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New species and records of Uncispionidae and *Pygospiopsis* (Polychaeta, Spionida) from deep water off the east and west coasts of North America, the Gulf of Mexico, the Antarctic Peninsula, and Southeast Asia

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Abstract

Five new species and one new genus of the obscure spioniform family Uncispionidae are described together with three new species of the rare and unusual spionid genus *Pygospiopsis* Blake, 1983. All species are from offshore habitats with most from deep-sea continental slope depths. Among the Uncispionidae are the second and third species of the genus *Uncopherusa* Fauchald & Hancock, 1981, collected from off Brunei in the South China Sea and off Louisiana in the Gulf of Mexico; two new species of *Uncispio* Green, 1982, the third and fourth to be described, from deep water off the U.S. Atlantic coast and the Gulf of Mexico; and a new species of a new genus, *Rhamphispio* **n. gen.,** from off the U.S. Atlantic coast. All species of Uncispionidae are compared and a key to the known species is presented. The genus *Pygospiopsis* Blake, 1983, is currently known for only two species: *P. dubia* (Monro, 1930) from Antarctic and sub-Antarctic waters and *P. occipitalis* Blake, 1996, from shelf depths off southern California. In the present study, new collections of the type-species *P. dubia* from the Antarctic Peninsula include post-larvae and juveniles as well as adults, thus permitting documentation of the development of some key adult morphology. Three new species of *Pygospiopsis* are described from deep water off the U.S. Atlantic and Pacific coasts and from the Antarctic Peninsula. A review of all species of *Pygospiopsis* suggests that, based on branchial distribution patterns, the closely related *Pseudatherospio fauchaldi* Lovell, 1994, should be referred to *Pygospiopsis*, bringing the total known species to six. All of these are compared and contrasted and the generic definition of *Pygospiopsis* updated. The status of *Pygospiopsis* within the Spionidae relative to the closely related genus *Atherospio* Mackie & Duff, 1986, is discussed.

Key words: *Uncopherusa*, *Uncispio*, *Rhamphispio*, *Pygospiopsis*, deep-sea, Annelida, Spionidae, new species, new genus, post-larvae

Introduction

Specimens of eight new species belonging to rare and poorly known spioniform polychaetes were encountered during extensive surveys of the continental slope along the east coast of the United States in the 1980s, baseline surveys in deep-water in the Gulf of Mexico in 2008, and off Brunei in the South China Sea in 2011 as part of the characterization of sites intended for oil and gas exploration and on-going development; a survey along the eastern Antarctic Peninsula in 2000; and at deep-water sites off northern California surveyed for the US EPA in 1991. These specimens yielded five new species belonging to the obscure family Uncispionidae, of which only three species are presently known, and three new species of the genus *Pygospiopsis* of the family Spionidae, of which only two species are presently known. In addition, adults and postlarvae of the type-species of *Pygospiopsis, P. dubia* (Monro, 1930), originally collected from near South Georgia Island, were newly collected from the eastern Antarctic Peninsula at the site of the former Larsen A Ice shelf.

The family Uncispionidae was established by Green (1982) to include *Uncopherusa bifida* Fauchald & Hancock, 1981, described from deep water off Oregon, and *Uncispio hartmanae* Green, 1982, described from off southern California. The family name is derived from the Latin *uncus*, referring to the characteristic giant modified hooks present in two or more posterior setigers, and *Spio*, referring to the supposed close relationship of these species to the family Spionidae. Similar large, modified hooks had been reported earlier from posterior fragments

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of an unknown species collected from deep water off northeastern South America by Hartman (1965) and again from off New England (Hartman & Fauchald 1971). A new species of *Uncispio, U. reesi* Darbyshire & Mackie, 2011, was recently described from the southern Irish Sea. Darbyshire & Mackie (2011) also redescribed the two previously known species and redefined the family and both genera. Fauchald & Rouse (1997), Rouse & Pleijel (2001), and Jumars *et al*. (2015) provided brief summaries of the Uncispionidae. Blake & Maciolek (2018a) recently prepared a review of the family for the Handbook of Zoology.

The genus *Pygospiopsis* was established for *Pygospio dubia* Monro, 1930 by Blake (1983), who determined that the nature of the branchiae, neuropodial hooks, and pygidial morphology did not agree with the well-known genus *Pygospio*. A second species, *P. occipitalis* Blake, 1996, was later described from the southern California shelf.

In the present study, five new species of Uncispionidae, all from deep water, are newly described, including a new species of *Uncopherusa* from off Brunei and another from the Gulf of Mexico; a new species of *Uncispio* from off New England and another from the Gulf of Mexico; and a new genus and species collected from off New England to the Carolinas. In addition, three new deep-water species of *Pygospiopsis* are described from off the Antarctic Peninsula and the U.S. Atlantic and Pacific coasts, together with new records including descriptions of adults and larvae of the type species, *P. dubia* (Monro, 1930), from Antarctic waters.

Material and methods

The U.S. Atlantic Continental Slope and Rise Program (ACSAR, aka ASLAR) was conducted between 1983 and 1987 and included 18 oceanographic surveys conducted in three distinct regions: (1) the North Atlantic region off New England, (2) the Mid-Atlantic region off New Jersey and Delaware, and (3) the South Atlantic region off North and South Carolina. Benthic biology samples were collected with a 0.25-m^2 box core partitioned into 25 subcores (10 x 10 x 50 cm), nine of which were processed for benthic infaunal biology; other subcores were used for sediment grain-size, total organic carbon, sediment chemistry, and meiofauna. Samples were collected over a depth range of 250–3000 m. Each of the nine subcores processed for benthic biology was cut to a 10-cm depth with a specially designed core cutter and sieved through a 300-µm-mesh sieve. In most instances, all nine subcores were combined into a single sample and fixed in 10% formalin. Upon completion of each survey, the samples were transferred to 80% ethyl alcohol (ETOH). In the laboratory, each sample was carefully re-sieved and sorted to major taxonomic category; polychaetes were sorted to family. A team of taxonomists then identified and counted the individual species. The taxonomic team was trained to recognize rare taxa such as the uncispionids. The results of these studies were documented in reports by Blake *et al*. (1985, 1987) and Maciolek *et al*. (1987a–b).

The benthic biology samples from the eastern Pacific were collected as part of a study to designate an offshore ocean disposal site for dredged material off San Francisco (Blake *et al*. 1992). Forty-five sites were sampled with a box core from depths of 500–3000 m. A survey off Louisiana in the Gulf of Mexico in 2008 and another off Brunei in 2011 were at deep-water sites intended to characterize areas planned or in use for oil and gas development. The samples from these studies were treated in a similar manner except that each box core sample included ten subcores that were used for biology. These samples were also sieved with a 300-µm-mesh sieve. An elutriation method was used to wash the sediment onto the sieves. A survey to the east Antarctic Peninsula in May 2000 was implemented to describe the geology and biology of sediments in an area newly opened to the sea following the collapse of the Larsen A Ice shelf in late 1990s. Biology samples were collected from a grab and similarly elutriated using a 300-µm-mesh sieve and preserved as in the other surveys.

All specimens were examined with light microscopy using a Wild M-5 stereomicroscope and a Zeiss RA research compound microscope equipped with phase contrast and Nomarski differential interference optics. Photomicrographs were taken with a Nikon D7100 camera mounted on both the stereo- and compound microscopes. Some specimens were stained with a solution of Shirlastain A in water to highlight difficult-to-see surficial morphology; other specimens were further stained with a saturated solution of Methyl Green in ETOH in order to elucidate distinct patterns of subdermal glands evident on some species. Both stains dissipate completely in ETOH. Line drawings were developed in pencil using a drawing tube or camera lucida on the Zeiss RA and later transferred to drawing paper and inked. Specimens of *Pygospiopsis dubia* and *P. antennata* **n. sp.** were prepared for scanning electron microscopy (SEM) at Hofstra University by dehydrating in an ascending ethanol series of

70–95% ETOH for 10 min each, followed by three changes of 100% ETOH for 15 min each. Specimens were critical-point dried with a Samdri 795 Critical Point Dryer, mounted on aluminum stubs, coated with gold using an EMS-550 Sputter coater, and viewed with a Hitachi S-2460N SEM.

Measurements were taken with a calibrated micrometer when specimens were observed on the microscope under a coverslip. For drawings prepared with the camera lucida, several scales were also sketched directly from the stage micrometer at different magnifications and later used to accurately measure the specimens that were illustrated. Plates were prepared and edited using Microsoft PowerPoint, Adobe Acrobat, and Adobe Photoshop software.

Specimens collected as part of the ACSAR program are deposited in the National Museum of Natural History, Washington, DC (USNM); the specimens from the Gulf of Mexico, Brunei and Antarctica are deposited in the Museum of Comparative Zoology, Harvard University (MCZ). Type specimens of *Uncopherusa bifida*, *Uncispio hartmanae* and *U. reesi* present in the collections of the Los Angeles County Museum of Natural History (LACM-AHF Poly) were also examined. Previously collected specimens of *Pygospiopsis dubia* from King George Island were provided by Drs. Jacek Siciński and Krzysztof Pabis, University of Łodź, Łodź, Poland. Syntypes of *Pygospio dubia* Monro, 1930, from off South Georgia were examined at the Natural History Museum, London (BMNH).

Systematics

Family Uncispionidae Green, 1982

Diagnosis. (Emended). Small, slender polychaetes with palps inserted dorsally at junction between pro- and peristomium (postectal prostomial margins). Occipital antenna present or absent. Peristomium dorsally expanded with lateral wings, extending ventrally encompassing mouth; separate pair of large ciliated peristomial lobes typically located on dorsal lip of mouth anterior to prostomium; a separate unpaired lobe on ventral lip visible if extruded; a pair of lobes present or absent lateral to expanded pharyngeal area ventral to mouth opening. Parapodia biramous with reduced, simple postchaetal lobes. Branchiae present on some anterior and middle setigers, basally fused or separate from notopodial lobes. Setae simple, including capillaries (smooth, with fringe of fibrils or spinose), bidentate hooded hooks, and enlarged, modified hooks on two or more posterior neuropodia. Neuropodial capillaries of setiger 1 long, thick, directed anteriorly forming cephalic cage; notopodia of setiger 1 with shorter, thin capillaries or with thick spines (genus *Uncopherusa*). Setiger 3 enlarged with heavy crested spinous setae in neuropodia (genus *Rhamphispio*) or setiger 3 not expanded and setae not modified. Terminal anus surrounded by up to eight digitate lobes or cirri.

Remarks. Darbyshire & Mackie (2011) modified the original diagnosis of the family based on details taken from their new species of *Uncispio* and reexamination of the type specimens of the other two known species. The family definition is here emended following the discovery of five new species including a new genus, *Rhamphispio* **n. gen.**, which has an enlarged setiger 3 with large crested spinous setae in the neuropodia.

Study of these new taxa has resulted in a reevaluation of the unusual oral morphology of uncispionids. All species in the family appear to have a pair of ciliated peristomial lobes anterior to the prostomium on the upper lip of the mouth; these have been considered as attached to a proboscis (Green 1982; Darbyshire & Mackie 2011); these are here referred to as anterior oral lobes and appear to be present on all species. In addition, an unpaired lobe that is visible only if extruded is present on the ventral lip of the mouth in most species. Ventral and posterior to the mouth opening is an expanded buccal area, usually swollen and triangular in shape, which is the external manifestation of the pharynx. This swollen buccal area typically has a thickened ridge or border that may bear a pair of lobes near or lateral to the mouth opening. In addition to the various lobes associated with the oral opening, a pair of rudimentary palps with a ventral groove can be discerned lateral to the prostomium and posterior to the anterior oral lobes; well-developed palps are present in *Uncispio greenae* **n. sp.** Presumably, the palps and large ciliated anterior oral lobes serve to move and manipulate food particles to the oral opening. The unpaired lobe on the lower lip of the mouth likely serves to further direct particles into the oral opening where they are ingested. Details of the oral morphology are presented for each species described in this paper.

The three genera, *Uncopherusa* Fauchald & Hancock, 1981, *Uncispio* Green, 1982, and *Rhamphispio* **n. gen.**, are distinguished from one another based on modification to setiger 3, presence or absence of notopodial spines on setiger 1, presence and number of lateral flanges or teeth on the enlarged neuropodial hooks, and the presence or absence of spinous or hirsute notosetae on anterior and middle body setigers. Historically, the number of segments bearing posterior neuropodial hooks has been considered a generic-level character, with *Uncispio* species having two posterior setigers with hooks and *Uncopherusa* having five or more setigers with hooks. However, the description of *Uncispio hamata* **n. sp.,** with ten posterior segments with enlarged hooks and *Rhamphispio tridentata* **n. gen., n. sp.** with three hook-bearing segments, precludes using the number of hook-bearing segments as a generic character. The following key serves to separate the three known genera and seven species. However, several species are known from only one or a few specimens and more material is needed to fully characterize them and understand their morphological variability.

Key to the genera and species of Uncispionidae

1A. Setiger 3 greatly enlarged, bearing heavy curved spines with a fimbriated crest; both notopodial and neuropodial hooded hooks present . . . . *Rhamphispio tridentata* **n. gen., n. sp.**
1B. Setiger 3 not enlarged; neuropodial crested setae, if present, not enlarged and not spinous; neuropodial hooded hooks present; notopodial hooded hooks absent 2
2A. Cephalic cage formed of both capillary neurosetae and notosetae …Genus *Uncispio*. 3
2B. Cephalic cage formed of long capillary neurosetae only; notosetae consist of a curved row of short, thickened spines and a few companion capillaries…Genus *Uncopherusa* 6
3A. Anterior and middle notopodia with long, spinous, hirsute capillaries; occipital antenna present. 4
3B. Anterior and middle notopodia with long, simple capillaries, not spinous, hirsute, or with lateral fringe; occipital antenna absent. 5
4A. Pygidium with four digitate anal lobes; hooded hooks from setiger 9; branchiae from setiger 6 continuing to 11; long spinous hirsute capillaries present from about setiger 15. . . . . *Uncispio hartmanae*
4B. Pygidium with six to eight short anal lobes; hooded hooks from setigers 8–12; branchiae from setiger 6–8, usually 7, continuing for 22 segments (holotype); long spinous hirsute capillaries from notopodia of setiger 10–17. . . . . *Uncispio reesi*
5A. Prostomium rounded on anterior margin; hooded hooks from setiger 7; posterior recurved neuropodial spines present on last two setigers, with penultimate spine having a secondary tooth on concave side . . . . *Uncispio greenae* **n. sp.**
5B. Prostomium incised on anterior margin; hooded hooks from setiger 9; posterior recurved neuropodial spines on last ten setigers; spines flattened or weakly concave on ventral side; accessory tooth or flange entirely absent. . . . *Uncispio hamata* **n. sp.**
6A. Branchiae from setiger 5, straplike; surface of body smooth, with or without subdermal glands, distinct papillae absent; occipital antenna present or absent 7
6B. Branchiae from setiger 9–10, short, oval; surface of body covered with numerous sessile papillae; occipital antenna absent. . . . . *Uncopherusa papillata* **n. sp.**
7A. Occipital antenna absent; notosetae of setiger 1 in transverse row; dorsal and ventral crests absent. . . . . . . *Uncopherusa bifida*
7B. Occipital antenna present; notosetae of setiger 1 in curved longitudinal row; setiger 3 with dorsal crest with numerous subdermal papillae; ventral crests present on anterior margin of setigers 5–6 . . . . *Uncopherusa cristata* **n. sp.**

Genus *Uncopherusa* Fauchald & Hancock, 1981

Type-species: *Uncopherusa bifida* Fauchald & Hancock, 1981 by monotypy.

Diagnosis. (Emended). Cephalic cage formed from neurosetae of setiger 1; notopodia of setiger 1 with acicular spines and few companion capillaries. Occipital antenna present or absent. Setae include smooth and fringed capillaries, acicular setae, bifid neuropodial hooded hooks, and enlarged posterior neuropodial hooks. Some parts of body covered with numerous small glandular papillae, or body smooth. Anus surrounded by four short lobes.

Remarks. *Uncopherusa bifida* is known only from a single specimen collected off Oregon in deep water (Fauchald & Hancock 1981). Two specimens of a second species, *U. papillata* **n. sp.** have been collected off Brunei in the South China Sea and a single specimen of a third species, *U. cristata* **n. sp.**, has been collected from off Louisiana in the Gulf of Mexico. These species differ from *Uncispio* and *Rhamphispio* **n. gen.** in having the cephalic cage formed by only the neurosetae, rather than both noto- and neurosetae. The notosetae of chaetiger 1 of the three species of *Uncopherusa* consist of short, thick, pointed acicular spines accompanied by a few short companion capillaries. In *U. bifida*, the spines are in transverse rows; in *Uncopherusa papillata* **n. sp.**, the spines are in curved rows with the emergent spines forming a rosette. In *U. cristata* **n. sp.**, the spines are arranged in diagonal rows directed posteriorly.

In their description of *U. bifida*, Fauchald & Hancock (1981) reported that the anterior segments were papillate and encrusted with sand, as were subsequent parapodial bases and the entire posterior end, but subsequent observers did not confirm the presence of papillae on the holotype; papillae were not observed during our examination of the holotype. However, *U. papillata* **n. sp.** from off Brunei has numerous small sessile glandular papillae on anterior segments and elsewhere on the body and *U. cristata* **n. sp.** from the Gulf of Mexico has conspicuous subdermal glands on the dorsal surface of setigers 1–4.

Despite the two specimens of *Uncopherusa* from off Brunei and the single specimen from off Louisiana being incomplete and lacking the enlarged posterior spines that characterize other uncispionids, we feel justified in describing and naming these species because they exhibit other morphology, some newly reported for uncispionids that is unique within the family. Further, the morphology of the oral lobes found on these two species combined with similar results from other species described in this paper provides new information that increases our understanding of how these worms may manipulate particles as part of their feeding.

Read (2004) listed *Uncopherusa* sp. A in a checklist of polychaetes from New Zealand; according to Darbyshire & Mackie (2011) those specimens had enlarged neuropodial hooks on the last five setigers, but no additional information was provided.

Uncopherusa papillata **new species**

Figure 1

Material examined. **Off Brunei, Island of Borneo**, R/V *Emma*, coll. P. Neubert, box corer, Sta. ME7, coll. 04 Jul 2011, 05°22.13688′N, 113°37.43300′E, 1725 m, **holotype** (MCZ 147896) and 1 **paratype** (MCZ 147897).

Other material examined. *Uncopherusa bifida* Fauchald & Hancock, 1971, off central Oregon, USA, Sta. AD-89, NAD-22A, 44°38.5′N, 126°16.1′W – 44°38.1′N, 126°16.4′W, 2860 m, **holotype** (LACM-AHF Poly 1147).

Description. Body long and thin, cylindrical throughout, fragile. Both specimens incomplete; holotype 5.6 mm long, 0.4 mm wide, with 26 setigers; paratype 3.8 mm long, 0.3 mm wide, with 19 setigers. Dorsal surface of both specimens with numerous sessile glandular papillae (Fig. 1A); setigers 1–4 of holotype with papillae in separate groups, some isolated; densest concentrations across entire dorsal surface from setiger 5 to about setiger 11–12 (Fig. 1A); papillae small, surficial, staining lightly with Methyl Green. Color of body in alcohol, light tan, without pigmentation.

Setiger 1 with noto- and neuropodia directed anteriorly, bearing long capillary neurosetae and short, thickened, spinous notosetae (Fig. 1A); long neurosetae forming cephalic cage partially encompassing prostomium and peristomium. Prostomium narrow, bluntly rounded on anterior margin, continuing posteriorly as low ridge to near border of setiger 1 (Fig. 1A); occipital tentacle absent; eyespots absent; nuchal organs not observed. Palps not observed. Peristomium short dorsally, extending laterally and onto venter, forming lips around mouth opening; with a pair of prominent anterior oral lobes, each with a digital process anterior to prostomium, located on dorsal lip of mouth (Fig. 1A–B); a broad triangular-shaped posterior oral lobe present on ventral lip of mouth when everted (Fig. 1B); two lateral oral lobes arising from lateral margins of mouth opening (Fig. 1B). Enlarged buccal area posterior to mouth due to muscular pharynx (Fig. 1B). Parapodia biramous throughout; podial lobes short, low throughout; largest on setiger 1 with notopodia broad and lamellate, neuropodia digitiform. Branchiae from setiger 9 or 10 continuing to setiger 14 or 15; each branchia short, oval, free from notopodia (Fig. 1A).

Notosetae of setiger 1 include 6–7 short, thick, pointed spines (Fig. 1A, C–D), arranged in curved row or rosette, with three thin companion capillaries in ventrolateral group (Fig. 1A); spines not extending beyond anterior end. Neurosetae of setiger 1 include one row of long, thin capillaries and a second row of shorter capillaries, all capillaries stiff; longer setae extending beyond anterior end about twice length of combined pre-setiger area and setiger 1, shorter capillaries directed anteromedial (Fig. 1A).

Setiger 2 with 4–5 short, thin, capillary notosetae; setiger 3 with about 6–8 capillaries, subsequent setigers with 12–14 curved capillaries; each notoseta with thin fringe of fibrils along one edge (Fig. 1E–F); notosetae of far posterior segments longer, thicker, also with thin fringe of fibrils along one edge (Fig. 1G).

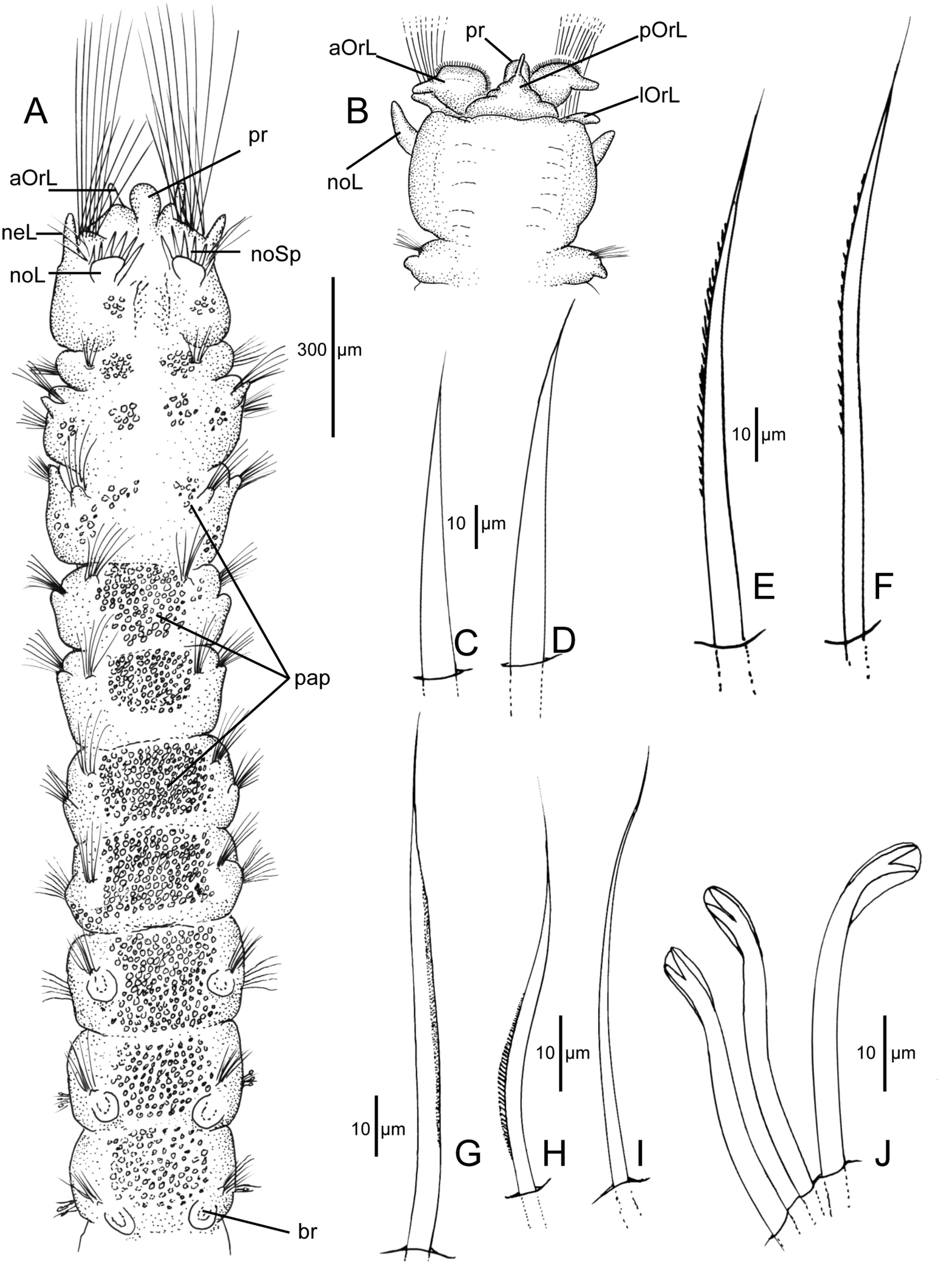

FIGURE 1. *Uncopherusa papillata* **n. sp.** Holotype (MCZ 147896: A) and paratype (MCZ 147897: B–J): A, anterior end, dorsal view; B, anterior end, ventral view; C–D, Notopodial spines from setiger 1; E–F, notopodial capillaries from setiger 3; G, notopodial capillary from setiger 19; H, neuropodial capillary from setiger 5; I, capillary neurosetae accompanying hooded hooks from setiger 12; J, three neuropodial hooded hooks from setiger 12. Abbreviations: aOrL, anterior oral lobe; br, branchiae; lOrL, lateral oral lobe; neL, neuropodial lamella; noL, notopodial lamella; noSp, notopodial spines; pap, papillae; pOrL, posterior oral lobe; pr, prostomium.

Neurosetae from setiger 2 through setiger 8–9 all curved capillaries, with thin fringe of fibrils along one edge (Fig. 1H); no distinct modified setae on any anterior segment; capillaries numbering about 10 per neuropodium on setiger 2, increasing to 10–12 through setiger 7, then decreasing to about 8 per neuropodium on setigers 8–9 or 10; capillaries mostly replaced by bidentate hooded hooks from setiger 9 or 10; hooks numbering 2–4 per neuropodium, accompanied by 3–4 thin smooth capillaries (Fig. 1I); from setiger 14 companion capillaries becoming thicker, curved ventrally, appearing similar to sabre setae of some spionids. Hooded hooks with long curved shaft bearing two narrow teeth, apical tooth longer or subequal to main fang, with narrow angle between teeth and wide angle between main fang and shaft; hood prominent, extending down shaft (Fig. 1J).

Posterior end missing; presence and nature of modified neuropodial hooks and pygidium unknown.

Methyl Green staining. Holotype with a curved band of stain posterior to and between fascicles of notopodial spines on setiger 1; paratype with lateral segmental patches on setigers 2–5. Small glandular papillae imparting diffuse but not heavy stain to those segments where they occur.

Remarks. *Uncopherusa papillata* **n. sp.** is referred to the genus *Uncopherusa* because the cephalic cage is formed only by the neurosetae, rather than both noto- and neurosetae as in species of *Uncispio* and *Rhamphispio* **n. gen**. In *Uncopherusa* species, the notochaetae of setiger 1 are short, thick, acicular spines that in *U. papillata* **n. sp.** are sharply pointed (Fig. 1C–D) and occur in a curved row resembling a rosette. In *U. bifida*, the spines, as illustrated by Darbyshire & Mackie (2011: Fig. 7A), taper to a narrow blunt tip; these spines are accompanied by two capillaries that are about twice as long and half the thickness and are anterior to the larger spines; they do not alternate with the spines as stated by Darbyshire & Mackie (2011) (NJM, pers. obs.). Companion capillaries in *U. papillata* **n. sp.** number about three on a side and are grouped in a bundle lateral to the curved row of spines.

The branchiae of *U. bifida* are short, straplike, and limited to setiger 5. In *U. papillata* **n. sp.** the branchiae occur from setiger 9 or 10 and continue to setiger 14 or 15; each branchia is short, oval-shaped, and free from the notopodium. In *U. cristata* **n. sp.** the branchiae are straplike and on setigers 5–8.

Dense patches of small glandular papillae occur on the anterior surface of *U. papillata* **n. sp.** Surficial papillae covered with sand were mentioned in the original description of *U. bifida* by Fauchald & Hancock (1981), but were not observed in subsequent examinations of the holotype by Green (1982), Darbyshire & Mackie (2011), or in the present study. In fact, Darbyshire & Macke (2011: 73) stated that “the epidermis was smooth, no papillae.” Green (1982) suggested that the papillae mentioned by Fauchald & Hancock (1981) might have actually been part of the worm’s tube. It is also possible that the papillae observed originally on *U. bifida* were actually subdermal glands that would not be readily visible externally unless stained or otherwise viewed with phase contrast optics. This is the exact situation observed for *Uncopherusa cristata* **n. sp.** (see below). As part of our observations of the holotype of *U. bifida*, the specimens were not stained, but were studied with phase contrast optics; no subdermal glands were observed.

Although the two available specimens of *U. papillata* **n. sp.** are incomplete, and therefore lack the enlarged posterior hooks of other known uncispionids, they are readily referred to the Uncispionidae by having a cephalic cage on setiger 1 and neuropodial bidentate hooded hooks. Other spioniforms such as *Poecilochaetus* that also have a cephalic cage do not have hooded hooks. The comparison of *U. bifida* and *U. papillata* **n. sp.** demonstrates the close affinity of these two species.

Etymology. The species name *papillata*, is from the Latin, *papilla*, for nipple or bud, referring to the numerous papillae on the surface of this species.

Habitat. The specimens were collected from fine-grained deep-sea sediments having the following characteristics: 62% silt + 37% clay and a total organic carbon content of 2.1%.

Distribution. South China Sea, off Brunei, 1725 m.

Uncopherusa cristata new species

Figure 2

Material examined. **Gulf of Mexico, off Louisiana**, Matterhorn Platform survey, R/V *Brooks McCall*, coll. J.A. Blake, box corer, Sta. 5S, coll. 10 Nov 2008, 28°43.4126′N, 88°49.5373′W, 955 m, **holotype** (MCZ 147898).

Description. A single anterior fragment with 10 setigerous segments measures 1.5 mm long and 0.36 mm wide across anterior end; mature female with large ova in setigers 8–10. Body cylindrical, individual segments through setiger 7, about three times wider than long. Color in alcohol opaque white. Setiger 1 with broad curved mass of glandular papillae extending between notopodial postsetal lamellae (Fig. 2A); glandular papillae also present on dorsal surface of setiger 2 and on dorsal crest on setiger 3; a few papillae present on setiger 4 (Fig. 2A). Ventral surface with elevated crests on anterior margin of setigers 5–6. Ovigerous segments 8–10 enlarged, about two times wider than long. Setiger 8 greatly distended due to two large eggs on either side, each about 180 µm in longest diameter (Fig. 2A); germinal vesicle clearly seen on eggs in ventral view. Setiger 9 with large elongate lateral tears suggesting eggs were previously discharged; setiger 10 with elongate narrow eggs in same position.

Setiger 1 with noto- and neuropodia directed anteriorly, bearing long capillary neurosetae and short, thickened, spinous notosetae (Fig. 2A); long neurosetae forming cephalic cage partially encompassing prostomium and peristomium.

Prostomium short, bluntly rounded on anterior margin (Fig. 2A–B), continuing posteriorly to about mid-way along setiger 1; with short occipital antenna near posterior margin (Fig. 2A); prostomium terminating at low curved ridge extending between postsetal notopodial lamellae (Fig. 2A); eyespots absent; nuchal organs not observed.

Peristomium short dorsally, extending laterally and onto venter, forming lips around mouth opening. Oral morphology complex, consisting of a pair of broad ciliated lobes immediately anterior to and ventral to prostomium on dorsal lip of mouth (Fig. 2A–B), two short lobes lateral to mouth, and a single medial lobe appearing on ventral most margin of ventral lip of mouth (Fig. 2B). Palp rudiments present arising lateral to prostomium, best seen in ventral view as short lobe with ventral groove (Fig. 2B). Ventral surface of setiger 1 posterior to mouth with enlarged buccal area due to muscular pharynx (Fig. 2B); followed by narrow esophagus on setiger 2 (Fig. 2B).

Parapodia biramous throughout; podial lobes short, low throughout; largest on setiger 1 with notopodia broad and lamellate, neuropodia fingerlike. Postsetal lamella short, broadly rounded. Branchiae from setiger 5 continuing to setiger 8; each branchia elongate, straplike, basally free from notopodia (Fig. 2A).

Notosetae of setiger 1 include 6–7 short, thick, pointed spines (Fig. 2A, C), arranged in curved longitudinal row, with 4–5 thin companion capillaries anterior to spines (Fig. 2A); spines not extending beyond anterior end. Neurosetae of setiger 1 include a fascicle of long, thin, stiff capillaries; longest setae extending beyond anterior end about as long as length of combined pre-setiger area and setiger 1.

Setiger 2 with 4–5 short, thin, capillary notosetae; setiger 3 with about 6–7 capillaries, subsequent setigers with 8–10 curved capillaries; each notoseta with thin fringe of fibrils along one edge; notosetae of far posterior segments longer, thicker, also with a thin fringe of fibrils along one edge.

Neurosetae of setiger 2 include 6–7 thin, simple capillaries. Setiger 3 with two rows, each with 7–8 heavier capillaries, each expanded in middle and with surface covered with short fibrils (Fig. 2D). Setigers 4–7 with 6–8 thin simple capillaries per neuropodium; setiger 8 with 4–5 short capillaries; these replaced by 2–4 bidentate hooded hooks on setigers 9 and 10; hooks accompanied by two thin smooth capillaries; hooks with apical tooth slightly shorter and thinner than main fang, with narrow angle between teeth and wide angle between main fang and shaft (Fig. 2E).

Posterior end missing; presence and nature of modified neuropodial hooks and pygidium unknown.

Methyl Green staining. Stain concentrated in subdermal glandular papillae on setigers 1–3; weaker stain on glandular cells in neuropodia of setigers 2–6.

Remarks. *Uncopherusa cristata* **n. sp.** is referred to the genus *Uncopherusa* because the notopodia of setiger 1 include a row of spines with alternating thin capillaries instead of only capillaries as seen in *Uncispio*. The presence of dorsal and ventral crests on this species are treated as species-level characters as in some genera of Spionidae. Although the specimen is incomplete, we are justified in describing it because it is sexually mature and exhibits characters that allow it to be easily recognized among uncispionids.

Uncopherusa cristata **n. sp.** exhibits several unique features that separate it from its two congeners. The curved mass of glandular papillae glands between the notopodial postsetal lamellae on setiger 1 is unique in the family as is the prominent dorsal crest on setiger 3. The ventral crests on setigers 5–6 are also unique; such crests have not been recorded in other uncispionids, but are known from some Spionidae (Blake *et al.* 2017). An occipital antenna is present in *U. cristata* **n. sp.** that is absent in both *U. bifida* and *U. papillata* **n. sp.** Large straplike branchiae occur on setigers 5–8 in *U. cristata* **n. sp.** whereas *U. bifida* has a single pair of branchiae on setiger 5 and *U. papillata* **n. sp.** has short, rounded branchiae from setiger 9–15. Dorsal subdermal glands are present on setigers 1–4 in *U. cristata* **n. sp.**; these are absent in *U. bifida* and present as glandular papillae over numerous segments on *U. papillosa* **n. sp.**

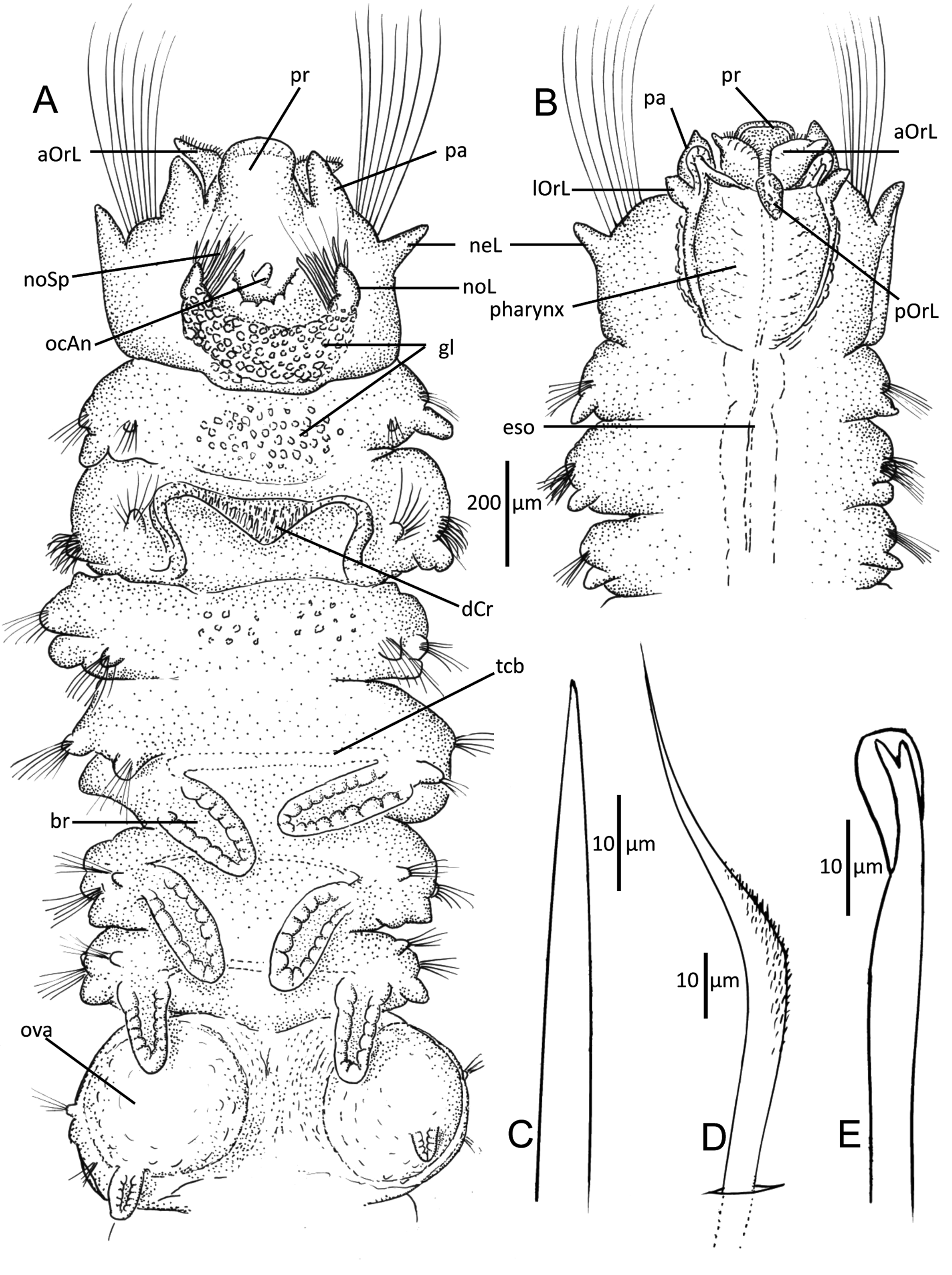

FIGURE 2. *Uncopherusa cristata* **n. sp.** Holotype (MCZ 147898). A, anterior end, dorsal view; B, anterior end, ventral view; C, notopodial spine, setiger 1; D, neuroseta, setiger 3; E, neuropodial hooded hook, setiger 10. Abbreviations: aOrL, anterior oral lobe; br, branchiae; dCr, dorsal crest; eso, esophagus; gl, glands; lOrL, lateral oral lobe; neL, neuropodial lamella; noL, notopodial lamellae; noSp, notopodial spines; ocAn, occipital antenna; pa, palp; pOrL, posterior oral lobe; pr, prostomium; tcb, transverse ciliary band.

Large yolky eggs that distend the body are present on setigers 8–10 in *U. cristata* **n. sp.**; the eggs are about 180 µm in diameter and occur two on each side of a segment. The eggs appear to be discharged through a rupture of the body wall as observed on setiger 9. On setiger 10, smaller eggs are present on either side of the segment. These observations suggest that egg production and release may be an on-going process in this deep-water polychaete. Gametes have not been recorded in the other *Uncopherusa* species.

Etymology. The species name is from the Latin for *crista*, referring to the dorsal and ventral crests that help characterize this species.

Habitat. The specimen was collected in sediments having a high silt (34%) and clay (64.14%) content and a total organic carbon content of 4.40 mg or 1.24%.

Distribution. Gulf of Mexico, off Louisiana, 955 m.

Genus *Uncispio* Green, 1982

Type-species: *Uncispio hartmanae* Green, 1982 by monotypy.

Diagnosis. (Modified from Darbyshire & Mackie, 2011). Body somewhat flattened dorsoventrally, cylindrical medially; three distinct regions defined by setae and branchiae sometimes apparent. Occipital antenna present or absent. Cephalic cage formed by smooth capillaries of both noto- and neuropodia of setiger 1. Some anterior setigers with short limbate capillaries with one edge bearing fringe of fine fibrils. Median notopodia with or without long, spinose capillaries in addition to short haired capillaries. Median neuropodia with bidentate hooded hooks and inferior bundle of long, curved, smooth capillaries. Posterior notopodia with simple fringed capillaries or long smooth capillaries with thick shafts and bent tips; neuropodial bidentate hooded hooks present. Posterior neuropodia with enlarged modified hooks. Anus terminal with up to eight anal cirri.

Remarks. *Uncispio* and *Rhamphispio* **n. gen.** both differ from *Uncopherusa* in having notopodial capillaries in setiger 1 instead of a row of spines. *Uncispio* also differs from *Rhamphispio* **n. gen.** in having setiger 3 of the same relative size and width as setiger 2 and following segments instead of setiger 3 being greatly enlarged with thick and heavy spinous crested neurosetae. The genus *Uncispio* now includes four species: (1) the type-species *U. hartmanae* from 222 m off southern California, (2) *U. reesi* from 120–171 m in the southern Irish Sea, (3) *U. greenae* **n. sp.** from deep-water (2110 m) off New England, and (4) *U. hamata* **n. sp**. from deep-water (825 m) in the Gulf of Mexico.

Uncispio greenae new species
Figure 3

Material Examined. **Off New England, south of Cape Cod**, U.S. North Atlantic ACSAR Program, R/V *Oceanus*, Cruise NA-1, coll. G. Hampson, box corer, Sta. 14, coll. 09 Dec 1984, 39°40.85′N, 70°54.31′W, 2110 m, **holotype** (USNM 1480968).

Comparative material examined: *Uncispio hartmanae* Green, 1982, off Santa Cruz Island, California, USA, Sta. 80901, 222 m, **holotype** (LACM-AHF Poly 1365); *Uncispio reesi* Darbyshire & Mackie, 2011, Anglesey, Wales, UK, 171 m, **paratype** (LACM-AHF Poly 2652).

Description. Holotype complete, small, probably a juvenile, 1.1 mm long, 0.15 mm wide with 16 setigerous segments. Body elongate, thin, fragile, cylindrical throughout with last two hook-bearing segments and pygidium somewhat flattened; individual segments well defined with obvious setal fascicles and short podial lobes. Branchiae not observed. Distinct esophagus visible through body, extending through setiger 5 (Fig. 3A), continuing to posterior end as intestine filled with dark silt particles. Color in alcohol light tan.

Prostomium narrow, rounded on anterior margin (Fig. 3A); occipital tentacle not observed; eyes absent; nuchal organs not observed. A single curled palp present on left side of dorsum arising posterior and lateral to prostomium (Fig. 3A). Peristomium reduced, surrounding mouth ventrally. Anterior oral lobes lateral to mouth (Fig. 3B), small posterior oral lobe on lower lip of mouth (Fig. 3B) present; lateral lobes and ridges not evident. Enlarged ventral pharyngeal or buccal area posterior to mouth on setiger 1 oval shaped (Fig. 3B); esophagus continuing over setigers 2–4 with intestine evident from setiger 5 (Fig. 3A).

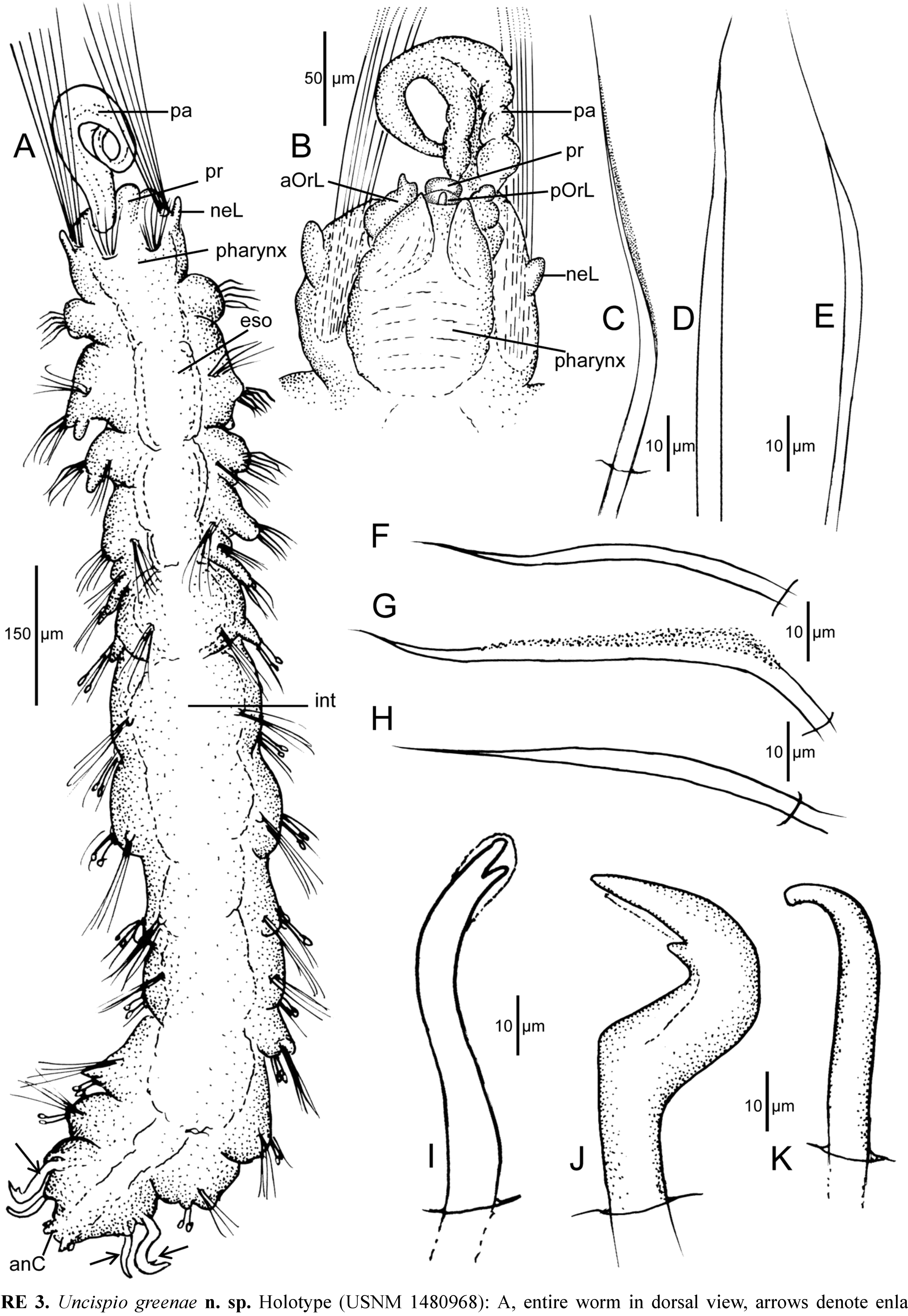

FIGURE 3. *Uncispio greenae* **n. sp.** Holotype (USNM 1480968): A, entire worm in dorsal view, arrows denote enlarged modified hooks; B, anterior end, ventral view; C–D, notosetae from setiger 5; E, notoseta from setiger 10; F, neuroseta from setiger 2; G, neuroseta from setiger 3; H, neuroseta from setiger 4; I, neuropodial hooded hook from setiger 9; J, enlarged modified neuropodial hook from setiger 15; K, modified hook from setiger 16. Abbreviations: anC, anal cirrus; aOrL, anterior oral lobe; eso, esophagus; int, intestine; neL, neuropodial lamella; pa, palp; pOrL, posterior oral lobe; pr, prostomium.

Parapodia biramous except for last two segments where notosetae not evident. Podial lobes small, best developed in anterior neuropodia as short, rounded lobes; elsewhere reduced to low mounds. Setiger 1 with parapodia and capillary setae directed anteriorly forming cephalic cage (Fig. 3A). Neurosetae long, thick, extending anteriorly about 2–3 times length of first setiger; notosetae also directed anteriorly, but short and thin, not extending beyond prostomium (Fig. 3A).

Notosetae not observed on setiger 2; notosetae of setigers 3–6 simple capillaries, some with narrow fringe of fibrils (Fig. 3C), most with fringe not evident (Fig. 3D); spinous notosetae absent. Notosetae of middle and posterior setigers long, with smooth edges, tapering to fine capillary tips (Fig. 3E).

Neurosetae of setigers 2–6 simple capillaries, some curved; capillaries of setigers 2, 4–6 smooth (Fig. 3F, H); capillaries of setiger 3 slightly thicker with fringed border (Fig. 3G); hooded hooks first present from setiger 7, with two hooks per neuropodium; individual hooks sigmoidally curved, with apical tooth longer than subdistal tooth (Fig. 3I). Neurosetae of last two segments include an enlarged modified hook or spine; penultimate hook greatly enlarged, sharply curved, with short secondary tooth on convex side, hood remnant present (Fig. 3J); spine of last segment smaller, simple, curved (Fig. 3K).

Anus terminal with four short digitate cirri (Fig. 3A).

Methyl Green staining. No staining pattern evident.

Remarks. This single specimen is easily referred to the genus *Uncispio* because it has notopodial capillaries in setiger 1 instead of a row of spines and setiger 3 is not enlarged or modified with large spines. *Uncispio greenae* **n. sp.** is readily separated from the two previously known species and *U. hamata* **n. sp.** by the lack of elongate notosetae in anterior and middle segments that are either spinous, hirsute, or large and thickened with bent tips. *Uncispio greenae* **n. sp.** is further separated from *U. hamata* **n. sp.** by having only two posterior neuropodia with enlarged hooks instead of ten and by having a secondary tooth on the concave side of the same hooks instead of lacking one.

The oral morphology on the ventral side includes similar anterior and posterior oral lobes associated with the mouth opening that we have observed in other species described in this study. Unlike other species, however, a palp is fully developed on the holotype of *U. greenae* **n. sp.** It is likely that the palps work together with the oral lobes to guide and manipulate particles into the mouth and pharynx. It is also probable that there is some level of particle selection during feeding.

Etymology. This species is named for Ms. Karen Green, polychaete systematist and friend, who first described the genus *Uncispio* and established the family Uncispionidae.

Habitat. The specimen was collected from deep-sea sediments with mixed coarse and fine-grained components: sand (46.4%), silt (26.9%), and clay (26.7%). CHN results were: organic carbon (1.48%), hydrogen (0.56%), and nitrogen (0.18%). Data from Maciolek *et al.* (1987b).

Distribution. Western North Atlantic Ocean, in slope depths off New England, 2110 m.

Uncispio hamata new species

Figures 4–5

Material examined. **Gulf of Mexico, off Louisiana**, Matterhorn Platform survey, R/V *Brooks McCall*, coll. J.A. Blake, box corer, Sta. 2N, 10 Nov 2008, 28°44.7798′N, 88°49.5337′W, 825 m, **holotype** (MCZ 147899).

Description. Holotype complete, 4.73 mm long, 0.60 mm wide across setiger 4, with 26 setigerous segments. Body dorsoventrally flattened and widest over anterior 8–9 setigers with each segment about 3.5 times as wide as long; middle body segments as long as wide, cylindrical in cross section; far posterior segments again becoming wider than long with dorsum weakly rounded and venter flattened. Oocyte measuring 60 x 48 µm with distinct germinal vesicle observed in parapodia of setiger 10. Color in alcohol opaque white, body lacking any additional pigment markings; gut retaining MG stain.

Setiger 1 with well-developed noto- and neuropodia bearing long capillaries directed anteriorly, forming cephalic cage only partially encompassing pre-setiger region (Figs. 4A, 5A); setae of neuropodia about three times longer than those of notopodia; noto- and neuropodial postsetal lobes elongate, more or less triangular in shape (Fig. 4A). Prostomium broad on anterior margin, distinctly incised, extending posteriorly as short caruncle to anterior border of setiger 2 (Fig. 4A); occipital antenna absent; eyespots absent; nuchal organs not observed. Palp rudiments present, arising lateral to prostomium, best seen in ventral view as short lobe with ventral groove (Fig. 4B). Peristomium limited to two ciliated triangular oral lobes located anterior to prostomium on dorsal lip of mouth (Figs. 4A–B, 5B) and forming upper and lower lips of mouth; two additional oral lobes located lateral to large V-shaped pharyngeal or buccal area (Fig. 4B), extending to setiger 1, then leading to esophagus on setiger 2 (Figs. 4B, 5B).

Parapodia biramous throughout; postsetal lamellae present along entire body; individual podial lobes generally elongate, weakly triangular and rounded on their tips. Branchiae from setigers 5–8, each elongate, straplike, basally fused with notopodia; branchiae on setigers 5–7 extending across dorsal midline (Fig. 4A). Transverse ciliary band extending across dorsum of each branchial segment (Fig. 4A); bands consist of cells or individual patches of cilia. Setigers 10–12 with additional glandular notopodial postsetal papilla, attached to body by a peduncle (Fig. 4A, inset).

Notosetae of anterior segments limited to single row of capillaries; setiger 2 with eight capillaries; setigers 3–7 with 10–14 capillaries; capillaries becoming longer and decreasing to 6–8 per notopodium over setigers 8–13; from setiger 14 capillaries becoming distinctly longer, thicker, some having the tips bent near distal end and a distinctly striated appearance (Fig. 4D). Notopodia of far posterior segments with 1–2 long, heavy capillaries.

Neurosetae of setiger 2 all thin simple capillaries in two rows, first row with 8–10 curved setae, overlapping 6–8 straighter setae of second row. Setiger 3 with capillaries in three rows, those of first two rows weakly modified with fringe of fibrils along one edge (Fig. 4E), overlapping straighter smooth setae of third row (Fig. 4F). Setigers 4–7 with simple smooth capillaries in two rows; setiger 8 with only eight capillaries in a single row. Bidentate hooded hooks from setiger 9; each fascicle with four hooks accompanied by five thin capillaries. Hooded hooks continuing over setigers 10–16, numbering 3–4 per fascicle accompanied by up to five capillaries that become longer and thicker. Individual hooded hooks with a main fang only slightly longer than apical tooth (Fig. 4G); hooks with a wide angle between main fang and shaft and narrow angle between the two teeth (Fig. 4G); hood closely applied. Large golden-colored recurved modified hooks or spines first present from setiger 17; setiger 17 with a single spine accompanied by one hooded hook and two thick and three thin capillaries. Spines completely replace hooded hooks by setiger 19, accompanied by 2–3 heavy capillaries; two spines present on right side of setiger 19 and left side of setiger 20 (Fig. 5C–D); setigers 21–25 with a single spine and a single large, thick capillary; setiger 26 with tip of spine just emerging. Thus, hooded hooks occur over setigers 9–18 and large recurved spines occur over setigers 17–26 (10 setigers). Recurved spines without accessory teeth or flanges; concave side of spines flattened or weakly grooved (Fig. 4H).

Posterior end with pygidium bearing four tapering anal cirri (Figs. 4C, 5C–D).

Methyl Green staining. Methyl Green most evident in ventral view, staining glands on dorsal and lateral peristomial oral lobes around mouth and parapodial glands of anterior neuropodia (Fig. 5B). Ventral surface of posterior segments with a pair of medial glands staining as well as pygidial glands (Fig. 5D).

Remarks. *Uncispio hamata* **n. sp.** is referred to the genus *Uncispio* because the notosetae of setiger 1 are all capillaries instead of acicular spines as in the genus *Uncopherusa*. In addition, setiger 3, while having some additional capillary neurosetae with a fringe of fibrils along one edge, is not enlarged and heavily modified as in *Rhamphispio* **n. gen.** By having the last ten posterior setigers with enlarged recurved spines, *U. hamata* **n. sp**., however, approaches *Uncopherusa bifida*, which has six. All other complete specimens of uncispionids have either two or three posterior segments with enlarged spines. In previous definitions of the genera, *Uncopherusa* was defined in part by having more than two posterior segments with these spines. Our opinion is that the number of posterior segments with enlarged spines is not a generic-level character and that *Uncopherusa* should be defined as having acicular notosetae on setiger 1 instead of all capillaries.

Uncispio hamata **n. sp.** is the fourth species of *Uncispio* to be discovered, and can be separated from the other species by using the key above. Both *U. hartmanae* and *U. reesi* have spinous or bristled capillaries in some anterior and middle notopodia, but similar setae are absent in both *U. greenae* **n. sp.** and *U. hamata* **n. sp.** However, *U. hamata* **n. sp.** has long, thick capillaries often with a bent tip in the posterior third of the body; in addition, similar capillaries are present as companions to the enlarged neuropodial spines. These thick capillaries have no fringe of fibrils or bristles; they are entirely smooth on the surface but have prominent internal striae.

The oral morphology of *Uncispio hamata* **n. sp**. and other uncispionids described in this paper includes two relatively large ciliated lobes, here termed anterior oral lobes, each of which has a terminal digitiform process. In *U. hamata* **n. sp**. the cilia of these lobes appear to be continuous with the entrance to the mouth and a narrow

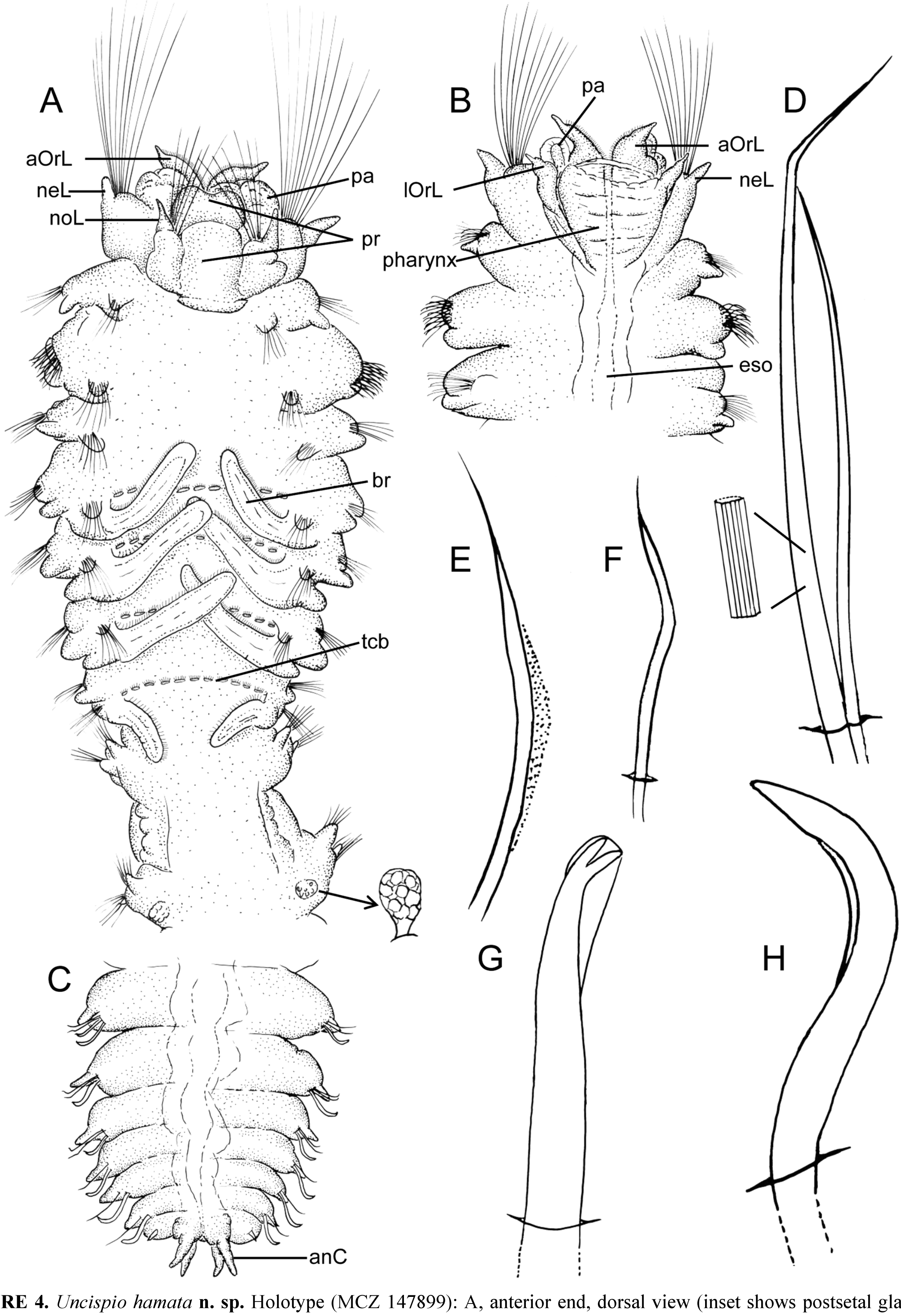

FIGURE 4. *Uncispio hamata* **n. sp.** Holotype (MCZ 147899): A, anterior end, dorsal view (inset shows postsetal glandular papilla, not to scale); B, anterior end, ventral view; C, posterior end, ventral view; D, capillary notosetae from posterior segment (inset not to scale); E, capillary neuroseta from first row of setiger 3; F, capillary neuroseta from third row of setiger 3; G, neuropodial hooded hook; H, posterior neuropodial spine. Abbreviations: anC, anal cirrus; aOrL, anterior oral lobe; br, branchiae; eso, esophagus; lOrL, lateral oral lobe; neL, neuropodial lamella; noL, notopodial lamellae; pa, palp; pr, prostomium; tcb, transverse ciliary band.

ciliated tube that continues internally through the pharynx into the esophagus. Two additional lobes, each with a terminal digital process, are located ventral and lateral to the dorsal lobes on either side of the muscular or buccal area that extends posteriorly from the oral opening. It appears that these four lobes are in close proximity to the palps and probably play a role in capturing and directing food particles to the mouth where they are ingested. There is no evidence of a posterior oral lobe as found on other species; however, this lobe might be present but not everted in *U. hamata* **n. sp**.

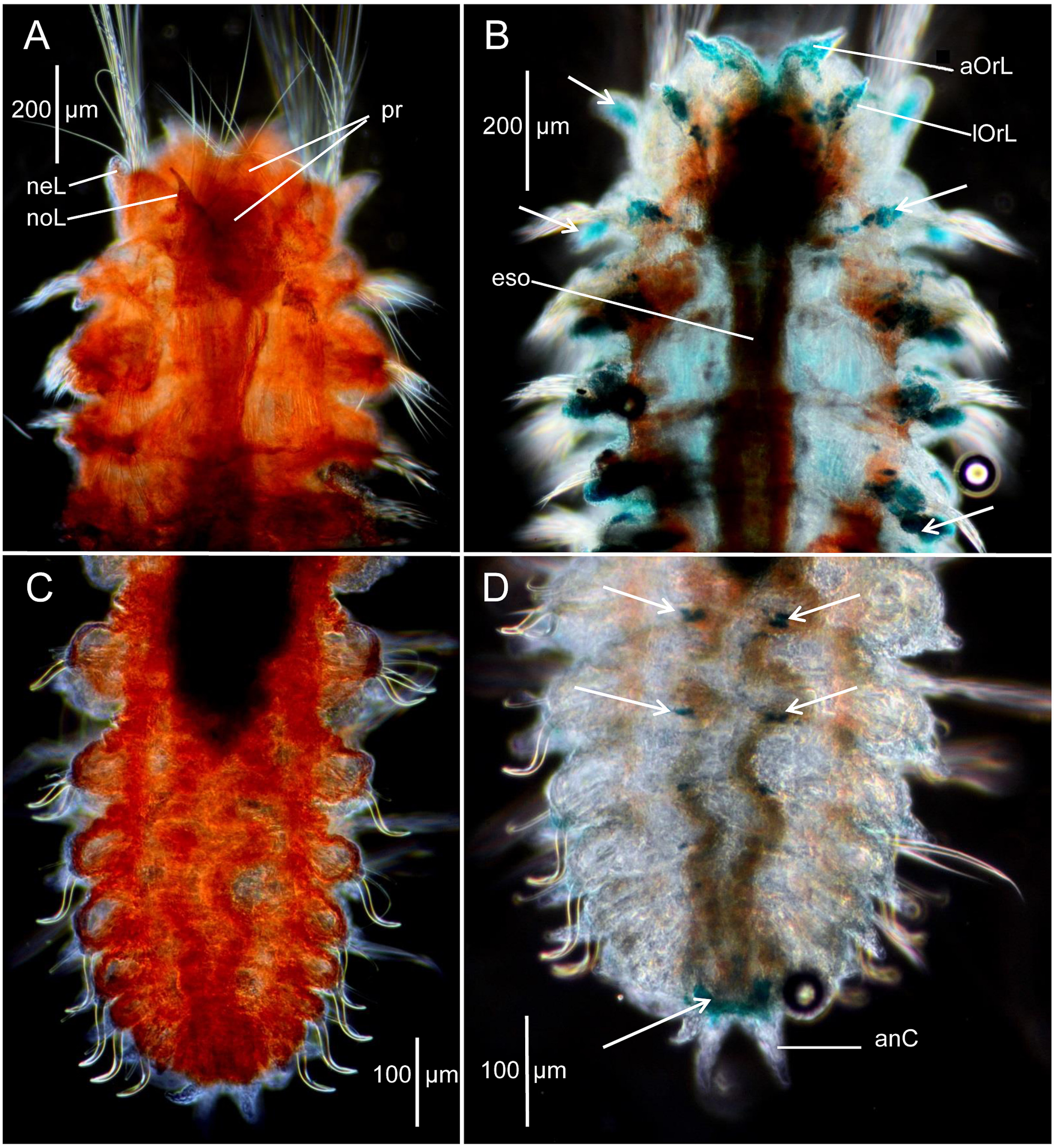

FIGURE 5. *Uncispio hamata* **n. sp.** Holotype (MCZ 147899): A–B, anterior end dorsal view; C–D, posterior end, ventral view with enlarged neuropodial spines visible. A, C stained with Shirlastain A; B, D stained with Methyl Green, arrows denote location of key MG stain. Abbreviations: anC, anal cirrus; aOrL, anterior oral lobe; eso, esophagus; lOrL, lateral oral lobe; neL, neuropodial lamella; noL, notopodial lamellae; pr, prostomium.

The posterior neuropodial spines of *U. hamata* **n. sp**. lack accessory teeth or flanges, but do have a flattened or weakly grooved surface on the concave side. This species is, therefore, the only known uncispionid with recurved spines that lack an accessory structure. The presence of these simple spines over ten setigers is an impressive armature.

The Methyl Green staining pattern is more prominent in *U. hamata* **n. sp.** than in the other species we have examined in that the above-mentioned oral lobes, parapodial glands, mid-ventral glands, and pygidial glands all stain prominently.

Etymology. The epithet is from *hamatus*, Latin for hooked and refers to the large recurved neuropodial hooks that lack accessory teeth or flanges and resemble boat hooks.

Habitat. The specimen was collected in sediments having a high silt (30.94%) and clay (67.39%) content and a total organic carbon content of 4.69 mg or 1.33%.

Distribution. Gulf of Mexico, off Louisiana, 825 m.

***Rhamphispio* new genus**

Type species: *Rhamphispio tridentata* **new species**

Diagnosis. Setiger 1 with both noto- and neuropodial capillary setae directed forward forming a cephalic cage. Occipital antennae present. Setiger 3 greatly enlarged, with wide, curved, spinous golden capillaries with fimbriated crest, in neuropodia. Neuropodia with bidentate hooded hooks in median and posterior setigers; notopodia with capillary setae in anterior and median setigers and bidentate hooded hooks in far posterior setigers. Hirsute or spinous capillary notosetae absent. Enlarged modified hooks or spines with two lateral teeth present in posterior neuropodia. Pygidium with four anal cirri.

Etymology. *Rhamphispio* is derived from the Greek, *rhamphis*, feminine for hook and *Spio*, Latin for sea nymph.

Remarks. *Rhamphispio* **n. gen.** differs from both *Uncopherusa* and *Uncispio* in having an expanded setiger 3 that bears enlarged crested spinous neurochaetae, notopodial hooded hooks in far posterior setigers, and enlarged posterior neuropodial hooks with two lateral teeth or flanges, which impart a tripartite appearance to the hooks. The enlarged setiger 3 and large modified spines are reminiscent of similar modifications to setiger 3 found on species of *Trochochaeta*, suggesting a closer relationship of the Uncispionidae to the Trochochaetidae than was suggested by Green (1982). Smaller limbate neurosetae occur on setiger 3 and subsequent anterior setigers in other uncispionids (Darbyshire & Mackie 2011; this study) but these are not large and spinous as in *R. tridentata* **n. sp.**

***Rhamphispio tridentata* new species**

Figures 6–8

Uncispionidae n. gen., n. sp. 1: Blake *et al*. 1987: Appendix C-6; Maciolek *et al*. 1987b: Appendix D-5; Hilbig 1994: 944.

Material Examined. **Off New England**, U.S. North Atlantic ACSAR Program. G. Hampson (WHOI), Chief Scientist: East of Lydonia Canyon, R/V *Cape Hatteras*, Cruise NA-1, Sta. 05, Rep.3, 5 Nov 1984, 40°05.29′N, 67°29.96′W, 2045 m, 2 **paratypes** (USNM 1480956); R/V *Oceanus*, Cruise NA-2, Sta. 05, Rep. 3, 29 Apr 1985, 40°05.07′N, 67°29.88′W, 2065 m, **Holotype** (USNM 1480957) and 3 **paratypes** (USNM 1480958); R/V *Cape Hatteras*, Cruise NA-6, Rep. 2, 26 July 1986, 40°05.03′N, 67°29.95′W, 2078 m 1 **paratype** (USNM 14880959); Sta. 05, Rep. 3, 40°05.09′N, 67°29.67′W, 2055 m, 1 **paratype** (USNM 1480960); east of Cape Cod, R/V *Cape Hatteras*, Cruise NA-5, Sta. 15, Rep. 1, 04 May 1986, 39°40.02′N, 70°54.21′W, 2162 m, 1 **paratype** (USNM 1480961).—**Off North Carolina,** U.S. South ACSAR Program, J.A. Blake (Battelle), Chief Scientist: Off Cape Lookout, North Carolina, R/V *Gyre*, Cruise SA-3, Sta. 3, 14 Jul 1984, 34°14.50′N, 75°40.30′W, 1509 m, 1 **paratype** (USNM 1480962); R/V *Gyre*, Cruise SA-2, Sta. 4, 20 May 1984, 34°11.90′N, 75°38.70′W, 2029 m, 1 fragment (JAB); R/V *Cape Hatteras*, Cruise SA-4, Sta. 4, Rep. 3, 23 May 1985, 34°11.29′N, 75°38.67′W, 2015 m, 1 **paratype** (USNM 1480963); R/V *Gyre*, Cruise SA-5, 24 Sta. 4, Rep. 3, Sep 1985, 34°11.22′N, 75°38.56′W, 2051 m, 1 **paratype** (USNM 1480964); R/V *Cape Hatteras*, Cruise SA-6, Sta. 4, Rep. 2, 24 Nov. 1985, 34°11.21′N, 75°38.61′W, 2057 m (4 **paratypes**, USNM 1480965).—**Off Charleston, South Carolina**, R/V *Cape Hatteras*, Cruise SA-4, Sta. 14, Rep. 1, 20 May 1985, 32°23.64′N, 7701.13′W, 803 m, 1 **paratype** (USNM 1480966); R/V *Cape Hatteras*, Cruise SA-6, Sta. 14, Rep. 3, 18 Nov. 1985, 32°23.70′N, 77°01.06′W, 799 m, 2 **paratypes** (USNM 1480967).

Description. Twenty specimens available, 19 designated as types, most incomplete, thin, elongate, and fragile. Holotype complete with 43 setigers; 6.8 mm long, 0.32 mm wide across enlarged setiger 3 and 0.2 mm wide across setiger 6. An incomplete paratype (USNM 1480964), with 43 setigers, 7.1 mm long, 0.23 mm across setiger 3, and 0.16 mm across setiger 6; two complete paratypes (USNM 1480964) less than 5 mm long. Body generally cylindrical throughout except for laterally expanded setiger 3. Color in alcohol opaque white.

First setiger with noto- and neuropodia directed anteriorly, bearing long noto- and neurochaetae forming a prominent cephalic cage that encompasses peristomium and prostomium (Figs. 6A–C; 8A–B). Prostomium bluntly rounded anteriorly, continuing to near posterior border of setiger 1 (Fig. 6A–B); short conical occipital tentacle present near posterior margin (Figs. 6A–B); eyes absent; nuchal organs not observed under light microscope. Palps missing on all specimens. Peristomium dorsally forming low lateral wings (Fig. 6A–B); ventrally surrounding mouth (Fig. 6C). Oral morphology includes a pair of large ciliated lobes with a terminal digital process present anterior to prostomium on dorsal lip of mouth; a short, clavate medial lobe present on lower lip of mouth, seen only if everted; lateral oral lobes absent, but V-shaped pharyngeal or buccal area posterior to mouth with thickened lateral ridge (Fig. 6C). Esophagus extending from pharynx on setiger 2, intestine present from setiger 5 (Figs. 6A, 8A–B).

Parapodia biramous throughout; podial lobes small, digitate on setiger 1, becoming low, conical on some anterior segments, then low and rounded in median setigers, small papilliform lobes in far posterior setigers. Branchiae present on setigers 6–12, short, apinnate, separate from dorsal lamellae (Fig. 6A).

Neurosetae of setiger 1 long, thick capillaries directed anteriorly; notosetae of setiger 1 shorter and thinner than neurosetae (Fig. 6A–B). Setiger 2 with short, thin capillaries in both noto- and neuropodia. Setiger 3 enlarged, up to twice as long as setiger 4 and conspicuously wider than setigers 2 and 4 (Figs. 6A–C; 8A–B); with thin simple notosetae, with or without thin fringe of fibrils along one edge (Fig. 7A–B) and large, prominent neurosetae arranged in two rows (Fig. 6E); setae of posterior row include 4–6 large golden spinous setae with expanded apex bearing prominent crest of numerous fibrils or fimbriae (Fig. 7C–F), setae of anterior row not as expanded, with narrow fimbriated border (Fig. 7F).

Notopodia of setiger 4 and following with simple short capillaries, some with narrow fimbriated border; spinous or otherwise modified setae absent. Notosetae of posterior segments becoming longer; complete specimens with single bidentate hooded hook from about setiger 20–30 accompanied by 3–4 long thin capillaries, hooks long, thin, weakly curved. Neurosetae of setigers 4–7 fimbriated capillaries (Fig. 7G), smaller versions of enlarged spinous setae of setiger 3. Bidentate hooded hooks in neuropodium from setiger 8; 2–3 hooks per fascicle; hooks with curved shaft tapering to narrow apex bearing two teeth (Figs. 7H–I; 8D); main fang longer than or of equivalent length to apical tooth, with about a 45° angle between them; with wide angle between main fang and shaft (Figs. 7H–I; 8D). Neuropodial hooded hooks accompanied by 2–4 simple, strongly curved capillaries (Fig. 7J), similar to sabre setae found in neuropodia of some Spionidae.

Last 2–3 setigers with enlarged, modified neuropodial hooks replacing hooded hooks and capillaries (Figs. 6D; 8F–G); penultimate hook typically largest, bluntly falcate, with a pair of flanges giving tripartite appearance to end of hook (Figs. 7L–N; 8C, G); partial hood present or absent. Last spine simple, with or without lateral flanges (Fig. 7K); one paratype (USNM 1480965) with large tripartite hooks on 3rd and 2nd last segments and a simple smooth spine on last segment.

One paratype (USNM 1480958) an ovigerous female: ovaries visible through body as paired sacs in middle segments, each bearing oocytes up to about 50 µm in diameter and arising from anterior septa of individual segments; these sacs extending about halfway along each segment (Fig. 8E). Gametes not observed in other specimens. Several specimens with esophagus and intestine evident (Figs. 6A, 8A–B). Esophagus a narrow tube extending to about setiger 4–5, intestine expanded in each segment continuing to posterior end where it again narrows near anal opening.

Pygidium with two dorsal and two ventral cirri; anus terminal (Figs. 6D; 8F–G).

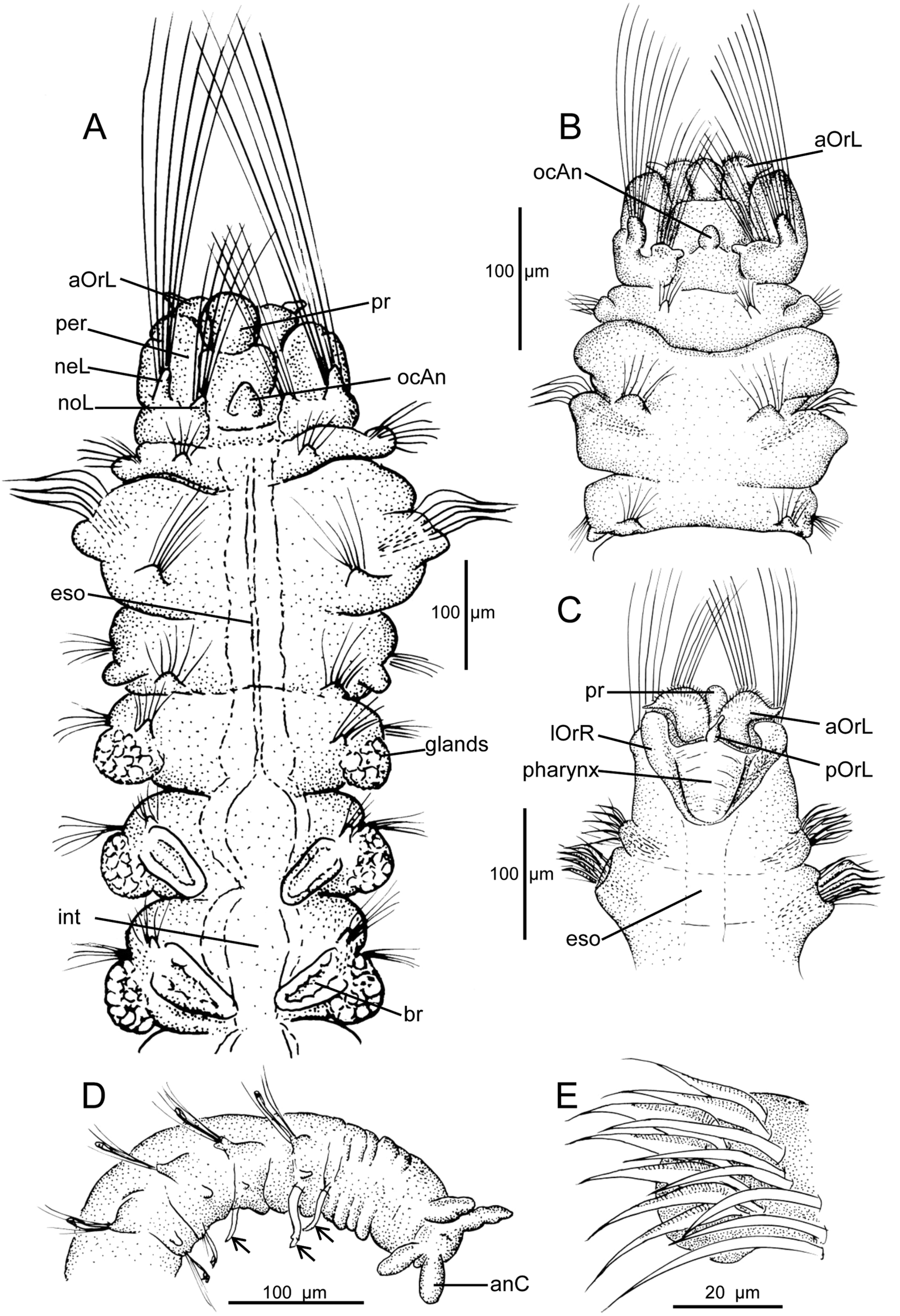

FIGURE 6. *Rhamphispio tridentata* **n. sp.** Holotype (USNM 1480957: A, D, E) and paratypes (USNM 1480965: B–C). A, anterior end, dorsal view; B–C, anterior end in dorsal (B) and ventral (C) views. D, posterior end in left lateral view, arrows denote enlarged modified hooks; E, fascicle of enlarged neuropodial crested setae from setiger 3, ventral view. Abbreviations: anC, anal cirrus; aOrL, anterior oral lobe; br, branchiae; eso, esophagus; int, intestine; lOrR, lateral oral ridge; ocAn, occipital antenna; per, peristomium; pOrL, posterior oral lobe; pr, prostomium.

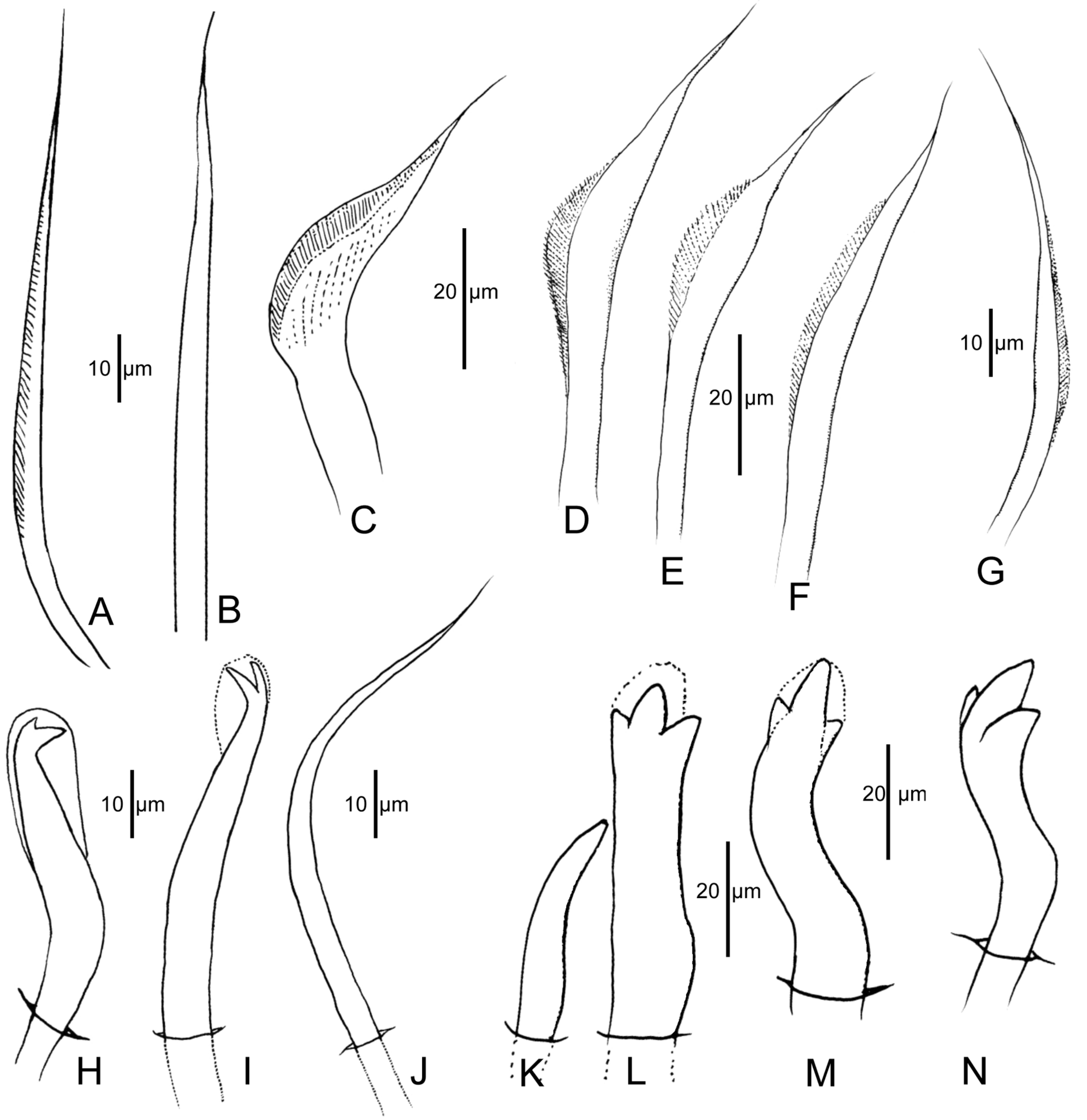

FIGURE 7. *Rhamphispio tridentata* **n. sp.** Setae: A–B, notopodial capillaries, setiger 3; C–F, enlarged neuropodial crested setae from setiger 3; G, neuropodial capillary from setiger 4; H–I, neuropodial hooded hooks; J, capillary neuroseta with hooded hooks; K–N, enlarged modified neuropodial hooks from far posterior parapodia; dotted line denotes outline of hood. Paratypes (USNM 1480965: A–B); (USNM 1480965: C); (USNM 1480962: D–F); (USNM 1480964: H–J); holotype USNM 1480957: K–N).

Methyl Green staining. Dorsal glands on the posterior lateral borders of anterior segments extend down and across the venter. These glands stain prominently with MG imparting a distinct pattern (Fig. 8B). Additional MG staining is evident in a V-shaped area posterior to the mouth that extends to the anterior border of setiger 3 (Fig. 8B).

Remarks. The enlarged posterior neuropodial hooks of *Rhamphispio tridentata* **n. gen. n. sp.** differ from those present in species of *Uncopherusa* and *Uncispio* in having two lateral flanges instead of one or none, imparting a tripartite appearance to the hooks. *Rhamphispio tridentata* **n. gen. n. sp.** also differs from *Uncopherusa* and *Uncispio* in having notopodial hooded hooks instead of lacking them, and by the presence of an enlarged setiger 3 that bears large, crested spinous neurosetae. In other uncispionids, the third setiger is not enlarged and neuropodial setae while sometimes having a low crest are not greatly enlarged relative to those on other segments.

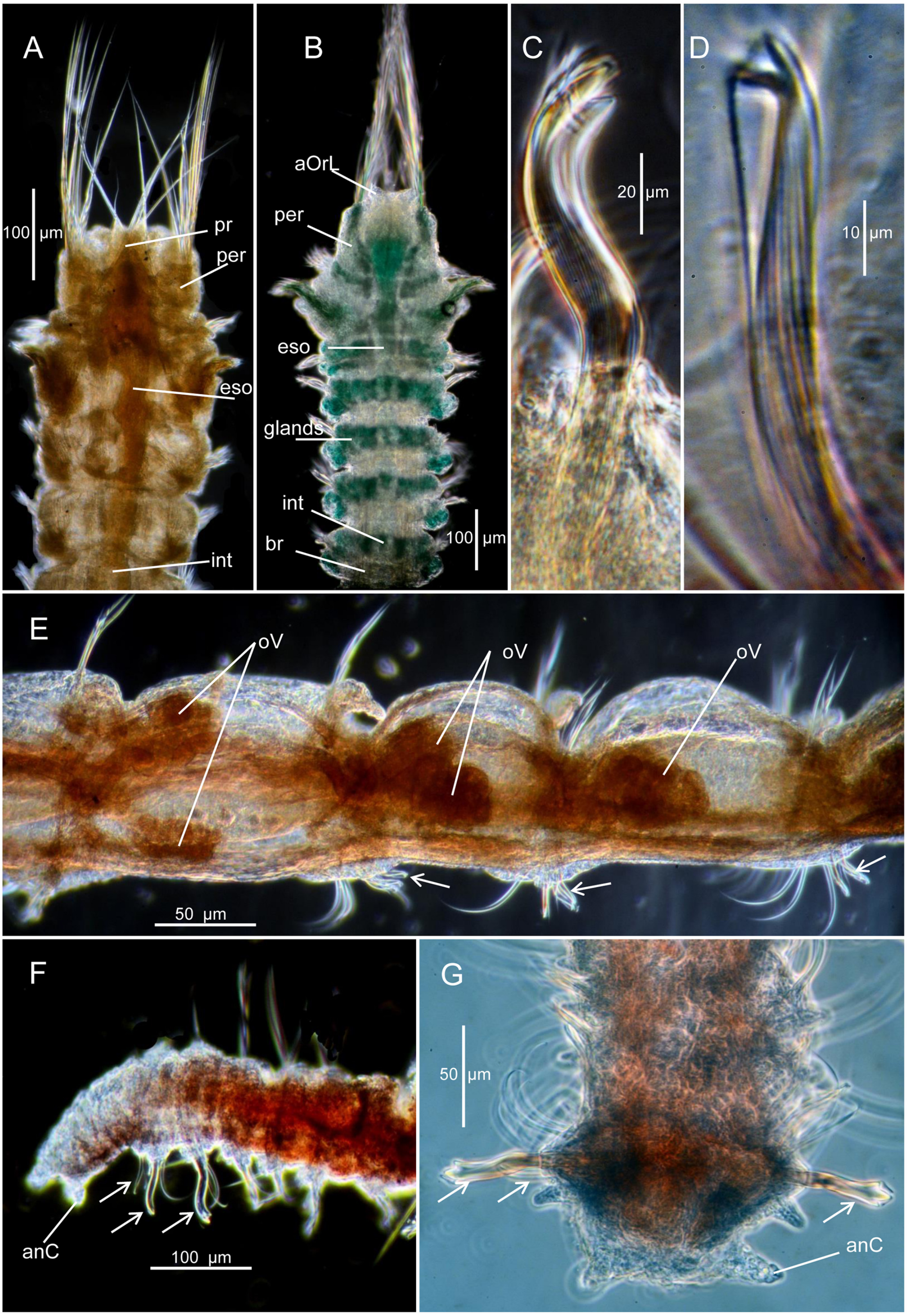

FIGURE 8. *Rhamphispio tridentata* **n. sp.** A, anterior end, dorsal view; B, anterior end, dorsum stained with Methyl Green; C, enlarged modified hook from a posterior neuropodium; D, hooded hook from a middle segment; E, mid-body segments of an ovigerous paratype; F, posterior end, right lateral view (USNM 1480965); G, posterior end, dorsal view. Arrows denote enlarged modified hooks. Abbreviations: anC, anal cirrus; aOrL, anterior oral lobe; br, branchia; eso, esophagus; int, intestine; oV, ovaries; per, peristomium; pr, prostomium. A, E, F, G stained with Shirlastain A; B, stained with Methyl Green. Paratypes (USNM 1480958: A, C–E); (USNM 1480963: B); (USNM 1480965: F); (USNM 1480962: G).

Etymology. The name *tridentata* refers to the enlarged neuropodial hooks of far posterior segments; the two lateral teeth produce a diagnostic tridentate morphology that is characteristic for the species.

Habitat. The sediment in the areas where *Rhamphispio tridentata* **n. sp.** was collected is variable, with specimens being collected from different depths and types of slope environments. Stations from off New England are from an area cut with canyons and gullies, whereas the U.S. South Atlantic stations are in an area of the continental slope that is influenced by complex current systems.

Data for selected stations are taken from Blake *et al*. (1987) and Maciolek *et al.* (1987b):

- North Atlantic, Lydonia Canyon, off Massachusetts (2065 m), sediments with high sand content: sand (73.4%), silt (15.9), clay (10.8); low organic carbon (0.28%).
- South Atlantic off Cape Lookout, North Carolina (~2000 m), mixed sediments: sand (19.9%), silt (41.3%), clay (38.7%); low organic carbon (1.8%).
- South Atlantic off Charleston, South Carolina (~800 m), mixed sediments: sand (38.5%), silt (33.9%), clay (28.3%); moderate organic carbon (3.8%).

Distribution. U.S. Atlantic continental slope off New England, North Carolina, and South Carolina; 800–2078 m.

Family Spionidae Grube, 1850

Genus *Pygospiopsis* Blake, 1983

Type-species: *Pygospio dubia* Monro, 1930, designated by Blake 1983.
Synonym: *Pseudatherospio* Lovell, 1994, type-species *P. fauchaldi* Lovell, 1994, by monotypy. **New Synonymy.**

Diagnosis. (Emended). Prostomium wider than long, sometimes bell shaped, flaring anteriorly, with bilobed frontal margin; frontal horns absent; occipital antenna present; eyes present or absent; nuchal organs as narrow slits or grooves near posterior margin of prostomium. Branchiae from setiger 1, 2, or 7, or on setiger 2, 2–3, 4–6, or 6, and resuming on setiger 7, continuing posteriorly; branchiae anterior to setiger 7 generally simple, free from notopodial lamellae or only basally fused; branchiae from setiger 7 enlarged, broad, heavily ciliated, and fully fused with notopodial lamellae. Transverse ciliary bands on dorsum between branchiae. Interparapodial pouches and dorsal crests absent. Notosetae all capillaries. Neurosetae include simple capillaries, some with distinct fringe of fibrils along one edge, or weakly aristate, but never heavily modified. Neuropodial hooks present in middle and posterior segments; hooks unidentate or weakly bidentate, hooded or unhooded, shaft narrow, straight, or heavier and curved; subapical tooth on concave side present as knob, short tooth, longer flange, or entirely absent; inferior sabre setae absent. Pygidium with up to 12 anal cirri.

Remarks. *Pygospiopsis* was established by Blake (1983) for *Pygospio dubia* Monro, 1930, a subantarctic species that differed from *Pygospio* species by having (1) unidentate, unhooded, neuropodial hooks with bristled tips instead of bidentate hooded hooks and (2) a pygidium surrounded by a ring of anal cirri instead of four lobes. Mackie & Duff (1986) later observed that some neuropodial hooks of the syntypes of *P. dubia* have a small subapical tooth. Lovell (1994) also examined the types of *P. dubia* and determined that modified neuropodial crested setae were present in anterior setigers. These additional features allied *P. dubia* with *Atherospio disticha* Mackie & Duff, 1986, from off Scotland, and *Pseudatherospio fauchaldi* Lovell, 1994, from the southern California outer continental shelf. All three species have similar prostomial shapes, an occipital antenna, modified anterior neurochaetae, branchiae that are either basally or entirely fused to notopodial lamellae, and unusual bidentate neuropodial hooded or unhooded hooks with a small tooth or knob on the concave side subapical to the terminal shaft or main fang. In other spionids, the small tooth (teeth) is (are) superior to the main fang on the convex side. In both *Pygospiopsis dubia* and *A. disticha*, the shaft of these hooks is more or less straight or only gently curved, whereas in *Pseudatherospio fauchaldi*, the shaft is strongly recurved. Blake (1996) reviewed these taxa as part of his description of a new species, *Pygospiopsis occipitalis*, and suggested that *Atherospio* species and *Pygospiopsis* species were part of the same genus and that *Pseudatherospio* was separate because branchiae began on setiger 1. Meißner & Bick (2005) did not support this synonymy as part of their redescription of *Polydora* *guillei* Laubier & Ramos, 1974, which they referred to *Atherospio* due to the highly modified neuropodial spines on setiger 5. Prior to the present paper, there have been no additional records of any of the three genera.

The major difference between these three genera as currently understood is in the branchial distribution. In *Pygospiopsis dubia*, slender branchiae that are free from the dorsal lamellae occur on setigers 2 and 3, then are absent on setigers 4–6, followed by larger branchiae from setiger 7 that are basally fused to notopodial lamellae; these continue for another 9–10 setigers. In *P. occipitalis*, branchiae also occur from setiger 2 and are mostly separate from the notopodial lamellae; these branchiae continue on following segments with an increasing degree of fusion with the notopodial lamellae and by setiger 7 the branchiae and lamellae are mostly fused along their length. In *Atherospio disticha*, thickened branchiae are fully fused with the dorsal lamellae from setiger 7, and are present for six setigers; there are no branchiae anterior to setiger 7. The same branchial arrangement is present in *A. guillei* (Laubier & Ramos, 1974) redescribed by Meißner & Bick (2005). In *Pseudatherospio*, branchiae are first present from setiger 1 and continue posteriorly to near the end of the body; these branchiae are basally fused with notopodial lamellae over most of the body and fully fused in some middle setigers.

In the present study, a new collection of the type-species, *P. dubia*, was obtained from the site of the former Larsen A Ice Sheet (LIS) on the east side of the Antarctic Peninsula. Two specimens collected from King George Island (KGI) in the South Shetlands off the West Antarctic Peninsula by Siciński (2000, 2004) were also examined. In addition to redescribing the adults with SEM and light microscopy, post-larvae and juveniles also collected from LIS are described and illustrated. Also, three new species have been encountered: (1) from another site on the Antarctic Peninsula, (2) from deep water off northern California, and (3) from the U.S. Atlantic continental slope. These records bring the total number of known species of *Pygospiopsis* to five. These species are all compared and contrasted with the closely related *Atherospio disticha*, *A. guillei*, and *Pseudatherospio fauchaldi*.

The results of the present study are that three additional branchial patterns are evident among the species of this complex and a different approach to the generic-level classification of this group is required. First, all species have broad branchiae from setiger 7 that are fused, partially or fully, with the notopodial lamellae. The two species of *Atherospio*, *A. disticha* and *A. guillei*, have their first branchiae on setiger 7; the two known and three new species of *Pygospiopsis* described in this paper and *Pseudatherospio fauchaldi* have simple or partially fused branchiae anterior to setiger 7 in different patterns. As will be evident in the following descriptions and accounts, there is little support for retaining *Pseudatherospio* as a separate genus; therefore, that genus and species, *P. fauchaldi,* are here referred to the genus *Pygospiopsis*. The genus *Atherospio* remains valid. The following list of species of *Pygospiopsis* includes the new species described herein and *P. fauchaldi* transferred from the genus *Pseudatherospio*:

Pygospiopsis dubia (Monro, 1930). Off South Georgia and Antarctic Peninsula, 25–713 m.
Pygospiopsis antarctica **n. sp.** Off East Antarctic Peninsula, 385 m.
Pygospiopsis antennata **n. sp.** Off northern California, 1820 m.
Pygospiopsis fauchaldi (Lovell, 1994) **new combination.** Off central and southern California, 197–530 m.
Pygospiopsis occipitalis Blake, 1996. Off Point Arguello, southern California, 930 m.
Pygospiopsis profunda **n. sp.** Off the U.S. Atlantic continental slope, 1509–2155 m.

***Pygospiopsis dubia* (Monro, 1930)**

Figures 9–11

Pygospio dubia Monro, 1930: 146–147, Fig. 55a-i; Hartman, 1966: 21, pl. 5, Figs. 4–7; Richardson & Hedgpeth, 1977: 186.
Pygospiopsis dubia: Blake 1983: 242–244, Fig. 20; Hartmann-Schröder & Rosenfeldt 1988: 57–58; Siciński 2000: 164; 2004: 82; Blake 2006: 623–624, Fig. 13.22 A–B, not Fig. 13.22C; Blake *et al.* 2017: Fig. 46A–C.

Material examined. **East Antarctic Peninsula, Larsen Ice Shelf A Area, Greenpeace Trough,** RVIB *Nathaniel B. Palmer* Cruise 2000-03, coll. J.A. Blake, Smith McIntyre grab, 19 May 2000, Sta. 16, 64°43.897′S, 059°55.745′W, 713 m, 3 specimens (MCZ 147900); 1 on SEM Stub (MCZ), 4 post-larvae (MCZ 147901); 2 post-larvae on SEM stub (MCZ).—**Off West Antarctic Peninsula, South Shetland Islands, King George Island**, Admiralty Bay, Section T, coll. J. Siciński, 08 Feb 1985, 88 m, 2 specimens (MCZ 147905).

Additional material examined. Off South Georgia, R/V *Discovery* Sta. 29, 16 March 1926, 25 m, **syntypes** (BMNH 1930.10.8.1576–1600).

Description. All adult specimens from Larsen Ice Shelf site (LIS) small. One complete specimen 2.08 mm long, 0.43 mm wide for 25 setigers; one incomplete specimen a female with oocytes in last few segments, oocytes with considerable yolk, largest 85 µm in widest diameter. Color in alcohol, opaque white. One complete specimen from King George Island (KGI) 8 mm long, 0.8 mm wide for 52 setigers. Largest syntype examined 12 mm long, 1.0 mm wide for 54 setigers.

Prostomium truncate on anterior margin, forming two weak lobes, weakly incised, extending posteriorly to setiger 1, caruncle absent (Fig. 9A, C); short, bulbous occipital antenna present at posterior margin of prostomium (Fig. 9A–C); nuchal organs present as paired slits posterior and lateral to occipital antenna (Fig. 9C); eyespots absent. Palps missing on all adults, present on juveniles (see below); palp scars evident lateral to prostomium as two large oval openings (Fig. 9A, C). Peristomium inflated, extending dorsally forming upper lip of mouth (Fig. 9A, C) and ventrally forming lower lip of mouth (Fig. 9B); entire oral area inflated, with relatively smooth surface; papillae few, best observed on lateral margins of mouth.

Setigers 1–6 with well-developed noto- and neuropodial postsetal lamellae (Figs. 9A–B, 10A–B); notopodial lamellae generally short, triangular; neuropodial lamellae initially short, triangular, becoming more rounded and elliptical; from setiger 7, notopodia fully fused with branchiae (Figs. 9A, 10C); podial lobes of post-branchial setigers triangular, broad basally, tapering to narrow tip (Fig. 10D). Neuropodial lamellae elliptical, rounded through branchial region (Fig. 10C), then becoming triangular and tapering to narrow tip (Fig. 10D).

Branchiae present on setigers 2–3 and 7–11 (Fig. 9A) in LIS specimens; 2–3, 7–12 in KGI specimens, and 2–3 and 7–16 in largest syntype from off South Georgia; anterior branchiae of setigers 2–3 cirriform, narrowing apically, entirely free from notopodial lamellae (Figs. 9C, 10A); branchiae from setiger 7 broad, flattened, with lateral undulating membrane fully fused with notopodial lamellae (Figs. 9A, 10C); each of these branchiae with a short digitate process on the distal end (Fig. 9A). Transverse ciliary bands extending across dorsum between branchiae from setiger 7 (Fig. 9A).

Setae include capillaries throughout in both noto- and neuropodia and long hooks or spines in posterior neuropodia; hooks first present from setigers 15–20; each with a curved narrow tip; entire tip of shaft covered with a bristled sheath when observed in SEM (Fig. 9E, F); a few fine bristles observed in light microscopy. Shafts of hooks narrowing to a blunt tip (Fig. 9E–F); separate knob on concave side not observed on LIS and KGI specimens, although some spines with a slight subapical swelling near tip of shaft, likely due to sheath of bristles. Capillary notosetae of anterior setigers 1–10 longer than neurosetae, in spreading fascicles of up to 10–12 curved capillaries in two rows, with setae of anterior row shorter and more curved than those of posterior row; each capillary seta with fringe of fibrils along one edge. Capillary neurosetae similar to those of notosetae, with fringe of fibrils along one edge (Fig. 9D), but generally shorter; a few very thin capillaries accompany long spines of posterior setigers (Fig. 9E).

Pygidium with terminal anus surrounded by at 6–10 short anal cirri in the LIS material; complete specimen from KGI with eight cirri surrounding anal opening.

Methyl Green staining. No pattern is evident; however, at least one specimen from LIS exhibited a weak staining of gland cells in the anterior notopodia; the same specimen exhibited similar staining of glands on the inner border of the upper lip of the mouth.

Remarks. The specimens described here from the LIS area differ from those reported from the type collection from off South Georgia (Blake 1983), mainly by being smaller. Thus, the large branchiae that occur over setigers 7–16 in the types occur only on setigers 7–11 in the smaller specimens. The specimens from KGI are more similar in size to the types, although branchiae occur only to setiger 12. The nature of the prostomium, occipital antenna, podial lobes, branchiae on setigers 2–3 and on setiger 7–10, as well as the morphology of posterior neuropodial hooks on both the LIS and KGI specimens agree well with the original materials. There is no evidence of modified neurosetae on any anterior segment.

The type collection of *Pygospiopsis dubia* was reexamined by Mackie & Duff (1986) as part of their description of *Atherospio disticha* Mackie & Duff, 1986, a species that shares some characters with *Pygospiopsis*. These authors observed a secondary tooth on the smallest spines and this was reduced or entirely absent on the other larger ones. Lovell (1994) also examined types of *P. dubia* and made the same observations as Mackie & Duff (1986). In the new materials, a careful inspection of each specimen did not yield any examples of spines having a secondary tooth or knob.

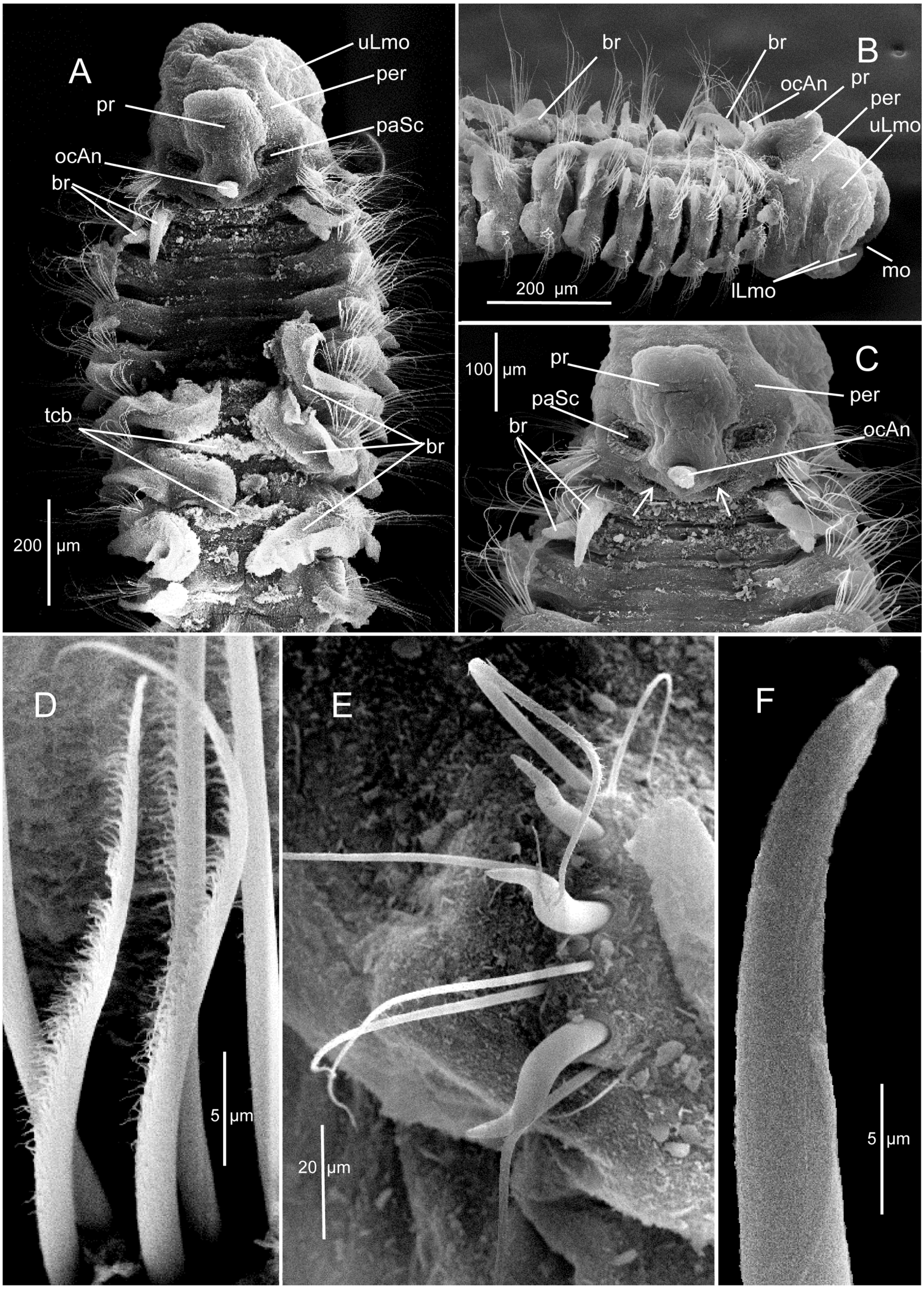

FIGURE 9. *Pygospiopsis dubia*. SEMs of adult (NBP Sta. 16): A, anterior end, dorsal view showing branchial segments; B, anterior end, right lateral view; C, anterior end, dorsal view, arrows indicate nuchal organs; D, capillary neurosetae from an anterior setiger; E, neuropodial hooked setae and capillaries from about setiger 15; F, detail of hooked seta. Abbreviations: br, branchiae; lLmo, lower lip of mouth; mo, mouth; ocAn, occipital antenna; paSc, palp scar; per, peristomium; pr, prostomium; tcb, transverse ciliary bands; uLmo, upper lip of mouth. Note SEMs are not archived as stubs, but as images.

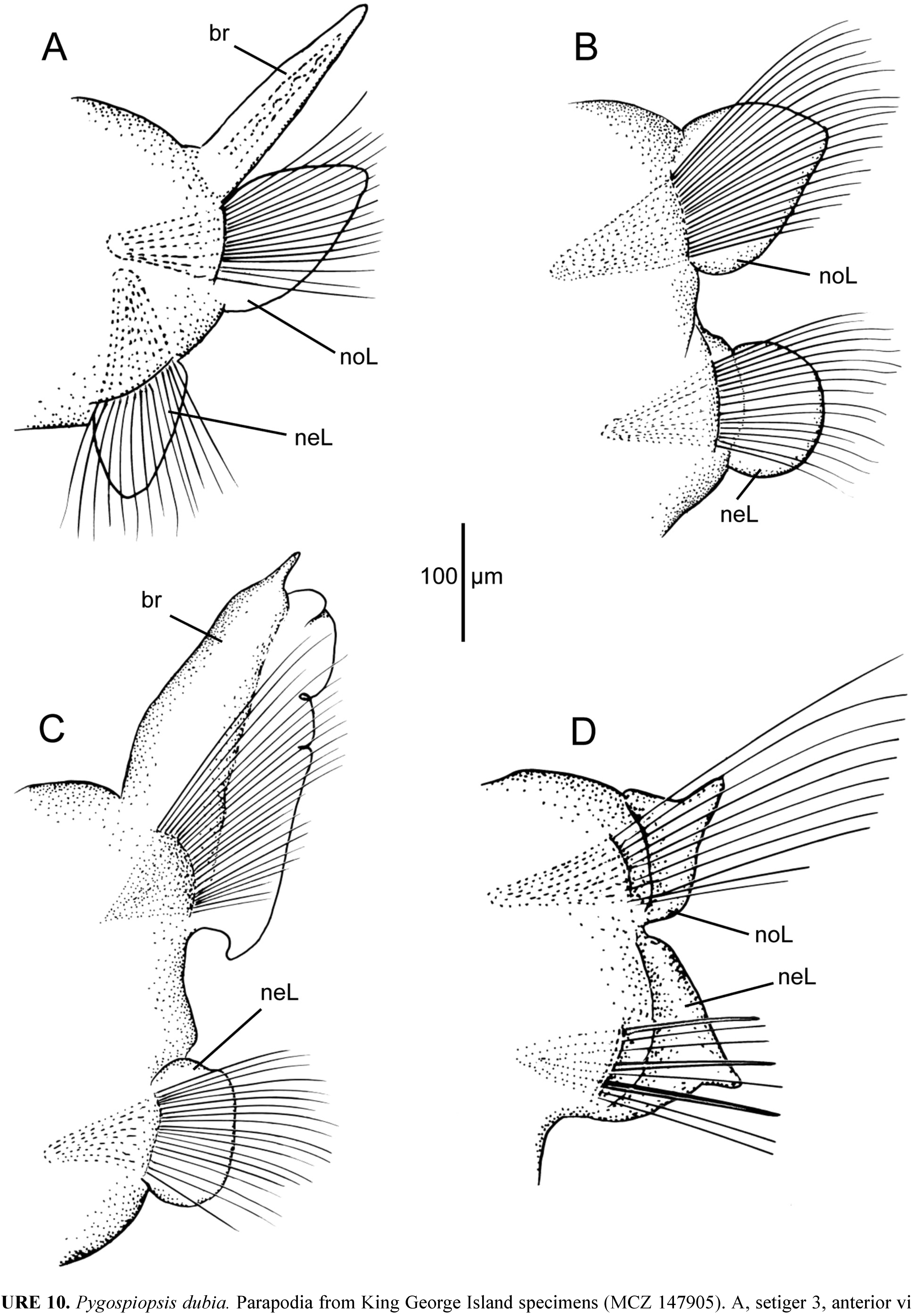

FIGURE 10. *Pygospiopsis dubia.* Parapodia from King George Island specimens (MCZ 147905). A, setiger 3, anterior view; B, setiger 5, anterior view: C, setiger 11, anterior view; D, setiger 32, anterior view. Abbreviations: br, branchia; neL, neuropodial lamella; noL, notopodial lamella.

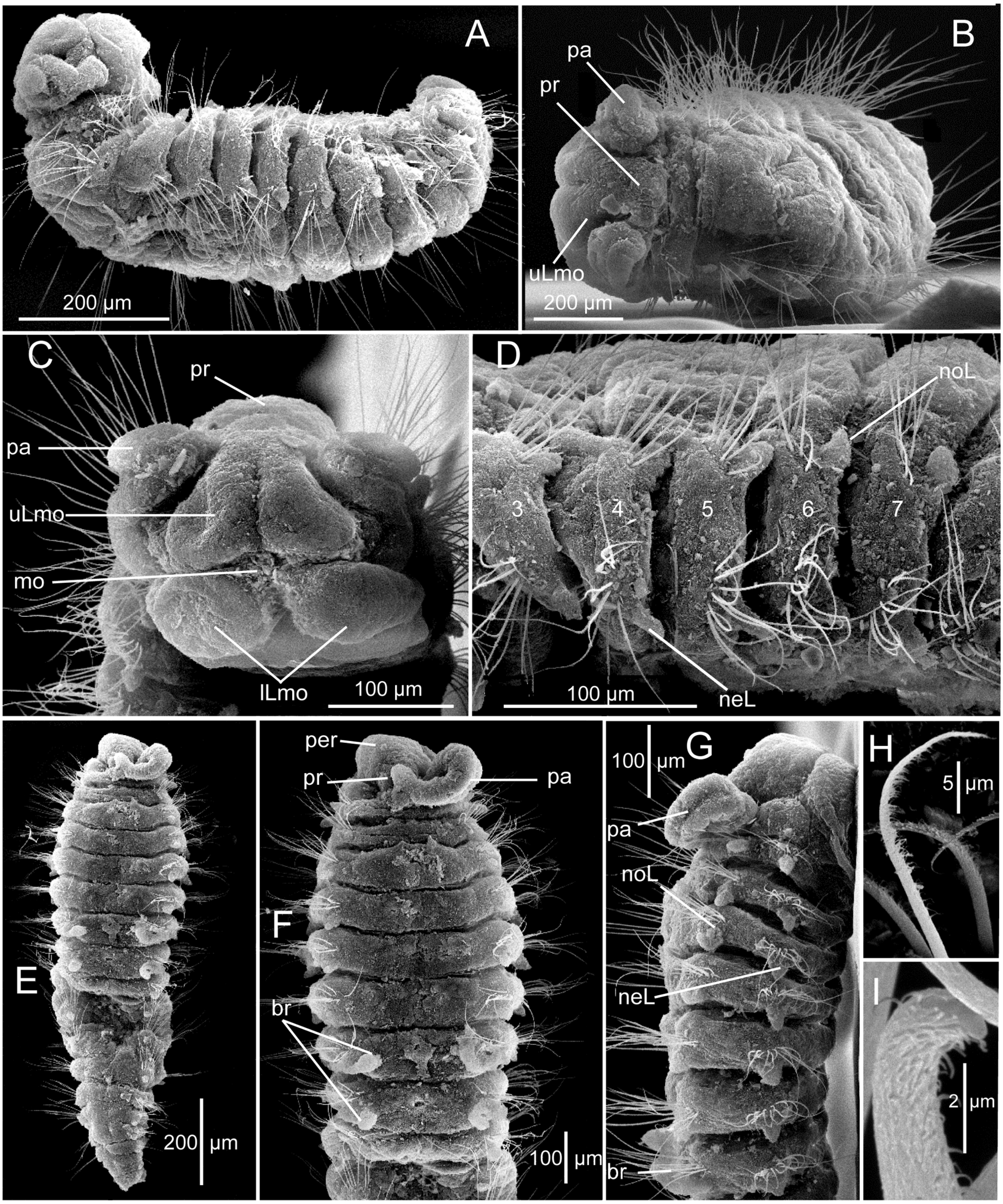

FIGURE 11. *Pygospiopsis dubia*. SEMs showing post-larval and juvenile morphology (NBP Sta. 16). A–D, 14-setiger postlarva: A, entire specimen, lateral view; B, anterior dorsal view; C, anterior end, frontal view; D, lateral view of setigers 3–7. E–I, 16 setiger juvenile: E, entire specimen, dorsal view; F, anterior 10 setigers, dorsal view; G, anterior end lateral view; H, capillary neuroseta anterior setiger; I, distal end of neuropodial hook from setiger 12. Abbreviations: br, branchiae; lLmo, lower lip of the mouth; mo, mouth; neL, neuropodial lamellae; noL, notopodial lamella; pa, palp; pr, prostomium; uLmo, upper lip of mouth. Numbers on Fig. 7D identify setigers 3–7. Note: SEMs are not archived as stubs, but as images.

During a visit short visit to the Natural History Museum (London) in 2007, one of us (JAB) was able to reexamine a few of the syntypes of *Pygospio dubia*. The greater majority of the neuropodial hooks on these specimens were unidentate with a secondary tooth or protuberance only infrequently apparent and only on smaller hooks that were newly developed. As noted, a subapical tooth or knob, was not observed on any hooks in specimens from the new samples examined in this study.

After the original description of *P. dubia* from the subantarctic island of South Georgia by Monro (1930) there were no further collections of the species until Richardson & Hedgpeth (1977) recorded it from Anvers Island on the Antarctic Peninsula. The species was subsequently reported from King George Island by Hartmann-Schröder & Rosenfeldt (1988) and Siciński (2000, 2004). The current records extend the range of the species to the East Antarctic Peninsula and into deeper water in the newly discovered Greenpeace Trough at the site of the former Larsen A Ice shelf.

Post-larval and Juvenile Morphology. During the separation of the four adults found at the LIS Sta. 16, six post-larvae and juveniles were found in the tube of one of the adults. Two specimens were prepared for SEM. A brief description of post-larvae and juveniles from this collection was reported by Blake (2006).

The earliest stage of development recovered from the sample was a 14-setiger post-larva (Fig. 11A). This specimen measures 780 µm long and 270 µm wide. It is short, thick, and does not appear capable of swimming in the plankton. A pair of short palps is present (Fig. 11A–C). The prostomium is short and not differentiated at this stage and an occipital antenna is not present. The peristomium is developed laterally and extends over and around the mouth, forming upper and lower lips (Fig. 11B–C). Parapodia are well-developed with short noto- and neuropodial lamellae (Fig. 11D). Both noto- and neurosetae are present with about 9–10 capillaries per fascicle in the noto- and neuropodia of most segments; these capillaries are not serrated as in provisional setae of planktic spionid larvae, but have a thin fringe of fibrils along one edge. There appear to be cilia on the ventral surface of this post-larva, but defined ciliary bands are absent. These post-larvae should be capable of slow crawling movements within a parental burrow or tube.

A 16-setiger juvenile is shown in Fig. 11E–G and is 1.17 mm long and 390 µm wide; three other juvenile specimens with 15–16 setigers were of a similar size. All have a similar tumid body shape and short palps. The prostomium is poorly developed, and appears to be bluntly rounded on the anterior margin; there is no occipital antenna; a single intact palp with a distinct ventral groove is present and considerably longer than in the previous stage, but still shorter than in other spionids at this stage of development (Fig. 11E–G). Two pair of short, broad branchiae are present on setigers 7–8 (Fig. 11F), but no branchiae are present on setigers 2–3 as in adults. There is no evidence of transverse dorsal ciliary bands at this stage.

Capillary setae are present on all setigers; in SEM these are observed to be thin and to have a thin fringe of fibrils along one edge (Fig. 11H); there is no evidence of modified or otherwise enlarged neurosetae on any anterior segment. Neuropodial hooks are first present from setigers 11 or 12; these hooks are long, with a straight bristled shaft and a smooth rounded tip (Fig. 11I); there is no evidence of a subapical tooth or protuberance. One or two thin capillaries accompany the hooks. The pygidium has 5–6 short rudimentary lobes.

Remarks. These observations, while limited, suggest that the basic morphology of the pre-setigerous region including peristomium, oral lips, palps, and occipital antenna develop early along with the large branchiae from setiger 7; the shorter branchiae on setigers 2–3 develop later. The prostomium is largely undifferentiated in these juveniles and there is no occipital antenna present. The presence of hooked neuropodial spines from setigers 11–12 suggests that they appear with the development of about 15 setigers. The spines are similar to those of the adults.

In most spionids studied to date, larval ciliary nototrochs of planktic larvae are likely retained in adults and contribute to the transverse ciliary bands (Blake & Arnofsky 1999; Blake 2006). The absence of transverse ciliary bands between the branchiae of the 16-setiger juvenile reported here, and in any segment of the earlier 14- or 15-setiger post-larval stages, suggest that dorsal segmental nototrochs, characteristic of planktic larvae of most spionids, do not develop in this species. Based on the overall morphology of the 14-setiger stage, and its presence in the tube of the adult, it is likely that the development is direct in this species and that there is no planktic dispersal stage.

Habitat. Biological and sediment samples were collected from sediments in the Greenpeace Trough, a nearshore feature discovered during the May 2000 survey of the former Larsen-A ice shelf area approximately two years after its breakup (Domack *et al.* 2001). Due to the glacial cover over Larsen A, the sediments contain high concentrations of sand in the surficial sediments from particles dropped to the seafloor. Percent sand is high (20–40%) in surficial sediments (0–5 cm) of the Greenpeace Trough according to Gilbert & Domack (2003). In their report of *P. dubia* from King George Islands, Hartmann-Schröder & Rosenfeldt (1988) noted that the species was collected from a substrate consisting of silt with stones. These observations suggest that *P. dubia* may be limited to sediments having a mixture of coarse and fine grains.

The four adult specimens were found in a single sample from the Greenpeace Trough at a depth of 713 m. In addition to the four adult specimens, six post-larval forms were found with one of the adults in a soft silty tube fragment. Other abundant invertebrates in the sample were polychaetes (Cirratulidae, Hesionidae, Opheliidae, Paraonidae, Scalibregmatidae), and at least two species of Scaphopoda (Blake & Maciolek unpublished).

Distribution. Off South Georgia, 25 m; South Shetland Islands, 88–200 m; West Antarctic Peninsula, off Anvers Island; East Antarctic Peninsula, site of the former Larsen Ice shelf A, 713 m.

Pygospiopsis antarctica **new species**

Figure 12

Material examined. **East Antarctic Peninsula, off Lindenberg Island, east of the Larsen A ice shelf area,** RVIB *Nathaniel B. Palmer* Cruise 2000-03, coll. J.A. Blake, Smith McIntyre grab, 15 May 2000, Sta. 03, 64°53.533′S, 059°30.694′W, 385 m, **holotype** (MCZ 147902).

Description. Holotype posteriorly incomplete, 6.8 mm long, 0.78 mm wide for 28 setigers. Body dorsoventrally flattened throughout, anterior and middle segments similar, about three times wider than long. Most podial lobes and a few areas of prostomium and peristomium with large glands; these glands stain with Methyl Green (see below). Color in alcohol light tan.

Prostomium short, incised on anterior margin, extending posteriorly to setiger 1, caruncle absent (Fig. 12A); short digitiform occipital antenna, arising from near posterior prostomial margin; eyespots absent; a pair of slit-like nuchal organs present near posterior margin of prostomium and posterior to occipital antenna (Fig. 12A). Palps arising lateral to prostomium (scars evident); one intact palp (broken off during handling) long, curled, tapered apically, with shallow ventral groove. Peristomium extending lateral to prostomium forming upper lip of mouth (Fig. 12A), and extending ventrally forming ventral lip of mouth (Fig. 12B); thick everted proboscis or pharynx present (damaged on holotype), dorsal surface of oral lips and pharynx relatively smooth; distinct papillae absent.

Setigers 1–6 with well-developed noto- and neuropodial postsetal lamellae, each bearing fascicles of long capillary setae. Notopodial lamellae of setigers 1–6 mostly broad basally, but some narrower than those of neuropodia (Fig. 12A). Neuropodial lamellae broad, leaflike to heart-shaped (Fig. 12B). Short, simple, digitiform branchiae present on setigers 2–6, followed by broad, thick branchiae on setigers 7–10 and shorter, simple branchiae again on setigers 11–14, each becoming smaller and more digitiform (Fig. 12A). Broad branchiae of setigers 7–10 with thick central core tapering to narrow apex bearing a short digitate process (Fig. 12A); core bearing thin anterior and posterior membranes; anterior membrane heavily ciliated. Notopodia from setiger 7 basally fused with branchiae; from setiger 11 notopodial lamellae separate from branchiae, but becoming smaller and digitate in remaining setigers. Neuropodia of setigers 7–12 leaflike, broad basally (Fig. 12A), then becoming short and papillate in remaining segments. Transverse ciliary bands extending across dorsal surface between bases of branchiae on setigers 7–13 (Fig. 12A).

Setae include noto- and neuropodial capillaries throughout; simple spines or hooks occur in neuropodia from setiger 14. Capillaries relatively thin, arranged in two rows in anterior and middle segments, with up to 20 setae per fascicle. Individual capillaries appear smooth in light microscopy; a narrow fringe of fibrils observed along one edge of some setae, but difficult to observe on a consistent basis. Neuropodial hooks or spines number 1–3 per fascicle, with 2–4 very thin capillaries. Individual spines narrow, with a weakly curved shaft tapering to a rounded, sometimes pointed, tip (Fig. 12C–E); no subapical knobs or teeth present on spines in this specimen. Very fine fibrils observed near tip of hooks, but their presence difficult to observe in light microscopy.

Methyl Green staining. Anterior podial lobes and glands in a few areas of the prostomium and peristomium stain with Methyl Green.

Remarks. *Pygospiopsis antarctica* **n. sp.** is unique among the five known species of the genus in having simple branchiae from setigers 2–6 that are free from the notopodia followed by large broad branchiae from setiger 7–10 that are only basally fused with the notopodia; these are then followed by additional simple branchiae over setigers 11–14. The only other species of the genus having branchiae from setiger 2 and on a series of following segments is *P. occipitalis* from California; in that species, however, the first two pairs of anterior branchiae on setigers 2–3 are simple and free from the notopodia, with those of 4–6 becoming larger and basally fused to the notopodia. *Pygospiopsis fauchaldi* has simple branchiae from setigers 1–6, basally fused to the notopodia, followed by fully fused branchiae from setiger 7. Other species of *Pygospiopsis* have anterior branchiae followed by setigers lacking branchiae, before the broad, basally fused branchiae of setiger 7.

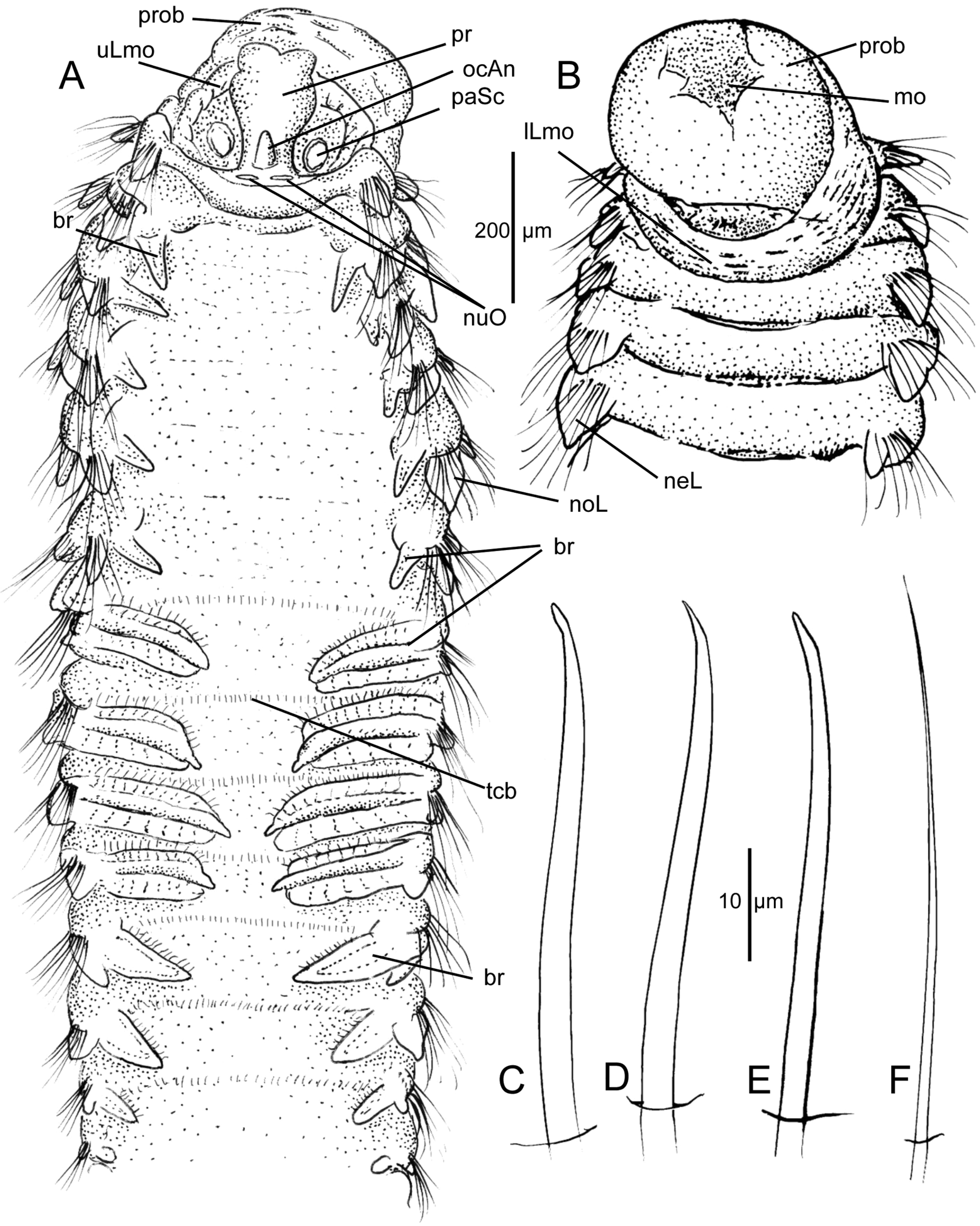

FIGURE 12. *Pygospiopsis antarctica* **n. sp.** Holotype (MCZ 147902): A, anterior end, dorsal view; B, anterior end, ventral view; C–E, neuropodial hooks from posterior neuropodia; F, capillary occurring with hooks. Abbreviations: br, branchiae; lLmo, lower lip of mouth; mo, mouth; neL, neuropodial lamella; noL, notopodial lamella; nuO, nuchal organs; ocAn, occipital antenna; paSc, palp scar; pr, prostomium; prob, proboscis; tcb, transverse ciliary band; uLmo, upper lip of the mouth.

The only other species of *Pygospiopsis* reported to have neuropodial spines or hooks lacking a subapical knob or tooth is the type-species, *P. dubia* (see Blake 1983 and description above). Mackie & Duff (1983), however, reexamined the type collection and observed a secondary tooth on the smallest spines, but this tooth was reduced or entirely absent on all other larger spines. A reexamination of syntypes of *P. dubia* confirmed that a few newly emergent hooks did indeed have a subapical knob protuberance, albeit this knob was small and difficult to observe. In the new materials of *P. dubia* reported in this paper, a careful inspection of each specimen did not yield any examples of spines having a secondary tooth or knob. It is also apparent that the spines of *P. dubia* are larger and more robust than those of *P. antarctica*.

Etymology. The name of this species is derived from its collection site off the Antarctic Peninsula.

Habitat. The holotype was collected in May 2000 from a site in Weddell Sea, east of the main Larsen A ice shelf area, at a depth of 385 m. Surficial sediments throughout the study area in and around the Larsen A survey site have high sand content (>40%) (Gilbert & Domack 2003).

Distribution. Known only from the east Antarctic Peninsula in 385 m.

Pygospiopsis antennata **new species**

Figures 13–14

Spionidae new genus 1: Blake *et al*. 1992: Appendix A: A-8.

Material examined. **Eastern North Pacific, off Half Moon Bay, California, South of Pioneer Canyon**, US EPA 102 Site survey, R/V *Point Sur*, coll. J.A. Blake, box corer, Sta. 4-5, 17 Sept. 1991, 37°13.54′N, 123°16.84′W, 1820 m, **holotype** (MCZ 147903 and 2 **paratypes, (**MCZ 147904); 1 **paratype** on SEM stub (MCZ).

Description. A small species, holotype complete, 2.1 mm long, 0.55 mm wide across setiger 5, with 29 setigers; complete paratype (on SEM stub) 1.7 mm long, 0.45 mm wide, with 24 setigers. Body expanded and dorsoventrally flattened for first 9–10 setigers with widest segments five times wider than long, then body narrowing, becoming cylindrical in cross-section (Figs. 13A, 14A); middle body segments about as wide as long; far posterior segments about four times as wide as long. Most podial lobes and a few areas of the prostomium and peristomium with large glands that stain with Methyl Green (see below). Color in alcohol light tan.

Prostomium short, expanded, incised on anterior margin, extending posteriorly to setiger 1, caruncle absent (Figs. 13A, 14A, C); digitiform occipital antenna arising from posterior margin, long on some specimens, up to two-thirds length of prostomium (Figs. 13A, 14B), some specimens with antenna broken, appearing shorter (Fig. 14A); two slit-like nuchal organs posterior to base of occipital antenna (Figs 13A, 14A, arrows); eyespots absent. Palps arising in narrow grooves between prostomium and setiger 1; each palp relatively short, cylindrical, with shallow ventral groove (Fig. 14B). Peristomium inflated, dorsally forming two upper lips of mouth (Figs. 13A, 14A, C) and ventrally forming lower lip of mouth (Figs. 13B, 14C); inflated oral area with dorsal surface covered with small papillae (Fig. 13A), fewer papillae on ventral lip (Fig. 13B).

Setigers 1–5 abranchiate, with well-developed noto- and neuropodial postsetal lamellae, each bearing long capillary setae (Figs. 13A, 14A–C). Notopodial lamellae of setigers 1–2 short, fingerlike; lamellae of setigers 3–5 becoming broader, triangular in shape, then rounded and elliptical on following (branchial) segments (Figs. 13A, 14A). Neuropodial lamellae narrow, digitiform on setigers 1–4 (Figs. 13B; 14C), then becoming wider, more elliptical on branchial segments and then fingerlike again in middle and posterior segments; post-branchial segments with short, digitate notopodial lamella (Fig. 13A).

Branchiae on setigers 6–10; branchiae of setiger 6 short, digitiform, basally attached to notopodial lamella (Figs. 13A, 14A–C); branchiae of setigers 7–10 larger, flattened, with thick, rounded core and thin, flattened undulating membrane on anterior and posterior margins (Figs. 13A, 14A, C); these branchiae entirely fused with notopodial lamellae. A transverse band of short cilia extends across dorsum between branchial bases on setigers 6–10 (Figs. 13A, 14C); ciliated band thicker on setiger 7, consisting of numerous cilia in multiple rows.

Setae include capillaries throughout and long uni- or bidentate hooded hooks in posterior neuropodia. Capillary notosetae of anterior setigers 1–10 in spreading fascicles of up to 15–16 curved capillaries in two rows; longer than neurosetae; from about setiger 11 capillaries becoming even longer, straight or stiff in posterior segments. Capillary neurosetae of setigers 1–3 numbering about 9–11 setae in a single row; neurosetae from setiger

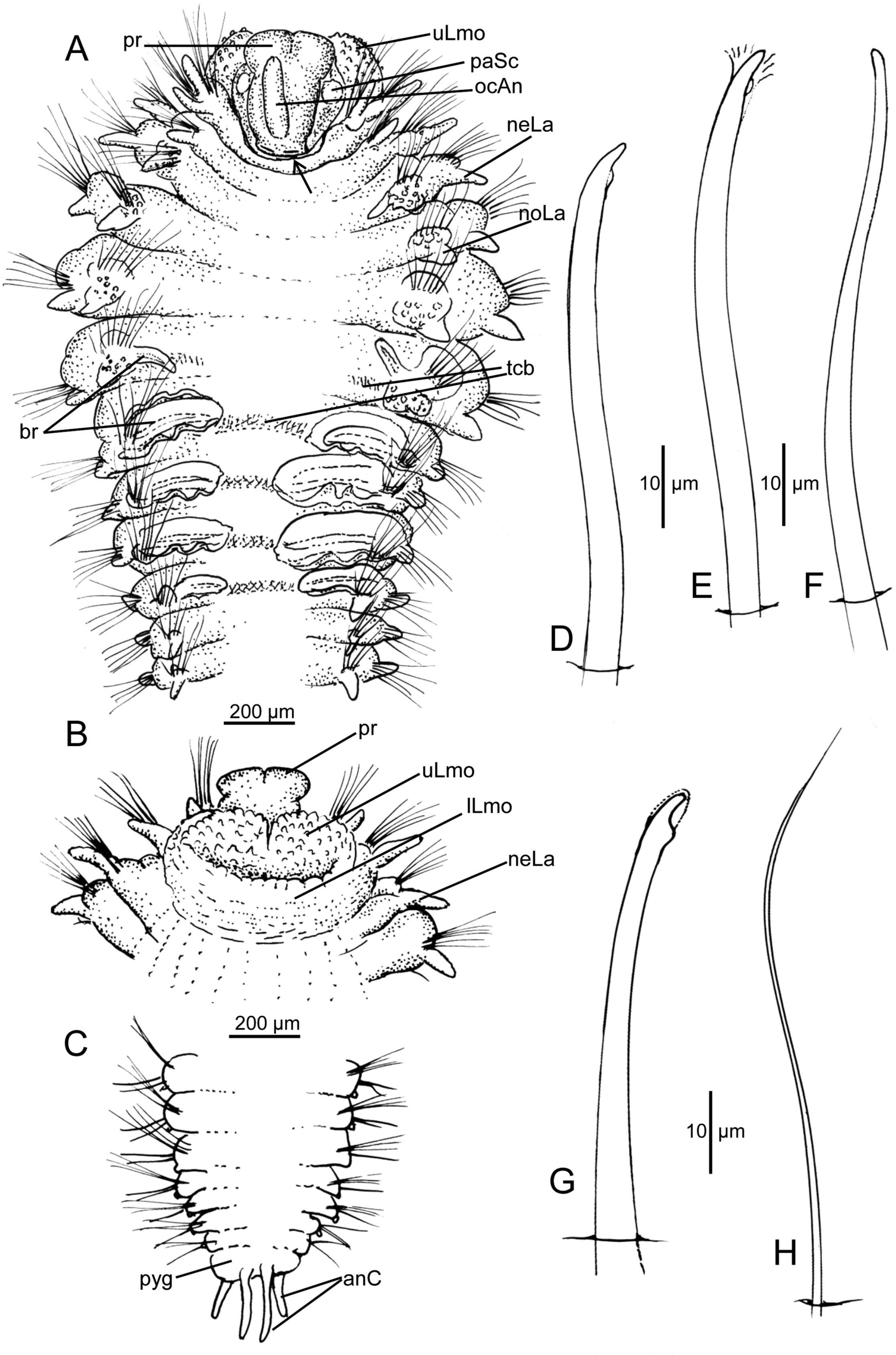

FIGURE 13. *Pygospiopsis antennata* **n. sp.** Holotype (MCZ 147903): A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end, dorsal view; D–G, long neuropodial hooks from posterior setigers; H, thin capillary seta accompanying long hooks. Arrow denotes nuchal organs. Abbreviations: anC, anal cirri; br, branchiae; lLmo, lower lip of mouth; neLa, neuropodial lamella; noLa, notopodial lamella; ocAn, occipital antenna; pr, prostomium; pyg, pygdium; tcb, transverse ciliary band; uLmo, upper lip of mouth.

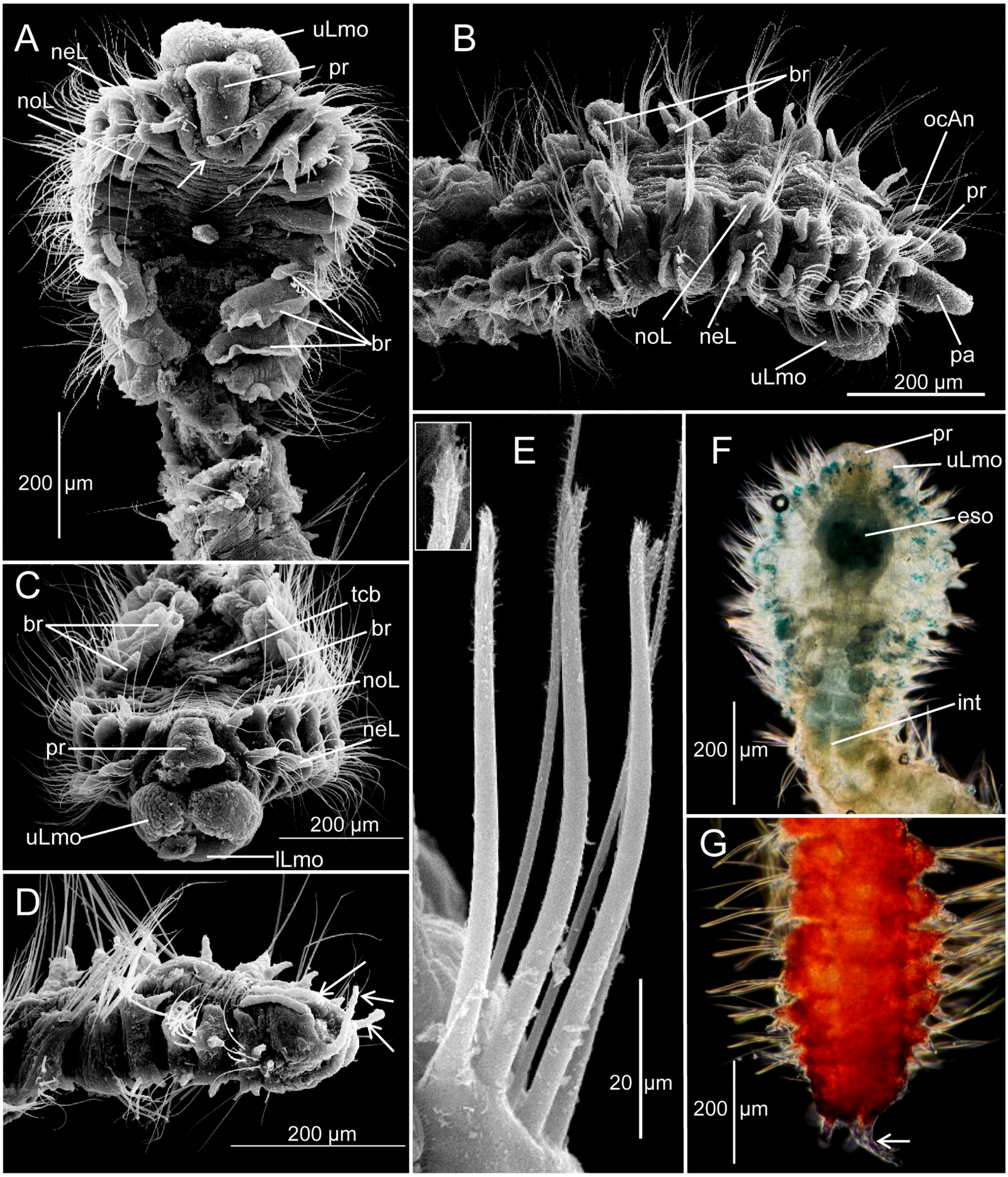

FIGURE 14. *Pygospiopsis antennata* **n. sp.** SEMs (US EPA Sta. 4-5: A–E); photomicrographs of paratype (MCZ 147904: F–G): A, anterior end, dorsal view (arrow indicates nuchal organ); B, anterior end, right lateral view; C, anterior end, frontal view; D, posterior end, left lateral view (arrows denote anal cirri); E, long neuropodial hooks from posterior setigers and accompanying thin capillaries (inset: tip of another hook, not to scale); F–G F, dorsal view, stained with Methyl Green; G, paratype, posterior end, dorsal view, stained with Shirlastain A (arrow indicates anal cirri). Abbreviations: br, branchiae; eso, esophagus; lLmo, lower lip of mouth; int, intestine; neL, neuropodial lamella; noL, notopodial lamella; ocAn, occipital antenna; pa, palp, pr, prostomium; tcb, transverse ciliary band; uLmo, upper lip of mouth. Note: SEMs are not archived as stubs, but as images.

4 number 15 capillaries arranged in two rows, with setae of second row more or less alternating or offset from those of first row; no evidence of heavily modified or enlarged neurosetae in any anterior segment (Fig. 14B–C). Subsequent neurosetae reduced in number to 5–6 per neuropodium until about setiger 17–20 when 1–3 long hooks first appear. Each neuropodial hook with a curved narrow tip; most hooks with a low rounded subapical knob or protuberance on convex side of shaft (Fig. 13D–E, G); entire tip of shaft covered with a narrow "hood" visible in light microscopy, but with SEM observed as bristled sheath obscuring shaft and subapical knob (Fig. 14E and inset); some hooks lacking subapical knob (Fig. 13F). Hooks accompanied by 3–4 very fine capillaries (Figs. 13H, 14E).

Pygidium with terminal anus surrounded by two long dorsal and two ventrolateral cirri (Figs. 13C, 14D, G).

Methyl Green staining. Methyl Green stains the glands in the anterior podial lobes plus a few isolated glands on the prostomium and peristomium. The overall pattern imparted by the stain is thus concentrated in the noto- and neuropodia and highlights those structures (Fig. 14F). The glands themselves are subdermal and relatively large compared with similar glands that stain in spionids and other polychaetes.

Remarks. *Pygospiopsis antennata* **n. sp.** differs from its congeners by having the branchiae first present from setiger 6 as a short simple gill only basally attached to the notopodium; the following branchiae on setigers 7–10 are large, broad, flattened, with a rounded apex and a lateral undulating membrane along both anterior and posterior sides; these branchiae are entirely fused with the notopodium. Branchiae are absent in middle and posterior setigers. In contrast, the type-species, *P. dubia*, has a pair of simple branchiae on setigers 2–3 and larger flattened branchiae from setiger 7. In *P. profunda* **n. sp.**, there is a single branchia on setiger 2 and larger flattened branchiae from setiger 7. In *P. occipitalis*, the branchiae are present from setiger 2 and continue to near the posterior end of the body; these branchiae are all flattened and basally fused to the notopodia, they are small at first, then become larger, broader, and full-sized by setiger 7. In contrast, *P. antarctica* **n. sp.** has simple branchiae on setigers 2–6 followed by larger flattened branchiae that are basally fused to the notopodial lamellae from setiger 7. *Pygospiopsis antennata* **n. sp.** is one of four species, including *P. fauchaldi*, *P. occipitalis*, and *P. profunda* **n. sp.** that have papillae on the oral lips and hooks with a subapical knob or tooth consistently on the concave side of shaft.

Etymology. The name *antennata* is from the Latin, *antenna*, a sensory appendage, and refers to the unusually long occipital antenna found on some specimens of this species.

Habitat. EPA 102 survey Sta. 4-5 is at a depth of 1820 m is on the continental slope adjacent to Pioneer Canyon, off Half Moon Bay near the entrance to San Francisco Bay. Sediment samples for grain size and CHN analysis were taken from box cores subsampled to a depth of 10 cm. Sediments at Sta. 4-5 were sand (54.3%), silt (45%), and clay (0.7 %) with a mean phi of 4.30 (SD=1.74). CHN data included organic carbon (1.64%), hydrogen (0.73%), and nitrogen (0.20%); C/N was 9.27 (Blake *et al.* 1992). Dominant invertebrates at the site were paraonid and cirratulid polychaetes, nemerteans, an amphipod *Parapano* sp., an isopod *Prochelator* sp., and a bivalve *Adontorhina* sp. (Blake *et al.* 1992).

Distribution. Off northern California, in slope depths, 1820 m.

Pygospiopsis profunda new species

Figure 15

Uncispionidae n. gen. n. sp. 2: Maciolek *et al*, 1987a–b.

Material Examined. **U.S. Mid-Atlantic ACSAR Program**, **off Delaware Bay**, Cruise Mid-1 leg 2, R/V *Gyre*, R. Petrecca, Chief Scientist, 07 May 1984, Sta. 10, rep. 2, 37°51.80′N, 73°19.96′W, 2095 m, **holotype** (USNM 1480969).—**U.S. North Atlantic ACSAR Program**, **off Massachusetts**, R/V *Oceanus*, Cruise NA-6, G. Hampson, Chief Scientist, Aug 1986, Sta. 15, recolonization tray 3, 39°40.05′N, 70°54.27′W, 2155 m, 1 **paratype** (post-larva) (USNM 1480970).—**U.S. South Atlantic ACSAR Program, off Cape Lookout, North Carolina**, R/V *Gyre*, Cruise SA-3, J.A. Blake, Chief Scientist, 14 Jul 1984, Sta. 3, 34°14.50′N, 75°40.30′W, 1509 m, 1 **paratype** (USNM 1480971).

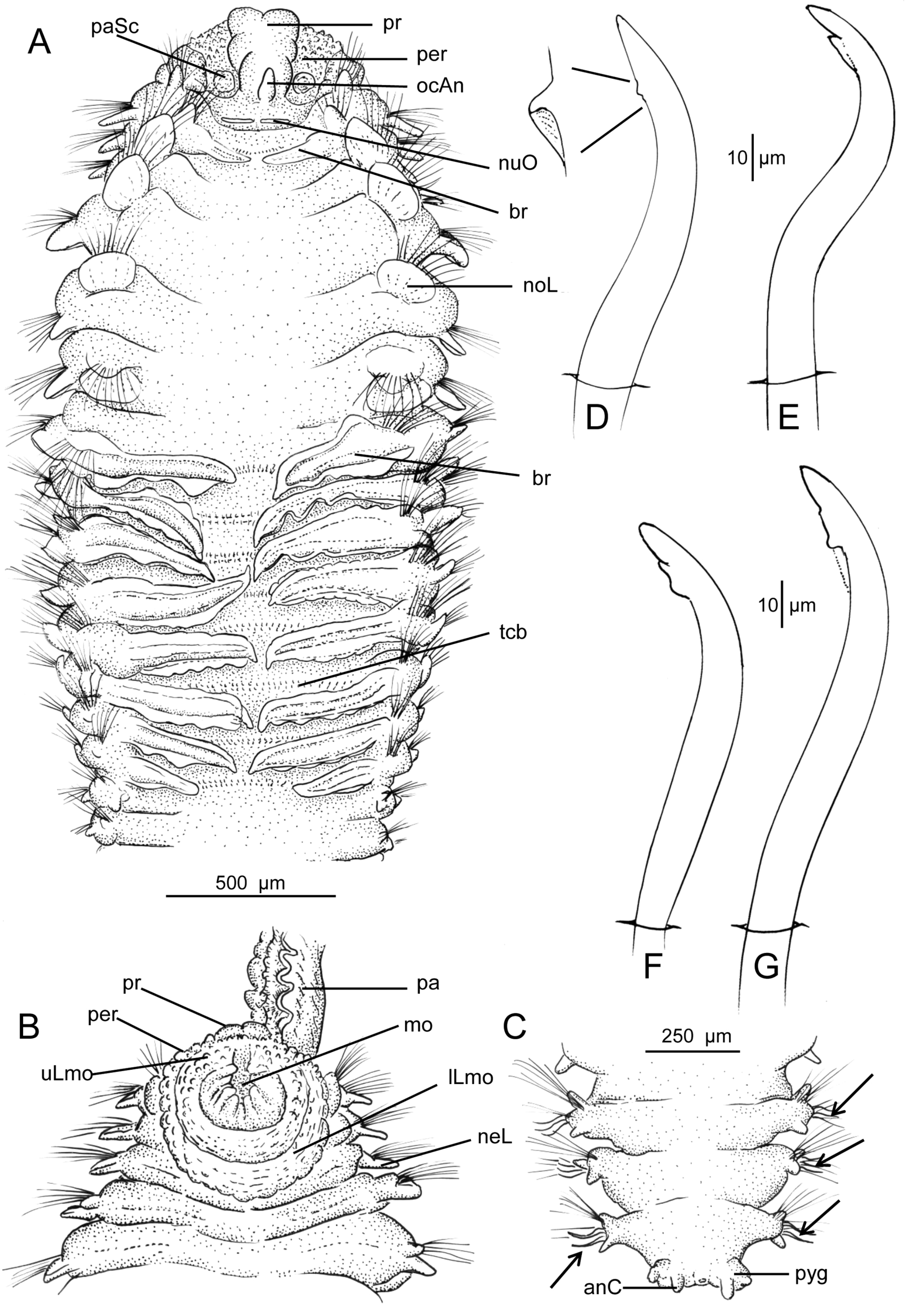

FIGURE 15. *Pygospiopsis profunda* **n. sp.** A–B, D–G, Holotype (USNM 1480969: A–B, D–G) and paratype (USNM 1480971: C): A, anterior end, dorsal view, palps omitted for clarity; B, anterior end, ventral view, with palp; C, posterior end, dorsal view (arrows denote neuropodial hooks); D–G, different posterior neuropodial hooks (D, inset of tip of subapical knob, not to scale). Abbreviations: anC, anal cirrus; br, branchia; lLmo, lower lip of mouth; neL, neuropodial lamella; noL, notopodial lamella; nuO, nuchal organ; ocAn, occipital antenna; pa, palp; paSc, palp scar; per, peristomium; pr, prostomium; pyg, pygidium; tcb, transverse ciliary band; uLmo, upper lip of mouth.

Description. Holotype posteriorly incomplete with 22 setigers, measuring 3.4 mm long; greatest width 1.0 mm at setiger 5; body more or less dorsoventrally flattened, widest from about setigers 5–8, then tapering posteriorly to narrow pygidium. Both paratypes small, juveniles; specimen from SA-3, Sta. 3, complete, grublike with 19 setigers, 1 mm long, 0.25 mm wide. Color in alcohol opaque white; no pigmentation.

Prostomium short, widest anteriorly with blunt tip divided into two rounded anterior lobes (Fig. 15A); continuing posteriorly as medial extension onto dorsum at level of setiger 1; with short digitiform occipital antenna arising from near base of posterior extension (Fig. 15A); eyespots absent; nuchal organs two narrow transverse slits posterior to occipital antenna (Fig. 15A). Palps arising from notch lateral to prostomium; each palp elongate, thick initially, then tapering to narrow tip; each with ciliated ventral groove having undulating margins (Fig. 15B). Peristomium inflated, heavily papillated, forming upper and lower lips around mouth and anterior surface of partially everted pharynx or proboscis (Fig. 15A–B).

Branchiae present on setigers 2 and 7–14 of holotype. Branchiae on setiger 2 separate from notopodial lamellae, extending from base of notopodia across dorsum to near midline (Fig. 15A); branchiae on setigers 7–14 larger, broad, flattened, with thin membranes on anterior and posterior surfaces, sometimes undulating (Fig. 15A); each branchia ciliated ventrally, cilia extending from base across dorsum, producing transverse ciliary band on setigers 2 and 7–14 (Fig. 15A).

Notopodia of setigers 1–3 conical, becoming broader and elliptical on setigers 4–6, then elliptical lamellae basally fused with branchiae on setigers 7–14 (Fig. 15A). Posterior notopodia short, conical (Fig. 15C). Neuropodial lamellae narrow, digitiform on setigers 1–2, then becoming broader and elliptical through branchial segments 7–14, then digitiform again in middle and posterior segments.

Setae include capillaries throughout and heavy hooked setae in posterior neuropodia. Capillary notosetae generally longer than neurosetae, in spreading fascicles of up to 14–20 thin curved capillaries through branchial region, then reduced to 8–12 capillaries in middle and posterior notopodia. Neuropodia of setigers 1–2 with about 10 capillary setae in single row; from setiger 3 with 20 capillaries arranged in two rows, with setae of second row more or less alternating or offset from those of first row; setiger 5 with 24 capillaries in two rows. Subsequent neurosetae reduced in number to about 10 per neuropodium until ca. setiger 17 when hooked setae first appear; no heavily modified neurosetae of any kind in anterior neuropodia. Neuropodial hooked setae from setiger 17 continuing to posteriormost setiger 22; one hook present on neuropodia of setiger 17, then increasing to 2–3 hooks per neuropodium over setigers 18–20, then with four hooks on setiger 21, decreasing to two hooks on setiger 22. Hooks large, strongly curved, each hook golden in color. Morphology of individual hooks variable, but each having a recurved, sigmoid-shaped shaft tapering to a narrow pointed tip (Fig.15 D–G); a subapical cusp, tooth (Fig. 15D and inset), or more elongate flange (Fig. 15E–G) present on concave side. Cusp-like structure appears as a simple knob that upon careful study appears to be a curved cusp covered with a thin sheath (Fig. 15D, inset). Other hooks have narrow flanges that are either entire or divided into two parts, probably from wear; remnants of a hood or worn sheath visible on some hooks (Fig. 15G).

Pygidium with two short dorsal cirri and two lateral cirri (Fig. 15C).

Methyl Green staining. Body stains more or less uniformly; no pattern after differentiation.

Remarks. The neuropodial hooks of *P. profunda* **n. sp.** are larger and more strongly curved than the hooks of any other species of *Pygospiopsis*; the size and prominence of these hooks resulted in the specimens being referred to the family Uncispionidae during the original laboratory identifications (Maciolek *et al*, 1987a–b). The branchial distribution of *P. profunda* **n. sp.** includes simple, digitiform branchiae on setiger 2, no branchiae present on setigers 3–6, and broad, thick branchiae that are basally fused to the notopodia on setigers 7–14. This branchial pattern distinguishes *P. profunda* **n. sp**. from all other *Pygospiopsis* species except for the type species, *P. dubia*, from Antarctic waters, which has simple branchiae on setigers 2–3 and broad thick branchiae from setiger 7–16 in the type collection (Blake 1983) and up to setiger 11 in the smaller specimens reported in the present paper (see above). The two species differ considerably, however, in the morphology of the neuropodial hooks. In *P. dubia,* the hooks are mostly unidentate and not strongly curved with only a few newer setae exhibiting a small subapical protuberance, or such a protuberance is entirely absent. In contrast, the hooks of *P. profunda* **n. sp.** are strongly recurved and have prominent subapical protuberances or flanges. Another apparent difference between the two species is that *P. profunda* **n. sp.** has numerous papillae on the oral lips that are lacking on *P. dubia*.

Etymology. The epithet is from the Latin, *profundus* for deep, recognizing the deep-sea habitat of this species.

Habitat. In the more than 550 0.25-m^2 box core samples collected along the U.S. Atlantic slope from the

Canadian boundary to off the Carolinas, only three specimens of *Pygospiopsis profunda* **n. sp**. were collected, one from each of the three survey areas. The holotype (USNM 1480969) is from Mid-Atlantic Sta. 10 at 2095 m, where sediments were roughly an equal mixture of sand (34.2%), silt (34.2%), and clay (31.6%). CHN analysis included carbon (0.90%), hydrogen (0.64%), and nitrogen (0.11%) (Maciolek *et al.* 1987a). One paratype is from Station SA3 (USNM 1480971), off Cape Lookout, North Carolina, in 1509 m. In this sample, fine-grained sediments were dominant: sand (14%), silt (45.3%), and clay (40.7%). CHN analysis included carbon (2.68%), hydrogen (0.88%), and nitrogen (0.29%) (Blake *et al.* 1985). The post-larval form from Sta. NA-5 (USNM 1480970) off New England was taken from an experimental recolonization tray filled with sterile mud collected from the same location and deployed for 15 months at a depth of 2155 m (Maciolek *et al.* 1987b).

Distribution. U.S. Atlantic continental slope off New England, off Delaware, and Cape Lookout, North Carolina; 1509–2155 m.

Discussion

Family Uncispionidae. Apart from *Uncispio reesi*, where nearly 150 specimens were available for study by Darbyshire & Mackie (2011), the other six species of the family are known from only a handful of specimens, some incomplete, others juveniles, species here listed with number of specimens in brackets: *Uncopherusa bifida* (1); *U. papillata* **n. sp.** (2), *U. cristata* **n. sp.** (1), *Uncispio hartmanae* (3), *U. greenae* **n. sp.** (1), *U. hamata* **n. sp.** (1), *Rhamphispio tridentata* **n. gen. n. sp.** (20). Uncispionids are therefore only rarely collected, and this paucity of material contributes to a general lack of information regarding morphological variability within a species, and in general, how these polychaetes feed, reproduce, and partition their habitat with other invertebrates.

The taxonomic characteristics that define uncispionids and in combination separate them from other spioniform polychaetes and from each other include: (1) the parapodia and setae of setiger 1 project anteriorly forming a cephalic cage; both the notopodia and neuropodia contribute capillaries to the cage in *Uncispio* and *Rhamphispio* **n. gen.**, whereas in *Uncopherusa*, only the neurosetae are long capillaries and the notosetae are acicular spines; (2) bidentate hooded hooks occur in the neuropodia of all genera and also in the notopodia of *Rhamphispio* **n. gen.**; the hooded hooks have both teeth subequal or have the upper tooth longer than the ventral tooth; (3) enlarged, "giant" neuropodial hooks are found in far posterior setigers; (4) one genus, *Rhamphispio* **n. gen.**, has setiger 3 greatly expanded and bearing enlarged, curved, crested spinous neurosetae; other uncispionids may have curved crested unilimbate neuropodial capillaries, but these are not prominent or conspicuous; and (5) spinous or hirsute capillaries are found in the notopodia of some species of *Uncispio*. In addition, branchiae are present on a few anterior and middle segments of most species and while not unique to uncispionids do vary in form and distribution among species. The pygidium is surrounded by digitate lobes or cirri, the number and form of which vary among species.

The species described in this study provide considerable new detail on the unique oral apparatus of the Uncispionidae. The oral apparatus of *Uncopherusa cristata* **n. sp.,** *Uncopherusa papillata* **n. sp.**, *Uncispio greenae* **n. sp.**, *Uncispio hamata* **n. sp.,** and *Rhamphispio tridentata* **n. gen, n. sp.** each exhibit up to three distinct lobes that surround the mouth opening and are associated with the oral lips. Two paired anterior ciliated lobes are clearly peristomial and located on the upper lip of the mouth of each species. An unpaired lobe is medial to the two anterior lobes and appears to be attached to the ventral lip of the mouth opening. In addition, two smaller lobes are located posterior to the two anterior lobes and appear to be associated with the lateral margins of the mouth opening. A similar arrangement has been observed with some differences in *Uncopherusa papillata* **n. sp.** and *Uncispio hamata* **n. sp.** In *U. papillata* **n. sp.**, the anterior and lateral lobes are similar, but the medial lobe instead of being a narrow lobe is a broad triangular structure that terminates in a narrow digitate process. In *U. hamata* **n. sp.**, the medial lobe is not present on the holotype but may be inverted. *Rhamphispio tridentata* **n. gen. n. sp.** has been found to have a similar arrangement with two large anterior ciliated lobes present together with a narrow, clavate unpaired medial lobe attached to the ventral lip of the mouth. There are no lateral lobes in *R. tridentata* **n. gen. n. sp.**, but the border of the buccal swelling is enlarged and thickened where the lobes would be. In their description of *Uncispio reesi*, Darbyshire & Mackie (2011: Fig. 1) identified structures that appear to be the same as the anterior, lateral, and posterior oral lobes; the latter was apparent only when everted. However, in our examination of a paratype of *U. reesi* (LACM-AHF Poly 2652), only the lateral oral lobes were evident, suggesting that both the anterior and posterior oral lobes are eversible in this species. The only other spioniform polychaete described as having lobes associated with the oral lips is *Poecilochaetus* which bears a single elongate peristomial lobe, termed a facial tubercle, ventral to the prostomium and associated with the upper lip of the mouth (Allen 1904; Blake & Maciolek 2018b).

Each of the five species described in this study has an enlarged or swollen ventral buccal or pharyngeal area that is present posterior to the mouth on setiger 1 and leads into a narrow esophagus, usually on setiger 2. The digestive system of uncispionids is thus similar to that of some spionids such as *Prionospio* where the mouth opens into a muscular ventral pharyngeal organ followed by a narrow esophagus and hindgut (Purschke & Tzetlin 1996; Tzetlin & Purschke 2005; Blake *et al*. 2017). However, the enlarged external manifestation of the pharynx in the uncispionids is larger and more prominent than in any spionids we have observed.

The oral morphology as described (above) differs from all other known spioniform polychaetes. The anterior, posterior, and lateral lobes that are associated with the oral or mouth opening suggest a role in particle selection for feeding and possibly tube building. Like other spioniforms, a pair of palps with a ventral ciliated groove likely serves in initial capture of particles that are transported toward the mouth along the ciliated groove. The ciliated pair of anterior oral lobes likely plays an important role in further selecting and manipulating particles into the oral opening. Based on the appearance of different specimens of *Uncopherusa papillata* **n. sp.** and *Rhamphispio tridentata* **n. gen., n. sp.**, it appears as if the pharynx is capable of expansion and contraction, which results in the mouth opening being reduced or greatly enlarged. There does not appear to be a distinct, separate proboscis everted, but more likely changes with the configuration of the pharynx as particles are manipulated and ingested. Study of living specimens and histological study is required before the role of these unusual oral structures and the structure of the pharynx can be confirmed. Given the rarity of uncispionids, this will be difficult.

The first report of eggs and egg morphology in an uncispionid was by Darbyshire & Mackie (2011) for *Uncispio reesi*. These authors described and illustrated eggs of about 100–120 µm that had a thick honeycombed egg envelope and numerous cortical alveoli, similar to eggs of some Spionidae reported by Blake & Arnofsky (1999). In the present study, eggs were observed in three species: *Rhamphispio tridentata* **n. gen, n. sp.**, *Uncispio hamata* **n. sp.**, and *Uncopherusa cristata* **n. sp.** Paired ovaries were observed in *R. tridentata* **n. gen, n. sp.** The ovaries were paired sacs arising from anterior septa and were releasing oocytes having a diameter of 40–50 µm into the coelom. The holotype of *Uncopherusa hamata* **n. sp.** was observed to have oocytes of about 60 µm in diameter, but these were few. *Uncopherusa cristata* **n. sp.** was observed to have a pair of extremely large, rounded eggs on either side of one segment; these measured up to 180 µm in diameter. External tears in a following segment suggested that similar eggs had been released.

The type of eggs found in *Uncispio reesi* by Darbyshire & Mackie (2011) with thick egg membranes and cortical alveoli are characteristic of spioniforms that discharge their eggs into the plankton and produce planktotrophic larvae (Blake & Arnofsky 1999). Such species typically occur in shallow waters where larvae can feed on the rich phytoplankton found on continental shelves; *U. reesi* was described from 121–170 m depth. In contrast, all of the eggs from three species observed in this study had thin egg membranes, considerable yolk, and lacked cortical alveoli; mature eggs of about 180 µm were observed for the one species, *Uncopherusa cristata* **n. sp.**, where eggs were mature. This suggests that deep-water uncispionids likely produce relatively large eggs with the considerable yolk reserves that are required to sustain lecithotrophic or direct development. Ecologically, the finding of mature eggs in one segment, evidence of egg discharge in the following segment, and smaller developing eggs in a subsequent segment suggest that, at least for *U. cristata* **n. sp.**, reproduction may be an on-going process in this deep-water species.

The present study adds one new genus and five new species to the family, bringing the total number of species to eight. As noted, the family itself is rarely encountered and there are few specimens available for study. Six of the eight known species are from deep-sea habitats: *Uncopherusa bifida*, the first species of this family to be described (Fauchald & Hancock 1981), was collected from off Oregon in 2800 m and the five new species described here are all from depths of 800 m and greater. Our own effort was enhanced by participation in several deep-sea reconnaissance and monitoring programs off the U.S. Atlantic and Gulf coasts of North America and Brunei in SE Asia, but even when sampling was as intensive as in those programs, few specimens of these unusual and rare uncispionids were collected.

Based on the nature of the specimens we have collected and those previously collected, we suggest that uncispionids are generally small, slender polychaetes that are fragile and fragment readily during sample processing. In our deep-sea programs, we have, where possible, used an elutriation method to initially wash specimens gently from the sediment on to a 300-µm-mesh sieve rather than direct a stream of water onto sediment placed on a sieve, which is likely to fragment small fragile polychaetes such as the uncispionids.

Habitat. Among the eight known species of Uncispionidae, all except *Uncopherusa bifida*, the first species to be described, have sediment data or habitat information associated with their sampling localities. Of the seven species with habitat information, *Uncopherusa greenae* **n. sp**., *Uncispio hartmanae*, *U. reesi*, and *Rhamphispio tridentata* **n. sp**. are associated with mixed sediment types. Sediments where the deep-sea species *U. greenae* **n. sp**. and *R. tridentata* **n. sp**. were found had high percentages of sand together with the usual deep-sea silt and clay fractions. *Uncispio hartmanae* and *U. reesi* are both from shelf depths and reported to occur in sediments with clay and pebbles or gravel. In contrast, *Uncopherusa papillata* **n. sp.**, *U. cristata* **n. sp.**, and *Uncispio hamata* **n. sp**. are deep-sea species associated with typical slope sediments having high silt and clay fractions and a reduced sand fraction. Therefore, there does not appear to be a consistent pattern of sediment types associated with uncispionids and it is likely that other factors such as current flow at the sediment-water interface and availability of organic material is more important in determining their habitat preferences.

Relationships with other spioniform polychaetes. In her establishment of the family Uncispionidae, Green (1982) noted that these worms shared some characteristics with poecilochaetids and trochochaetids in having long, anteriorly directed setae on the first setiger, but were also closely related to spionids due to the presence of hooded hooks, branchiae, and the presence of an occipital antenna.

Blake & Arnofsky (1999), as part of a review of the reproduction and larval development of spioniform polychaetes, developed a preliminary phylogenetic analysis using 38 characters of 36 genera of Spionidae, Apistobranchidae, Trochochaetidae, Poecilochaetidae, Longosomatidae, and Uncispionidae. This analysis emphasized reproductive and larval characteristics in addition to adult morphology. One of the results was the indication of a close relationship of *Uncispio* with *Poecilochaetus* and *Trochochaeta*, largely based on the unique egg morphology of these genera and certain Spionidae. In those genera, the egg membranes are thick, honeycombed, and have prominent cortical alveoli as recently confirmed for *U. reesi* by Darbyshire & Mackie (2011).

In the present study, the morphology of the newly described *Rhamphispio tridentata* **n. gen., n. sp.,** a species with an enlarged setiger 3 bearing heavy neurosetae, suggests a closer relationship to *Trochochaeta* than to other spioniforms. However, to date, there have been no additional phylogenetic studies using uncispionids; molecular sequence data has not been collected for any species of this group.

Family Spionidae, Genus *Pygospiopsis* and related taxa. The most important taxonomic characters that serve to separate the six species of *Pygospiopsis* and two species of *Atherospio* recognized in this study are: (1) branchial patterns along the body, especially branchiae that occur on setigers anterior to setiger 7; (2) the presence or absence of modified neurosetae in one or more anterior setigers; (3) the nature of the posterior neuropodial hooks; (4) and the presence or absence of papillae on the peristomium or upper lip of the mouth. Other characters such as the length and shape of the occipital antenna and form of the anterior noto- and neuropodial lamellae are variable and less consistent between specimens. The main characteristics of *Pygospiopsis* species and of the closely related species of *Atherospio* are presented in Table 1 and discussed below.

Branchial patterns. All species of *Pygospiopsis* and *Atherospio* have in common large, broad branchiae from setiger 7 that are fused to some degree with the notopodial lamellae. Species of *Pygospiopsis* also have simple branchiae anterior to setiger 7 in different configurations that are either entirely free from the notopodium or only basally fused. These different patterns serve as a first-level character to separate the species. In the two species of *Atherospio*, no branchiae occur anterior to setiger 7. The different anterior branchial patterns exhibited by the six species of *Pygospiopsis* are illustrated in Fig. 16. The three species in the first row (Fig. 16A–C) have only one or two pairs of branchiae anterior to setiger 7, which are limited to either setiger 2 (*P. profunda* **n. sp.**), setigers 2–3 (*P. dubia*), or setiger 6 (*P. antennata* **n. sp.**). The three species in the second row (Fig. 16D–F) have branchiae extending over either setigers 2–6 (*P. antarctica* **n. sp.** and *P. occipitalis*) or setigers 1–6 (*P. fauchaldi*). In *P. antarctica* **n. sp.**, the anterior branchiae are all simple and free from the notopodial lamellae. In *P. occipitalis* and *P. fauchaldi*, the branchiae are initially free from the notopodial lamellae, but become variously fused basally to the lamellae from setigers 3 or 4.

Neurosetae of anterior segments. While the anterior neurosetae of the two species of the closely related genus *Atherospio* are enlarged and modified, there is little evidence of modified anterior neurosetae in species of *Pygospiopsis*. *Atherospio disticha* has two rows of conspicuous neurosetae on setigers 4–5 that are enlarged and have a fringed tip of bristles and terminate in a thin mucron (Mackie & Duff 1986); these setae are of the same size as the posterior hooded hooks according to the published figures. *Atherospio guillei* has large and small modified spines in the neuropodia of setiger 5 (Meiβner & Bick 2005). None of the species of *Pygospiopsis* described in the present study has any modified neurosetae in anterior setigers. Lovell (1994) reported fringed neurosetae in *P. fauchaldi* (as *Pseudatherospio*), but setae of this type are present in all species; they are best seen with SEM (see Fig. 9D for *P. dubia*, this study). Blake (1996) reported slightly modified anterior neurosetae with a fringed apex on setigers 2–6 of *P. occipitalis*. These capillaries, while similar, were not as large as those reported for *A. disticha* by Mackie & Duff (1986: Figs. 3A, F); in that species, the capillaries were fully as large as the posterior neuropodial hooded hooks. In *P. occipitalis*, all capillaries are smaller than the hooks.

Neuropodial hooks of middle and posterior segments. The morphology of the posterior hooded or unhooded hooks of species of *Atherospio* and *Pygospiopsis* are similar and unique among spioniform polychaetes in having a subapical secondary tooth or protuberance on the concave side of the shaft instead of surmounting the main fang on the convex side. A thin hood may be apparent in light microscopy or absent, with the subapical structure visible where present. Under SEM, the anterior end of the shaft is covered with a cloak of fibrils, with the tip emergent, obscuring any subapical structure present. A distinct bidentate hooded or unhooded hook is evident in *A. disticha*, *P. antennata* **n. sp.**, *P. fauchaldi*, *P. occipitalis*, and *P. profunda* **n. sp.** Species having unidentate unhooded hooks include *A. guillei*, *P. dubia*, and *P. antarctica* **n. sp.** In the majority of these species, the hooks have relatively straight narrow shafts that are only slightly curved along the length. The shafts of the hooks of *P. fauchaldi* and *P. profunda* **n. sp.**, however, are strongly recurved; the hooks of *P. profunda* **n. sp.** being noticeably large and conspicuous, approaching the modified hooks found in species of Uncispionidae.

Peristomial papillae and prostomial morphology. The peristomium of species of *Atherospio* and *Pygospiopsis* extends laterally and ventrally and surrounds the mouth opening. Upper and lower lips are identified in this study. In some species, these peristomial lips are covered with papillae to varying degrees. Papillae appear to be absent in *A. disticha*, *P. dubia*, and *P. antarctica* **n. sp.**, but are present in *P. profunda* **n. sp.**, *P. antennata* **n. sp.**, *P. occipitalis*, and *P. fauchaldi*. They are also clearly visible in Fig. 1 of Laubier & Ramos (1974) and in Fig. 2C of Meiβner & Bick (2005), for *A. guillei*. The presence or absence of these papillae serve as a useful taxonomic character; their occurrence is indicated in Fig. 16 for the six species of *Pygospiopsis*.

The prostomium of all eight species of *Atherospio* and *Pygospiopsis* are generally similar in having the anterior end expanded and incised, often formed into two distinct lobes. The prostomium is short, extending posteriorly only to the anterior border of setiger 1; a caruncle is absent (Fig. 16). There is some variability likely due to stage of development and preservation. Each species, except *A. guillei*, has an occipital antenna. The form of the antenna is similar in all species except that it appears larger in *P. antennata* **n. sp**. (Fig. 16). Nuchal organs have been identified in most species: in *P. dubia*, *P. antarctica* **n. sp.**, *P. antennata* **n. sp.**, *P. fauchaldi*, and *P. profunda* **n. sp.** nuchal organs have been identified as paired grooves or slits at the posterior lateral margins of the prostomium posterior to the occipital antenna (Lovell 1994; this study). Mackie & Duff (1986) identified triangular-shaped nuchal organs on either side of the posterior end of the prostomium in *A. disticha* and Meiβner & Bick (2005) noted inconspicuous nuchal organs near the posterior end of the prostomium in *A. guillei*.

In the early developmental stages of *P. dubia* described in this study, the peristomium and oral morphology appear to differentiate before the prostomium (Fig. 11C, F). At the stage at which the peristomium, oral lips, and palps are well developed, the prostomium has little or no overall shape and there is no occipital antenna present.

Habitat. All four species reported in this study, *Pygospiopsis dubia*, *P. antarctica* **n. sp.**, *P. antennata* **n. sp.**, and *P. profunda* **n. sp.**, occur in mixed sediments with relatively high sand content. *Pygospiopsis fauchaldi* and *P. occipitalis* are also reported from mixed sediments but with a high silt fraction. The only sediment data reported for *Atherospio disticha* is its occurrence in mud. For *A. guillei*, however, the original report by Laubier & Ramos (1974) was from gravel and sand; Meissner & Bick (2005) reported it from fine sands with a moderate silt content. These observations suggest that most species of the *Atherospio*-*Pygospiopsis* complex occur in coarse sediments.

There is no information regarding the mode of life of species of *Pygospiopsis*. However, the presence of paired palps suggests that they are interface feeders as in other spionids (Jumars *et al.* 2015). The presence of a soft tube containing post-larvae associated with one adult of *P. dubia* collected in the present study suggests a tube-dwelling habit similar to other spionids.

TABLE 1. Taxonomic Characteristics of Eight Species of *Pygospiopsis* and *Atherospio*

Species/Character	Prostomium: Anterior Margin	Occipital Antenna	Peristomial Papillae	Anterior Notopodial Lamellae^1	Anterior Neuropodial Lamellae^1	Branchial Distribution^1
P. dubia (Monro, 1930)	Expanded, weakly incised	Short	Absent	1–2: short, triangular; 3–6: broad elliptical	1: triangular; 2–6: elliptical	2–3: simple; 7–16: broad, membranous, fully fused to dorsal lamellae
P. antarctica **n. sp.**	2 short lobes	Short	Absent	1–6: broad, triangular, leaflike	1–6: broad, leaflike to heart–shaped	2–6: simple; 7–10: broad, membranous, basally fused to dorsal lamellae; 11–14: simple
P. antennata **n. sp.**	Expanded, weakly incised	Long	Present	1–2: digitate; 3–5: broad, triangular	1–4: narrow, digitiform; 6^+: rounded, elliptical	6: simple; 7–10: broad, membranous, fully fused to dorsal lamellae
P. fauchaldi (Lovell, 1994)	2 lobes, deeply incised	Short	Present	1: long, triangular; 2–5: short, broad	1: broad, triangular; 2–6: low, rounded	1–6: simple; 7–15: broad, fully fused to dorsal lamellae; 16^+: simple
P. occipitalis Blake, 1996	Expanded, weakly incised	Long	Present	1: long, digitiform; 2–6: broad, membranous, fused to branchiae	Low, thin, membranous	2–6: elongate, basally fused to dorsal lamellae; 7^+: broad, fully fused to dorsal lamellae
P. profunda **n. sp.**	2 rounded lobes	Short	Present	Most broad, elliptical	1–2: narrow, digitiform; 3^+: broad, elliptical	2: simple; 7–14: broad, membranous, basally fused to dorsal lamellae
A. disticha Mackie & Duff, 1986	2 rounded lobes	Short	Absent	1–2: digitate; 3–6: broad, triangular	1–2: broad, triangular; 3–6: elliptical	7–12: broad, fully fused to dorsal lamellae
A. guillei (Laubier & Ramos, 1974)	2 lobes, deeply incised	Absent	Present	1: digitate; 3–6: broad, triangular	1: digitate; 3–6: broadly rounded	7–13: long, thick, fully fused to dorsal lamellae

……*continued on the next page*

TABLE 1.(Continued)

Species/Character	Anterior Neurosetae	Posterior Neuropodial Hooks	Pygidium	Methyl Green	Distribution	References
P. dubia (Monro, 1930)	Smooth or limbate capillaries	Unidentate bristled spines with weakly curved shaft; subapical knob rare	6–12 cirri	Weak staining of parapodial glands	Off South Georgia, 25 m; E & W Antarctic Peninsula, 125–713 m	Monro 1930; Blake 1983; Hartmann–Schröder & Rosenfeldt 1988; This study
P. antarctica **n. sp.**	Smooth or limbate capillaries	Unidentate, narrow, weakly curved spines	Unknown	Podial lobes and few prostomial and peristomial glands stain	E Antarctic Peninsula, 385 m	This study
P. antennata **n. sp.**	Smooth or limbate capillaries	Bidentate with subapical knob; shaft weakly curved, hood closely adhering	4 cirri	Anterior podial glands and isolated glands stain	Off Northern California continental slope, 1820 m	This study
P. fauchaldi (Lovell, 1994)	Smooth or limbate capillaries	Bidentate shaft strongly recurved, hood closely adhering	Unknown	Not tested	Central and southern California in shelf and slope depths, 197–530 m	Lovell 1994; Blake 1996
P. occipitalis Blake, 1996	Anterior row of capillaries short, thick, with smooth dark shaft; with aristate tip	Bidentate with subapical knob; shaft weakly curved, hood absent	Unknown	Not tested	Off Central California continental slope, 930 m	Blake 1996
P. profunda **n. sp.**	Smooth or limbate capillaries	Bidentate, heavy, strongly curved shaft; subapical tooth or flange present; hood closely adhering	4 cirri	No pattern	U.S Atlantic continental slope, New England to North Carolina, 1509–2155 m	This study
A. disticha Mackie & Duff, 1986	Setigers 4–5 with double row of aristate spines	Bidentate hooks with narrow, curved shaft	6–9 cirri	Not tested	West coast of Scotland, 27 m	Mackie & Duff 1986
A. guillei (Laubier & Ramos, 1974)	Setiger 5 with 2–3 heavy spines and 3^+ thin spines	Unidentate and bidentate with curved shaft; hood absent	8 cirri	No pattern	North Sea, 38–41 m; Mediterrean Sea, 44–99 m	Laubier & Ramos 1974; Meiβner & Bick 2005

[1] Numbers refer to the setigers on which the character appears.

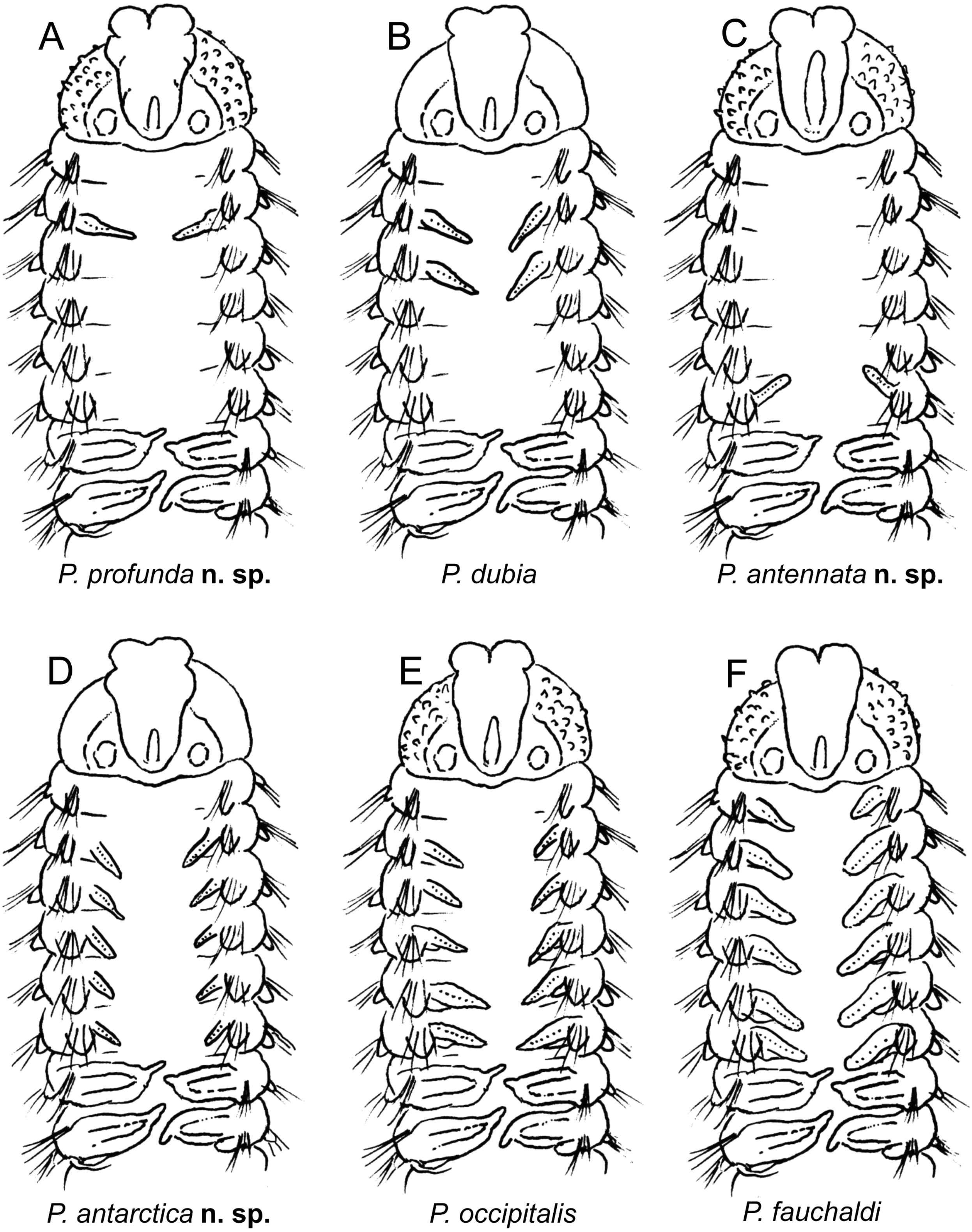

FIGURE 16. Diagrams of the six species of *Pygospiopsis* emphasizing branchial patterns and morphology, peristomial papillae, and general shape of the prostomium and occipital antenna. Not to scale.

Relationships with other spioniform polychaetes. *Pygospiopsis* and *Atherospio* are related to the Spionidae based on the presence of hooded hooks, straplike branchiae, palps, and occipital antennae. In their phylogenetic analysis using reproductive and adult characters, Blake & Arnofsky (1999) recovered *Pygospiopsis* (including *Atherospio*) as a separate clade of the Spionidae.

There are several features of these worms that are unusual among spioniforms: (1) the hooded hooks have the accessory tooth or knob, when present, on the concave side of the shaft instead of on the convex side or superior to the main fang; in some species the tooth or knob is entirely absent leaving the hooks as a unidentate neuropodial spine; the "hood" is closely applied and often missing or not apparent; (2) the prostomium is short, lacks a caruncle and except for *Atherospio guillei*, always has an occipital antenna; (3) the nuchal organs are narrow transverse slits or grooves located on the posterior margin of the prostomium instead of longitudinal or U-shaped grooves as in most spionids; (4) the branchiae from setiger 7 are always broad and completely fused to the notopodial lamellae whereas setigers 1–6 have simple narrow branchiae in different combinations or they are entirely absent.

These characters in and of themselves are not sufficient to link *Pygospiopsis* with other spionids or spioniforms; however, we note that the large recurved hooded hooks of *P. profunda*, although smaller, have some similarity to the giant modified neuropodial hooks or spines of some uncispionids in having a tooth, knob, or flange on the concave side of the hook. To date, as for the uncispionids, there have not been any molecular sequences collected for any species of *Pygospiopsis* or *Atherospio* that might offer additional clues as to possible relationships within the spioniform polychaetes.

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