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A New Species of *Dipolydora* (Annelida, Spionidae) from deep-water methane seep habitats off Louisiana (Gulf of Mexico), a borer in shells of the gastropod *Kanoia meroglypta*

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Abstract

A new shell-boring spionid polychaete of the genus *Dipolydora* is described from the gastropod, *Kanoia meroglypta* (Family Trochidae), collected from mussel beds on the continental slope off Louisiana at a depth of 617 m in an area of methane seepage. The new species belongs to a large group of Spionidae comprising the *Polydora* complex (ca. 178 species) having a modified setiger 5. The new species, *Dipolydora walkerae* **sp. nov.**, belongs to a small group of *Dipolydora* having large hooked spines on setiger 5 surmounted with a crest or cloak of fine bristles or fibrils and has posterior notopodia with modified acicular spines. The majority of polydorins are from intertidal or continental shelf depths; deep-water accounts are few and poorly documented. The new species is compared with its closest congener, *Dipolydora armata*. Previous accounts of shell-boring polydorins from offshore are tabulated by the depth of occurrence and discussed. The new species represents the deepest confirmed record for a shell-boring spionid polychaete.

Key words: Deep-sea, shell borer, polychaete, Trochidae

Introduction

Spionid polychaete species of the *Polydora* complex are well-known from nearshore and coastal waters as inhabitants of soft sediment, sponge matrices, or as commensals or borers in molluscan shells and other calcareous substrates. However, there are few if any verified records of species of *Polydora* or related genera as shell borers from deep-water continental slope depths (>200 m).

During environmental surveys to support oil and gas exploration of the continental slope off Florida, Louisiana, and Texas in the 1980s, methane seeps having faunas resembling those of hydrothermal vents were discovered in continental slope sediments (Paull *et al*. 1984; Brooks *et al*. 1987). As part of surveys off Louisiana, shells of *Kanoia meroglypta* (McLean & Quinn, 1987), a common gastropod in the seep habitats, were noticed to have their shells tunneled with burrows that were identified as belonging to polychaetes of the "Polydorinae" (Warén & Bouchet 2001). Specimens of this gastropod species with the polydorin burrows had previously been collected from a mussel bed in the Green Canyon area off Louisiana in June 1987 as part of an HOV *Johnson Sea-Link* Dive. These gastropods were eventually examined and found have polydorin polychaetes in burrows in the shells. After initial dissection and removal of the worms from the shells, they were provided to the author for examination and determined to represent an undescribed species of the genus *Dipolydora*, which is here reported and described.

Material and Methods

The specimens on which this study is based were collected from a mussel bed in the Minerals Management Service (MMS) now Bureau of Ocean Energy Management (BOEM) Green Canyon 234 Lease Block off Louisiana. Samples

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were collected using a scoop sampler, with the submersible HOV *Johnson Sea-Link* on Dive 2059 in June 1987. Specimens of the gastropod, *Kanoia meroglypta*, were preserved in ethanol (ETOH) and subsequently examined by Dr. Sally E. Walker, who removed the worms from the shell and sent them to Dr. Janet Voight of the Field Museum of Natural History, Chicago (FMNH) and archived. Upon request, Dr. Voight shipped them to the author for study. Two additional specimens of *K. meroglypta* from the similar depths off Louisiana and archived in the mollusc collections of the Museum of Comparative Zoology, Harvard (MCZ) were also examined, but no shell borers were present.

Specimens were examined using a Wild M-5 stereomicroscope and a Zeiss RA research microscope equipped with phase contrast optics. Photomicrographs were taken with a Nikon D7100 camera mounted on both the stereo- and compound microscopes. For observation, specimens were first stained with an aqueous solution of Shirlastain A to highlight difficult-to-see surficial morphology. The holotype was also stained with a saturated solution of Methyl Green in 70% ETOH in order to identify staining patterns of any subdermal glands. Measurements were taken with a calibrated micrometer on the compound microscope. Line drawings were first sketched in pencil using a drawing tube or camera lucida on the Zeiss RA microscope and later transferred to Dura-Lar® matte film and inked. The photographs and drawings were subsequently edited in Photoshop CS3®.

Abbreviations in text: BOEM, Bureau of Ocean Energy Management; ETOH, Ethyl alcohol; FMNH, Field Museum of Natural History, Chicago; HOV, Human Occupied vehicle; MCZ IZ, Museum of Comparative Zoology, Department of Invertebrate Zoology, Harvard University; MMS, Minerals Management Service.

Results

Systematic Account

Annelida, Polychaeta

Family Spionidae Grube, 1850

Genus *Dipolydora* Verrill, 1881

Diagnosis. (after Blake *et al*. 2020): Prostomium entire or incised anteriorly, extending posteriorly as caruncle; eyespots present or absent. Setiger 1 with notosetae. Setiger 5 modified, with major spines of one type, with or without accompanying companion setae; spines arranged in single curved row; spines simple, falcate, with lateral flanges, teeth, and/or apical bristles, with superior notosetae dorsal to modified spines and companion setae. Posterior notopodial spines present or absent. Neuropodial hooded hooks bidentate, usually with recurved shaft without constriction or manubrium, main fang forming wide angle with shaft and narrow, acute angle with apical tooth; hooks first present from setigers 7 to 17. Pygidium disc-like, cuff-shaped, with 2, 3, or 4 lobes of various forms, or with four or more small papillae. Anterior part of digestive tract sometimes with enlarged, thick, gizzard-like structure.

Remarks. The genus *Dipolydora* Verrill, 1881 was revalidated and redescribed by Blake (1996), thus subdividing the formerly large genus *Polydora* into two genera. *Dipolydora* differs from *Polydora* in having notosetae on setiger 1 rather than lacking them; bidentate hooded hooks with a recurved shaft without a constriction or manubrium and with the main fang forming a wide angle with the shaft and a narrow, acute angle with the apical tooth rather than a distinct constriction on the shaft and with the apical tooth closely applied to the main fang. The pygidial morphology is variable rather than simple; and some *Dipolydora* species have a gizzard-like structure in the digestive tract, which *Polydora* species lack. To date, approximately 47 species of *Dipolydora* are recorded (Read & Fauchald 2024a), including several that are poorly known and require study. In the present study, a new species of *Dipolydora* has been discovered as a borer in shells of the gastropod, *Kanoia meroglypta* from deep-water methane seep habitats in the Gulf of Mexico off Louisiana.

***Dipolydora walkerae* new species**
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Figures 1–2

Material examined. Gulf of Mexico, off Louisiana, continental slope, BOEM Green Canyon Lease Block 234, HOV *Johnson Sea Link* Dive 2059, June 1987, coll. WR Callender; worms removed from burrows in the columella of the gastropod *Kanoia meroglypta* collected from the mussel bed with a scoop sampler, 27.733°N, 91.253°W, 617 m, **holotype** (FMNH 223654), 1 **paratype** (MCZ IZ 173000).

Description. Body elongate, slightly wider anteriorly; holotype complete with 60 setigers, 8.4 mm long and 0.7 mm wide anteriorly, 0.4 mm wide posteriorly; paratype larger, also complete but damaged and not as well preserved, with 85 setigers, 17 mm long, 0.8 mm wide anteriorly, 0.5 mm wide posteriorly. Color in alcohol: light tan; only pigment from two large, curved reddish-colored peristomial glands lateral to oral vestibule.

Prostomium narrow, distinctly rounded on anterior margin (Figs. 1A, 2B–C), posteriorly extending to anterior border of setiger 1 as a caruncle (Fig. 1A); occipital antenna absent; eyes absent. Palps thick, relatively short when preserved, only about as long as first 4–5 setigers (Fig. 2A); each palp with narrow ventral groove lined with short cilia; cilia not observed on dorsal surface. Peristomium wide and long, rounded anteriorly and laterally (Fig. 1A), interrupted dorsally by caruncle (Fig. 1A) and ventrally by oral vestibule (Fig. 2C).

Setiger 1 with capillary setae and postsetal lamellae in both rami; lamellae short, rounded on setigers 1–4 (Fig. 1A); notosetae of setiger 1 shorter, fewer (4–5) than on setigers 2–5 (8–10); neurosetae of setiger 1 as long those on setiger 2, but fewer (6–8) than on setigers 2–4 (8–10). Posterior to setiger 5, notopodia with a row of 8–10 moderately long capillaries continuing posteriorly; these replaced in last 11–12 setigers by 6–8 long, narrow acicular spines arranged in a rosette and producing a distinct spinous appearance to the posterior end of body (Fig. 1B). Each spine narrowing to pointed tip (Figs. 1I, 2G–H).

Setiger 5 twice as large as setigers 4 and 6, with 5–6 dorsal superior capillaries, six large falcate spines arranged in an oblique row, and 7–8 capillaries ventral to major spines (Fig. 1A); companion setae absent between falcate spines. Dorsal superior and ventral capillaries geniculate, winged with crest of short fibrils along one edge (Fig. 1F); these capillaries shorter and fewer than on setigers 4 and 6. Distal convex sides of falcate spines surmounted by a distinct dorsal crest formed by numerous fibrils (Figs. 1C–E, 2E).

Hooded hooks in neuropodia from setiger 7, up to 6–8 in a row, accompanied by 1–3 inferior winged capillaries. Hooks bidentate, with slightly recurved shaft without constriction and with wide angle between shaft and main fang in hooks from anterior and middle segments (Fig. 1G–H); posterior hooks with more acute angle between teeth (Fig. 2F).

Branchiae from setiger 7, full-sized from setiger 8 (Fig. 1A), absent from posterior setigers from about setiger 30 in holotype and setiger 40 in paratype, or about mid-body; branchiae arising from base of notopodial postsetal lamellae, flattened, directed toward dorsal midline, but not reaching entirely across dorsum (Fig. 1A); each branchia broad, with distinct blood loop (Fig. 1A).

Pygidium with four large lobes (Figs. 1B, 2D), surface covered with numerous papillae; a rounded medial lobe also present between the dorsal lobes, dorsal to anal opening (Fig. 1B).

Due to opaque nature of body, internal morphology not visible; thus neuropodial glandular pouches, nephridia, and digestive system not observed.

Methyl green staining. Anterior ventral and lateral border of anterior setigers retaining stain; rest of body with no staining reaction.

Remarks. *Dipolydora walkerae* **sp. nov.** belongs to a group of species having the modified spines of setiger 5 with an apical cloak or crest of fibrils and acicular spines in posterior notopodia (Blake 1996). In *D. walkerae* **sp. nov.**, the posterior acicular spines are uniquely arranged in a rosette and provide a spinous appearance to the posterior end of the body. Only two other species of *Dipolydora* have a similar configuration: *D. armata* (Langerhans, 1880) and *D. paracaulleryi* Meißner, Bick, Guggolz & Götting, 2014.

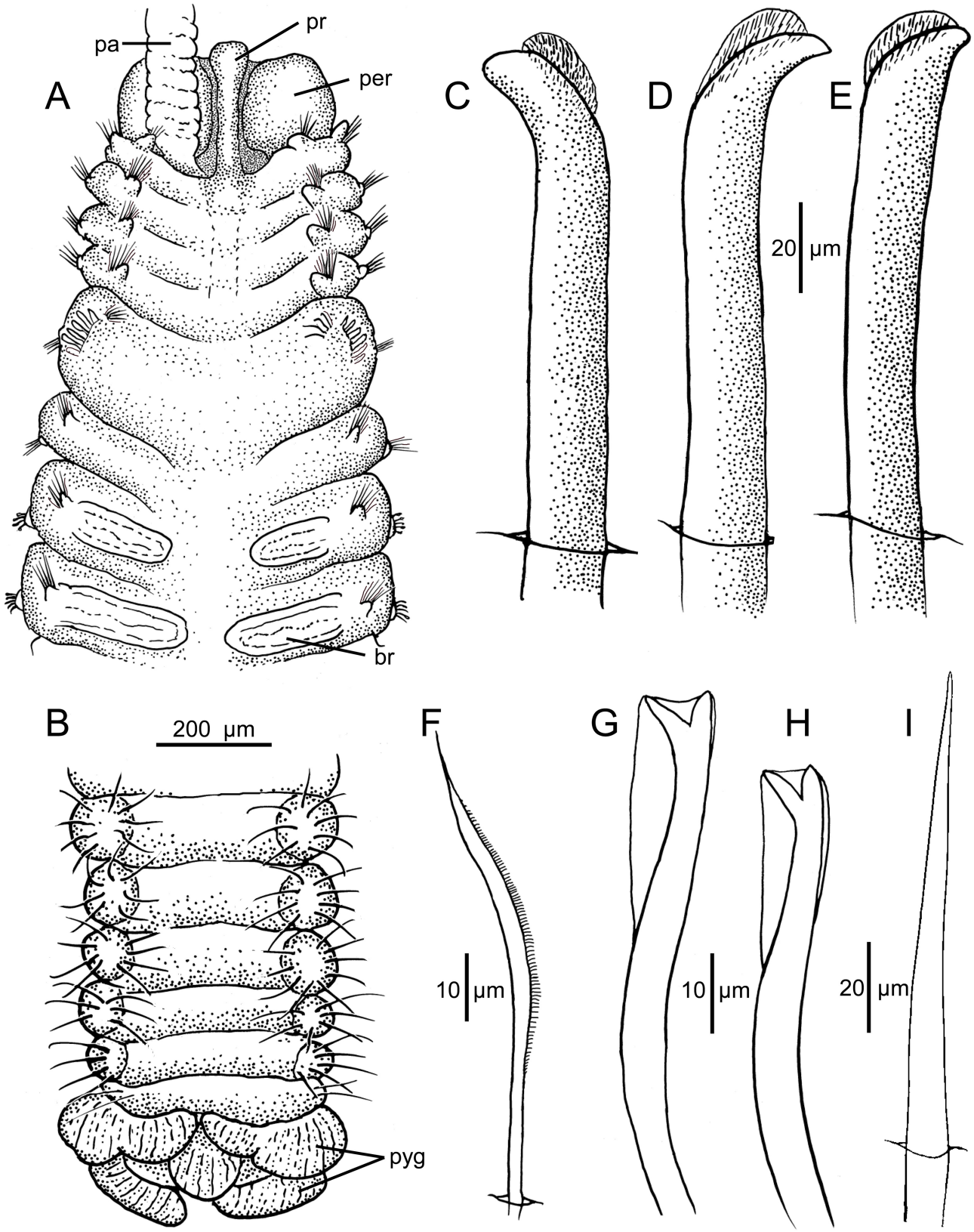

FIGURE 1. *Dipolydora walkerae* **sp. nov.** (A) Anterior end, dorsal view, right palp missing. (B) Posterior end, dorsal view. (C, D, E) Major falcate spines of setiger 5. (F) Dorsal superior notoseta of setiger 5. (G, H) Hooded hooks, posterior neuropodium. (I) Acicular spine, posterior notopodium. A, G, H, I from holotype (FMNH 223654); C, D, E from paratype (MCZ 173000). Abbreviations: br, branchia; pa, palp; per, peristomium; pr, prostomium; pyg, pygidium.

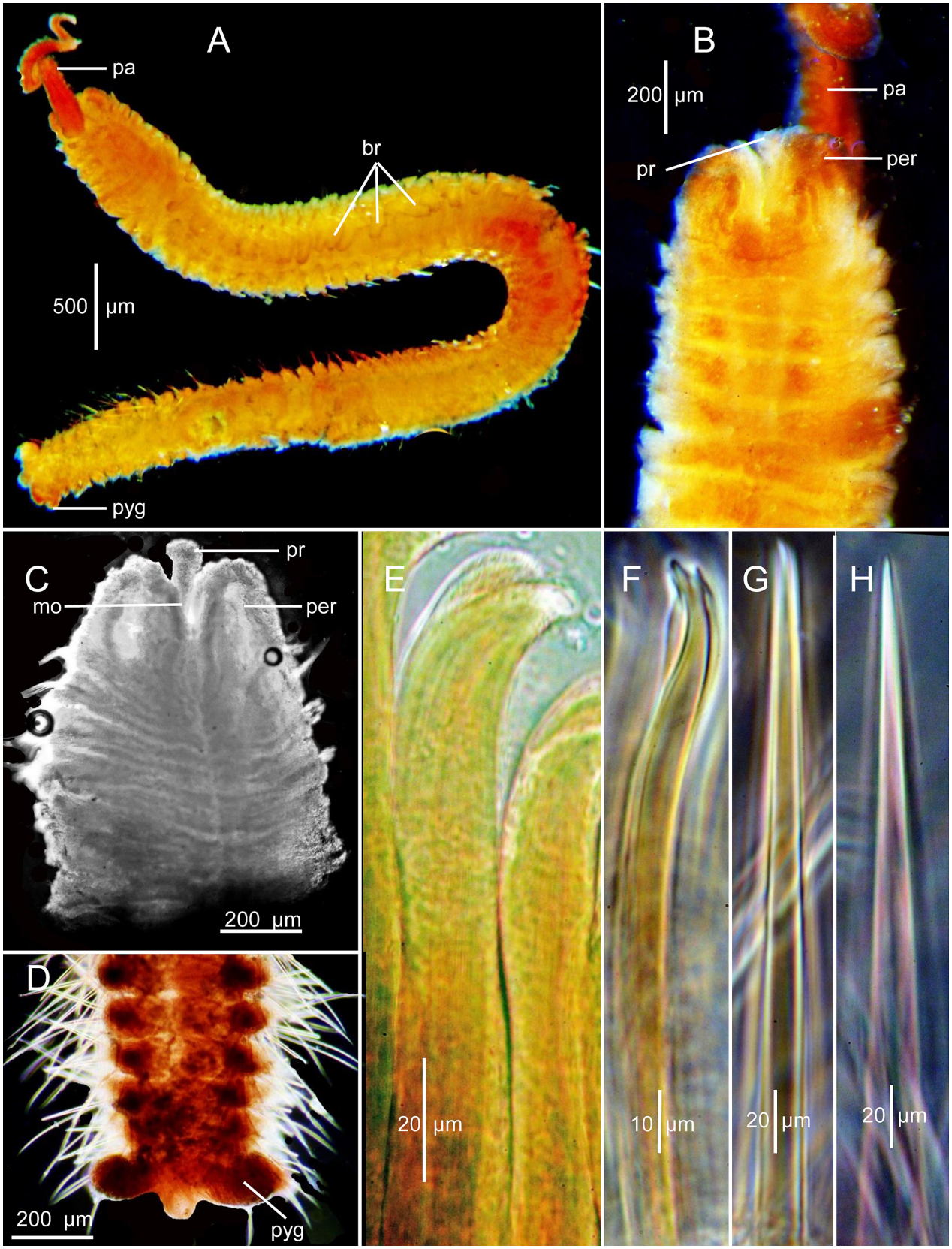

FIGURE 2. *Dipolydora walkerae* **sp. nov.** (A) Entire holotype, dorsal view. (B) Same, ventral view of anterior end. (C) Ventral view of anterior end, paratype. (D) Posterior end, dorsal view. E Major spine of setiger 5. (F) Hooded hook at oblique angle, posterior neuropodium. (G, H) Acicular spines, posterior notopodium. A–B, D from holotype (FMNH 223654); C, E–H from paratype (MCZ 173000). A, B, D stained with Shirlastain A. Abbreviations: br, branchia; mo, mouth; pa, palp; per, peristomium; pr, prostomium; pyg, pygidium.

Dipolydora armata is a widespread shallow-water tropical and sub-tropical coralline boring species (Woodwick 1964; Blake & Kudenov 1978; Blake 1983, 1996; Radashevsky & Nogueira 2003). *Dipolydora walkerae* **sp. nov.** differs from *D. armata* in that the major spines of setiger 5 have a shaft that curves apically to a narrowly pointed tip that is surmounted by a distinct crest formed of bristles or fibrils; the posterior notopodial spines are narrow with a pointed tip and the pygidium has four large papillated lobes and a fifth medial dorsal lobe. In contrast, *D. armata* has major spines with a main fang, a large lateral tooth and wide cowling or third tooth, all of which are covered with a cloak of bristles, the posterior spines that form the rosette are thick and awl-shaped, and the pygidium is a simple cup that opens dorsally.

Dipolydora paracaulleryi is known from the Meteor Seamounts west of the Canary Islands in the North Atlantic Ocean, dredged from coral and crushed shell gravel at a depth of 300 m (Meißner *et al*., 2014). This species is similar to *D. walkerae* **sp. nov.** in having curved major spines on setiger 5 with pointed tips surmounted by a bristled crest and with a narrow prostomium, but this is weakly incised on the anterior end rather than entire. In addition, the prostomium of *D. paracaulleryi* continues posteriorly as a caruncle over setigers 1–2 instead of bluntly ending anterior to setiger 1 as in *D. walkerae* **sp. nov.** Ventrally, the peristomium of *D. paracaulleryi* continues posteriorly over several anterior setigers as a ventral ridge whereas a posterior extension is absent in *D. walkerae* **sp. nov.** Both species have four pygidial lobes, but these are distinctly unequal in *D. paracaulleryi* with the dorsal lobes being smaller; whereas in *D. walkerae* **sp. nov.** all four lobes are of an equivalent size and there is, in addition, a fifth medial lobe dorsal to the anal opening. While the posterior notopodial spines of *D. walkerae* **sp. nov.** form a rosette, these are few in *D. paracaulleryi* and are arranged in a curved row. *Dipolydora paracaulleryi* also has a distinctive methyl green staining pattern on the venter of setigers 6–7 where stained glands are concentrated medially from which a pair of bands extends laterally.

Biology. *Dipolydora walkerae* **sp. nov.** was found boring in the shells of the gastropod *Kanoia meroglypta* collected from mussel beds in methane seep habitats off Louisiana at an upper continental slope depth of 617 m. MacDonald *et al*. (1990a: fig. 4) and (1990b: fig. 2A) illustrated mussels with attached specimens of the gastropod *K. meroglypta* on their shells. The mussels were likely *Gigantidas childressi* (Gustafson, Turner, Lutz & Vrijenhoek, 1998), originally described in the genus *Bathymodiolus*.

In a letter to the author dated 05 June 1992 regarding the availability of the worms described here that were collected in June 1987, Dr. Sally E. Walker stated that "*the spionid is large in comparison to the living snail. It has burrowed through the protoconch, then, through the columella and umbilicus.*" Warén & Bouchet (2001: 133) later stated "*Several specimens* (*of Kanoia meroglypta;* then in the genus *Cataegis*) *from the Bush Hill Seep* (off Louisiana) *had the shell tunneled by polychaetes of the subfamily Polydorinae, in one case so wide a tunnel that both the in and outside of the shell had been broken through. Usually the tubes were restricted to the umbilicus of the shell*." These observations suggest that *D. walkerae* **sp. nov.** is likely widespread in upper slope depths across the northern Gulf of Mexico where the gastropod, *K. meroglypta* is present. The degree of infestation of *D. walkerae* **sp. nov.** on these gastropods and other molluscs is unknown.

Fragmented egg capsules were present with yellow eggs and early 4-cell cleavage stages; eggs measured 138–143 μm in diameter. Although the capsules are broken into separate pieces, they appear to have an elongate tubular shape rather than as strings of beads; attachment threads were not evident.

Etymology. This species is named for Dr. Sally E. Walker, Professor of Paleontology, University of Georgia, Athens, Georgia, USA. Dr. Walker initially discovered and removed these worms from their burrows and identified them as spionids. Having known Dr. Walker from her student days, she notified me of their availability.

Distribution. Gulf of Mexico, off Louisiana, in deep-water methane seep habitats, a borer in shells of the gastropod, *Kanoia meroglypta*, 617 m.

Discussion

Review of deep-water species of the *Polydora* complex. The Family Spionidae is one of the largest among annelids with 38 genera and about 525 species (Blake *et al*. 2020; Read & Fauchald 2024b). Of these, genera having a modified fifth setiger belonging to the *Polydora* complex are collectively called the polydorids or polydorins and include nine genera and approximately 178 species. Of these, *Polydora* is the largest genus with 64 species followed by *Dipolydora* with 47 species (Blake *et al*. 2020); Read & Fauchald 2024a; this study). The new species in the present paper is added to the latter genus.

Collectively, the polydorins are known mostly from the intertidal zone and offshore to about 200 m on the outer continental shelf. Very few species have been reported deeper than 200 m (Blake *et al*. 2020); of those that have been reported most occur either in soft sediments or their habitats are not identified. The lack of deep-water records for shell-boring species may simply be that no one has looked for them. Large offshore surveys typically utilize a team of systematists to identify different taxa; the annelid experts rarely see the molluscs.

Table 1 is a partial list of confirmed shell or other calcareous substrate boring species of polydorins with depth records compiled from recent literature and the author's records. It is noteworthy that nearly all confirmed records of offshore or deep-water species of polydorins as borers of mollusc shells or other calcareous habitats belong to the genus *Dipolydora* (Table 1). The one notable exception is *Polydora pygidialis* Blake & Woodwick, 1972 from intertidal to 90 m shelf depths from central California to British Columbia. The depth of 617 m for *Dipolydora walkerae* **sp. nov.** in the present study represents the deepest confirmed record for a shell-boring spionid polychaete.

TABLE 1. Documented Records of Offshore *Dipolydora* species from Shell or Coralline Boring Habitats by Increasing Depth.

Species/Data	Geographic Distribution	Depth	References
D. elegantissima (Blake & Woodwick, 1972)	E North Pac Ocean, California	Intertidal to 49 m	Blake & Woodwick 1972; Radashevsky *et al*. 2023
D. bidentata (Zachs, 1933)	W North Pac Ocean; Sea of Japan, Russia, Japan	Intertidal to 54 m	Radashevsky *et al*. 2023
D. barbilla (Blake, 1981)	E North Pac Ocean; Gulf of California; S. California	15–55 m	Blake 1981: Radashevsky *et al*. 2023
D. magellanica (Blake, 1983)	E South Pac Ocean, off Peru	64 m	Blake 1983
D. carunculata (Radashevsky, 1993)	E North Pac Ocean; Sea of Japan, Russia	Intertidal to 70 m	Radashevsky *et al*. 2023.
D. concharum (Verrill, 1879)	W North Atl Ocean, off New England; W North Pac Ocean, Japan, Sea of Japan, Russia	15–55 m (Atl); 5–70 m (Pac)	Blake 1971; Radashevsky *et al*. 2023
D. akaina Blake, 1996	E North Pac Ocean, California	75–168 m	Blake 1996
D. alborectalis (Radashevsky, 1993)	W North Pac Ocean, Sea of Japan, Russia, Japan; Sakhalin, Kurile Islands.	33–180 m	Radashevsky 1993; Radashevsky *et al.* 2023
D. giardi (Mesnil, 1893)	Widespread in the Pac Ocean, likely introduced to NE Atl (English Channel, original description)	Intertidal to 200 m	Blake 1996; Radashevsky *et al*. 2023
D. paracaulleryi Meißner *et al*. 2014	NE Atl Ocean, seamounts	300 m	Meißner *et al*. 2014
D. walkerae **sp. nov.**	Gulf of Mexico, methane seeps	617 m	This study

Abbreviations: Atl, Atlantic; E, eastern; m, meter(s); NE, northeast; Pac, Pacific; W, western.

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