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A new species of *Afrolaophonte* (Copepoda, Harpacticoida, Laophontidae) from Korea and cladistic tests of species-groups

Tomislav Karanovic*

Hanyang University, College of Natural Sciences, Department of Life Science, Seoul 04763, Republic of Korea

**Correspondent: tomislav.karanovic@gmail.com*

Afrolaophonte koreana sp. nov. is described from the intertidal zone of two sandy beaches on the south coast of Korea. This is the first record of the genus *Afrolaophonte* Chappuis, 1960 in the Northern Pacific. The new species is most similar to *A. aequatorialis* Cottarelli and Mura, 1981, described from the Maldives and subsequently also found in Papua New Guinea, but could be distinguished by numerous characters, including the segmentation of the third leg endopod in male, armature formula of the second leg in both sexes, length of caudal rami in both sexes, and length of some setae on the fourth leg in female. *Afrolaophonte ensiger* Wells and Rao, 1987 from the Andaman and Nicobar Islands is established as a junior subjective synonym of *A. aequatorialis*. To test previous phylogenetic hypotheses based on intuitive methods, a parsimony based cladistic analysis of 13 valid congeners is performed using 15 morphological characters and one outgroup. Only one of three previously proposed species-groups is supported with a synapomorphy, while one was clearly based on symplesiomorphies. Our current knowledge of morphology in this genus is not sufficient for postulating interspecific phylogenies, which also renders previous zoogeographical hypotheses untestable.

Keywords: intertidal sand, meiofauna, new species, Northern Pacific, phylogeny, taxonomy

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Introduction

Afrolaophonte is one of 75 valid laophontid genera (Walter and Boxshall, 2021). It was established by Chappuis (1960) to accommodate one new species he described in the same paper from Senegal. Lang (1965) revised the generic diagnosis to include two more species, originally described in the genus *Laophontina* Norman and T. Scott, 1905. Fiers (1990) provided an overview of all species descried until then, unintentionally omitting only one species described from India by Wells and Rao (1987). Fiers (1990) also informally divided the genus into three species-groups and provided the most recent key to species. No new species were described subsequently in this genus.

Today *Afrolaophonte* contains 13 species (Walter and Boxshall, 2021), all of which are small vermiform animals that live exclusively in the interstitial realm of the intertidal zone of sandy beaches (Sönmez *et al*., 2018). The genus has a wide distribution, with one species known from the Mediterranean Sea (Masry, 1970; Cottarelli *et al*., 1992; Alper *et al*., 2010; 2015; Sönmez *et al*., 2018), two from the Atlantic coast of Africa (Chappuis, 1960; Cottarelli and Mura, 1981), two from the Caribbean (Chappuis and Delamare Deboutteville, 1956; Fiers, 1990), two from the Pacific Coast of South America (Mielke, 1981; 1982; 1985; 2003), and six species from different islands in the Indian Ocean and the Indo-Pacific (Chappuis, 1954; Cottarelli and Mura, 1981; Cottarelli, 1986; Wells and Rao, 1987; Fiers, 1990). It has never been recorded in the Northern Pacific.

Compared to its small size, marine interstitial harbours a disproportionate level of biodiversity (Giere, 1993; Gray, 1997; Thrush *et al*., 2006; Karanovic, 2008), which is yet to be fully appreciated and understood (Armonies and Reise, 2000; Gray, 2002; Zeppelli *et al*., 2015). Harpacticoid copepods are one of the dominant animal groups here (Giere, 1993). Recent discoveries in this habitat in Korea include a record for the number of syntopic copepod congeners (Karanovic, 2020a), second members of two genera that were considered monotypic for a long time (Karanovic and Cho, 2018), records of species previously known only from the Western Pacific (Karanovic, 2019), and numerous new species (Karanovic and Cho, 2016; Karanovic, 2020b). Korea has 12,478 kilometers of coastline along three seas (Pruett and Cimino, 2000).

Globally nearly three-quarters of the ice-free coastlines consist of sandy shores (Brown and McLachlan, 2006). Unfortunately, this ecosystem is under constant anthropogenic pressure and, being a marginal habitat, is rarely included in protected natural reserves.

Materials and Methods

Specimens were collected from the intertidal zone, using the Karaman-Chappuis method (see Karanovic, 2008). It consisted of digging a hole down to the water level and then decanting the inflowing interstitial water and filtering it through a plankton hand-net (mesh size 30 µm). All samples were fixed in 99% ethanol and sorted in the laboratory also in 99% ethanol using an Olympus SZX12 dissecting microscope with PLAPO objectives and magnification of up to 200×. Locality data and number of specimens are listed in the species description below and the holotype is deposited in the National Institute of Biological Resources (NIBR), in Inchon, South Korea.

Two specimens (holotype female and allotype male) were dissected and mounted on a microscope slide in Faure's medium (see Stock and von Vaupel Klein, 1996), and dissected appendages were then covered by a coverslip; they were used for all illustrations. Prior to that, for the purpose of illustrating the urosome or the entire animal, two human hairs of appropriate thickness were mounted between the slide and coverslip, so the parts would not be compressed. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, equipped with N-PLAN (5×, 10×, 20×, 40× and 63× dry) or PL FLUOTAR (100× oil) objectives. One specimen was observed *in toto* under 63× dry objective and preserved in alcohol.

The terminology for macro-morphological characters follows Huys and Boxshall (1991), except for the numbering of setae on the caudal rami (their terminology is here based on the relative position) and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as in other crustacean groups (see Karanovic, 2019; 2020a). Sensilla and pores on each somite and caudal rami were numbered consecutively from anterior to posterior end of body and from dorsal to ventral side; sensilla were numbered using Arabic numerals, and pores using Roman numerals (see Karanovic and Cho, 2016; Karanovic *et al*., 2016).

To estimate the phylogenetic relationships between the known species of *Afrolaophonte*, characters for morphological cladistic analyses were coded and optimized using the computer program WinClada, version 1.00.08 (Nixon, 1999), and then analysed using NONA, version 2 (Goloboff, 1999). Analyses were performed with both unweighted and weighted characters, always using heuristic searches and default settings (100 maximum trees to keep; 1 number of replicates: 1 starting tree per replicate: 0 random seed: 1 name of stem: Multiple TBR + TBR search strategy; and unconstrained search). *Arenolaophonte stygia* Lang, 1965 from California (see Lang, 1965) was used as an outgroup. All characters were scored from published descriptions and redescriptions, and no material was consulted except for the new Korean species. No assumption of apomorphy or plesiomorphy was assigned to character states a priori.

Results

Taxonomy

***Afrolaophonte koreana* sp. nov.**
(Figs. 1–4)

Type locality. South Korea, South Sea, Dangdong, small beach, intertidal sand, interstitial water from a Karaman-Chappuis hole, 34°59.629′ N 128°26.201′ E.
Specimens examined. Holotype female and allotype male, dissected on one slide each, both collected from the type locality, 4 April 2012, leg. T. Karanovic.

Paratype male in alcohol, collected from South Korea, South Sea, Busan, Songjeong Beach, intertidal sand, interstitial water from a Karaman-Chappuis hole, 35°10.741′ N 129°12.317′ E, 6 May 2016, leg. T. Karanovic.
Etymology. The species name refers to South Korea. It is an adjective, agreeing in gender with the feminine genus name.
Description. Holotype female. Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae and appendages) about 500 µm. Colour of preserved specimens yellowish. Nauplius eye not visible. Prosome comprising cephalothorax with completely fused first pedigerous somite and three free pedigerous somites; urosome comprising six urosomites; although second and third urosomites fused into genital double-somite, original segmentation still visible in dorsal and lateral views. Habitus (Fig. 1A–C) vermiform, slightly tapering posteriorly, not particularly slender, without distinct demarcation between prosome and urosome, prosome slightly shorter than urosome, cephalothorax about 1.15 times as wide as genital double-somite in dorsal view. Body length/width ratio about 5.6. Integument of all somites relatively well sclerotized, generally coarse but clean (with hardly any bacterial growth, mucus, or accumulated sediment), and without cuticular windows. Hyaline fringe of all somites relatively narrow; that of cephalothorax smooth, those of other so-

mites finally serrated on lateral and dorsal sides. Minute spinules present on all somites except on cephalothorax, their frequency and size increasing towards posterior end. Cuticular sensilla present on all somites except fifth urosomite (preanal somite), their number generally decreasing towards posterior end, with 32 pairs on cephalothorax (including one pair on rostrum), six on first free prosomite, eight on second free prosomite, seven on third free prosomite, six on first urosomite, three on second urosomite, five on third urosomite, three on fourth urosomite, and one on sixth urosomite (anal somite). Cuticular pores not present, except one pair on caudal rami.

Rostrum (Fig. 1A, C), small, demarcated at base, triangular but with lateral notches at insertion of sensilla, about half as long as first segment of antenulla.

Cephalothorax (Fig. 1A–C) about 1.2 times as long as wide, slightly tapering towards anterior end in dorsal view, with pronounced ventro-lateral wings of tergites midlength partly covering mouth appendages.

Pleurons of free prosomites and first urosomite short, with convex sides, widely spaced, with short pseudosomites between them.

Genital double-somite (Figs. 1A, B, 2A) slightly wider than long in ventral view, with posterior ventro-lateral corners expanded into small rounded wings, each with one large sensilla and several large spinules; posterior margin in ventral view with row of hair-like spinules.

Fourth urosomite (Figs. 1A, B, 2A) about half as long as genital double-somite, half as long as wide in ventral view, with similar ventro-lateral wings as in genital double-somite, and also with posterior row of hair-like spinules on ventral side.

Fifth urosomite (Fig. 2A) only slightly shorter than fourth urosomite, without ventro-lateral wings, but with posterior row of hair-like ventral spinules.

Sixth urosomite (Figs. 1A, B, 2A) 1.2 times as long as fifth urosomite, covered with minute spinules on all sides and larger spinules along anal operculum and posterior margin on ventral side; anal operculum convex, very short and narrow.

Caudal rami (Fig. 2A) only about half as long as sixth urosomite, nearly cylindrical (although slightly tapering towards posterior end), covered with minute spinules on all sides, with one ventral cuticular pore and six setae (three lateral, one dorsal, and three terminal); dorsal seta slender and smooth, about 1.4 times as long as ramus, inserted at 2/3 of ramus length; two proximal lateral setae inserted very close to each other at about 3/4 of ramus length, ventral one minute (shorter than most sensilla), dorsal one slender and smooth, 1.1 times as long as ramus; distal lateral seta also slender and smooth, inserted at about 4/5 of ramus length, as long as ramus; innermost terminal seta smooth, slender, about 0.65 times as long as ramus; outermost terminal seta strong, pinnate, with breaking plane, about three times as long as ramus; central terminal seta strongest, smooth, with breaking plane, about ten times as long as.

Antennula (Fig. 3A) about half as long as cephalothorax, five-segmented, with several rows of minute spinules on first segment, recurved caudal cuticular beak on second segment, long and slender aesthetasc on fourth segment, and setal formula 1.9.5.2.12; aesthetasc fused at base with one long seta and three apical setae on fifth segment also fused at base; six lateral setae on fifth segment biarticulate (inserted on short pseudojoint), all other setae uniarticulate; second segment longest while fourth segment shortest.

Antenna (Fig. 3C) comprising coxa, allobasis (fused basis and first endopodal segment), one-segmented endopod, and much smaller but also one-segmented exopod; coxa very short, slightly wider than long, unarmed, and unornamented; allobasis cylindrical, almost twice as long as wide and nearly three times as long as coxa, unornamented, with single short seta in distal half; endopod about as long as allobasis but significantly narrower, with narrower base than distal part, with one anterior row of large spinules, one distal surface frill, one smooth and short lateral spine, slender and smooth seta on posterior surface flanked by lateral spine, and six smooth apical elements (three of them geniculate setae, longest one fused at base to slender seta); exopod also with slightly narrower base than distal part, 0.3 times as long as endopod, three times as long as wide, with longitudinal row of minute spinules and four pinnate setae.

Labrum (Fig. 1C) trapezoidal, rigidly sclerotized, with slightly convex cutting edge, with numerous slender apical and subapical spinules, those in central part of cutting edge longest.

Mandibula (Fig. 3D) small, heavily chitinized, composed of large curved coxa and small palp; palp one-segmented, cylindrical, 2.8 times as long as wide, with two minute smooth lateral setae and one longer but also smooth apical seta; cutting edge of coxa narrow, with one large ventral tricuspidate tooth, one smooth dorsal seta, and four unicuspidate teeth in between.

Maxillula (Fig. 3E) slightly larger than mandibula, composed of praecoxa, coxa, basis, and minute exopod; endopod completely fused with basis and probably represented by single bare seta; praecoxa large, quadrate, unornamented; praecoxal arthrite mobile, with row of anterior spinules in proximal half, five strong and unipinnate apical spines, one ventral smooth spine, and two smooth and slender anterior setae; coxa represented by very small, unornamented endite, with one long unipinnate spine and one smooth seta; basis more than twice as long as coxal endite, slender, tapering distally, unornamented, about 2.5 times as long as wide, with one unipinnate spine (shorter than that on coxa) and one smooth

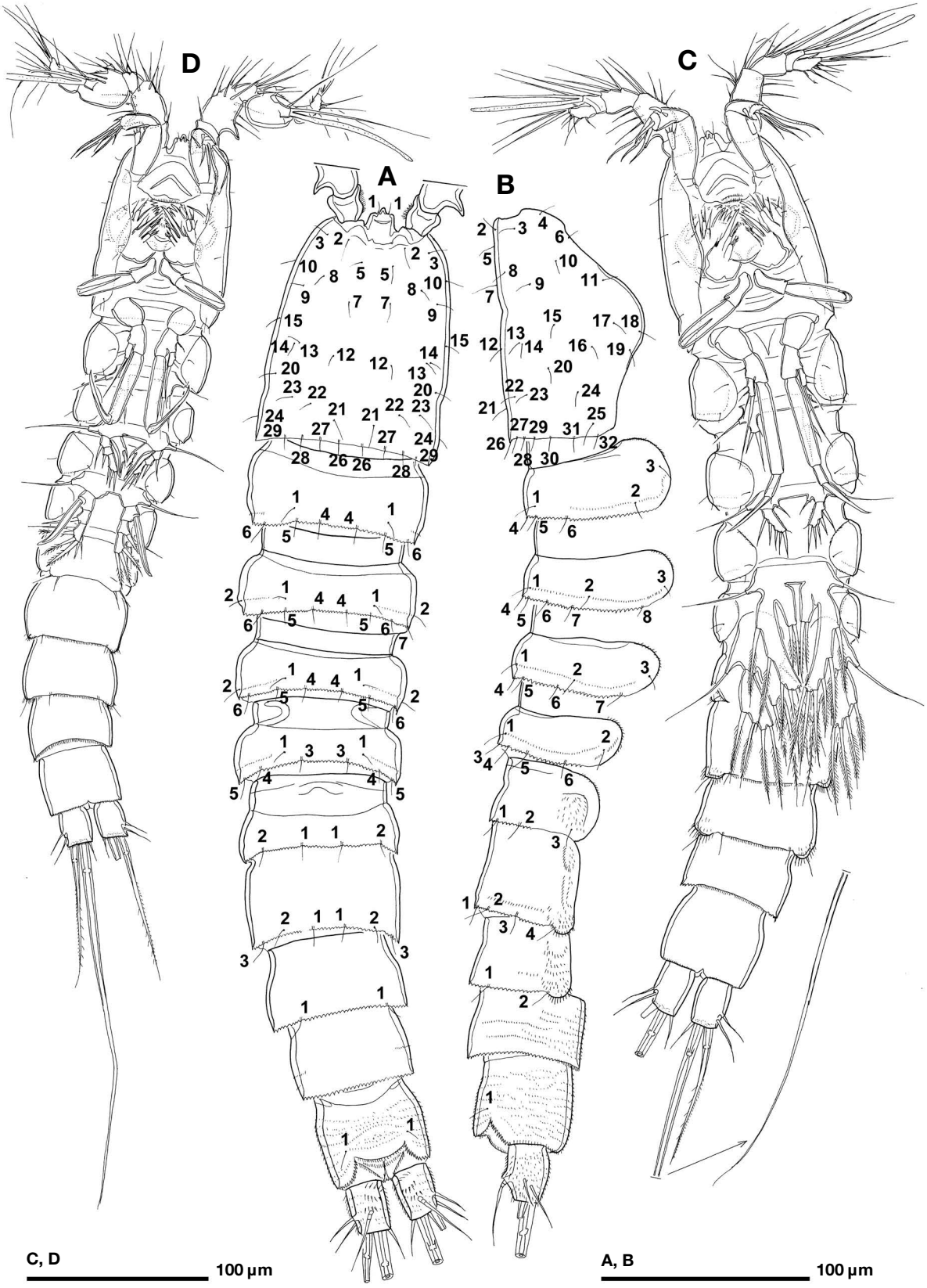


Fig. 1. *Afrolaophonte koreana* sp. nov.: A, female habitus, dorsal; B, female habitus, lateral, omitting appendages; C, female habitus, ventral; D, male habitus, ventral. Arabic numerals indicating same sensilla on corresponding somites in different view.

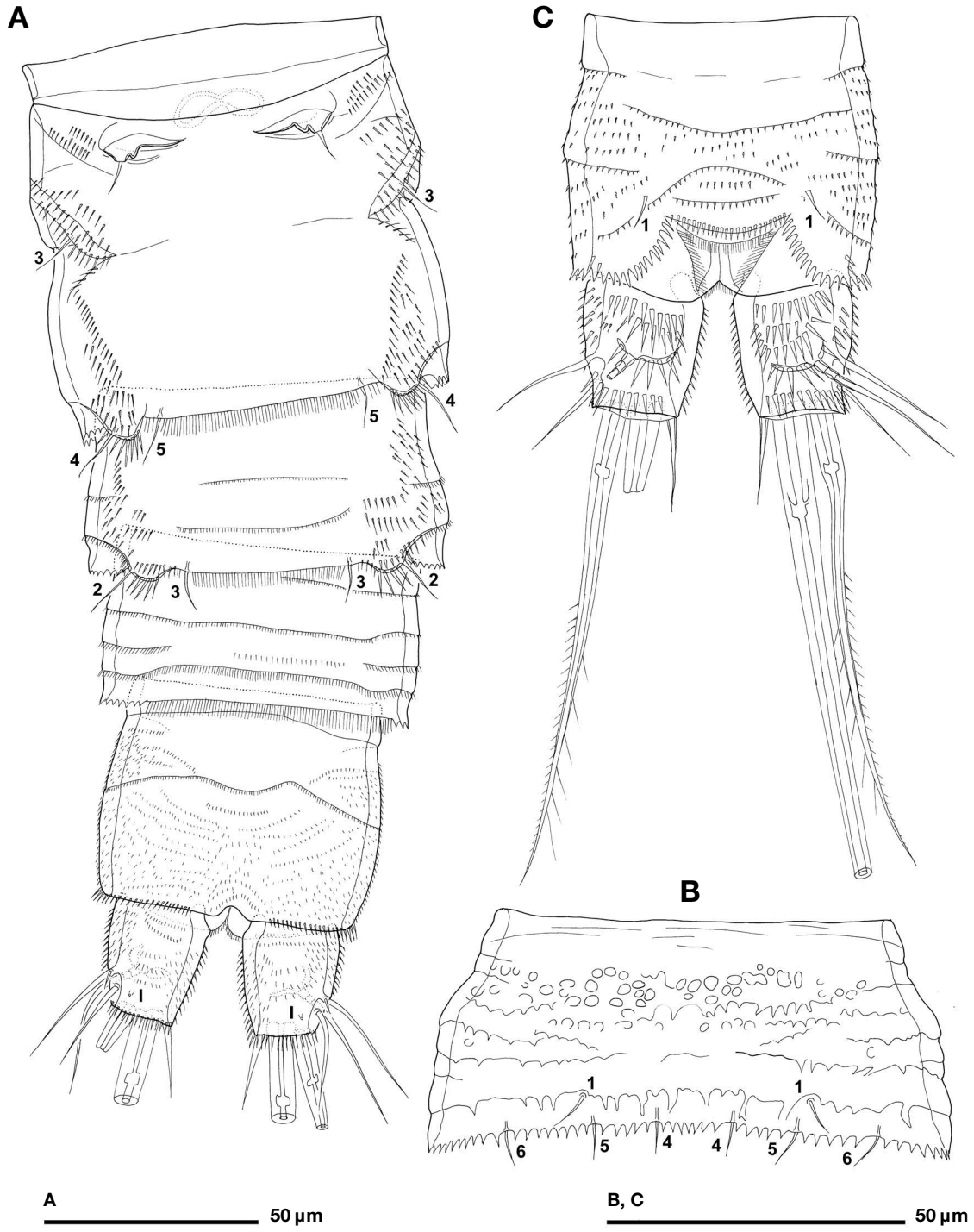


Fig. 2. *Afrolaophonte koreana* sp. nov.: A, female abdomen, ventral; B, male pleuron of second pedigerous somite (first free prosomite), dorsal; C, male anal somite and caudal rami, dorsal. Arabic numerals indicating sensilla as in Fig. 1.

seta on endite in addition to endopodal smooth seta; exopod with single smooth seta.

Maxilla (Fig. 3F) about as large as maxillula, composed of large syncoxa with two endites and small basis (exopod reduced without trace, while endopod probably represented by single seta); syncoxa ovoid, with heavily chitinized outer half and weakly chitinized inner half, with outer row of large spinules and inner row of smaller spinules; proximal endite short, with two strong unipinnate setae; distal endite twice as long as proximal endite, with two

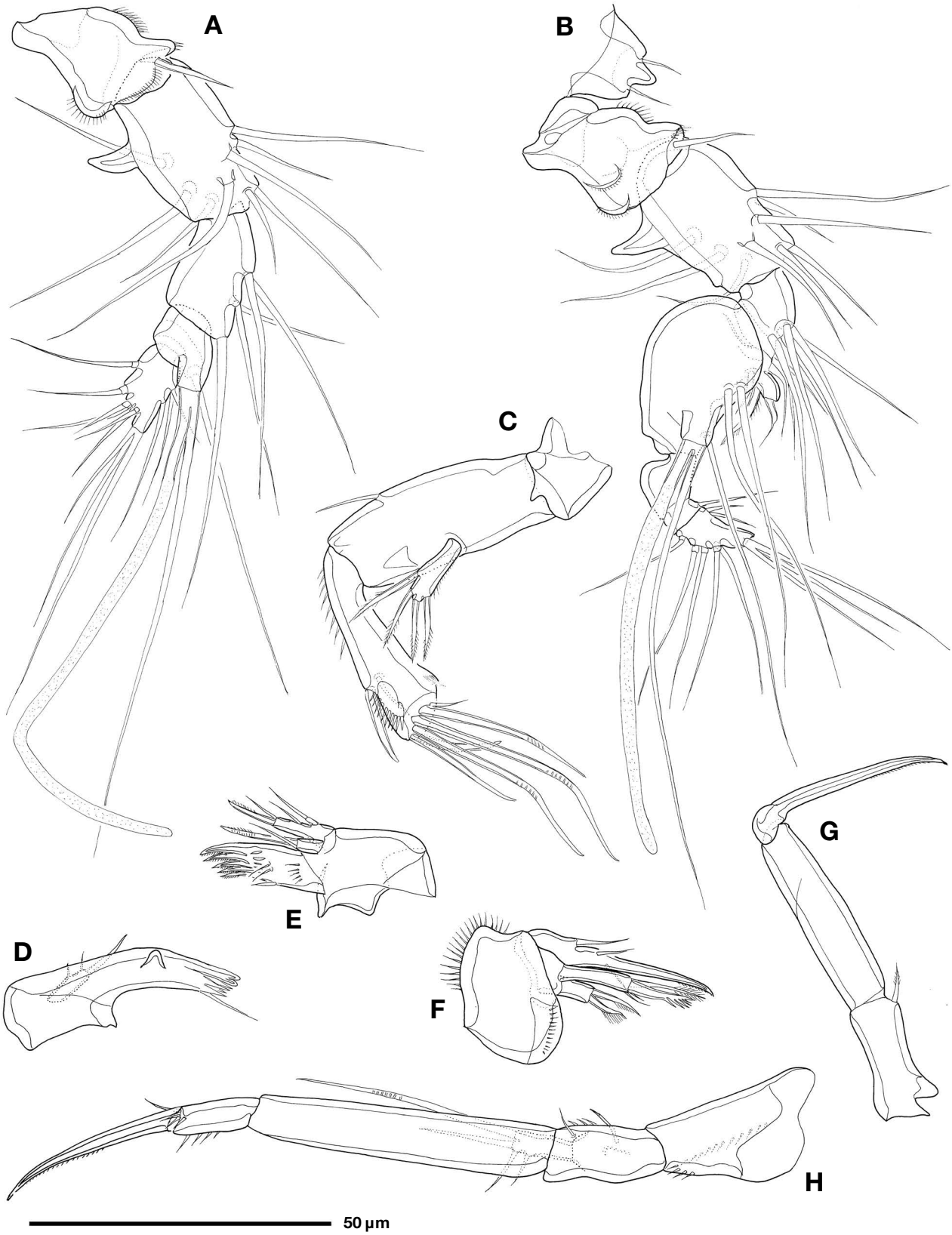


Fig. 3. *Afrolaophonte koreana* sp. nov.: A, female antennula, posterior; B, male antennula, posterior; C, female antenna, anterior; D, female mandibula, posterior; E, female maxillula, anterior; F, female maxilla, posterior; G, female maxilliped, anterior; H, female first swimming leg, median (slightly twisted).

strong pinnate setae and one minute smooth seta; basis elongate, fused with strong apical spine into claw-like structure, unornamented, with three smooth setae.

Maxilliped (Fig. 3G) twice as long as maxilla, slender, prehensile, three-segmented, composed of syncoxa, basis, and one-segmented endopod; syncoxa 2.5 times as long as wide, with single short seta on inner-distal corner; basis 1.7 times as long as syncoxa, nearly four times as long as wide, unarmed and unornamented; endopod minute, fused completely with apical claw-like spine, unornamented; apical spine nearly as long as basis.

First swimming leg (Figs. 1C, 3H) long and slender, composed of minute praecoxa, large coxa, short and wide intercoxal sclerite, large basis, short one-segmented exopod, and long and prehensile two-segmented endopod; praexoca triangular, unarmed and unornamented; coxa trapezoidal, with two rows of large spinules, unarmed; basis pentagonal, somewhat smaller than coxa, with one row of spinules, one inner seta, and one outer seta; exopod cylindrical, shorter than basis, about 2.8 times as long as wide, unornamented, with two outer spines and two apical seta (outer apical seta geniculate); first endopodal segment longest, about five times as long as exopod, 5.4 times as long as wide, unarmed and unornamented; second endopodal segment slightly longer than exopod, with two rows of large spinules, one short and smooth seta and long and curved apical spine; apical endopodal spine about 2.5 times as long as second endopodal segment.

Second swimming legs (Figs. 1C, 4A) small, fused medially, each simple bilobate cuticular plate, with slender outer basal seta on long setophore and two apical spines (outer one shorter) and single innermost minute seta as only remnants of exopodal armature; distal lobe (probably ancestral exopod) with minute spinules along inner and outer margins; endopod reduced without any trace.

Third swimming legs (Figs. 1C, 4C) slightly bigger than second legs, also fused medially, but with distinct one-segmented exopod and endopod represented by small lobe; slender outer basal seta on long setophore; endopodal lobe with single apical spiniform seta; exopod slightly more than twice as long as wide, with five spines (proximalmost longest) and innermost slender and short seta; exopod and basal setophore with several rows of minute spinules.

Fourth swimming leg (Figs. 1C, 4E) significantly larger than third leg but with same segmentation; endopodal lobe larger than in third leg and with two slender plumose setae; exopod about 4.4 times as long as wide, with six long and plumose armature elements (four outer spines and two apical setae); basal setophore, endopodal lobe and exopod with several rows of slender spinules.

Fifth legs (Fig. 4G) similar in size and segmentation to fourth legs but not fused medially; exopod ovoid, shorter than in fourth leg, 2.2 times as long as wide, with long and selender spinules along outer and distal margins but with smooth inner margin, with four long and plumose setae; endopodal lobe larger than in fourth leg, with two inner short unipinnate spines, and two long plumose apical setae (inner one almost twice as long as outer one).

Sixth leg (Fig. 2A) minute cuticular flap covering gonopore, with single smooth seta about as long as smaller sensilla.

Male. Body length about 400 μm. Second and third urosomites not fused, but habitus shape (Fig. 1D), ornamentation of somites (Fig. 2B), caudal rami (Fig. 2C), rostrum (Fig. 3B), antenna, mouth appendages, and first swimming leg as in female.

Antennula (Fig. 3B) seven-segmented, prehensile, slightly larger than in female; first two segments and seventh segment very similar to female; third segment short, as well as fifth and sixth, while fourth segment largest, ovoid, with basal notch; only aesthetasc on fourth segment slightly shorter and wider than in female; seta formula 1.9.5.8.0.1.10; two setae on basal notch of fourth segment spiniform (one smooth, other unipinnate), all others smooth and slender.

Second swimming leg (Fig. 4B) slightly smaller than in female, but with similar segmentation, armature, and ornamentation.

Third swimming leg (Fig. 4D) similar in size to female, but with three-segmented exopod and one-segmented endopod; endopod conical, 1.25 times as long as endopod, unornamented, with two inner smooth and short setae; first and second exopodal segments quadriform, each with single short outer spine (that on first segment longer); third exopodal segment about twice as long as second exopodal segment, with three short spines and single innermost slender and short seta.

Fourth swimming leg (Fig. 4F) much smaller than in female, without endopodal lobe, and with three segmented exopod; first and second exopodal segments quadriform, each with single strong outer spine (that on first segment longer, recurved, and especially strong); second exopodal segment with three strong spines and single innermost slender and short seta.

Fifth legs (Fig. 4H) much smaller than in female, fused medially, unornamented, without endopodal lobe, with basal seta on long setophore, and three setae on minute exopod.

Sixth legs (Fig. 4I) fused fused medially into simple cuticular flap with two smooth setae on each corner.

Variability. Paratype male from Busan was only examined *in toto* and at lower magnification (63× objective), but was no different from the allotype in any characters.

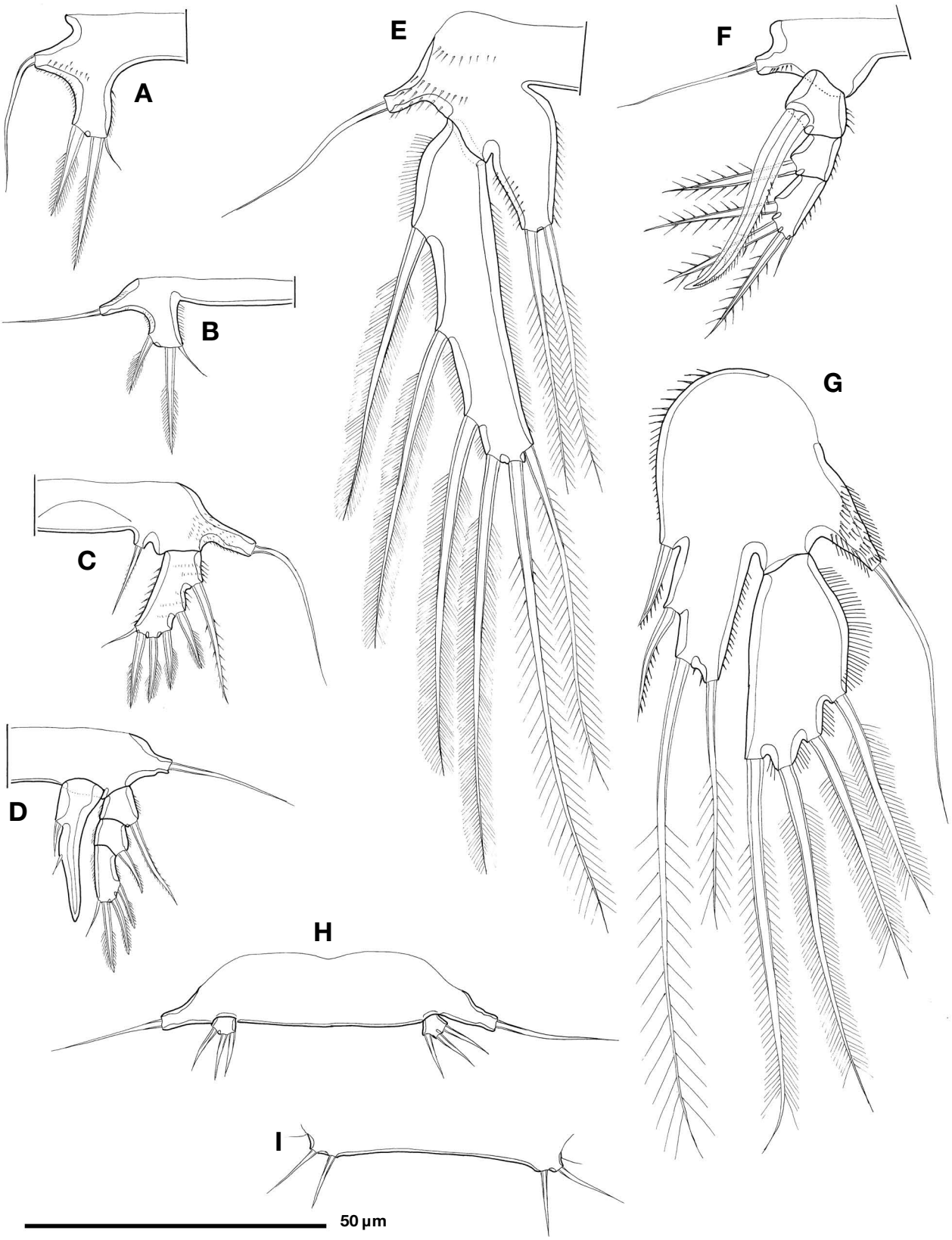


Fig. 4. *Afrolaophonte koreana* sp. nov.: A, female second swimming leg; B, male second swimming leg; C, female third swimming leg; D, male third swimming leg; E, female fourth swimming leg; F, male fourth swimming leg; G, female fifth leg; H, male fifth legs; I, male sixth legs. All in anterior view.

Table 1. Character states scored for 13 species of *Afrolaophonte* and one outgroup, *Arenolaophonte stygia* from California. Missing characters are marked with a dash for species with unknown males. NONA requires characters to start from zero.

Characters	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
A. stygia Lang, 1965	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. aequatorialis Cottarelli & Mura, 1982	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0
A. brevipes (Chappuis, 1954)	0	1	1	1	1	0	1	1	0	1	0	1	0	0	0
A. brignolii Cottarelli, 1986	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0
A. chilensis Mielke, 1985	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
A. koreana sp. nov.	1	1	0	1	1	1	1	0	1	1	0	1	0	1	1
A. leonis Cottarelli & Mura, 1982	1	1	1	1	1	0	0	0	0	0	0	1	0	–	–
A. michae Cottarelli, 1986	1	1	0	1	1	0	1	1	0	1	0	1	0	–	–
A. michaelae Cottarelli & Mura, 1982	1	1	0	1	1	1	1	1	0	1	1	1	1	0	0
A. monodi Chappuis, 1960	1	1	1	1	1	0	1	0	0	0	0	1	0	0	1
A. pori Masry, 1970	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0
A. renaudi (Chappuis & Delamare, 1956)	1	1	1	1	0	1	1	0	0	0	0	1	0	–	–
A. schmidti Mielke, 1981	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
A. stocki Fiers, 1990	1	1	1	0	1	0	1	0	0	0	0	1	0	0	0

Cladistics

Unfortunately, many species are known from a very limited set of morphological characters, so any characters related to the presence and relative position of cuticular organs on prosomites, armature and ornamentation of antennae and mouth appendages, and most male characters had to be omitted. The following 15 binary characters were selected, with character states in parentheses (note: NONA requires characters to start from zero, rather than one):

0. Female second leg exopod: distinct (0); fused to basis (1).
1. Female second leg exopod, number of spines: more than two (0); two (1).
2. Female second to fourth legs, inner apical seta: present (0); absent (1).
3. Female third leg endopod, number of setae: more than one (0); one (1).
4. Female third leg endopod: distinct (0); fused to basis (1).
5. Female third leg exopod, first segment: distinct (0); fused (1).
6. Female third leg exopod, second segment: distinct (0); fused (1).
7. Female third leg exopod, number of spines: five (0); four (1).
8. Female fourth leg exopod, first segment: distinct (0); fused (1).
9. Female fourth leg exopod, second segment: distinct (0); fused (1).
10. Female fourth leg exopod, number of spines: five (0); four (1).
11. Female fifth leg exopod, number of setae: five (0); four (1).
12. Female fifth leg endopod, number of setae: four (0); three (1).
13. Male third leg endopod: two-segmented (0); one-segmented (1).
14. Male fourth leg, endopodal seta: present (0); absent (1).

A character matrix was constructed (Table 1) to contain all character states for all species, except for two male characters (nos. 13 and 14) for three species (*A. leonis*, *A. michae*, and *A. renaudi*), for which males are unknown. Three characters (nos. 1, 12, and 14) proved to be autapomorphies (found in only one species) and are thus uninformative for this phylogenetic analysis, but are kept here nevertheless to help future taxonomic and systematic research on this genus.

Cladistic analysis with all characters unweighted resulted in 12 equally parsimonious trees (Fig. 5), with a length of 29 steps, a consistency index (Ci) of 0.51, and a retention index (Ri) of 0.62. Low Ci and Ri values were not a consequence of missing characters because an analysis with the last two characters excluded also resulted in 12 equally parsimonious trees; although the trees were slightly shorter (26 steps), the Ci of 0.5 and Ri of 0.63 were equally low. A strict consensus of these 12 trees resulted in a perfect comb (not shown). The most significant difference between these 12 trees was in the position of *A. aequatorialis*: six suggested a basal position (Fig. 5A), while the other six suggested a terminal position for this species (Fig. 5B). Korean new species always had a terminal position, being sister to *A. aequatorialis* in six trees (Fig. 5B), to *A. michaelae* in four trees, to *A. michae* in

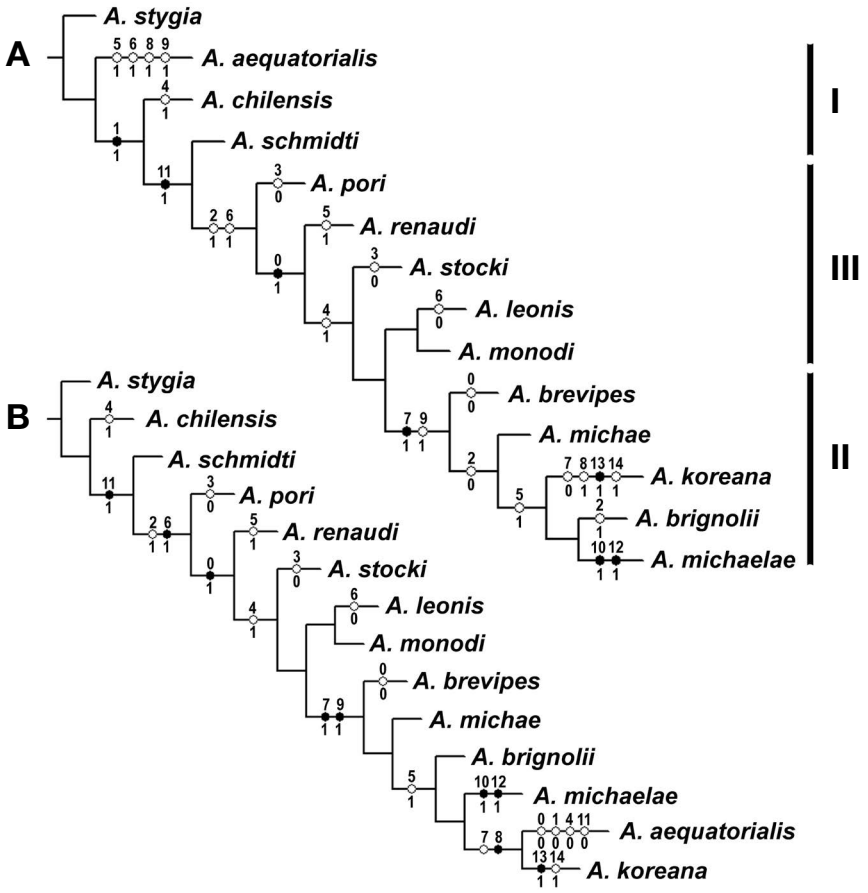


Fig. 5. Two out of 12 equally parsimonious trees resulting from an analysis of 15 unweighted morphological characters (Table 1) scored for 13 species of *Afrolaophonte* Chappuis, 1960 and one outgroup, *Arenolaophonte stygia* Lang, 1965. The trees were constructed using Winclada/NONA and heuristic search method. Full circles represent presumed synapomorphies, empty circles presumed plesiomorphies or homoplasies, Arabic numerals above circles characters, Arabic numerals below circles character states, and Roman numerals indicate species-groups proposed by Fiers (1990). *Afrolaophonte aequatorialis* Cottarelli and Mura, 1981 has a basal position in six trees (as in A) and terminal position in six trees (as in B).

one tree, and to *A. brignolii* + *A. michaelae* in one tree (Fig. 5A).

An analysis based on the same dataset, but with down-weighted characters 0, 2–4, and 11–14, resulted in 20 equally parsimonious trees, with a length of 9 steps, a consistency index (Ci) of 0.77, and a retention index (Ri) of 0.88. Their strict consensus collapsed four unsupported nodes (Fig. 6). Korean new species was sister to *A. aequatorialis*, and this clade was supported by a single synapomorphy: fused first exopodal segment of the female fourth leg (resulting in a one-segmented exopod). Another clear group of four species (*A. brevipes*, *A. brignolii*, *A. michae*, and *A. michaelae*) was also supported by a single synapomorphy: a reduced number of spines on the female third leg exopod. These two groups were united as a teminal brunch on the consensus tree by the fused second exopodal segment on the female fourth leg (Fig. 5), but no other groups of species were suggested. Despite many morphological similarities between *A. chilensis* and *A. schmidti*, the cladistic analysis shows that they are all symplesiomorphies. The cladistic analysis also exposed many homoplastic characters, two most common ones being the separation of second leg exopod (character 0) and the separation of third leg endopod (character 4).

Discussion

The new species is probably most closely related to *A. aequatorialis*, which was described by Cottarelli and Mura (1981) from a small island in the Maldives. *Afrolaophonte ensiger*, which was described by Wells and Rao (1987) from five beaches on the Andaman and Nicobar Islands (also in the Indian Ocean), is an obvious junior synonym of *A. aequatorialis*. It is clear that Wells and Rao (1987) were not aware of the Maldivian species,

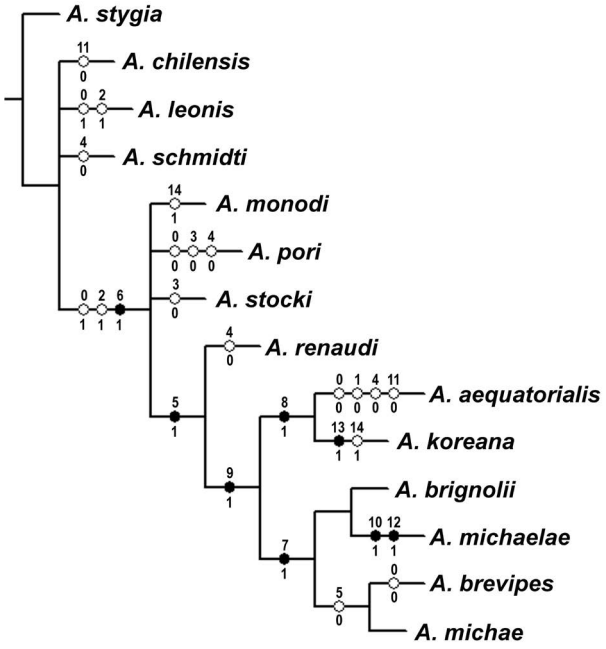


Fig. 6. Strict consensus tree resulting from 20 equally parsimonious trees from an analysis of 15 weighted morphological characters (Table 1) for 13 species of *Afrolaophonte* Chappuis, 1960 and one outgroup, *Arenolaophonte stygia* Lang, 1965. Characters 0, 2–4, and 11–14 were down-weighted to 0.5, while others were left at the default weight of 1. Full circles represent presumed synapomorphies, empty circles presumed plesiomorphies or homoplasies, Arabic numerals above circles characters, and Arabic numerals below circles character states.

because they emphasized the one-segmented exopod of the fourth leg as a major distinguishing character of *A. ensiger*. *Afrolaophonte aequatorialis* and *A. koreana* are the only two congeners with a one-segmented exopod of the fourth leg, and they also share the segmentation of other swimming legs, as well as most armature formulae. However, the Korean species has shorter caudal rami and genital double-somite, longer endopod of the first leg, exopod of the second leg with one less spine and also completely fused to basis, much longer outer endopodal and innermost exopodal setae on the female fourth leg, fused all endopodal segments on the male third leg, female fifth leg exopod with one less seta (although this is sometimes variable in *A. aequatorialis*), and no prominent cuticular tubes on the caudal rami. Unfortunately, mouth appendages were not illustrated for *A. aequatorialis*, so they cannot be compared with the Korean new species. Cuticular organs were also not carefully mapped in *A. aequatorialis*, but the female urosomal ornamentation looks remarkably similar to that in *A. koreana*. Cuticular sensilla and pores were surveyed in more detail by Sönmez *et al.* (2018) for the Mediterranean *A. pori* and by Fiers (1990) for the Caribbean *A. stocki*, but their patterns seem to be quite different, especially on the cephalothoracic shield. Both of these species differ from *A. koreana* in the sensilla and pores pattern, as well as in numerous macro-morphological characters.

Mouth appendages were examined and illustrated for only eight species in this genus so far: *A. aequatorialis*; *A. brignolii*; *A. chilensis*; *A. leonis*; *A. michae*; *A. michaelae*; *A. pori*; and *A. schmidti*. Note that figure captions were erroneously partly swapped in Cottarelli and Mura (1981) (their figures 3 and 4), and in the text they referred to a non-existent figure 5. Also note that the illustration of a maxillula for *A. aequatorialis* provided by Cotttarelli and Mura (1981) in their figure 4D (figure caption below their figure 3) is far too complex to belong to the family Laophontidae (see Boxshall and Halsey, 2004). All these eight species have two setae on the mandibular palp, while *A. koreana* has three. Maxillula, maxilla, and maxilliped were illustrated in sufficient detail only for *A. chilensis*, *A. pori*, and *A. schmidti*, and they are remarkably similar to those in *A. koreana*. Sönmez *et al.* (2018) illustrated (their figure 4D) and described a maxillula without a distinct exopod, but this minute segment is clearly visible in their SEM photo in figure 5A. It seems that the endopod of maxilliped bears a minute seta in *A. chilensis* and *A. schmidti*, while this is absent in *A. koreana* and *A. pori*. Males are still unknown for three *Afrolaophonte* species (*A. leonis*; *A. michae*; and *A. renaudi*), but their morphology was considered to be very conservative (Fiers, 1990; Sönmez *et al.* 2018). However, males of *A. koreana* differ from all others by a one-segmented endopod of the third leg; they also lack endopodal seta on the fourth leg, which is a character shared only with *A. monodi*.

Fiers (1990) divided the genus into three species groups based on intuitive methods and extremely convoluted rhetoric. Based on his system, *A. koreana* could probably be assigned to the first group, as it is most similar to *A. aequatorialis*. However, the parsimony based cladistic analysis performed here suggests that the first group (also called the *chilensis*-group) was based on symplesiomorphies. His third group (also called the *monodi*-group) also was not supported by any synapomorphies. The only group that received some support was his second group (also called the *brevipes*-group), but this was based on a single synapomorphy. It is quite clear that our current knowledge of morphology in this genus is not sufficient for postulating interspecific phylogenies. The number of homoplasies suggested by the cladistic analysis additionally calls for caution when using morphology in this genus with preference for interstitial habitats that favours vermiform habitus and reductions in appendage segmentation and armature. In interstitial harpacticoids where phylogenetic relationships were tested with molecular markers, it has been proven that similar reductions can happen a number of times independently in one genus

(Karanovic *et al*., 2015).

Fiers (1990) suggested a Tethyan origin of the genus, with vicariance as a major driver of diversification. This is despite the fact that his model could not explain the presence of one species on the volcanic Galapagos Islands and that he found *A. aquaetorialis*, originally described from the Maldives, in Papua New Guinea (a distance of over 8300 kilometers). Presence of this species in the Andaman and Nicobar Islands (as *A. ensiger*; see above) is a further testament of enormous dispersal potential of these small animals, despite the fact that they have never been observed outside the interstitial environment and that their reduced swimming legs suggest very modest active dispersal abilities. Today we have solid genetic evidence that copepods with seemingly enormous active dispersal potential do not necessarily have very large ranges (Handschumacher *et al*., 2010; Peterson *et al*., 2013; Karanovic *et al*., 2018) and that some with seemingly limited dispersal potential sometimes do, often facilitated with anthropogenic translocation (Reid and Pinto-Coelho, 1994; Lee, 1999; Horvath *et al*., 2001; Karanovic and Krajicek, 2012). Even in undisturbed calcrete aquifers of Western Australia, which act as an archipelago of tiny subterranean islands, dispersal plays a vital part in species diversification (Karanovic and Cooper, 2012; Karanovic *et al*., 2016). Absence of reliable phylogeny renders previous zoogeographical hypotheses in the genus *Afrolaophonte* untestable.

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