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Kuayguara etymatee sp. nov., a New Genus and Species of Artotrogidae (Copepoda: Siphonostomatoida) with an Uncommonly Atrophied Leg 1

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Artotrogidae Brady, 1880 is a cosmopolitan family with 23 valid genera and 131 known species. However, a considerable number of these species were subject of reexaminations and redescriptions recently. With the crescent number of new species discovered, it is becoming possible to better understand their boundaries. This study presents a new genus and species of Artotrogidae, recovered from unidentified hosts in debris of benthonic samples from Todos-os-Santos Bay, northeastern coast of Brazil. *Kuayguara etymatee* gen. et sp. nov. exhibits an underdeveloped first leg, which possess an unsegmented protopod and 1-segmented exopod, a unique set of morphological characteristics that differentiates it from all other genera of the family.

Key words: Invertebrate associate, Symbiotic copepods, Systematics, Uncommon leg, Taxonomy

BACKGROUND

Artotrogidae Brady, 1880 is a cosmopolitan family with species found associated with a wide variety of invertebrate hosts, ranging from sponges to urochordates. Even so, many species of the family were recovered from mixed benthonic samples (Boxshall and Halsey 2004; Ivanenko et al. 2018; Lee and Kim 2023). Nowadays the family includes 23 valid genera and 131 known species (Walter and Boxshall 2025).

A significant part of the family species was described between the second half of the nineteenth and the early decades of the twentieth century (Boeck 1859; Thorell 1859; Brady and Roberston 1876; Brady 1880 1899 1910; Thomson 1883; Scott 1888 1898 1905 1912; Giesbrecht 1895 1899; Sars 1918; Hansen 1923; Wilson 1923 1924), period known as the "golden age of the copepodology" (Damkaer 2002). However, since the 1960s, the genera and species described during this period have been the target of extensive reexaminations and redescriptions that, allied with new species recently discovered, have expanded the understanding about their boundaries (Eiselt 1961 1965; Stock 1965 1966; McKinnon 1988; Kim 1996; Johnsson and Rocha 2002; Johnsson and Neves 2005; Lee and Kim 2023). Nonetheless, a significant number of genera of the family is remaining monospecific (Walter and Boxshall 2025).

Despite the great number of known species, only five artotrogid species are recorded from the South Atlantic Ocean: *Bradypontius ancistronus* Neves and Johnsson, 2008; *Cryptopontius aesthetascus* Neves and Johnsson, 2008; *Cryptopontius expletus* Neves and Johnsson, 2008; *Cryptopontius pentadikos* Farias, Neves

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and Johnsson, 2020 e *Cryptopontius phyllogorgius* Farias, Neves and Johnsson, 2020 (Neves and Johnsson 2008; Farias et al. 2020). Aiming to cover this knowledge gap this study investigations bring to light the description of a unique new artotrogid genus and species with a unique underdeveloped leg 1.

MATERIALS AND METHODS

The copepods were found at seven different locations of Todos-os-Santos Bay (Fig. 1). Samples were collected on the submersed surface of pier decks incrusted with a diverse benthonic community, such as sponges, barnacles, mollusks, hydroids, bryozoans, ascidians, and corals. The material was fixed in 10% formalin for 48 hours and posteriorly preserved in 70% ethanol.

The copepods were sorted out under a stereo microscope Zeiss Stemi 508. Specimens were analyzed immersed in glycerin and mounted on temporary slides with adhesive plastic rings to avoid crushing (Kihara and Rocha 2009). Examination, photos, measurements, and drawings were made with the aid of a Zeiss Axio Lab.A1 microscope equipped with a digital camera AxioCam ERc 5S connected to an iPad (7th generation) with Zeiss Labscope Software (version 4.0.2). The holotype and allotype were dissected directly on a

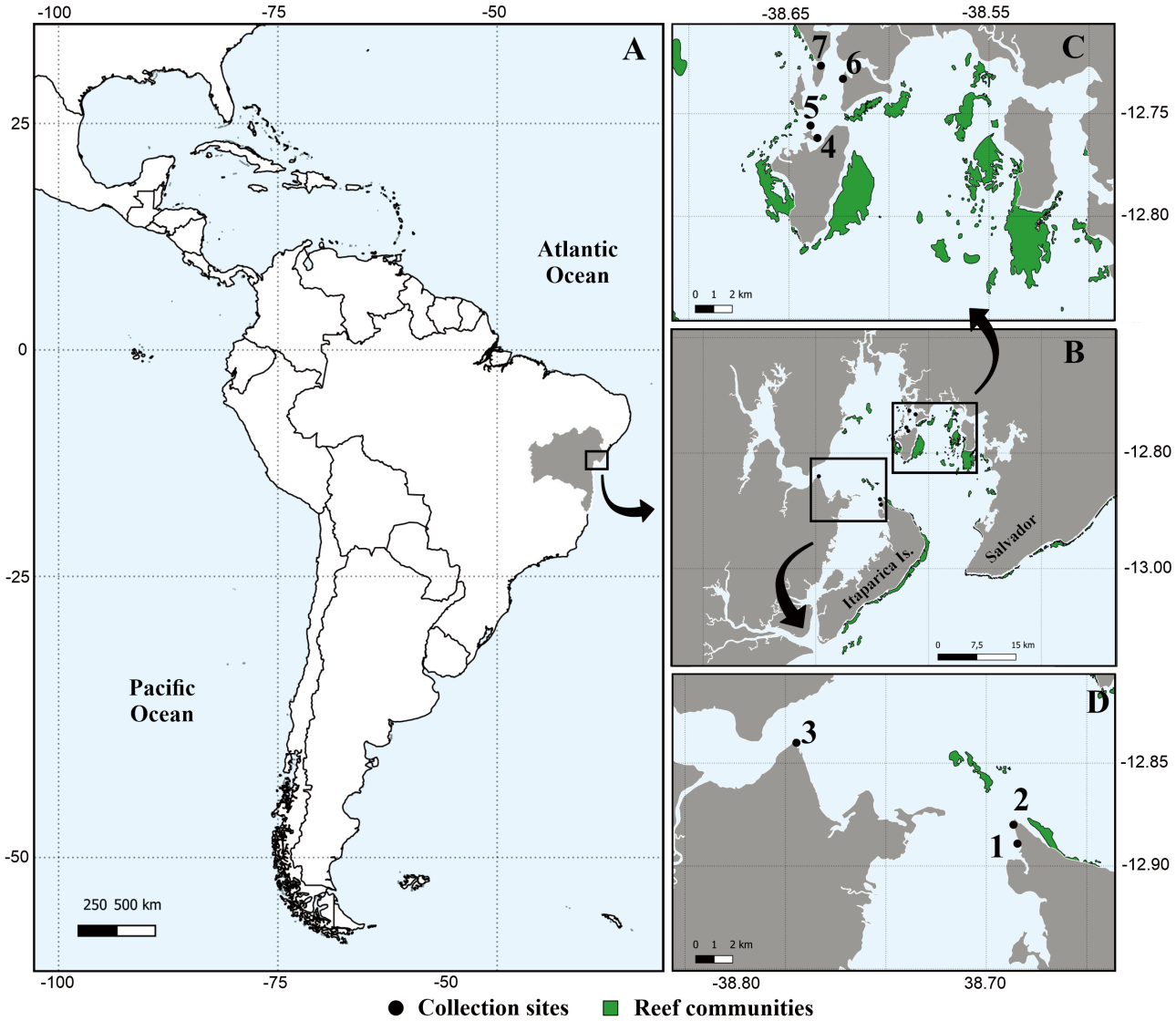

Fig. 1. Collection sites: A) Bahia state highlighted on the South America continent; B) Todos-os-Santos Bay; C) Sample area of: Private pier on Bom Jesus dos Passos Is. [4], Public pier on Bom Jesus dos Passos Is. [5], Private pier on Madre de Deus Is. [6], and, Private pier on Bimbarras Is. [7]; D) Sample area of: Marina de Itaparica pier [1], Estação de Medidas Magnéticas de Itaparica pier [2], and, Public pier on Barra do Paraguaçu beach [3].

permanent slide with CMC-9 mounting media for the appendages analysis (Kihara and Rocha 2009). The Illustrations were vectorized with CorelDRAW 2021 software (version 23.1.0.389).

For the leg armature formula, Roman numerals represent spines and Arabic numerals represent setae (Huys and Boxshall 1991). For antennule armature, Roman numerals represent ancestral segments (Huys and Boxshall 1991).

The type material analyzed was deposited in the Crustacea Zoological Collection of the Museu de História Natural da Bahia of the Universidade Federal da Bahia, Brazil.

For Confocal Laser Scanning Microscopy, a female paratype and a male paratype were stained with a 1:1 solution of Congo Red and Acid Fuchsin overnight, following the procedure described by Corgosinho et al. (2017). The specimens were examined using an Axio Observer.Z1 equipped with LSM900; images were obtained through an experiment of extended depth of focus on ZEN 3.0 (blue edition) and the final images were post-processed using the maximum projection method, detailed acquisition information on table 1.

RESULTS

TAXONOMY

Order Siphonostomatoida Burmeister, 1835
Family Artotrogidae Brady, 1880

Kuayguara gen. nov.

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Diagnosis: Artotrogidae. Body cyclopiform, dorso-ventrally flattened. Cephalic shield ornamented with scale-like structures showing integumental organs. Prominent dorsal crest and rostrum. Radial bands on the lateral margins of the cephalosome. Epimera of the cephalosome, second, and third pedigerous somites projected posteriorly. Medio-posterior margin of the second and third pedigerous somites with posteriorly elevated projections medially aligned. Urosome 5-segmented on female, genital double-somite with two pairs of produced posteriorly projected epimera. Male urosome 6-segmented, genital somite and first post-genital somite with a pair of projected epimera produced posteriorly. Both female and male with paired genital apertures, equal sized and ventrally located. Female antennule 8-segmented. Male antennule 9-segmented, with additional aesthetascs, showing an incomplete segmentation on the terminal segment; and significantly large spine on segment 7. Antennal exopod represented by seta, and 2-segmented endopod. Maxillule bilobed. Maxilliped 5-segmented. Leg 1 uncommonly reduced, with single-segmented ramus. Leg 1, 3, and 4 with coxa and basis fused. Leg 2 and 3 biramous and 3-segmented. Leg 4 lacking endopod.

Type species: *Kuayguara etymatee* sp. nov. by original designation.

Etymology: The genus name *Kuayguara* is a junction of the words "*Kûa*" (= bay) and "*-ygûara*" (= inhabitant), from old-Tupi language, referring to the Tupinambá people, the ethnic group that inhabited Todos-os-Santos Bay before the arrival of the Portuguese colonizers.

Remarks: When redefining Artotrogidae, Eiselt (1961) described, among other characteristics, the legs 1 to 4 as being: "*normal ausgebildet oder in verschiedenem Ausbaße reduziert, P4 bis zu seinem völligen Fehlen*", (normally developed or reduced to various degrees, leg 4 to its complete absence). In fact, the different levels of reduction patterns of leg 4 on Artotrogidae performed an important role in the differentiation of the genera, splitting the family in a few groups: (1) Leg 4 biramous with 3-segmented exopod and endopod (*Abyssopontius* Stock, 1985; *Antarctopontius* Eiselt, 1965; *Artogordion* Ivanenko, Bandera and Conradi, 2018; *Bradypontius* Giesbrecht, 1895; *Cribropontius* Giesbrecht, 1899; *Glannapontius*

Table 1. Confocal laser scanning microscopy (CLSM) detailed acquisition settings

Figure	Objective	Pinhole	Laser Wavelength	Detection Wavelength	Detector Gain
Fig. 5a	N-Achroplan 5x/0.15 M27	0.96 AU / 35 µm	561 nm; 2.00 %	555–607 nm	840 V
		0.84 AU / 35 µm	640 nm; 3.00 %	615–700 nm	877 V
Fig. 5b	N-Achroplan 5x/0.15 M27	0.95 AU / 35 µm	561 nm; 1.00 %	568–621 nm	840 V
		0.84 AU / 35 µm	640 nm; 5.00 %	594–700 nm	877 V
Fig. 6b	Plan-Apochromat 10x/0.45 M27	1.46 AU / 35 µm	561 nm; 0.30 %	555–593 nm	840 V
		1.26 AU / 35 µm	640 nm; 2.00%	605–700 nm	877 V
Fig. 6b	Plan-Apochromat 10x/0.45 M27	1.46 AU / 35 µm	561 nm; 0.20 %	555–593 nm	840 V
		1.26 AU / 35 µm	640 nm; 3.00%	605–700 nm	877 V

Holmes, 1998; *Myzopontius* Giesbrecht, 1895; *Neobradypontius* Eiselt, 1961, *Neopontius* Scott T., 1898; and; *Sestropontius* Giesbrecht, 1899). (2) Leg 4 biramous with 3-segmented exopod and 2-segmented endopod (*Arctopontius* Sars G.O., 1915 and *Metapontius* Hansen, 1923). (3) Leg 4 with 3-segmented exopod, without endopod (*Ascidipontius* Kim IH, 1996; *Chejupontius* Lee J and Kim IH, 2023; *Cryptopontius* Giesbrecht, 1899; *Dyspontius* Thorell, 1859; *Pteropontius* Giesbrecht, 1895; *Pulicitrogus* Kim I.H., 1998; and; *Sewellopontius* Ummerkutty, 1966). (4) Leg 4 reduced to a protopod (*Pseudotrogus* Eiselt, 1961). (5) Leg 4 absent (*Glyptotrogus* McKinnon, 1988; *Artotrogus* Boeck, 1859; and; *Tardotrogus* Eiselt, 1961).

Kuayguara gen. nov. shares the uniramous leg 4 with a 3-segmented exopod with the 7 genera included in the third group, but these taxa can be easily differentiated by the level of reduction patterns found on their leg 1: *Ascidipontius*, *Chejupontius*, *Cryptopontius*, *Dyspontius*, and *Pulicitrogus* exhibit a biramous 3-segmented leg 1, with the exopod formula: (I-0, 0-0; II, 3), (I-0; 0-1; II, I, 2 or II, I, 1), (I-1; I-1; III, 4 or III, 5), (I-1; I-1 or 0-1; II, 5 or II,4), (I-0; 0-1; II, 3), respectively, characterizing minor modifications in the pattern, showing only a few elemental reductions (Thorell 1859; Giesbrecht 1899; Sars 1918; Kim 1996 1998 2016; Johnsson 2001; Farias et al. 2021; Lee and Kim 2023). This is completely different from *Kuayguara* gen. nov. which shows only one-segmented ramus on leg 1.

Sewellopontius species can exhibit a moderate reduction pattern, with leg 1 exopod 2- or 3-segmented, with the formula (I-0 or 0-0; 0-1; II, 3) or (I-0; II, 3 or II, 4) (Ummerkutty 1966; Kim 1996; Lee and Kim 2023). Therefore, also differing from the one-segmented ramus of leg 1 in the new genus.

The species included in the genus *Pteropontius* exhibited the most reduced pattern known to the leg 1, with both exopod and endopod 2-segmented, with the formula (0-1 or I-0; II, 3 or II, 4). This pattern has been confirmed with the recent redescription of the type species by Lee and Kim (2023) and differentiates it from the new genus.

The species *P. pediculus* exhibits an exception to this pattern, it was described based on a single male specimen found in association with the coral *Echinopora lamellosa* (Esper, 1791) on Mauritius Is., Stock (1966) also classified the specimen as "somewhat aberrant", alluding to the uncommon morphology of its reduced first leg, which exhibit a single segmented ramus.

Considering the erection of the new genus, it is possible to observe other differences between *P. pediculus* from all other *Pteropontius* species, such as the 2-segmented antennal endopod (instead of 1-segmented); leg 1 and leg 3 with coxa and basis fused (instead of articulated). Thus, since these characteristics previously mentioned, plus the leg morphology, are diagnostic of the new genus, *P. pediculus* should be moved to *Kuayguara* gen. nov., with a new combination as *Kuayguara pediculus* (Stock, 1966) comb. nov.

***Kuayguara etymatee* gen. et sp. nov.**

(Figs. 2–5)

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Material examined: Holotype ♀ (UFBA4130), dissected on permanent slide; allotype ♂ (UFBA4133), dissected on permanent slide; from mixed benthonic samples, collected at public pier on Barra do Paraguaçu beach (Salinas da Margarida city – 12°50'25.0"S, 38°47'40.9"W). Paratypes: 1 ♂ (UFBA4131) and, 1 ♀ (UFBA4132) collected at public pier on Barra do Paraguaçu beach (Salinas da Margarida city – 12°50'25.0"S, 38°47'40.9"W). 1 ♀ (UFBA4092) and, 1 ♀ (UFBA4093) collected at Marina de Itaparica pier, Itaparica Is. (Itaparica city – 12°53'21.2"S, 38°41'04.2"W). 1 ♀ (UFBA4112) collected at a private pier on Bom Jesus dos Passos Is. (Salvador city – 12°45'42.4"S, 38°38'09.5"W). 1 ♂ (UFBA4098), 1 ♀ (UFBA4099), 1 ♂ (UFBA4100), 1 ♀ (UFBA4101), 1 ♀ (UFBA4102), 1 ♀ (UFBA4103), and 2 ♀ (UFBA4134), collected at Estação de Medidas Magnéticas de Itaparica pier, Itaparica Is. (Itaparica city – 12°52'47.9"S, 38°41'10.1"W). 1 ♂ (UFBA4137) and 1 ♂ (UFBA4138), collected at a private pier on Bimbarras Is. (Madre de Deus city – 12°43'36.1"S, 38°38'02.7"W). 3 ♀ (UFBA4316), 1 ♂ (UFBA4317), 2 ♀ and 1 ♂ (UFBA4139), 2 ♀ (UFBA4187), 1 ♀ (UFBA4353), 1 ♀ (UFBA4827), 4 ♀ (UFBA4826), and 1 ♂ (UFBA4827) collected at a private pier on Madre de Deus Is. (Madre de Deus city – 12°43'58.8"S, 38°37'22.8"W). 1 ♀ (UFBA4777), 1 ♀ (4778), and a juvenile (UFBA4779) collected at a public pier on Bom Jesus dos Passos Is. (Salvador city – 12°45'20.7"S, 38°38'21.5"W). All paratypes from mixed benthonic samples, preserved in ethanol.

Description of the female holotype: Body (Fig. 5a) cyclopiform, dorso-ventrally flattened, 888 µm long. Cephalic shield adorned with scale-like structures showing sensilla on each integumental organs (Fig. 5a, b), and radial bands along all margins (Fig. 2b); body length: width ratio 1.6:1. Cephalosome slightly wider than long (539 × 553 µm); with robust dorsal crest, ranging from posterior medial margin to prominent rostrum; also bearing radial bands along margins and ending in projected epimera. Second and third

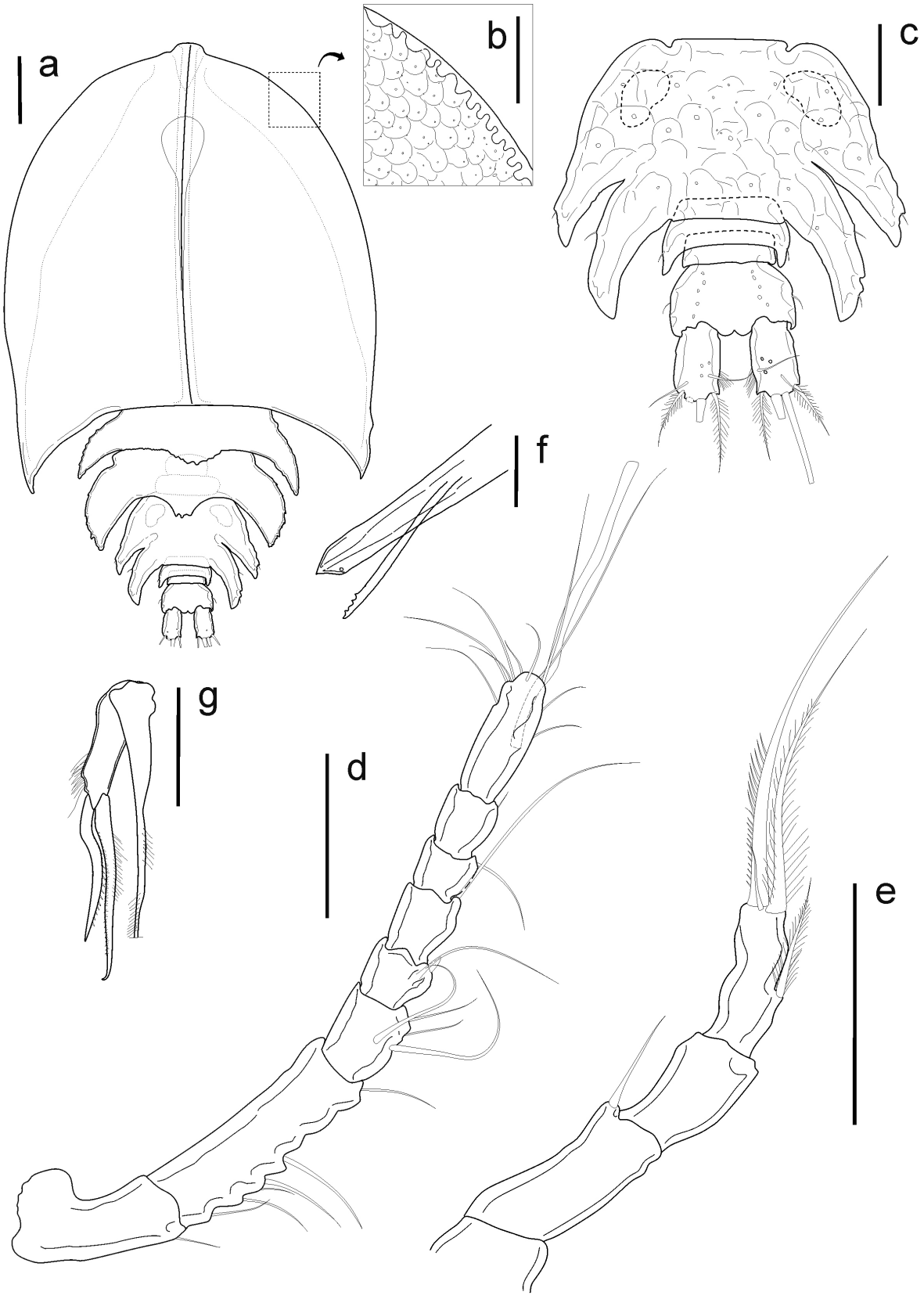

Fig. 2. *Kuayguara etymatee* sp. nov., Holotype female (UFBA4130): a, Body, dorsal view; b, radial bands and detailed ornamentation of the carapace; c, urosome; d, antennule; e, antenna; f, oral cone and stylet tip; g, maxillule. Scale bars: a–b = 100 µm; c–e = 50 µm; f = 20 µm; g = 50 µm.

pedigerous somites with serrulated margins, and showing medial posterior margins with dorsal elevated projections aligned with dorsal crest. Second pedigerous somite significantly wider than long (88 × 327 µm), with produced projected epimera. Third pedigerous somite wider than long (100 × 287 µm), with elevated structure on posterior medial margin projecting over fifth pedigerous somite. Fourth pedigerous somite twice as wide as long (31 × 62 µm), and strongly reduced. Prosome longer than wide (703 × 553 µm), prosome: urosome length ratio 1.2:1.

Urosome (Fig. 2c) 5-segmented, longer than wide (245 × 212 µm). Fifth pedigerous somite wider than fourth one (30 × 96 µm). Genital double-somite nearly twice as wide as long (110 × 214 µm) exhibiting two pairs of projected epimera. Paired genital apertures on the proximal region of the somite, equal sized, well-spaced and ventrally located. Egg sac not observed. First and second post-genital somites wider than long (28 × 78 µm, and 19 × 56 µm). First somite partially covered by genital one. Robust anal somite, wider than long (42 × 77 µm), showing row of five parallel perforations. Caudal rami longer than wide (49 × 28 µm), armed with two smooth and small dorsal setae, and distally armed with 4 setae. Caudal rami length: width ratio 1.7:1.

Antennule (Fig. 2d) 8-segmented, total length measuring 249 µm long. Length measurements made along medial margin = 51, 63, 25, 18, 20, 12, 19, and, 41 µm long, respectively. Segmental homologies and armature as follow: I – 1; II-VIII – 6; IX-XII – 4; XIII-XIV – 1+s; XV-XVI – 1; XVII-XVIII – 1; XIX-XX – 1; XXI-XXVIII – 10+ae. All setae naked, two distal long setae almost as long as aesthetasc, which is 93 µm long.

Antenna (Fig. 2e) 4-segmented, total length measuring 100 µm long (without distal setae), Coxa and basis unarmed, 10 and 35 µm long, respectively. Exopod reduced to seta, 22 µm long, almost as long as first endopodal segment. Endopod 2-segmented, first segment 25 µm long and unarmed, second segment 30 µm long, 1.2 times longer than first one, armed medially with plumose seta, and distally with 3 setae: a small slender seta, 2 stout ones, unequally sized, and elongated plumose seta.

Oral cone (Fig. 2a) 260 µm long, reaching basis of maxilliped. Mandible with long stylet inserted in oral cone, showing 4 teeth-like projections at the tip, palp absent (Fig. 2f).

Maxillule (Fig. 2g) bilobed, inner lobe longer than outer one, 109 µm long (broken, as long as the oral cone on paratypes), exhibiting a tapering shape and naked margins, with long plumose seta; outer lobe 55 µm long, with row of setules on outer margin, and two strong distal setae; longest seta has plumose inner margin and spinules along outer margin, shortest one shows spinules on inner margin and naked outer margin.

Maxilla (Fig. 3a) stout, syncoxa naked, measuring 202 µm long, with prominent bump on outer margin; (detached) strong basis (claw), 230 µm long, remarkably recurved, and armed with small stout seta on medio-distal margin. Maxilliped (Fig. 3b) 5-segmented, total length 291 µm long (not including distal claw); coxa 36 µm long, armed with single seta on inner margin, and row of setules on outer margin; basis unarmed, 136 µm long. Endopod 3-segmented, first segment unarmed, 28 µm long; second segment 38 µm long, armed with distal inner seta; third segment 53 µm long, armed with robust seta and terminal claw. Terminal curved claw measuring 82 µm long.

Leg 1 (Fig. 3c) showing no segmentation between coxa and basis, forming protopod, and exhibiting long seta on distal outer margin. Leg 1 (Fig. 3c) has a single-segmented ramus, armed with 3 distal unequal-sized setae.

Leg 1 to 4 armature formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	-	-	3	-
Leg 2	0–1	1–0	I-1, I-1, III, I, 5	0–1, 0–2, 1,2,3
Leg 3	0–0	1–0	I-1, I-1, III, I, 5	0–1, 0–2, 1, 1+I, 3
Leg 4	0–0	1–0	I-1, I-1, III, I, 4	absent

Outer margins of exopodal segments of legs 2 to 4 (Fig. 3d–f) armed with spinules. Endopodal segments of leg 2 (Fig. 3d) showing setules along outer margin. Third endopodal segment of leg 3 (Fig. 3e) exhibiting strong distal spine. Distal spine of the third exopodal segment of legs 3 and 4 (Fig. 3e–f) slightly bending on the proximal region.

Both protopod and exopod of leg 5 (Fig. 3g) extremely reduced, represented by 1 and 2 setae, respectively.

Description of the male allotype: Body (Fig. 4a) cyclopiform, longer than wide, smaller but comparatively slightly slender than female (530 × 292 µm), body length: width ratio 1.8:1. Body adorned as seen on female (Fig. 6a, b). Cephalosome longer than wide (319 × 292 µm), cephalosome length: width ratio: 1.1:1. Prosome longer than wide (402 × 292 µm), prosome: urosome length ratio 2.5:1. Urosome 6-segmented, longer than wide (158 × 110 µm). Genital somite (Fig. 4b) wider than long (63 × 148 µm), with only a pair of epimera posteriorly projected. Paired genital apertures, well-developed, equal-sized, and ventrally located. First post-genital somite almost as wide as genital somite (35 × 123 µm), also showing epimera posteriorly projected. Second post-genital somite almost entirely covered by first one,

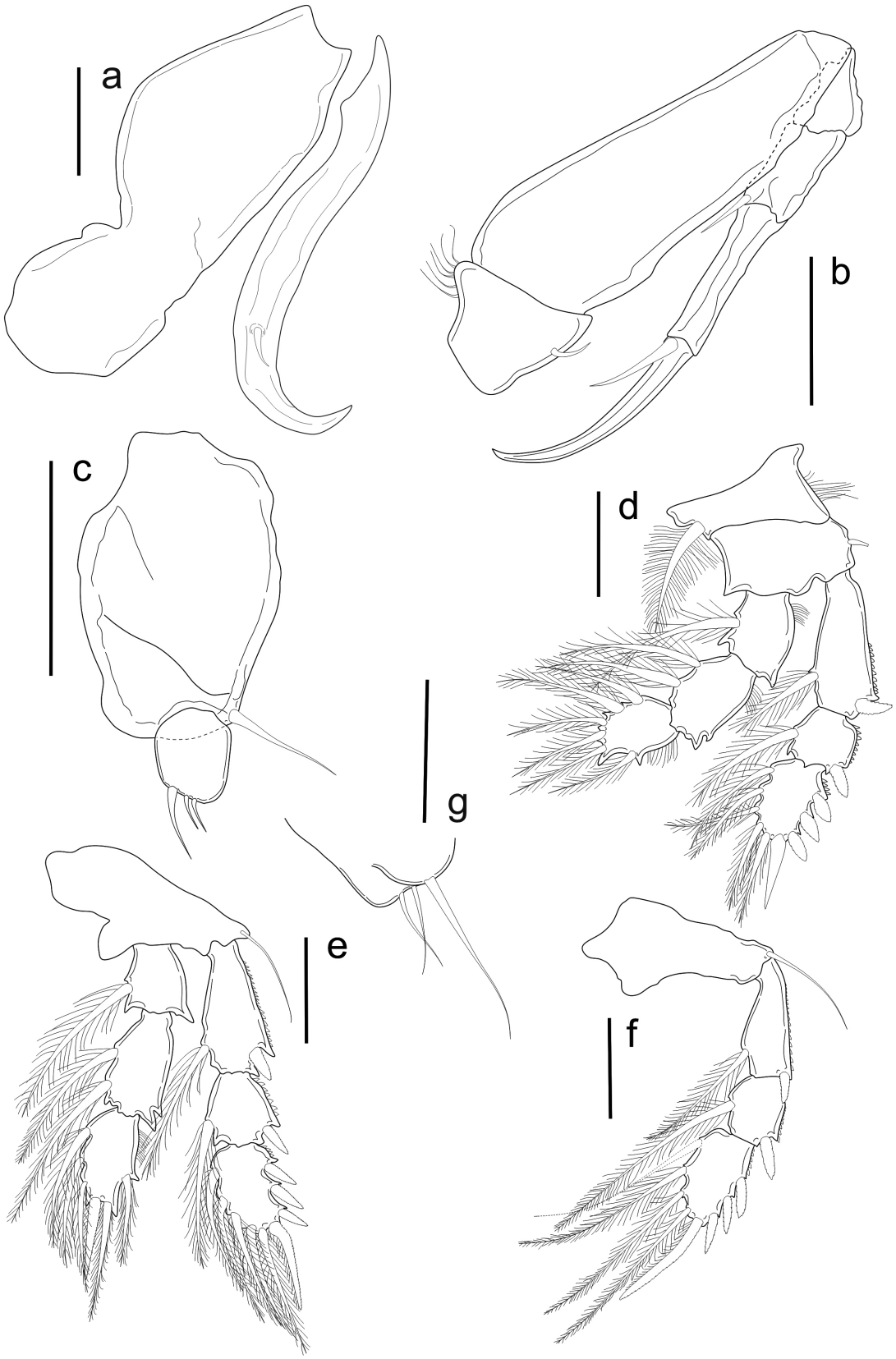

Fig. 3. *Kuayguara etymatee* sp. nov., Holotype female (UFBA4130): a, maxilla; b, maxilliped; c, leg 1; d, leg 2; e, leg 3; f, leg 4; g, leg 5. Scale bars: a–f = 50 μm; g = 20 μm.

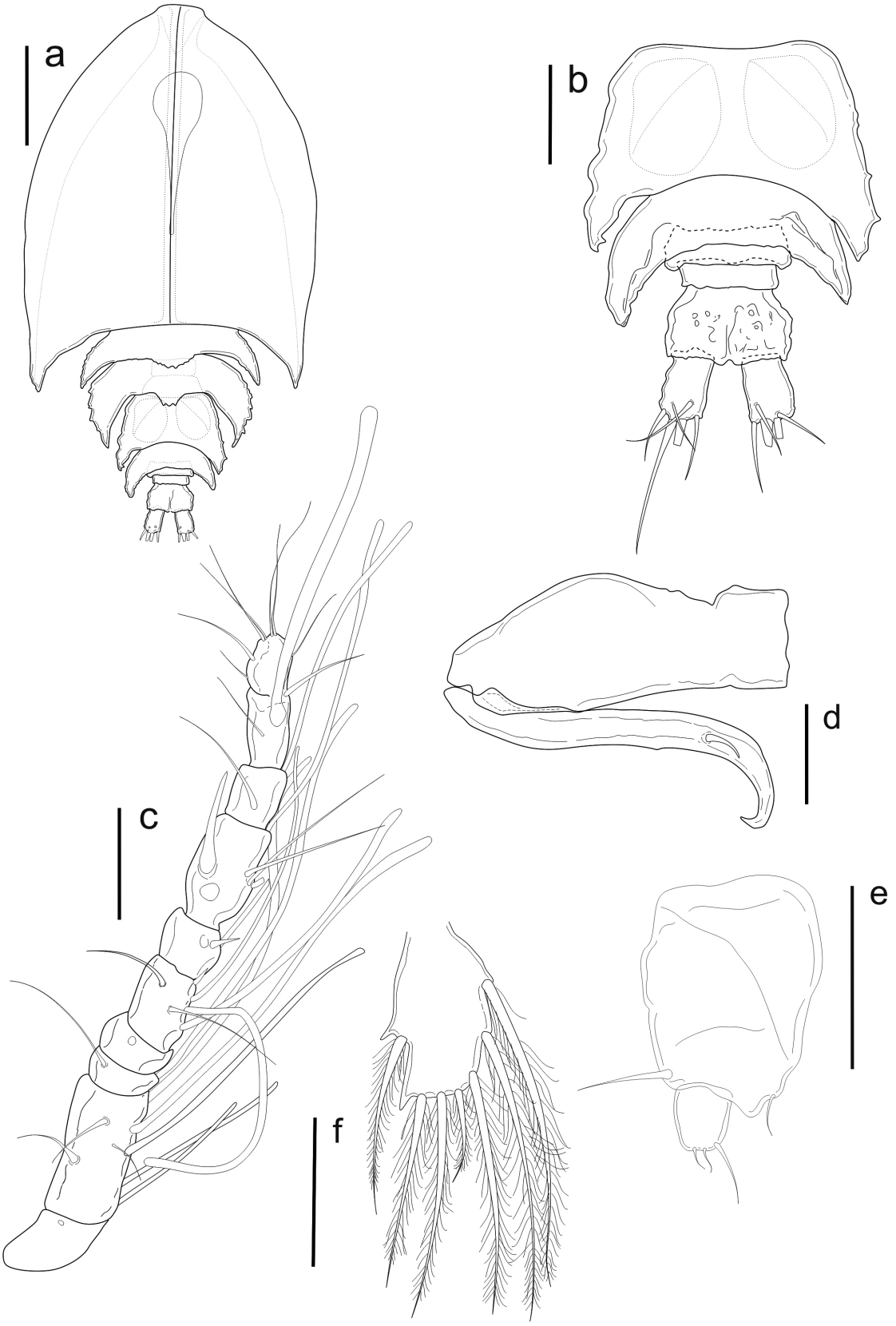

Fig. 4. *Kuayguara etymatee* sp. nov., Allotype male (UFBA4133): a, body, dorsal view; b, urosome; c, antennule; d, maxilla; e, leg 1; f, third exopodal segment of leg 3. Scale bars: a = 100 µm; b–e = 50 µm.

and followed by third somite, both wider than long (17 × 63 µm and 13 × 48 µm), respectively. Anal somite robust, almost twice wider than long (36 × 63 µm). Caudal rami longer than wide (31 × 22 µm), bearing two dorsal small naked setae and four terminal setae, caudal rami length: width ratio 1.4:1.

Antennule (Fig. 4c) 9-segmented, total length along medial margin measuring 312 µm long. Segments measurements: 31, 60, 12, 15, 35, 23, 49, 27, and, 60 µm long, respectively. Segmental homologies as follows: I – 0; II-VI – 3+5ae; VII – 1+ae; VIII – 0; IX-XII – 2+s+3ae; XIII-XIV – 1+ae; XV-XVIII – 3+s+ae; XIX-XX – 1+ae; XXI-XXVIII – 9+ae. All setae naked. Large spine on segment XV-XVIII measuring 46 µm long, almost reaching proximal margin of the last segment. Terminal aesthetasc measuring 147 µm long.

Maxilla (Fig. 4d) with unarmed syncoxa, 179 µm long, narrower than in female; and strong basis (grasping claw) 208 µm long, armed with small stout seta on medio-distal margin.

First leg (Fig. 4e) sharing female uncommon reduced morphology. Protopodal segment bulkier (65 µm long × 49 µm wide), exhibiting small seta on distal inner margin in addition to long seta on distal outer margin. And finally, third leg (Fig. 4f) showing small distal seta on third exopodal segment.

All other features as seen on female.

Etymology: The species name etymatee is a junction on the words "*etymã*" (= leg) plus "*teé*" (= very different), both from old-Tupi language, alluding to the uncommon morphology of leg 1 of the new species.

Remarks: The only congener of the new species, *Kuayguara pediculus* (Stock, 1966) comb. nov., was described based on a male, and some sexual dimorphic features can only be compared with the male of the new species (Table 2). The male body from both species is similar, *Kuayguara etymatee* gen. et sp. nov. differs from *K. pediculus* comb. nov. based on features such as the circular-shaped radial bands on the lateral margins of the cephalosome (instead of elongated); the medio-posterior projection of the third pedigerous somite not only covering the fifth but also covering the proximal part of the genital somite (instead of not reaching the genital somite); and finally, the second post-genital somite not exhibiting posteriorly projected epimera (instead of the projected epimera observed on *K. pediculus* comb. nov. (Stock 1966).

The antennule of the new species exhibits no aesthetasc on segment 4, three on segment 5, none on segment 7; and the terminal aesthetasc is only twice thicker than the others. While the male antennule of *K. pediculus* comb. nov. shows an aesthetasc on segment 4, two on segment 5, two on segment 7; and the terminal aesthetasc is 4 times thicker than the others (Stock 1966).

The antenna *Kuayguara etymatee* gen. *et* sp. nov. exhibits a naked exopodal seta, and unadorned endopodal margins. While the male antenna of *K. pediculus* comb. nov. shows features not seen in the new species, such as a plumose exopodal seta, a row of setules on the first endopodal segment, and the crest-like structures on the inner margin of the first and second endopodal segments (Stock 1966).

The maxillule of *K. pediculus* comb. nov. shows a row of setules on the proximal inner margin, and a minute lateral seta on the distal margin of the inner lobe (Stock 1966); both features not observed in the new species.

The maxilla basis (grasping claw) of *Kuayguara etymatee* gen. et sp. nov. exhibits only one stout seta; while *K. pediculus* comb. nov. shows 3 spine-like projections and a row of denticles (Stock 1966).

The maxilliped of the new species shows a naked seta on the first segment, a smooth second segment,

Table 2. Comparison between *Kuayguara* gen. nov. species

	Kuayguara etymatee gen. et sp. nov.	*Kuayguara pediculus* (Stock, 1966) comb. nov.
Radial bands shape	circular-shaped	elongated
Dorsal medio-posterior projection of the 3rd ped. somite	covers the proximal part of the genital somite	did not reach the genital somite
Antennule terminal aesthetask	2x thicker than others	4x thicker than others
Antenna exopod seta	naked	plumose
Antenna endopod margins	unadorned	adorned with setules and crest-like structures
Maxillule inner lobe inner margin	unadorned	adorned with setules and minute seta
Maxilla basis	stout seta	3 spine-like projections and denticles
Maxilliped armature formula	(0, 1, 1)	(2, 1, 1)
Leg 1 exopod	smooth margins	adorned with setules
Leg 3 third exopodal segment armature formula	(1, 1+I, 3)	(1, 2, 3)
Leg 5 seta	2 setae	3 setae

and endopodal armature formula (0, 1, 1); while *K. pediculus* comb. nov. shows a plumose basal inner seta on the first segment; two rows of long setules, and a medial serrated spine on the second segment; and endopodal armature formula (2, 1, 1) (Stock 1966).

Despite sharing the uncommon morphology of the legs, such as the reduction of the first, and the fusion of the coxa and basis on the third and fourth legs; *Kuayguara etymatee* gen. et sp. nov. exhibits a few more differences to point out from *K. pediculus* comb. nov.: on the first leg, the single-segmented ramus shows smooth margins (instead of row of setules on outer margins); the armature formula of the third endopodal segment of leg 3 is (1, 1+I, 3) (instead of (1, 2, 3)); and the fifth leg exopod is represented by 2 (instead of 3) terminal setae (Stock 1966).

Key to Artotrogidae genera (adapted from Boxshall and Halsey 2004)

1. L4 biramous 2
- L4 uniramous, represented by protopod, or absent 13
2. Epimeral plates of third pedigerous somite not produced beyond anterior margin of genital double-somite 3
- Epimeral plates of third pedigerous somite produced with posterolateral lobes extending posteriorly to anterior margin of double-somite 9
3. Female antennule 14-segmented; leg 4 endopod 2-segmented .... *Metapontius* Hansen, 1923
- Female antennule 9 to 14-segmented; leg 4 endopod 3-segmented 4
4. Leg 5 reduced to single seta; antennary exopod absent, unarmed ..... *Abyssopontius* Stock, 1985
- Leg 5 with at least 1 free segment (exopod) bearing 3 to 5 setae; antennary exopod with free segment bearing 2 setae or without free segment and represented by 2 setae 5
5. Antennary exopod 1-segmented 6
- Antennary exopodal segment not expressed, represented by 2 setae on basis ..... *Glannapontius* Holmes, 1998
6. Antennary exopod 1-segmented, armed with 3 setae; leg 5 armed with 2 tooth-like processes .... *Artogordion* Ivanenko, Bandera & Conradi, 2018
- Antennary exopod 1-segmented, armed with 2 setae; leg 5 without tooth-like processes 7
7. Leg 5 with free segment bearing 5 setae; antennary exopod with 2 setae ..... *Antarctopontius* Eiselt, 1965
- Leg 5 with free segment bearing 3 setae; antennary exopod with 2 setae 8
8. Oral cone with long distal siphon; maxillule outer lobe longer than inner lobe ..... *Myzopontius* Giesbrecht, 1895

Fig. 5. Confocal Laser Microscopy. *Kuayguara etymatee* sp. nov., Paratype female (UFBA4353) a, body, dorsal view; b, body, ventral view. Scale bars: a–b = 200 µm.

- Oral cone short, pear-shaped, without siphon; maxillule outer lobe shorter than inner lobe ..... *Neopontius* Scott T, 1898
9. Epimeral plates of third pedigerous somite reaching mid-region of genital double-somite 10
- Epimeral plates of third pedigerous somite extending beyond genital double-somite and reaching second free abdominal somite ..... *Neobradypontius* Eiselt, 1961
10. Endopod and exopod of leg 4 with similar length .... *Sestropontius* Giesbrecht, 1899
- Endopod of leg 4 shorter than exopod 11
11. Posterolateral angle of dorsal cephalic shield bifid .... *Cribropontius* Giesbrecht, 1899
- Posterolateral angle of dorsal cephalic shield simple 12
12. Leg 1 with 3 outer spines on exopodal segment 3; leg 4 with 3-segmented endopod ..... *Bradypontius* Giesbrecht, 1895
- Leg 1 with 2 outer spines on exopodal segment 3; leg 4 with 2-segmented endopod ..... *Arctopontius* Sars GO, 1915
13. Leg 4 absent 21
- Leg 4 present 14
14. Leg 4 reduced to protopod bearing 1 or 2 setae on process at outer distal angle ..... *Pseudotrogus* Eiselt, 1961
- Leg 4 uniramous, lacking endopod (or rarely biramous with endopod represented by a single seta on minute segment as seen in *Cryptopontius digitatus* Kim IH, 1996) 15
15. Leg 1 showing some level of segmentation reduction 16
- Both rami of leg 1 3-segmented 18
16. Leg 1 biramous 17
- Leg 1 uniramous, exopod 1-segmented ..... *Kuayguara* gen. nov.
17. Both rami of leg 1 2-segmented .... *Pteropontius* Giesbrecht, 1895
- Exopod of leg 1 2- or 3-segmented, endopod 3-segmented .... *Sewellopontius* Ummerkutty, 1966
18. Leg 1 with 3 outer spines and 4 or 5 setae (III,4/5) on third exopodal segment ..... *Cryptopontius* Giesbrecht, 1899
- Leg 1 with 2 outer spines on third exopodal segment 19
19. Leg 1 with 2 inner setae on second endopodal segment 20
- Leg 1 with 1 inner seta on second endopodal segment 21
20. Leg 1 with 2 spines and 4 setae (II,4) on third exopodal segment ..... *Dyspontius* Thorell, 1859
- Leg 1 with 2 spines and 3 setae (II, 3) on third exopodal segment ..... *Pulicitrogus* Kim IH, 1998
21. Second exopodal segment of leg 1 unarmed .... *Ascidipontius* Kim IH, 1996
- Second exopodal segment of leg 1 armed with inner seta .... *Chejupontius* Lee J & Kim IH, 2023
22. Exopod of antenna 1-segmented, bearing 3 setae .... *Glyptotrogus* McKinnon, 1988
- Exopod of antenna represented by single seta on small papilla 23
23. Leg 1 with 2 inner setae on second endopodal segment and typically with 3 outer spines on third exopodal segment .... *Artotrogus* Boeck, 1860
- Leg 1 with 1 inner seta on second endopodal segment and typically with 2 outer spines on third exopodal segment .... *Tardotrogus* Eiselt, 1961

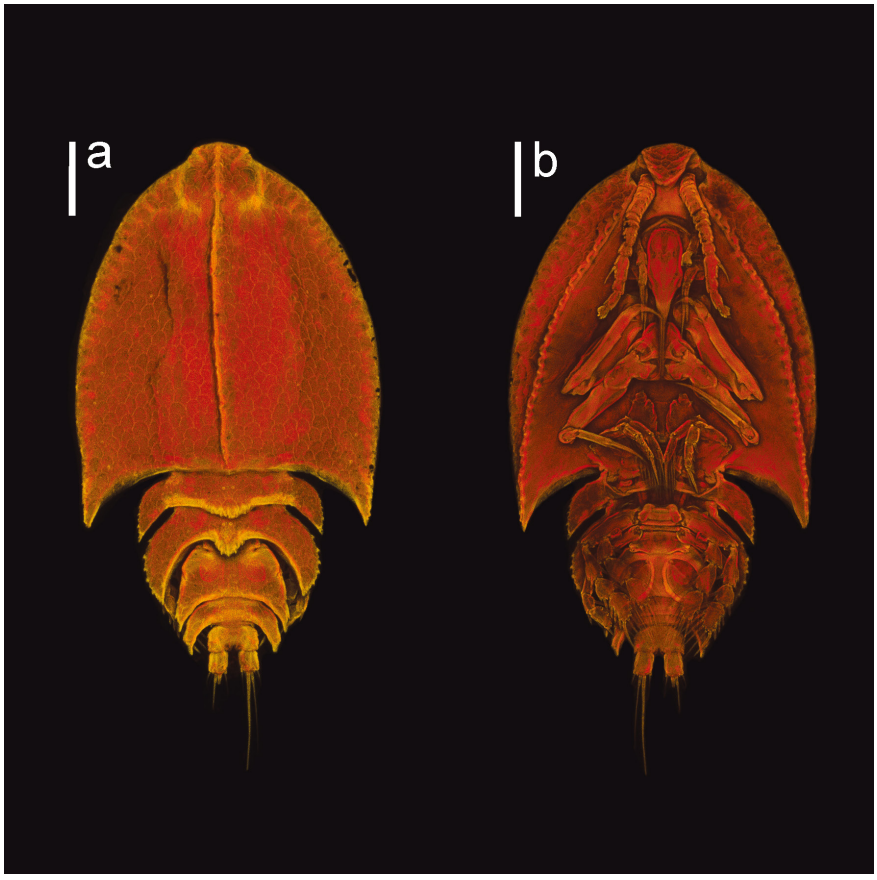

Fig. 6. Confocal Laser Microscopy. *Kuayguara etymatee* sp. nov., Paratype male (UFBA4827) a, body, dorsal view; b, body, ventral view. Scale bars: a–b = 100 µm.

DISCUSSION

The discovery of new taxa has allowed the unraveling of known and until then unnoticed taxonomical problems, as an example, the description of the *Neobradypontius* Eiselt, 1961 and *Metapontius* Hansen, 1923 that allowed Eiselt to propose that the Artotrogidae family should be merged with Dyspontiidae and Myzopontiidae (Eiselt, 1961). Most recently, in a study with artotrogid species from Korean waters, Lee and Kim (2023) described a new genus and 7 new species for the family; among them, two new species to the genus *Sewellopontius*, until then monospecific (Lee and Kim 2023). With the knowledge about the newly discovered *Sewellopontius* species it was possible to observe that *Pteropontius trimerus* Kim IH, 1996 exhibited features more related to the latter, which resulted in the combination novae for the species, as *Sewellopontius trimerus* (Kim IH, 1996) (Lee and Kim 2023). The same process occurred with the combination novae proposed in this study, with the erection of the new genus it was possible to observe that *K. pediculus* comb. nov. exhibits many differences from other *Pteropontius* species, and shares diagnostic features with the new taxon.

The variation in leg armature formula is a crucial systematic tool to understand the diversity of the associated copepods, from species to ordinal level. Moreover, fusions or losses of ramal segments can be observed in most copepod orders, being one, both rami, or the entire leg absent (Huys and Boxshall 1991). The uncommon morphology of the first leg exhibited by *Kuayguara* gen. nov. diverged from the most recent artotrogid diagnosis, which states that "*legs 1 to 4 biramous, typically with 3-segmented rami except endopod of leg 4 reduced or absent; leg 4 entirely absent in some genera. Leg 1 sometimes with reduced segmentation in one or both rami, as in Pteropontius*" (Boxshall and Halsey 2004, p. 710). Consequently, the diagnosis of the family should be extended to include the possibility of a single-segmented ramus. The first leg shall be diagnosed as "*typically biramous and 3-segmented, sometimes with reduced segmentation in one or both rami in some genera, exhibiting 2-segmented rami or a single-segmented ramus*".

Contrarily to the observed on the extended diagnosis of Entomolepididae in Farias et al. (2021), in which the inclusion of a newly discovered biramous and 3-segmented leg 4 possibly approaches the family with Asterocheridae, the changes reported on the Artotrogidae diagnosis brought new evidences to distance it from its sister family. The uncommon morphology of leg 1 on the new Artotrogidae genus indicates a transformation towards reduction of the limb, characterizing an apomorphy.

The study of the development of the legs of *Dioithona oculate* (Farran, 1913) made by Ferrari (1998) may help understand the odd morphology of leg 1 exhibited by *Kuayguara* gen. nov. species. On this investigation, five developmental stages were described, corresponding to copepodid I to V. In the first stage, the leg exhibited a bilobed bud with 3 and 2 setae, presumably indicating the initial formation of the exopod and endopod, respectively. In the second stage, the segment bearing the setae is transformed on a biramous limb. And posteriorly, during the next stages, new segments are added proximally on the distal segment forming the 3-segmented biramous leg (Ferrari 1998). The morphology of leg 1 of *Kuayguara* gen. nov. suggests that the development of the limb was suppressed in the first stage, not undergoing the transformation expected to appear on copepodid II.

Despite the comprehension of the development process involved on the leg 1 formation of the new genus, its functional implications may also be considered. On a study about copepods from hydrothermal ecosystems, Heptner and Ivanenko (2002) made a functional analysis on the morphology of locomotory limbs; characterizing swimming, crawling, and swimming-crawling types of copepods. Features used on the characterization of crawling copepods are the fused coxa and basis [1] (legs 1, 3, and 4) forming a wide protopod [2] (legs 3 and 4), the way leg branches are positioned folded up [3] to the flattened body [4]. These characteristics are observed on *Kuayguara* gen. nov. While the presence of intercoxal plates [1] (legs 1, 2, and 3), the articulated and similar-sized coxa and basis (leg 2) [2], and the swimming seta on all legs [3] are features described as found on the swimming type copepods. By exhibiting traits of both types, *Kuayguara* gen. nov. features suggest the intermediate characteristics of the swimming-crawling type of copepods.

Ultimately, among the siphonostomatoid species, there are some highly modified families in which one or many legs are absent; but only Nanaspididae Humes and Cressey, 1959 (holothurians parasites); Pseudocycnidae Wilson, 1922 (fish parasites); and Stellicomitidae Humes and Cressey, 1958 (starfish parasites) species are recorded to have a reduced biramous and 1-segmented leg 1 (Boxshall and Halsey 2004). Thus, leg 1 with a single-segmented ramus of *Kuayguara etymatee* gen. et sp. nov. is so far a unique feature on Siphonostomatoida.

CONCLUSIONS

A new artotrogid genus and species, *Kuayguara etymatee* sp. nov., is described from Todos-os-Santos Bay, Northeastern Brazil, from mixed benthonic samples. The new genus is the first artotrogid genus to be described for Southwestern Atlantic waters, and add up the number of Artotrogidae species registered on the Brazilian coast to 6. In this study, Confocal Laser Microscopy is used for the first time in the family, showing details of some morphological traits, as the first leg exhibiting a single-segmented ramus, an unprecedented leg morphology on the order Siphonostomatoida.

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