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A new species of *Longipedia* Claus, 1863 (Copepoda: Harpacticoida: Longipediidae) from Caribbean mesophotic reefs with remarks on the phylogenetic affinities of *Polyarthra*

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ORIGINAL ARTICLE

A new species of *Longipedia* Claus, 1863 (Copepoda: Harpacticoida: Longipediidae) from Caribbean mesophotic reefs with remarks on the phylogenetic affinities of Polyarthra

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Abstract

Mesophotic coral reefs are largely unexplored nearshore habitats. We present illustrations of both sexes of a new copepod species of the family Longipediidae Sars, 1903 collected via scuba-diving with tri-mix rebreathers from mesophotic coral reefs in Puerto Rico as an example of the rich fauna encountered in these habitats. The new species, *Longipedia gonzalezi*, displays a conservative morphology that characterizes the genus by having a robust body, first pedigers fused to the cephalosome, P4 exp-2 with only 1 medial seta, number of enp-1 medial setae of P1–P4 = 1:1:1:1, number of enp-2 medial setae of P1–P4 = 1:1:2:1, and caudal rami of cylindrical shape about twice as long as wide. The new species belongs to the *helgolandica* species-group and is morphologically similar to *L. helgolandica* and *L. americana*. Species distinction within the genus *Longipedia* based on morphological characters is challenging because of the conservative morphology of the genus, so we provide the first DNA sequences (28S gene) for future comparisons within the genus. The phylogenetic position of the Polyarthra (a taxon consisting of the families Longipediidae and Canuellidae, whose affinities with Harpacticoida have been questioned) is discussed within Copepoda and other Crustacea. The 28S DNA analysis confirms that Polyarthra are very closely related and are included in the strongly supported Copepoda clade. Polyarthra were not found within the Harpacticoida, which, therefore, remained not as a monophyletic, but as a paraphyletic taxon. Therefore, our 28S data indicate that the claim by Dahms and previous authors for the exclusion of Polyarthra from the Harpacticoida may be valid, and warrants further investigation.

Key words: *Harpacticoida*, *Longipedia*, *mesophotic coral ecosystems*, *phylogenetics*, *Polyarthra*, *Puerto Rico*

Introduction

In the Caribbean, mesophotic coral ecosystems (MCEs) are found on the insular and continental slopes of islands and provide habitats for a highly diverse and specialized benthic fauna. MCEs are characterized by the presence of zooxanthellate corals, sponges and algae typically found at depths of 40–50 m and reaching down to more than 100 m

(Kahng et al. 2010). The fauna of MCEs is largely unexplored because MCEs are typically found at depths too deep for conventional scuba-diving. New technical diving equipment combining tri-mix diving and rebreathers allow researchers to do research and safely collect from these depths. Divers can selectively sample substrata and minimize habitat alterations compared to more destructive methods such as benthic dredging.

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The renewed scientific interest in MCEs has resulted in the identification of new taxa (e.g. algae: Ballantine & Ruiz 2010, 2011; crustaceans: Petrescu et al. 2012, 2013; Corgosinho & Schizas 2013), suggesting that MCEs may represent a transition zone between the shallow and deeper habitats, at times harboring a unique fauna. Because MCEs have a possible areal extent comparable to shallow reefs (Locker et al. 2010), there is the potential for MCEs to be biodiversity hotspots. The identification and description of new benthic taxa is part of a larger research effort of a National Oceanic and Atmospheric Administration-sponsored mesophotic coral reef ecosystem study (DeepCres).

After preliminary examination of the harpacticoid copepod fauna associated with substrata from MCEs in Puerto Rico, we recovered several specimens of the family Longipediidae Sars, 1903, which are easily distinguished by an elongated P2. The presence of *Longipedia* Claus, 1862 in mesophotic reefs stimulated further investigations because longipediids are usually found in small numbers in shallow-water habitats or in inshore plankton (Boxshall & Halsey 2004; Dahms et al. 2012; Tseng et al. 2012). In Puerto Rico, González & Bowman (1965) collected *Longipedia americana* Wells, 1980 (originally identified as *L. helgolandica* Klie, 1949) from Bahía Fosforescente, a shallow embayment near La Parguera. Species of the monogeneric Longipediidae Sars, 1903 are unique in having extremely long second legs, but are also notorious for minute differences existing among species. The only genus of this family, *Longipedia*, comprises 13 valid species (Boxshall & Halsey 2004): *Longipedia americana* from the Atlantic coast of North America, Jamaica and Mexico; *L. andamanica* Wells, 1980 from the Andaman Islands and Japan; *L. brevispinosa* Gurney, 1927 from the Suez Canal; *L. coronata* Claus, 1862 from Iceland, NW Europe and the Mediterranean Sea; *L. corteziensis* Gómez, 2001 from NW Mexico; *L. helgolandica* from NW Europe and SW Africa; *L. kikuchii* Itô, 1980 from Japan, India and Singapore; *L. minor* T. & A. Scott, 1893 from NW Europe, the Mediterranean Sea and the Black Sea; *L. nichollsi* Wells, 1980 from Australia; *L. santacruzensis* Mielke, 1979 from the Galapagos Islands; *L. scotti* G.O. Sars, 1903 from NW Europe, the Mediterranean Sea, Mozambique, Australia and Samoa; *L. spinulosa* Itô, 1981 from Japan; and *L. weberi* A. Scott, 1909 from Japan, the Suez Canal and the Addu Atoll.

The concomitant use of morphological and molecular data sets will be useful to elucidate taxa relationships within the Harpacticoida and Copepoda (Chullasorn et al. 2011), including the morphologically conservative Longipediidae. Dahms

(2004) excluded the Polyarthra (consisting of the families Longipediidae and Canuellidae) from the Harpacticoida and allocated them to Copepoda, as an underived taxon. He claimed that there is no reasonable autapomorphy for the taxon Harpacticoida (sensu Lang 1948), based on naupliar and adult-stage characters, and suggested that Harpacticoida should be represented solely by the monophyletic taxon Oligoarthra (all remaining harpacticoid families).

The purpose of the present study is to describe a new species of Longipediidae from a mesophotic Caribbean reef and to discuss the phylogenetic relationship of Polyarthra within a wider circle of Copepoda and other crustacean taxa. We used newly generated molecular data to explore the phylogenetic affinities of Polyarthra with the order Harpacticoida.

Materials and methods

Collection and processing

Divers equipped with tri-mix rebreathers collected substrata (loose rubble, corals, sponges and algae) from MCEs located near the shelf-edge of southwestern Puerto Rico. Whole colonies of the coral *Agaricia lamarcki* Milne Edwards & Haime, 1851 were placed over 1 mm and 0.125 mm mesh sieves and washed with filtered seawater. The portion of fauna retained in the 0.125 mm mesh sieve was extracted, preserved in 100% ethanol and examined under the microscope. Prior to light microscopic examination, specimens were cleared in lactic acid. The material was examined using bright-field and differential interference contrast optics. All measurements and dissections were made under a Leica MZ8 dissection microscope. The length of habitus was measured from the anterior lateral corner of the cephalothorax (noted by an arrow in Figure 1A) to the posterior margin of the caudal rami, after the specimen was placed under a coverslip to straighten the urosomal bend. Drawings were made with the aid of a camera lucida mounted on a Nikon compound microscope. The description is based on the holotype female and one of the paratype males (USNM 1272447). For long-term preservation, the holotype and paratypes were mounted on slides in glycerol and sealed with Eukitt (O. Kindler GmbH & Co.).

Terminology and acronyms

The references for the genus *Longipedia* were Bodin (1997), Fiers (1984), Huys & Boxshall (1991), Huys et al. (1996), Mu & Huys (2004), Por (1983), Wells (2007), and Wells & Rao (1987). Terminology and the establishment of the homology of maxillary and maxillipedal structures follow Ferrari & Ivanenko

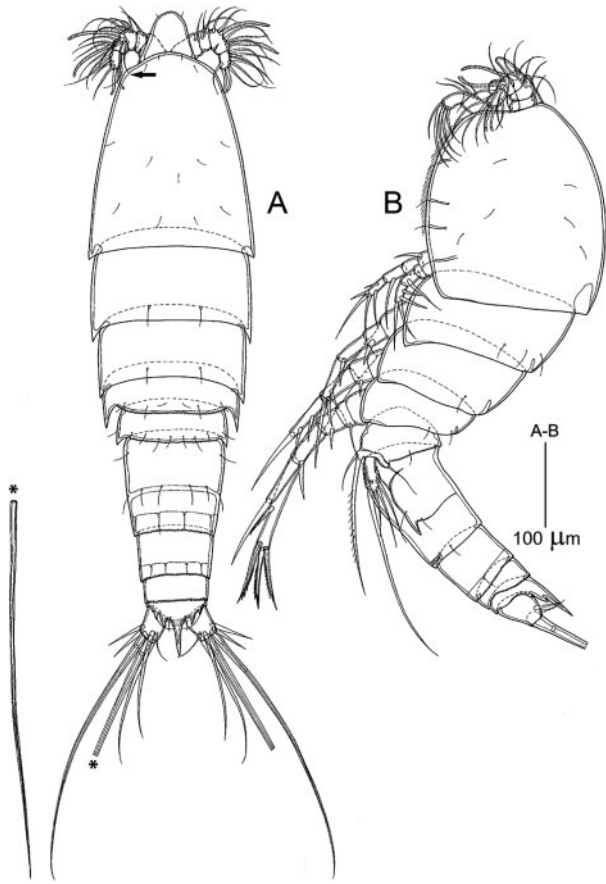


Figure 1. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) habitus, dorsal view; (B) habitus, lateral view. Arrow points to anterior lateral corner of cephalothorax.

(2008) and Ferrari et al. (2013). The terms seta, setules, spines and spinules are used according to Huys & Boxshall (1991) and Song et al. (2012). The following abbreviations are used in the text: A1, antennule; A2, antenna; ae, aesthetasc; benp, baseopod; enp, endopod; enp-1 (2,3), proximal (middle, distal) segment of endopod; exp, exopod; exp-1 (2,3), proximal (middle, distal) segment of exopod; Md, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; P1–P6, first to sixth thoracopod; CR, caudal rami; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (Department of Invertebrate Zoology).

Molecular procedures and analysis

We extracted DNA from two specimens of the new species preserved in 100% ethanol using the DNeasy Blood & Tissue Kit (Qiagen Inc.) following the manufacturer's guidelines. We also extracted DNA from 12 harpacticoid species from Puerto Rico belonging to nine families (Laophontidae, Ancorabolidae, Ameridae, Darcythompsoniidae, Hamondiidae,

Metidae, Peltidiidae, Tetragonicipitidae and Thales-tridae; Table I) to augment the representation of Harpacticoida in our analysis. A region (v–x) of the 28S rDNA was polymerase chain reaction (PCR)-amplified using universal primer sets described in Hillis & Dixon (1991). We also downloaded publicly available 28S sequences from 31 species of crustaceans including all available copepod species (Table I). The primers 28Sv and 28Sx were used because they have been shown to be variable at the species level in crustaceans (Syme & Oakley 2012; Hou et al. 2013) and amplify the target area easily. PCR amplifications took place in 25 µl reactions containing 0.5 µl of extracted DNA solution, 0.5 µl (5 pmol) of each primer (28S v–x), 12.5 µl of 2x BioMix (Bioline Inc.) and 11 µl of molecular-grade water. We ran the PCR in a Bio-Rad thermal cycler machine; after an initial denaturation of 2 min at 94°C, we programmed the thermal cycler to perform 40 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 1 min and extension at 72°C for 90 s followed by a final extension at 72°C for 6 min. We checked for successful PCR reactions by loading 5 µl of the amplicon on a 1% TBE agarose gel stained with ethidium bromide under UV light and catalogued electronically. Sequencing reactions were set up with Big Dye™ terminators (dideoxynucleotides) in both directions and sequencing took place in an ABI 3130xl 16-capillary Genetic Analyzer.

DNA data analysis

DNA trace files were imported in CodonCode Aligner (CodonCode Corporation) for base calling, quality assessment, contig assembly, visualization and manual editing. DNA sequences were aligned with the online MAFFT v7 software (Katoh & Toh 2008) using the E-INS-i alignment strategy, which is recommended for < 200 sequences with multiple conserved domains and long gaps, adjusting direction according to the first sequence and with the default parameters (gap opening penalty 1.53, offset value 0.0). The resulting 28S alignment contained highly variable regions for which we could not assign homology, and those regions were removed by Gblocks v.0.91b (Castresana 2000). The Gblocks parameters were: minimum number of sequences for a conserved position (33), minimum number of sequences for a flanking position (33), maximum number of contiguous non-conserved positions (8), minimum length of a block (5), and allowed gap positions (with half). After quality control, end trimming and removal of uncertain alignment blocks by Gblocks (Castresana 2000), a 505 bp region of 28S of *Longipedia gonzalezi* sp. nov. and of the other taxa was used for phylogenetic analysis. 28S sequences were

Table I. Species and GenBank accession numbers of 28S sequences used in this study. Numbers after species name signify sample identifiers.

Class	Subclass	Order	Species	GenBank no.
Maxillopoda	Copepoda	Siphonostomatoida	<i>Sphyrion lumpi</i> (Krøer, 1845)	DQ180345
Maxillopoda	Copepoda	Siphonostomatoida	<i>Clavella stellata</i> (Krøyer, 1838)	DQ180339
Maxillopoda	Copepoda	Siphonostomatoida	<i>Lepeophtheirus pollachius</i> Bassett-Smith, 1896	DQ180343
Maxillopoda	Copepoda	Siphonostomatoida	<i>Parabrachiella merluccii</i> (Bassett-Smith, 1896)	DQ180347
Maxillopoda	Copepoda	Siphonostomatoida	<i>Echthrogaleus coleoptratus</i> (Guérin-Méneville, 1837)	DQ180344
Maxillopoda	Copepoda	Siphonostomatoida	<i>Lepeophtheirus salmonis salmonis</i> (Krøyer, 1837)	DQ180342
Maxillopoda	Copepoda	Siphonostomatoida	<i>Caligus curtus</i> O. F. Müller, 1785	DQ180338
Maxillopoda	Copepoda	Siphonostomatoida	<i>Clavellopsis</i> sp.	HM545894
Maxillopoda	Copepoda	Calanoida	<i>Calanus simillimus</i> Giesbrecht, 1902	EU914255
Maxillopoda	Copepoda	Calanoida	<i>Paraechaeta antarctica</i> (Giesbrecht, 1902)	AF169732
Maxillopoda	Copepoda	Harpacticoida	<i>Tigriopus fulvus fulvus</i> (Fischer, 1860)	EU370444
Maxillopoda	Copepoda	Harpacticoida	<i>Tigriopus japonicus</i> Mori, 1938	EU054307
Maxillopoda	Copepoda	Harpacticoida	<i>Tigriopus californicus</i> (Baker, 1912)	AF363350
Maxillopoda	Copepoda	Harpacticoida	<i>Canuella perplexa</i> T. & A. Scott, 1893	EU370445
Maxillopoda	Copepoda	Harpacticoida	<i>Longipedia gonzalezi</i> sp. nov.	KP410722
Maxillopoda	Copepoda	Harpacticoida	<i>Eupelte</i> sp.	KP410721
Maxillopoda	Copepoda	Harpacticoida	Ancorabolidae sp.	KP410720
Maxillopoda	Copepoda	Harpacticoida	<i>Darcythompsonia fairliensis</i> (T. Scott, 1899) 2_1	KP410719
Maxillopoda	Copepoda	Harpacticoida	Darcythompsoniidae 1	KP410718
Maxillopoda	Copepoda	Harpacticoida	Darcythompsoniidae 2	KP410717
Maxillopoda	Copepoda	Harpacticoida	<i>Laophontella armata</i> (Willey, 1935)1	KP410716
Maxillopoda	Copepoda	Harpacticoida	<i>Laophontella armata</i> 2	KP410715
Maxillopoda	Copepoda	Harpacticoida	<i>Metis ignea ignea</i> Philippi, 18432 female	KP410714
Maxillopoda	Copepoda	Harpacticoida	<i>Metis ignea</i> 3	KP410713
Maxillopoda	Copepoda	Harpacticoida	<i>Lucayostratiotes cornuta</i> (Geddes, 1969) female	KP410712
Maxillopoda	Copepoda	Harpacticoida	<i>Lucayostratiotes cornuta</i> male	KP410711
Maxillopoda	Copepoda	Harpacticoida	<i>Lucayostratiotes cornuta</i> pair	KP410710
Maxillopoda	Copepoda	Harpacticoida	<i>Eudactylopus robustus</i> (Claus, 1863) 3	KP410709
Maxillopoda	Copepoda	Harpacticoida	<i>Eudactylopus robustus</i> 2	KP410708
Maxillopoda	Copepoda	Harpacticoida	<i>Eudactylopus robustus</i> 1	KP410707
Maxillopoda	Copepoda	Harpacticoida	<i>Echinolaophonte armiger armiger</i> (Gurney, 1927) male1	KP410706
Maxillopoda	Copepoda	Harpacticoida	<i>Echinolaophonte armiger</i> male	KP410705
Maxillopoda	Copepoda	Harpacticoida	<i>Echinolaophonte armiger</i> large	KP410704
Maxillopoda	Copepoda	Harpacticoida	Ameridae sp. 2	KP410703
Maxillopoda	Copepoda	Harpacticoida	Ameridae eggs	KP410702
Maxillopoda	Copepoda	Cyclopoida	<i>Cyclops insignis</i> Claus, 1857	EF532821
Maxillopoda	Copepoda	Cyclopoida	Cyclopidae sp.	AY210813
Maxillopoda	Copepoda	Cyclopoida	<i>Cyclops kolensis</i> Lilljeborg, 1901	EF532820
Maxillopoda	Copepoda	Cyclopoida	<i>Paracyclops nana</i> Smirnov, 1935	FJ214952
Maxillopoda	Copepoda	Poecilostomatoida	<i>Chondracanthus lophii</i> Johnston, 1836	DQ180341
Maxillopoda	Copepoda	Poecilostomatoida	<i>Chondracanthus merluccii</i> (Holten, 1802)	DQ180340
Malacostraca	Phyllocarida	Leptostraca	<i>Nebalia</i> sp.	AY859590
Maxillopoda	Branchiura	Arguloidea	<i>Argulus foliaceus</i> (Linnaeus, 1758)	EU370442
Maxillopoda	Mystacocarida	-	<i>Derocheilocaris typica</i> Pennak & Zinn, 1943	EU370443
Malacostraca	Eumalacostraca	Mysida	<i>Siriella okadai</i> Ii, 1964	AB432983
Malacostraca	Eumalacostraca	Mysida	<i>Heteromysis</i> sp.	AY859578
Malacostraca	Eumalacostraca	Anaspidacea	<i>Anaspides tasmaniae</i> Thomson, 1892	AY859549
Malacostraca	Hoplocarida	Stomatopoda	<i>Pseudosquilla ciliata</i> (Fabricius, 1787)	HM180076
Malacostraca	Hoplocarida	Stomatopoda	<i>Squilla empusa</i> Say, 1818	AY210842
Malacostraca	Eumalacostraca	Decapoda	<i>Penaeus vannamei</i> Boone, 1931	AF124597
Malacostraca	Eumalacostraca	Decapoda	<i>Limnarus trigonus</i> (von Siebold, 1824)	AY113665
Malacostraca	Eumalacostraca	Decapoda	<i>Jasus edwardsii</i> (Hutton, 1875)	AF169741
Malacostraca	Eumalacostraca	Decapoda	<i>Homarus americanus</i> Milne Edwards, 1837	AY859581
Malacostraca	Eumalacostraca	Decapoda	<i>Eriocheir sinensis</i> Milne Edwards, 1853	GU362671
Branchiopoda	Phyllopoda	Diplostraca	<i>Daphnia pulex</i> Leydig, 1860	FJ177015
Maxillopoda	Ostracoda	Myodocopa	Philomedidae sp. 69	KP410723
Maxillopoda	Ostracoda	Myodocopa	Sarsiellidae sp. 8	KP410724
Maxillopoda	Ostracoda	Myodocopa	Cylindroleberididae sp. 67	KP410725
Maxillopoda	Ostracoda	Podocopa	Xestoleberididae sp. 18	KP410727
Maxillopoda	Ostracoda	Podocopa	Bairdiidae sp. 41	KP410728
Maxillopoda	Ostracoda	Podocopa	Bairdiidae sp. 4	KP410726
Insecta	Hexapoda	Trichoptera	Phryganeidae sp.	JQ259059

imported into MEGA v.6.0.6 (Tamura et al. 2013) and MrBayes v.3.2 (Ronquist et al. 2012) to construct Maximum Likelihood (ML) trees and Bayesian Inference (BI) genealogies, respectively. Within MEGA, the most appropriate model of DNA substitution for the resulting 28S data set was estimated and applied to the ML analysis. Clade support was assessed with 500 bootstrap replicates. Corrected pairwise distances between species were also estimated in MEGA. The condition for the MCMC-based BI were 10,000,000 generations, four independent chains, sampling every 1000 generations and discarding 25% of the first sampled trees. Summary information about sample trees was produced using LogCombiner and TreeAnnotator v.1.7.4. To check the performance of MrBayes output for an adequate convergence and mixing quality of all parameters, we used Tracer v.1.5 by examining the log likelihood values across generation number. In addition, Tracer was used to confirm that post-burn-in trees yielded an effective sample size (ESS) of > 200 for all parameters. DNA sequences were submitted to GenBank (Table I).

Results

Taxonomy

Class Copepoda Milne Edwards, 1830
Order Harpacticoida Sars, 1903
Family Longipediidae Sars, 1903
Genus *Longipedia* Claus, 1863

Longipedia Claus, 1863: type species *L. coronata* Claus, 1863

***Longipedia gonzalezi* sp. nov.**
 (Tables I, II, III; Figures 1 to 12 and S1)

Type locality

The specimens were collected from the edge of the insular shelf (location 'Hole-in-the-Wall'; 17° 53.4239'N, 66°59.3209'W), 46–52 m depth, La Parguera, southwest Puerto Rico. The copepods were collected together with samples of the scleractinian coral *Agaricia lamarcki*. It was, however, impossible to discern the level of association with the coral, as other taxa (e.g. algae and small sponges) and some sediment were also attached to the coral colonies.

Material examined

Holotype: USNM 1272446, adult female dissected on seven slides. Paratype: USNM 1272447, adult male dissected on 10 slides. Paratype: USNM 1270863, whole adult female on one slide. Allotype: USNM

1270864, whole adult male on one slide. Paratype: USNM 1270865, whole adult male on one slide. 11 whole specimens (six females, five males) in one vial (USNM 1272448) and dissected parts of adult female on one slide USNM 1272449. All specimens were collected during 2007 by tri-mix rebreather divers.

Description

Holotype

Body (Figure 1A,B): 0.75 mm long, large, fusiform in dorsal view, without marked distinction between prosome and urosome. Cephalothorax ornamented with setules along ventrolateral margin; with lateral tubular internal structures (Figure 2A). Cephalothorax and posterior part of pedigerous somites of P2–P4 furnished with sensilla; fourth somite with sensilla and hyaline frill.

Urosome (Figure 3A,B): ancestral two somites of genital double somite distinct dorsally, but shells completely fused; with ventrolateral processes at position of posterior margin of ancestral sixth

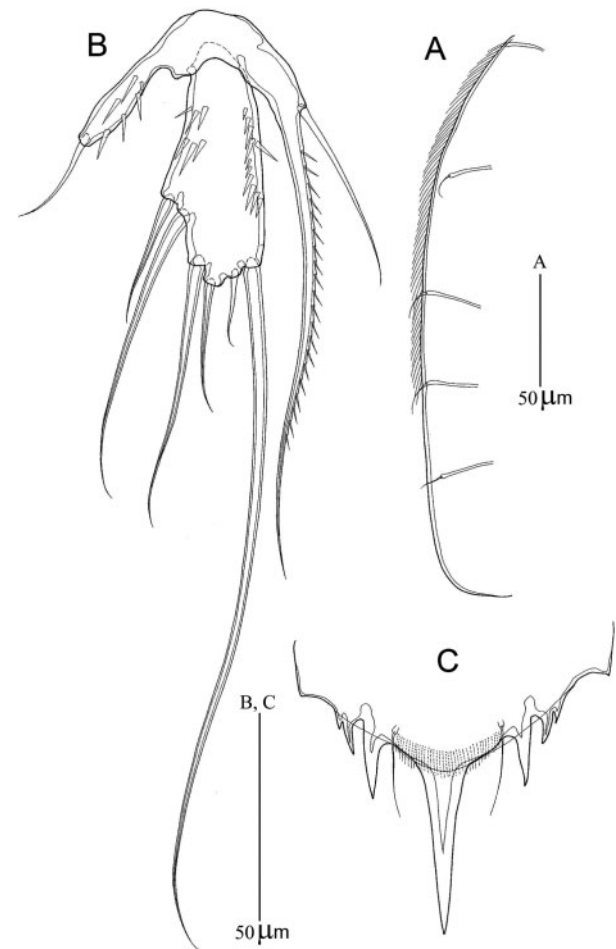


Figure 2. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) detail of the anterolateral edge of the cephalic shield; (B) P5; (C) projection of the anal operculum.

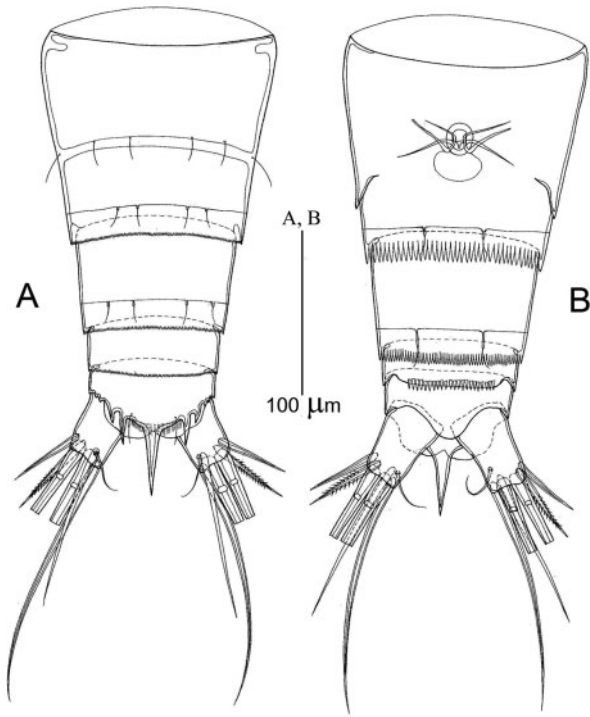


Figure 3. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) urosome excluding the fifth thoracic somite, dorsal view; (B) urosome excluding the fifth thoracic somite, ventral view.

thoracic somite. Urosomites 1–3 with sensilla along posterior part dorsally and urosomites 2–4 with finely serrated hyaline frill, but more pronounced ventrally. Genital field compact, with median copulatory pore immediately posterior to common genital aperture. Anal operculum well developed, furnished with fringing setules; dorsally with strong median projection (Figure 2C) reaching beyond posterior margin of furcal rami, and with four pairs of projections (two of which more pronounced) and sensillum on each side.

Furca (Figure 3A, B) of somewhat conical shape, twice as long as wide in ventral view, each ramus armed with seven setae.

Rostrum (Figure 4A) massive, bell-shaped, defined at base, and with two very small sensilla dorsally on both sides of apex.

A1 (Figure 4B) non-discrete, with five segments, two aesthetascs each on segments 3 and 4, and two modified aesthetascs (noted with arrow) apically on terminal segment. Armature formula: 3-9-11+1 ae-9+1 ae-8+2 ae.

A2 (Figure 4C) biramous, with separate coxa and basis. Exopod 7-segmented; exp-1 with one spiniform and one short, simple seta; exp-2–6 with one spiniform seta; exp-7 with four spiniform setae. Endopod 3-segmented; enp-1 with one smooth and one spiniform seta; enp-2 with four spiniform setae and one simple seta; enp-3 with six robust spiniform setae.

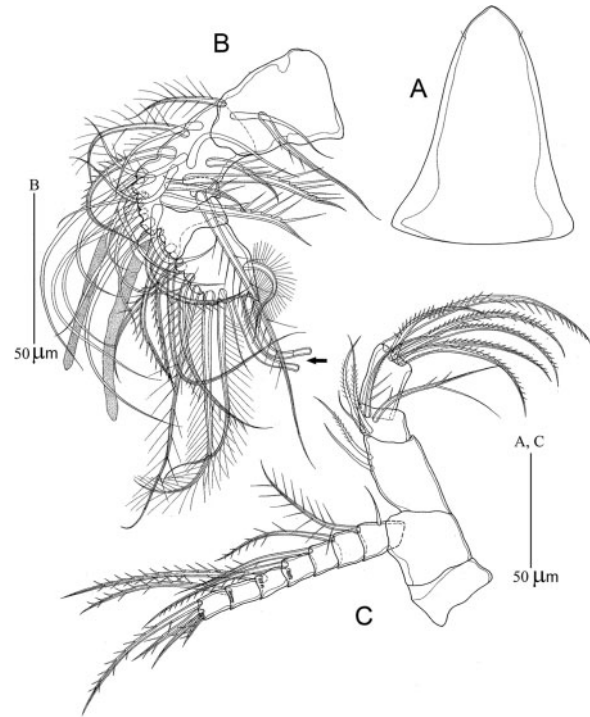


Figure 4. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) rostrum; (B) antennule; (C) antenna. Arrow points to the two modified aesthetascs on the apical segment of the antennule.

Md (Figure 5A) biramous; coxa with well-developed gnathobase. Basis armed with two plumose setae and row of fine, long setules. Exopod 3-segmented; exp-1 with one simple seta and one plumose seta; exp-2 and exp-3 each with two plumose setae. Endopod 2-segmented; enp-1 with two unipinnate setae and one simple seta; enp-2 with six setae: three plumose, one unipinnate, and two simple setae.

Mx1 (Figure 5B) biramous; praecoxa with short spinules and well-developed arthrite bearing seven distal spines, one lateral bipinnate seta, two lateral simple setae, and two surface setae. Coxa with two spines and two setae on medial margin and five plumose setae on lateral margin; basis ornamented with short spinules on anterior surface and eight setae on medial margin. Endopod 2-segmented with three plumose and one naked setae on proximal segment and five plumose setae on distal segment; round exopod 1-segmented with seven plumose setae on distal margin and two rows of fine spinules on anterior surface.

Mx2 (Figure 6A) praecoxa with two endites, proximal endite with six plumose setae, distal endite with three spiniform setae; coxa with two endites, each with three elements ornamented with strong spinules; basis with seta laterally, two setae medially, and three setae on medial lobe. Endopod

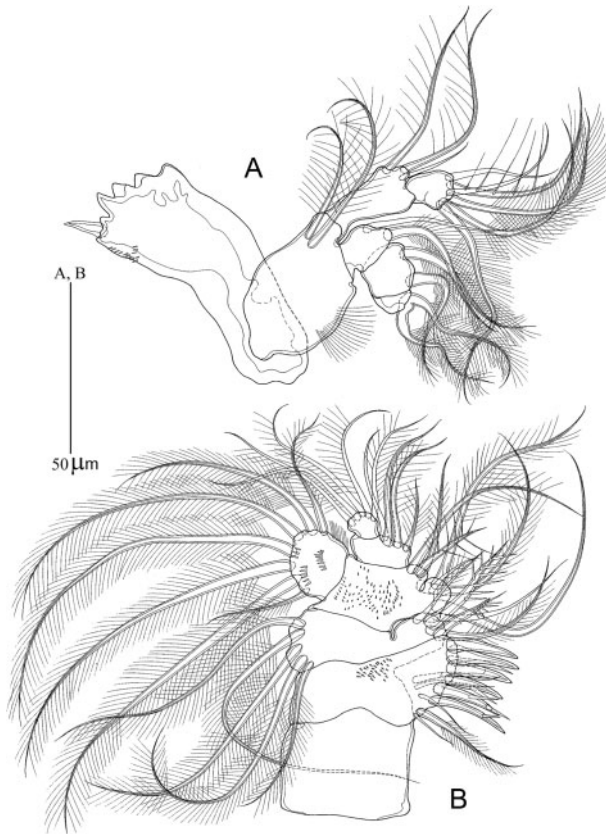


Figure 5. *Longipedia gonzalezi*, sp. nov. Holotype. Female: (A) mandible; (B) maxillule.

2-segmented; first segment with four setae, second segment with three setae.

Mxp (Figure 6B) phyllopodial. Syncoxa with eight plumose setae. Basis with two setae and 1-segmented endopod with 11 plumose setae.

P1 (Figure 7A) praecoxa with rectangular, smooth intercoxal sclerite. Anterior face of coxa with strong spinules and furnished with many transverse rows of small spinules. Basis with one medial pinnate spine and one lateral plumose seta. Exopod 3-segmented; exp-1 with one smooth lateral spine and one plumose medial seta; lateral spine of exp-2 very long and curved, ornamented with small spinules, and one medial slender seta; exp-3 with three lateral smooth spines, one spine apically, and two medial plumose setae. Endopod 3-segmented, slightly longer than exopod; enp-1 with one large plumose seta; enp-2 with strong spinules along lateral margin and with one plumose seta; enp-3 with two smooth spines at lateral margin, one bipinnate spine apically, and two plumose setae along medial margin.

P2 (Figure 7B) praecoxa with rectangular, smooth intercoxal sclerite. Coxa with one small medial seta and two rows of strong spinules close to lateral distal corner and distally. Basis with one spiniform lateral seta; with small spinules at base of endopod and

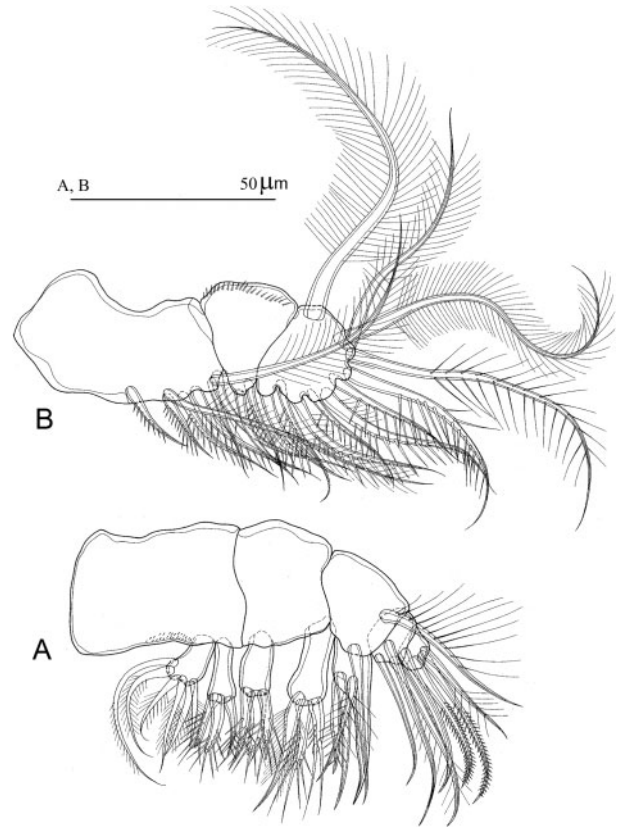


Figure 6. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) maxilla; (B) maxilliped.

sharp projection between endopod and exopod. Exopod 3-segmented; lateral distal corners of exp-1 and exp-2 produced, anterior surface furnished with numerous strong spinules; exp-1 with one lateral spine and one spiniform surface seta; exp-2 with one lateral spine and one medial spiniform seta; exp-3 with two lateral spines, one terminal spine and one terminal seta, and two medial spiniform setae. Endopod 3-segmented; enp-1 and enp-2 sub-equal; enp-3 four times longer than end-2; enp-1 with small projection on distal corner, with one plumose seta, anterior surface ornamented with oblique row of strong spinules; enp-2 furnished with one longitudinal row of spinules and a few spaced out minute spinules laterally; enp-3 with one lateral, two medial, and three apical spines ornamented with teeth unilaterally.

P3 (Figure 8A) praecoxa with rectangular, smooth intercoxal sclerite. Coxa with one pinnate medial spine. Basis with one lateral seta, with very small spinules at base of endopod. Exopod 3-segmented; lateral distal corner of exp-1 and exp-2 produced, and with oblique rows of strong spinules along lateral margin; exp-1 with one lateral spine and one anterior, slender surface seta; exp-2 with one lateral spine and one plumose seta; exp-3 with two lateral

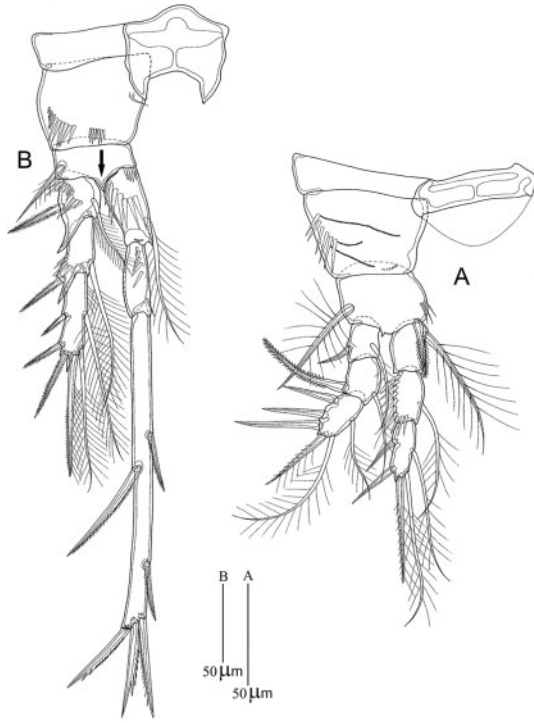


Figure 7. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) P1, anterior; (B) P2, anterior. Arrow indicates the sharp projection of the basis between the endopod and exopod, one of the major differences between *L. gonzalezi* and *L. americana*.

spines, two unequal distal spines, and two medial plumose setae. Endopod 3-segmented; lateral distal corner of enp-1 and enp-2 produced, and with longitudinal rows of strong spinules along lateral margin; enp-1 furnished with numerous minute spinules on anterior surface distally; enp-1 with one medial plumose seta; enp-2 with two medial plumose setae; enp-3 with one lateral spine, two spines and one plumose seta apically, and two plumose setae along medial margin.

P4 (Figure 8B) praecoxa with rectangular, smooth intercoxal sclerite. Coxa with one strong pinnate medial element. Basis with one lateral smooth seta, with minute spinules at base of endopod. Exopod 3-segmented; exp-1 and exp-2 with longitudinal rows of strong spinules on anterior surface; lateral distal corner of exp-2 produced; exp-1 with one lateral spine; exp-2 with one lateral and one medial spine; exp-3 with one lateral spine, three terminal unequal spines, and one medial plumose seta. Endopod 3-segmented; lateral distal corner of enp-1 and enp-2 produced, with almost transverse rows of strong spinules along lateral margin; enp-1 furnished with row of minute spinules on anterior surface; enp-1 with one medial seta in proximal third; enp-2 with one small seta and one plumose medial seta apically; enp-3 with three unequal spines apically and one lateral simple spine.

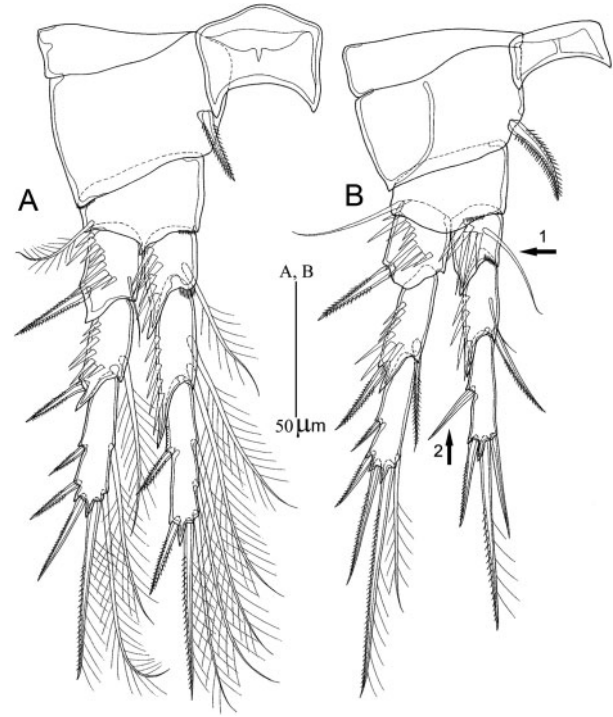


Figure 8. *Longipedia gonzalezi* sp. nov. Holotype. Female: (A) P3, anterior; (B) P4, anterior. Arrow 1 indicates the setiform element, which defines the *helgolandica* species-group and arrow 2 indicates the lateral spine, which differentiates *L. gonzalezi* sp. nov. from *L. helgolandica*.

P5 (Figure 2B) baseoendopod and 1-segmented exopod. Tubercle present. Exopod with six simple setae, medial-most seta more than three times as long as exopod, with numerous minute spinules on anterior surface. Endopod with long ornamented attenuation and one medial simple seta.

Paratype

Habitus (Figure 9A,B): body type same as female but smaller and less slender. Body length 0.70 mm measured from anterior lateral corner of cephalothorax to posterior margin of caudal rami.

Urosome (Figure 10A,B) similar to that of female in gross morphology except for obvious sexual dimorphism. In addition, ventrolateral corners of cephalothorax and pedigers 2–4 produced posteriorly with pointed tips in male but without pointed tips in female. Serration of frills along ventral margins of urosomites much finer in male, and ventral row of spinules present in male but absent in female.

A1 (Figure 11A) chirocer, 5-segmented, with four aesthetascs. Armature arrangement of setae and aesthetascs: 3-13-5+1 ae-10+1 ae-3+2 ae.

P2 (Figure 11B) praecoxa with rectangular and smooth intercoxal sclerite. Anterior face of coxa with one group of spinules and with one small medial seta.

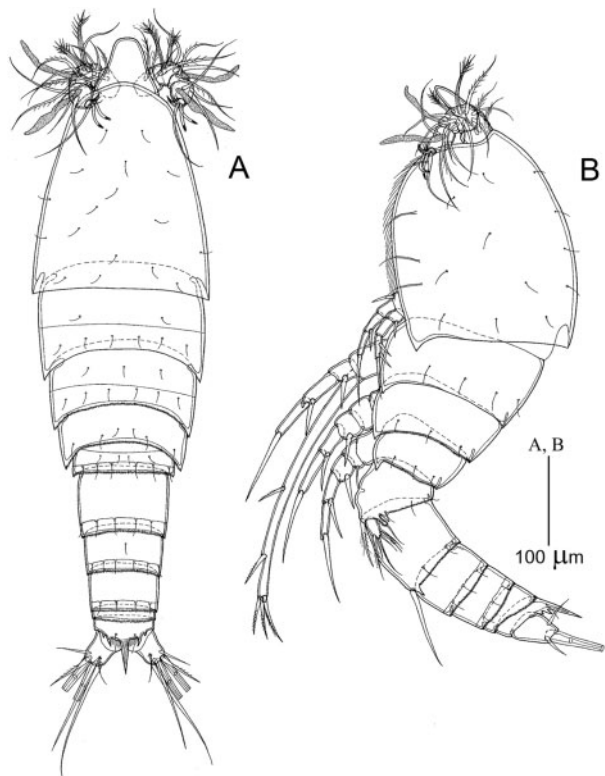


Figure 9. *Longipedia gonzalezi* sp. nov. Paratype. Male: (A) habitus, dorsal view; (B) habitus, lateral view.

Basis with one lateral plumose seta, anterior surface ornamented with one row of slender spinules. Exopod 3-segmented, exp-1 with large projection at distal corner, one plumose seta, exp-2 furnished with one row of spinules. Anterior surface of exp-3 smooth, with four spines and two setae. Endopod 3-segmented, enp-1 and end-2 subequal, enp-3 extremely elongate, with strong spines. Enp-1 with row of 11 slender spinules and two additional rows of fine, short spinules; enp-2 smooth, anterior surface of enp-3 smooth, with one lateral, two medial, and three terminal spiniform spines.

P5 (Figure 11C) with endopod confluent and tubercle present. Exopod 1-segmented, armed with four long and two short setae. Exopod approximately two times shorter than exopod of female. Baseoendopodal lobe lacks long attenuation of female, present by plumose seta about two times longer than exopod and reduced accessory seta fused to base.

P6 (Figure 10B) highly reduced to one medial spine and two lateral long setae.

Etymology

The new species '*gonzalezi*' is named in honor of Dr Juan Gerardo González Lagoa, Emeritus Professor of the Department of Marine Sciences, University of Puerto Rico at Mayagüez, who has relentlessly

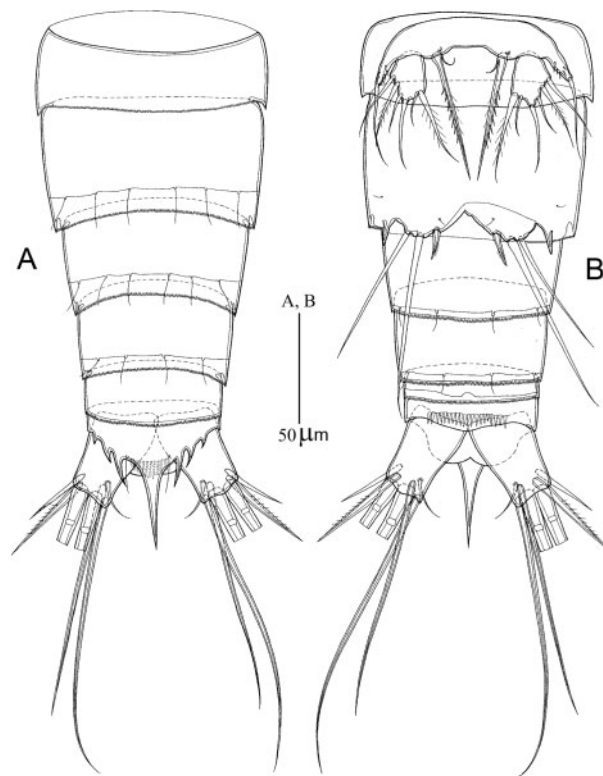


Figure 10. *Longipedia gonzalezi* sp. nov. Paratype. Male: (A) urosome, dorsal view; (B) urosome, ventral view.

educated the public and students about research in the field of marine sciences over the span of several decades.

Variation

No notable variation was observed among the additional female and male specimens.

Differential diagnosis

The presumed apomorphies of the new species *Longipedia gonzalezi* sp. nov. are the endopod of P2, which is extremely long, extending beyond the end of the caudal rami, and the conservative setation formula of the swimming legs (Table II). The male specimens carry four aesthetascs on each antennule.

Table II. Armature formulae of legs 1–4 of *Longipedia gonzalezi* sp. nov. Setae are denoted by numbers, and spines are denoted by Roman numerals. Segments are separated by a colon.

	Exopod	Endopod
P1	1: 1: 2, I, III	1: 1: 1, 1+I, II
P2	1: 1: 2, II, II	1: 0: II, III, I
P3	1: 1: 2, II, II	1: 2: 2, 1+II, I
P4	0: 1: 1, II, II	I: I: 0, III, I

Table III. Comparison of characters between *Longipedia helgolandica*, *L. americana*, *L. santacruzensis*, *L. corteziensis* and *L. gonzalezi* sp. nov. Table updated from Wells (1980) and Gómez (2001).

	<i>L. helgolandica</i>	<i>L. americana</i>	<i>L. gonzalezi</i> sp. nov.	<i>L. santacruzensis</i>	<i>L. corteziensis</i>
Abdominal ornamentation	Sparse but with some well-developed rows of spinules	Extremely sparse; spinulation very restricted	Extremely sparse; spinulation very restricted	Extremely sparse; spinulation very restricted	Extremely sparse; spinulation very restricted
P2 Coxa	Medial seta well-developed, spine-like. Proximal spinule row long, of short spinules	Medial seta reduced. Proximal spinule row short, of long spinules	Medial seta reduced. No proximal spinule row	Reduced, setiform inner element. Short proximal spinule row, with spinule row with long spinules	Very reduced, setiform inner element. Short proximal spinule row, spinule row with long spinules
P2 Basis	With lateral spine?; with sharp projection between End and Exp	With lateral seta? with blunt projection between Exp and End	With lateral spine?; with sharp projection between End and Exp	–	With lateral seta; with sharp projection between End and Exp
P2 exp-1	Unguiform projection normally developed	Unguiform projection massive	Unguiform projection massive	Unguiform projection massive	Unguiform projection massive
P2 end-3	Lateral spine absent	Lateral spine present	Lateral spine present	Male unknown	Lateral spine present
P3-P4 Coxa	Spinule rows of different form	Spinule rows of different form	No spinules	–	–
P4 end-2	Proximal inner seta moderately developed	Proximal inner seta small and weak	Proximal inner seta small and weak	Proximal inner seta small and weak	Proximal inner seta small and weak
P5 benp	Not articulated	Not articulated	Not articulated	Articulated; with 2-seg endopodal lobe	Articulated; with 2-seg endopodal lobe
P5 exp	Without ornamentation on posterior face. Without tubercle	With minute spicules on posterior face. With tubercle	With minute spicules on posterior face. With tubercle	Omitted	With minute spicules on posterior face. With tubercle
P5 exp	Without tubercle	With tubercle	With tubercle	Male unknown	With tubercle

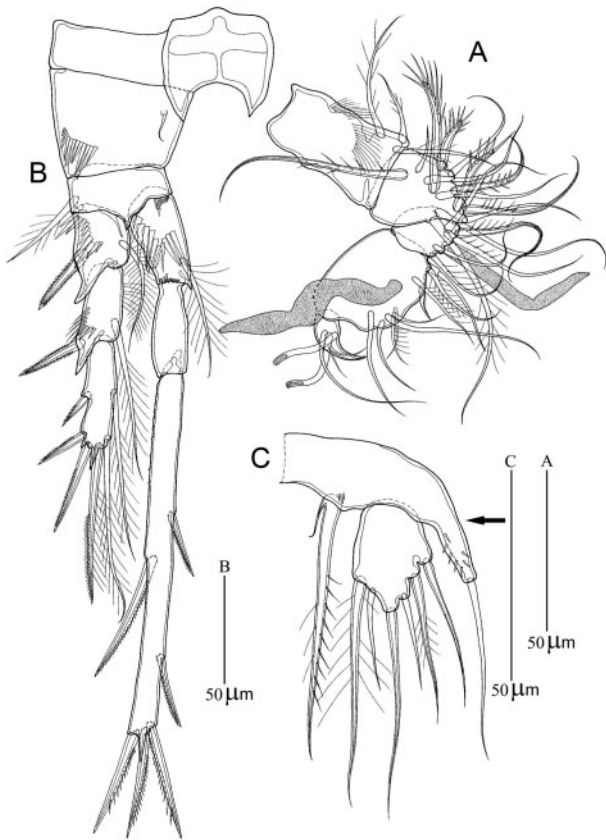


Figure 11. *Longipedia gonzalezi* sp. nov. Paratype. Male: (A) antennule; (B) P2, anterior; (C) P5, anterior. Arrow indicates the tubercle of P5 exp.

The autapomorphies of *L. gonzalezi* are the sparse, very restricted spinulation patterns on the abdomen and the seminal receptacle on the genital double somite of the females, which is different from its congeners. *Longipedia gonzalezi* belongs to the helgolandica species-group (Table III) as defined by Gómez (2001). Gómez grouped the species *L. helgolandica*, *L. americana*, *L. santacruzensis* and *L. corteziensis* in the helgolandica species-group based on the reduction of the medial spine of P4 enp-1 to a setiform element, denoted by arrow 1 in Figure 8; all other longipediids exhibit a spiniform element. *Longipedia gonzalezi* can be differentiated from *L. santacruzensis* and *L. corteziensis* by the non-articulated baseoendopod of P5 in females (Table III). *Longipedia gonzalezi* is more similar to *L. helgolandica* and especially to *L. americana*. *Longipedia gonzalezi* can be differentiated from *L. helgolandica* based on the presence of the lateral spine on P4 end-3 and the tubercle of P5 exp in males (both structures are indicated with arrows in Figures 8 and 11, respectively). *Longipedia gonzalezi* can be differentiated from *L. americana* based on the presence of a sharp projection of the basis between the endopod and the exopod of P2 (denoted

by an arrow in Figure 7A) and the absence of any spinules on the coxa of P3 and P4.

Phylogenetic analysis

The Tamura 3-parameter + Γ model of DNA substitution (Tamura 1992) was applied to the maximum likelihood in MEGA and the genetic distance analysis. The smallest genetic pairwise distance of *Longipedia gonzalezi* sp. nov. was observed against *Canuella perplexa* A. & T. Scott, 1893 (4.9% divergence, corrected distance), and against the three harpacticoid *Tigriopus* species (4.5–6.2%). The sequence divergence between *L. gonzalezi* and other harpacticoids did not exceed 10% except compared to the ancorabolid specimen (11.2%). Among all other copepod species, including the poecilostomatoid, siphonostomatoid, calanoid and cyclopoids, the sequence divergence ranged from 10.6% (cyclopoid *Cyclops insignis* Claus, 1857) to 17.4% (siphonostomatoid *Sphyrion lumpi* (Krøyer, 1845)). The next higher genetic distance was observed against the malacostracan mantis shrimp *Squilla empusa* Say, 1818 (43.1%). When only transversions are included in the genetic distance analysis, *L. gonzalezi* sp. nov. is more closely related to *Canuella perplexa* (1.3%), and the corrected distances against Harpacticoida and Siphonostomatoida ranged 1.9–8.1% and 3.8–6.8%, respectively. The phylogenetic analyses of the v-x region of 28S strongly support the monophyly of Copepoda (Figures 12, S1 [supplementary material]). The expected sister taxon-relationship of the two polyarthran taxa is evidenced by the small genetic distance and ML topology (Figure 12) but not by the BI tree (Figure S1, supplementary material). The ML and the BI trees are generally characterized by the lack of resolution among the ‘crown’ group of copepods, as evidenced by the branches with less than 50% bootstrap support in the ML tree (Figure 12) and polytomies in the Bayesian tree (Figure S1, supplementary material). The Polyarthra were not placed with other Harpacticoida; rather, they were placed together with the Poecilostomatoida and the Siphonostomatoida. However, support for this grouping is not significant in the ML tree. Similarly, the Polyarthra taxa have been placed basally in the clade leading to the Siphonostomatoida in the Bayesian tree with a high posterior probability (pP) value (0.96; Figure S1, supplementary material). The monophyly of Siphonostomatoida is well supported with both analyses, but no strong inferences can be made for Calanoida and Poecilostomatoida because they are not well represented and their placement is still unstable, especially for the Poecilostomatoida. Calanoida and Poecilostomatoida were sister taxa in the BI tree (pP = 0.87). Three species of Cyclopoida

formed a well-supported clade (91%), but the position of the cyclopoid copepod *Paracyclopina nana* Smirnov, 1935 is inconclusive in both analyses.

Another robust phylogenetic grouping in the phylogenetic analysis contained the malacostracan taxa with the exception of *Nebalia* sp. The shrimp *Penaeus vannamei* Boone, 1931 is characterized by a long branch in the BI tree and a position outside the malacostracans in the ML analysis. Each of the ostracod taxa Podocopa and Mydocopa were recovered as monophyletic in both analyses, but the monophyly of Ostracoda was supported only in the ML analysis.

Discussion

Suárez-Morales et al. (2006) published a list of known records of harpacticoid copepods in the Caribbean and included *Longipedia helgolandica* from Costa Rica and Barbados and *Longipedia* sp. from Bonaire, in addition to the records of *L. americana* listed in Wells (1980). The few references in the literature indicate that the genus *Longipedia* is probably underreported in the Caribbean and as more samples are collected more new records and new species are expected to be found. The genus *Longipedia* is distributed worldwide, particularly in shallow marine habitats with sandy and muddy sediments, on macroalgae, and in the marine plankton (Wells 1980; Boxshall & Halsey 2004). However, the new species described here was collected from substrata deeper than 46 m, which is unusual because very few *Longipedia* species have previously been recovered from greater depths (Wells 1980).

Previous workers (Sewell 1940; Itô 1980, 1981, 1985; Wells 1980; Fiers 1982; Chullasorn & Kangtia 2008) have raised concerns about the difficulty in correctly identifying representatives of *Longipedia* because of inadequate past descriptions and the morphological conservatism observed throughout the genus. Because the identification of *Longipedia* species is problematic, the best approach in identification is to examine in both genders: (1) the form of the abdominal ornamentation and of the hyaline frill, (2) the setation of the P2 endopod, and (3) the shape and setal lengths of the P5 exopod. Because of the high degree of morphological conservatism, *Longipedia* is possibly a perfect copepod genus to apply, and perhaps require, molecular sequences to corroborate species demarcations based on morphology. The appropriateness of the 28S region and/or other markers (e.g. COI, cytochrome b) remains to be tested. Previous workers (Chullasorn et al. 2011) have suggested that new descriptions of copepods should be accompanied by DNA sequences (i.e. barcoding) to test whether sequence divergence is

concordant with morphological divergence. Specifically for the COI gene of most metazoan species, which is the most widely used locus for molecular barcoding, we expect the within-species sequence divergence not to exceed 2%, especially in sympatry, whereas between-species divergence is usually larger (Hebert et al. 2003a, 2003b). There are glaring exceptions, such as in the harpacticoid copepod *Tigriopus californicus* (Baker, 1912), where population differences may exceed 20% (Burton & Lee 1994; Edmands 2001). In the case of rare specimens or revisions based on museum material, molecular tools may not be applicable.

Species of the monogeneric Longipediidae are unique in having extremely long second legs. The only genus (*Longipedia*) belonging to this family comprises 13 valid species (Boxshall & Halsey 2004). The new species exhibits distinctive features of the genus *Longipedia*: the P2 endopod is extremely elongated and the median apical spine of the P2 endopod third segment has a large tooth at mid-length (Wells 1980; Itô 1980).

Phylogenetic placement of Longipedia and Polyarthra within Copepoda

Our 28S analysis confirmed the close relationship of Canuellidae (*Canuella perplexa*) and Longipediidae (*Longipedia gonzalezi* sp. nov.), as they were only 4.9% divergent for this concatenated section of the 28S region. The two Polyarthra taxa did not group with the Harpacticoida, even though according to the corrected genetic distance estimates they were relatively closely related. Corrected genetic distances based on transversions only show an approximately equal distance between the Polyarthra versus the Harpacticoida and the Siphonostomatoida. The Bayesian and the Maximum Likelihood approaches (Figures 12, S1) suggested that Harpacticoida may be a paraphyletic taxon, implying that the taxon is defined by convergent morphological characters. Our Bayesian analysis supports the claim by Por (1984) and Dahms (2004) that the Polyarthra should be excluded from the Harpacticoida. The monophyly of Harpacticoida was proposed by Huys & Boxshall (1991) as the result of *a priori* reasoning where characters were defined as apomorphic and plesiomorphic at the level of order, therefore assuming that the copepod orders are monophyletic *a priori*. Perhaps an ideal approach would be to define a less-inclusive taxonomic level as working taxa. By doing this, the position of the families of Polyarthra could be different than currently proposed. Seifried (2003) also recovered a monophyletic Harpacticoida, with a narrow outgroup comparison, limited to Calanoida and Misophrioida. A molecular

approach with greater taxon sampling of more harpacticoid families would be more useful to further assess the phylogenetic status of Harpacticoida. The two Polyarthra are grouped robustly with the Siphonostomatoida in the Bayesian analysis of the present study, but their position is inconclusive in the ML analysis. This result is similar to that presented by Huys & Boxshall (1991), in which the Harpacticoida have a sister-group relationship with the Siphonostomatoida, Poecilostomatoida and Monstrilloida. The exact placement of several species is sensitive to the phylogenetic algorithm used (e.g. Poecilostomatoida, *Paracyclops nana*), suggesting the need for more genetic data and denser taxon sampling. The monophyly of Copepoda (see Chullasorn et al. 2012) is highly supported by high posterior probabilities in BI and high bootstrap values in maximum likelihood.

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Supplementary material (Figure S1)

The supplementary material for this article is available via the Supplemental tab of the article's online page at <http://dx.doi.org/10.1080/17451000.2015.1013556>

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