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# Two new deep-sea species of Argestidae and Ameiridae (Copepoda: Harpacticoida) from the Eastern Mexican Pacific and Gulf of California, with proposal of a new genus of the family Argestidae

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## ABSTRACT

A handful of benthic harpacticoid species are known from the Gulf of California. Here I describe *Argestes analongises* sp. n. (Argestidae), and *Argestigens celibis* sp. n. (Ameiridae) from the deep sea of the Tropical Eastern Pacific and Gulf of California. *Argestes analongises* sp. n. fits in the subfamily Argestinae (Argestidae) and was attributed to the genus *Argestes* by the presence of small spinules covering the body surface of, at least, the urosome, and by the presence of an extremely elongated distal seta on the sixth segment of the female antennule. This new species seems to be allied to *A. angolaensis* by the situation of all the caudal setae, and by the ventral position of caudal seta III. They differ in the relative length of the female caudal rami, size, shape and relative position of the sensilla-bearing tubercles associated to the anal somite, armature of the mandibular basis, shape of the exopodal and endopodal segments of swimming legs, and relative length of the setae on the female P5 endopodal lobe and position of the innermost seta of the exopod of the female fifth leg. *Argestigens celibis* sp. n. was attributed to the family Ameiridae based on the non-argestid maxilla, on the presence of a more or less well-developed endopodal lobe of the male fifth leg and three inner setae on the third endopodal segment of the third leg, and on the presence of the typically modified ameirid-like inner spine on the basis of the male first leg. The new species was attributed to *Argestigens* based on the non-prehensile endopod of first leg and presence of long inner spinules on the basis of second to fourth legs. Additionally, a new genus, *Georgus* gen. n., is proposed for *Bodinia peterrumi*, and some comments are given on the monophyly of that genus.

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## Introduction

Extensive oceanographic campaigns (Talud IV–XVI cruises) have been carried out from 2000 to 2014 in the Gulf of California, western coast of the Baja California Peninsula, and Eastern Tropical Pacific to study the diversity of deep-sea meiofauna, among other components of

the deep-sea benthic fauna of this region (see also Hendrickx 2012). Preliminary personal observations revealed a high diversity of benthic and hyperbenthic copepods, and three species of the family Ancorabolidae, *Ancorabolus hendrickxi* Gómez and Conroy-Dalton 2002, *Ceratonotus elongatus* Gómez and Díaz 2017 and *Dendropsyllus californiensis* Gómez and Díaz 2017, one species of the family Rhizothrichidae, *Rhizothrix longiseta* Gómez 2018a, and five species of the family Argestidae, *Mesocletodes brevisetosus* Gómez 2018c, *M. simplex* Gómez 2018c, *M. unisetosus* Gómez 2018c, *Eurycletodes paraehippiger* Gómez 2018b, and *Odiliacletodes secundus* Gómez 2018b, have been described so far from the deep sea of the Gulf of California and Eastern Tropical Pacific. Extensive areas in the deep sea of the Atlantic, Gulf of Mexico, Gulf of California and Pacific Ocean are still *terra incognitae* of deep-sea meiofauna. However, preliminary results indicate some predictable affinities between the deep-sea harpacticoid fauna from the Gulf of California and the San Diego Trough (Gómez and Díaz 2017), as well as some unexpected relationships between some deep-sea harpacticoids from the Gulf of California, and Norway and Sweden (Gómez and Conroy-Dalton 2002), Inhaca Island (Mozambique) (Gómez 2018a), and the Angola Basin (Gómez 2018c). Future investigations will shed some light on such affinities that could be the result of our poor knowledge about the diversity of deep-sea harpacticoids and other meiofaunal taxa from vast areas of the world ocean.

In this paper I propose a new species of the family Argestidae, *Argestes analongises* sp. n., and a new species of the family Ameiridae, *Argestigens celibis* sp. n., from the deep sea of the Eastern Tropical Pacific and from the deep sea of the Gulf of California. The first species is hypothesized to hold a close relationship with *A. angolaensis* George 2008 from the Angola Basin. The affinities of the second species remain uncertain. Additionally, I give some comments on the monophyly of the genus *Bodinia* George 2004, and I propose a new genus, *Georgus* gen. n., for *B. peterrumi* George 2004.

## Materials and methods

### Fieldwork

Sediment samples for meiofaunal analyses were taken in two oceanographic cruises on board the research vessel 'El Puma' of the Universidad Nacional Autónoma de México (UNAM). Talud IV cruise took place in the Southern Gulf of California from Carmen basin to off Nayarit State during August 2000. During this cruise sediment samples were collected at depths ranging from about 520 m to 2120 m using a multiple sediment corer equipped with six cores of 30 cm in length and sampling surface of 3.9 cm<sup>2</sup>. Talud X cruise took place in the Southern Trough of Guaymas Basin during February 2007, and sediment samples were collected at depths ranging from about 379 m to 1902 m using a box corer from which triplicate sub-samples were taken with 69 cm<sup>2</sup> cores of 20 cm in length.

### Sample processing and morphological examination

The upper 3 cm layer of sediment was preserved in 70% ethanol, sieved through 500 and 38 µm sieves to separate macro- and meiofauna, and stained with Rose Bengal.

Meiofauna was sorted at a magnification of 40× using an Olympus SZX12 stereomicroscope (Center Valley, Pasadena, USA) equipped with DF PLAPO 1× objective and WHS10× eyepieces, and harpacticoid copepods were stored separately in 1 ml vials with 70% ethanol. Illustrations and figures were made from whole individuals and their dissected parts using a Leica DMLB microscope (Wetzlar, Germany) equipped with L PLAN 10× eyepieces, N PLAN 100× oil immersion objective, and a drawing tube. The dissected parts were mounted on separate slides using lactophenol as mounting medium. Huys and Boxshall (1991) was followed for general terminology. Ferrari and Ivanenko (2008) was considered for the description of the maxilla.

### **Abbreviations used in the text**

acro, acrotheke (two setae fused basally to aesthetasc); ae, aesthetasc; art, articulated at its base; ENP, endopod; EXP, exopod; EXP (ENP)1 (2,3), first (second, third) exopodal (endopodal) segment; P1–P6, first to sixth legs; se, naked, setiform setae; sp, spinulose setae.

### **Depository of the type material and acronym of the collection**

The type material was deposited in the Copepoda collection of the Instituto de Ciencias del Mar y Limnología, Unidad Académica Mazatlán (ICML-EMUCOP).

## **Taxonomy**

Family **ARGESTIDAE** Por 1986a

Genus **Georgus** gen. nov.

### **Type species**

*Bodinia peterrumi* George 2004, by monotypy.

### **Diagnosis (based on the description of the type species by George (2004))**

Argestidae. Habitus semi-cylindrical. Posterior margin of cephalothorax and free prosomites plain. P3-bearing somite with pair of conspicuous pores. Posterior margin of P5-bearing somite, genital somite, and free urosomites coarsely serrated. Genital somite and third urosomite distinct in both sexes. Anal somite square from dorsal view, with strongly chitinized area ('apron') ventrally. Caudal seta VII arising dorsally from conspicuous knob; caudal seta III shifted ventrally on distal fourth of ramus. Antennule seven-segmented in the female, with 10 segments and haplocer in the male. Antenna with allobasis; exopod one-segmented, small, with one seta. Mandibular palp biramous; basis with one seta; endopod one-segmented with four setae; exopod incorporated to basis and represented by one seta. Exopod and endopod of the maxillule incorporated into basis, with five setae in all. Syncoxa of maxilliped with two setae. P1 with three-segmented exopod and two-segmented endopod; endopod non-prehensile, longer than exopod; armature formula of exopod/endopod 0,1,023/1,220; P2–P4 EXP and ENP three-segmented, exopod longer than endopod; P2–P4 EXP1 and ENP1 with inner seta; P2–P3 EXP2 and ENP2 with inner seta; P4 EXP2 with, ENP2 without inner seta; armature

formula of P2–P4 EXP3/ENP3, 223/121, 223/121, and 123/121, respectively (note that the legs in George's (2004, p. 254) figure 10a,b are not P2 and P3 as in the legend, but P3 and P4, respectively, and that in the text and in George's (2004) figure 10b the P4 ENP2 is described without inner seta, but his table (George 2004, p. 249) shows an inner seta on this segment). Female P5 endopodal lobe poorly developed, with three setae, exopod with five setae and a subapical, inner, long tube pore. Male P5 with endopodal lobe poorly developed bearing one seta; exopod with five setae, and one subapical, inner, long tube pore.

### ***Etymology***

The genus is dedicated to Dr Kai Horst George for his contribution to the knowledge of the Argestidae. The name is a noun in the nominative singular, gender masculine.

### ***Remarks***

See below.

## **Subfamily ARGESTINAE Por 1986a** **Genus *Argestes* Sars 1910**

### ***Type species***

*Argestes mollis* Sars 1910, by original designation.

### ***Other species***

*Argestes angolaensis* George 2008, *A. longiseta* Apostolov 2011, *A. reductus* Itô 1983, *A. tenuis* Sars 1921 *tenuis* Sars 1921, *A. tenuis* Sars 1921 *arcticus* Lang 1936, *A. analongises* sp. n.

## ***Argestes analongises* sp. n.** (Figures 1–6)

### ***Material examined***

Female holotype (ICML-EMUCOP-230800-01) dissected and mounted onto seven slides; Talud IV cruise; 23 August 2000; coll. S. Gómez.

### ***Type locality***

Off Nayarit State, NW Mexico, few miles north of Islas Mariás (22°01'2"N, 106°40'2"W), 1540 m depth.

### ***Diagnosis (based on the female only)***

Posterior margin of second urosomite to anal somite smooth, with spinules dorsally and ventrally. Genital somite and third urosomite distinct. Anal somite slightly longer than two preceding somites combined, tapering distally; anal operculum shifted medially. Caudal rami four times as long as wide, with six setae. Antennule seven-segmented. Antenna with allobasis, with one-segmented exopod bearing one seta. Mandibular palp biramous. Syncoxa of maxilla with two endites; proximal (praecoxal) endite with one, distal (coxal) endite with three elements. P2–P4 with three-segmented rami. Syncoxa of

maxilliped with two setae. P1 EXP1 without, P2–P4 EXP1 with inner seta; P1–P4 EXP2 with inner seta; P1–P4 EXP3 with five, seven, eight, and seven setae/spines, respectively; proximal inner seta of P4 EXP3 reduced, spiniform. P1–P4 ENP1–2 with inner seta; P1 ENP3 with three, P2–P4 ENP3 with five setae/spines. P5 endopodal lobe poorly developed, with two setae; P5 EXP elongated, with six setae.

### **Description of female**

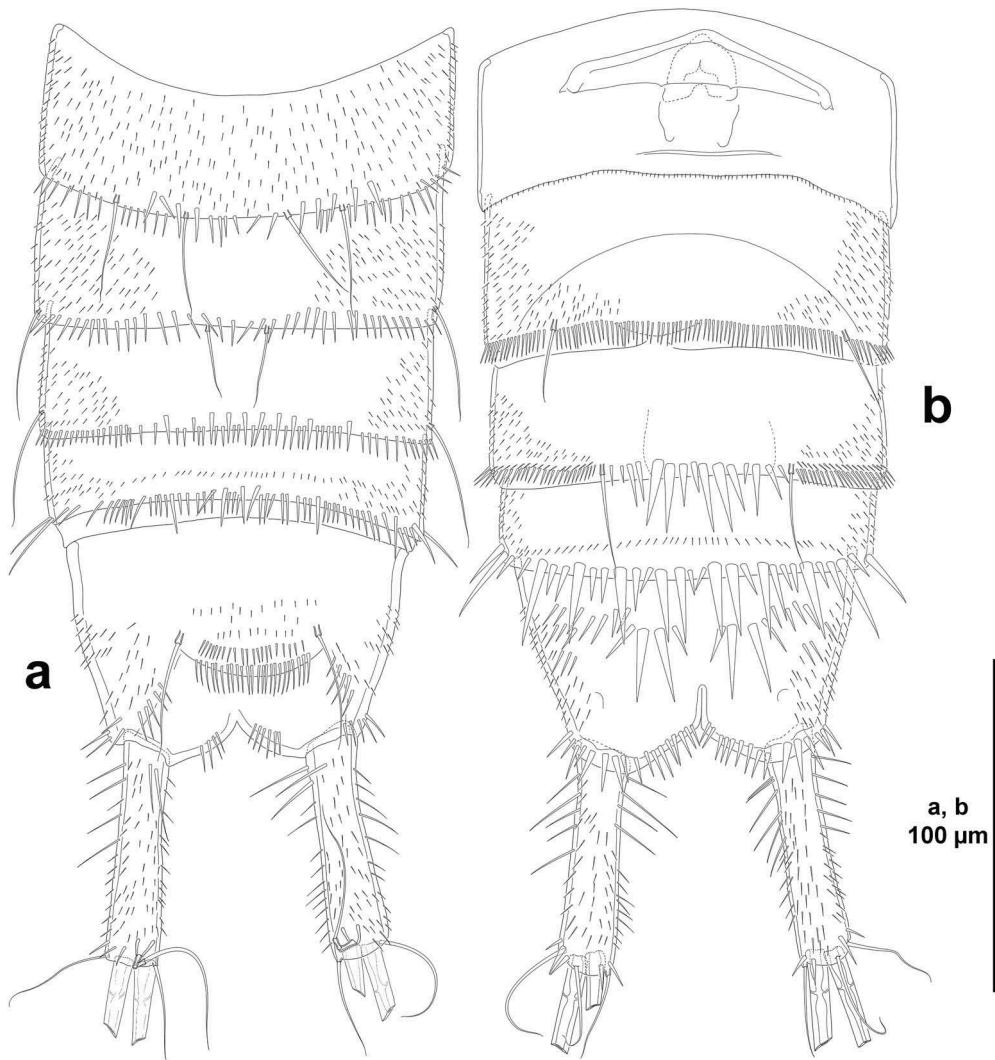
**Body.** Total body length undetermined due to bad condition of the only specimen; subcylindrical, tapering slightly posteriorly. Second to fifth urosomite with small surface spinules dorsally (Figure 1(a)) and ventrally (Figure 1(b)) as figured; posterior margin with continuous transverse row of strong spinules dorsally; sensilla along posterior margin of somites arising from small tubercles. Genital somite with transverse row of minute spinules along posterior margin ventrally; third urosomite with continuous row of visibly less strong spinules ventrally; fourth urosomite with lateroventral transverse row of visibly less strong spinules, with row of strong spinules midventrally; fifth urosomite with strong spinules ventrally as shown.

**Anal somite (Figure 1(a,b)).** Tapering posteriorly, slightly longer than two preceding somites combined, posterior margin medially cleft; dorsal (Figure 1(a)) and ventral (Figure 1(b)) surface covered with spinules as figured; anal operculum shifted rather medially, ornamented with two transverse rows of spinules, and flanked by one seta on each side.

**Caudal rami (Figure 1(a,b)).** Cylindrical, elongated, four times as long as wide (width measured at widest distal part), covered with spinules as shown, with six setae, all issuing distally, as follows: seta I lost; homologation of setae II and III difficult, probable seta II arising on outer distal corner, seta III shifted ventrally; setae IV and V longest; seta VI issuing at inner distal corner; dorsal seta VII subdistally, tri-articulated, arising from small tubercle.

**Antennule (Figure 2(a)).** Seven-segmented; all segments covered with minute denticles; first, and third-fifth segments with medium to small sized spinules, second segment with medium sized spinules proximally and subdistally, and with set of stronger and longer medial spinules; sixth and seventh segments without spinular ornamentation; sixth segment with very long single naked seta distally. Armature formula as follows: 1-[1se], 2-[4sp+ 5se], 3-[2sp+ 5se], 4-[1sp+ 1se+(1se+ ae)], 5-[1sp+ 1se], 6[1sp+ 2se], 7-[1sp+ 2se+ 6 art+ acro].

**Antenna (Figure 2(b)).** Allobasis elongated, as long as free endopodal segment, with suture indicating original division between basis and first endopodal segment, without abexopodal seta, with inner longitudinal row of spinules. Exopod one-segmented, with one seta. Endopod with inner longitudinal row of strong spinules, with smaller spinules on surface and with stronger ones subdistally, with few outer spinules; with two inner lateral spines medially, and with six elements apically (three single geniculated setae, one geniculate seta fused basally to small naked element, and one slender seta).

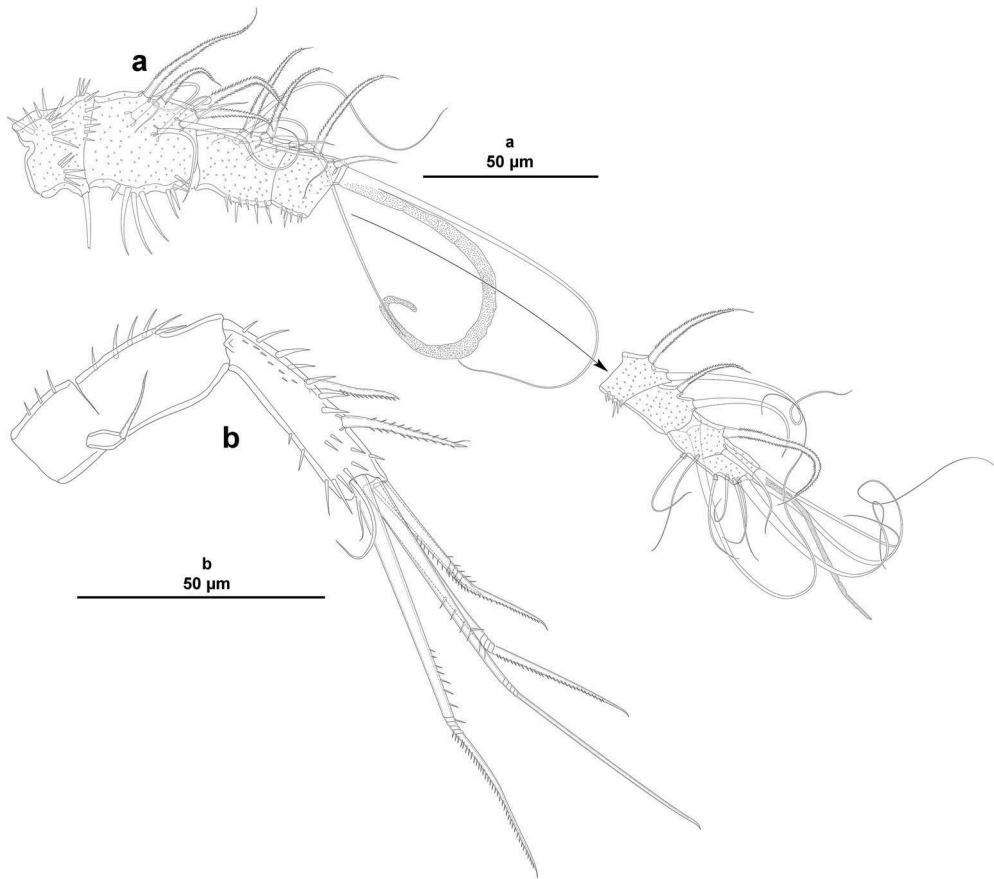


**Figure 1.** *Argestes analogises* sp. n., female holotype. (a) urosome, dorsal, P5-bearing somite omitted; (b) urosome, ventral, P5-bearing somite omitted.

**Mandible (Figure 3(a)).** Gnathobase with acute tooth-like projections. Palp biramous, covered with spinules; basis with one pinnate seta, and one strong flame-shaped spine; endopod with one inner, three subapical and two apical pinnate setae; exopod visibly smaller, with three bipinnate setae.

**Maxillule (Figure 3(b)).** Praecoxal arthrite with row of spinules proximally, with two surface setae, one lateral pinnate spine, and seven distal spines of which two single and bare, two with articulated tip and bare, and three pinnate elements of which two with long spinules and one with small spinules. Coxa with one subdistal seta, and apically with one slender seta and one very strong, pinnate element. Basis with some median





**Figure 2.** *Argestes analongises* sp. n., female holotype. (a) antennule; (b) antenna.

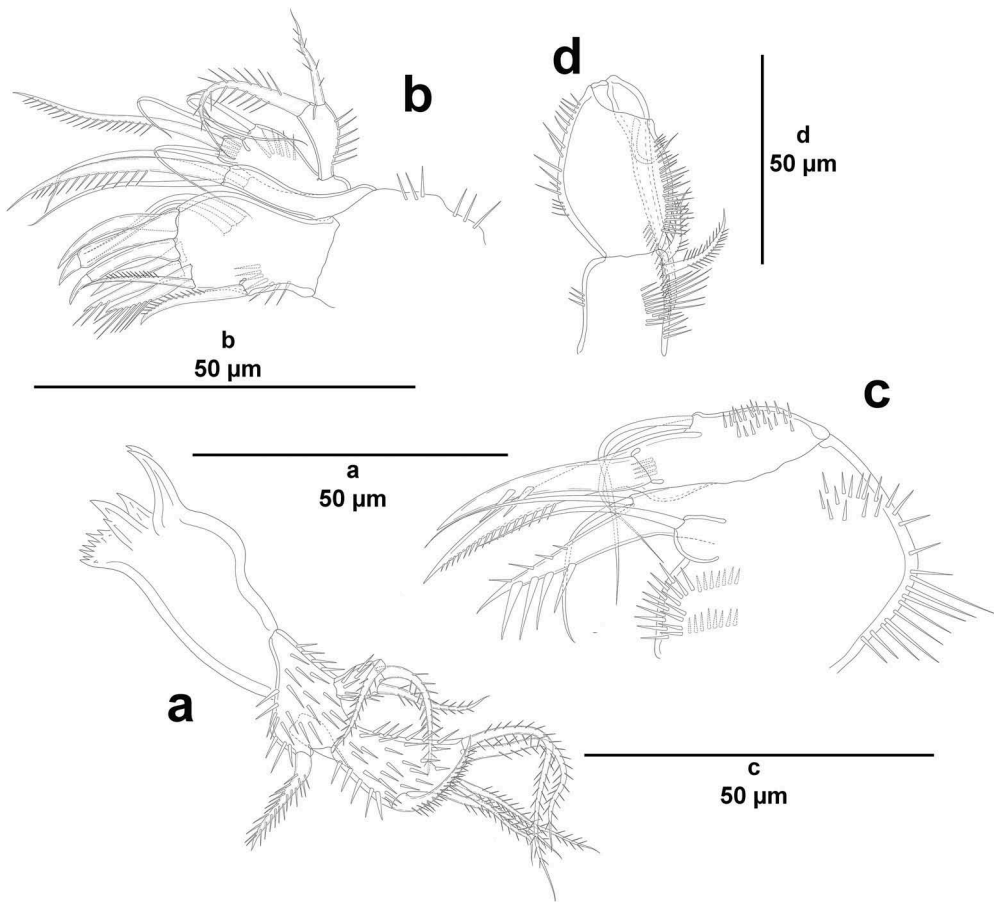
and some subdistal spinules, with two apical setae. Endopod fused to basis, represented by two setae. Exopod one-segmented, elongated, with two bipinnate setae.

**Maxilla (Figure 3(c)).** Syncoxa with spinules as shown; with two endites; proximal (praecoxal) endite small, with one slender seta; distal (coxal) endite with one strong spinulose element fused to endite, and two bare setae. Allobasis with spinules proximally and at base of strong spinulose claw, the latter fused to allobasis, and with one strong spine. Endopod represented by two setae.

**Maxilliped (Figure 3(d)).** Subchelate, strong. Syncoxa with inner long and outer small spinules as shown, with two bipinnate setae subequal in length. Basis unarmed, with inner and outer longitudinal rows of spinules. Endopod one-segmented, fused to strong spinulose claw, with one accompanying bare seta.

**P1 (Figure 4(a)).** Coxa with small spinules close to inner corner proximally, and medially close to basis, the latter with inner and outer spiniform elements, with some spinules in the middle, at the base of endopod, and at the base of outer element. Endopod three-

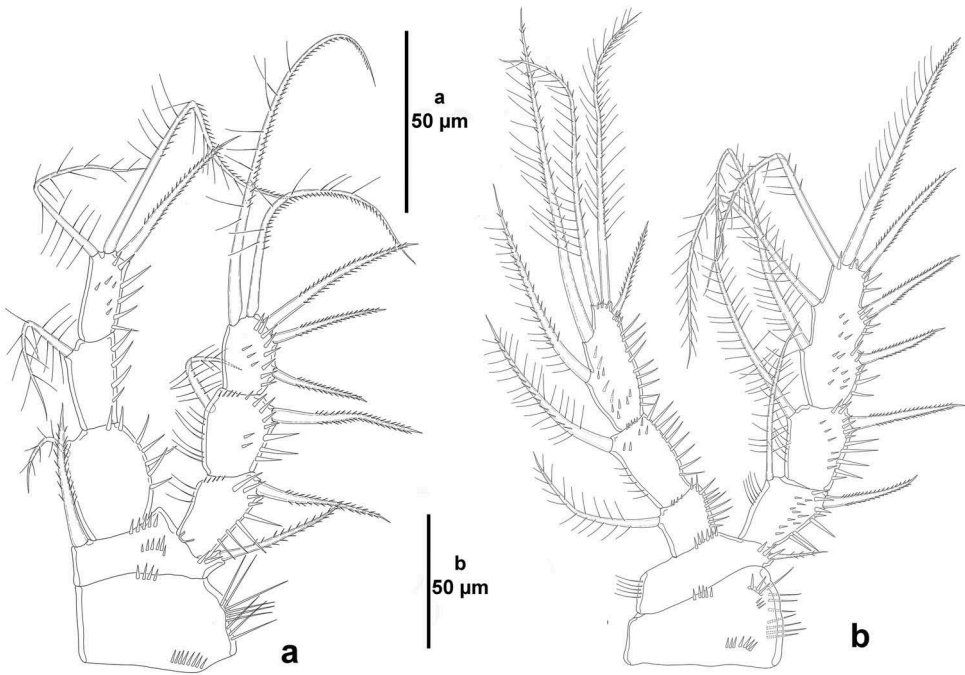




**Figure 3.** *Argestes alongis* sp. n., female holotype. (a) mandible; (b) maxillule; (c) maxilla; (d) maxilliped.

segmented, visibly longer than exopod; ENP1 and ENP2 with inner seta; ENP3 with three elements, outermost a spine. Exopod three-segmented; EXP1 without, EXP2 with inner seta; EXP3 with five elements.

**P2–P4 (Figures 4(b), 5(a–c)).** Coxa and basis covered with detritus, making spinular ornamentation difficult to see. Coxa with anterior set of strong spinules close to distal outer corner, and with additional small spinules close to proximal outer corner, posteriorly with longitudinal row of long, slender outer spinules. Basis of P2 and P3 with long slender inner spinules, with small spinules at base of endopod and at base of outer seta, of P4 with comparatively shorter inner spinules, and with spinules at base of endopod and at base of outer seta; outer basal seta of P2 spiniform, of P3 and P4 slender and long. Endopod three-segmented, reaching middle of EXP3; ENP1 and ENP2 with inner seta; ENP3 with two inner and two apical setae, and one outer spine. Exopod three-segmented; EXP1 and EXP2 with inner seta; P2 EXP3 with three outer, two apical and two inner elements, P3 EXP3 with three outer, two apical and three inner elements; of P4 with three outer, two apical and two inner elements, of which proximal reduced, spine-like.



**Figure 4.** *Argestes alongises* sp. n., female holotype. (a) P1, anterior; (b) P2, anterior.

**P5 (Figure 6).** With some spinules on baseoendopodal setophore. Endopodal lobe poorly developed, with two setae subequal in length, with some slender, long spinules between both baseoendopods. Exopod distinct, elongated, slender, four times as long as wide (maximum width measured at its base), with spinules as figured, with six setae.

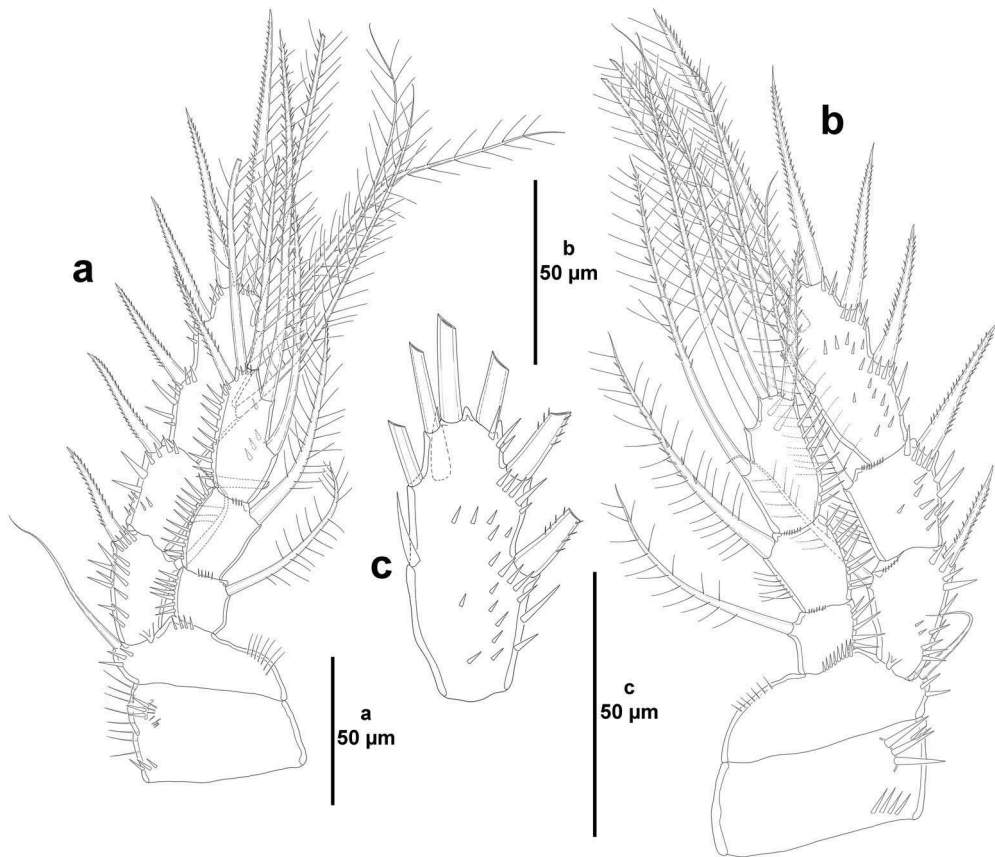
**Armature formula.**

	EXP	ENP
P1	0.1.023	1.1.111
P2	1.1.223	1.1.221
P3	1.1.323	1.1.221
P4	1.1.223	1.1.221
P5	330	2

**Male.** Unknown.

**Etymology**

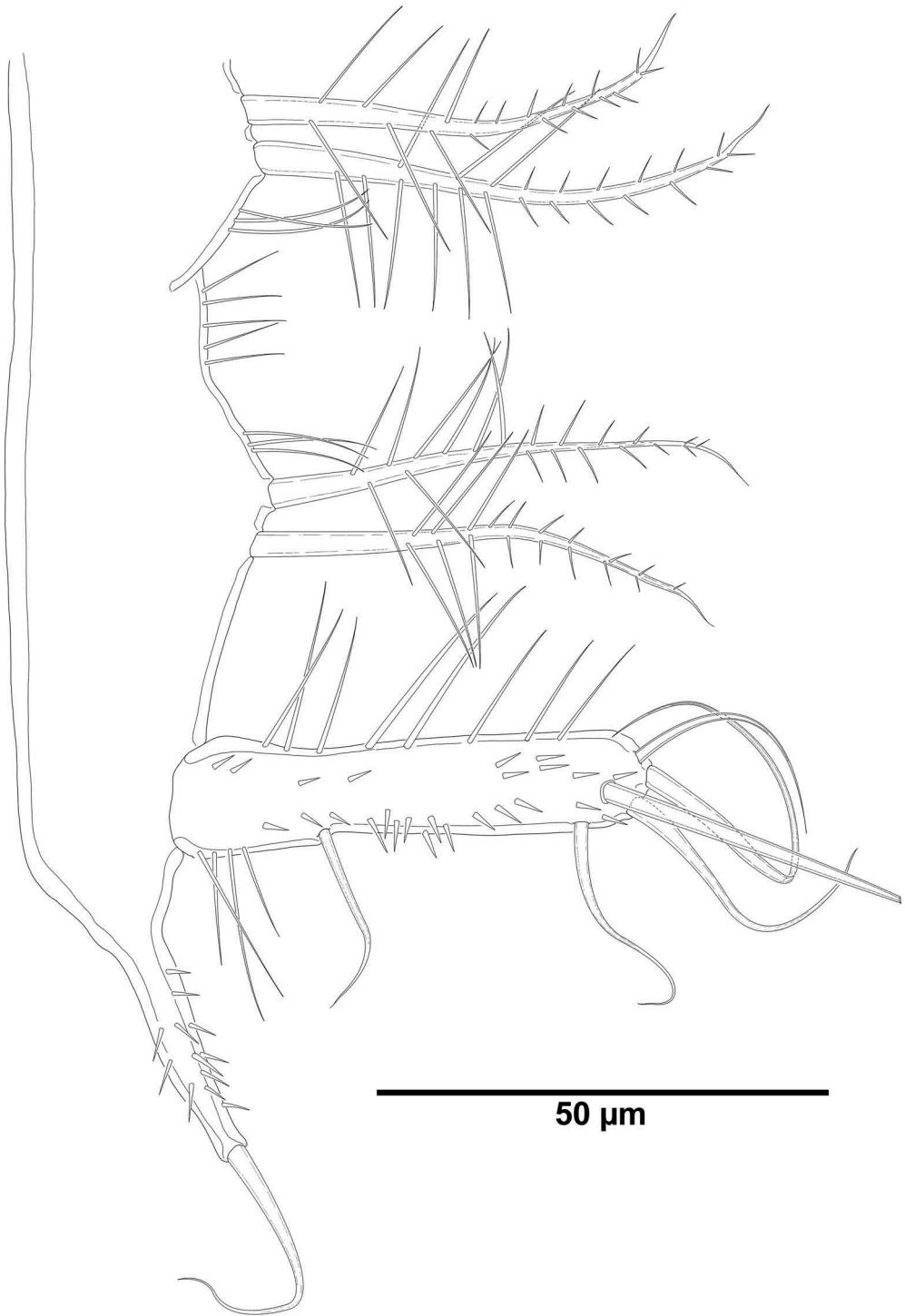
The specific epithet is an anagram of the specific epithet of *A. angolaensis*, its probable most closely related species.



**Figure 5.** *Argestes analogises* sp. n., female holotype. (a) P3, anterior; (b) P4, anterior; (c) P4 EXP3.

### Remarks

The new species, *A. analogises* sp. n., fits the morphological description of Argestidae as presented by Por (1986a) and George (2004). Also, the new species proposed herein possesses elongate sensilla on the urosomites (these sensilla are assumed to be present also on the thoracic somites), thus fitting the sub-familial diagnosis for Argestinae by George (2011). George (2008) presented a generic diagnosis for *Argestes* and proposed the monophyly of the genus based on three synapomorphies [plesiomorphies] for *A. angolaensis*, *A. mollis*, and *A. reductus*, viz. body densely covered with small cuticular spinules [body not covered with spinules], sixth segment of the female antennule (penultimate/antepenultimate segment in the male antennule) with a very strong sub-apical seta [without such a strong seta], and caudal setae I, II, III and VI of 'rat-tail' shape [setae normal]. Pending the redescription of *A. reductus*, he suggested that the presence of sensilla-bearing cylindrical tubercles on the free thoracic somites could constitute an additional synapomorphy for the genus. Additionally, George (2008) commented on the similarity between *Argestes* and *Parargestes* Lang 1944, the latter created by Lang (1944) for *A. tenuis* Sars 1921, and suggested that *P. tenuis arcticus* should be reallocated into *Argestes*. This was formally done by George (2011) who dissolved the genus *Parargestes* and reallocated *P. tenuis arcticus* again into *Argestes* based on a partial redescription of



**Figure 6.** *Argestes analogises* sp. n., female holotype. P5, anterior.

the subspecies, while implicitly relegating *P. tenuis tenuis* (Sars 1921) as *incertae sedis* within Argestidae because the material of that subspecies is no longer available and the presence of the synapomorphies for the genus as presented by George (2008) could not be verified. Additionally, George (2011) proposed the subfamily Argestinae for *Argestes* and *Fultonia* Scott 1902 based on three synapomorphies, viz. body densely covered with small cuticular spinules [body not covered with spinules], sixth segment of the female antennule with a very strong subapical seta [without such a strong seta], and presence of elongate sensilla on thoracic somites dorsally [sensilla of normal length]. With the description of *A. longiseta* from Iceland, the number of species of the genus increased to five. The placement of *A. analongises* sp. n. into *Argestes* was thus problematic and controversial. Although I could only observe six caudal setae, of which setae I–III and seta IV seem to be of normal type, i.e. not rat-tailed, *A. analongises* sp. n. was placed into that genus since it fits the generic diagnosis given by George (2008), and by the presence of (a) small spinules covering the body surface of, at least, the urosome (the only specimen available was badly damaged and the surface ornamentation of prosomites could not be assessed), and (b) an extremely elongated distal seta on the sixth segment of the female antennule, both of which are synapomorphies for *Argestes* (George 2008).

As noted above, George (2011) could not confirm the synapomorphies for *Argestes* in *P. tenuis tenuis* since the material of that subspecies is no longer available. However, from Sars' (1921, plate LXVI) illustration of the female antennule of *P. tenuis tenuis*, the presence of a very long seta on the sixth segment of the antennule is evident. In his description of *A. tenuis arcticus*, Lang (1936) already noted some important differences between his newly proposed subspecies and the nominotypical species, viz. presence of a reduced proximal element on P4 EXP3 in *A. tenuis tenuis*, but absent in *A. tenuis arcticus*, and comparatively shorter setae on the endopodal lobe of the female P5 of the nominotypical subspecies. In my opinion, these differences render the conspecificity of these two subspecies questionable. Until the redescription of *A. tenuis tenuis* based on new material is available, I propose to reallocate *P. tenuis tenuis* into *Argestes* as *A. tenuis tenuis* Sars 1921, assuming the conspecificity of both subspecies.

The phylogenetic relationships between *A. mollis*, *A. reductus*, *A. angolaensis*, *A. longiseta*, *A. tenuis arcticus*, *A. tenuis tenuis*, and *A. analongises* sp. n. are uncertain. Among the species of *Argestes*, both sexes are known only for *A. angolaensis*, *A. mollis*, and *A. tenuis tenuis*. *Argestes longiseta*, *A. tenuis arcticus*, and *A. analongises* sp. n. are known from the female only, and *A. reductus* is known only from the male. The males of *A. angolaensis*, *A. mollis*, and *A. reductus* possess two well-developed inner setae on the P4 EXP3, but the condition for the male of *A. tenuis tenuis* remains unclear. George (2008) noted that few females of *A. angolaensis* showed some variability consisting of the occasional presence of a proximal reduced, spine-like element on the same segment, instead of one 'normal', well-developed seta, suggesting that, despite the male possessing two inner setae on the P4 EXP3, the normal condition in the female is the possession of only one inner seta on the same segment. Such reduced, proximal inner element on the P4 EXP3 is also present in the females of *A. mollis*, *A. longiseta*, *A. tenuis tenuis*, and *A. analongises* sp. n., and has been observed also in the only species of *Dizahavia* Por 1979, *D. halophila* Por 1979, known from a single female. The low prevalence (defined here as the number of specimens (%) of a given sex showing

a particular variable character in relation to the total number of inspected individuals of that sex) of such a spine-like element on the P4 EXP3 observed by George (2008) in the females of *A. angolaensis* is misleading, and suggests that the normal condition in the female is the presence of one seta on the P4 EXP3. However, the presence of such reduced element in all the females (nine specimens) of *A. mollis* inspected by George (2008), in all the females (10 specimens) of *A. longiseta* inspected by Apostolov (2011), in the single female of *A. analongises* sp. n. presented herein, presumably in all the females of *A. tenuis tenuis* inspected by Sars (1921), and in the only female of *D. halophila*, suggests that the normal condition in the female of these species is the possession of two inner elements, being the proximal visibly reduced, and that the condition of the females of *A. angolaensis* inspected by George (2008) in which he observed only one well-developed inner seta, is actually the variable state of the inner armature of the female P4 EXP3. If this view is correct, the significance of the presence of this reduced, spine-like element in the females of the species of *Argestes* and *Dizahavia*, but its complete absence in, for example, the three females of *A. tenuis arcticus* inspected by George (2011), needs to be assessed.

*Argestes tenuis arcticus*, *A. tenuis tenuis*, *A. angolaensis*, and *A. analongises* sp. n. share the elongated caudal rami. Both subspecies of *A. tenuis* share caudal setae I and II arising laterally from the distal fifth of ramus, and seta III issuing from the distal outer corner. *Argestes angolaensis*, known from the Angola Basin, and *A. analongises* sp. n. share the distal situation of all the caudal setae and the ventral position of caudal seta III, suggesting a close relationship between these two species. These two species differ, however, in the relative length of the female caudal rami (about as long as the anal somite in the Mexican species, but considerably longer in *A. angolaensis*), size, shape and relative position of the sensilla-bearing tubercles associated to the anal somite (flanking the anal operculum and of normal size and shape in *A. analongises* sp. n., but shifted medially on the anal operculum and very large in *A. angolaensis*), armature of the mandibular basis (with one bipinnate seta and a strong flame-shaped spine in *A. analongises* sp. n., but with two bipinnate setae in *A. angolaensis*), shape of the exopodal and endopodal segments of swimming legs (comparatively more elongated and slenderer in *A. angolaensis*), and relative length of the setae on the female P5 endopodal lobe (both subequal in length in *A. analongises* sp. n., but outermost smaller in *A. angolaensis*) and position of the innermost seta of the female P5 exopod (subapical in *A. analongises* sp. n., but lateral in *A. angolaensis*).

Supposed close relationships between deep-sea harpacticoids from the Angola Basin and from the Gulf of California have been documented earlier by Gómez (2018b) for *Mesocletodes brevisetosus* (Carmen Basin, Gulf of California) and *M. dorsiprocessus* Menzel and George 2009 (Angola Basin), *M. simplex* (Guaymas Basin, Gulf of California) and *M. meteorensis* Menzel and George 2009 (Angola Basin), and *M. unisetosus* (Carmen Basin, Gulf of California) and *M. angolaensis* Menzel and George 2009 (Angola Basin). Undoubtedly, the relationships between deep-sea Argestidae from the western Atlantic and Gulf of California will remain hypothetical until future investigations on this fauna from the eastern Atlantic and Gulf of Mexico reveal new interesting clues about the phylogenetic relationships between the species of this interesting group of deep-sea crustaceans.



Family **AMEIRIDAE** Boeck 1865  
Genus **Argestigens** Willey 1935

**Type species**

*Argestigens uniremis* Willey 1935, by original designation.

**Other species**

*Argestigens abyssalis* Becker 1979, *A. difficilis* (Smirnov 1946), *A. glacialis* Lang 1936, *A. celibis* sp. n.

***Argestigens celibis* sp. n.**  
(Figures 7–11)

**Material examined**

Dissected male holotype mounted onto nine slides (ICML-EMUCOP-110207-02); Talud X cruise; 11 February 2007; coll. S. Gómez.

**Type locality**

Southern Trough of Guaymas Basin, Gulf of California, México, between Isla San Pedro Nolasco and Isla Tortuga (27°42'N, 111°38'W), 1570 m depth.

**Diagnosis (based on the male only)**

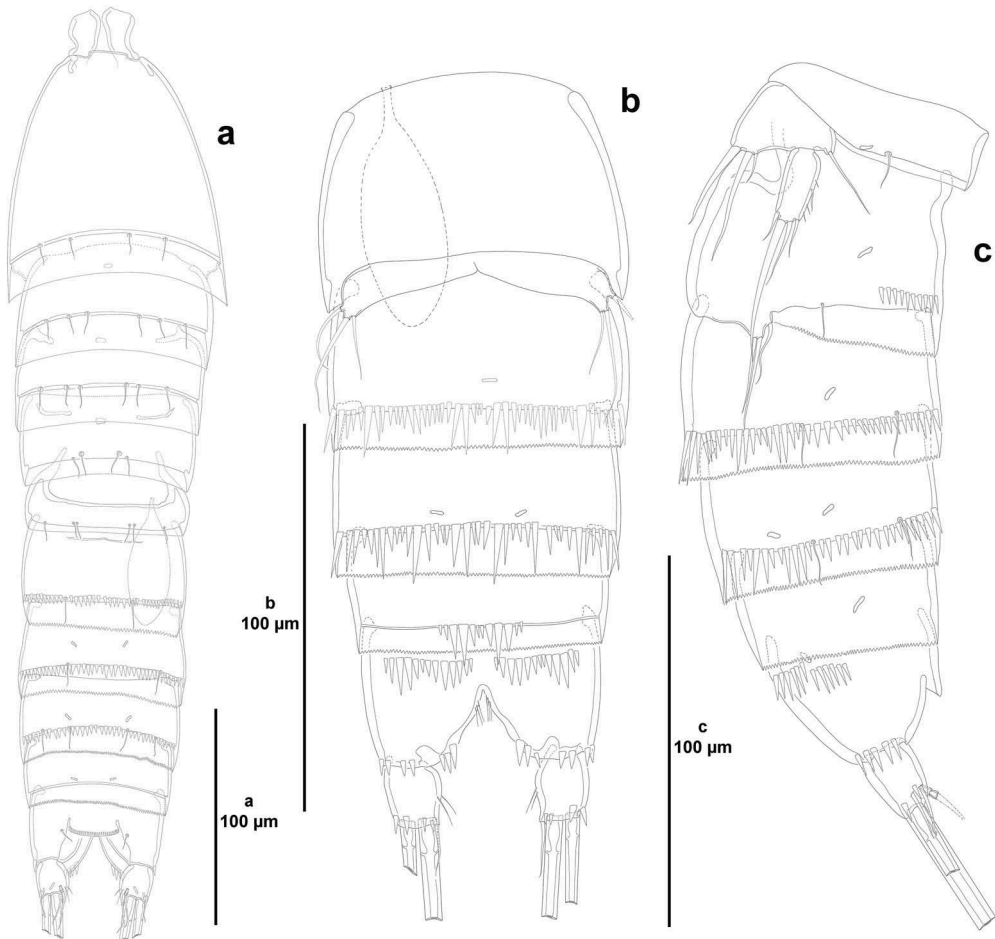
Body subcylindrical. Surface of cephalothorax and prosomites and P5-bearing somite smooth, with few sensilla along posterior margin; hyaline frill of cephalothorax and P2–P4-bearing somites plain. Posterior hyaline frill of genital somite and fourth to fifth urosomites finely serrated. Anal somite slightly shorter than two preceding somites combined, quadrate from dorsal view, posterior margin deeply cleft medially, anal operculum situated in the middle of somite. Caudal rami short, 1.2 times as long as wide, with six setae. Antennule eight-segmented, haplocer.

**Description of male**

**Body.** Total body length, 387  $\mu\text{m}$  measured from anterior margin of rostrum to posterior margin of caudal rami, subcylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome (Figure 7(a)). Rostrum (Figure 7(a)) fused to cephalothorax, the latter 0.3 times as long as entire body length; without surface ornamentation except for few sensilla along posterior margin; posterior hyaline frill smooth.

**P2–P5-bearing somites (Figure 7(a)).** Without surface ornamentation except for sensilla close to posterior margin; posterior hyaline frill smooth; P2–P4-bearing somites with, P5-bearing somite without medial pore. Second urosomite (P6-bearing somite) seemingly without surface pores, without surface ornamentation except for posterior continuous spinular row dorsally and some sensilla close to posterior margin, posterior hyaline frill finely serrated (Figure 7(a–c)). Third and fourth urosomites with paired pores dorsally; third urosomite with one, fourth urosomite with two pores ventrally; both urosomites with continuous row of spinules of moderate sized dorsally (Figure 7(a)) and laterally (Figure 7(c)), ventrally





**Figure 7.** *Argestigens celibis* sp. n., male holotype. (a) habitus, dorsal; (b) urosome, ventral, P5-bearing somite omitted; (c) urosome, lateral.

(Figure 7(b)) with spinular pattern consisting of sets of larger spinules alternating with sets of smaller ones, posterior hyaline frill finely serrated. Fifth urosomite with paired pores dorsally, without any other surface ornamentation dorsally and laterally (Figure 7(a,c)); ventrally (Figure 7(b)) with medial row of spinules consisting of two sets of larger spinules flanked by sets of smaller ones, hyaline frill finely serrated.

**Anal somite (Figure 7(a–c)).** Quadrate, slightly longer than preceding somite, posterior margin deeply cleft medially, without surface ornamentation dorsally except for two sensilla associated to anal operculum, the latter shifted anteriorly and with row of minute spinules close to posterior margin; ventrally (Figure 7(b)) with two anterior sets of spinules, each consisting of two sets of larger spinules flanked by smaller ones, and with some sets of spinules close to caudal rami as shown; with lateral spinules anteriorly and close to joint with caudal rami (Figure 7(c)).

**Caudal rami (Figure 7(a–c)).** Cylindrical, short, 1.2 times as long as wide (width measured at the widest medial part), without surface ornamentation except for few spinules close to posterior margin, with six setae, all issuing from distal fifth, as follows: seta I lost; homology of setae II and III difficult, both visible from lateral view, probably seta II dorsal to seta III, both setae subequal in length; setae IV and V longest; seta VI issuing at inner distal corner; dorsal seta VII issuing subdistally, tri-articulated.

**Antennule (Figure 8(a)).** Eight-segmented, haplocer, with three segments distal to geniculation; first segment with few spinules proximally, other segments without surface ornamentation. Armature formula as follows: 1-[1se], 2-[1se], 3-[7se], 4-[5se], 5-[4se+ 3 sp + ae], 6[2se+ 1sp], 7-[3se], 8-[2se+ 5art+ acro].

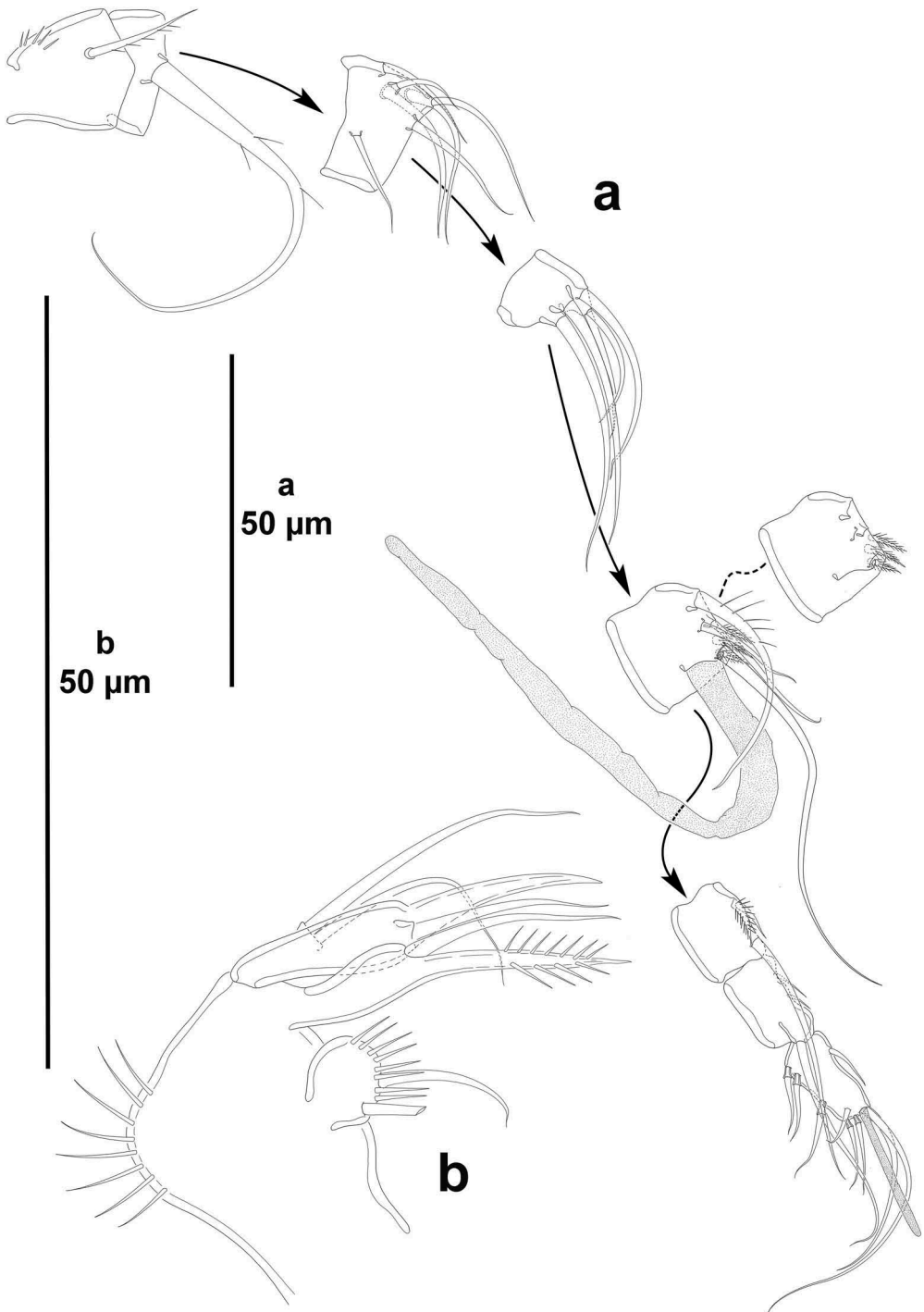
*Antenna, mandible, maxillule, and maxilliped.* Lost during dissection.

**Maxilla (Figure 8(b)).** Syncoxa with outer spinules, seemingly without any other surface ornamentation; with two endites; proximal (praecoxal) endite small, rounded, with apical row of spinules, with two setae; distal (coxal) endite elongated, with one strong spinulose element fused to endite, and one bare seta. Allobasis seemingly without spinules, drawn out into strong, un-ornamented claw, and accompanied by one seta. Endopod represented by two setae.

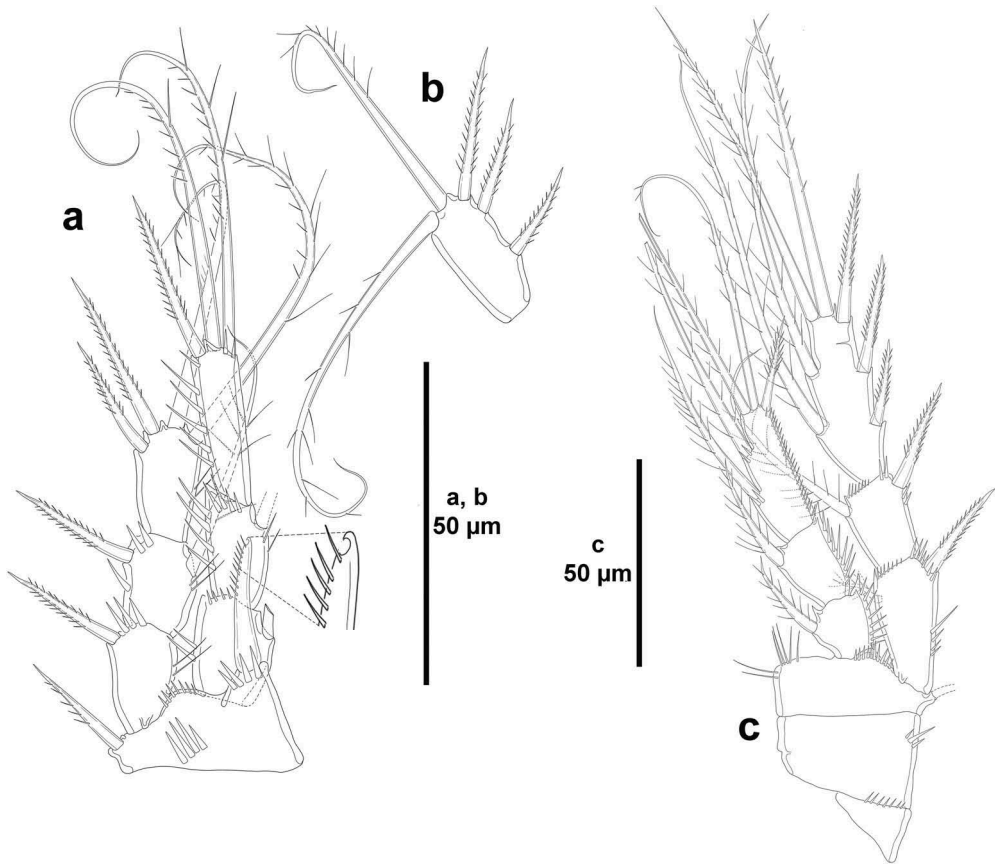
**P1 (Figure 9(a,b)).** Basis with inner and outer strong spinulose spines, inner one modified; with strong spinules medially, between rami and at base of inner spine. Exopod three-segmented; exopodal segments subequal in length, with spinules as depicted; EXP1 without, EXP2 with inner seta, EXP3 with five elements. Endopod three-segmented, longer than exopod; ENP1 and ENP2 with inner seta; ENP3 with three elements, outermost a spine.

**P2–P4 (Figures 9(c), 10(a,b)).** Praecoxa as in P2 and P4 (see Figures 9(c), 10(b)), small, triangular, with a transverse row of spinules close to joint with coxa, the latter with some spinules close to distal outer corner. Basis with spinules between rami and at base of outer seta, and with slender, long spinules (setules?) at distal inner corner. Outer basal seta of P2 lost during dissection, of P3 and P4 slender, naked. Exopod three-segmented, longer than endopod, with spinular ornamentation as shown; EXP1 and EXP2 with inner seta; P2 EXP2 (Figure 9(c)) with two inner setae, two apical elements (innermost setiform, outermost spine-like), and three outer spines; P3–P4 EXP3 (Figure 10(a,b)) with three inner setae (all setae of P3 bipinnate and slender, medial seta of P4 strong and spinulose), two apical elements (innermost setiform, outermost spine-like) and three outer spines. Endopod three-segmented, with spinular ornamentation as shown; P2–P4 ENP1 and ENP2 (Figures 9(c), 10(a,b)) with one inner seta; P2 ENP3 (Figure 9(c)) and P4 ENP3 (Figure 10(b)) with two inner and two apical setae, and one outer spine; P3 ENP3 (Figure 10(a)) with three inner and two apical setae, and one outer spine.

**P5 (Figure 11(a)).** Seemingly without spinules on baseoendopod and on baseoendopodal setophore. Endopodal lobe poorly developed, with three setae of which outermost and medial element close to each other (outermost smallest), innermost separated from the former two elements by wide gap. Exopod distinct, oval, two times as long as



**Figure 8.** *Argestigens celibis* sp. n., male holotype. (a) antenna; (b) maxilla.



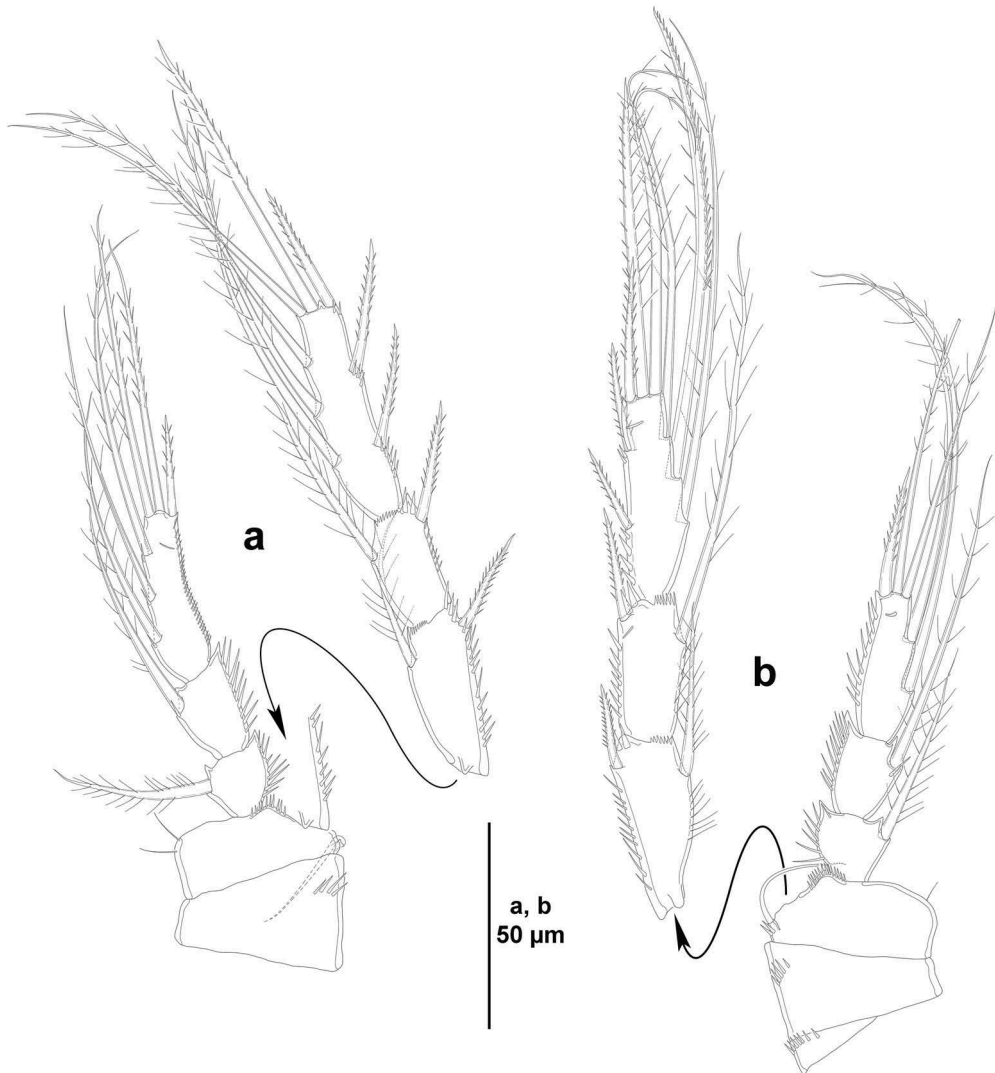
**Figure 9.** *Argstigens celibis* sp. n., male holotype. (a) left P1, anterior, with aberrant EXP3; (b) right P1 EXP3, anterior; (c) P2, anterior.

wide (maximum width at medial part); only one small spinule was observed on medial outer margin; with three outer, one apical and two inner setae.

**Armature formula.**

	EXP	ENP
P1	0.1.023	1.1.111
P2	1.1.223	1.1.221
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221
P5	312	3

**Female.** Unknown.



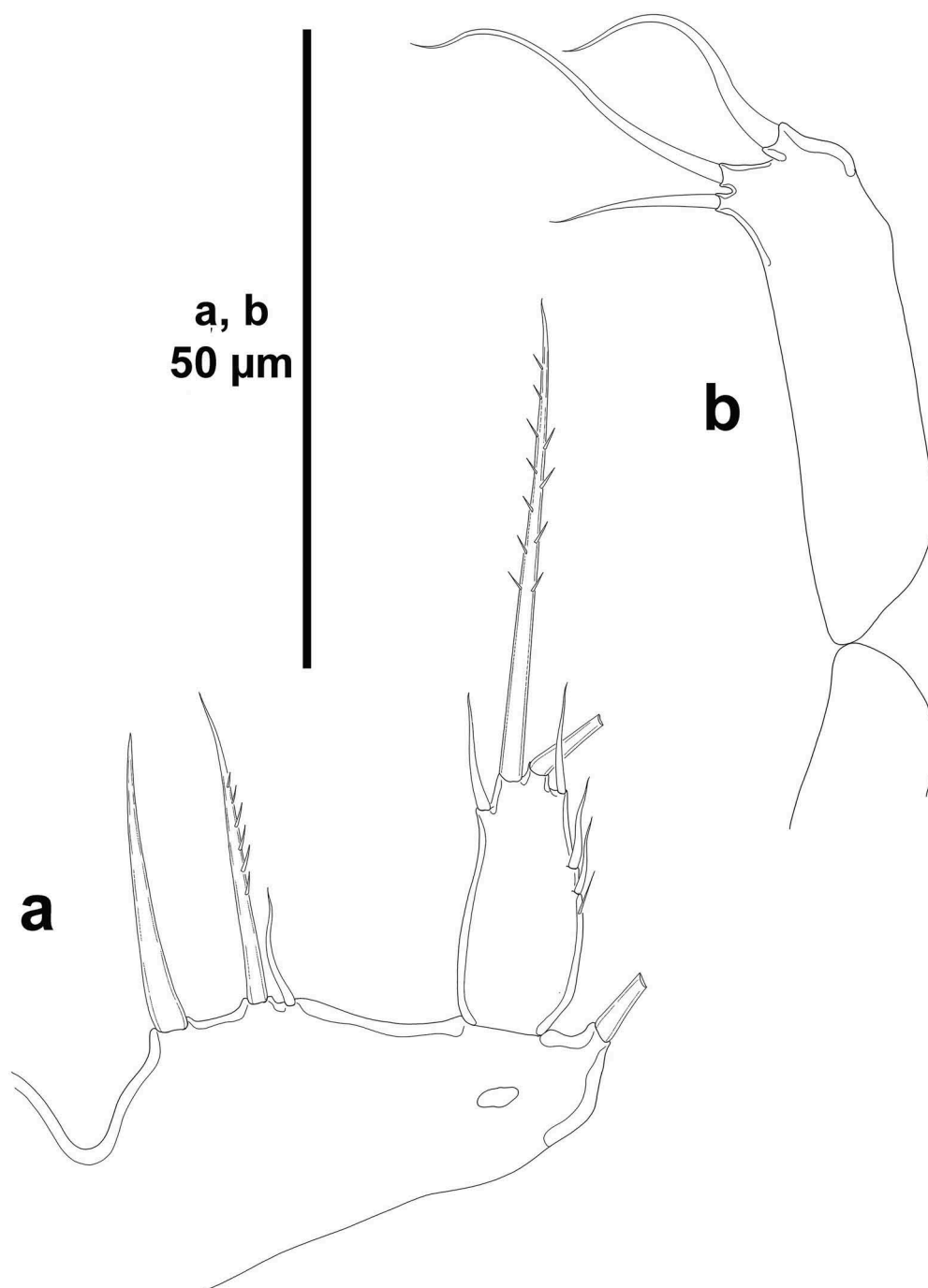
**Figure 10.** *Argestigens celibis* sp. n., male holotype. (a) P3, anterior; (b) P4, anterior.

### ***Etymology***

The specific epithet from the Latin *celibis*, single, refers to the missing female of the species. The name is an adjective in the nominative singular, gender masculine.

### ***Remarks***

The phylogenetic relationships and systematic position of some Argestidae have always been problematic and controversial, due to the lack of apomorphies, blurring the boundaries, for example, between the Argestidae and the Ameiridae (Huys et al. 2009). Becker (1974) hypothesized an evolutionary lineage composed of *Parameiopsis* Becker 1974 (which he regarded as similar to Lang's (1948) hypothetical ameirid



**Figure 11.** *Argestigens celibis* sp. n., male holotype. (a) P5, anterior; (b) P6.

ancestor), *Argestes*, *Parargestes* and *Argestigens*, which, following Becker (1974, 1979), should be removed from the Cletodidae and reallocated into the Ameiridae. Huys et al. (1996) believed that *Argestigens* really belonged to the Ameiridae and Huys and Conroy-

Dalton (1997) suggested that the monotypic genus *Argestoides* Huys and Conroy-Dalton 1997 (currently considered as *genus incertae* within Argestidae) could represent part of a lineage holding an intermediate position between the Ameiridae and Argestidae. In their analysis, Huys et al. (2009) presented a detailed account on the systematic history of the genus and concluded that the position of *Argestigenes* within the Argestidae 'is highly questionable, being entirely based on plesiomorphic character states' (Huys et al. 2009, p. 153). After a thorough analysis, they removed *Argestigenes* from the Argestidae and reallocated that genus into the Ameiridae as the sister group of the 'traditional' genera of that family (Huys et al. 2009, p. 153), holding a close relationship with *Sarsameira* Wilson 1924. Huys et al. (2009, p. 154) supported the sister-group relationship between *Argestigenes* and *Sarsameira* on the shared uniramous two-segmented mandibular palp, primitive setal formula on the swimming legs with three inner setae on P3 ENP3, triangular endopodal lobe of P5 with four or five setae and both endopodal lobes medially separated, and non-argestid (unmodified) mandibles, maxillules and maxillae. Corgosinho and Martínez Arbizu (2010) accepted, with some reservations, the scheme by Huys et al. (2009), and also considered *Argestoides prehensilis* Huys and Conroy-Dalton 1997 as part of the Ameiridae. Additionally, Corgosinho and Martínez Arbizu (2010) concluded that *Parameiropsis* could not be attributed to the Ameiridae nor to the Podogenonta, and decided to create a new family, Parameiropsidae Corgosinho and Martínez Arbizu 2010, for *Parameiropsis* and all its species. Finally, as noted above, George (2011) dissolved the genus *Parargestes* and reallocated *P. tenuis arcticus* again into *Argestes*. The exclusion of *A. celibis* from Argestidae, and its inclusion in the Ameiridae, was based on the non-argestid (unmodified) maxilla, on the presence of a more or less well-developed endopodal lobe of the male P5 which is more of the ameirid type, but above all because of the armature formula of P2–P4 ENP3 (221, 321, 221; i.e. with three inner setae on the P3 ENP3; which is common in the Thalestridae, Miraciidae and Ameiridae (Lang 1948), and particularly in the more basal ameirid genera *Sarsameira*, *Ameiropsis* Sars 1907, and *Stenocopia* Sars 1907 (Huys et al. 2009)), and on the presence of the typically modified ameirid-like inner spine on the male P1 basis. The exclusion of the new species from *Sarsameira* and its inclusion in *Argestigenes* was difficult given the lack of synapomorphies for these two genera (but see also Huys et al. 2009, p. 154), because the female of the new species is still unknown, and because, amongst the mouth parts, I could recover the maxilla only. The new species presented herein was attributed to *Argestigenes* based on the non-prehensile endopod of P1 and presence of long inner spinules (setules?) on the basis of P2–P4, the latter already observed by Willey (1935) for the type species *A. uniremis*, and used by Huys et al. (2009) as a criterion for the removal of *Parameira difficilis* Smirnov 1946 from *Parameira* Sars 1907 and reallocation into *Argestigenes*. The female of *A. celibis* remains unknown, and all other species of *Argestigenes* are known from the female only, making impossible any comparison and phylogenetic inference. In the meantime, and until the female of the Mexican specimen is found, *A. celibis* sp. n. is proposed for this material.

## Discussion

The family Argestidae is one of the dominant harpacticoid taxa of muddy substrates (Hicks and Coull 1983, George 2004, 2008, Menzel and George 2009, Menzel 2011) and



even though the family is considered a typical deep-sea taxon (Hicks and Coull 1983, Huys and Conroy-Dalton 1997, George 2004) some of its genera have been found in shallow locations (see George 2004, Menzel 2011, Menzel and George 2012, Gómez 2018a). Within the family, the genera *Mesocletodes* Sars 1909 (41 species) and *Eurycletodes* Sars 1909 (27 species) are the most species-rich. Eight genera (*Argestes*, *Bodinia*, *Corallicletodes* Soyer 1966, *Fultonia*, *Hypalocletodes* Por 1967, *Leptocletodes* Sars 1920, *Neoargestes* Drzycimski 1967, and *Odiliacletodes* Soyer 1964) possess from five to two species, and seven genera (*Actinocletodes* Fiers 1986, *Argestoides*, *Austrocletodes* Pallares 1979, *Dizahavia*, *Hemicletodes* Lang 1936, *Megistocletodes* Por 1986b, and *Pontocletodes* Apostolov 1980) are monotypic. The monophyly of the Argestidae has not been proved yet (George 2004, 2008, 2011), but some important advances have been presented towards the monophyly of the family and its relationships with the Ameiridae: (a) the proposal that the monotypic genus *Argestoides*, currently considered *incertae sedis* within Argestidae, could represent a new family occupying an intermediate position between the Ameiridae and Argestidae (Huys and Conroy-Dalton 1997); (b) the proposal of the shape and armature of the maxilla as a useful character towards the monophyly of the Argestidae (Corgosinho and Martínez Arbizu 2010); (c) the proposal of the monophyly of *Bodinia*, currently regarded as *incertae sedis* within Argestidae (George 2004); (d) the proposal of the monophyly of *Argestes* (George 2008); (e) the proposal of the monophyly of *Mesocletodes* and of the *Mesocletodes abyssicola*-group (Menzel and George 2009); (f) the allocation of *Argestigens* into the Ameiridae (Huys et al. 2009); (g) the proposal of the monophyly of *Fultonia*, along with the proposal of the subfamily Argestinae for *Fultonia* and *Argestes*, and transfer of *P. tenuis tenuis*, Sars 1921 and *P. tenuis arcticus* to *Argestes* (George 2008, 2011); (h) the proposal of the monophyly of *Eurycletodes* and its subgenera, *E. (Eurycletodes)* Sars 1909 and *E. (Oligocletodes)* Lang 1944, and allocation of *E. profundus* Becker 1979 into the subgenus *E. (Oligocletodes)* (Menzel 2011); and (i) the hypothesized monophyly of a group of derived *Mesocletodes* whose males lack mouth parts, and of a group of species of the *M. abyssicola*-group with bifid dorsal processes on P2–P4-bearing somites and second half of genital-double somite (Menzel and George 2009; see also Gómez 2018b). However, the monophyly and position of some genera within Argestidae, e.g. *Odiliacletodes*, still needs confirmation (Gómez 2018c), and the monophyletic status of some genera is still questionable. For example, George (2004) established the monophyly of *Bodinia* based on the presence of a strongly sclerotized ventral fold ('apron') on the anal somite of *B. meteorensis* George 2004 and *B. peterrumi*. However, some strong differences between these species render their congeneric nature questionable. One of these species, *B. peterrumi*, likely occupies a comparatively more basal position within Argestidae than the type species, *B. meteorensis*. This is evidenced by the possession, in the former, of a biramous mandibular palp (but see below) with a tetrasetose endopod, two setae on the syncoxa of the maxilliped, four setae on the P1 ENP2, five setae on the P1 EXP3, an inner seta on the P2–P4 EXP1, three outer spines on the P2–P4 EXP3, three-segmented P2–P4 endopods (with an inner seta on P2–P3 ENP2, but without inner seta in P4 ENP2), and by the general structure of the caudal rami (seta VII issuing from a long protrusion) and the coarsely serrated posterior margin of urosomites. In contrast, the type species of the genus, *B. meteorensis*, seems to occupy a comparatively more derived position as evidenced by the presence of

a uniramous mandibular palp (but see below) with a tri-setose endopod, one seta on the syncoxa of the maxilliped, three setae on the P1 ENP2, four setae on the P1 EXP3, but also by the loss of an inner seta on the P2–P4 EXP1, the loss of an outer spine on the P2–P4 EXP3, and by the possession of two-segmented P2–P4 endopods, and by the general structure of the caudal rami (comparatively more simple), and the lack of a serrated posterior margin of urosomites. George (2004) interpreted the mandible of *B. peterrumi* as biramous, with an exopod represented by two setae, one of which is strong and bipinnate, and a one-segmented endopod with four elements, and that of *B. meteorensis* as biramous, with the exopod represented by a strong bipinnate seta and a one-segmented endopod with three setae. The strong bipinnate seta on the mandibular palp of both species seem to be homologous and are reinterpreted here as the basal setae, rendering the mandibular palp of *B. meteorensis* uniramous, and that of *B. peterrumi*, biramous. In my opinion, these arguments are strong enough to suggest the presence of an ‘apron’ in both species as the result of convergence, and to propose a new genus, *Georgus* gen. n., for its type and only species, *B. peterrumi*. Probably, *Georgus* gen. n. holds a close position either to *Fultonia*, *Odiliaclatodes* or *Dizahavia*. George (2004) already commented on the possible relationship between *Bodinia sensu* George (2004) and *Dizahavia* based on the setation and shape of the swimming legs, but since I could not find any apomorphy to objectively define the new genus proposed herein, its position within Argestidae remains uncertain. Also, with this course of action, the genus *Bodinia*, with its type and only species, *B. meteorensis*, remains undefined since the only synapomorphy uniting both species of *Bodinia sensu* George (2004), the ventral ‘apron’ on the anal somite, is regarded here as a result of convergence and no other apomorphy for *B. meteorensis* has been detected.

## Disclosure statement

No potential conflict of interest was reported by the author.

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## Geolocation information

Eastern Mexican Pacific (point): 22°01'2"N, 106°40'2"W; Gulf of California (point): 27°42'N, 111°38'W.

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## References

- Apostolov A. 1980. Description de deux genres nouveaux de la famille Cletodidae Sars (Copepoda, Harpacticoida) de la Mer Noire. Acta Musei Maced Sci Nat Skopje. 10:167–174.
- Apostolov A. 2011. Les harpacticoides marins (Crustacea, Copepoda) d'Islande. First. Bourgas (Bulgaria): Libra Scorp Publisher.
- Becker K. 1974. Eidonomie und Taxonomie abyssaler Harpacticoida (Crustacea, Copepoda) Teil I. Cerviniidae-Ameiridae. Meteor Forschungsergebnisse R D. 18:1–28.
- Becker K-H. 1979. Eidonomie und taxonomie abyssaler Harpacticoida (Crustacea, Copepoda) Teil II. Paramesochridae, Cylindropsyllidae und Cletodidae. Meteor Forschungsergebnisse R D - Biol Suppl. 31:1–37.
- Boeck A. 1865. Oversigt over de ved Norges Kyster jagttagne Copepoder henhørende til Calanidernes, Cyclopidernes og Harpacticidernes Familier. Forh i Vidensk i Kristiania. 1864:226–282.
- Corgosinho PHC, Martínez Arbizu P. 2010. Ameiridae Boeck and Argestidae Por revisited, with establishment of Parameiropsidae, a new family of Harpacticoida (Crustacea, Copepoda) from deep-sea sediments. Helgol Mar Res. 64:223–255.
- Drzycimski I. 1967. Zwei neue Cletodidae (Copepoda Harpacticoida) aus dem Westnorwegischen Küstengebiet. Sarsia. 29:199–206.
- Ferrari FD, Ivanenko VN. 2008. The identity of protopodal segments and the ramus of maxilla 2 of copepods (Copepoda). Crustaceana. 81:823–835.
- Fiers F. 1986. New and interesting copepods (Crustacea, Copepoda) from brackish waters of Laing Island (northern Papua New Guinea) Leopold III Biological Station, Laing Island - Contribution no. 196. Bull R des Sci Nat Belgique Biologie. 56:99–120.
- George KH. 2004. Description of two new species of *Bodinia*, a new genus incertae sedis in Argestidae Por, 1986 (Copepoda, Harpacticoida), with reflections on argestid colonization of the Great Meteor Seamount plateau. Org Divers Evol. 4:241–264.
- George KH. 2008. *Argestes angolaensis* sp. nov. (Copepoda: Harpacticoida: Argestidae) from the Angola Basin (Southeast Atlantic), and the phylogenetic characterization of the taxon *Argestes* Sars, including the redescription of *A. mollis* Sars, 1910, and *A. reductus* (Itô, 1983). Zootaxa. 262:223–262.
- George KH. 2011. Revision of the taxon *Fultonia* T. Scott (Copepoda: Harpacticoida: Argestidae), including the (re) description of some species, discontinuation of the genus *Parargestes* Lang. Meiofauna Mar [Internet]. 19:127–160. [http://www.pfeil-verlag.de/04biol/pdf/mm19\\_11.pdf](http://www.pfeil-verlag.de/04biol/pdf/mm19_11.pdf)
- Gómez S. 2018a. A new record and a new species of the genus *Rhizothrix* (Copepoda: Harpacticoida: Rhizothrichidae) from the deep sea of the Gulf of California. Proc Biol Soc Washingt [Internet]. 131:7–18. <http://www.bioone.org/doi/10.2988/17-00021>
- Gómez S. 2018b. New species of the genus *Mesocletodes* Sars, 1909 from the deep Gulf of California (Copepoda, Harpacticoida). Zookeys. 751:75–112.
- Gómez S. 2018c. New species of *Eurycletodes* Sars, 1909 and *Odiliacletodes* Soyler, 1964 from the deep Gulf of California (Copepoda, Harpacticoida, Argestidae). Zookeys. 764:1–25.
- Gómez S, Conroy-Dalton S. 2002. Description of *Ancorabolus hendrickxi* sp. nov. (Copepoda: Harpacticoida: Ancorabolidae) from the neotropics and notes on caudal ramus development within oligoarthran harpacticoids. Cah Biol Mar. 43:111–129.

- Gómez S, Díaz K. 2017. On some new species of Ancorabolidae Sars, 1909 from the Gulf of California: the genera *Ceratonotus* Sars, 1909, and *Dendropsyllus* Conroy-Dalton, 2003 (Crustacea, Copepoda, Harpacticoida). *Zookeys*. 657:43–65.
- Hendrickx ME. 2012. Operaciones oceanográficas en aguas profundas: los retos del pasado, del presente y del proyecto Talud en el Pacífico mexicano (1989-2009). In: Zamorano P, Hendrickx ME, Caso M, editors. Biodiversidad y comunidades del talud Continental del Pacífico Mexicano. Mexico City: Instituto Nacional de Ecología, Secretaría de Medio Ambiente y Recursos Naturales; p. 466.
- Hicks GRF, Coull BC. 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanogr Mar Biol Annu Rev*. 21:67–175.
- Huys R, Boxshall GA. 1991. Copepod evolution. London: The Ray Society.
- Huys R, Conroy-Dalton S. 1997. Discovery of hydrothermal vent Tantulocarida on a new genus of Argestidae (Copepoda: Harpacticoida). *Cah Biol Mar*. 38:235–249.
- Huys R, Gee J, Moore C, Hamond R. 1996. Marine and brackish water harpacticoid copepods. Part 1. In: Barnes R, Crothers J, editors. Synopses Br fauna. New Ser. London: Published for The Linnean Society of London and The Estuarine and Coastal Sciences Association by Field Studies Council Shrewsbury; p. 352.
- Huys R, Mackenzie-Dodds J, Llewellyn-Hughes J. 2009. Cancrincolidae (Copepoda, Harpacticoida) associated with land crabs: A semiterrestrial leaf of the ameirid tree. *Mol Phylogenet Evol* [Internet]. 51:143–156.
- Ito T. 1983. Harpacticoid copepods from the Pacific abyssal off Mindanao. II. Cerviniidae (cont.), Thalestridae, and Ameiridae. *Publ Seto Mar Biol Lab*. 28:151–254.
- Lang K. 1936. Die während der Schwedischen Expedition nach Spitzbergen 1898 und nach Grönland 1899 eingesammelten Harpacticiden. *K Sven Vetenskapsakademiens Handl*. 15:1–55.
- Lang K. 1944. Monographie der Harpacticiden (vorläufige Mitteilung). Uppsala: Almqvist & Wiksells Boktryckeri AB.
- Lang K. 1948. Monographie der Harpacticiden. Vol. I & II. Stockholm: Nordiska Bokhandeln.
- Menzel L. 2011. A new species of *Eurycletodes* Sars, 1909 (Copepoda: Harpacticoida: Argestidae) from the southern hemisphere including remarks on the phylogeny of the genus and its subgenera. *Helgol Mar Res*. 65:479–493.
- Menzel L, George KH. 2009. Description of four new species of *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae) and redescription of *Mesocletodes robustus* Por, 1965 from the South Atlantic, including remarks on the *Mesocletodes abyssicola*-group. *Zootaxa*. 2096:214–256.
- Menzel L, George KH. 2012. Copepodid and adult Argestidae Por, 1986 (Copepoda: Harpacticoida) in the southeastern Atlantic deep sea: diversity and community structure at the species level. *Mar Biol*. 159:1223–1238.
- Pallares RE. 1979. Copepodos harpacticoides marinos de Tierra de Fuego (Argentina). Isla de los Estados III. *Cent Investig Biol Mar Estac Puerto Deseado Estac Austral Contrib Cient*. 142:1–22.
- Por FD. 1967. Level bottom Harpacticoida (Crustacea, Copepoda) from Elat (Red Sea), Part I. *Isr J Zool*. 16:101–165.
- Por FD. 1979. The Copepoda of Di Zahav pool (Gulf of Elat, Red Sea). *Crustaceana* [Internet]. 37:13–30.
- Por FD. 1986a. A re-evaluation of the family Cletodidae Sars, Lang (Copepoda, Harpacticoida). In: Schriever G, Schminke C-T Shih HK, editors. Proceeding of Second International Conference Copepoda, 1984 Aug 13-17. Vol. 58. Ottawa (Canada): Syllogeus; p. 420–425.
- Por FD. 1986b. New deepsea Harpacticoida (Copepoda) of Cletodid type, collected in the Indian Ocean by R/V "Anton Bruun" in 1964. *Crustaceana*. 50:78–98.
- Sars G. 1907. Copepoda Harpacticoida. Canthocamptidae (concluded), Laophontidae (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. V. Bergen: Bergen Museum.
- Sars GO. 1909. Copepoda Harpacticoida. Parts XXV & XXVI Laophontidae (concluded), Cletodidae (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. V. Bergen: Bergen Museum.

- Sars GO. 1910. Copepoda Harpacticoida. Tachidiidae (concluded), Metidae, Balaenophilidae, supplement (part). An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. V. Bergen: Bergen Museum.
- Sars GO. 1920. Copepoda. Supplement. Parts VII & VIII Harpacticoida (continued). An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. VII. Bergen: Bergen Museum.
- Sars GO. 1921. Harpacticoida (concluded), Cyclopoida. An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. VII. Bergen: Bergen Museum.
- Scott T. 1902. Notes on gatherings of Crustacea collected by the fishery steamer "Garland", and the steam trawlers "Star of Peace" and "Star of Hope", of Aberdeen, during the year 1901. In: 20th Annu Rep Fish Board Scotland. Glasgow: James Hedderwick & Sons. Part III: p. 447–485.
- Smirnov SS. 1946. Novye vidy Copepoda Harpacticoida iz severnogo ledovitogo okeana (New species of Copepoda-Harpacticoida) from the northern Arctic Ocean. Tr Dreif Eksped Glav Na Ledokol Parokh G Sedov. 1937–1940:231–263.
- Soyer J. 1964. Copépodes Harpacticoides de l'étage bathyal de la région de Banyuls-sur-Mer: V. Cletodidae T. Scott. Vie Milieu. 15:573–643.
- Soyer J. 1966. Copépodes harpacticoides de Banyuls-Sur-Mer. III. Quelques formes du coralligène. Vie Milieu, Sér B Oceanogr. 17:303–344.
- Willey A. 1935. Harpacticoid Copepoda from Bermuda. Part II. Ann Mag Nat Hist Ser 10. 15:50–100.
- Wilson C. 1924. New North American parasitic copepods, new hosts, and notes on copepod nomenclature. Proc United States Natl Museum. 64:1–22.