidiphonte* also displays no sexual dimorphism in mouthparts and P1 – P4, and possesses an spinous process on the second antennular segment.

*Paralaophonte harpagone* has stout maxillipeds. The other shared features with *Vostoklaophonte* and *Microchelonia* include the rectangular rostrum, the number of segments of antennule in both sexes, the number of setae on the antennary exopod, the mandibular palp with only four elements, the two segmented endopod of P1. The species

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**Comment [R57]:** Please compare also M. californiensis.

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**Comment [R58]:** Please compare also M. californiensis.

**Comment [R59]:** Here the authors compared their new genus with only one species of Microchelonia, M. koreensis…..what about M. californiensis? Or these two species are so similar that there is no point in comparing both species with the new one? And if so, why not to compare the new species with the generic diagnosis in Ho & Perkins (1977)?

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**Comment [R60]:** What about P4?

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**Comment [R61]:** Does this refer to P4? It is not clear…please elaborate more on this.

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**Comment [R62]:** 4?

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**Comment [R63]:** Then, Peltidiphonte is not closely related to the new genus. The flatteded body shape in these two generamust be the result of convergence.

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**Comment [R64]:** Most of these characters are for the family has more primitive segmentation of P2–P4 than that of the two highly derived symbiotic genera. Since there are too many reductions in mouthparts and legs in *Vostoklaophonte* and *Microchelonia*, it is premature to claim that they are close to *Paralaophonte* lineage (Gheerardyn et al., 2006b).

The reduction of segmentation in P1-P4 found in several interstitial laophontids is different from that of *Vostoklaophonte and Microchelonia*. *Aequinoctiella* has one segmented exopod in P1–P4, no endopod in P2–P4, and P1 with 2-segmented endopod.

Morphological features of *Vostoklaophonte* and *Microchelonia* living in symbiosis with holothurians suggest their close phylogenetic relationships and belonging to one monophyletic group distinguishing it from other laophontids. This is supported by phylogenetic tree based on 18s rDNA sequences (Fig. 8). Meanwhile lack of molecular data for most genera of laophontids limits our analysis of the laophontid phylogenetic relationships.


## Acknowledgements

We would like to express our thanks to Raehyuk Jeong for reading and correcting the manuscript in English. Anton Chichvarkhin (A.V. Zhirmunsky Institute of Marine Biology) hosted MN and VI during the field trip.

## Funding

This study was supported by the BK21 Plus Program (Future oriented innovative brain raising type, 22A20130012806) funded by the Ministry of Education (MOE, Korea). Fieldwork and molecular laboratory work were conducted with support from the Russian Foundation for Basic Research (#15-29-02601 and #15-54-78061, respectively); molecular data analyses were supported by the Russian Science Foundation (#14-50-00029).


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**Comment [R65]:** In fact, I do not think they are related. The similarity observed in the maxilliped could be due to convergence.

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**Comment [R66]:** Probably, the similarities observed between these two genera are due to convergence, since these two genera are associated to holothurians.

**Comment [R67]:** Why? Please explain. This is interesting but the authors should elaborate more on this. Is there any synapomorphy supporting the monophyly of these two genera?

**Comment [R68]:** I do not see the point to show the phylogenetic tree of harpacticoids based on nuclear 18S ribosomal DNA data. The table and figure 8 were not discussed in detail. The only thing I can see is that the Laophontidae is different from all the other families, and that, with the small amount of data available, Microchelonia seems to be the sister group of Vostoklaophonte. The first is of little or no use to the present ms. The second is highly questionable.

**Comment [R69]:** I do not think this is enough to stablish the monophyly of these two genera, especially because of the small data base (i.e. molecular data of more species of the two subfamilies are needed to support this). This is implicitly suggested in the following line.

**Comment [R70]:** Please check that the references cited in the text appear in this list and vice versa.

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**Comment [R71]:** This reference deals with the genus Coullia. Please check this reference. I think the right reference is:
Huys, R. 2009. Unresolved cases of type fixation, synonymy and homonymy in harpacticoid copepod nomenclature (Crustacea: Copepoda). Zootaxa 2183: 1-99.

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**Table**

Table 1. GenBank numbers of sequences used in phylogenetic analyses in this study.

**Figures**

Fig. 1. *Vostoklaophonte eupenta* gen. & sp. nov. (♀). (A) Habitus, dorsal.

Fig. 2. *Vostoklaophonte eupenta* gen. & sp. nov. (♀). (A) Antennule, dorsal (setae of segment 6 omitted). (B) 6th segment of antennule. (C) Urosome, ventral (excluding the somite bearing P5). (D) Fifth urosomite, anal somite and caudal rami, dorsal.

Fig. 3. *Vostoklaophonte eupenta* gen. & sp. nov. (♀). (A) Antenna. (B) Mandible. (C) Maxillule. (D) Maxilla. (E) Maxilliped.

Fig. 4 *Vostoklaophonte eupenta* gen. & sp. nov. (♀). (A) P1. (B) P2. (C) P3. (D) P4. (E) P5.

Fig. 5. *Vostoklaophonte eupenta* gen. & sp. nov. (♂). (A) Habitus, dorsal (B) Antennule (setae of 5th & 7th segments omitted). (C) 5th antennulary segment. (D) 7th antennulary segment.

Fig. 6. *Vostoklaophonte eupenta* gen. & sp. nov. (♂). (A) P2, anterior. (B) P3, anterior. (C) P4, anterior. (D) P5, anterior. (E) Urosome, ventral (excluding the somite bearing P5).

Fig. 7. *Vostoklaophonte eupenta* gen. & sp. nov. SEM photographs. (A) P3 (♀, abnormal inner seta arrowed). (B) Genital area (♀, genital pore arrowed). (C) Caudal ramus, ventral (♀, tube pore arrowed). (D) Antennule (♂). (E) Antenna (♂). (F) P2 & P3 (♂).

Figure 8. Phylogenetic tree of harpacticoids based on nuclear 18S ribosomal DNA data. A 50% majority consensus of 5000 trees generated using PhyloBayes 3.3 (Lartillot et al., 2009) under the CAT-GTR model. Numbers at nodes represent Bayesian posterior probabilities. Members of the family Laophontidae showed in bold. Symbionts of holothurians are marked with asterisk (*).

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placed within “siphonostome” Cyclopoda (Ho & Perkins, 1977)

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Ho (1986) concluded that Namakosiramiidae “should have been placed in the order Harpacticoida”, but its position within Harpacticoida remained unclear until Huys’ (1988) paper.. Please add some lines about this here. The complete reference is: Ho, J.-s. (1986) Phylogeny of Cyclopoida. Syllogeus 58: 177-183. The paper is available at: https://ia800708.us.archive.org/32/items/syllogeus58nati/syllogeus58nati.pdf

Also, please mention that Huys (2016) gave a complete account on the taxonomic history of Namakosiramia. This is important because Huys (2016) mentioned some references not included in the present ms.

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, and 2 outer pinnate spines (1 abnormal short inner seta observed in one paratype specimen as arrowed in Fig. 7A)

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, and 2 outer pinnate spines (1 abnormal short inner seta observed in one paratype specimen as arrowed in Fig. 7A)

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, and 2 outer pinnate spines (1 abnormal short inner seta observed in one paratype specimen as arrowed in Fig. 7A)

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, ornamented with row of spinules along outer margin

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with 1 naked outer seta, and a row of spinules along outer margin

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Please add here why you think the genus Vostoklaophonte is unique among the other Laophontinae. Please give the apomorphies for the new genus and a brief discussion.

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All these correspond to the character states for the subfamily Laophontinae as diagnosed by Huys & Lee (2000), and, in my opinion, do not define objectively the new species.

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Where is the diagnosis of the genus? Huys (2016: 614-615) only gave an historical account around Microchelonia and Namakosiramia and gave some hints to identify the genus Microchelonia, but did not give a diagnosis of the genus. The diagnosis of Namakosiramia was given in Ho & Perkins (1977: 368) and an amended diagnosis was proposed by Huys (1988: 1518)

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This term should be used cautiously. It could mean that the genera mentioned here are phylogenetically related, or just that they resemble each other. Since 1) the authors did not give a phylogenetic analysis based on morphology, and 2) the dorso-ventrally compressed body shape shared with Peltidiphonte and Microchelonia, and the reduced postmaxillipedal legs shared with Afrolaophonte and Aequinoctiella could be due to convergent adaptation, I suggest to change “close” for “similar”.

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I suggest to delete these references. It seems to me that these references support the idea that the new genus is similar or close to the other genera.

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But the authors compared their new genus with one species of Microchelonia only, M. koreensis….what about M. californiensis? The mandible, maxillule and maxilla of these two species seem to me very different and the diagnosis of the genus is not available, except for the generic diagnosis of Namakosiramia in Ho & Perkins (1977: 368) and in Huys (1988: 1518) which were based on M. californiensis only.

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Ornamentation? Spinules and setules? Or do the authors mean armature? Spines? Also, note that that the mandible possess a gnathobase…the maxillule possess an arthrite of the praecoxa.

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I'm not sure here. The structure of the gnathobase looks different indeed, but Kim omitted any comment on the "palp". I think the authors should compare their new genus and species with the generic diagnosis of Huys (1988) and not only with one species of Microchelonia. Also, the authors can compare their material with the two descriptions of M. californiensis (Ho & Perkins (1977) and Huys (1988)) and M. koreensis.

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The maxilla looks different to me. Also, the authors were comparing their new genus and species with M. koreensis only. Also, the maxilla of koreensis and californiensis are different (compare Huys (1988) and Kim (1991)).

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The endopod of P3 in both sexes is two segmented, however each segment shows reduction of an inner seta in male.

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