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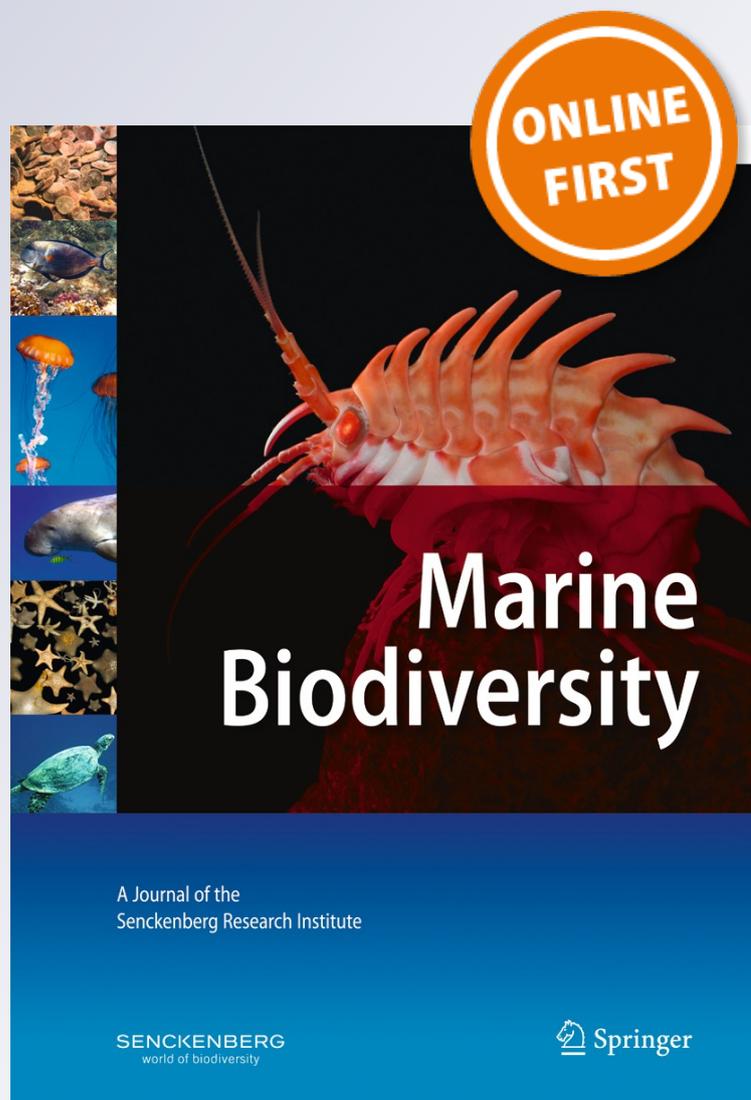
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**Marine Biodiversity**

ISSN 1867-1616

Mar Biodiv

DOI 10.1007/s12526-016-0446-9



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# A new species of *Atergopedia* (Copepoda: Harpacticoida: Novocriniidae) from a Caribbean mesophotic reef

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**Abstract** Coordinated research efforts in mesophotic coral reefs are only a decade old, but have already produced exciting findings in ecology, physiology, geomorphology, population genetics, biodiversity, and taxonomy. In this taxonomic contribution, we describe both sexes of a new copepod species of the family Novocriniidae Huys and Iliffe in Zool Scr 27(1):1–15, 1998 from a mesophotic coral reef off southwestern Puerto Rico. This is only the fifth species of the family and the fourth of the genus *Atergopedia* Martínez Arbizu and Moura in Zool Beitr NF 38:189–210, 1998. The new species, *Atergopedia dowgialli* sp. nov., shares the following characters with its three congeners: 1) antenna without seta on the first endopodal segment; 2) lateral armature of the female antenna shows a multiplication of distinct setae and consists of one geniculate seta followed by five or more slender setae; 3) the first endopod segment of the first swimming leg P1

bears no inner seta; 4) male fifth leg with two spines on endopodal lobe; and 5) the exopod of the fifth swimming leg fused to basendopod in the female. *Atergopedia dowgialli* sp. nov. is characterized by the loss of the basal seta in both antenna and maxilliped, the loss of the first maxilla endite, the presence of a long process between the outer and distal elements of the leg 1 exopodite 3, which is stronger and longer in the female, and the possession of a very short and strongly ornamented furca in both sexes. The genus *Atergopedia* has been found in deep and relatively shallow habitats from the Arctic Ocean to the Caribbean. In contrast, almost all species of the taxon Novocrinidimorpha, which includes the families Novocriniidae, Superornatiremidae Huys 1996, and Rotundiclipeidae Huys 1988, have been found associated with anchialine caves, indicating a derived distribution for *Atergopedia*.

Communicated by P. Martínez Arbizu

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monica.alfaro@upr.edu<sup>1</sup> Department of Water Science and Engineering, UNESCO-IHE, Westvest 7, 2611AX Delft, The Netherlands<sup>2</sup> Department of Marine Sciences, University of Puerto Rico at Mayagüez, Call Box 9000, Mayagüez, PR 00681, USA<sup>3</sup> Department of Biology, University of Puerto Rico at Mayagüez, Call Box 9000, Mayagüez, PR 00681, USA**Keywords** Biodiversity · Mesophotic coral ecosystems · Puerto Rico · Meiofauna · Crustacea · tropical habitat

## Introduction

Caribbean Mesophotic Coral Ecosystems (MCEs) are found on the insular and continental slopes of islands and are visually dominated by sponge and algal species, as well as scleractinian corals (*Agaricia* and *Undaria* spp.), which may be abundant until 90–100 m depth, in waters with high visibility (Kahng et al. 2010; Locker et al. 2010; Sherman et al. 2010). These species provide habitats for a highly diverse, specialized benthic fauna, which is oftentimes new to science (e.g., algae - Ballantine and Ruiz 2010, 2011; crustaceans - Petrescu et al. 2012, 2013; Schizas et al. 2015; mites - Pesic et al. 2012).

The copepod order Harpacticoida is well represented in the meiofauna associated with MCEs and the most common families are the Cletodidae, Ectinosomatidae, Laophontidae, Longipediidae, Miraciidae, and Porcellidiidae (Corgosinho and Schizas 2013). In this paper we describe the adult female and male of a new species of Novocriniidae belonging to the genus *Atergopedia*. The motivation for working on this taxon stems from the peculiar distribution of the crown group, the Novocrinidimorpha, formally proposed by Seifried (2003). All species of the Novocrinidimorpha, except the genus *Atergopedia* and *Gideonia noncavernicola* George and Martínez Arbizu 2005 (Family Superornatiremidae) are from anchialine caves (Fig. 1). This is indicative of the direction of adaptive radiation of Novocrinidimorpha from the archialine caves to other marine environments.

## Materials and methods

### Collection and processing

A team of technical divers using tri-mix Rebreathers collected various substrata (loose rubble, corals, sponges, and algae) from an MCE, off La Parguera, southwestern Puerto Rico.

Upon return to the laboratory, the substrata were placed on a 1-mm sieve and washed with filtered seawater. Any fauna that passed through the 1-mm sieve and was retained in the 0.125-mm sieve was extracted, preserved in 100 % ethanol, and examined under a microscope. Prior to light microscopic examination, specimens were cleared, dissected in lactic acid, and mounted on slides with glycerine. All observations and drawings were conducted with the aid of an Olympus BX51 compound microscope equipped with Normarsky interference contrast and using a drawing tube, at 400× and 1000× magnification. Terminology and homologization of maxillary and maxillipedal structures follow the methods of Ferrari and Ivanenko (2008). The terms seta, setules, spines, and spinules are used according to the terminology proposed by Huys and Boxshall (1991). The following abbreviations are used in the text: A1, antennule; A2, antenna; benp, basendopod; enp, endopod; enp-1 (2,3), proximal (middle, distal) segment of endopod; exp, exopod; exp-1 (2,3), proximal (middle, distal) segment of exopod; Md, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; P1–P6, first to sixth thoracopod; sap, synapomorphy; spl, symplesiomorphy; UPRM-MMI, University of Puerto Rico, Mayagüez - Museum of Marine Invertebrates, PR, USA (Department of Marine Sciences).



**Fig. 1** Distribution map of Novocrinidimorpha. Type locality of taxa is represented by different colors. Modified from Iliffe (2000)

**Systematics**

Class COPEPODA H. Milne Edwards, 1830

Order HARPACTICOIDA Sars 1903

Family Novocriniidae Huys and Iliffe 1998

Genus *Atergopedia* Martínez Arbizu and Moura 1998

*Atergopedia dowgialli* sp. nov.

Additional species: *Atergopedia vetusta* Martínez Arbizu and Moura 1998; *Atergopedia longicaudata* Gheerardyn et al. 2009; *Atergopedia confluenta* (Kornev and Chertoprud 2008).

**Descriptive part**

*Atergopedia dowgialli* sp. nov. (Figs. 2–6)

**Etymology**

The species epithet is in honor of Dr. Michael Dowgiallo, Branch Chief, Regional Ecosystem Research Branch, NOAA/NCCOS/Center for Sponsored Coastal Ocean Research, who was one of the key protagonists initiating research and management on mesophotic coral ecosystems through NOAA's Deep Coral Reef Ecosystems Studies program and additional research cruises within the US Caribbean.

**Type material**

Holotype female, dissected on six slides (UPRM-MMI no 10097).

**Type locality**

The *Atergopedia* specimens were collected on October 21, 2008, on the shelf edge of southwest Puerto Rico, near La Parguera (Fig. 1). The type locality is called Hole-in-the-Wall, a well known location of mesophotic reefs (Latitude° 17.88476, Longitude° -67.02192, 77 m depth).

**Description of female holotype**

Habitus (Fig. 2a) fusiform, tapering posteriorly, with a slight demarcation between prosome and urosome. Total body length 468 µm measured from anterior margin of rostrum to posterior margin of telson. First pedigerous somite incompletely fused to cephalosome, lacking a tergite and concealed beneath an extension of the cephalic shield and the rugged hyaline frill. Cephalic shield with sensilla as figured; increasing in width posteriorly. Rostrum broad, triangular with simple blunt tip, fused to cephalic shield, with two sensilla. Hyaline frills non-striated and rugged. Fifth pedigerous somite and the first half of the genital double somite with oblique row of spinules ranging from their middle to the distal portion and less developed in the first portion of the genital double somite. Second half of the

genital double somite and the following somite with a continuous distal row of spinules. Last urosomite with a continuous median row of spinules. Telson with two rows of spinules inserted middle ventrally and a continuous row of spinules near the insertion of the furca. Anal operculum convex. Furca rectangular, short, two times broader than long, with six setae (Fig. 2a, e). Seta I not observed or missing; seta II smooth, short and inserted distolaterally; seta III of the same size of seta II, and disto-ventrally inserted; setae IV and V the longest; seta VI as long as seta II and III, inserted beneath seta V; seta VII biarticulate at the base and dorsally inserted.

Antennule (Fig. 2b) 9-segmented, slender, with aesthetascs on fourth and last segments. Second segment with an inner row of 3 long spinules. Armature formula: 1/9/5/1+(1+ae)/1/3/2/2/6+(1+ae).

Antenna (Fig. 3a, b) basis without seta, completely separate from endopod. Exp 4-segmented; segments 1–3 each with 1 seta; segment 4 with 2 long setae and 1 minute smooth seta. Enp 2-segmented, enp-2 with 7 distal setae, 3 of them geniculate, and 5 setae at the oral margin, the innermost geniculate.

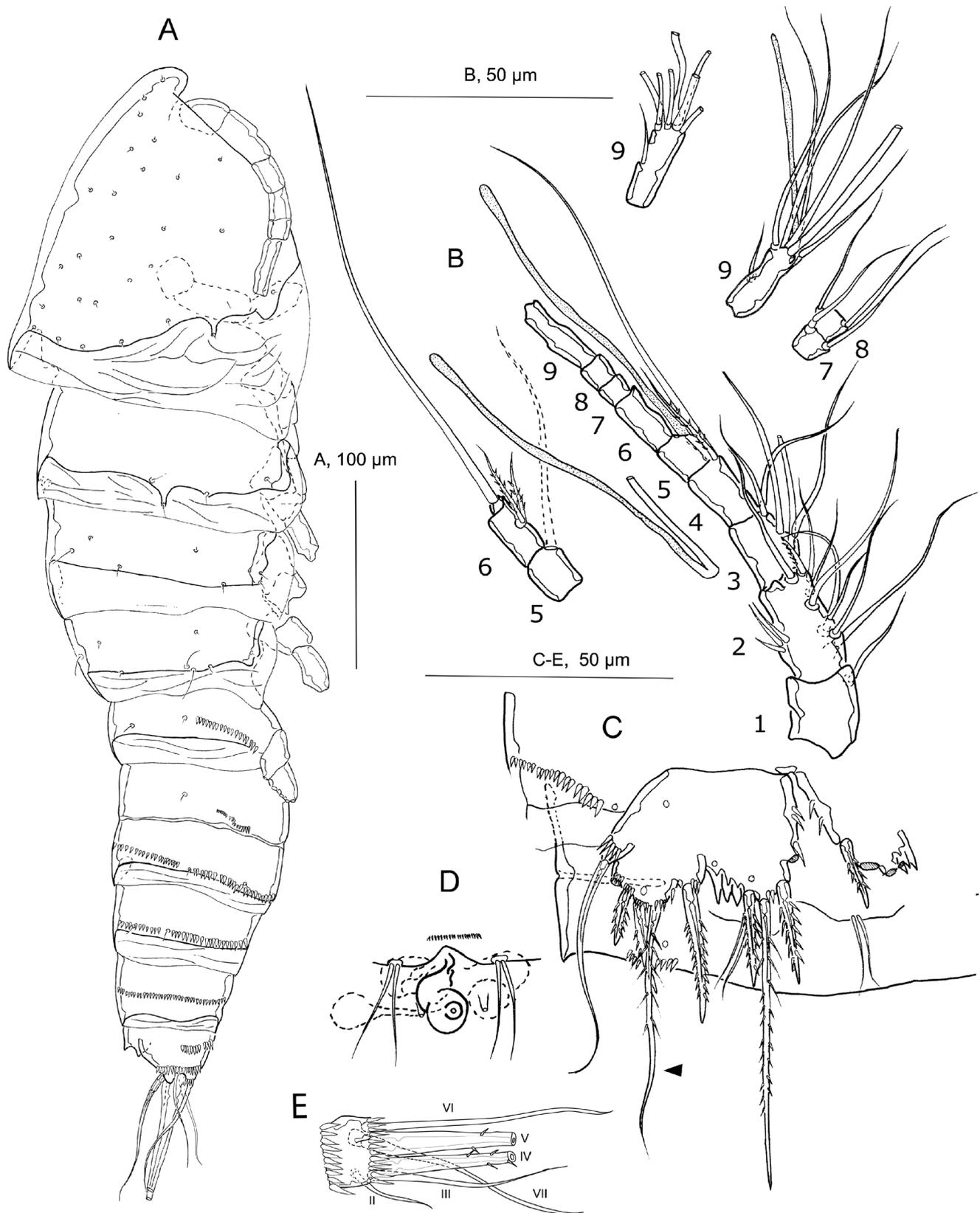
Mandible (Fig. 3i–k). Coxa elongate, gnathobase with 1 pinnate seta and several distal teeth. Basis with 1 inner seta; exp 4-segmented, with setal formula 1/1/1/2 and a 1-segmented enp bearing 1 inner and 4 distal setae.

Maxillule (Fig. 3n–o). Praecoxa with 9 terminal setae and 2 surface setae. Coxal endite cylindrical, with 5 setae. Basis with two endites bearing 3 setae each. Exopod 1-segmented, small and cylindrical, outwardly directed, bearing two apical setae. Endopod 1-segmented, bearing 4 distal and 2 subdistal setae.

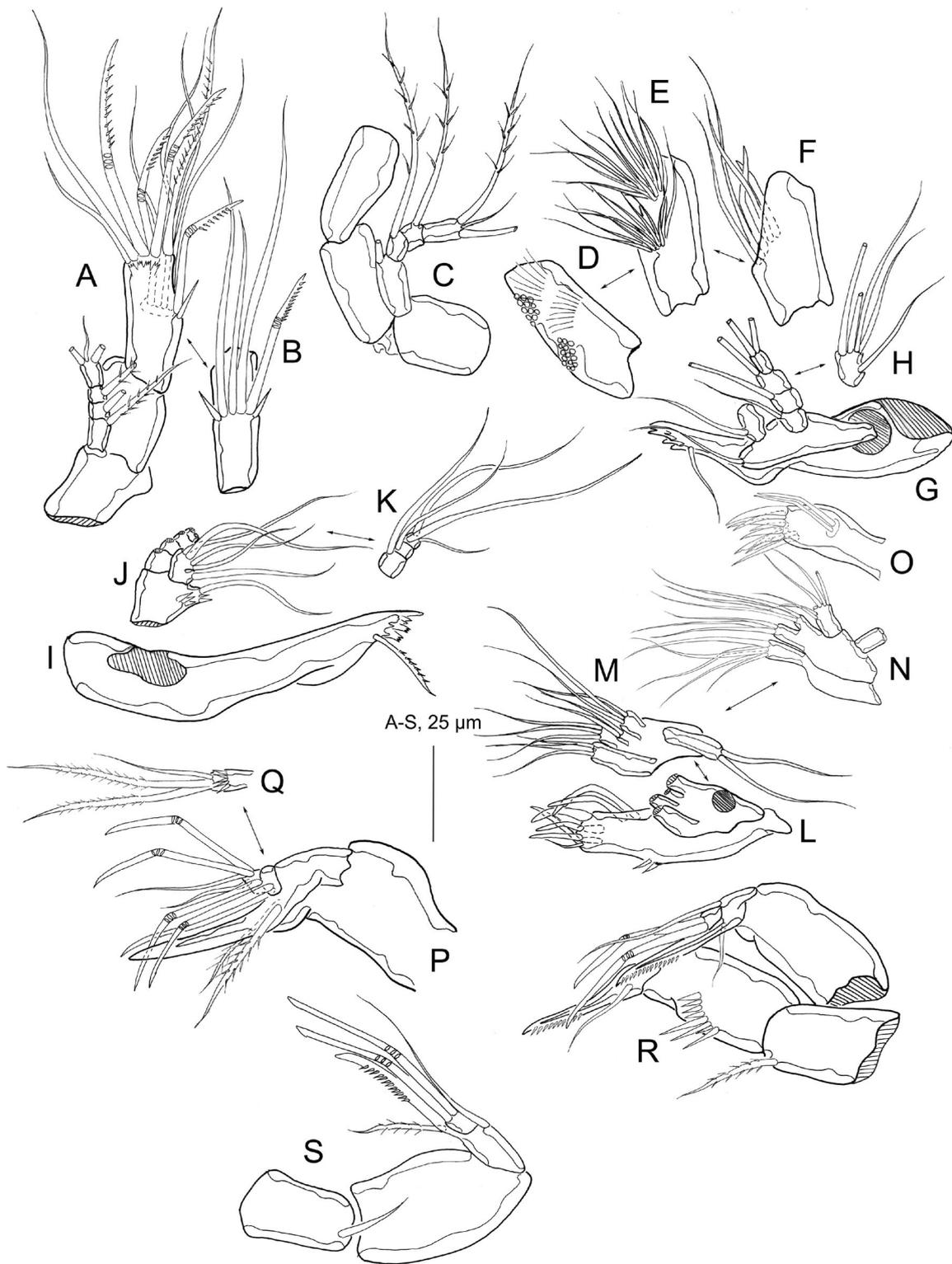
Maxilla (Fig. 3p–q). Syncoxa with 1 endite bearing 3 setae, 2 long, bipinnate and a small smooth seta. Basis drawn out into strong claw; accessory armature consisting of 2 pinnate setae. Endopod 2-segmented, with 2 geniculate setae on proximal segment and 2 geniculate setae as well as 2 slender setae on distal segment.

Maxilliped (Fig. 3r) subchelate, well developed. Syncoxa with 1 bipinnate inner seta at distal corner. Basis without seta and with a row of long spinules. Endopod 2-segmented; first endopodal segment with 1 short, inner seta, and distal margin produced into a strong, pinnate claw; second endopodal segment with 1 slender seta proximally inserted on base of segment, and 2 distal, geniculate setae.

Swimming legs P1–P4 (Fig. 4a–f) with well-developed praecoxae, coxae, bases, and 3-segmented rami; with pattern of pores and long and minute spinules as figured. Intercoxal sclerites rectangular; of P1 with distal spinules, P4 without distal spinules, P2 and P3 not observed. Bases with outer pinnate spine (P1) or smooth seta (P2–P4; broken in P2); inner distal corner with inner seta (P1).

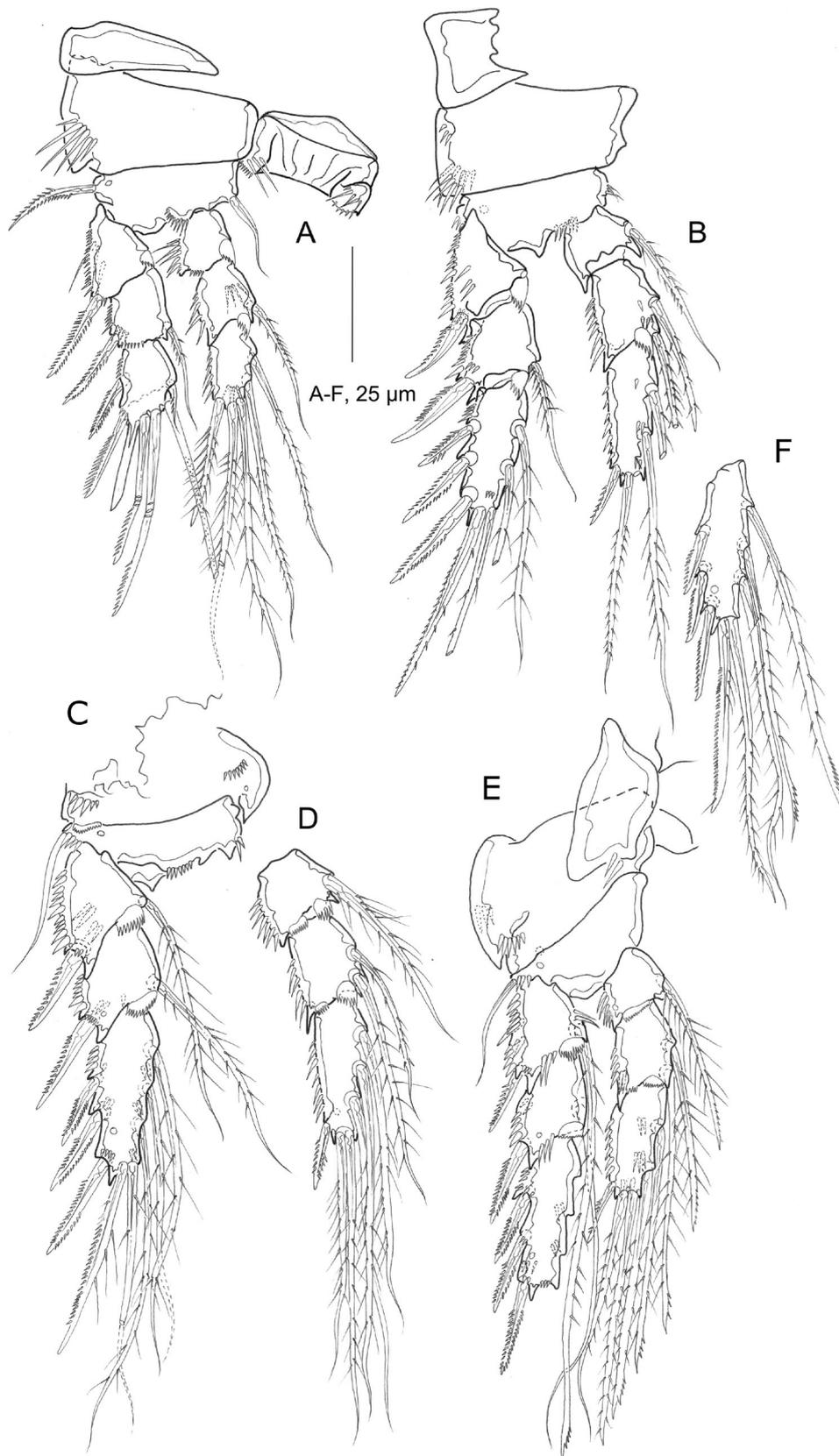


**Fig. 2** *Atergopedia dowgialli*, sp. nov. Female: **a** habitus, lateral view; **b** antennule; **c** P5, anterior; **d** genital field. Segments 5–9 of A1 have been drawn separately for clarity



**Fig. 3** *Atergopedia dowgialli*, sp. nov. Female: **a** antenna; **b** antenna ep-2; **i** mandible, gnathobasis; **j** basis, endopod, and exopod of mandible, exopod without setation (see **k**); **k** exopod-2, -3, -4 of mandible with setation; **n–o** slightly tilted coxal and basal endites of maxillule, exopod reduced setation as in male (see **m**); **r** maxilliped. Male: **c** antenna with setation of

endopod removed; **d** antenna ep-2; **e** antenna ep-2 showing cluster of setoid elements; **f** antenna ep-2; **g** mandible with reduced setation on endopod (see **h**); **h** mandible, endopod; **l** praecoaxal arthritis of maxillule; **m** coxal and basal endites, endopod, and exopod of maxillule; **p** damaged maxilla; **q** syncoxa of maxilla; **s** maxilliped



**Fig. 4** *Atergopedia dowgialli*, sp. nov. Female: **a** P1, anterior; **b** P2, anterior; **c** P3, anterior; **d** P3 endopod (detached from basis during dissection); **e** P4 with exopod 3 without full armature for clarity; **f** P4 exp-3

Endopod of P1 as long as exopod; endopods of P2-P4 reaching to middle of respective exp-3.

P1 (Fig. 4a). Coxa with outer row of long spinules; basis with a row of spinules near the insertion of the enp. exp-1-3 and enp-1-3 approximately of the same size. Exp-3 with 6 elements; two outer spines, two distal geniculated setae, one long seta on the distal inner corner and a reduced inner seta. A long hyaline process occurs between the outer spine and the first geniculate seta.

P2-P4 (Fig. 4b-f). Coxa and basis ornamented as depicted. Outer exopodal spines more strongly developed than in P1. Outer distal corners of exopodal segments 1 and 2 and inner and outer distal corners of endopodal segments 1 and 2 forming spinous processes. Presence of inner setae with modified tip on the enp1-3 of P4 (Fig. 4f). P4 exp-1 (Fig. 4e) with modified seta longer than the whole exopod, exp-3 with 2 modified setae at the inner margin. Swimming-leg setal formulae as in Table 1.

P5 (Fig. 2c). Benp and exp fused, forming one wide plate; with 4 pores on anterior surface; with outer basal seta arising from short setophore. Endopodal lobe with 3 spines and one a long seta. Three spinous processes between endopodal and exopodal lobe. Exopodal lobe with 5 elements, of which at least 3 are strong spines and one is a long seta. Small intercoxal sclerite present.

Genital double-somite wider than long; with subcuticular ridge ventrally and laterally, representing original segmentation. Genital field (Fig. 2d) located in distal half of genital double-somite. Copulatory pore located medially, covered in the holotype by a copulatory plug. Sixth legs represented by two plates medially fused, armed with 2 setae each.

**Male**

Allotype dissected on 11 slides (UPRM-MMI no 10098).

Total body length 311µm measured from anterior margin of rostrum to posterior margin of telson. Sexual dimorphism in antennule, antenna, maxillule, P1-P6, and genital segmentation. Abdominal male ornamentation with exactly the same pattern as in female, but stronger (Fig. 5d-e).

**Table 1** Swimming-leg setal formulae of female *Atergopedia dowgialli* sp. nov

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	I-1	I-0, I-1, II-3-1	0-0, 0-1, I-2-2
P2	0-0	I-0	I-1, I-1, III-I+1-2	0-1, 0-2, I-2-2
P3	0-0	I-0	I-1, I-1, III-I+1-3	0-1, 0-2, I-2-3
P4	0-0;	I-0	I-1, I-1, III-I+1-3	0-1, 0-2, I-2-2

Antennule (Fig. 6b) 9-segmented, slender; haplocer with aesthetascs on the 3rd, 5th, and 9th segments. Armature formula: 1/10/4+(1+ae)/2/4+(1+ae)/1/1/2/10+(1+ae).

Antenna (Fig. 3c-f) basis, exopod and enp-1 essentially as in female. Armature of enp-2 as in female, with two additional cluster of setoid elements.

Mandible (Fig. 3g, h). Essentially as in female except gnathobase with 1 naked seta.

Maxillule praecoxal arthritis with reduced number of distal elements (Fig. 3l); coxa, basis, exp and enp (Fig. 3m) as in female.

Maxilliped (Fig. 3s). Essentially as in female except syncoxa with 1 naked inner seta at distal corner and basis without row of long spinules.

P1-P4 (Fig. 6a-f). Armature as in female. P1 (Fig. 6a) basis with pinnate inner seta; exp-3 with two distal bipinnate spines and a bipinnate longer inner seta, hyaline process shorter. Transformed setae not observed on P3 (Fig. 6e-f) and P4 (Fig. 6c-d). Swimming-leg setal formulae as in Table 2.

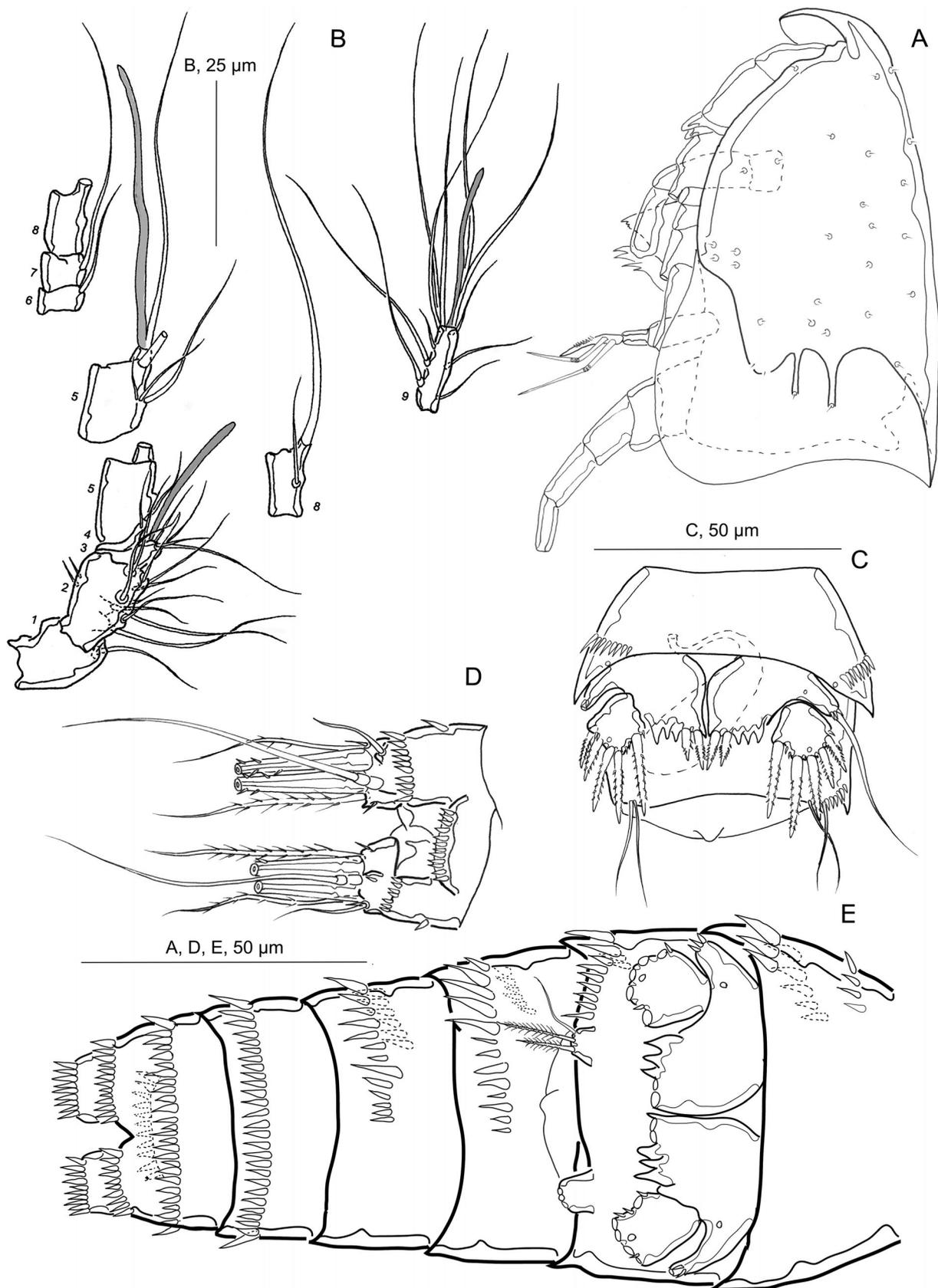
P5 (Fig. 5c, e). Benp and exp not fused; with 1 pore at the basis of the benp setophore and 1 pore at the exp. Outer basal seta arising from long setophore. Endopodal lobe with 2 stout spines, three spinous processes between endopodal lobe and the exp. Exp armed with 5 strong spines. No intercoxal sclerite present.

P6 (Fig. 5c, e). Represented by a continuous plate with 2 long setae on each side of the body.

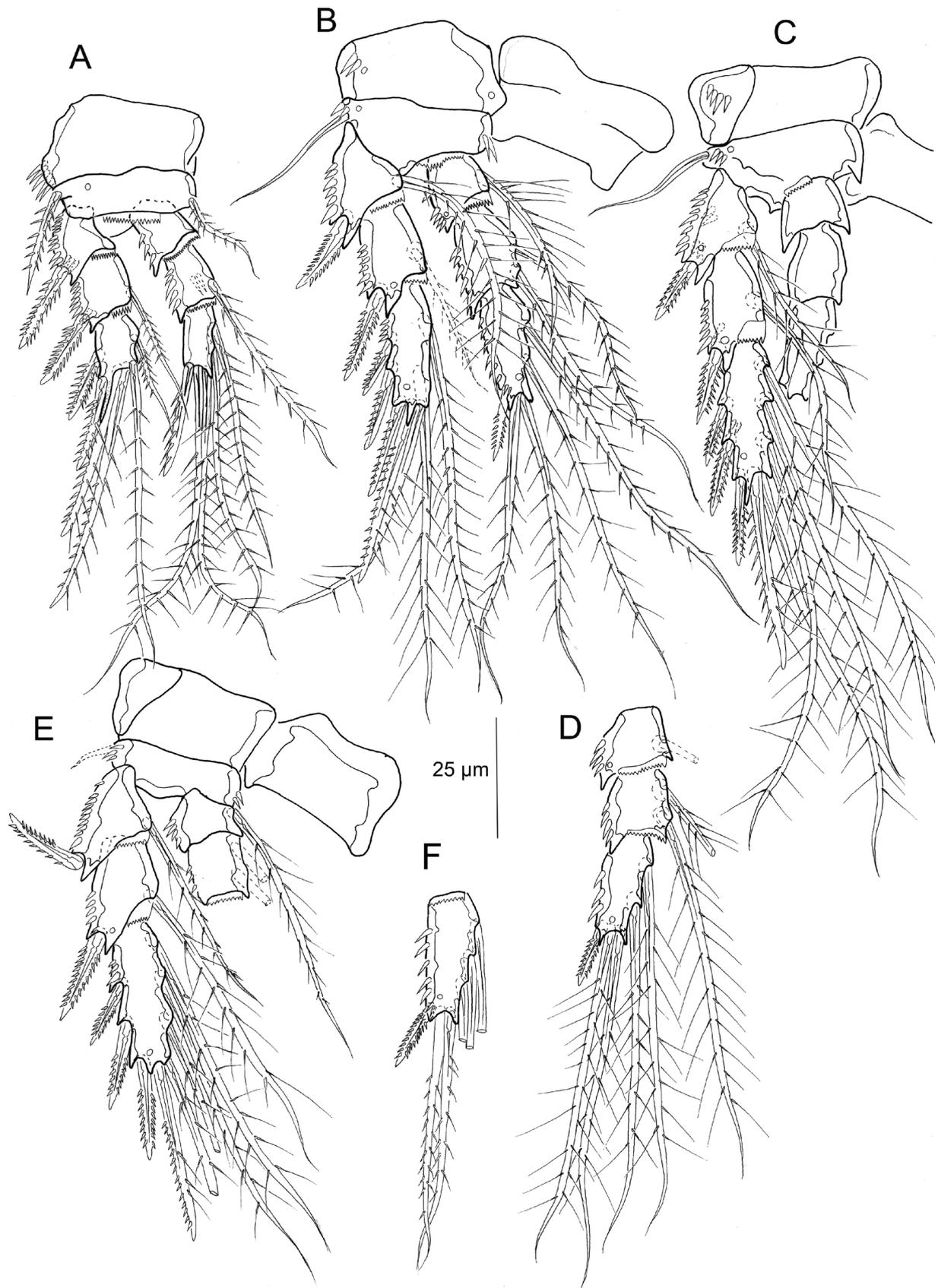
**Discussion**

The family Novocriniidae was proposed by Huys and Iliffe (1998) to accommodate the species *Novocrinia trifida* Huys and Iliffe 1998 from anchialine caves in Belize. Martínez Arbizu and Moura (1998) established the family Atergopediidae to house the species *Atergopedia vetusta* from Arctic oligotrophic sediments, but this became a junior synonym as Huys and Iliffe (1998) had established the name Novocriniidae earlier in the same year (Gheerardyn et al. 2009). Gheerardyn et al. (2009) described *Atergopedia longicaudata* from cold water corals in the Porcupine Seabight (NE Atlantic). In the same publication these authors synonymized the genus *Archeotisbe*, previously proposed by Kornev and Chertoprud (2008), with *Atergopedia*. The morphological similarity of *Atergopedia confluenta* with *Atergopedia vetusta* and their geographical proximity (i.e., *A. confluenta* was sampled from shallow, shelly bottoms in the White Sea) raises questions about its validity. Pending new studies, *A. confluenta* must be considered valid and closely related to *A. vetusta*.

In this work we describe a fifth species from the Caribbean mesophotic reefs of Puerto Rico. *Atergopedia dowgialli* sp.



**Fig. 5** *Atergopedia dowgialli*, sp. nov. Male: **a** cephalothorax, lateral view; **b** antennule, segments 5–9 drawn separately for clarity; **c** P5, P6; **d** furca, dorsal view; **e** urosome, ventral view



**Fig. 6** *Atergopedia dowgialli*, sp. nov. Male: **a** P1, anterior; **b** P2, anterior; **c** P4, anterior with unarmed endopod; **d** P4 endopod; **e** P3, anterior with broken endopod 3; **f** P3 endopod 3

**Table 2** Swimming-leg setal formulae of male *Atergopedia dowgialli* sp. nov

Leg	Coxa	Basis	Exopod	Endopod
P1	0–0	I-1	I-0, I-1, II-II+1-1	0–0, 0–1, I-2-2
P2	0–0	I-0	I-1, I-1, III-I+1-2	0–1, 0–2, I-2-2
P3	0–0	I–0	I-1, I-1, III-I+1-3	0–1, 0–2, I-2-3
P4	0–0	I–0	I-1, I-1, III-I+1-3	0–1, 0–2, I-2-2

*nov.* is a typical novocriniid, sharing the following characters with other novocriniid species [synapomorphies (sap) and symplesiomorphies (spl) within brackets]: First pedigerous somite incompletely fused to cephalosome and lacking a tergite (sap); female and male A1 9-segmented (spl), haplocer and with supranumerary aesthetascs in the male (spl); A2 enp-2 with setoid tufts in the male (sap), which are the result of a secondary multiplication of setal elements (Huys and Iliffe 1998; Martínez Arbizu and Moura 1998); Md with elongated gnathobasis (spl); Mxp morphology of the Novocrinidomorpha kind (spl) (viz. Seifried 2003), P1–P4 with 3-segmented exp and enp, without marked sexual dimorphism (spl) and setiform element IV (arrowed) on female P5 exp (sap) (Fig. 2c).

The new species can be easily placed within the genus *Atergopedia*, sharing the following synapomorphies with its congeners: 1) A2 without seta on the first endopodal segment; 2) Lateral armature of the female A2 shows a multiplication of distinct setae and consists of 1 geniculate seta followed by 5 or more slender setae; 3) P1 enp-1 without inner seta; 4) male fifth leg with two spines on endopodal lobe and 5) female P5 exp fused to benp; 6) female fourth exopodal element transformed into a long seta.

The new species differs from the previous species included within *Atergopedia* by the following *hitherto* unknown character within the family, which we consider autapomorphic, supporting the establishment of the new species: (1) The presence of a long process between the outer and distal elements of the leg 1 exopodite 3 which is stronger and longer in the female, and (2) a bilobed male and female leg 5 benp and exopodal lobe; (3) the presence of a row of spiniform processes between the leg 5 benp and exp; (4) female P5 spines are of unequal sizes, with the largest appearing in the inner margin of the exopodal lobe; (5) female P6 with two setae on each halph opercular plate; (6) possession of a very short and strongly ornamented furca in both sexes. The *Atergopedia* species are similar to each other, differing in some few characters involving body ornamentation, furcal size, mouth parts, and pereopods shape and armature. Within the genus *Atergopedia*, *A. dowgialli* sp. nov. seems to be closely related to *Atergopedia longicaudata*, sharing with this species the loss of the basal seta of both A2 and Mxp and the loss of the

first Mx2 endite. *Atergopedia dowgialli* sp. nov shares with *A. vetusta* the same morphology of the seta II of the female P5 endopodal lobe, which is transformed into a spine in *A. longicaudata*.

The correct placement of the new species within the genus *Atergopedia* cannot be properly addressed without a formal phylogenetic analysis, which is out of the scope of this contribution.

## Distribution

The distribution of the Novocriniidae fauna (Fig. 1) reveals no bathymetric pattern, with species occurring in both shallow and deep-sea ecosystems. With the exception of *Atergopedia confluenta*, from the mesotrophic White Sea (viz. Filatov et al. 2005), the other Novocriniidae species were sampled from oligotrophic systems. The genus *Novocrinia* encompasses a single species, *Novocrinia trifida* Huys and Iliffe 1998, from a shallow anchialine cave in Belize (8–10 meters deep). The genus *Atergopedia*, instead, is not coupled with the anchialine environments. *Atergopedia vetusta*, for example, is recorded at 534 meters deep at the Barents Sea (Martínez Arbizu and Moura 1998). Kornev and Chertoprud (2008) described *A. confluenta* from 10 m deep samples taken at the mesotrophic Karelian Coast in the White Sea. Gheerardyn et al. (2009) described *A. longicaudata* from dead coral fragments at 969 meters depth of the Porcupine Sea Bight. In this study we describe a new species of *Atergopedia* sampled at 77 m depth from the mesophotic zone of southwest Puerto Rico.

The emerging pattern, therefore, implies an initial colonization of oligotrophic environments such as deep sea or stygobiont environments such as anchialine caves by novocriniids. Food in the stygobiotic environment may be scarce overall or at best patchy (Iliffe and Kornicker 2009); the same applies to the deep sea (Gage and Tyler 1991). In these environments, the distensible P1 somite and the long mandible gnathobasis [viz. Syngnathartha (Seifried and Schminke 2003); i.e. Parameiropsidae Corgosinho and Martínez Arbizu 2010] form an oral cone with the labrum, similar to which appears in some parasitic orders such as Siphonostomatoida, which could represent adapted tools for acquisition of large pieces of scarce food or even for a commensal or parasitic life. Though the question remains whether Novocriniidae originated in anchialine caves or if they spread from deep-sea environments to anchialine ones. A deep-sea origin has been proposed for some anchialine species having close relatives that inhabit bathyal depths (Hart et al. 1985). Both caves and the deep sea are old, climatically stable, lightless, and non-rigorous environments (Iliffe and Kornicker 2009). Anchialine habitats on islands and continental margins could be connected via a continuum of crevicular corridors extending from shallow depths to the deep sea (Iliffe 1990).

Seifried (2003) proposed the Novocrinidomorpha to hold the families Novocriniidae, Superornatiremidae, and Rotundiclipeidae. With exception of the genus *Atergopedia* and the Superornatiremidae species *Gideonia noncavernicola* from the Patagonian continental slope (Chile) (George and Martínez Arbizu 2005), all the remaining Novocrinidomorpha are from anchialine caves (Fig. 1), which is an indicative of the origin and diversification of its composing families within this kind of environment. In the karst environments of Puerto Rico there are anchialine caves; however, the *Atergopedia* specimens were clearly collected from a deep reef system, with no anchialine caves in the vicinity. This distribution of the Novocrinidomorpha suggests an origin and diversification, which could have happened inside the Tethys Sea, before its closure, when the Novocrinidomorpha would have adapted to shallow oligotrophic zones and anchialine caves. In fact, the strongest alternative to a deep-sea origin is that suggested by the clear Tethyan distribution patterns exhibited by anchialine taxa that never penetrate into the fresher parts of the cave systems (Boxshall and Jaume 1999). With the separation of the landmasses, the anchialine caves would act as refuges of the Tethyan fauna; relicts of the once widespread, warm-water fauna of the Tethys Sea (Boxshall and Jaume 1999).

In accordance with Hennig's (1966) progression rule, in a monophyletic group, the spatial distribution of taxa parallels the character transformation series. The species that accumulates more plesiomorphies is found closer to its center of origin, while derived species, undergoing peripheral allopatric speciation, accumulate more apomorphies and are found at the peripheries. Today's data support the origin of the Novocrinidomorpha and the Novocriniidae in anchialine environments. Within Novocriniidae, the genus *Novocrinia* is closer to its center of origin and accumulates a higher number of plesiomorphic structures such as A2 with seta on the enp-1, md palp with two basal seta, P1 enp-1 with inner seta, P5 of male and female with 1-segmented exp and P5 of male and female with the same number of the same number of elements in the exp and in the enp. Therefore, it seems probable that *Novocrinia*, by remaining in the anchialine environment, has retained these plesiomorphies, while *Atergopedia* shows the apomorphic conditions as the result of their colonization of other oligotrophic environments and adaptation to life outside the anchialine environment. Nonetheless, structures compatible with what Danielopol et al. (1996) described as the "darkness syndrome" are retained unaltered, such as the increase in number of the sensorial structures in the male A1. In accordance with these authors, those continental shelf species that acquired traits, which fit the darkness syndrome in shallow depths will more easily spread into the subsurface and/or deep-sea habitats. Modifications of sensory structures are also mentioned by Iliffe and Kornicker (2009) as adaptations to the life inside anchialine caves and other stygobiotic

environments. Although some phylogenetic analyses of morphological characters support independent colonization of deep-sea and anchialine habitats (Stock 1986; Danielopol 1990), the presence of Novocrinidomorpha families basically in anchialine caves and some few derived species in the deep sea (especially Novocriniidae) advocate a secondary colonization of the last, similarly to Misophrioida (see Boxshall and Jaume 1999). We hypothesize that with the rearrangement of the ocean current northwards, during post Eocene glacial periods, some novocrinidomorphid fauna could have migrated between shallow and deep-sea areas via crevicular corridors. This migration included the *Atergopedia* species, which spread to other Atlantic as well as northern oligotrophic environments via the deep sea.

Evidence against fauna exchange between shallow environments and the deep sea includes the questionable ability which species show to cross the oceanic thermocline (Iliffe and Kornicker 2009). Nevertheless, the eurybathic distribution of some species [e.g. *Argestes mollis* Sars, 1910; *A. tenuis* Sars, 1921; *Eurycletodes (O.) abyssi* Lang, 1936 (George 2004)], ranging from the littoral down to deepest bathyal areas, is well known.

**Acknowledgments** The UPRM-CCRI-DMS technical rebreather divers (C. Sherman, M. Nemeth, I. Bejarano, H. Ruiz, M. Carlos) collected all samples. Partial funding was provided by the National Oceanographic and Atmospheric Administration Coastal Ocean Programs under award #NA06NOS4780190 to the Department of Marine Sciences, University of Puerto Rico at Mayagüez.

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