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On two new paraonids (Annelida, Paraonidae) from Bahía de los Angeles, Gulf of California, Mexico

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Abstract

Two new species of Paraonidae (Annelida) belonging to the genera *Aricidea* (*Acmira*) Hartley, 1981 and *Paradoneis* Hartman, 1965, are described from soft bottoms of Bahía de Los Angeles, Gulf of California. *Aricidea* (*Acmira*) *blackei* **sp. nov.** is characterized by having a short, digitiform antenna with a discrete swollen base; by possessing notopodial postchaetal lobes in prebranchial and branchial region, changing gradually in size and shape from the first two chaetigers to the last pair of branchiae; last pair of branchiae being shorter than the rest; and by having curved hooks with a very strong hood and a fragile arista. *Paradoneis mackiei* **sp. nov.** is characterized by the presence of lyrate notochaetae with tines of different thickness along body, showing an evident increament in size from anterior to posterior end. Identification keys to all species of *Aricidea* (*Acmira*) and *Paradoneis* are included.

Key words: Cortez Sea, *Aricidea*, *Paradoneis*, new species, Biosphere Reserve

Introduction

Paraonidae Cerruti, 1909, is a family of polychaetes that comprises small burrowing worms that rarely exceed 20 mm in length. The family is organized into eight genera and 170 accepted nominal species (Blake, 2019, Read & Fauchald, 2024). Paraonids are present in all oceans, inhabit soft substrates and appear to be most common in continental shelf and slope depths, where they are frequently among the dominant species of infaunal benthic communities (Blake & Hilbig, 1994, Blake *et al*. 2009, Blake, 2019). Nonetheless, several species are known from shallow waters and even from intertidal environments (e.g. de Léon-González & Díaz-Castañeda, 2011, Romano *et al*. 2016, Ribeiro *et al.* 2018).

The phylogenetic placement of Paraonidae has been intriguing for decades, with reconstructions changing depending on morphological or molecular approaches. Based on morphology, Paraonidae was nested within the Clade Scolecida in the earlier study by Rouse & Fauchald (1997), with Orbiniidae and Questidae (now combined) as the most closely grouped families. This arrangement was also recovered by Rouse & Pleijel (2001) based on a compilation of various polychaete phylogenetic hypotheses. Afterwards, many molecular studies included a few paraonids within large datasets, showing a closer affinity of Paraonidae with Cirratuliformia, rather than with the Scolecida. The latter was identified as a polyphyletic group, with morphological affinities driven mostly by evolutionary convergence rather than common descent (Rousset *et al*. 2007, Struck *et al.* 2007, 2008, Bleidorn 2009, Zrzavý *et al*. 2019).

The first molecular phylogeny of Paraonidae was assessed by Langeneck *et al.* (2019), who analyzed 16S rDNA, COI and 18S rDNA sequences of 38 species. Their study provides interesting findings. First, the monophyly of Paraonidae was confirmed. Second, despite the strong morphological divergence between Paraonidae and

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Sternaspidae, the analysis by Langeneck *et al.* (2019) supports a close relationship between these two families, as previously suggested by Bleidorn (2005). Second, the phylogenetic reconstruction of Paraonidae does not reflect the current taxonomic scheme. Before 2019, the family was organized in eight genera: *Aparaonis* Hartman, 1965 (monotypic), *Aricidea* Webster, 1879 (with 4 subgenera), *Cirrophorus* Ehlers, 1908, *Levinsenia* Mesnil, 1897, *Paradoneis* Hartman, 1965, *Paraonella* Strelzov, 1973, *Paraonis* Cerruti, 1909 and *Sabidus* Strelzov, 1973 (monotypic) (Blake, 2019). The phylogenetic reconstruction obtained by Langeneck *et al.* (2019) recovered five clades within Paraonidae, where *Aricidea*, *Cirrophorus* and *Paradoneis* were not monophyletic. Third, *Levinsenia* and *Paraonis* were each retrieved as monophyletic where the sampling of the latter was restricted to one nominal species and two terminals. Fourth, Langeneck *et al.* (2019) established the genus *Blakeia* for an isolated, morphologically homogeneous group of *Aricidea* species (with *Aricidea* (*Acmira*) *simplex* Day, 1963 as type species), but it is a preoccupied homonym by a Lepidoptera that requires a new name (Read & Fauchald, 2024). Fifth, none of the subgenera traditionally recognized within *Aricidea* were monophyletic (*Aricidea*, *Aedicira* Hartman, 1957, *Acmira* Hartley, 1981, *Strelzovia* Aguirrezabalaga, 2012). Thus, there are inconsistencies between the current systematics of Paraonidae and the available phylogenetic reconstructions. Besides, no cladistic analysis of Paraonidae based on morphology has been performed to family-genera-species levels that allow a better comprehension of features useful to recognize groups. In addition, a vast number of descriptions of new species of paraonids are being documented from everywhere (Blake, 2019, and references therein), but few of them analyzes and propose the use of new characters to distinguish species and genera (e.g. Erdoğan-Dereli & Çinar, 2020).

In the Gulf of California, Mexico, 12 species of paraonids were included in the compilation by Hendrickx (2005). Since then, the number of species has increased to 28 based on ecological and taxonomical studies (de León-González *et al.* 2006, Hernández-Alcántara & Solís-Weiss, 2013, Hernández-Alcántara *et al.* 2017, Cuéllar-Mercado *et al*. 2019).

Bahía de los Ángeles is part of a Biosphere Reserve located in the Gulf of California Midriff Island region on the eastern coast of the Baja California peninsula (DOF, 2007). This bay is important for its biodiversity, high productivity and tourism. The family Paraonidae was first reported from the Bahía de los Angeles by Reish (1968), who found *Aricidea uschakowi* Zachs, 1925 (accepted as *A*. (*Allia*) *suecica* Eliason, 1920 *fide* Strelzov, 1973, but as a controversial synonym it demands a deep revision), *Paradoneis lyra* Southern, 1914 and *Paraonis gracilis oculata* Hartman, 1957 (currently recognized in *Levinsenia* Mesnil, 1897 and raised to the status of species), and also described *Aricidea rosea* as a new species. Since then, no one has reported additional paraonids in the locality.

In the present work two new species belonging to the genera *Aricidea* (*Acmira*) and *Paradoneis* were found in a survey held in 2013 and here are formally described from Bahía de los Angeles. A key to the world's species is provided for each genus.

Methods

Field work

Sediment samples were taken in 12 stations using a Petit Ponar grab (0.023 m^2). Five grabs were taken per station, four replicates for macrofauna analysis and the fifth for granulometry and organic matter analyses. Sediments were sieved using a 1.0 mm mesh size and retained material was relaxed for 10 min in 8% $MgSO_4$ solution and then fixed in 7% buffered sea-water-formalin solution. In the laboratory, samples were washed using a 0.5 mm sieve and transferred to 70% ethanol. Macrofaunal organisms were sorted and counted; polychaetes were separated to be identified to species level.

Identification

Observations and body measurements were undertaken with an Olympus BX51 microscope with differential interference contrast (DIC). Microphotographs were taken with a Nikon D610 camera, using the Helicon Focus program for capturing and superimposing images. Drawings were made with a camera lucida. A specimen was dehydrated in a series of increasing concentrations of hexamethyldisilazane (HMDS). Once air-dried, they were

mounted on aluminum stubs and gold-coated for observation in a JEOL JSM-6010Plus-LA scanning electron microscopy at the Scanning Electron Microscopy Laboratory (LMEB), ECOSUR-Chetumal. In order to standardize and facilitate comparison between species of *Aricidea* Webster, 1879, the length of antenna is classified in terms of chaetigers reached backwards: short if the antennae do not exceed chaetiger 1 and long if the antennae exceed chaetiger 2.

Data resources

Type material and additional materials were deposited in the Colección Poliquetológica, Universidad Autónoma de Nuevo León (UANL, NL-INV-002-05-09).

Results

Paraonidae Cerruti, 1909

Genus *Aricidea* Webster, 1879

Subgenus *Aricidea* (*Acmira*) Hartley, 1981

Type species. *Aricidea catherinae* Laubier, 1967

Diagnosis: Prostomium subtriangular, pear-shaped to oval, with rounded anterior margin; antenna simple, usually unbranched and unarticulated. Posterior lip of mouth extending through ventral surface of first two chaetigers. Chaetae of three types: limbate in the anterior part, thin capillaries in the post-branchial region, and modified neurochaetae which are heavy, curved spines with or without hood, with or without accessory filaments, teeth or bristles, always thicker than notochaetae and accompanying capillary neurochaetae (Blake, 2019).

Aricidea (*Acmira*) *blakei* sp. nov.

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Figures 1–4

Type material

Holotype (UANL-8171), 2 paratypes (UANL-8172), Bahía de los Angeles, Baja California, Gulf of California, Mexico, Station M3-2, November 14, 2013, N28.89534 W113.50281, 17 m depth.

Additional material

12 specimens. 1 specimen, (UANL-8173), Bahía de los Angeles, Baja California, Gulf of California, Mexico, Station M2-4, November 14, 2013, N28.90032 W113.48569, 17 m depth; 1 specimen, (UANL-8174), Station M4-2, N28.89650 W113.51538, 14 m depth; 1 specimen, (UANL-8175), Station M5-4, N28.90727 W113.52895, 16 m depth; 1 specimen, (UANL-8176), Station M8-1, N28.94241 W113.55211, 10.8 m depth; 1 specimen, (UANL-8177), Station M8-3, N28.94241 W113.55211, 10.6 m depth; 1 specimen, (UANL-8178), Station M11-1, N28.97932 W113.54205, 12.8 m depth; 3 specimens, Station M11-2, (UANL-8179), N28.97932 W113.54205, 12.9 m depth; 4 specimens, (UANL-8180), Station M11-3, N28.97932 W113.54205, 11.1 m depth; 1 specimen, (UANL-8181), Station M12-1, N28.99071 W113.54576, 11.4 m depth.

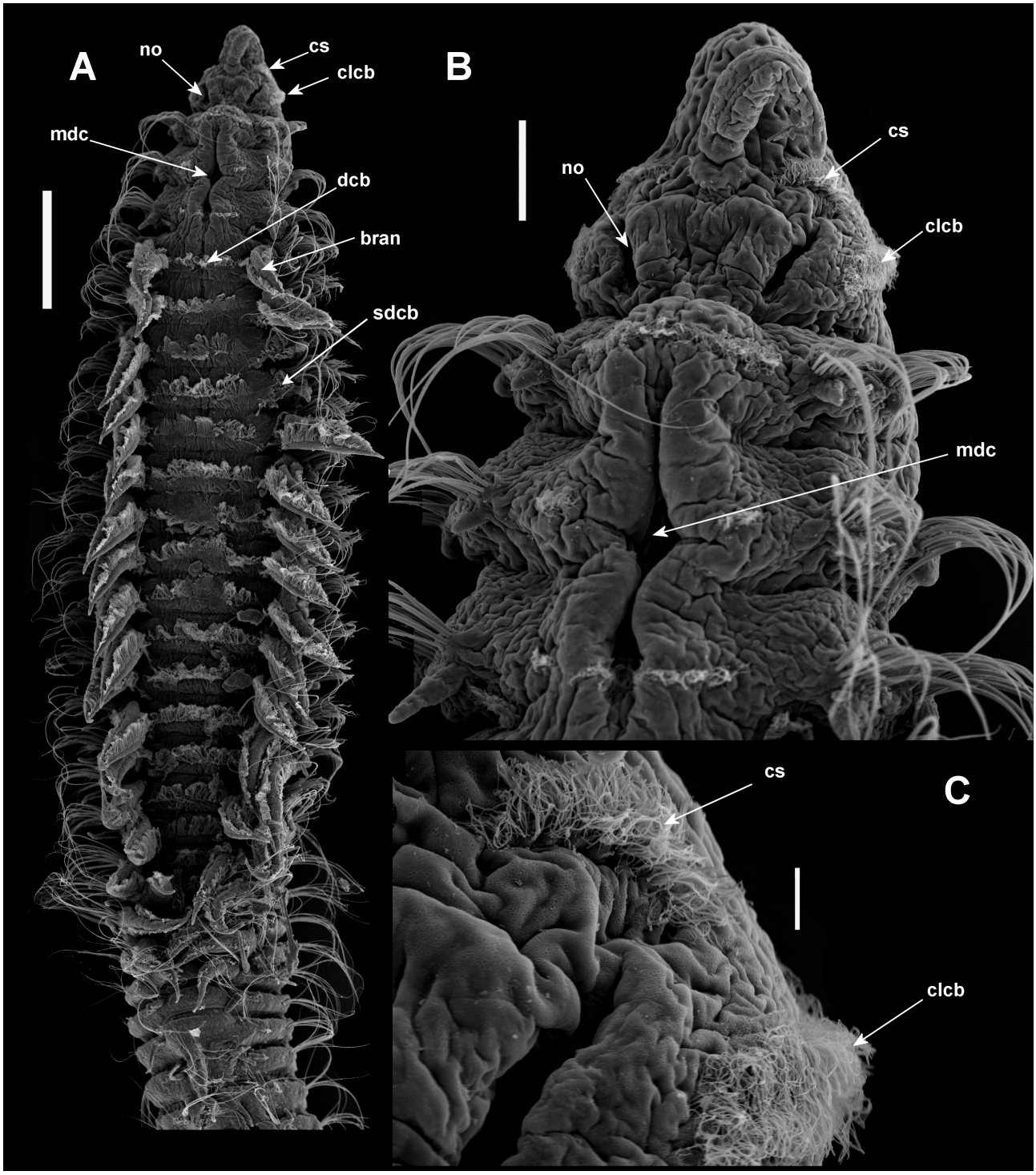

FIGURE 1. *Aricidea* (*Acmira*) *blakei* **sp. nov.** (Paratype) A. Anterior end, dorsal view; B. Prostomium and first three chaetigers, dorsal view; C. Detail of the right nuchal organ and bands of cilia. Abbreviations: bran, branchia; clcb, crown-like ciliary band; cs, ciliary slits; dcb, dorsal ciliary band; mdc, median dorsal crest; no, nuchal organ, sdcb, short dorsal ciliary band. Scale bars: A, 200 µm; B, 50 µm; C, 10 µm.

Description

Holotype complete, 11 mm long (8–11 mm in paratypes), 0.5 mm wide (0.3–0.7 mm in paratypes) with 140 chaetigers (124–140 in complete paratypes). Color in preserved worms pale yellowish. Body cylindrical and robust, branchial region thicker than pre- and postbranchial regions (Fig. 1A). First three segments with a median dorsal crest (mdc) (Figs 1A–B, 3B, 4A), in specimen prepared for SEM, crest appears as a dorsally cleft elevation, whereas in specimens examined under light microscopy, the crest is an uncleaved elevation (Figs 3A, 4A). Prostomium subtriangular, wider than long, anterior margin rounded (Figs 1A–B, 3A). Eyes absent in all specimens. With a pair of crown-like ciliary bands (clcb) inserted in postero-lateral side of prostomium. A pair of ciliary slits (cs) located anteriorly to nuchal organs, semicircular in shape (Fig. 1B–C). Antenna digitiform, short, extend back to mid part of first chaetiger, with discrete swollen base and small group of cilia surrounding base (Fig. 2A). A pair of nuchal organs present, as diagonal, narrow, deep, short and slanted slits placed on dorso-lateral sides of posterior prostomium; dense internal ciliation not reaching outer margin of slits (Figs 1A–B, 2A).

A dorsal ciliary band present on mid-dorsal transversal line of each pre-branchial and branchial chaetiger: that of chaetiger #1 form a complete ciliary band with short cilia, that of chaetiger #2 divided in two small bands with short cilia, those of chaetiger #3 forming almost an entire band of medium length cilia. From chaetiger #5 to end of branchial region all ciliary bands are entire with very long cilia (Fig. 1A). A pair of short dorsal ciliary bands (sdcb) present just posterior to base of each branchia (Figs 1A, 2B). Intersegmental ciliary bands not present.

Branchiae numbering 20 pairs in holotype (15–24 pairs in paratypes), starting on chaetiger #4, foliaceous with wide base, tapering towards distal part and digitiform tip, slightly longer in middle branchial region, last pair of branchiae shorter than others (Fig. 1A); dense ciliary bands on both sides of branchiae from the basal part to subdistal region, bare distal part (Figs. 1A, 2B, 4B); branchiae shorter than segment width. Branchiae length/wide: 254.9 μm/110.8 μm in anterior region (chaetiger #4); 376.8 μm/110.8 μm in middle region (chaetiger #11), 221.6 μm/55.4 μm in posterior region (chaetiger #23).

Notopodial papillae absent. Notopodial postchaetal lobes present in prebranchial region; short, conical on first two chaetigers (Figs. 1B, 3C); increasing in length and becoming stout, digitiform with asymmetrical swollen base on chaetiger #3 (Figs. 1B, 3D, 4A); in the branchial region they increase in size until penultimate pair of branchiae, cirriform and thin tips (Figs. 3E, 4B), from last pair of branchiae onwards cirri are thin and long, filiform (Figs. 3F–G). Neuropodial postchaetal lobe as hemispherical tubercle present from chaetigers 1 to 32.

Lateral sense organs present on all chaetigers, located between noto- and neuropodia, closest to and slightly behind postchaetal lobe (Fig. 1B), with flexible cilia distinctly protruding from opening or embedded into pore.

Three main types of chaetae present: limbate, capillary and modified neurochaetae (Figs. 2C–E). First 17 chaetigers with very numerous limbate chaetae, thick basally, attenuating towards distal part. In chaetiger #18 thin capillary chaetae appear, of lesser abundance. Modified neuropodial chaetae present from chaetiger #32 (21–36 in paratypes) to the last chaetigers, absent on 2 prepygidial segments, numbering 1–3 in each neuropodium. Anterior parapodia with only one modified neurochaeta 2.8 μm wide; median parapodia with three modified neurochaeta of different widths (inferior 5.6 μm wide, middle 2.8 μm wide, superior 8.4 μm wide); posterior parapodia with modified neurochaetae also of different widths (inferior 5.6 μm, middle 8.4 μm, superior 11.2 μm wide (Figs. 2E, 4C). Modified neurochaetae accompanied by thin capillary chaetae (Fig. 2E); neurochaetae as curved hooks (90° degrees towards terminal region), with strong hood, hood with numerous fibrils and encompassing curved end of shaft except for small subdistal gap (Fig. 2C); with a short, thin and fragile arista arising from terminal region, in most of the specimens the arista is missing, but insertion scar of where it was implanted is visible only using SEM imaging (Fig. 2D).

Pygidium with three cirri, two inserted ventro-laterally, one cirrus placed mid-ventrally, short, all digitiform with the base wider, tapering towards the distal part (Fig. 2F). Pygidium surrounded by a band of cilia, much denser in the dorsal region than in the ventral region, usually each cilium emerges from a pore, in ventral region with groups of cilia emerging from a single pore. Anal cirri with clusters of cilia emerging from pores (Fig. 2F).

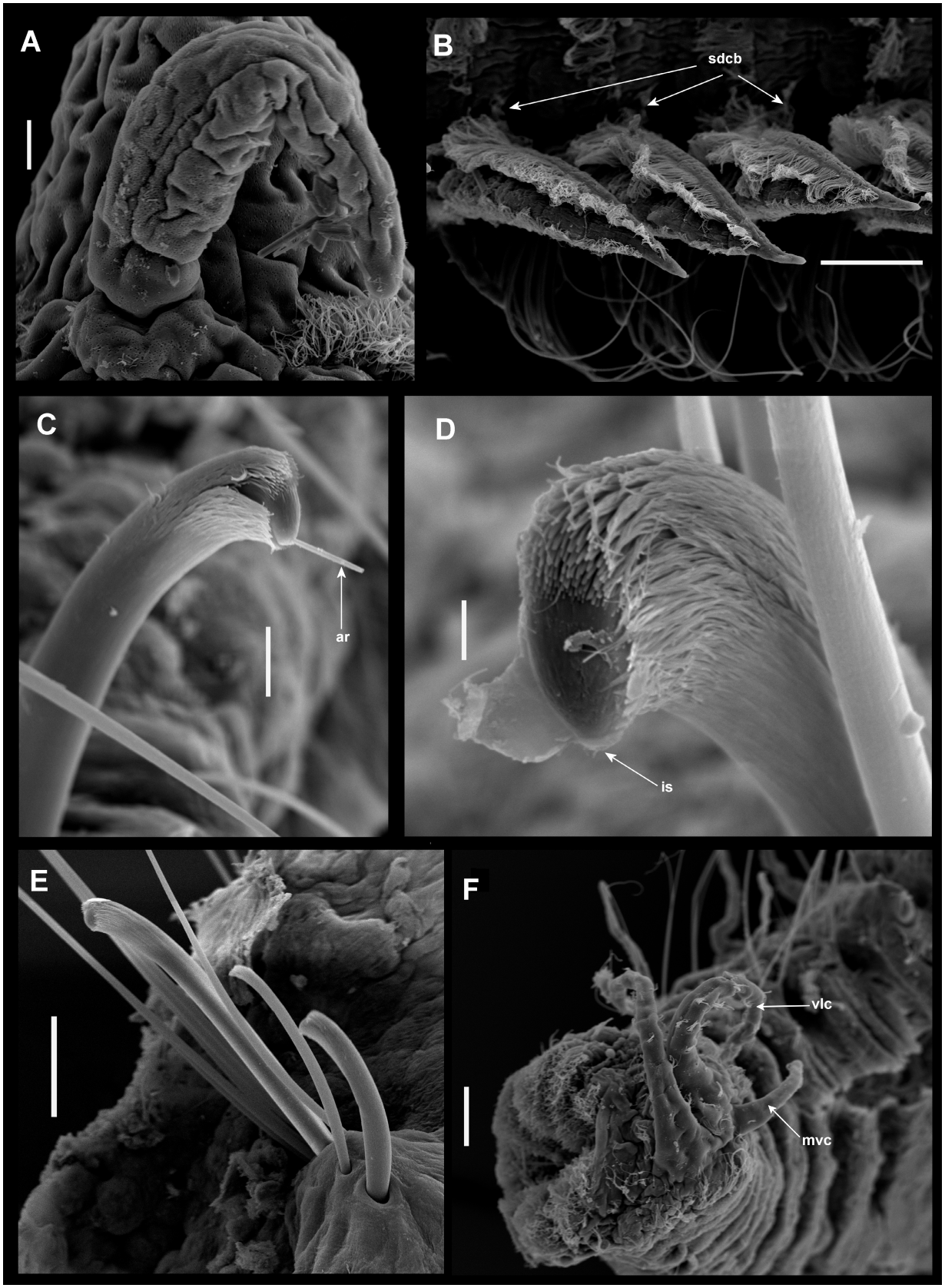

FIGURE 2. *Aricidea* (*Acmira*) *blakei* **sp. nov.** (Paratype) A. Antenna, detail; B. Branchiae area, dorsal view; C. Modified neurochaetae with broken arista; D. Modified neurochaetae shown trace of implantation of the arista; E. Posterior neuropodia showing three sizes of modified neurochaetae; F. Posterior end, ventral view. Abbreviations: ar, anterior arista; is, insertion scar of modified neurochaeta; mvc, mid- ventral cirrus; sdcb, short dorsal ciliary band; vlc, ventro-lateral cirrus. Scale bars: A, 10 µm; B, 50 µm; C, 5 µm; D, 2 µm; E, 20 µm; F, 20 µm.

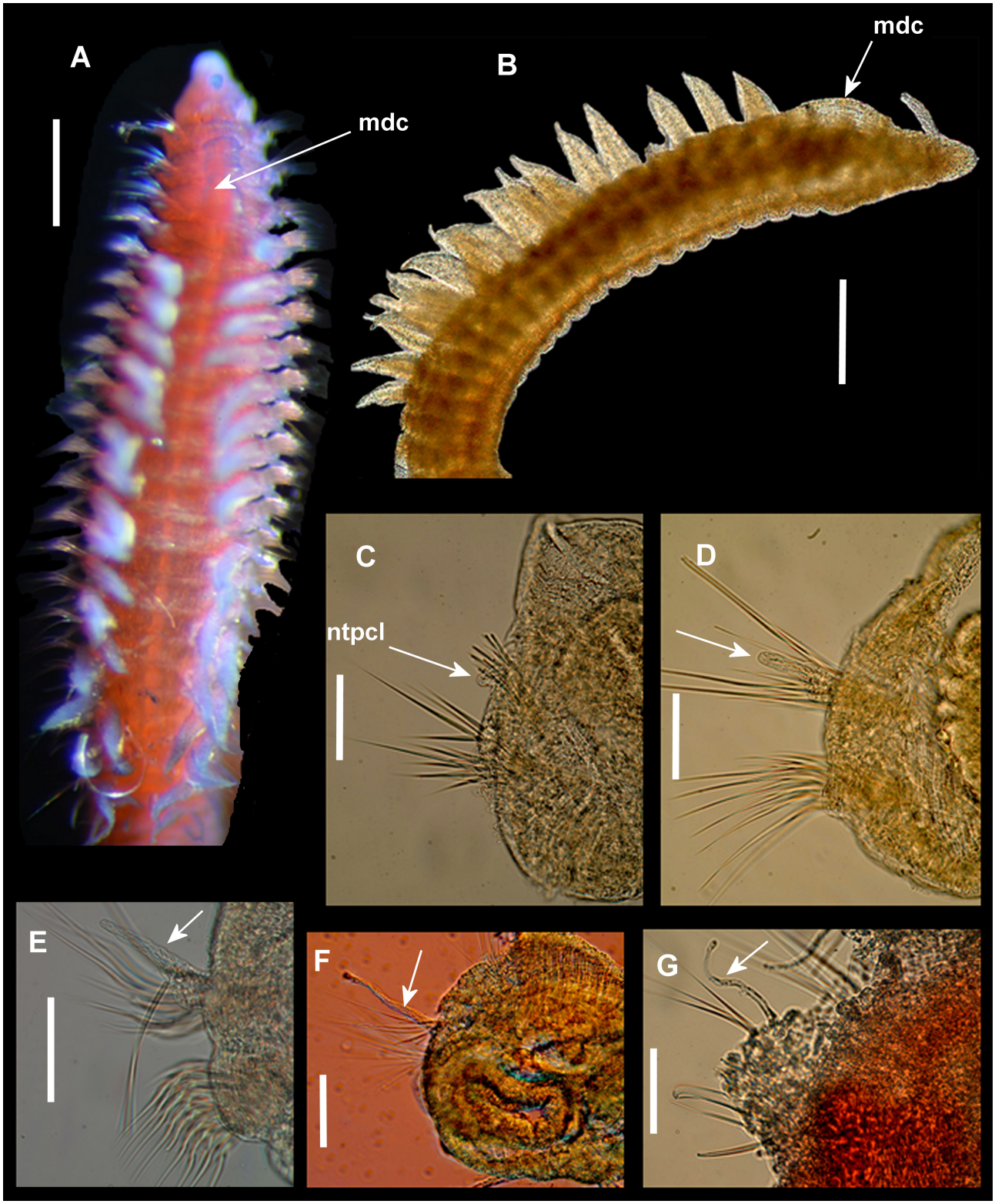

FIGURE 3. *Aricidea* (*Acmira*) *blakei* **sp. nov.** A. Anterior end, dorsal view, stained with Shirla stain A (Holotype); B. Anterior end, lateral view (Paratype); C. Parapodium # 1; D. Parapodium # 3; E. Parapodium # 9; F. Parapodium from median region; G. Parapodium from posterior region (C–G Specimen from station 11–3). Abbreviations: mdc, median dorsal crest; ntpcl, notopodial postchaetal lobe. Scale bars: A–B, 332.5 µm; C–G, 110.8 µm. Arrows in D–G point to notopodial postchaetal lobe.

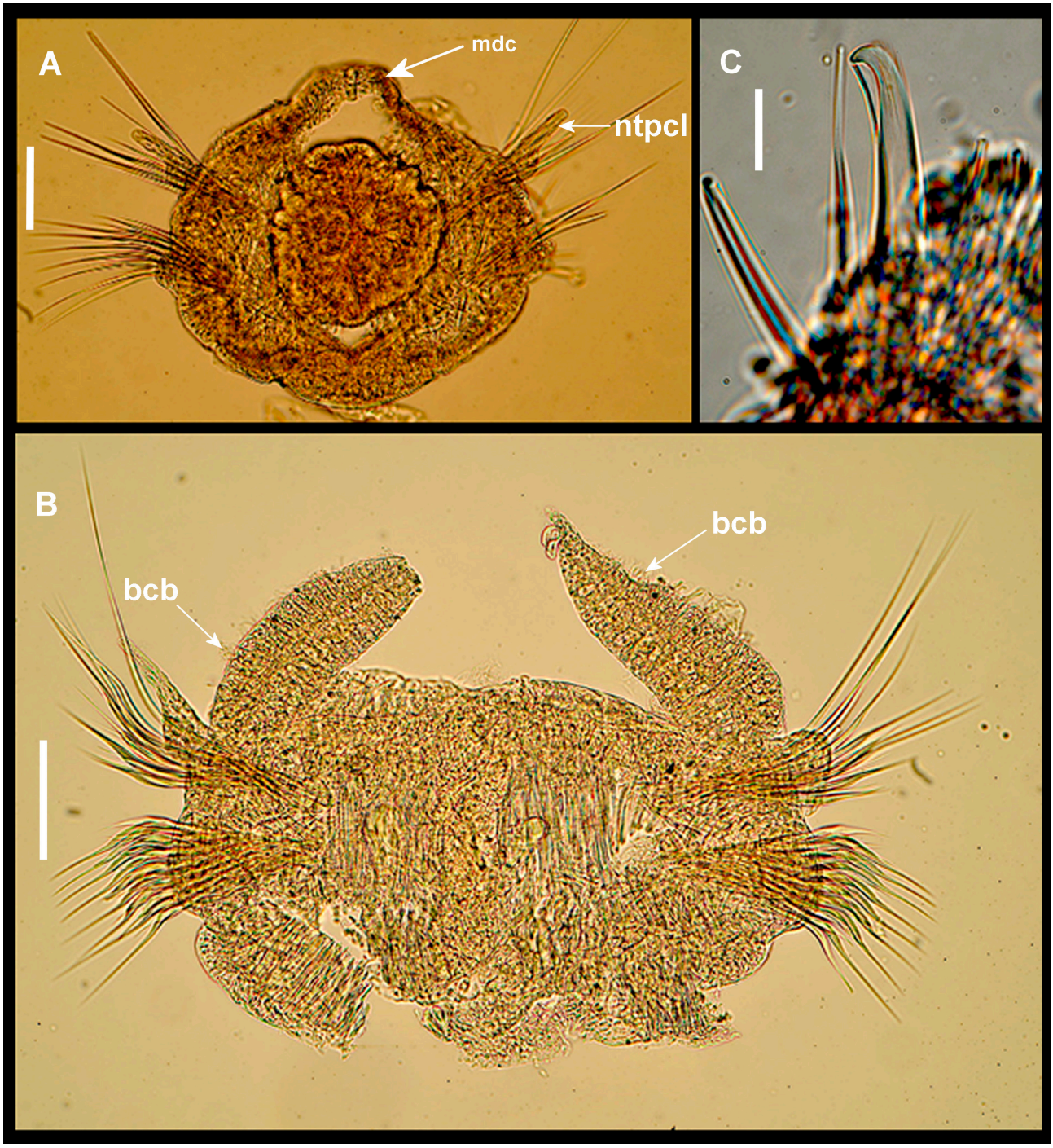

FIGURE 4. *Aricidea* (*Acmira*) *blakei* **sp. nov.** (specimen from station M11–3) A. Transversal section of chaetiger # 3; B. Transversal section of chaetiger # 9; C. Modified neurochaetae from a posterior chaetiger. Abbreviations: bcb, branchial ciliary band; ntpcl, notopodial postchaetal lobe, mdc, median dorsal crest. Scale bars: A–B, 110.8 µm; C, 11.2 µm.

Etymology

Specific name is in honor of James A. Blake, a great American polychaetologist whose trajectory and excellent work on the knowledge of annelid polychaetes, including paraonids, made systematics easier and inspired many generations.

Remarks

The subgenus *Acmira* has traditionally been used to place species easily recognized by having a variety of modified neurochaetae (Blake, 2019), which are thick or thin curved spines, with or without hoods, filaments, teeth or accessory spines. Before this work, *Aricidea* (*Acmira*) was represented by 34 species and two subspecies after Blake (2019), Barroso *et al.* (2020), Erdoğan-Dereli & Çinar (2020) and Plathong *et al*. (2020).

Aricidea (*Acmira*) *blakei* **sp. nov.**, is mainly characterized by having a short digitiform antenna (not exceeding chaetiger 1) with a discrete swollen base; by possessing notopodial postchaetal lobes with asymmetrical base swollen in prebranchial and branchial region, changing gradually in size and shape from the first two chaetigers to the last pair of branchiae; last pair of branchiae being shorter than the rest; and by having curved hooks with a very strong hood and a fragile arista.

Aricidea (*Acmira*) *blakei* **sp. nov.**, *A. elongata* Imajima, 1973, *Aricidea eximia* Imajima, 1973, *Aricidea katzmanni* Erdoğan-Dereli & Çinar, 2020 and *Aricidea catherinae sensu* Aguirrezabalaga (2012) belong to a small group of species characterized by possessing a rather slender antenna, reaching back to the 1st, 2nd-3rd chaetigers, without inflated median region; relatively long, tapered branchiae; modified neurochaetae which gradually become thicker towards the pygidium, with a thin terminal arista that easily breaks. *Aricidea* (*Acmira*) *blakei* **sp. nov.** differ from these species in terms of the following characteristics: (1) the shape and size of antenna: digitiform, short, extends back to mid part of first chaetiger in *A*. (*A*.) *blakei* **sp. nov.**; slender, long, extends to the anterior part of third chaetiger, basally swollen in *A*. (*A*.) *eximia*; slender, long, extends back to second to fourth chaetiger in *A*. (*A*.) *elongata*; digitiform, with more or less swollen region above mid-region, with cilia, extends to chaetiger 2 in *A*. (*A*.) *katzmanni*; thicker in the middle zone, becomes attenuated and ends in a thin point, inserted slightly in front of the middle of the prostomium, long, extends to the chaetiger 3 in *A*. (*A*.) *catherinae sensu* Aguirrezabalaga 2012. (2) The shape and size of last pairs of branchiae: last pair of branchiae shorter than the anterior ones but similar in shape in *A*. (*A*.) *blakei* **sp. nov.**; last two pairs of branchiae extremely long with filamentous distal part, each branchia is about two times as long as the former in *A.* (*A*.) *eximia*; posterior four pairs of branchiae are noticeably longer and slender, each is longer than the width of the segment, and ends as slender filamentous tip in *A*. (*A*.) *elongata*; last two pairs of branchiae are cylindrical, smaller than the previous ones, the last pair is the smallest and thinnest in *A*. (*A*.) *katzmanni* and *A*. (*A*.) *catherinae sensu* Aguirrezabalaga 2012. (3) The shape of first two postchaetal notopodial lobes: conical in *A*. (*A*.) *blakei* **sp. nov.**; extremely small, barely visible in *A.* (*A*.) *eximia*; cirriform in *A*. (*A*.) *elongata* and *A*. (*A*.) *katzmanni*; digitiform in *A*. (*A*.) *catherinae sensu* Aguirrezabalaga 2012. (4) Shape of the postchaetal notopodial lobe base in anterior parapodia: with asymmetrical swollen bases in *A*. (*A*.) *blakei* **sp. nov.**, *A.* (*A*.) *eximia* and *A*. (*A*.) *elongata*, and with symmetrical bases in *A*. (*A*.) *katzmanni* and *A*. (*A*.) *catherinae*; (5) The presence and shape of neuropodial lobe: absent in *A.* (*A*.) *eximia* and *A*. (*A*.) *elongata*; as short ridges on chaetigers 1–11 in *A*. (*A*.) *katzmanni*; as hemispherical tubercles in postbranchial region, from chaetigers 1–29 in *A*. (*A*.) *catherinae sensu* Aguirrezabalaga 2012, and from chaetigers 1–32 in *A*. (*A*.) *blakei* **sp. nov.**

Key to species of *Aricidea* (*Acmira*) of the world. In square brackets is the region where the type locality is contained.

1	Modified neurochaetae with arista 2
-	Modified neurochaetae without arista 23
2(1)	Modified neurochaetae with hood 3
-	Modified neurochaetae without hood 11
3(2)	Modified neurochaetae generally with distal pubescence 4
-	Modified neurochaetae without pubescence 8
4(3)	Pubescence in most of the modified neurochaetae, distal arista inserted subdistally; median antenna with thin base and inflated, rounded tip, not extending beyond posterior margin of prostomium . . . . . *A*. (*A*.) *filamentosa* Barroso, Paiva & Ranauro, 2020 [Espírito Santo Basin, Brazil].
-	All neurochaetae modified with pubescence; antenna extending beyond posterior margin of prostomium 5
5(4)	Antenna inserted anteriorly, reaching middle of chaetiger 1, digitiform, with two sub-distal constrictions and rounded distally; last pair of branchiae narrow and long; modified neurochaetae bearing a tuft of distal pubescence and sometimes a short distal arista . . . . . *A*. (*A*.) *bbkingi* Barroso, Paiva & Ranauro, 2020 [Espírito Santo Basin, Brazil]
-	Antennae smooth, without constrictions, inserted medially; modified neurochaetae with distal or subdistal arista on convex side of shaft 6

6(5) Antenna extend back to mid part of first chaetiger, digitiform; notopodial postchaetal lobe short and conical in first two chaetigers; modified neurochaetae with distal arista only seen by SEM . . . . . *A.* (*A.*) *blakei* **sp. nov.** [Bahía de los Angeles, Gulf of California]

- Antenna extend back to chaetiger 2 or beyond; notopodial lobe short and cirriform in first two chaetigers 7

7(6) Antenna extending to chaetiger 2; digitiform with more or less swollen region above mid-region; notopodial postchaetal lobe in postbranchial segments long, stout, finger-like; with 10–21 pairs of branchiae; modified neurochaetae with distal arista . . . . . *A.* (*A.*) *katzmanni* Erdoğan-Dereli & Çinar, 2020 [Sea of Marmara]

- Antenna extending to chaetigers 3–6, slightly thicker initially, then tapering, sometimes weakly telescoping then tapering to pointed tip; notopodial lobe in postbranchial segments filiform; with up to 50 pairs of branchiae; modified neurochaeta with subdistal arista on convex side of shaft . . . . . *A.* (*A.*) *lopezi* Berkeley & Berkeley, 1956 [Eastern Pacific, British Columbia]

8(3) Antenna thick, not reaching posterior margin of prostomium; with 28–30 pairs of branchiae, last pair somewhat longer, narrower; modified neurochaetae curved, acicular, with hooked tip bearing 3–4 spines, with subapical hood on concave side of tip . . . . . *A.* (*A.*) *rubra* Hartman, 1963 [off California, USA]

- Antenna reaching chaetiger 4 9

9(8) Antenna long (extends back to chaetiger 2–4), slender; with 19–20 pairs of branchiae, last four pairs are noticeably longer than the width of segment, with a slender filamentous tip; notopodial papilla absent; notopodial lobe in first two prebranchial chaetigers short and cirriform . . . . . *A.* (*A.*) *elongata* Imajima, 1973 [Japan][1]

- Antenna short (not exceeding chaetiger 2), broad near base or medially; with up to 16 pairs of branchiae; notopodial papilla present 10

10(9) Antenna with thin base, central part swollen, then thin and cylindrical in its distal part; notopodial postchaetal lobe thick, short, digitiform in first two chaetigers, becoming thicker and longer with weakly asymmetrical basal swelling from chaetiger 3 to branchial region, long and filiform in postbranchial region . . . *A.* (*A.*) *catherinae* Laubier, 1967 [Mediterranean Sea, France]

- Antenna clavate, unequally bifid distally, with small subterminal process; notopodial postchaetal lobe small, spherical in first two chaetigers, more elongate in the third chaetiger, subulated in branchial region, becoming slenderer and cirriform in postbranchial region . . . . . *A.* (*A.*) *philbinae* Brown, 1976 [East and west coasts of Florida, USA]

11(2) Modified neurochaeta with subterminal pubescence 12

- Modified neurochaeta without subterminal pubescence 21

12(11) Antenna does not extend beyond the posterior margin of first chaetiger 13

- Antenna extending to chaetiger 2 or beyond 14

13(12) Antenna inserted medially, it reaches back to about the midline of the first chaetiger; notopodial papilla present in first 14 chaetigers; modified neurochaetae with arista inserted medially . . . . . *A.* (*A.*) *laubieri* Hartley, 1981 [Smith Bank, Moray Firth, Scotland]

- Antenna inserted anteriorly, extending to posterior part of prostomium; notopodial papilla absent; modified neurochaetae with arista inserted distally . . . . . *A. (A.) pseudoassimilis* Erdoğan-Dereli & Çinar, 2020 [Sea of Marmara]

14(12) Modified neurochaetae with arista inserted subdistally on convex side 15

- Modified neurochaetae with arista or long fibrils inserted basally on convex side 18

15(14) Antenna inserted medially, extended beyond the second chaetiger; neuropodial postchaetal lobe present. 16

- Antenna inserted distally, extended back to chaetiger 2, moderately inflated in proximal region; neuropodial postchaetal lobe absent; notopodial postchaetal lobe cirriform in prebranchial and branchial region . . . . . *A.* (*A.*) *bispinata* Cantone, 1994 [Ross Sea, Antarctica]

16(15) Notopodial postchaetal lobe with asymmetrical basal enlargement on branchial region. Modified neurochaetae of two types, with or without terminal arista 17

- Notopodial postchaetal lobes short, thick and cirriform on first two chaetigers; long and thick between chaetiger 3–6; filiform on posterior chaetigers. Modified neurochaetae of three types: type I long, relatively thin, with a strong and thick arista at tip; type II short, thicker than others, with a distal end curving at 90°, fibrils (hirsute) subterminally; type III short, thick, with a curved distal end and a strong arista at tip, hirsute subterminally . . . . . *A.* (*A.*) *annae* Laubier, 1967 [Western Mediterranean]

17(16) Antenna extends back to chaetiger 3–4; with 20–28 pairs of branchiae; modified neurochaetae from chaetiger 20–22; with notopodial papilla . . . . . *A.* (*A.*) *finitima* Strelzov, 1973 [Scotia Sea][2]

- Antenna extends back to chaetiger 6; with 12 pairs of branchiae; modified neurochaetae from chaetiger 28–30; notopodial papilla absent . . . . . *A.* (*A.*) *mirifica* Strelzov, 1973 [Antarctica]

18(14) Neuropodial postchaetal lobe present 19

- Neuropodial postchaetal lobe absent 20

19(18) Antenna extending to posterior margin of chaetiger 1, inserted centrally; neuropodial postchaetal lobe from chaetiger 1–19, short, digitiform anteriorly; short, cirriform posteriorly, does not exceed half the size of the neurochaetae . . . . . *A.* (*A.*) *meridionalis* Laubier & Ramos 1974 [Western Mediterranean]

- Antenna extends back to chaetiger 5, inserted distally; neuropodial postchaetal lobe from chaetiger 1–37, slender digitate, as long as the size of the neurochaetae . . . . . (*A.*) (*A.*) *horikoshii* Imajima, 1973 [Japan]

20(18) Antenna clubbed, thin in the proximal part, thickening towards the distal part; notopodial postchaetal lobe short, cylindrical in first two chaetigers, long and subulated on chaetiger 3 and branchial chaetigers . . . . . *A.* (*A.*) *taylori* Pettibone, 1915 [Florida, USA]

- Antenna long, thin, extends back to chaetiger 3–10; notopodial postchaetal lobe short and cirriform in first two chaetigers, long and thin on chaetiger 3 and branchial chaetigers, with strongly developed asymmetrical basal enlargement . . . . . *A.* (*A.*) *assimilis* Tebble, 1959 [Mediterranean Sea]

21(11) Antenna extends back to chaetiger 2, cirriform; notopodial postchaetal lobe in first two prebranchial chaetigers short and

cylindrical; with 10–13 pairs of branchiae . . . . . *A.* (*A.*) *strelzovi* Hartmann-Schröder & Rosenfeldt, 1990 [Off Elephant Island, Antarctica]

- Antenna does not reach posterior margin of prostomium; notopodial postchaetal lobe in first two prebranchial chaetigers conical or cirriform 22

22(21) Antenna oval; notopodial prechaetal lobe in first two prebranchial chaetigers conical; modified neurochaetae from chaetiger 13, with small arista; interramal lobe absent . . . . . *A.* (*A.*) *brevicornis* (Hartmann-Schröder, 1962) [Peru]

- Antenna club-shaped; notopodial prechaetal lobe in first two prebranchial chaetigers cirriform, from chaetiger 3 to 5 with a weak asymmetrical basal enlargement; modified neurochaetae from chaetigers 24–25, with long distal arista; interramal lobe present on branchial segments . . . . . *A.* (*A.*) *punctata* (Hartmann-Schröder, 1962) [Peru]

23(1) Modified neurochaetae with hood 24

- Modified neurochaetae without hood 29

24(23) Modified neurochaetae with distal pubescence; antenna does not reach posterior margin of prostomium 25

- Modified neurochaetae without pubescence; antenna extending beyond posterior margin of prostomium 26

25(24) Claviform antenna, reaches posterior margin of prostomium; last pair of branchiae shorter than anterior ones; prebranchial notopodial postchaetal lobes short and conical in first two chaetigers, the third three times longer than anterior ones; lobes of branchial chaetigers cirriform, 1/3 the length of branchiae . . . . . *A.* (*A.*) *pigmentata* Carrasco, 1976 [Chile]

- Antenna swollen basally, extends back to anterior part of third chaetiger; last two pairs of branchiae extremely elongate, with filamentous distal part, two times as long as former; notopodial postchaetal lobe in first two chaetigers extremely small; those of branchial region slender, digitate, 2/3 as long as accompanying branchiae . . . . . *A.* (*A.*) *eximia* Imajima, 1973 [Japan][3]

26(24) Neuropodial postchaetal lobe present; branchiae from chaetiger 3; with 48–68 pairs of branchiae, last one shorter than anterior ones; notopodial postchaetal lobe from first chaetiger long, digitiform, that of the second chaetiger slightly longer; postchaetal lobe cirriform in branchial and postbranchial region . . . . . *A.* (*A.*) *anusakdii* Plathong, Hernández-Alcántara, Harris & Plathong, 2020 [Gulf of Thailand][4]

- Neuropodial postchaetal lobe absent 27

27(26) Interramal lobe present as rudimentary ridges in branchial region; antenna thick, finger like, with dense ciliation, inserted in mid prostomium, not reaching chaetiger 1; notopodial postchaetal lobe short and cirriform in first two chaetigers, longer, thick, finger like from chaetigers 3 to 20; thin, long and filiform in postbranchial chaetigers . . . . . *A.* (*A.*) *cerruti* Laubier, 1966 [Western Mediterranean Sea]

- Interramal lobe absent 28

28(27) Antenna inserted in mid prostomium; notopodial postchaetal lobe tuberculate in chaetigers 1–5, cirriform from chaetiger 6 to the end of branchial region, long and filiform with spherical tip in postbranchial region . . . . . *A.* (*A.*) *pearti* Barroso, Paiva & Ranauro, 2020 [Eastern Brazil]

- Antenna inserted in mid anterior prostomium; notopodial postchaetal lobe bulbous in first two chaetigers, digitiform from third chaetiger and branchiate region, becoming filiform posteriorly . . . . . *A.* (*A.*) *cerruti pacifica* Imajima, 1973 [Japan]

29(23) Modified neurochaetae with distal pubescence 30

- Modified neurochaetae without pubescence 31

30(29) Antenna proximally inflated, tapering to short blunt end, does not reach posterior margin of prostomium; last four pairs of branchiae smaller than others; modified neurochaetae from chaetiger 18 with blunt shaft surrounded by pubescence in median and distal end of chaetae, some with one or two distal filaments clearly long; neuropodial postchaetal lobe absent . . . . . *A.* (*A.*) *hirsuta* Arriaga-Hernández, Hernández-Alcántara & Solís-Weiss, 2013 [Southern Gulf of Mexico]

- Antenna slender, extending back to anterior part of chaetiger 3; posterior branchiae longer than anterior ones; modified neurochaetae from chaetiger 31, with hirsute tip, anterior filaments noticeably long; neuropodial postchaetal lobe present as inconspicuous low tubercles . . . . . *A.* (*A.*) *flava* Zhou & Reuscher, 2013 [Chinese Sea]

31(29) With up to eight pairs of branchiae 32

- With more than 14 pairs of branchiae 33

32(31) With four pairs of branchiae increasing slightly in size posteriorly; neuropodial modified neurochaetae present from chaetiger 40, curved, falcate; notopodial postchaetal lobe in first chaetiger inconspicuous, digitiform in second and third; cirriform in branchial chaetigers . . . . . *A.* (*A.*) *tetrabranchia* Hartman & Fauchald, 1971 [Western North Atlantic]

- With four to eight pairs of branchiae (very fragile, have fallen off on all specimens of the type description, only distinguished by the branchial bases); modified neurochaetae from chaetiger 20–22, with three types: slightly curved and strongly pointed hooks, thick, but with elongated tip, and with strongly curved tip; notopodial postchaetal lobe in first two chaetigers minute, semispherical, those of third chaetiger digitiform; in branchial region cirriform, increasing in size to posterior chaetigers . . . . . *A.* (*A.*) *jeaneteae* Langeneck, Busoni, Aliani & Castelli, 2017 [Western Ionian Sea]

33(31) Modified neurochaetae thick, curved distally at an angle of 90° 34

- Modified neurochaetae thin, slightly curved 35

34(33) With 16 to 18 pairs of branchiae; notopodial postchaetal lobe in first chaetiger conical; in second and third chaetigers and branchial region digitate, but in branchial region shorter than in chaetigers 2 and 3; in postbranchial region thin, filiform . . . . . *A.* (*A.*) *neosuecica nipponica* Imajima, 1973 [Japan]

- With 30 pairs of branchiae; notopodial postchaetal lobe in first two chaetigers cirriform, in third chaetiger longer than previous chaetigers; in branchial region cirriform, 2/3 the branchial size; in postbranchial region similar, slightly shorter than those of branchial region . . . . . *A.* (*A.*) *simplex* Day, 1963 [West of Cape Town, South Africa]

35(33) Antenna does not reach the posterior margin of prostomium 36

- Antenna slender, inserted medially, reaching chaetiger 2; prostomium distally trilobate; modified neurochaetae of two kinds: with mucronate tips, and thin, slightly recurved; notopodial postchaetal lobe in first two chaetigers extremely small, inconspicuous

. . . . . *A*. (*A*.) *trilobata* Imajima, 1973 [Japan]

36(35) Prostomium subtriangular, with frontal eversible palpode; antenna papilliform, inserted medially; branchiae from chaetiger 3, with 18–30 pairs of branchiae, last two pairs smaller than previous ones; notopodial postchaetal lobe in first two chaetigers cirriform . . . . . *A*. (*A*.) *simonae* Laubier & Ramos, 1974 [Mediterranean, France][6]

- Prostomium trilobate, wider than long; antenna short, slender, inserted posteriorly; with 13–14 pairs of branchiae, last five pairs decrease evenly in size, slender tips become less distinct than in anterior branchial segments; notopodial postchaetal lobe in first two chaetigers short and digitate . . . . . *A*. (*A*.) *crassicapitis* Fauchald, 1972 [Cedros Island, Off Western Mexico]

Notes

[1] Langeneck (pers. comm.) mentioned that *A*. (*A*.) *elongata* is probably synonymous with *A*. (*A*.) *eximia*, since all the individuals on which the description was based are incomplete posteriorly. This does not enable knowledge of the evolution of modified neurochaetae towards the pygidium. In this key we keep both species until a revision confirms or invalidates the synonym. The shape of the prostomium, the development of the first two postchaetal notopodial lobes, and the development of the branchiae are used in the key to discern among morphs.

[2] Strelzov's description was based on specimens from three different regions (California, South Africa and Uruguay). The distribution of the notopodial papilla is only known in two of these regions. In the specimen from California notopodial papilla is found on chaetigers 6–13, whereas in the South African specimen it is found on chaetigers 9–28.

[3] *Aricidea* (*Acmira*) *eximia* Imajima, 1973 and *A*. (*A*.) *elongata* Imajima, 1973 were synonymized with *A*. (*A*.) *catherinae* Laubier, 1967 by Lovell (2002). However, despite having reviewed the type material of both species, Lovell does not provide an explanation for said synonymy. In this work we prefer to keep these species separated until a comparative analysis is carried out, because there are notable morphological differences between the species.

[4] The appearance of branchiae in chaetiger 3 have only been reported for *A*. (*A*.) *simonae* and *A*. (*A*.) *anusakdii* Plathong *et al*. (2020). However, Hartley (1981) emphasized that small-sized specimens of *A. simonae* presented branchiae from chaetiger 4 onwards (Hartley, 1981). Thus, it is important to verify if this pattern also occurs in *A*. (*A*.) *anusakdii* Plathong *et al.* (2020).

[5] Pettibone (1965) describes the antenna of *A*. (*A*.) *taylori* as club-shaped, however she illustrated a paratype with a bifid antenna and mentioned that it is a clear abnormality. This could create confusion and the reader might mistake this characteristic. In this key we include only the primary character of the species.

[6] Kurt-Sahin *et al*. (2019) mentioned variation in the number of branchiae among different populations of *A*. (*A*.) *simonae*, possibly due to ontogeny: 7–36 pairs of branchiae in the British and North Sea specimens (Hartley, 1981); 14 pairs of branchiae in the Atlantic specimens (Aguirrezabalaga & Gil, 2009); 18–30 pairs of branchiae in the western Mediterranean specimens (Laubier & Ramos, 1974); and 16 pairs of branchiae in the Black Sea specimens. However, Hartley (1981) emphasized that in North Sea specimens with 12 pairs or less, branchiae appear for first time on chaetiger 4, and those with more than 16 pairs appear from chaetiger 3. Furthermore, in the different reported populations there are differences in the size and insertion of the antenna (short, thin, button-shaped, inflated at the tip, some reaching the posterior edge of the prostomium, and are inserted in middle or middle anterior part of prostomium), demanding further studies on the high variability.

Genus *Paradoneis* Hartman, 1965

Type species: *Paraonis lyra* Southern, 1914

Diagnosis: Body long, thin, slightly enlarged anteriorly. Prostomium variable in shape (conical, triangular, subtriangular, rounded or truncated anteriorly). Median antenna absent. Eyes usually absent. Prostomial ciliary bands present or absent. Longitudinal nuchal grooves along posterior prostomium margin. Peristomium indistinct or distinct dorsally. Three to six prebranchial segments; branchiae from chaetigers 4–7, numbering 5–48 pairs. All segments with notopodial postchaetal lobes; neuropodial lobes absent. Notochaetae include capillaries and either lyrate chaetae, modified spines, or simple curved spines; neurochaetae capillaries, a few species with curved neuropodial spines in posterior segments. Pygidium rounded terminally, with three anal cirri (Magalhães *et al.* 2018, Blake, 2019).

***Paradoneis mackiei* sp. nov.**
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Figures 5–7

Type material

Holotype, (UANL-8182), two paratypes (UANL-8183) Bahía de los Angeles, Baja California, Gulf of California, Station M4-2, November 14 2013, N28.89650, W113.51538, 14 m depth.

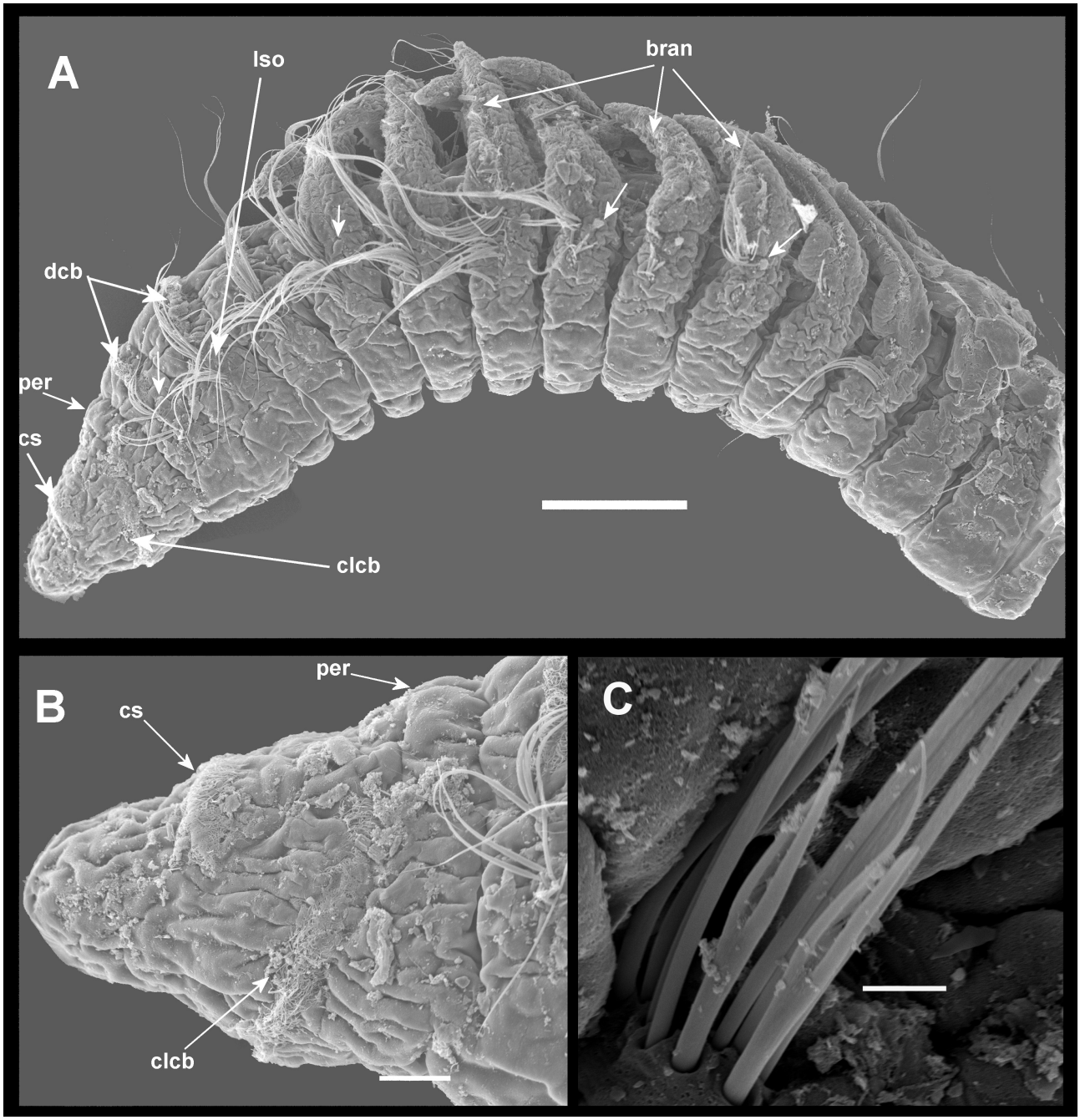

FIGURE 5. *Paradoneis mackiei* **sp. nov.** (Paratype) A. Anterior end, lateral view (Arrows indicate postchaetal lobes); B. Prostomium, lateral view; C. Lyrate notochaetae from mid-body. Abbreviations: bran, branchia; bcb, branchial ciliary band; dcb, dorsal ciliary band; clcb, crown-like ciliary band; cs, ciliary slits; lso, lateral sense organ; nacb, nuchal associated ciliary band; ntpcl, notopodial postchaetal lobe; per, peristomium; tcb, transversal ciliary band. Scale bars: A, 100 µm; B, 20 µm; C, 5 µm.

Additional material

11 specimens. 2 specimens, (UANL-8184) Los Angeles Bay, Baja California, Gulf of California, Station M1-2, November 14 2013, N28.90927, W113.48156, 18 m depth; 1 specimen, (UANL-8185), Station M1-4, N28.90927, W113.48156, 18 m depth; 3 specimens, (UANL-8186), Station M2-4, N28.90032, W113.48569, 17 m depth; 5 specimens, (UANL-8187), Station M3-1, N28.89534, W113.50281, 17 m depth.

Description

Holotype complete, 9 mm long (4.5–10 mm long in paratypes), 0.2 mm wide (0.15–0.2 mm wide in paratypes) with 84 chaetigers (83–89 chaetigers in paratypes). Color in ethanol pale yellowish. Body thin, cylindrical; significantly thicker at beginning of postbranchial region; gradually thinner towards posterior end. Prostomium subtriangular, slightly longer than wide, anterior end distinctly conical; eyespots present (Fig. 7A). Nuchal organs elongated, located dorsally (Fig. 7A). Two ciliated bands on the prostomium, dorsal one (ciliary slits) extended laterally, ventral one (crown like ciliary band) extended latero-dorsally without reaching the nuchal organs (Fig. 5A–B). Peristomium fused with prostomium ventrally indistinct, starting point posterior to nuchal organs (Fig. 7A–B), observed dorsally as a small fold overlapping posterior end of prostomium. Dorsal ciliary bands present on prebranchial segments, not seen posteriorly (Fig. 5A).

Branchiae lanceolate, ciliated on the outer margin from the proximal part to near distal end on each branchia. Beginning from chaetiger 4, holotype with 9 pairs, paratypes 9–10 pairs. Branchial length variable along the body; branchiae overlapping dorsally on chaetigers 6 to 10 (Figs 5A, 6A, 7A–B), slightly longer than body width, then becoming progressively shorter. Last pair of branchiae cirriform in shape (Fig. 7B). Notopodial postchaetal lobes shorter and subtriangular with wide base on prebranchial chaetigers (Figs 5A, 7B–C), globular to subtriangular on branchial segments (Figs 5A, 6A–B, 7D), becoming subtriangular and thinner slightly longer on postbranchial, median and posterior segments (Figs 6C–D, 7E–G), last eight notopodial prechaetal lobes (preanal region) progressively longer and thinner (Fig. 6E). Notopodial postchaetal lobe easily detached and lost in many median and posterior chaetigers. Lateral sense organs visible from chaetiger 2, seen on pre- and branchial chaetigers as depression on ventral side of notopodial postchaetal lobes (Fig. 6B). Neuropodial postchaetal lobes as low ridges, indistinct from body wall. Notopodial chaetae numbering 4–10 long capillaries in a tuft, reduced in number and length posteriorly, and 1–2 lyrated notochaetae from chaetigers 2. Lyrate notochaetae with tines of different size and thickness along body, each with an inner row of 7–8 spines, shorter branch slightly thicker, appears rigid, ending in a more or less blunt tip, the longer branch has a very thin and flexible distal part, ending in a point (Fig. 5C); long tine 2.4 times longer than short tine on anterior chaetigers, 2 times longer on median and posterior chaetigers; short tine 1.2 to1.4 times thicker than long tine. Lyrated notochaetae increase in size from anterior to posterior parapodia: 17.2µm from the base of the chaeta to the distal end of the short tine in branchial parapodia, 18.8 µm in middle parapodia and 20.2 µm in posterior parapodia (Fig. 7H–J). Neuropodial chaetae long capillaries in two rows, four capillaries on first neuropodium, 12–14 capillaries anteriorly, reduced to 4–8 posteriorly.

Pygidium oval, pygidial region with nine cirri, one pair corresponding to notopodial postchaetal lobes of a normal sized segment, two pairs corresponding to two preanal segments, migrate to ventral side, and three elongated anal cirri, two dorso-lateral and one mid-ventral, mid-ventral cirrus slightly thicker and shorter than lateral ones (Fig. 6D–E).

Etymology

This species is named in honor of Andrew S.Y. Mackie, a great British polychaetologist who inspired the first author to study paraonid polychaetes.

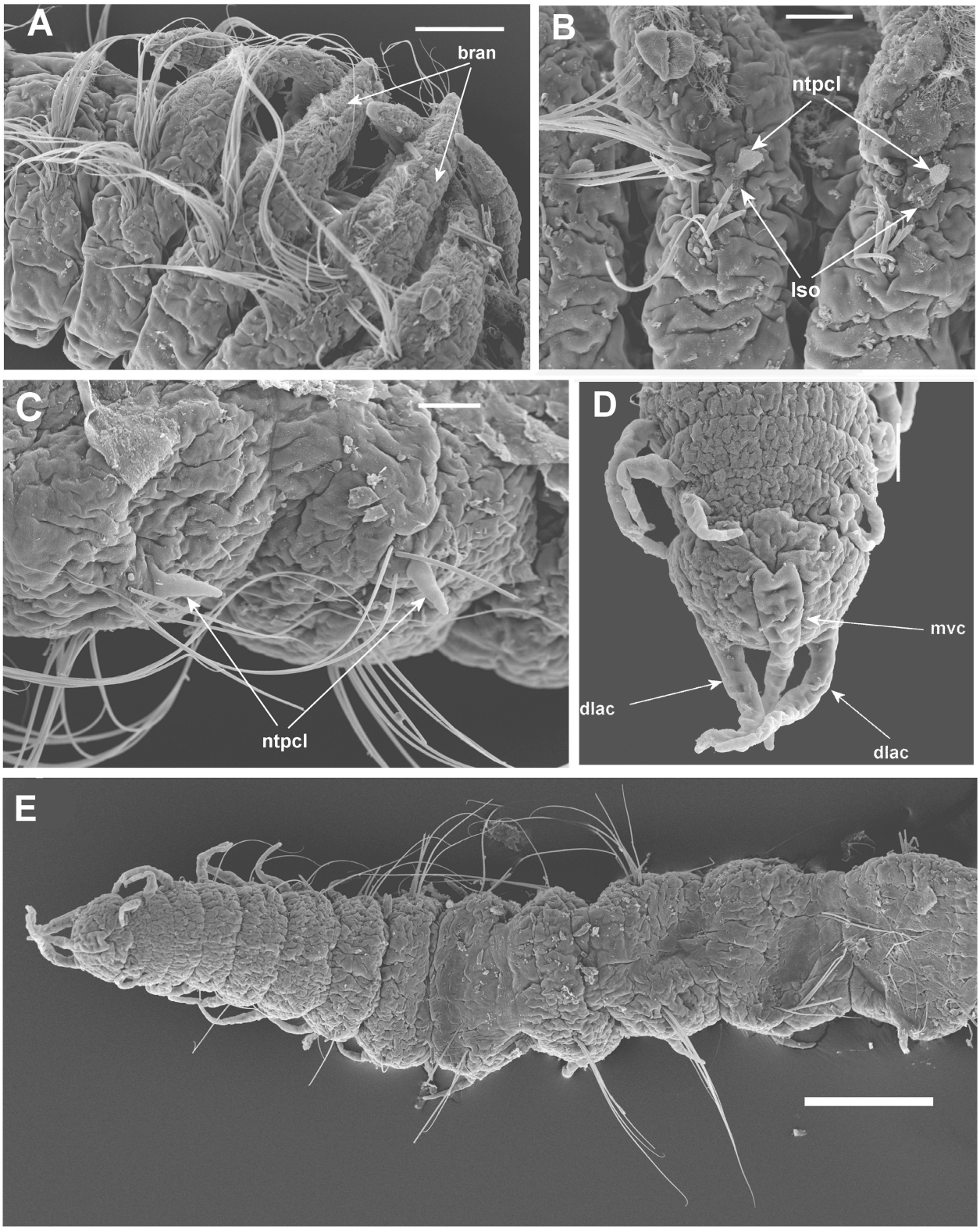

FIGURE 6. *Paradoneis mackiei* **sp. nov.** (Paratype) A. Branchial segments in lateral view; B. Lateral sense organs and notopodial postchaetal lobe from branchial region; C. Posterior parapodia, lateral view; D. Pygidial region, ventral view; E. Posterior end, ventral view. Abbreviations: bran, branchiae; dlac, dorso-lateral anal cirrus; lso, lateral sense organs; mvc, mid-ventral cirrus; ntpcl, notopodial postchaetal lobe. Scale bars: A, E, 50 µm; B–D, 20 µm; E, 100 µm.

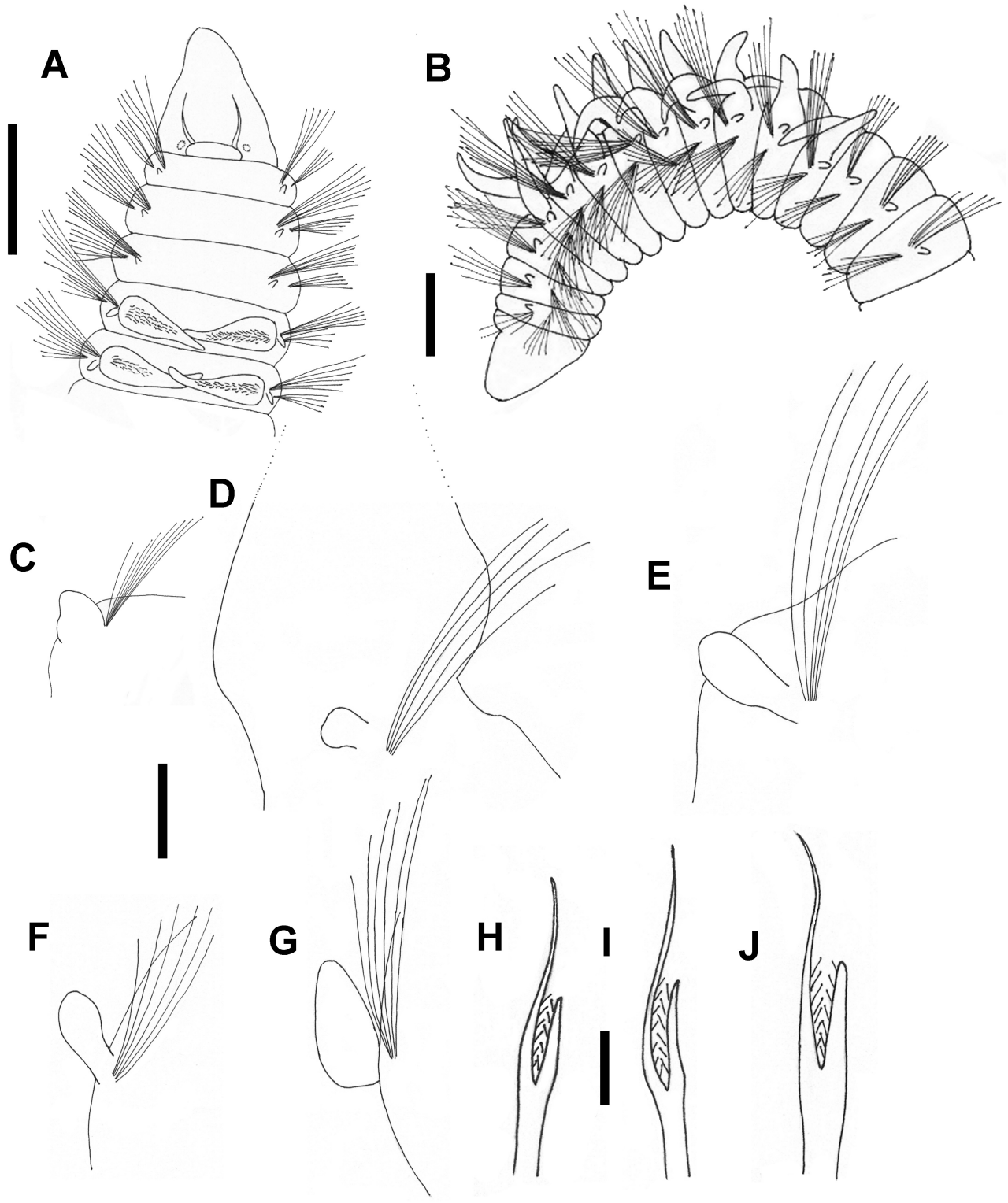

FIGURE 7. *Paradoneis mackiei* **sp. nov.** (Holotype) A. Anterior end, dorsal view; B. Anterior end, lateral view (specimen from station M3-1); C–G. Notopodial postchaetal lobes chaetigers 2, 11, 15, median and posterior respectively; H–J. Lyrate notochaetae from branchial region, median and posterior parapodia respectively. Scale bars: A–B, 0.1 mm; C–G, 20 µm; H–J, 10 µm.

Remarks

The genus *Paradoneis* is composed of 30 valid species including two subspecies: *P. lyra capensis* (Day, 1955) and *P. lyra guadalupensis* (Amoreux, 1985).

Paradoneis mackiei **sp. nov.**, belongs to the group of *Paradoneis* species with three pre-branchial chaetigers, lyrate notochaetae and without modified neurochaetae. Other species that share these characteristics are *Paradoneis lyra* (Southern, 1914) from Clare Island, Ireland, *P. lyra capensis* (Day, 1955) from South Africa, *P. forticirrata* (Strelzov, 1973) from Kuril Islands, *P. nipponica* Imajima, 1973 from Japan, *P. ilvana* Castelli, 1985 from Italy, *P. lyra guadalupensis* Amoreoux, 1985 from Guadeloupe Island, Antilles, *P. brunnea* (Hartmann-Schröder & Rosenfeldt, 1988) from Antarctica, *P. perdidoensis* (McLelland & Gaston, 1994) from Northwest Florida, Perdido Key, *P. carmelitensis* Arriaga-Hernández, Hernández-Alcántara & Solís-Weiss, 2013 from Terminos Lagoon, southern Gulf of Mexico, *P. kamaehu* Magalhães, Bailey-Brock & Barroso, 2018 from Mamala Bay, Oahu, Hawaii, *P. campechensis* Quintanar-Retama, Hernández-Alcántara & Solís-Weiss, 2019 from Campeche Sound, Mexico, *P. heterochaeta* Erdoğan-Dereli & Çinar, 2019 from Sea of Marmara, *P. idoiae* Martínez, 2019 from Abra de Bilbao, Spain, *P. longifurcata* Erdoğan-Dereli & Çinar, 2019 from Sea of Marmara, *P. mexicanensis* Quintanar-Retama, Hernández-Alcántara & Solís-Weiss, 2019 from Southern Gulf of Mexico and *P. yucatanensis* Quintanar-Retama, Hernández-Alcántara & Solís-Weiss, 2019 from Southern Gulf of Mexico.

Of these species, *P. ilvana*, *P. heterochaeta*, *P. mexicanensis* and *P. nipponica*, and *P. mackiei* **sp. nov.**, have lyrate chaetae with tines of different thickness at least in part of the body, the rest of species have these kinds of chaetae with both tines of the same thickness. However, *P. mackiei* **sp. nov.** differs from them in terms of the following characters: (1) Lyrate notochaetae: the new species and *P. nipponica* present lyrate notochaetae with tines of different thickness along body, however, *P. mackiei* **sp. nov.** show a slight increase in size of lyrate chaetae from anterior to posterior end, this character is unknown for *P. nipponica*; *P. ilvana* presents lyrate chaetae with tines of equal thickness in the anterior region, tines of different thickness in the posterior region; *P. heterochaeta* has lyrate chaetae with tines of equal thickness in the anterior region, while midbody and posterior chaetigers show the co-occurrence of chaetae with tines of both equal and unequal thickness in the posterior region; *P. mexicanensis* with two types of lyrate chaetae, on branchial region with distal end longer and thin with the short tine 3/4 the size of the long tine, longer than normal one in other species, in postbranchial region, with distal end shorter and stouter; in posterior chaetigers lyrate chaetae becoming thin again. (2) Prostomium shape: subtriangular, slightly longer than wide, anterior end distinctly conical in *P. mackiei* **sp. nov.**; triangular with anterior end weakly conical in *P. ilvana*; triangular, with anterior end distinctly conical in *P. heterochaeta*; conical, longer than wide in *P. mexicanensis*; and a subtriangular lobe, little longer than wide in *P. nipponica*. (3) Notopodial postchaetal lobes: short and subtriangular with wide base in the prebranchial region, globular to subtriangular in the branchial region, becoming subtriangular and thinner slightly longer in the postbranchial region, last eight progressively longer and thinner in the preanal region in *P. mackiei* **sp. nov.**; short and cirriform in prebranchial region, indistinctly digitiform in branchial region, short and triangular in postbranchial region in *P. heterochaeta*; short and rounded in prebranchial region, rudimentary in branchial region and long and triangular in postbranchial region in *P. ilvana*; in first two chaetigers of prebranchial region short and rounded, digitiform and increase in length from chaetiger 3 throughout branchial region, small as cylindrical protuberance in postbranchial region, becoming longer at chaetigers before pygidium in *P. mexicanensis*; short, digitate in prebranchial region, getting longer in branchial region, as small conical lobes in postbranchial region, filiform in preanal region in *P. nipponica*.

Key to species of *Paradoneis* modified from Martínez (2019). In square brackets is the region where the type locality is contained

1	Branchiae present	2
-	Branchiae absent	*Paradoneis abranchiata* Hartman, 1965 [Western North Atlantic]
2(1)	One pair of branchiae	*Paradoneis juvenalis* (Hartmann-Schröder, 1974)
-	Three or more pairs of branchiae	3
3(2)	One kind of modified notochaetae	4
-	Two kinds of modified notochaetae: lyriform in anterior chaetigers, acicular on median and posterior chaetigers	31

4(3) Modified notochaetae acicular or spinelike 5
- Modified notochaetae lyriform 8

5(4) Modified notochaetae spinelike 6
- Modified notochaetae acicular 7

6(5) Spinelike notochaetae straight, distally pointed; 6 prebranchial chaetigers; 8–10 pairs of branchiae . . . . . *Paradoneis drachi* Laubier & Ramos, 1974 [Mediterranean Sea]
- Spinelike notochaetae curved, distally rounded; 4–5 prebranchial chaetigers; 12–20 pairs of branchiae . . . . . *Paradoneis spinifera* (Hobson, 1972) [Puget Sound, Washington]

7(5) Acicular notochaetae beginning in prebranchial chaetigers, three prebranchial chaetigers; 3–4 pairs of branchiae . . . . . *Paradoneis perkinsi* (McLelland & Gaston, 1994) [Northwest Florida]
- Acicular notochaetae beginning in branchial chaetigers, four prebranchial chaetigers; 10 pairs of branchiae . . . . . *Paradoneis magdalenaensis* (de León-González, Hernández-Guevara & Rodríguez-Valencia, 2006) [Western Mexico]

8(4) Posterior chaetigers with spinelike neurochaetae 9
- All neuropodia with capillary chaetae 11

9(8) Up to 18 pairs of branchiae; notopodial postchaetal lobes on prebranchial region papiliform; pygidium with four anal cirri . . . . . *Paradoneis andreae* López & Sikorski, 2017 [Northeast Atlantic]
- Up to 12 pairs of branchiae; notopodial postchaetal lobes on prebranchial region tuberculate or triangular; pygidium with three anal cirri 10

10(9) Up to 12 pairs of branchiae, marginally ciliated; notopodial postchaetal lobes on prebranchial region tuberculate; three long anal cirri, two ventrolateral and one midventral shorter than ventrolateral . . . . . *Paradoneis eliasoni* Mackie, 1991 [Northern Europe]
- Up to 7 pairs of smooth branchiae; notopodial postchaetal lobes on prebranchial region distinctly triangular; three short, subequal anal cirri . . . . . *Paradoneis strelzovi* de León-González & Díaz-Castañeda, 2011 [Western Mexico]

11(8) Three prebranchial chaetigers 12
- Four prebranchial chaetigers 29

12(11) Lyrate notochaetae starting on prebranchial region 13
- Lyrate notochaetae starting on branchial region 21

13(12) Fifteen or more pairs of branchiae 14
- Up to 10 pairs of branchiae 26

14(13) More than 20 pairs of branchiae 15
- Up to 20 pairs of branchiae 16

15(14) Lyrate neurochaetae from chaetiger 2; with 23–26 pairs of branchiae . . . . . *Paradoneis nipponica* (Imajima, 1973) [Japan]
- Lyrate neurochaetae from chaetiger 3; with 25–48 pairs of branchiae . . . . . *P. kamaehu* Magalhães, Bailey-Brock & Barroso, 2018 [Hawaii]

16(14) With 8–14 pairs of branchiae, longer than segment width; notopodial postchaetal lobes on branchial and postbranchial region (except in the last 4–5 chaetigers) similar in size. . . . . *Paradoneis lyra guadalupensis* (Amoureux, 1985) [Caribbean Sea, Guadaloupe Island][1]
- Up to 15 pairs of branchiae 17

17(16) A single type of lyrate notochaetae 18
- Several types of lyrate notochaetae 20

18(17) Branchiae of middle branchial region thin, digitiform; notopodial postchaetal lobes on prebranchial region digitiform . . . . . *P. lyra* (Southern, 1914) [Irish Exclusive Economic Zone]
- Branchiae of middle branchial region cirriform, elongated, basally thickened 19

19(18) Notopodial postchaetal lobes short, cirriform, increasing gradually in length on prebranchial region; in anterior part of branchial region digitiform, in middle and posterior part thick, finger-like, weakly jointed. . . . . *P. longifurcata* Erdoğan-Dereli & Çinar, 2019 [Sea of Marmara]
- Notopodial postchaetal lobes short, oval, getting longer on prebranchial region; on branchial region longer, finger-like; short, finger-like or elongated spindle-shaped to oblong oval on prebranchial region . . . . . *P. brunnea* (Hartmann-Schröder & Rosenfeldt, 1988) [Southern Ocean]

20(17) Lyrate notochaetae on prebranchial and branchial region with equal branch thickness and pilose handle; those of postbranchial region similar to anterior ones but without pilose handle; from chaetiger 19, two types of lyrate chaetae (equal and unequal branch thickness) present on the same parapodium . . . . . *P. heterochaeta* Erdoğan-Dereli & Çinar, 2019 [Sea of Marmara]
- Lyrate notochaetae of two types, from branchial region having distal portion long with thin inner teeth; postbranchial lyriform notochaetae with distal part short and stout, with inner teeth stouter . . . . . *P. mexicanensis* Quintanar-Retama, Hernández-Alcántara & Solís-Weiss, 2019 [Southern Gulf of Mexico]

21(12) Postbranchial lyrate notochaetae with tines of equal thickness along body. 22
- Lyrate notochaetae with equal tine thickness in anterior region; unequal thickness in posterior region . . . . . *Paradoneis ilvana* Castelli, 1985 [Mediterranean Sea]

22(21) Notopodial postchaetal lobes on prebranchial region not visible. . . . . *Paradoneis lyra capensis* (Day, 1955) [South Africa][2]
- Notopodial postchaetal lobes on prebranchial region remarkably visible 23

23(22) Notopodial postchaetal lobes on prebranchial region conical, uniform in length; 15–17 pairs of branchiae in adult specimens, slightly shorter than segment width . . . . . *Paradoneis forticirrata* (Strelzov, 1973) [West Pacific]
- Notopodial postchaetal lobes on prebranchial region conical or triangular, progressively increases in size; up to 14 pairs of branchiae. 24

24(23) Branchiae longer than body width, pygidium with two long mid-lateral cirri and one short mid-ventral cirrus. . . . . *P. carmelitensis* Arriaga-Hernández, Hernández-Alcántara & Solís-Weiss, 2013 [Southern Gulf of Mexico]
- Branchiae shorter than body width, pygidium with three short equal anal cirri 25

25(24) Prostomium bluntly conical . . . . . *Paradoneis lyra* (Southern, 1914) *in partim* [North Atlantic]
- Prostomium triangular, slightly longer than wide . . . . . *Paradoneis campechensis* Quintanar-Retama, Hernández-Alcántara & Solís-Weiss, 2019 [Southern Gulf of Mexico]

26(13) Three (rarely 4) pairs of branchiae; all notopodial postchaetal lobes on branchial region uniform in length . . . . . *Paradoneis perdidoensis* (McLelland & Gaston, 1994) [Northwest Florida]
- With up to 10 pairs of branchiae; last notopodial postchaetal lobe on branchial region clearly shorter than remainder. 27

27(26) With 4–6 pairs of branchiae; lyrate chaetae with tines of equal thickness; notopodial postchaetal lobe digitiform on branchial chaetigers 28
- With 9–10 pairs of branchiae; lyrate notochaetae with tines of unequal thickness; notopodial postchaetal lobe on branchial chaetigers globular to subtriangular . . . . . *P. mackiei* **sp. nov.**

28(27) With 4–5 pairs of branchiae; pygidium with three anal cirri of similar size . . . . . *P. yucatanensis* Quintanar-Retama, Hernández-Alcántara & Solís-Weiss, 2019 [Southern Gulf of Mexico]
- With 5–6 pairs of branchiae; pygidium with three anal cirri, two laterals filiform, and one ventral long and thick . . . . . *Paradoneis idoiae* Martínez, 2019 [Bay of Biscay]

29(11) Postbranchial lyriform notochaetae with tines of similar thickness. 30
- Postbranchial lyriform notochaetae with tines of unequal thickness . . . . . *Paradoneis bathyilvana* Aguirrezabalaga & Gil, 2009 [Northeast Atlantic]

30(29) Up to 7 pairs of branchiae; postbranchial lyriform notochaetae with long hairs basally. . . . . *Paradoneis hirsuta* Sardá, Gil, Taboada & Gili, 2009 [Mediterranean Sea]
- Up to 12 pairs of branchiae; postbranchial lyriform notochaetae with smooth shaft. . . . . *Paradoneis mikeli* Aguirrezabalaga & Gil, 2009 [Northeast Atlantic]

31(3) Up to 19 pairs of branchiae, blunt distally; modified notochaetae lyriform in anterior chaetigers, acicular with subterminal spine on median and posterior chaetigers . . . . . *Paradoneis armata* Glémarec, 1966 [Northeast Atlantic]
- Up to 10 pairs of branchiae, rounded distally; modified notochaetae lyriform in anterior chaetigers, harpoon like in posterior chaetigers . . . . . *Paradoneis harpagonea* (Storch, 1967) [Red Sea]

Notes

[1] *Paradoneis lyra gadalupensis* is a species very closely related to *P. lyra*, but it differs from it in the length of its branchiae and the habitat where it is found. In the case of the former, it has extremely long branchiae and lives in mangrove areas, while *P. lyra* has short branchiae and is marine. The fact that the branchiae are greatly developed may be due to an adaptation to shallow environments with low oxygen (J. Langeneck pers. comm.). If this were the case, both species could be the same.

[2] *Paradoneis lyra capensis*, despite having a branchial development pattern similar to that of *P. lyra guadalupensis*, differs from *P. lyra* Southern 1914 in the shape and size of the prechaetal notopodial lobe, as well as in the beginning of the lyrate notopodial chaetae. It should be considered as an independent species.

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