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

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Definición de estilo: Revisión

Abstract

The ectosymbiotic copepods, *Vostoklaophonte eupenta* gen. & sp. nov. associated with the sea cucumber *Eupentacta fraudatrix*, and *Microchelonia koreensis* (Copepoda: Harpacticoida: Laophontidae) associated with the spiked sea cucumber *Apostichopus japonicus*, were found in the subtidal zone of Peter the Great Bay, East/Japan Sea. The new genus, *Vostoklaophonte*, is similar to *Microchelonia* in the flattened body form, reduced mandible, maxillule and maxilla, but with well-developed prehensile maxilliped, and in the reduced segmentation and setation of legs 1–5. Most appendages of the new genus are more primitive than those of *Microchelonia*. The inclusion of the symbiotic genera *Microchelonia* and *Vostoklaophonte* gen. nov. in Laophontidae as well as their close phylogenetic relationships are supported by morphological observations and molecular data. This is the third record of laophontid harpacticoid copepods living in symbiosis with sea cucumbers recorded 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, Avdeev, 2017). Among harpacticoids, only 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* in washings of *Holothuria tubulosa* Gmelin, 1791 collected in the Bay of Banyuls. *Microchelonia californiensis* was found associated with the holothurian *Apostichopus parvimensis* (Clark, 1913) on the Californian coast. *Microchelonia californiensis* was originally described as *Namakosiramia californiensis* Ho & Perkins, 1977, and was designated by Ho & Perkins (1977) as the type of their newly established “siphonostome” cyclopoid family Namakosiramiidae. Ho (1986) concluded that Namakosiramiidae “should have been placed in the order Harpacticoida”, but its position within Harpacticoida remained unclear until 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 found and

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

The family Laophontidae consists of 325 valid species in 73 genera and two subfamilies (Walter & Boxshall, 2017) and includes forms with cylindrical or dorsoventrally flattened bodies, and with reduced armature complement and segmentation of the 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 associated with the sea cucumber *Eupentacta fraudatrix* (D'yakonov & Baranova in D'yakonov, Baranova & Savel'eva, 1958) is found and described herein.

Materials and methods

The laophontid harpacticoid copepods *Vostoklaophonte eupenta* gen. & sp. nov. associated with the sea cucumber *Eupentacta fraudatrix* , and *Microchelonia koreensis* associated with the spiked sea cucumber *Apostichopus japonicus*, were collected on 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 *E. fraudatrix* and five specimens of *A. japonicus*) were collected by hand. The sea cucumbers were placed in plastic bags and rinsed *in situ* with 10% ethanol to anesthetize and detach the copepods. The washings were sieved using a 60µm sieve, and copepods were sorted with a pipette under an Olympus SZX 7 dissecting microscope. Copepods were fixed in 70% ethanol for morphological observations.

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 (ZM LMSU).

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DNA was extracted from ethanol-preserved specimens using Diatom DNA Prep 100 kit (Isogene, Moscow, Russia). Nuclear 18S rDNA was amplified using Encyclo Plus PCR kit (Evrogen) and universal primers Q5 and Q39 (Medlin et al, 1988). DNA amplification through PCR was as follows: 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 for 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.

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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 45 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 MrBayes 3.2.6 (Ronquist et al., 2012). Two MCMC chains were run in parallel and the analyses were stopped when average standard deviations of split frequencies between chains was below 0.01. 1500 000 tree generations were produced Burn-in was set at 500 000 trees.

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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 µm.

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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. Laophontinae. 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 genital segmentation. Rostrum large, rectangular and fused to cephalothorax; antennule 6-segmented in female and 7-segmented subchirocer in male, aesthetascs present on segments 4 and 6 in female, on segments 5 and 7 in male; mandibular palp with 4 elements; coxal endite of the maxillule small, with 3 elements; syncoxa 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.

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Etymology. The generic name refers to the type locality, the Vostok research station, and to the type genus of the family. Gender, feminine.

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

Vostoklaophonte eupenta sp. nov.

urn:lsid:zoobank.org:act:67348997-40CB-4C48-92F6-066BEBE90B67

Figs. 1–8

Type locality. The subtidal zone at the Vostok research station (42°53'37.5"N 132°44'00.9"E), Peter the Great Bay, Russia, 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 (ZM LMSU 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. The specific name refers to the host of the new species, the holothurian *Eupentacta fraudatrix*.

DNA-barcode (18s rDNA). Sequence (1929 base pairs) was submitted to GenBank (Genbank Accession number: MG012753).

Host. Sea cucumber, *Eupentacta fraudatrix* (Echinodermata: Holothuroidea: Dendrochirotida).

Description of female. Total body length from anterior margin of rostrum to posterior margin of caudal rami 583 μm (holotype; paratypes, n=3, mean=563 μm). Maximum width 336 μm (holotype; paratypes, n=3, mean=331μm) 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 3 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 (Fig. 1A). Urosome (Figs. 1A, 2C–D, 7B) 5-segmented, comprising P5-bearing somite, genital double-somite, two free abdominal somites, and anal somite. Genital double-somite wide, with 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) forming single plate, with well-developed opercula closing off paired genital apertures, each leg represented by 2 naked setae. Anal somite 1.9 times as

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wide as long, with well-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 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–B) 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 1 row of spinules along posterior margin; segment 4 with 1 bare seta plus 1 slender seta fused basally with aesthetasc, the latter 2 elements issuing from sub-cylindrical process; segment 6 with 6 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 setae + acrothek].

Antenna (Fig. 3A) comprising coxa, allobasis, and 1-segmented endopod. Coxa small and 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, armature consisting of 3 strong and 1 pinnate spines, and 2 bare and 2 pinnate setae.

Mandible (Fig. 3B) small, with elongated gnathobase armed with several sharp teeth. Mandibular palp 2-segmented; proximal segment with 1 short inner and 1 long outer naked seta; 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 subdistal row of outer spinules, with 1 slender element consisting of 2 fused spines. Allobasis produced into strong curved pinnate claw. Endopod incorporated into allobasis, represented by 2 naked setae.

Maxilliped (Fig. 3E) 3-segmented. Syncoxa with 1 naked seta. Basis strong, ovoid, with 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.

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P1 (Figs. 4A) Coxa without ornamentation. Basis armed with 1 outer and 1 inner naked seta. Exopod 2-segmented; exp-1 with 1 outer spine; 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, 1 large robust claw and ornamented with inner and outer spinules.

P2 (Fig. 4B) Praecoxa triangular. Coxa without surface ornamentation. Basis with 1 outer pinnate seta, and row of spinules at base of 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 bipinnate 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, 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 setae (1 inner and 1 distal seta, and 1 outer spine).

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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 1 row of spinules along outer margin.

Armature formula as follows;

	Exopod	Endopod
P2	0.0.022	0.010
P3	0.0.022(0.113 in ♂)	1.111(0.020 in ♂)
P4	032(0.121 in ♂)	010

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 µm (n=2, mean=383µm) measured from anterior margin of rostrum to posterior margin of caudal rami. Maximum width 232µm (n=2, mean=220µm) measured at posterior margin of cephalothorax. General body shape and ornamentation as in female except for lack of sensilla on cephalothorax. Sexual dimorphism expressed in A1, P2, P3, P4, P5, P6 and genital field. One spermatophore present as in Fig.5A.

Comentado [R6]: Ax for the female. I suggest: “total body length measured from tip of rostrum to posterior margin of caudal rami ranging from XX µm to XX µm (n= 2).”
Note that in this case there is no point in giving the mean for two measurements.

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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 thick, 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], 7-[7 + acrothek]. Apical acrothek consisting of aesthetasc and 2 naked setae.

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Comentado [R8]: If this is the same for the female, I suggest to add a similar sentence for the female A1. Alternatively, the acrothek can be defined in Materials and Methods and deleted in the descriptions.

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 1 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 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 1 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 base of outer seta. Exopod 2-segmented; exp-1 with 1 pinnate outer spine and 1 row of outer 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); outer distal corner with one seta issuing from long setophore ornamented with some spinules.

Variability

A 1-segmented mandibular palp with 4 elements (not shown) was observed in a paratype. An abnormal short inner seta was observed in the P3 exp-3 of paratype NIBRIV0000812901 (arrowed in Fig. 7A).

Phylogenetic position

It is difficult to suggest a phylogenetic position of the new genus based on morphological characters due to the extreme reductions of mouthparts, and unusual sexual dimorphism in swimming legs. However, a sister group relationship between *Vostoklaophonte* and *Microchelonia* can be hypothesized based on the 18S rDNA gene.

The phylogenetic tree, based on the nuclear 18S rDNA gene (Fig. 8) shows all three members of the family Laophontidae representing five genera (*Paralaophonte*, *Pseudonychocamptus, Laophontina*, *Microchelonia*, *Vostoklaophonte*) are grouped together with very high support (98% bootstrap support in NJ tree and 99% Bayesian posterior probability in Bayesian tree). The high support (100%) observed for *Vostoklaophonte* gen. nov. and *Microchelonia* suggests a close relationship between these two genera.

Discussion

Ho & Perkins (1977) established the “siphonostome” cyclopoid family Namakosiramiidae for *Namakosiramia californiensis* Ho & Perkins, 1977 found attached to the body surface of a holothurian, *Apostichopus parvimensis* (Clark, 1913) on the Californian coast. Later, Ho (1986) recognized that the family Namakosiramiidae “should have been placed in the order Harpacticoida” and, upon re-examination of the type material of *N. californiensis*, Huys (1988) removed the family from the Siphonostomatoida and tentatively placed it in the subfamily Laophontinae (Harpacticoida: Laophontidae), rendering Namakosiramiidae a junior synonym of Laophontidae (see also Huys 2009, 2016).

Boxshall & Halsey (2004) listed the genus *Microchelonia* (established by Brady (1918) for *M. glacialis* Brady, 1918 found in washings of *Laminaria* from Macquarie Island in the southwest Pacific Ocean) in their list of “generic names – not in current use” without any justification. Huys (2009) suggested that *Microchelonia* belongs to the family

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Comentado [R11]: On the contrary. I think that the extreme reduction of mouthparts at least (and probably the unusual sexual dimorphism), could be indicative of a derived clade within Laophontodinae. A similar approach was used to suggest the monophyly of a derived group of deep-sea Mesocletodes (Argestidae) in which the males are non-feeding and lack mouthparts. I wonder if such approach could be followed here. If so, please add some lines about this in the discussion. Also, I wonder if the authors detected any synapomorphy for Vostoklaophonte and Microchelonia to support a derived group of symbiotic genera. If so, please add some lines in the discussion.

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Also, I still don't see the point to add all the other species to the list in Table 1 and in Figure 8. None of these species were discussed in the MS.

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Comentado [R14]: Check the journal’s format….gen. nov. should be added here?

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Laophontidae, considered this genus a senior subjective synonym of *Namakosiramia*, and the latter as the junior objective synonym of *Microchelonia*. More recently, Huys (2016) included only two species, *M. californiensis* and *M. koreensis*, in his key to the species of *Microchelonia* because “the description of *M. glacialis* is grossly inadequate and its host is as yet unknown”.

The new genus, *Vostoklaophonte*, is attributed here to the family Laophontidae T. Scott, 1905 as diagnosed by (Boxshall & Halsey, 2004), based on the presence of the following characters: (1) the 6-segmented female antennule, and 7-segmented subchirocer in the male, (2) one abexopodal seta on the antennary endopod, and four elements on the 1-segmented antennary exopod, (3) one seta only on the syncoxa of maxilliped, (4) P1 with large prehensile endopod and small exopod, (5) sexual dimorphism in antennules, genital segmentation and P5 and P6. Furthermore, the new genus fits the diagnosis of the subfamily Laophontinae T. Scott, 1905 given by Huys and Lee (2000).

Vostoklaophonte eupenta displays the following unique combination of characters: (1) body dorso-ventrally flattened, (2) mouth parts highly reduced except for the well-developed maxillipeds, and (3) sexually dimorphic setation and segmentation of P2–P4. In addition, *V. eupenta* has syapomorphies including 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 as a member of Laophontinae.

Within Laophontidae, the compressed body of *Microchelonia* and *Vostoklaophonte* is also present in *Peltidiphonte* (Gheerardyn et al., 2006a). However, *Peltidiphonte* possesses well-developed mouthparts and swimming legs, lacks sexual dimorphism in mouthparts and P1–P4, and possesses a spinous process on the second antennular segment, suggesting that the compressed body in *Microchelonia* and *Vostoklaophonte*, and *Peltidiphonte* might be the result of convergence.

The reduction of segmentation in P1–P4 found in several interstitial laophontids, e.g. *Afrolaophonte* Chappuis, 1960 and *Aequinoctiella* Cottarelli, Bruno & Berera, 2008, is different from that of *Vostoklaophonte* and *Microchelonia*. For example, *Aequinoctiella* displays a 1-segmented exopod in P1–P4, P2–P4 lack endopods, and P1 possesses a 2-segmented endopod (Cottarelli et al., 2008).

Vostoklaophonte gen. nov. seems to be closely related to *Microchelonia* Brady, 1918 by the flattened body, the reduced mandible, maxillule, and maxilla, but well-

Comentado [R16]: Vostoklaophonte sp. nov.? Please check the journal’s format.

Con formato: Sangría: Primera línea: 1.27 cm

Comentado [R17]: Please check the journal’s format:”six-segmented” or “6-segmented”?

Comentado [R18]: Please check the journal’s format.

Eliminado: set of

Eliminado: is six-segmented

Eliminado: seven

Eliminado: setal

Eliminado: the

Eliminado: bearing only one seta

Comentado [R19]: All this is ok, but it would be even better to justify the inclusion of the new genus into the Laophontidae based in synapomorphies for the family. Is there any confirmed synapomorphy for the family? If so, please add some lines on this and give the respective references. The monophyly of the family has been confirmed?

Eliminado: All these characters correspond to the diagnosis of the family Laophontidae (Boxshall and Halsey, 2004).

Eliminado: to t

Eliminado: tic features

Comentado [R20]: Please mention the characters in Huys & Lee (2000) by which you attributed the new genus to Laophontinae (just as you did some lines above for the family). As before, this is ok, but it would be better to justify the allocation of the new genus into this subfamily based on synapomorphies. Is there any confirmed synapomorphy for the subfamily? If so, please write some lines about this and add the respective references. The monophyly of the subfamily has been confirmed? I think Huys & Lee (2000) did confirm the monophyly of the Laophontinae. In Huys & Lee (2000: 103) “The residual laophontids” —Laophontinae—……”have lost the inner seta on P1 enp-1 and the outer spine on P2 enp-2, and bear a maximum of 2 setae on the maxillipedal syncoxa (absence of proximal seta)”…..could these be the synapomorphies needed here? Please check.

Eliminado: (

Eliminado: ,

Eliminado: has

Eliminado: body form

Eliminado: mouth parts

Comentado [R21]: This is ok, but did you find any autapomorphy to define objectively the new genus?

Comentado [R22]: This is confusing. Please check.

Comentado [R23]: This is probably wrong. I don’t think all these are synapomorphies, but just a list of combined ...

Eliminado: Brady (1918) established the new genus ...

Eliminado: form

developed maxilliped, and by the reduced segmentation and setation of P1–P4. Most appendages of the new genus seem to be more primitive than those of *Microchelonia*. For example, (1) the female antennule of *Vostoklaophonte* gen. nov. is 6-segmented, but 4-segemented in *Microchelonia*, (2) the male antennule is 7-segmented in *Vostoklaophonte*, but 6-segmented in *Microchelonia*, (3) the mandible, maxillule, and maxilla of the new genus possess more setae than those of *Microchelonia*, (4) the mandibular palp of *Vostoklaophonte* possesses four elements (see Fig. 3B), instead of two as in *Microchelonia* (Ho & Perkins, 1977: 370, Huys, 1988: 1519, and Kim, 1991: 431, and Fig. 2C, present study), (5) the maxillule of *Microchelonia* is strongly reduced and is represented by an elongated arthrite bearing 4 spines (Ho & Perkins, 1977: 370, Huys, 1988: 1519, and Kim, 1991: 431, Fig. 2D), but maxillule with 1-segmented coxa bearing three elements in *Vostoklaophonte* gen. nov. (see Fig. 3C), (6) the maxillary syncoxa possesses 1 endite in *Vostoklaophonte* gen. nov., but maxillary syncoxa without endites in *Microchelonia* (Huys, 1988: 1519). On the contrary, some appendages of the new genus seem to be more derived than in *Microchelonia*. For example, (1) the antennary exopod has 4 setal elements in both genera, but the distal spine on the endopod is reduced in *Vostoklaophonte*, but more developed in *Microchelonia*, (2) the maxilla is similar in both genera, except for the endopod represented by 2 setae in *Vostoklaophonte*, but represented by 3 setae in *Microchelonia koreensis* (Fig. 2E in Kim, 1991, p. 431, and Fig. 3D in this study), and (3) the maxilliped is well developed and stout in both genera, but the maxilliped of *Microchelonia* possesses more dense spinular patches than in the new genus (compare *M. californiensis* in Ho & Perkins (1977: 369, Fig. 7) and Huys (1988: 1523, Fig. 3F) and *M. koreensis* in Kim (1991: 431, Fig. 2F), and *Vostoklaophonte* gen. nov. (Fig. 3E, present study).

Some other differences between *Vostoklaophonte* gen. nov. and *Microchelonia* were detected. The exopod of P1 is 1-segmented with 5 elements in *Microchelonia*, but 2-segmented with a total of 6 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 2-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. Also, sexual dimorphism of *Microchelonia* is expressed in the relative length of the

Comentado [R24]: I wonder if these could be regarded as synapomorphies to define a monophyletic group of genera.

Eliminado: -

Eliminado: The

Eliminado: has less derived states of most appendages

Eliminado: *the new genus*

Con formato: Fuente: Cursiva

Movido (inserción)[1]

Eliminado: , Also,

Eliminado: .

Movido (inserción)[2]

Eliminado: the arthrite of the praecoxa of the maxillule of *Microchelonia* lacks ornamentation, and that the coxal endite/basis is completely missing

Eliminado: the maxillule of

Eliminado: possesses a 1-segmented coxa with three elements

Eliminado: , present study

Eliminado: four

Eliminado: .

Movido (inserción)[3]

Eliminado: two

Eliminado: three

Movido hacia arriba[1]: Also, the mandible, maxillule, and maxilla of the new genus possess more setae than those of *Microchelonia*.

Eliminado: For example, the mandibular palp of *Vostoklaophonte* possesses four elements (see Fig. 3B), instead of with two as in *Microchelonia* (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 (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 represente ...

Movido hacia arriba[2]: the arthrite of the praecoxa of

Movido hacia arriba[3]: the maxilla is similar in both

Eliminado: is ornamented with

Eliminado: and species

Eliminado: *M. californiensis*

Eliminado: Ho & Perkins (1977: 369, Fig. 7), and in Huy ...

Eliminado: in the

Eliminado: five

Eliminado: six

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setae on P2–P4 (Kim, 1991, Figs. 2H-J, 3C-D), and in armature complement of P5 and P6 (Kim, 1991 Figs. 2K-L, 3F-G), but sexual dimorphism in *Vostoklaophonte* gen. nov. is expressed in P3 and P4 (e.g. the exopod of P3 is 3-segmented in the female, but 2-segmented in the male; the endopod of P3 in both sexes is 2-segmented, but the male P3 endopod possesses a reduced number of setae on both segments, and based on the position of its setae, the 2-segmented P3 exopod of the male is most probably the result of the fusion of P3 exp-3 and exp-2 of the female; the exopod of P4 is 1-segmented in the female, but 2-segmented in the male, the exopod of P4 possesses 5 setae in both sexes, but the homologous setae are difficult to define), and no significant dimorphism was observed in P1 and P2.

Paralaophonte harpagone Gheerardyn, Fiers, Vincx & De Troch, 2006 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 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).

Some morphological features shared by *Vostoklaophonte* and *Microchelonia* and the results of 18s rDNA sequences (Fig. 8) suggest a close relationship between these two genera. However, it is premature to claim a sister-group relationship or presence of a monophyletic lineage of symbiotic laophontids due to the lack of molecular data for most genera of the subfamily Laophontinae and for a number of undescribed symbiotic laophontids present in our collection.

Acknowledgements

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References

Eliminado: -

Eliminado: . ¶
Sexual dimorphism in the new genus and species *Vostoklaophonte* is expressed

Eliminado: For example, the exopod of P3 is 3-segmented in the female, but 2-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 1-segmented in the female, but 2-segmented in the male. The exopod of P4 possesses 5 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 five setae in the female, and four in the male. 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.

Eliminado: Besides *Microchelonia* and *Vostoklaophonte* the flatten body form is also present in *Peltidiphonte* (Gheerardyn et al., 2006a). However, *Peltidiphonte* possesses well-developed mouthparts and swimming legs. *Peltidiphonte* also displays no sexual dimorphism in mouthparts and P1–P4 and possesses a spinous process on the second antennular segment. This suggests that Peltidiphonte is not closely related to the new genus, and the flattened body shape in these two genera must be the result of convergence.¶

Comentado [R25]: Why did the authors include P. harpagone in their analysis and not the entire genus Paralophonte? 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, and the two-segmented endopod of P1 are symplesiomorphies and are not indicative of any relationship between the new genus and P. harpagone. I think this can be deleted.

Eliminado: 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 (Cottarelli et al., 2008). ¶

Eliminado: M

Eliminado: of

Eliminado: living in symbiosis with holothurians

Eliminado: the

Eliminado: m, and this is supported by phylogenetic tree based on 18s rDNA sequences (Fig. 8)

Eliminado: their

Eliminado: symbiotic

Eliminado: of laophontids

Comentado [R27]: This is interesting. The authors seem to have at their disposal more symbiotic laophontids. The find of more symbiotic genera could allow more in depth analyses to establish a monophylum of symbiotic laophontids.

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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 antennulary segment. (C) Urosome, ventral (excluding somite bearing P5). (D) 5th urosomite, anal somite and caudal rami, dorsal.

Con formato: Inglés (Reino Unido)

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.

Con formato: Español (América latina)

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

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).

Con formato: Inglés (Estados Unidos)

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 and P3 (♂).

Figure 8. Phylogenetic tree of harpacticoids based on nuclear 18S ribosomal DNA data. A 25% majority consensus of 1500 trees generated using MBayes 3.2.6 (Ronquist et al., 2012) under the GTR+G+I model. Numbers at nodes represent Bayesian posterior probabilities. Members of the family Laophontidae showed in **bold**. Symbionts of holothurians are marked with asterisk (*).