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New species and records of *Heterospio* (Annelida, Longosomatidae) from continental shelf, slope and abyssal depths of the Atlantic Ocean, Pacific Ocean, Indian Ocean and adjacent seas

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Abstract

Nineteen species of the rare polychaete genus *Heterospio* are reported, 15 of which are new to science. The status of *H. longissima* Ehlers, 1874, the type-species, is reviewed. The specimens examined are from several locations in the North Atlantic Ocean, Gulf of Mexico, Caribbean Sea, off Br azil, the Indian Ocean, the Pacific Ocean off California, New Zealand, Australia, and the South China Sea. Deep-water samples from the western North Atlantic Ocean collected by the late Drs. H.L. Sanders and R.R. Hessler that were reported by Hartman as *H. longissima* were re-examined and referred to two new species, *H. hartmanae* **n. sp**. (abyssal depths, New England to Bermuda transect) and *H. guiana* **n. sp**. (bathyal depths off Suriname). Other materials from the Sanders/Hessler North Atlantic collections were also examined and referred to two additional species, *H. canariensis* **n. sp**. (deep water off Canary Islands) and *H. southwardorum* **n. sp**. (Bay of Biscay) as well as *H*. cf. *reducta* from off SW Ireland in bathyal depths. New collections from the North Atlantic region include additional materials of *H. hartmanae* **n. sp**. (deep water off the Mid-Atlantic and SE USA), *H. aruba* **n. sp**. (Caribbean Sea), *H. bathyala* **n. sp**. (deep water off SE USA), and *H*. *dibranchiata* **n. sp.** (deep water, Gulf of Mexico). *Heterospio paulolanai* **n. sp**. is from shelf depths off southeastern Brazil. *Heterospio knoxi* **n. sp**. is from the North Island of New Zealand, *H. ehlersi* **n. sp**. is from the Gulf of Thailand, in the South China Sea, *H. bidentata* **n. sp**. is described from deep water in the Coral Sea off eastern Australia, and *H. alata* **n. sp**. and *H. brunei* **n. sp**. are described from deep water off the Island of Borneo in the South China Sea. *Heterospio africana* **n. sp**. and *H*. *antonbruunae* **n. sp**. are described from off east Africa in the Mozambique Channel. New records and descriptions of *H. catalinensis*, *H. indica*, and *H. peruana* are presented. The 15 new species reported here nearly triple the number of previously known species of *Heterospio*, with 23 species now recognized. All known species are tabulated and compared.

Key words: polychaetes, benthos, deep-sea, Ehlers, Hartman, *Longosoma*

Introduction

Species of *Heterospio* (family Longosomatidae) are rarely encountered in benthic surveys and when found they are few in number and invariably fragmented owing to their unusual morphology. Their elongated bodies are narrow and consist of a short thoracic region with crowded segments, an abdominal region with extensively elongated segments, and a bulbous posterior end armed with hooks that likely serve as an anchor. Complete specimens are rarely encountered because sampling to shallow depths within the sediment often results in the posterior end being lost when the samples are taken. The history and biology of the family were recently reviewed by Blake & Maciolek (2019).

The first species to be reported was *Heterospio longissima* by Ehlers (1874, 1875) from deep-water off Ireland. Ehlers (1874) introduced the genus and species*, Heterospio longissima,* in a brief diagnosis in Latin as part of an account of the results from the *Porcupine* Expedition. A complete work, with a description and illustrations, was subsequently published (Ehlers 1875). Throughout the present paper, both the 1874 and 1875 publications will be cited in reference to the species.

Hartman (1965) provided an illustrated description of what she identified as *H. longissima* from deep-water off the U.S. Atlantic coast, and despite Laubier *et al.* (1974)[1] observing differences between Ehlers' and Hartman's versions of the species, the latter has primarily been the one used to characterize the species. Over the years, many investigators have identified *Heterospio* in their collections as *H. longissima* following either Ehlers' (1874, 1875) or Hartman's (1965) concept of the species. These include Hartman (1974a–b: Arabian Sea, 34–88 m), Imajima (1974: Suruga Bay, Japan, 300–450 m), Intes & LeLoeuff (1977: E Africa, Ivory Coast, 30–100 m), Kirkegaard (1980: NE Atlantic, off Ireland, 4120–4165 m), and Uebelacker (1984: Gulf of Mexico, off Texas, 5–134 m). The specimens of *H. longissima* identified by Rosenfeldt (1989) from the Red Sea and referenced by Türkay (1996) and Wehe & Fiege (2002) were subsequently re-examined and referred to *H. indica* by Parapar *et al.* (2016) as part of their description of that species. The majority of these various records of *H. longissima*, however, have not been revisited despite the recent discounting of global or cosmopolitan reports of benthic species (Hutchings & Kupriyanova 2018) and the possibility that these records represent undescribed species. No modern collection or account of *H. longissima sensu* Ehlers has been published. Unfortunately, efforts to obtain Ehlers' original material have not been successful (Laubier *et al.* 1974; Borowski 1994).

Currently, eight species are recognized as valid (Blake & Maciolek 2019; Read & Fauchald 2022). After Ehlers (1874, 1875), there have been long intervals between the descriptions of new species: Hartman (1944, 1957) described *H. catalinensis* (as *Longosoma*) from off southern California, followed by *H. sinica* Wu & Chen, 1966 (East China Sea), *H. mediterranea* Laubier, Picard, & Ramos, 1974 (Mediterranean Sea), *H. reducta* Laubier, Picard, & Ramos, 1974 (Mediterranean Sea), *H. peruana* Borowski, 1994 (off Peru), *H. angolana* Bochert & Zettler, 2009 (off Angola), and *H. indica* Parapar, Vijapure, Moreira, & Sukumaran, 2016 (western India, Arabian Sea). However, it is certain that in addition to our own collections reported here, more species are present. These include the reports of *H. longissima*, Uebelacker's (1984) report of *Heterospio* sp. A from the Gulf of Mexico, off Florida and Alabama, at depths of 19–82 m and 177–182 m, respectively, and Borowski's (1994) report of *Heterospio* sp. 1 from the Peru Basin at 4142 m. In addition, the specimens identified as *H. longissima* by Imajima (1974) from Japan and Kirkegaard (1980) from abyssal depths off Ireland have not been re-examined.

The collections examined here include Hartman's original material that was published in 1965 as *H. longissima* from the Atlantic Ocean; this material is here referred to two new species: one from abyssal depths in the western North Atlantic and another from upper slope depths off Suriname. Thirteen additional new species are described from off the Carolinas, Caribbean Sea, Gulf of Mexico, Canary Islands, Bay of Biscay off Spain, Brazil, Eastern Australia, New Zealand, the South China Sea and Indian Ocean. The newly described 15 species bring the known number of described species to 23.

Materials and methods

Materials examined. Specimens of *Heterospio* were assembled from several surveys, most from deep water, in-

1 Vie et Milieu Vol. 23 encompassed papers planned for 1972–1973. The paper by Laubier, Picard, & Ramos on *Heterospio* was submitted in June 1972 and published in March 1974.

cluding the original materials collected by the late H.L. Sanders and R.R. Hessler and reported by Hartman (1965) and Hartman & Fauchald (1971) from the Atlantic Ocean as *H. longissima*. Other collections from the North Atlantic by H.L. Sanders not previously documented were also examined. In addition, specimens of *Heterospio* from the U.S. Atlantic Continental Slope and Rise (ACSAR) program, the Gulf of Mexico from offshore platform and pipeline surveys, the Caribbean Sea, SE Brazil, New Zealand, deep-water off Queensland, Australia, Gulf of Thailand, SE Asia (off Brunei) and the Indian Ocean collected as part of the International Indian Ocean Expedition (IIOE) and Southeast Pacific Biological Oceanographic Program (SEPBOP) have also been studied. These collections are deposited in the Los Angeles Museum of Natural History (LACM-AHF); the Museum of Comparative Zoology (MCZ), Harvard University; the National Museum of Natural History, Smithsonian Institution (USNM), Australian Museum, Sydney (AM) and the Museu de Zoologia, Universidade de São Paulo (MZUSP).

Sample handling and preservation. Samples from the Gulf of Mexico and off Brunei were collected with a 0.25-m^2 box core from which subcores measuring 10 x10 x 50 cm were obtained and extruded. The upper 10 cm of each of ten subcores were used for biology; other subcores were used for sediment chemistry, grain-size and total organic carbon analyses. During processing, the loose upper flocculent sediment was gently washed from the surface of each subcore directly into a jar and preserved without any sieving in the field. The more compact remainder of the sediment was extruded onto a 300-µm-mesh sieve and gently washed; the residue was retained and preserved in a separate jar. Both fractions were re-sieved in the laboratory. Samples from the earlier ACSAR program along the U.S Atlantic slope were similarly collected; however, a separate flocculent layer was not obtained.

The samples from the Sanders/Hessler deep-water surveys in the Atlantic Ocean and the more recent deep-water survey off Queensland, Australia, were mostly collected using towed sleds or dredges hauled over defined distances. These samples were also separated from the sediment with fine-mesh sieves. Earlier collections were mainly collected with grab samplers or trawls. In most instances the sieve sizes and sample processing methods are not known.

Morphological observations. 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. Some specimens were stained with a saturated solution of Methyl Green (MG) in 70% ethyl alcohol (ETOH) in order to identify staining patterns of subdermal glands evident on some species. 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 used on figures: br, branchiae; dCr, dorsal crest; dRdg, dorsal ridge; dT, dorsal tentacle; mo, mouth; neL, neuropodial lamella; nuO, nuchal organ; per, peristomium; pr, prostomium; pyg, pygidium; trMus, transverse muscle; vGr, ventral groove; vRdg, ventral ridge.

Other abbreviations: ACSAR, Atlantic Continental Slope and Rise Program; AD, anchor dredge; ant., anterior; BC, box core; EBS, epibenthic sled; fr/s., fragment/s; juv, juvenile; MG, Methyl Green stain; IIOE, International Indian Ocean Expedition; NC, North Carolina; NE, northeast; post., posterior; SEPBOP, Southeast Pacific Biological and Oceanographic Program; SC, South Carolina; SE, southeast; set, setiger; SW, southwest; U.S., United States; TOC, total organic carbon.

Terminology of *Heterospio* morphology. Palps vs. dorsal tentacles. Hartman (1965) described *Heterospio* as having "long spioniform palpi", which are grooved feeding structures; several subsequent papers also refer to "palps" in the description of *Heterospio* species (e.g., Wu & Chen 1966, Laubier *et al.* 1974, Borowski 1994). Blake & Maciolek (2019) also used the term "palps", but given recent evidence that longosomatids are more closely related to cirratulids than to spionids (Rouse *et al.* 2022), the cirratulid term "dorsal tentacles" is used here. The dorsal tentacles of cirratulids are lined with cilia and are only shallowly grooved.

Setal types. Longosomatids have several types of simple setae: capillaries, recurved or hooked spines or acicula, aristate spines, and subuluncini. Hartman (1957: 221; pl. 35, fig. 5, pl.37, figs. 5–6) introduced the term "subuluncini" for a certain type of seta found in Orbiniidae; she defined them as transitional between pointed setae (capillaries) and uncini (spines), with a thick base and a long, abruptly slender, pointed distal end. In the same publication (1957), she also used the term in reference to setae found in *Heterospio catalinensis,* saying that certain setae resembled subuluncini. Since that time, the term has been used for setae in both orbiniids and longosomatids. However, setae referred to as subuluncini in orbiniids are typically heavy ribbed neuropodial uncini or spines

that abruptly taper to an elongated and pointed tip; these often occur in fascicles with the blunt tipped uncini. In *Heterospio* setae referred to as subuluncini are not as large, never ribbed, and taper gradually to a pointed tip. Such setae often occur with thickened spinous capillaries and may also occur with aristate-tipped spines where the pointed tip is abruptly narrow. Borowski (1994) referred to the acicular setae in his species *H. peruana* as aristate setae and "subuluncini-like capillaries". The "subuluncini" illustrated by Parapar *et al.* (2014: figs. 4D–G) could just as well be termed aristate. The use of "subuluncini" in *Heterospio* has therefore not been consistent. Aristate spines were first reported for *H. sinica* by Wu & Chen (1966) and later for *H. peruana* by Borowski (1994), who distinguished among several transitional forms of aristate setae and subuluncini-like capillaries (Borowski 1994: fig. 2A–E). In this paper we distinguish between aristate spines and subuluncini.

Systematic Account

Family Longosomatidae Hartman, 1944

Type genus: *Heterospio* Ehlers, 1874.
Synonym: Heterospionidae Hartman, 1963. *Fide* Petersen 1992: 80, Borowski 1994.

Generic Diagnosis: Same as genus *Heterospio* (see below).

Remarks: Longosomatids are easily recognized by the unusually long segments of the middle body region; this character was considered a synapomorphy by Fauchald & Rouse (1997). Another unusual aspect of longosomatid segmentation is that the setal fascicles emerge on the anterior end of each of the short anterior and elongated middle segments, rather than from the middle of the segment as is typical of most polychaetes. The enlarged bulbous posterior end with pairs of curved spines likely serves as an anchor, which probably accounts for most specimens being fragmented when removed from sediment.

Ehlers (1874, 1875) originally placed his new genus in the Spionidae and even after being referred to a new family (Hartman 1944, 1965) it was considered a spioniform (Fauchald 1977, Rouse & Fauchald 1997, Blake & Arnofsky 1999; Read & Fauchald 2022). However, recent interpretation of morphology and newly obtained molecular data supports a close affiliation of Longosomatidae with Cirratulidae (Blake & Maciolek 2019; Rouse *et al.* 2022); this position was also taken by Wilson (2000) and Grosse *et al.* (2021). Longosomatids are similar to cirratulids in having long filamentous branchiae that differ from the broad flattened branchiae of spionids, a pair of long dorsal tentacles and in most species, the arrangement of abdominal setae into cinctures that mostly surround the body.

Genus *Heterospio* Ehlers, 1874

Type species: *Heterospio longissima* Ehlers, 1874, by monotypy.
Synonym: *Longosoma* Hartman, 1944. Type species: *Longosoma catalinensis* Hartman, 1944, by monotypy.

Generic Diagnosis. (emended): Body elongated, linear, divided into three regions: an anterior region with seven to nine short setigers, a median or abdominal region with greatly elongated segments, and a posterior bulbous region bearing three to five short segments. Prostomium narrow, conical, or broadly rounded to disk-like; nuchal organs narrow slits on posterior lateral margins. One pair of grooved peristomial dorsal tentacles, easily lost, arising from notches on dorsolateral surfaces of peristomium. Proboscis an eversible epithelial pouch. Anterior region with one to eight pairs of cirriform branchiae beginning on setiger 2, usually very long when present, arising above and near notopodia. Parapodia biramous with setal fascicles arising from near anterior margin of each segment. Anterior or thoracic region with simple capillaries in tightly defined fascicles, neuropodial acicular spines present or absent on setiger 1. Parapodia of abdominal segments with setae arranged in two elongate rows producing cinctures similar to those of some cirratulids. Abdominal setae include simple capillaries, acicular spines, aristate spines, and subuluncini. Posterior inflated section with acicular hooks.

Remarks. The number of branchial pairs, location of the first elongated segment, and the nature and arrangement of setae along the body are the characters most often used to separate species in the genus. However, there have been differing approaches to identify where the abdominal or elongated segments first begin, and other characters have proven to be equally important. See Discussion at end of paper.

The description of *Heterospio longissima* from off Ireland in 837 m by Ehlers (1874, 1875) was the first account of this unusual group of polychaetes. It was another 70 years before the second species, *H. catalinensis* (Hartman, 1944), (as *Longosoma*) was described from southern California followed by *H. sinica* Wu & Chen, 1960 from China, *H. mediterranea* Laubier *et al.*, 1974 and *H. reducta* Laubier *et al.*, 1974 from the Mediterranean Sea, and *H. peruana* Borowski, 1994 from off Peru in abyssal depths. The two most recently described species are *H. angolana* Bochert & Zettler, 2009 from West Africa, and *H. indica* Parapar *et al.*, 2016 from the Arabian Sea off India. Blake & Maciolek (2019) listed these eight valid species of *Heterospio* but noted that additional species from various deep-water collections were known to them.

In the present study, specimens have been accumulated from sites throughout the North Atlantic Ocean, Gulf of Mexico, off Brazil, California, SE Australia, New Zealand, the South China Sea, and the Indian Ocean. Most materials are from deep-water surveys. From these a total of 19 species have been identified, 15 new to science.

The following species of *Heterospio*, grouped by geographic area, are identified and treated in this study:

1. *Heterospio hartmanae* new species
2. *Heterospio aruba* new species
3. *Heterospio bathyala* new species
4. *Heterospio canariensis* new species
5. *Heterospio dibranchiata* new species
6. *Heterospio guiana* new species
7. *Heterospio* cf. *reducta* Laubier, Picard & Ramos, 1974
8. *Heterospio southwardorum* new species
9. *Heterospio paulolanai* new species
10. *Heterospio alata* new species
11. *Heterospio bidentata* new species
12. *Heterospio brunei* new species
13. *Heterospio catalinensis* (Hartman, 1944**)**
14. *Heterospio ehlersi* new species
15. *Heterospio knoxi* new species
16. *Heterospio peruana* Borowski, 1994
17. *Heterospio africana* new species
18. *Heterospio antonbruunae* new species
19. *Heterospio indica* Parapar, Vijapure, Moreira & Sukumaran, 2016

Comments on *Heterospio longissima* Ehlers, 1874

The original account of *Heterospio longissima*. The genus *Heterospio* was first described by Ehlers (1874, 1875) based on a single anterior fragment collected off SW Ireland (51.017°N, 11.35°W) in 458 fathoms (837 m). Ehlers (1874) introduced the genus and species names briefly in Latin as part of a summary of new or little known polychaetes collected as part of the *Porcupine* Expedition. The full description, however, with illustrations was not published until a year later (Ehlers 1875). Ehlers placed his new genus in the Spionidae and named the new species *H. longissima.* He provided relevant details and an illustration of the anterior end. Based on Ehlers' original description and figures (Ehlers 1875: Pl. 25, figs. 10–11) and our interpretation of his illustrations (Fig. 1), the type species can be characterized as follows:

Description of *Heterospio longissima* Ehlers, 1874. A 12-setiger anterior fragment, 25 mm long, 0.5–0.8 mm wide. Body with a short anterior or thoracic region about 2 mm long with prostomium, peristomium, and eight short setigers each wider than long (Fig. 1A–B); these followed by setiger 9, the first elongate segment, about as long as first 8 setigers combined (Fig. 1A–B). Branchiae present on setigers 2–9 posterior to setal fascicles, one long branchia on setiger 4, with rest mostly stubs or scars. Setigers 10–12 (abdominal) each long, with setiger 10 being 4.5 times as long as setigers 1–9 combined; last two segments each about 8 times as long as anterior segments. Prostomium short, broadly rounded on anterior margin (Fig. 1A), flattened dorso-ventrally. Peristomium a single

ring without dorsal crest; mouth surrounded by lobes (Fig. 1A). Setae arise from anterior border of each segment (Fig. 1A–B); setigers 1–9 with setae in discrete, narrow, fan-shaped fascicles; setigers 10–12 with setae arising in rows producing broad transverse fascicles along anterior and lateral margins, with dorsal, ventral, and lateral gaps; all setae capillaries. Presence of other types of setae not observed on available segments.

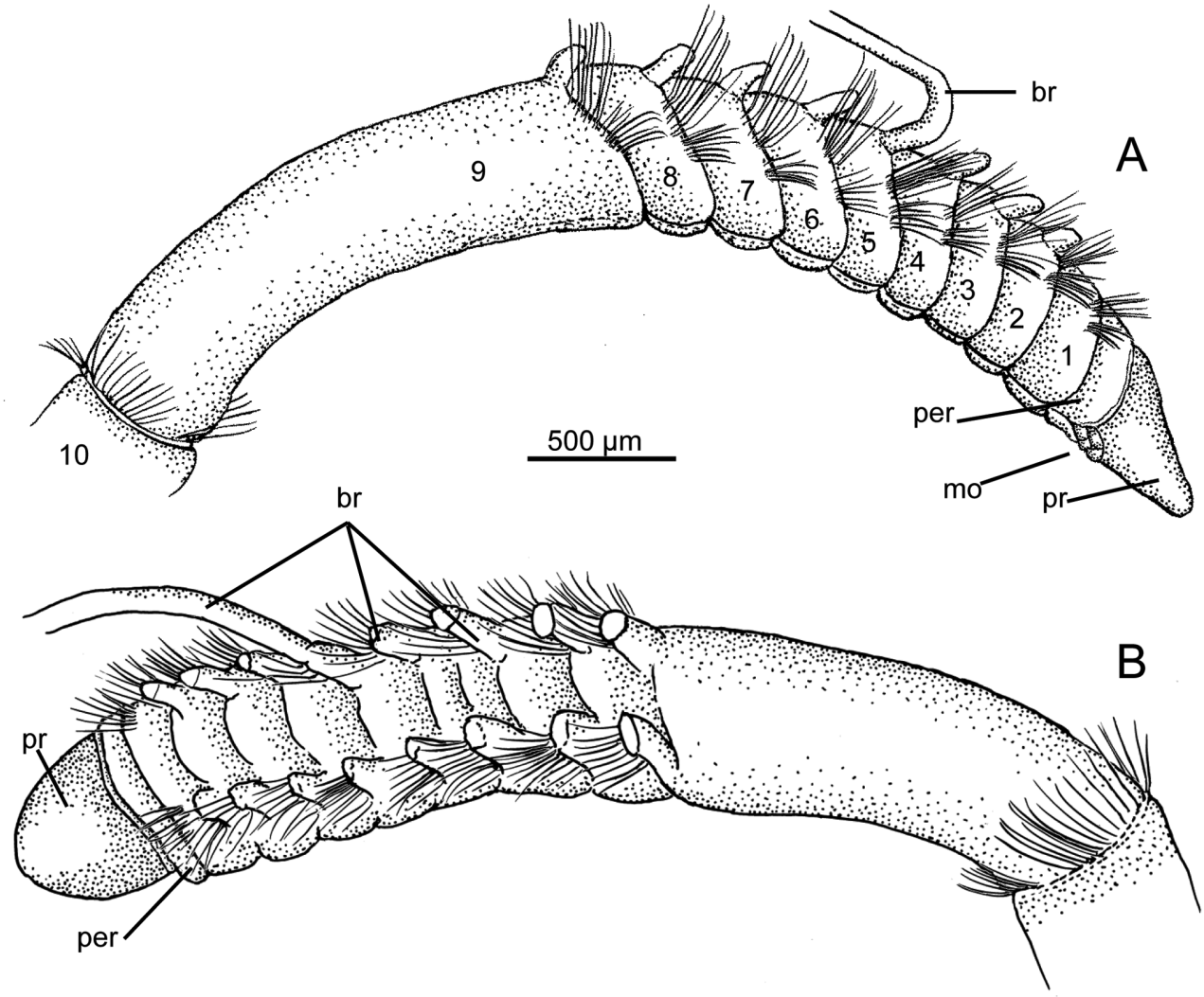

FIGURE 1. *Heterospio longissima* Ehlers, 1874. A, anterior end, right lateral view; B, anterior end, dorsal view. Redrawn from Ehlers (1875).

Remarks. This description is based on Ehlers' (1874, 1875) text and illustrations and is the best we can present based on the limited available information. Ehlers (1874, 1875) states that the mouth has two transverse lobes on the anterior lip but his Pl. 25, fig. 11 suggests that additional lateral lobes may also be present.

Based on information published by Laubier *et al.* (1974) and Borowski (1994) as well as correspondence by the first author with the late Drs. M.E. Petersen and G. Hartmann-Schröder (*in litt.*), Ehlers' type-specimen is not present in the Museum of Natural History, London, or the Zoological Museum of Hamburg and is presumed lost. It is noteworthy that despite additional surveys and collections from near the type locality off SW Ireland, no additional specimens that agree with Ehlers' (1874, 1875) description have been found. Although Amoureux (1982) reported specimens that he identified as *H. longissima*, he did not describe them. Conversely, specimens that agree well with a Mediterranean species, *H. reducta*, have been identified from the same general area and depths (Amoureux 1982; Parapar *et al.* 2014; this study).

Hartman's (1965) concept of *H. longissima*. Hartman (1965), as part of a monograph on deep-water polychaetes from the North Atlantic Basin collected by H.L. Sanders and R.R. Hessler, described and illustrated specimens she assigned to *Heterospio longissima*. As noted in the Introduction, Hartman's concept of the species has been used by many investigators to characterize the type species.

Laubier *et al.* (1974), as part of a paper describing two new species of *Heterospio* from the Mediterranean Sea, examined several specimens of *H. longissima* from the Sanders/Hessler collections loaned to them by Dr. Hartman but did not specify which stations they were from. This omission is problematic because there are two distinct species in Hartman's material (see below).

Laubier *et al.* (1974) determined that Hartman's concept of *H. longissima* differed from Ehlers' (1874, 1875) original description in that setiger 9, the first elongate segment, was only about 2.5 times longer than setiger 8 instead of setiger 9 being as long as the preceding eight setigers. However, there are additional differences between Ehlers' original description, brief as it is, and Hartman's version, which itself contains several errors. One is that Ehlers found only capillary setae on his 12-setiger specimen, whereas Hartman reported acicular spines. Nevertheless, the morphological concept presented by Hartman (1965) and slightly modified by Laubier *et al.* (1974) has been perpetuated and modified in several subsequent studies as "*H. longissima sensu* Hartman" (Laubier *et al.* 1974; Borowski 1994; Bochert & Zettler 2009; Parapar *et al.* 2014, 2016). It is generally assumed, although not specifically stated by these authors, that Hartman's (1965) concept of *H. longissima* represents the actual morphology of Ehlers' species.

However, based on an examination of Hartman's original materials, it is clear that the description presented by Hartman (1965) is incorrect in several aspects. There are major differences between Hartman's (1965) description of the specimens and our observations of the same material. The most striking differences are:

(1) The branchial distribution reported and illustrated (Hartman 1965: Pl. 30, fig. f) for a specimen from R/V *Atlantis* Sta. II-2 indicates long filamentous branchiae on setigers 2–9, whereas the present observations of more than 50 specimens, including five from the same sample (R/V *Atlantis* II-2), consistently have branchiae on setigers 2–5 with no evidence of scars or stubs of additional branchiae on more posterior setigers on any specimen.
(2) The prostomium on Hartman's Pl. 30 fig. f is shown as narrow and pointed; whereas none of the specimens examined from that station or others have such a prostomium. The conical prostomium, while narrowing anteriorly, definitely has a rounded, not pointed, tip.
(3) Hartman's Pl. 30, fig. f illustrates two dorsal tentacles arising from the peristomium. In the present study, no specimens from the Sanders/Hessler's collections had attached dorsal tentacles; however, one small specimen from ACSAR Sta. 16 had one dorsal tentacle arising from the right side of the peristomium. Hartman (1965:163) does indicate in the text that "several long grooved palpi are present in the sample". These were probably added to the illustration.
(4) The main illustration of the anterior end, Pl. 30, fig. f, does not correctly depict the relationship of the emergence of the setal fascicles on the segments of this species or *Heterospio* in general. The parapodia are depicted with the setal fascicles emerging from the middle of each segment rather than on or near the anterior margin, a character that defines the genus (and family). This incorrect depiction of the origin of the setal fascicles also includes an additional segmental furrow suggesting that an additional setigerous segment is present due to its placement after the eighth pair of branchiae. This error was pointed out by Laubier *et al.* (1974) who diagramed the correct segmental sequence. However, these authors did not comment on the number or placement of branchiae on the specimens they examined.

Contributing to the confusion is that Hartman (1965) wrote only of acicular spines and capillaries in abdominal parapodia and did not indicate that spines having an arista or other type of terminal extension were present. Borowski (1994) specifically stated that *H. longissima sensu* Hartman did not have aristate setae but mistakenly reported subuluncini in his Table 2 when referring to Hartman (1965). Parapar *et al.* (2014) evidently followed Borowski's table and included subuluncini in their description of *H. longissima sensu* Hartman based on specimens from off Iceland in bathyal depths (784–834 m). The specimens from Hartman's collection reported here as *H. hartmanae* **n. sp**. are from lower continental slope and abyssal depths (2470–4950 m) and have only acicular spines and capillaries in the abdominal cinctures from setiger 10. The specimens reported by Parapar *et al.* (2014) most likely represent an undescribed species.

There is no obvious reason why the account of *H. longissima* by Hartman (1965) contains so many errors. However, the collection date of the last sample used in the study was April 1963, leaving only two years between the final collection date and the release of the monograph in April 1965 to process over 27,000 specimens and identify,

describe, and illustrate more than 265 species, 70 of which were new to science. Further, four different illustrators were employed to assist Dr. Hartman on the project, including at least two technical assistants, perhaps students, one of whom is acknowledged as preparing Plate 30. It seems likely that morphological details in the illustrations and text were not rechecked against the actual specimens, or the text was edited after the illustrations were prepared and details were not confirmed.

Part of the problem may also be that the Sanders/Hessler collections examined by Hartman (1965) were from different locations. The main collections along the Gay-Head-Bermuda transect from off New England to Bermuda were mostly from abyssal depths and included the species with branchiae on setigers 2–5 described here as *H. hartmanae* **n. sp.** These collections differ from the original account as noted above. However, specimens were also collected from ca. 550 m off Suriname (then Dutch Guiana) and were also listed as *H. longissima* by Hartman (1965). These, however, are a different species, here described as *H. guiana* **n. sp.** These latter specimens agree more closely with Hartman's Pl. 30, fig. f in that some long branchiae were present and branchiae or stubs were found from setigers 2–8. It seems possible that Hartman and/or her illustrator may have consulted specimens from both areas and assumed that observed differences were variations of the same species. In those days, *Heterospio* was rare, nothing was known about morphological variability, and many polychaete species were often assumed to have global distributions. Since the first two described species of *Heterospio*, Ehlers' *H. longissima* and Hartman's *H. catalinensis* had branchiae on setigers 2–9 and we recently learned that specimens from New Zealand that the late Dr. George Knox carried with him during a visit with Dr. Hartman in 1959 also had branchiae on setigers 2–9 (see *Heterospio knoxi* **n. sp**. below), it might be that Dr. Hartman assumed that this was typical for the genus.

A final issue is that Ehlers's specimen came from an upper continental slope or bathyal site of about 837 m, whereas Hartman's North Atlantic collections were largely from abyssal depths of 3000 m and greater. In our experience, upper slope or bathyal species rarely range into abyssal depths.

Summary. Ehlers' type-specimen is apparently lost and no specimens having the same morphology described and depicted by Ehlers (1875) have been reported from the type-locality. Hartman's (1965) concept of *H. longissima* is shown in the present study to represent two different species, neither of which agrees with Ehlers' original account.

Species of *Heterospio* from the North Atlantic Ocean and Adjacent Seas

Heterospio hartmanae new species

Figures 2–3

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Heterospio longissima: Hartman 1965: 163–164, Plate 30, figs. F–H; Hartman & Fauchald 1971: 108–109 (in part). **Not** Ehlers 1874, 1875.

Heterospio cf. *longissima*: Blake & Grassle 1994: 861 (in part); Hilbig 1994: 941 (in part). **Not** Ehlers 1874, 1875.

Not *H. longissima sensu* Hartman: Laubier *et al.* 1974; Borowski 1994; Parapar *et al.* 2014, 2016.

Material examined. (*55 specimens in addition to many middle and posterior fragments*) **Western North Atlantic Ocean. Off New England, Gay Head Bermuda Transect**, coll. H. L. Sanders and R.R Hessler. R/V *Atlantis* Cruise 264, **Sta. II-2**, 24 May 1961, AD, 38.083°N, 69.6W, 3752 m, **holotype** (LACM-AHF Poly 13270); 4 **paratypes** and post. ends, (LACM-AHF Poly 13271); **Sta. HH-3**, 21 May 1961, AD, 38.783°N, 70.133°W, 2900 m (3, small, LACM-AHF Poly 13272); **Sta. II-1**, 22 May 1961, AD, 37.983N, 69.533W, 3742 m, 1 **paratype** and 2 post. ends (LACM-AHF Poly 13273); R/V *Atlantis* Cruise 273, **Sta. JJ-1**, 02 Oct 1961, AD, 37.45°N, 68.683W, 4436 m (4, dry, LACM-AHF Poly 13274); **Sta. GH-4**, 03 Oct 1961, AD, 39.8°N, 70.95W, 2470 m (1, small, LACM-AHF Poly 13275); R/V *Atlantis* Cruise 277, **Sta. JJ-3**, 25 May 1962, AD, 37.217°N, 68.66°W, 4540 m (1, LACM-AHF Poly 13276); **Sta. NN-1**, 29 May 1962, AD, 33.942°N, 66.567°W, 4950 m (1 juv, LACM-AHF Poly 13277); R/V *Atlantis* II Cruise 12, **Sta. 65**, AD, 21 Aug 1964, 38.78°N, 70.113°W, 2891 m (3 post. ends, LACM-AHF Poly 13278); **Sta. 71**, 24 Aug 1964, AD, 38.133°N, 71.792°W, 2946 m, 10 **paratypes** and 9 post. ends and fragments., (LACM-AHF Poly 13279); **Sta. 72**, 24 Aug 1965, EBS, 38.267°N, 71.783°W, 2864 m (1, ant., LACM-AHF Poly 13280); R/V *Chain*, Cruise 50, **Sta. Ch-85**, 05 Jul 1965, EBS, 37.987°N, 69.437W, 3834 m (2, LACM-AHF Poly 13281); R/V *Atlantis* II, Cruise 17, **Sta. 95**, EBS, 17 Dec 1965, 38.55°N, 68.533°W, 3573 m, 11 **paratypes**, 3 post.

ends (LACM-AHF Poly 13282).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR Program**, coll. R. Petrecca, Chief Scientist. **Sta. 12**, Cruise Mid-1, Rep. 2, 07 May 1984, BC, 38.489°N, 72.704°W, 2501 m, (1, USNM 1673091); Rep. 3, 07 May 1984, BC, 38.489°N, 72.704°W, 2500 m (1 juv, USNM 1673092).—**Off Cape Fear, North Carolina**, **U.S. South Atlantic ACSAR Program,** coll. J.A. Blake, Chief Scientist. **Sta. 13**, Cruise SA-4, Rep. 1, 21 May 1985, BC, 32.92°N, 73.83°W, 3015 m (1 post. end, USNM 1673093); Cruise SA-5, Rep. 1, 21 Sep 1985, BC, 32.921°N, 75.833°W, 3006 m (2, USNM 1673094); Rep. 2, 21 Sep 1985, BC, 32.919°N, 75.831° W, 3009 m (1, USNM 1673095); Cruise SA-6, Rep. 2, 20 Nov 1985, BC, 32.92°N, 75.837°W, 3002 m (1, USNM 1673096); Rep. 3, 21 Nov 1985, BC, 32.921°N, 75.835°W, 3006 m (1, USNM 1673097).—**Off Charleston, South Carolina,** coll. J.A. Blake, Chief Scientist. **Sta. 16**, Cruise SA-5, Rep. 1, 14 Sep 1985, 31.587°N, 75.173°W, 3009 m (1, USNM 1673098); Rep. 2, 16 Sep 1985, BC, 31.586′N, 75.171°W, 3011 m (2, USNM 1673099); Cruise SA-6, Rep. 2, BC, 20 Nov 1985, 31.585°N, 75.172°W, 3009 m (1, USNM 1673100); Rep. 3, 20 Nov 1985, BC, 31.586°N, 75.17° W, 3012 m (1, USNM 1673101).

Description. Body long, narrow, threadlike (Fig. 2A–C), divided into an anterior thoracic region with crowded, slightly flattened segments, abdominal region with elongate cylindrical segments, and posterior region terminating in a bulbous pre-pygidial region bearing hooked spines. All larger specimens fragmented: largest holotype (LACM AHF-Poly 13270) with 13 setigers, 14.1 mm long, 0.4 mm wide across anterior setigers; paratype (LACM AHF-Poly 13273) with 12 setigers, 14.9 mm long, 0.2 mm wide across anterior setigers. Only complete specimen (USNM 1673091) smaller, slender, with nine thoracic setigers, 15 abdominal setigers, and three setigers in posterior bulbous section for a total of 27 setigerous segments, this specimen 9.45 mm long, and 0.11 mm wide across thoracic segments (Fig. 2A–C). Color in alcohol opaque white to light tan; pigment entirely absent.

Pre-setiger region short, about as long as first 3 or 3.5 thoracic segments (Figs. 2D–E; 3A–C). Prostomium roughly rhomboid-shaped, tapering anteriorly from wide middle section to narrow, rounded tip; posteriorly narrowing, encompassed by first peristomial ring (Figs. 2D–E, 3A–C); eyespots absent; nuchal organs narrow slits on posterior lateral margins (Fig. 3A). Peristomium with two rings, both prominent dorsally and laterally; first ring surrounding prostomium dorsally like a yoke, continuing laterally but not onto ventral surface; second ring a large achaetous segment interrupted dorsally by posterior extension of prostomium and complete ventrally, encompassing mouth (Fig. 3A–C). Mouth a transverse opening with anterior lip formed by 7–8 short lobes and posteriorly by 3–4 narrow lobes (Fig. 3B); pharynx everted on some specimens, short, rounded sac-like. A single dorsal tentacle observed on right side of one small specimen (USNM 1673098); this tentacle long, thickened in middle, arising from groove between anterior and posterior peristomial rings, subsequently detached during examination.

Branchiae present on setigers 2–5 (Fig. 3A, C) on all specimens examined except juveniles; most branchiae short, stubby, a few longer ones basally thick, tapering to rounded tip; prominent stubs or branchial scars typically present if individual branchiae not evident; no evidence of branchiae or scars after setiger 5. Smallest juveniles with branchiae on setigers 2–3.

Thoracic region consisting of eight short setigers, each about as wide as long, and a ninth transitional setiger about 2.5 times longer than setiger 8 (Figs. 2D–E, 3A–C). All thoracic setigers slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum; similarly inflated ventrally. Abdominal setigers elongated from setiger 10, about 20–25 times longer than short thoracic setigers; setigers 10–24 elongate on complete specimen (USNM 1673091) and 10–14 on larger anterior fragments.

All parapodia biramous with setal fascicles arising from anterior edge of segment, lateral and dorsal gaps between setal fascicles defining noto- and neuropodia. All thoracic noto- and neuropodia of setigers 1–9 with 12–15 long capillaries in spreading fascicles; abdominal setae from setiger 10 arranged in two rows producing cirratulid-like cinctures with numerous (25+) acicular spines in both noto- and neuropodia on each side, thus 50–60 spines on each side or 100–120 per segment; spines in anterior row accompanied by 25–30 or more thin capillaries in posterior row. Abdominal acicular spines with thick, weakly curved shaft tapering to narrow tip (Figs. 2F–G, 3F); aristate setae not present. Spines present on all abdominal setigers except last 3–4 posterior segments where setae all capillaries; complete 27-setiger specimen (USNM 1673091) with spines absent on setigers 22–24.

Far posterior bulbous section with at least 2–3 parapodia each bearing two distinctly separated acicular spines in each ramus (Fig. 3D). Each spine yellow, curved, with blunt tip (Figs. 2C [inset], 3E).

Methyl Green staining. Prostomium and peristomium stain intensely; segmental bands most evident ventrally.

Remarks. The description of *Heterospio hartmanae* **n. sp**. presented here is based on the original materials collected from off New England to Bermuda by the late Drs. H.L. Sanders and R.R. Hessler and identified and reported as *H. longissima* Ehlers, 1874 by Hartman (1965) and Hartman & Fauchald (1971). A few additional

specimens collected as part the U.S. ACSAR program off the Carolinas and off Delaware and New Jersey are also included. The species occurs in lower continental slope and abyssal depths from about 2500–4950 m.

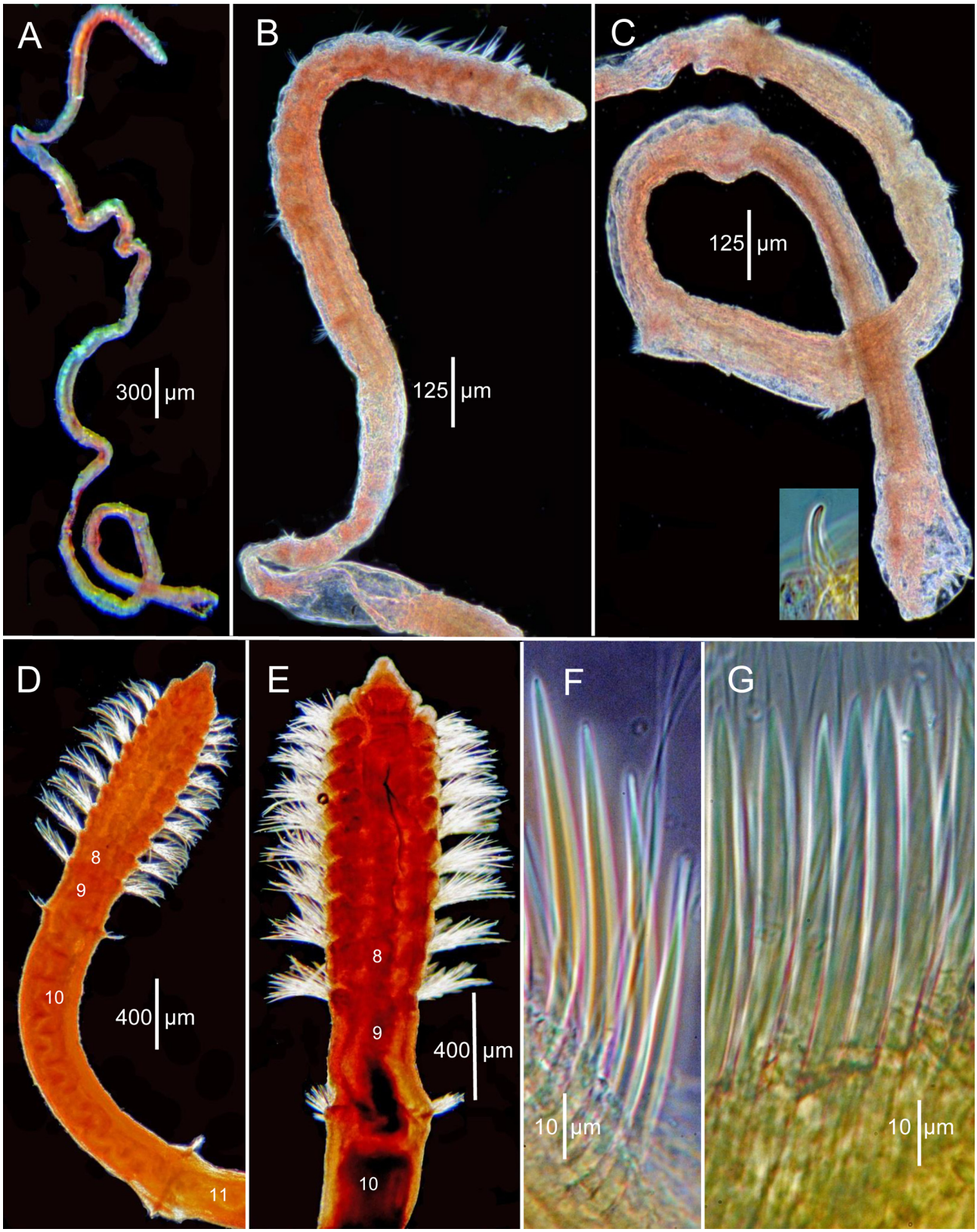

FIGURE 2. *Heterospio hartmanae* **n. sp**. A, complete specimen; B, anterior fourth of A; C, posterior fourth of A with inset of hook (not to scale); D, anterior end, setigers 1–11, dorsal view; E, anterior end, setigers 1–10, dorsal view; F, G, acicular spines and capillaries from middle setigers. A–C, E (USNM 1667391); D, holotype (LACM-AHF Poly 13270); F–G (paratype, LACM-AHF Poly13279). A–E stained with Shirlastain A.

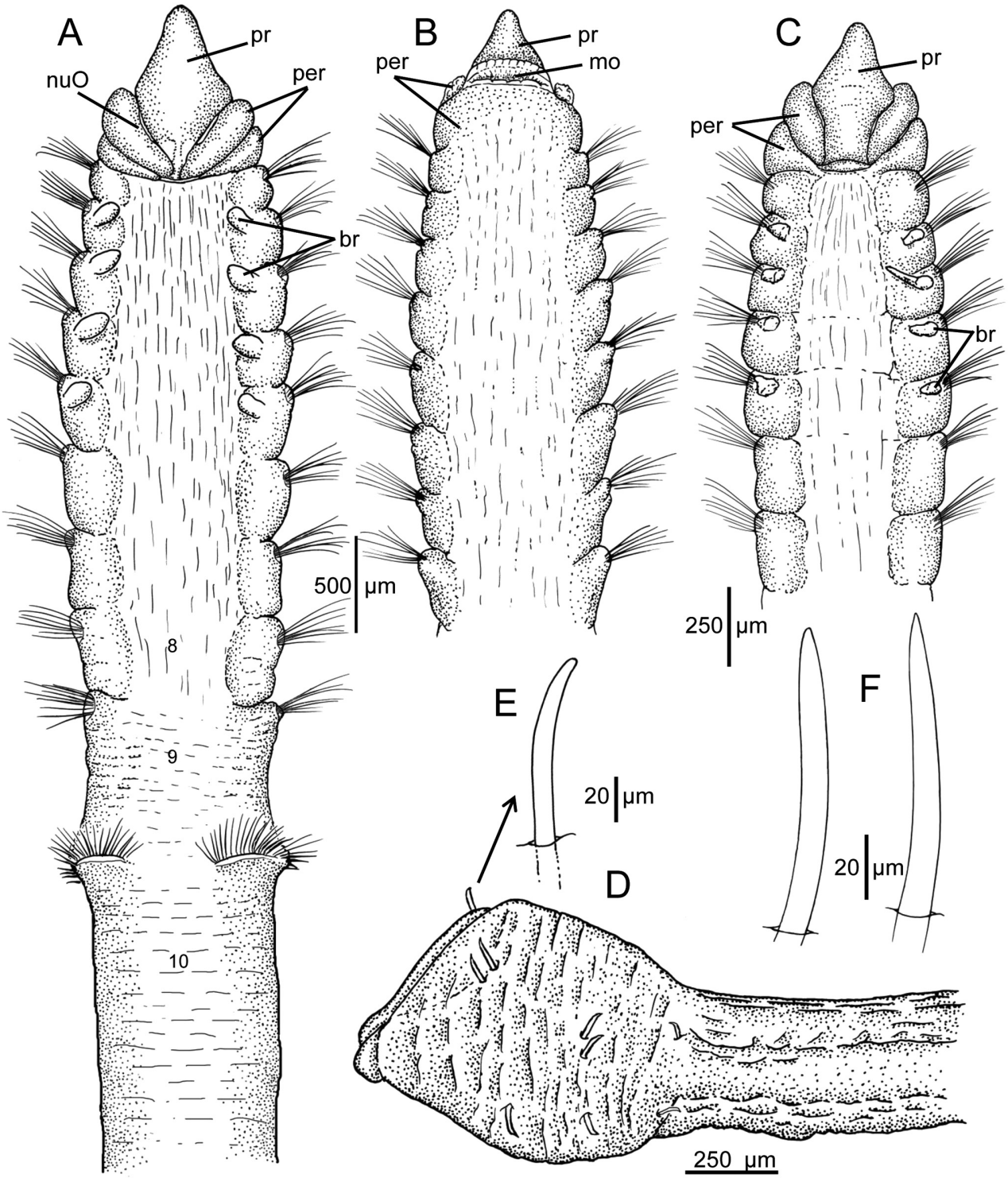

FIGURE 3. *Heterospio hartmanae* **n. sp**. A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end, dorsal view; D, posterior end, left lateral view; E, hook from D; F, acicular spines from setiger 12. A–B, D–F, holotype (LACM-AHF Poly 13270); C, paratype (LACM-AHF Poly 13282).

As detailed above in the previous section on *Heterospio longissima*, Hartman's (1965) version, which has been followed by recent investigators as representative of the type-species, has been found to differ from the original description by Ehlers (1874, 1875) and is also an incorrect description of the materials themselves. Major differences between Hartman's (1965) account and the present examination of the same specimens include the distribution of

branchiae (setigers 1–9 vs. 2–5), the shape of the prostomium (narrow and pointed vs. conical and rounded), the presence or absence of thick palps, and the origin of the setae from middle of segments vs. from the anterior margin.

With the morphological differences reported here, the placement of the species among the known species of *Heterospio* changes. Rather than *H. longissima*, the species most similar to *H. hartmanae* **n. sp**. are *H. peruana* Borowski, 1994, an abyssal species from off western South America, and *H. brunei* **n. sp**. from deep-water in the South China Sea (see below). All three species have branchiae limited to setigers 2–5, a 9-setiger thoracic region of which the first eight are short and a transitional ninth that is about 2.5 times longer than each of the first eight setigers; all nine thoracic setigers have capillary setae. The first setal cinctures occur on setiger 10, which is the first abdominal setiger. While the shape of the thick curved spines on the posterior bulbous section appears to be the same in all three species, the acicular spines in the abdominal setigers are different. In *H. hartmanae* **n. sp**. the abdominal spines in the cinctured segments are mainly simple spines with narrow rounded tips; only a few have pointed tips and none are aristate. In contrast, the acicular spines of cinctured segments in *H. peruana* are illustrated by Borowski (1993) as distinctly aristate or subuluncinate-like capillaries where the extended tip is thicker than the smoothly tapering tip of typical capillaries. *Heterospio brunei* **n. sp**. has a few aristate spines in the first one or two abdominal setigers, but most are acicular throughout. More importantly, *H. hartmanae* **n. sp**. has two prominent peristomial rings, whereas *H. brunei* **n. sp**. has only one.

Biology. Sediment grain size data are available for the two abyssal stations off the Carolinas where *Heterospio hartmanae* **n. sp**. was collected (Blake *et al.* 1987; Blake & Grassle 1994). Station 13 off Cape Fear, NC, and Station 16 off Charleston, SC, were adjacent sites along the 3000 m isobath and had similar sediment characteristics; both sites had high silt + clay fractions and a water content of about 56.3%. The nine sediment samples collected at each of station, averaged over all three surveys, included the following results for percent sand, silt and clay fractions: Sta. 13: sand (17.6 ± 5.1); silt (38.8 ± 4.1); clay (43.5 ± 3.7); Sta. 16: sand (6.0 ± 1.1); silt (38.3 ± 1.1); clay (52.4 ± 1.6).

Blake & Grassle (1994) reported that the polychaetes *Microrbinia linea* Hartman, 1965, *Prionospio* sp. 2, and *Myriochele* sp. 1 were the three most abundant species at Sta. 13 and *M. linea*, *Prionospio* sp. 2, and *Siboglinum* sp. 2 were the three most abundant species at Sta. 16. *Heterospio hartmanae* **n. sp**. ranked 14th at Sta. 16.

Etymology. This species is named after the late Dr. Olga Hartman, who recognized the unusual nature of *Heterospio*. Dr. Hartman's lifetime of work on polychaete systematics has been an inspiration to the present authors and polychaete researchers worldwide.

Distribution. Lower continental slope and abyssal depths of the Western North Atlantic Ocean, off eastern North America, 2470–4950 m.

Heterospio aruba new species

Figure 4

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Material examined. (*3 specimens*) **Caribbean Sea, off Island of Aruba**, R/V *Alpha Helix*, Cruise CARIB I, **Sta. ND-16**, 26 Jun 1977, dredge, 12.506°N, 70.045°W, 30 m, **holotype** (USNM 1673074), 2 **paratypes** (USNM 1673075).

Description. All three specimens incomplete. Body elongate, narrow; fragments with 11–13 setigers, nine anterior thoracic setigers with first eight crowded, each about four times wider than long, followed by an elongated setiger 9 about 3.5 times longer than each of first eight setigers (Fig. 4A–B). Following abdominal segments each about as long as entire thoracic region. Thoracic segments 1–9 with typical dorso-lateral setal fascicles confined to localized parapodia; these transitioning from setiger 10 to abdominal segments where setae arise from long transverse parapodia resulting in broad cincture-like fascicles or rows mostly surrounding anterior margin of each segment, with dorsal and lateral parapodial gaps. Dorsal surface relatively smooth along entire body; mid-ventral surface of setigers 1–8 with low ridge extending posteriorly from mouth over peristomium to about setiger 8 (Fig. 4B); ventral surface of setiger 9 and abdominal segments smooth, similar to dorsal surface.

Holotype (USNM 1673074) largest fragment, with 13 setigers, 5.8 mm long, 0.4 mm wide across thorax and 0.45 mm wide across abdominal segments. Larger paratype with 11 setigers, 3.93 mm long, 0.29 mm wide across thorax and abdomen; smaller paratype long, thin, threadlike, with 12 setigers, 4.36 mm long, 0.12 mm wide across thorax and 0.07 mm wide across abdominal segments. Color in alcohol light tan.

Pre-setiger region triangular in shape, about as long as first three thoracic setigers (Fig. 4A–B). Prostomium triangular, wide at base, tapering to narrow rounded tip; eyespots absent, nuchal organs narrow slits along posterior margin (Fig. 4A). Peristomium with two dorsolateral rings dorsally separated by groove; no dorsal tentacles present, but scars evident in medial notch in groove (Fig. 4A). Peristomial lobes not extending onto smooth ventral surface; mouth arising at level between the two peristomial lobes, consisting of simple narrow transverse slit (Fig. 4B), proboscis not emergent on any specimen.

Branchiae on setigers 2–8 on holotype (Fig. 4A), setigers 2–6 on larger paratype, and 2–3 on small paratype; branchiae or their stubs or scars clearly evident when present, not observed on setiger 9. Individual complete branchiae, when present, thin, rounded in cross section, tapering to rounded tip; with narrow ciliated groove; internal blood vessel extends along entire length.

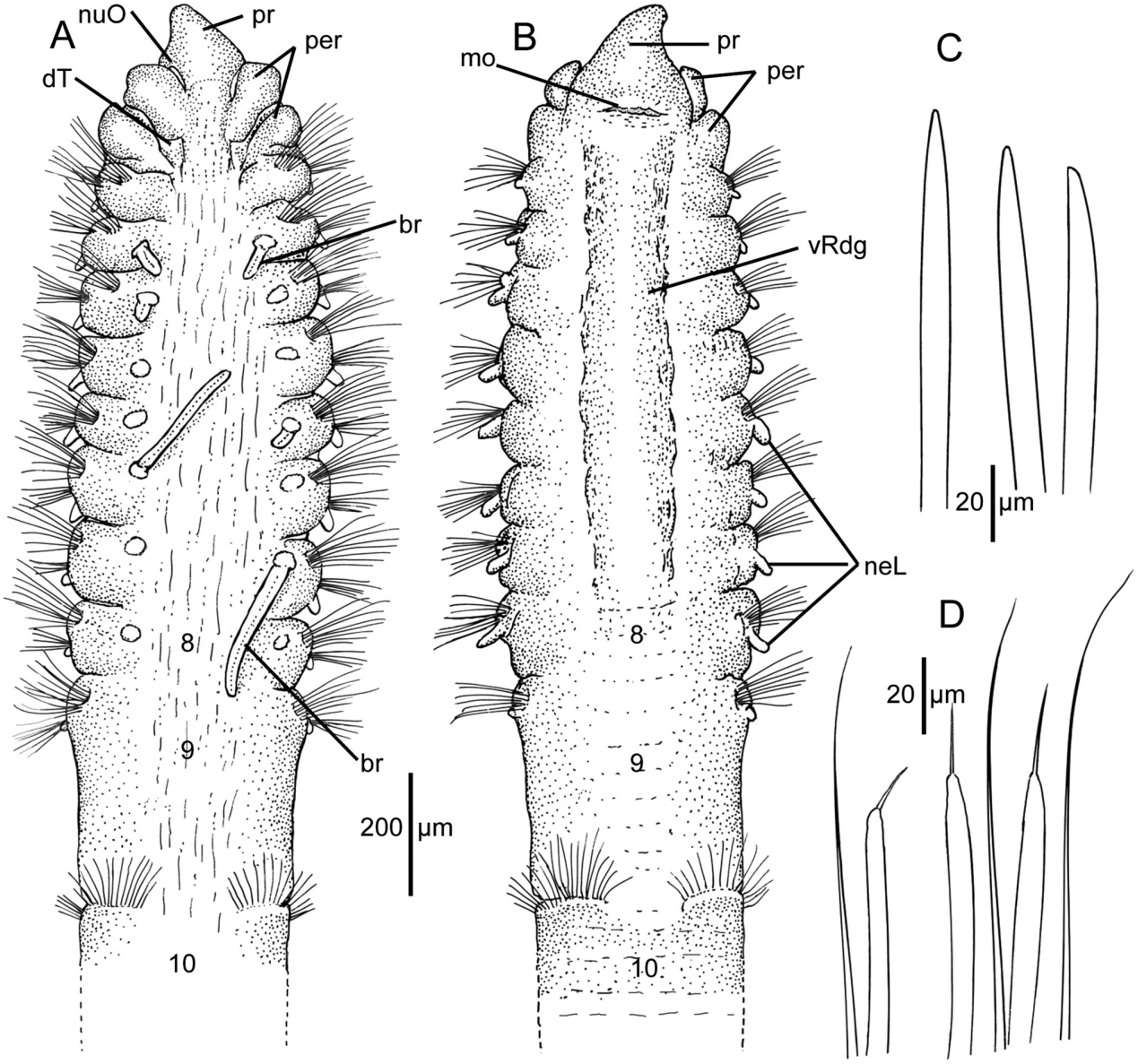

FIGURE 4. *Heterospio aruba* **n. sp**. Holotype (USNM 1673074): A, anterior end, dorsal view; B, anterior end, ventral view; C, acicular spines, setiger 13; D, acicular spines, aristate spines, and capillaries, setiger 12.

All parapodia biramous with setal fascicles arising from near anterior edge of segment. All thoracic setigers slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum and bearing setal fascicles in tight bundles. Neuropodia of holotype with prominent digitate postsetal lobes on all nine thoracic setigers, shortest on setigers 1–3, then longer on setigers 4–8, then short again on setiger 9 (Fig. 4B); these short, rounded lobes on larger paratype, rudimentary on smaller paratype. Abdominal setigers round in cross section and bearing setae

in transverse rows encircling anterior border of each segment. Abdominal parapodia from setiger 10 as narrow elongate lobes, becoming thicker and more prominent on setigers 11–13; noto- and neuropodia with distinct dorsal and ventral gaps between setal fascicles; lateral gaps between noto- and neuropodia narrower.

All thoracic notopodia of setigers 1–9 with 10–25 long capillaries in spreading fascicles; capillaries of neuropodia more numerous with up to 25–30 arranged in tight, dense fascicle. Noto- and neuropodia of setiger 10 with capillaries arranged in two transverse rows with distinct dorsal and lateral gaps; a few aristate spines also present in anterior row of neuropodia. Setigers 11–12 with noto- and neuropodia with aristate-tipped acicular spines in anterior row (Fig. 4D) and capillaries in posterior row; setiger 13 similar but with acicular spines (Fig. 4C) in neuropodia in first row and thin capillaries in second row, notopodia with aristate spines and few acicular spines in anterior row and capillaries in posterior row.

Posterior region not present among fragments.

Methyl Green staining. Body stains uniformly and de-stains with no pattern.

Remarks. *Heterospio aruba* **n. sp**. is similar to the original concept of *H. longissima* by Ehlers (1874, 1875) in having eight short thoracic segments and a longer ninth setiger, followed by even longer segments. However, *H. aruba* **n. sp**. has acicular and aristate spines among the abdominal setae from setiger 10 instead of only capillaries. It is possible that some acicular spines with rounded tips may simply be ones that have lost the fragile arista. *Heterospio aruba* **n. sp**. is unusual in having prominent digitate neuropodial postsetal lamellae on setigers 1–9. Short neuropodial lamellae were illustrated, but not described or discussed for *H. indica* from the Indian Ocean in about 20 m (Parapar *et al.* 2016: Fig. 2B). *Heterospio indica* is reported to have thickened capillary setae and a few subuluncini in abdominal parapodia, but no acicular or aristate spines (but see *H. indica* below); in contrast *H. aruba* **n. sp**. has both aristate and acicular spines.

Etymology. The epithet for *Heterospio aruba* **n. sp**. is based on its discovery offshore the Island of Aruba, in the Caribbean Sea.

Distribution. Caribbean Sea, off Island of Aruba, 30 m.

Heterospio bathyala **new species**

Figures 5–6

urn:lsid:zoobank.org:act:8CFC9701-A0C8-4E39-8ED7-85A67D30E7D4

Heterospio cf. *longissima*: Blake *et al.* 1987; Blake & Grassle 1994: 861; Hilbig 1994: 941 (in part). **Not** Ehlers 1874, 1875; Hartman 1965.

Material examined. (*27 specimens*) **Southeastern United States, U.S. South Atlantic ACSAR Program, off Cape Fear, North Carolina**, coll. J.A. Blake. **Sta. 11**, Cruise SA-4, Rep. 1, 22 May 1985, BC, 33.081°N, 76.418°W, 800 m, **holotype** (USNM 1673076), 2 juvs (USNM 1673077); Rep. 3, 22 May 1985, BC, 33.81°N, 76.423°W, 799 m, 1 juv (USNM 1673078); Cruise SA-5, Rep. 1, 23 Sep 1985, BC, 33.081°N, 76.42°W, 796 m, 1 **paratype** (USNM 1673079); Rep. 2, 23 May 1985, BC, 33.081°N, 76.2517°W 796 m, 2 **paratypes** (USNM 1673080); Rep. 3, 23 May 1985, BC, 33.081°N, 76.419°W, 797 m, 2 **paratypes** (USNM 1673081); Cruise SA-6, Rep. 2, 22 Nov 1985, BC, 33.083°N, 76.419°W, 804 m, 3 **paratypes** (USNM 1673082); **Sta. 14**, Cruise SA-4, Rep. 1, 20 May 1985, BC, 33.394°N, 77.019°W, 805 m (4, USNM 1673083); Rep. 2, 20 May 1985, BC, 33.394°N, 77.02°W, 802 m (3, USNM 1673084); Rep. 3, 20 May 1985, BC, 33.395°N, 77.019°W, 803 m (3, USNM 1673085); Cruise SA-5, Rep. 1, 19 Sep 1985, BC, 33.395°N, 77.02° W, 796 m, 1 **paratype** (USNM 1673086); Rep. 2, 19 Sep 1985, BC, 33.395°N, 77.021°W, 799 m, 1 juv (USNM 1673087); Cruise SA-6, Rep 1, 18 Nov 1985, BC, 33.396°N, 77.018°W, 799 m, 3 **paratypes** (USNM 1673088); Rep. 3, 18 Nov 1985, BC, 33.395°N, 77.018°W, 799 m (3, USNM 1673089).—**Off Cape Lookout, North Carolina**. **Sta. 3**, Cruise SA-3, 14 Jul 1984, BC, 34.242°N, 75.672°W, 1509 m (1, USNM 1673090).

Description. All specimens incomplete. Body long, narrow, threadlike; available anterior fragments with 11–14 setigerous segments, divided into thoracic region with 1–7 crowded setigers and setiger 8 as the first elongated segment; these followed 3–6 elongate cylindrical abdominal segments (Figs. 5A, 6A). Most specimens with a total of 11–12 setigerous segments. One posterior fragment terminating in bulbous pre-pygidial region bearing hooked spines (Fig. 6F). Holotype (USNM 1673076) anterior fragment with 12 setigers, 16.5 mm long and 0.23 mm across thoracic segments (Fig. 5A, C); paratype (USNM 1673081) with 12 setigers, 16.7 mm long, 0.28 mm wide; paratype

(USNM 1673082) with 13 setigers, 14.25 mm long, 2.7 mm wide. A few mid-body fragments suggest at least 14-setiger specimens collected, but not intact. Juvenile (USNM 1673086) anterior fragment with 11 setigers, 3.1 mm long and 0.1 mm wide. Color in alcohol opaque white to light tan; pigment entirely absent.

Pre-setiger region short, only as long as first 1.5 thoracic setigers (Figs. 5A–D, Fig. 6B). Prostomium flattened, disk-like, broadly rounded anteriorly (Fig. 5A–C), with middle of dorsal surface becoming elevated as broad crest extending over peristomium and merging with setiger 1 (Figs. 5A–B, D, 6B), eyespots absent; nuchal organs narrow posterior lateral grooves anterior to first peristomial ring (Fig. 6B). Peristomium with narrow anterior ring separated from large posterior ring by dorsolateral grooves from which dorsal tentacles arise (Figs. 5B, D, 6E); these located laterally; when present, tentacles elongate thickened filaments (Fig. 6A, E); peristomium interrupted by mid-dorsal crest; ventral surface relatively smooth; mouth located mid-ventrally between prostomium and peristomium, consisting of 4–6 short lobes surrounding oral opening (Fig. 5C).

Branchiae or their stubs present on setigers 2–4 on all specimens examined except juveniles (Figs. 5A–B, 6A–C, E); most branchiae long, thin, rounded in cross section, tapering to rounded tip; branchiae with narrow ciliated groove; internal blood vessel extends along entire length (Fig. 6B, E). Juveniles with branchiae observed only on setiger 2.

All parapodia biramous with setal fascicles arising from near anterior edge of segment. Thoracic region of all specimens including juveniles with seven short setigers, each slightly wider than long; with setiger 8 being first elongate setiger (Fig. 5A), about as long as setigers 1–6, shorter in juveniles; setiger 9 very elongate, about 20x longer than setigers 1–7; setigers 10–12 or 13 each 25–30x longer than thoracic setigers. All thoracic setigers slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum. Abdominal setigers similarly inflated ventrally; abdominal setigers round in cross section. Abdominal parapodia from setiger 10 with parapodia as narrow elongate lobes, becoming thicker and more prominent from setigers 11–12; noto- and neuropodia with distinct dorsal and ventral gaps; lateral gaps between noto- and neuropodia narrower.

All thoracic notopodia of setigers 1–8 with 12–16 long capillaries in spreading fascicles; capillaries of neuropodia more numerous with 25–30 setae arranged in tight, dense fascicle. Noto- and neuropodia of setigers 9–11 with capillaries in two short transverse rows with wide dorsal and ventral gaps and narrow lateral gaps between noto- and neuropodia; setiger 12 with capillaries (Fig. 5E) and usually a few acicular spines (Fig. 5F) and rarely an aristate spine or thickened capillary in anterior row; setigers 13–14 with numerous acicular spines in anterior row and narrow capillaries in posterior row; aristate spines present or absent. Spines and capillaries of noto- and neuropodia from setiger 13 in longer cinctures, each with 10–12 acicular spines in anterior row and about 25 or more capillaries in posterior row or about 20–24 acicular spines from noto- and neuropodia on a side. Spines flattened, tapering to narrow pointed tip (Fig. 5F), some with a very short aristate tip. Far posterior bulbous section with two parapodia, each bearing 1–2 hooked spines in each ramus. Each spine short, pointed, with curved tip (Fig. 5G).

Segments of elongate abdominal region with transverse muscle bands; these believed to support stretching of elongate segments (Blake & Maciolek 2019); continuing until posterior bulbous section. Posterior bulbous section oval-shaped, with terminal anal opening (Fig. 6F).

Methyl Green staining. Stain concentrates on peristomium and a few anterior thoracic setigers (Fig. 6C); prostomium not stained; abdominal setigers with stain retained laterally in bands anterior to parapodia and variably along individual segments as irregular speckles (Fig. 6C–D).

Remarks. *Heterospio bathyala* **n. sp**. is most similar to *H. reducta* Laubier, Picard & Ramos, 1974 originally reported from deep water (2335 m) in the Mediterranean Sea north of Algeria and *H. angolana* Bochert & Zettler, 2009 from shelf depths (105–146 m) off Angola, West Africa. All three species have a reduced number of branchiae (three pairs) and the first elongated segment is setiger 8. *Heterospio reducta* is reported to have only capillary setae in posterior cinctures; however, no specimens with more than 12 setigers have been reported (Laubier *et al.* 1974; Borowski 1994; Parapar *et al.* 2014; this study).

Heterospio angolana is therefore the species most similar morphologically to *H. bathyala* **n. sp**. The two species differ in that *H. bathyala* **n. sp**. has a broadly rounded, flattened, disk-like prostomium followed by a raised dorsal crest that extends posteriorly over the peristomium and onto setiger 1; in contrast, the prostomium of *H. angolana* is conical, narrowing to a rounded tip, and has no dorsal crest. In addition, *H. angolana* is described as having numerous aristate spines or subuluncini in the anterior setal row from setiger 12 and a posterior row of numerous simple acicular spines. In contrast, *H. bathyala* **n. sp**. has an anterior row of simple pointed acicular spines and a posterior row of simple capillaries. A few aristate spines may be present with acicular spines on setiger 12, but are not present on setigers 13–14.

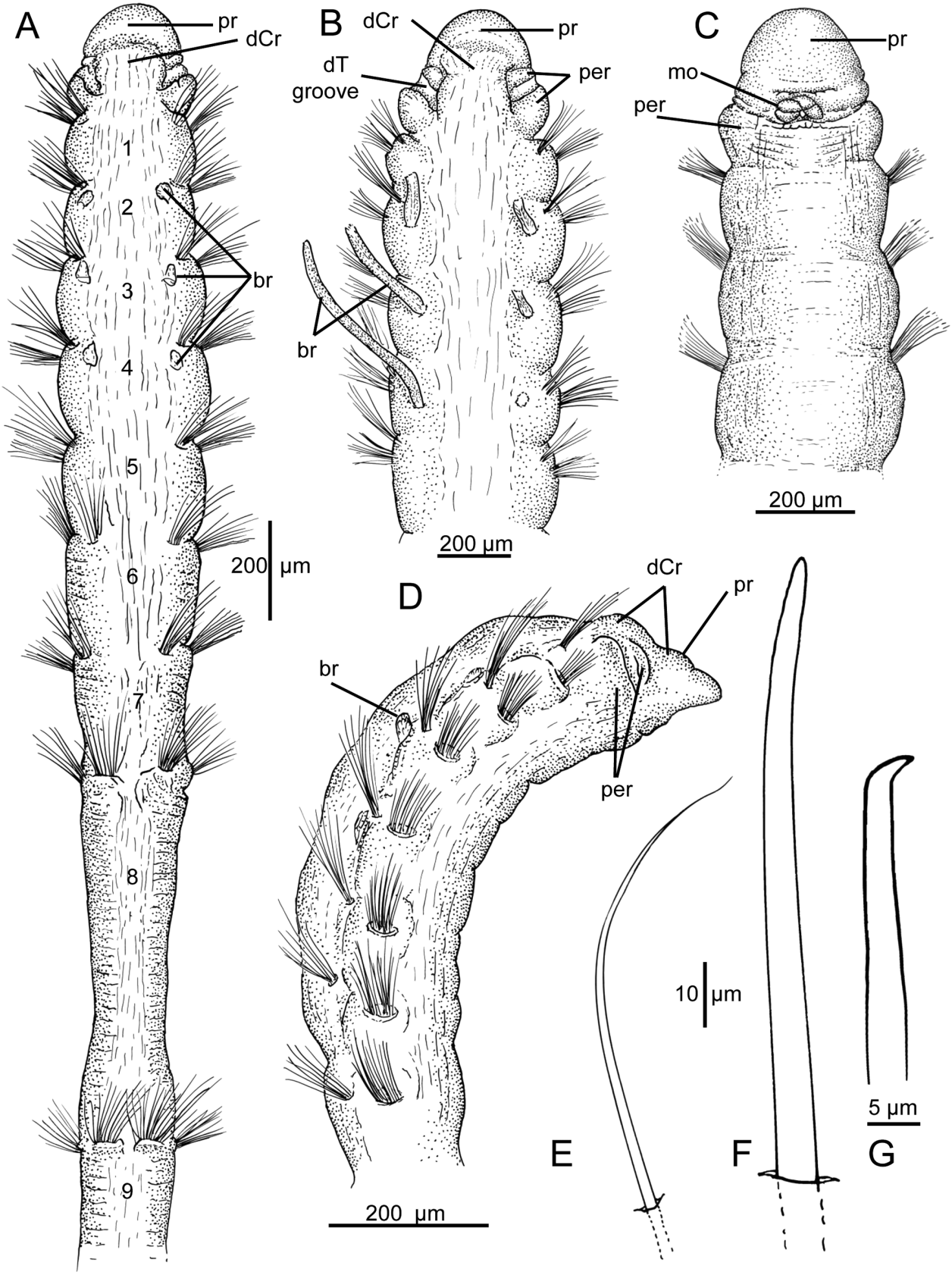

FIGURE 5. *Heterospio bathyala* **n. sp**. A, anterior 10 setigers, dorsal view; B, anterior end, dorsal view; C, anterior end, ventral view; D, anterior end, right lateral view; E, capillary notoseta setiger 12; F, acicular spine, setiger 12; G, hook from posterior end. A, C, E, F, holotype (USNM 1673077); B, D, paratype (USNM 1633079); G, (USNM 1673085).

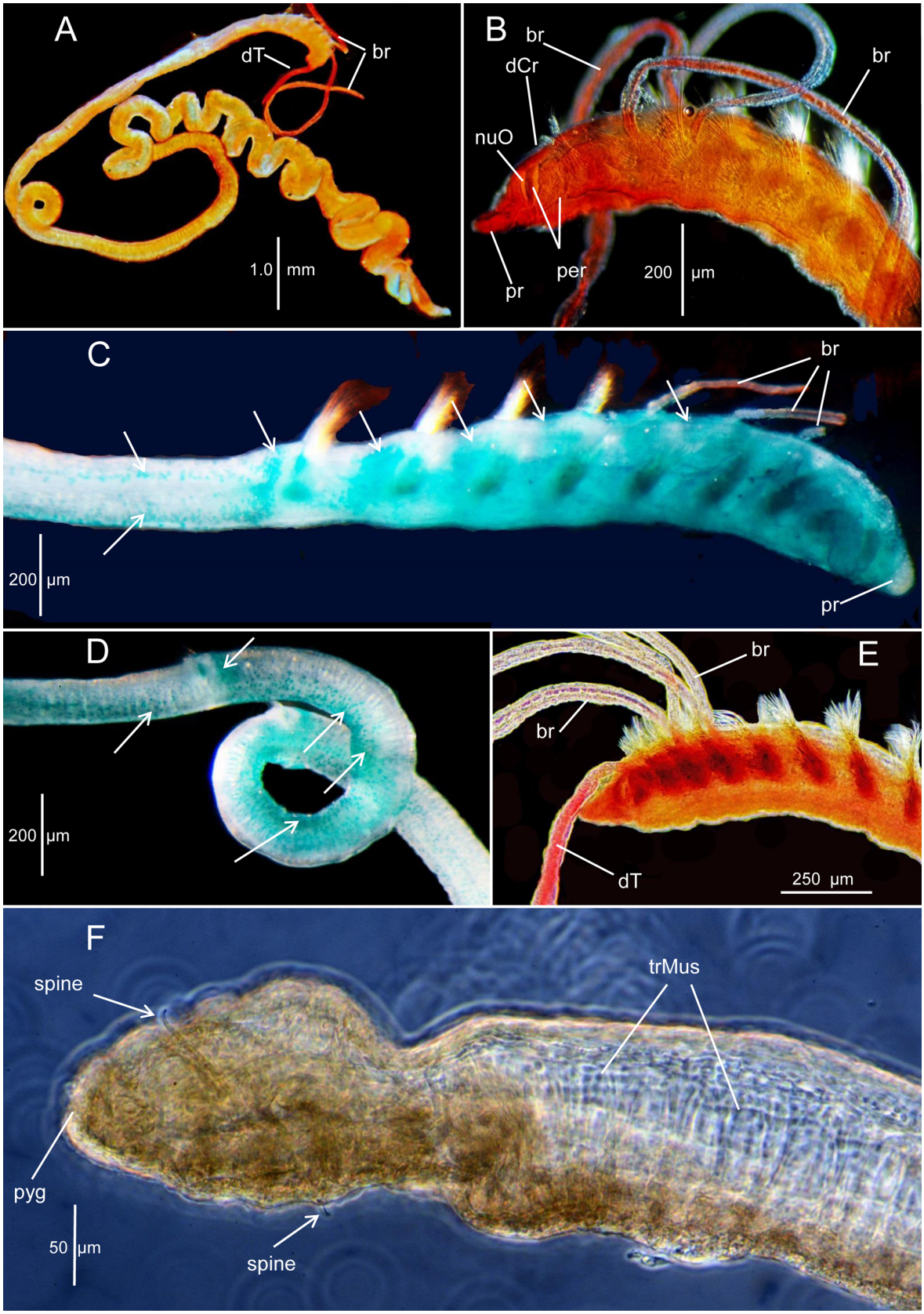

FIGURE 6. *Heterospio bathyala* **n. sp**. A, 13-setiger anterior fragment with dorsal tentacle attached; B, anterior end, left lateral view; C, anterior end, right lateral view; D, same, middle segments; E, anterior end, left lateral view with dorsal tentacle attached; F, bulbous posterior end, right lateral view. A–B paratype (USNM 1673082); C–D, paratype (USNM 1673080); E, paratype (USNM 1673081); F, (USNM 1673085). A–B, E stained with Shirlastain A; C–D stained with MG. C–D, arrows denote concentrations of MG.

Biology. *Heterospio bathyala* **n. sp**., although rare, was concentrated at Stations 11 (off Cape Fear, NC) and 14 (off Charleston, NC) along the 800-m isobath, with only a single specimen collected elsewhere in survey areas off the Carolinas. Station 14, with 436 species of benthic invertebrates collected from nine box core samples (0.81 m^2) over three surveys, had the highest species richness and diversity for any site during the entire U.S. ACSAR program sampled from the Canadian boundary to off the Carolinas (Blake *et al.* 1987; Blake & Grassle 1994). The dominant polychaete at both stations was *Microrbinia linea* Hartman, 1965, a small threadlike orbiniid that is widespread along the entire U.S. Atlantic continental slope (Blake 2021a).

Stations 11 and 14 were adjacent sites in areas influenced by the Gulf Stream and complex local bottom currents (Blake & Grassle 1994); both sites were thought to be depositional and had similar sediments that were well mixed with a water content of about 57%. The nine sediment samples each at Stations 11 and 14 averaged over all three surveys included the following results for percent sand, silt and clay fractions (Blake *et al.* 1987): Station 11: sand (39 ± 3), silt (33.9 ± 2.5), clay (26.9 ± 1.8); Sta. 14: sand (41 ± 0.7); silt (33.1 ± 1.5); clay (25.87 ± 2.3). Station 14 is in an area of high productivity and sedimentation with an average mean percent total carbon in the sediments of 3.67 ± 0.67.

Etymology. The epithet is derived from the Greek, *bathys*, for deep, denoting the bathyal depths from which this species was collected.

Distribution. U.S. continental slope off North Carolina; off Charleston, SC, and Cape Fear, NC, 796–804 m; off Cape Lookout, NC, 1509 m.

Heterospio cf. *reducta* Laubier, Picard & Ramos, 1974

Heterospio reducta Laubier, Picard & Ramos, 1974: 246, figs. 1B–C, 3; Amoureux 1982: 185; Parapar *et al.* 2014, 990–995, figs. 9–10; Langeneck *et al.* 2017: 143–144.

Material examined. **Off Ireland, R/V *Chain*, Cruise 106, J. F. Grassle, Chief Scientist, Sta. 310**, 17 Aug 1972, Anchor dredge, 51.552°N, 12.357°W, 984–978 m, 2 specimens (MCZ 100580).

Description. Both specimens incomplete, each, long, threadlike; largest with 11 setigerous segments, 16 mm long, 0.1 mm wide along most of body. Body with seven crowded thoracic segments followed by setiger 8 about as long as setigers 1–7; setiger 9 as long as setigers 1–8. Anterior setigers slightly flattened dorsoventrally, thicker than rest of body. From setiger 9 all segments cylindrical in cross section; from setiger 10 each segment elongate appearing stretched; with numerous transverse muscle bands. Color in alcohol light tan.

Prostomium broadly rounded anteriorly, flattened dorsoventrally; eyespots absent; nuchal organs grooves on posterolateral margin of prostomium. Peristomium with two rings, evident laterally, first ring narrow, second ring large, continuing across venter, interrupted dorsally by low crest. Dorsal tentacles and/or scars not present. Short, rounded pharynx everted on both specimens resulting in oral morphology not being apparent.

Branchiae present on setigers 2–4; these short, stubby. All parapodia biramous with setal fascicles well separated on all setigers. Encircling rows of setae or cinctures of setae not observed on any available segments. Noto- and neuropodia of setigers 1–8 each with about 12–15 capillaries arising from narrow setal fascicles; noto- and neuropodia of setigers 9–11 each with about 20–25 capillaries arising from two rows with broad dorsal and ventral gaps, not forming cinctures. Setae all capillaries; no neuropodial hooks in anterior setigers; acicular spines, aristate spines, and subuluncini not observed.

Posterior bulbous segments not present.

Methyl Green staining. No pattern, stain not retained anywhere along the body.

Remarks. These specimens from bathyal depths (984–978 m) off SW Ireland agree with the morphology of *Heterospio reducta* as originally described by Laubier *et al.* (1974) from deep water (2335 m) off Algiers in the Mediterranean Sea and by Parapar *et al.* (2014) from bathyal depths (270–922 m) off Iceland. Amoureux (1982, 1987) also reported, but did not describe, specimens he identified as *H. reducta* from off W Ireland (500–1400 m). Langeneck *et al.* (2017) reported the species as a dominant polychaete from the Malta Escarpment in the Mediterranean, but did not describe their specimens. The species is characterized as having a broadly rounded, disk-like prostomium, branchiae on setigers 2–4, with setiger 8 being the first elongated setiger, and all setae capillaries with no spines or segmental cinctures. However, no specimens having more than 12 setigers have ever been reported and therefore, complete absence of spines in abdominal segments cannot be fully confirmed until larger fragments or complete specimens are collected.

It has not escaped our notice that the type locality for *Heterospio longissima* Ehlers, 1874, the type-species of the genus, is also off SW Ireland in bathyal depths (837 m) and only 116 km from the location of our specimens. Ehlers' species was described for a specimen with 12 setigers with all capillary setae. Ehlers' (1875) illustration also shows a broadly rounded prostomium, but branchiae are illustrated on setigers 2–8 instead of 2–4 and setiger 9 is the first elongate one instead of setiger 8 (see also Fig. 1 this study). Unfortunately, the original materials examined by Ehlers (1874, 1875) appear to have been lost (Laubier *et al.* 1974; Borowski 1994). However, the possibility that the specimens from off Ireland identified here as *H.* cf. *reducta*, might actually represent the type species should be investigated given that we have determined that Hartman's (1965) version of *H. longissima* was misconstrued and her collections actually include two of our newly described species (*H. hartmanae* **n. sp**. and *H. guiana* **n. sp**.). We also note that Amoureux (1982) reported both *H. longissima* and *H. reducta* from off Ireland, but did not describe them. Amoureux (1987) later added *H. mediterranea* in a summary report of the "*Thalassia*" expeditions. A starting point might be to locate and examine his specimens. Some of his samples included two of these species.

Distribution. Mediterranean Sea, 1200–2100, 2335 m; Off SW Ireland, 500–1400 m; off Iceland, 270–922 m.

Heterospio canariensis new species

Figure 7

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Material examined. (*9 specimens*) **Eastern North Atlantic Ocean, off Canary Islands**, **SE of Gran Canaria Island**, coll. J. Allen, RRS *Discovery*, Cruise 21, **Sta. 6711**, 19 Mar 1968, EBS, 27.248°N, 15.605°W, 2988 m, **holotype** (LACM-AHF Poly 13266); 4 **paratypes** plus middle and post. fragments (LACM-AHF Poly 13267); **Sta. 6709**, 18 Mar 1968, EBS, 27.537°N, 15.427°W, 2351 m, 3 **paratypes** (LACM-AHF Poly 13264); **Sta. 6710**, 19 Mar 1968, EBS, 27.395N, 15.66°W, 2670 m, 1 **paratype** plus posterior fragments (LACM-AHF Poly 13265).

Description. An elongate, threadlike species; all specimens incomplete, material includes anterior fragments with 12–13 setigers, abdominal fragments, and posterior fragments with bulbous posterior ends containing at least three setigers. Holotype (LACM-AHF Poly 13266) an anterior fragment with 13 setigers, 16.6 mm long, 0.36 mm wide across thorax and 0.38 mm wide across abdominal segments. Paratype (LACM-AHF Poly 13267) with 12 setigers, 12.4 mm long, 0.41 mm wide across thorax and 0.21 mm wide across abdominal segments. Dorsal surface of thoracic region with parapodia weakly elevated producing flattened channel along first seven setigers (Fig. 7A); following abdominal segments with relatively smooth surface interrupted by numerous transverse muscle bands. Ventral surface with mid-ventral ridge extending from peristomium to about setiger 6 (Fig. 7B), thereafter ventral surface relatively smooth, similar to that of dorsum. Color in alcohol light tan.

Pre-setiger region about as long as first three thoracic setigers (Fig. 7A–B). Prostomium rhomboid-shape in dorsal view, widest medially, anteriorly tapering to broadly rounded apex, narrowing posteriorly, continuing as dorsal crest or ridge over peristomium to middle of setiger 3 (Fig. 7A); eyespots absent; nuchal organs distinct slits on posterior lateral margins anterior to first peristomial ring; dorsal surface with numerous small lumps extending over dorsal surface, not as obvious on ventral surface (Fig. 7A); ventrally prostomium broadly rounded anteriorly, merging posteriorly with upper lip of mouth (Fig. 7B). Peristomium with two rings; anterior ring unusually narrow (Fig. 7A), ventrally forming anterior lip of mouth (Fig. 7B); posterior ring as large as subsequent parapodia, interrupted dorsally by dorsal crest (Fig. 7A) and ventrally by posterior lip of mouth and ventral ridge (Fig. 7B). Mouth opening a transverse slit with about six large lobes on anterior lip and smaller indistinct lobes on posterior lip that merge with mid-ventral ridge (Fig. 7B). Proboscis partially everted on some specimens as simple rounded lobe. Dorsal tentacles not present on any specimen, but scars evident mid-dorsally in notches between two peristomial rings. Branchiae limited to setiger 1 on all specimens examined (Fig. 7A); branchiae short, thick, apparently broken or regenerating.

All parapodia biramous with setal fascicles arising from near anterior edge of segment. Thoracic region of all specimens with eight short setigers, twice as wide as long (Fig. 7A); setiger 9 elongate, about as long as thoracic setigers 5–8 combined (Fig. 7A). All thoracic setigers slightly flattened dorsally with parapodia inflated and elevated over dorsum, bearing setae in tight fascicles. Abdominal setigers from setiger 10 rounded in cross section, bearing setae in transverse rows encircling each segment similar to cinctures of some cirratulid polychaetes (Fig. 7A). Abdominal parapodia from setiger 10 narrow elongate lobes, noto- and neuropodia with distinct dorsal and ventral gaps between setal fascicles; lateral gaps between noto- and neuropodia narrower.

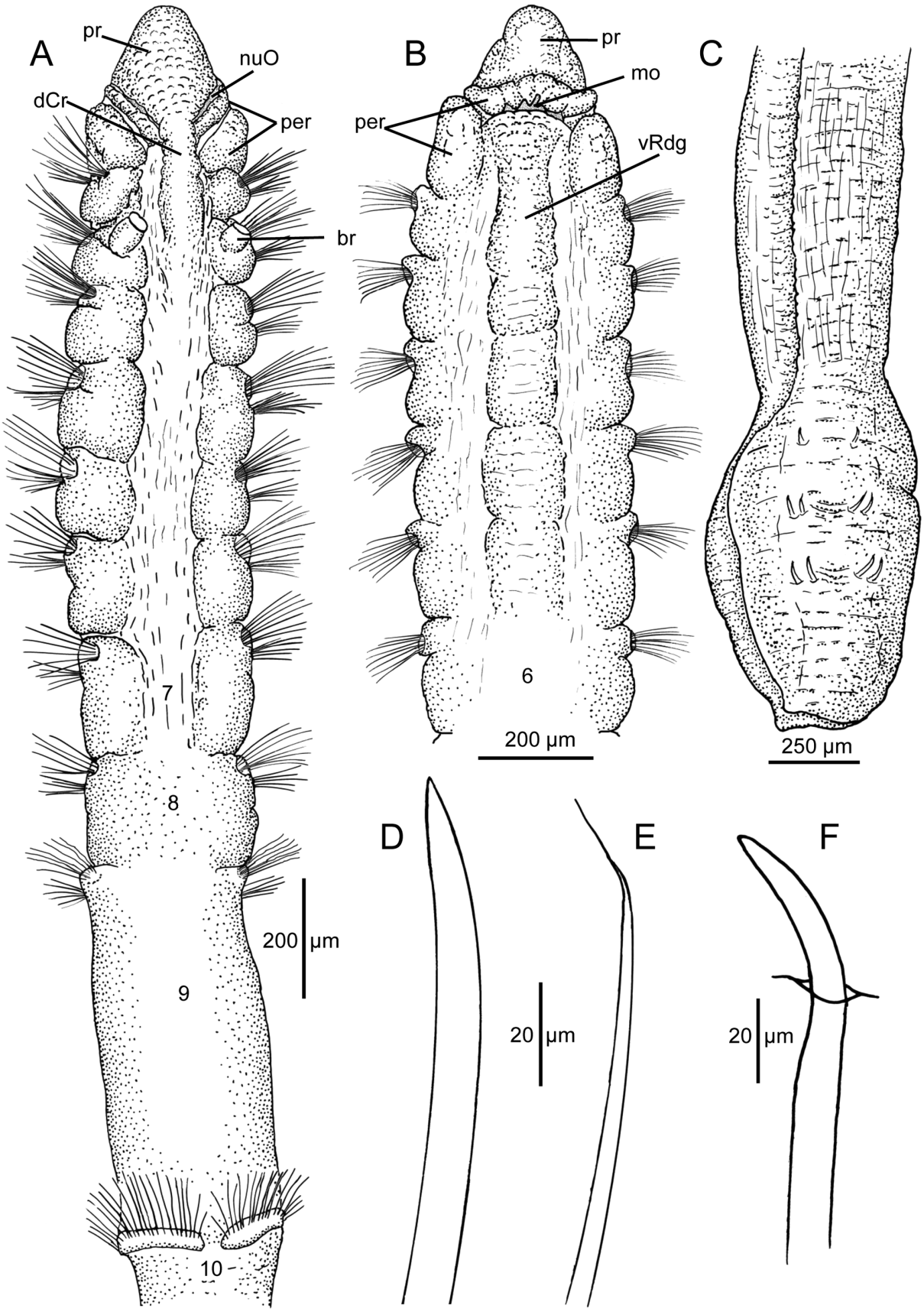

FIGURE 7. *Heterospio canariensis* **n. sp**. A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end, right lateral view; D, notopodial acicular spine setiger 11; E, notopodial capillary setiger 11; F, posterior notopodial hook. A, holotype (LACM-AHF Poly 13266); B–F, paratype (LACM-AHF Poly 13267).

All thoracic notopodia of setigers 1–9 with 10–15 long capillaries in spreading fascicles; capillaries of neuropodia more numerous with up to 20–25 setae arranged in tight, dense fascicle. Noto- and neuropodia of setigers 10–13 with both capillaries and acicular spines in two transverse rows forming cinctures similar to those of some cirratulid polychaetes; cinctures partial on setiger 10, fully developed on setigers 11–13. Spines present in anterior or first row of setae and more numerous capillaries in posterior row. Acicular spines thickened, tapering to narrow pointed tip (Fig. 7D), aristate spines not observed; capillaries thin, narrowing to long fine tip (Fig. 7E). Far posterior bulbous section oval-shaped, with dorsal groove and terminal anal opening; with three parapodia, each bearing 1–2 hooked spines in each ramus. Each spine short, with curved with narrow blunted tip (Fig. 7F).

Methyl Green staining. Prostomium and both peristomial rings staining intensely with unstained grooves between, producing distinct pattern; laterally, first eight setigers staining intensely between parapodia, also producing pattern; areas where setae emerge not staining. Rest of body not retaining stain, no pattern.

Remarks. *Heterospio canariensis* **n. sp**. is characterized by having: (1) two peristomial rings where the first is narrow and ventrally forms the anterior lip of the mouth, (2) a dorsal crest that extends from the prostomium posteriorly to about setiger 2, (3) a ventral crest or ridge that extends from the posterior lip of the mouth to about setiger 6, (4) only a single pair of branchiae (setiger 2), (5) setiger 9 is the first long setiger and is about as long as the preceding setigers 5–8, (6) acicular spines are simple and first present from setiger 10, and (7) the posterior bulbous section has at least three parapodia each with 1–2 curved hooked spines. No other species of *Heterospio* has this combination of characters.

Etymology. The epithet is derived from the type locality off the Canary Islands.

Distribution. Eastern North Atlantic Ocean, off Canary Islands, 2351–2988 m.

Heterospio dibranchiata new species

Figures 8–9

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Material examined. (*40 specimens*) **Gulf of Mexico, off Louisiana. Matterhorn Platform Survey,** coll. J. A. Blake, Chief Scientist. **Sta. M-5S**, 10 Nov 2008, BC, 28.724°N, 88.826°W, 955 m, **holotype** (MCZ 163727), 9 **paratypes** (MCZ 163728); **Sta. M-1S**, 10 Nov 2008, BC, 28.739°N, 88.826°W, 875 m (2, MCZ 163729); **Sta. M-2S**, 10 Nov 2008, BC, 28.738.738°N, 88.826°W, 878 m, 1 **paratype** (MCZ 163730); **Sta. M-3S**, 10 Nov 2008, BC, 28.737°N, 88.826°W, 884 m, 2 **paratypes** (MCZ 163731); **Sta. M-4S**, 10 Nov 2008, BC, 28.733°N, 88.826°W, 908 m, 1 **paratype** (MCZ 167732); **Sta. M-1E**, 10 Nov 2008, BC, 28.742°N, 88.822°W, 867 m, 1 **paratype** (MCZ 163733); **Sta. M-2E**, 10 Nov 2008, BC, 28.742°N, 88.821°W, 867 m, 1 **paratype** (MCZ 163734); **Sta. M-3E**, 10 Nov 2008, BC, 28.742°N, 88.82°W, 868 m, 2 **paratypes** (MCZ 163735); **Sta. M-4E**, 10 Nov 2008, BC, 28.742°N, 88.815W 891 m (1, MCZ 163736); **Sta. M-5E**, 09 Nov 2008, BC, 28.742°N, 88.805°W, 921 m, 3 **paratypes** (MCZ 163737); **Sta. M-2N**, 10 Nov 2008, BC, 28.746°N, 88.826°W, 825 m (1, MCZ 163738); **Sta. M-4N**, 10 Nov 2008, BC, 28.752°N, 88.826°W, 821 m, 1 **paratype** (MCZ 163739); **Sta. M-3W**, 10 Nov 2008, BC, 28.742N, 88.831°W, 850 m, 2 **paratypes** (MCZ 163740); **Sta. M-4W**, 10 Nov 2008, BC, 28.742°N, 88.837° W, 839 m, 1 **paratype** (MCZ 163741).—**Virgo Platform Survey,** coll. J.A. Blake, Chief Scientist. **Sta. V-1E**, 11 Nov 2008, BC, 29.182°N, 88.164°W, 340 m (1, MCZ 163742); **Sta. V-1W**, 11 Nov 2008, BC, 29.185°N, 88.172°W, 340 m (1 post end MCZ 167743); **Sta. V-1N**, 11 Nov 2008, BC, 29.185°N, 88.171°W, 335 m (1, MCZ 163744).—**Matterhorn Gas Pipeline Survey,** coll. P.A. Neubert, Chief Scientist. **Sta. 2C**, 05 Jun 2009, BC, 28.872°N, 88.88°W, 533 m (3, MCZ 163745); **Sta. 6C**, 04 Jun 2009, BC, 28.872°N, 88.941°W, 282 m (1, MCZ 163746); **Sta. 8C**, 04 Jun 2009, BC, 28.863°N, 88.984°W, 241 m (1, MCZ 163747); **Sta. 9C**, 04 Jun 2009, BC, 28.897°N, 88.946°W, 229 m (2, MCZ 163748).—**Matterhorn Oil Export Pipeline Survey**, coll. J.A. Blake, Chief Scientist, Sta. 4, 10 Jul 2008, 28.821°N, 88.985W, 364 m (1, MCZ 154127).

Description. An elongate, threadlike species. Holotype (MCZ 163727) complete, with 27 setigers (9 thoracic, 15 abdominal, 3 on posterior section), 14.9 mm long, 0.1 mm wide across narrow thoracic setigers, 0.26 mm wide across middle abdominal segments, and 0.22 wide across bulbous posterior section (Fig. 8A). A smaller complete specimen (MCZ 163744) with 28 setigers (9 thoracic, 15 abdominal, 4 on posterior section), 7.27 mm long, 0.08 mm wide across thoracic setigers, 0.12 mm wide across abdominal segments, and 0.07 mm across posterior section. One small complete juvenile also present (see below). Paratypes and other specimens incomplete. Large paratype (MCZ

163735) with 13 setigers, 23.3 mm long, 0.21 mm wide across thoracic setigers, and 0.71 mm across abdominal segments; small paratype (MCZ 163728) with 13 setigers, 5.71 mm long, 0.15 across thoracic setigers, 0.12 across abdominal segments. Body divided into thoracic region with nine setigers, setigers 1–6 short, slightly wider than long; setigers 7–9 becoming progressively longer with setiger 7 about 2 times longer than setiger 6, setiger 8 about 3.5 times longer than setiger 6; setiger 9 greatly elongated, about 9 times longer than setiger 6. Color in alcohol opaque white to light tan; pigment entirely absent.

Pre-setiger region short, as long as first two thoracic setigers (Fig. 9A–C). Prostomium narrow, triangular, tapering to narrow apex (Fig. 9A–C); eyespots absent; nuchal organs distinct slits on posterior lateral margins (Fig. 9A–B). Dorsal surface with narrow ridge or crest extending from prostomium mid-dorsally over peristomium (Fig. 9B). Peristomium a single ring, interrupted dorsally by dorsal ridge (Fig. 9A–B). Mouth narrow vertical opening bordered anteriorly by three short narrow lobes, laterally by two large protruding lobulated lobes that could be mistaken for protruding proboscis, and posteriorly by 7–9 lobes connecting to elongate narrow ridge extending posteriorly over peristomium and setigers 1–2 (Fig. 9C). Dorsal tentacles observed on one specimen, arising in groove or notch lateral to dorsal crest; tentacles thickened filaments.

Branchiae present on setigers 2–3 (Figs. 8A–B, 9A–B) on all specimens examined except smallest juveniles, where present only on setiger 2; branchiae long, thin (Fig. 8B), rounded in cross section, tapering to rounded tip; each with narrow ciliated groove; internal blood vessel extends along entire length.

All parapodia biramous with setal fascicles arising from near anterior edge of segment. All thoracic setigers slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum and bearing setal fascicles in tight bundles. Abdominal setigers 10 and following round in cross section and bearing setae in transverse rows encircling each anterior end of segment. Abdominal parapodia from setiger 10 narrow elongate lobes, becoming thicker and more prominent from setigers 11–12; noto- and neuropodia with distinct dorsal and ventral gaps between setal fascicles; lateral gaps between noto- and neuropodia narrower.

Thoracic notopodia of setigers 1–9 with 10–15 long capillaries in spreading fascicles; capillaries of neuropodia more numerous, with up to 20–25 setae arranged in tight, dense fascicle. Noto- and neuropodia of setiger 10 with capillaries arranged in two elongate transverse rows with distinct dorsal and lateral gaps. Setiger 11 with notosetae of both rows all capillaries; neuropodia with anterior row of acicular spines and posterior row with capillaries; setiger 12 with both noto- and neuropodia with anterior row of acicular spines and posterior row of capillaries. Setiger 13 and all subsequent abdominal setigers (to setiger 24 in holotype) with both noto- and neuropodia with anterior row of acicular spines and posterior row of narrower spines with long aristate tip. Acicular spines thick, tapering to narrow pointed tip (Figs. 8D–E, 9D); aristate spines narrower than acicular spines, with long, tapering tip (Figs. 8D–E, 9E–G). Far posterior bulbous section of holotype oval-shaped (Fig. 8C), with terminal anal opening; with three parapodia, each bearing 1–2 hooked spines in each ramus; each spine short, with curved pointed tip (Fig. 8F).

Juvenile morphology. A complete juvenile with 28 setigers (MCZ 163745) with nine thoracic, 16 abdominal, and three posterior setigers; 4.94 mm long and 0.06 mm across anterior setigers; body consistently narrow except for bulbous posterior end. A pair of long branchiae present on setiger 2 but absent on setiger 3. Setigers 7, 8, and 9 longer than individual setigers 1–6, but setiger 9 not as long proportionately as in adults; all abdominal segments of a relatively equal length. A second complete juvenile from Sta. 6C (MCZ 163746) with 28 setigers: nine thoracic, 15 abdominal, and four posterior, measuring 3.3 mm long, 0.73 mm across thoracic setigers, 1.22 mm across abdominal setigers, and 0.91 across the posterior section. This second juvenile with abdominal segments contracted, thus appearing shorter. Posterior bulbous section of juveniles similar in appearance to that of adults. Transverse setal fascicles of abdominal segments greatly reduced in juveniles, restricted to simple noto- and neuropodia with fewer setae (4–6 spines per fascicle), but have same arrangement of acicular spines and aristate spines in two rows as in adults from setiger 13. Short curved hooks in posterior region of same morphology, arrangement, and number as in adults.

These observations suggest that full segmental complement of 27–28 or more setigers of *Heterospio dibranchiata* **n. sp**. develop early in juveniles and that subsequent growth involves elongation, enlargement, and elaboration of individual segments and parapodia as well as an increase in number of setae. It is likely that this same growth pattern occurs in all species of *Heterospio*.

Methyl Green staining. Body stains uniformly; weak staining of pre-setigerous region not prominent.

Remarks. *Heterospio dibranchiata* **n. sp**. is unusual within the genus in having only two pairs of branchiae (setigers 2–3); these branchiae are remarkably long, and when complete are as long as one-third or more of the body length.

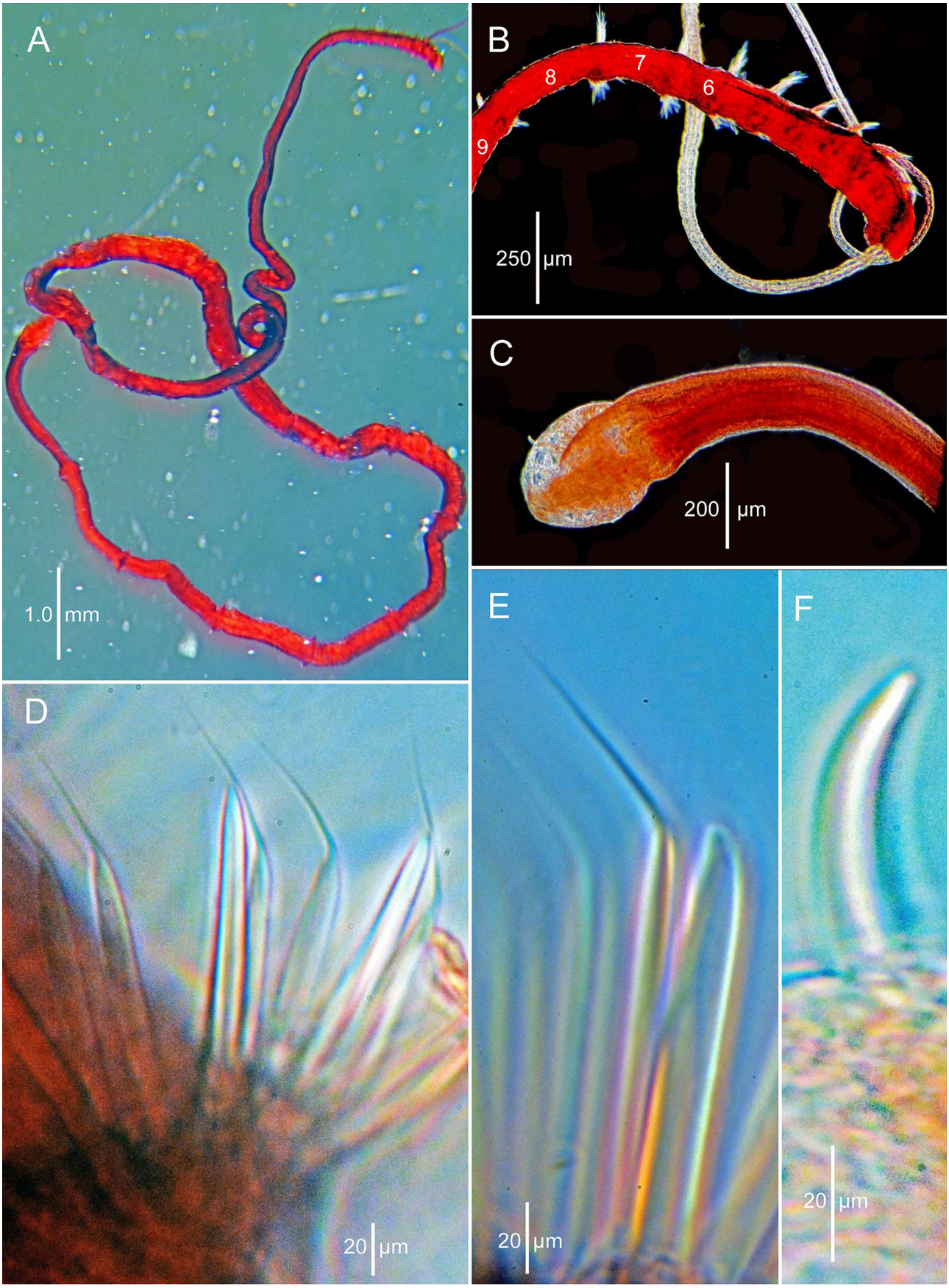

FIGURE 8. *Heterospio dibranchiata* **n. sp**. Holotype (MCZ 163727): A, entire worm; B, anterior end, right lateral view; C, posterior end, right lateral view; D, subuluncini setiger 16; E, subuluncini and acicular spine setiger 13; F, posterior hook. A–C, stained with Shirlastain A.

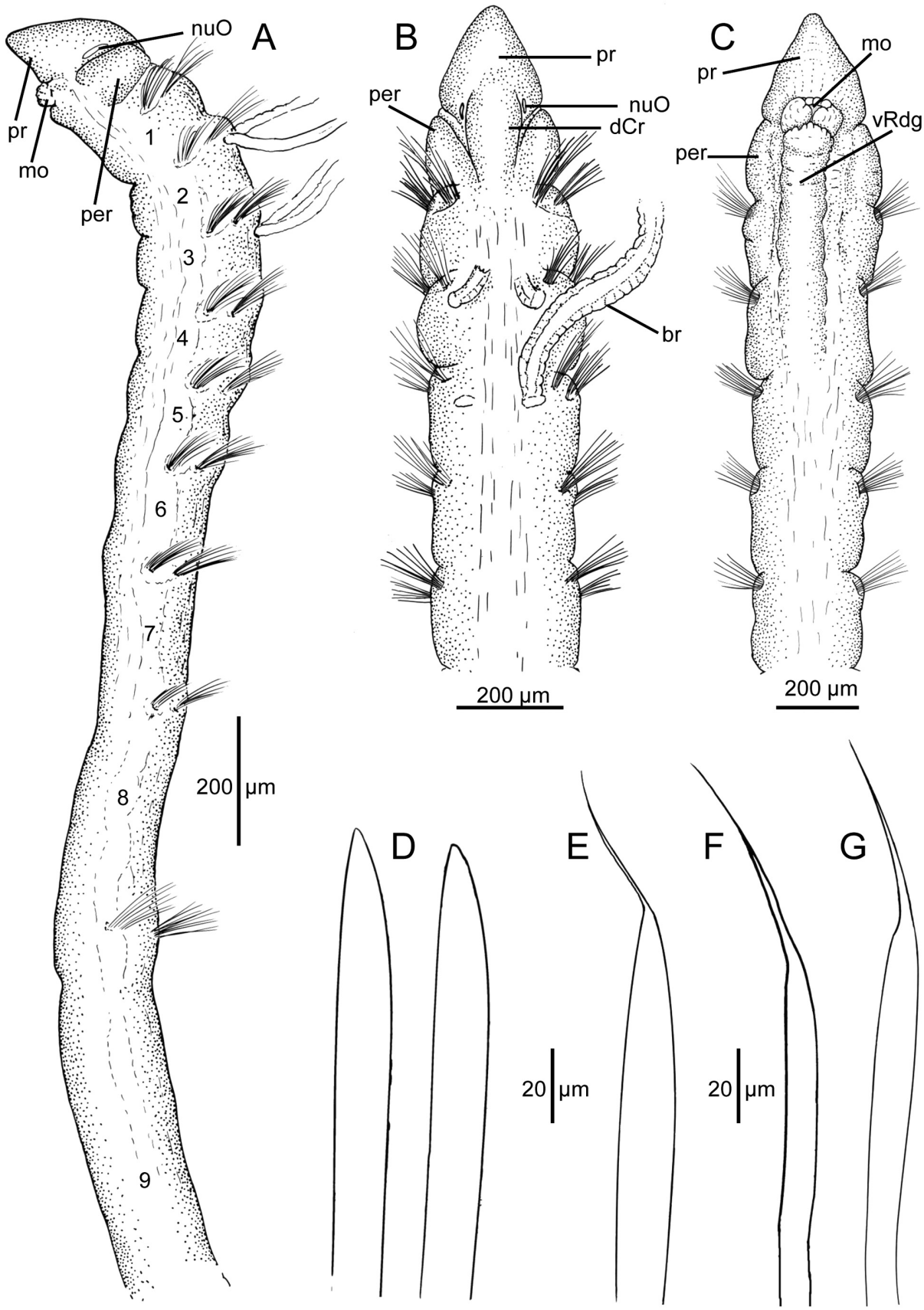

FIGURE 9. *Heterospio dibranchiata* **n. sp.** A, anterior end, left lateral view; B, anterior end, dorsal view; C, anterior end, ventral view; D, acicular spines; E–G, subuluncini. A, C, paratype (MCZ 163728), B, paratype (163735), D–G, holotype (MCZ 163727).

Other unusual characters include: (1) a conical prostomium with a narrow anterior apex and a posterior extension or caruncle that extends over the peristomium as a dorsal crest merging with setiger 1, (2) a single peristomial ring instead of two where the curved nuchal organs can be seen immediately anterior to the peristomium on the posterior lateral margin of the prostomium, (3) a notch on the anterior border of the peristomium where the dorsal tentacles are attached, (4) an unusual oral apparatus where a narrow vertical oral opening is bordered laterally by two large protruding lobes resembling a protruding pharynx, and (5) only six short thoracic segments with setigers 7, 8, and 9 becoming increasingly longer, and setiger 9 is as long as setiger 10 of other species. Other characters are more typical of known species, such as the first nine setigers (thorax) having widely spaced and well-defined noto- and neuropodia with setal fascicles in setiger 10 that transition to setae arranged in transverse rows across each noto- and neuropodia, nearly encircling the body; when spines are present, these encircling rows of setae resemble the cinctures of spines found in cirratulids of the genus *Chaetozone*. The hooked spines of the posterior bulbous section are similar to those reported for *H. hartmanae* **n. sp**. and others in this study. Another species in this study found to have only two pairs of branchiae and a single peristomial ring is *H. alata* **n. sp**. from off Brunei, Island of Borneo (see below). However *H. alata* **n. sp**. is one of only four known species to have neuropodial hooks on setiger 1, whereas *H. dibranchiata* **n. sp**. has only capillaries in that position.

Biology. The presence of four complete specimens in these samples is unusual for a species of *Heterospio* and likely represents the careful manner in which they were collected; gentle handling minimized fragmentation and damage (see Materials and methods).

Heterospio dibranchiata **n. sp**. was widely distributed in the various survey samples at the platform and pipeline locations ranging from 241**–**955 m. About a third of the specimens (10) were collected from a single sample at Station M-5S at a depth of 955 m, the deepest location from which the species was collected. Sediment grain size at Sta. M-5S was sand (1.86%), silt (34.00%), and clay (64.14%), with TOC at 1.24%. Station M-5S (955 m) was the only location where *H. dibranchiata* **n. sp**. was among the top 10 species. The station was dominated by aplacophoran molluscs, polychaetes including cirratulids, paraonids, and spionids, and a thyasirid bivalve mollusc (Blake *et al.* unpublished data).

Etymology. The epithet *dibranchiata* is from the Greek, *di*-, for two or double and *branchos* for gill in reference to this species having only two pair of branchiae.

Distribution. U.S. northern Gulf of Mexico, off Louisiana, 241–955 m.

Heterospio guiana new species

Figures 10–11

urn:lsid:zoobank.org:act:7D8FCC80-6876-4B88-A08F-85A01E3D1C1B

Heterospio longissima: Hartman 1965: 163–164 (in part). **Not** Ehlers 1874, 1875.

Material examined. (*10 specimens*) **Off Suriname (Dutch Guiana)**, coll. H.L. Sanders & R.R. Hessler, R/V *Chain*, Cruise 35, **Sta. DR 33**, 25 Apr 1963, AD, 07.867°N, 54.525°W to 07.917°N, 54.583°W, 520–550 m, **holotype** (LACM-AHF Poly 13268) and 9 **paratypes** (LACM-AHF Poly 13269).

Description. All specimens incomplete. Holotype (LACM-AHF Poly 13268) an anterior fragment with 11 setigers, 7.34 mm long and 0.50 mm across thoracic segments; 10-setiger paratype 7.12 mm long, 0.65 mm wide (Figs. 10B, 11A); 11-setiger paratype 7.54 mm long, 0.35 mm wide. Juvenile anterior fragment with 11 setigers, 3.1 mm long and 0.1 mm wide. Body long, narrow, threadlike; available anterior fragments divided into thoracic region of nine setigers, with first eight crowded, followed by setiger 9, a longer transitional segment about three times length of setiger 8 (Figs. 10A, 11A–B). Transition from thoracic segments with defined dorso-lateral setal fascicles to abdominal segments at setiger 10 denoted by entirely different setal arrangement with setae arising from broad cincture-like fascicles with rows of setae mostly surrounding anterior margin. Color in alcohol light tan, pigment entirely absent.

Pre-setiger region triangular in shape, about as long as first three thoracic setigers (Fig. 10A–C). Prostomium rhomboid to triangular shaped dorsally, triangular shaped ventrally, anteriorly tapering to narrow rounded tip; eyespots absent, nuchal organs narrow slits along posterior margin. Peristomium with two dorsolateral lobes separated by groove from which dorsal tentacles arise; no tentacles present but scars evident in grooves. Ventral surface relatively smooth, not crossed by peristomial grooves; mouth arising at level of first peristomial ring, consisting of simple opening between 6–8 lateral lobes (Fig. 10C); proboscis partially emergent on a few specimens.

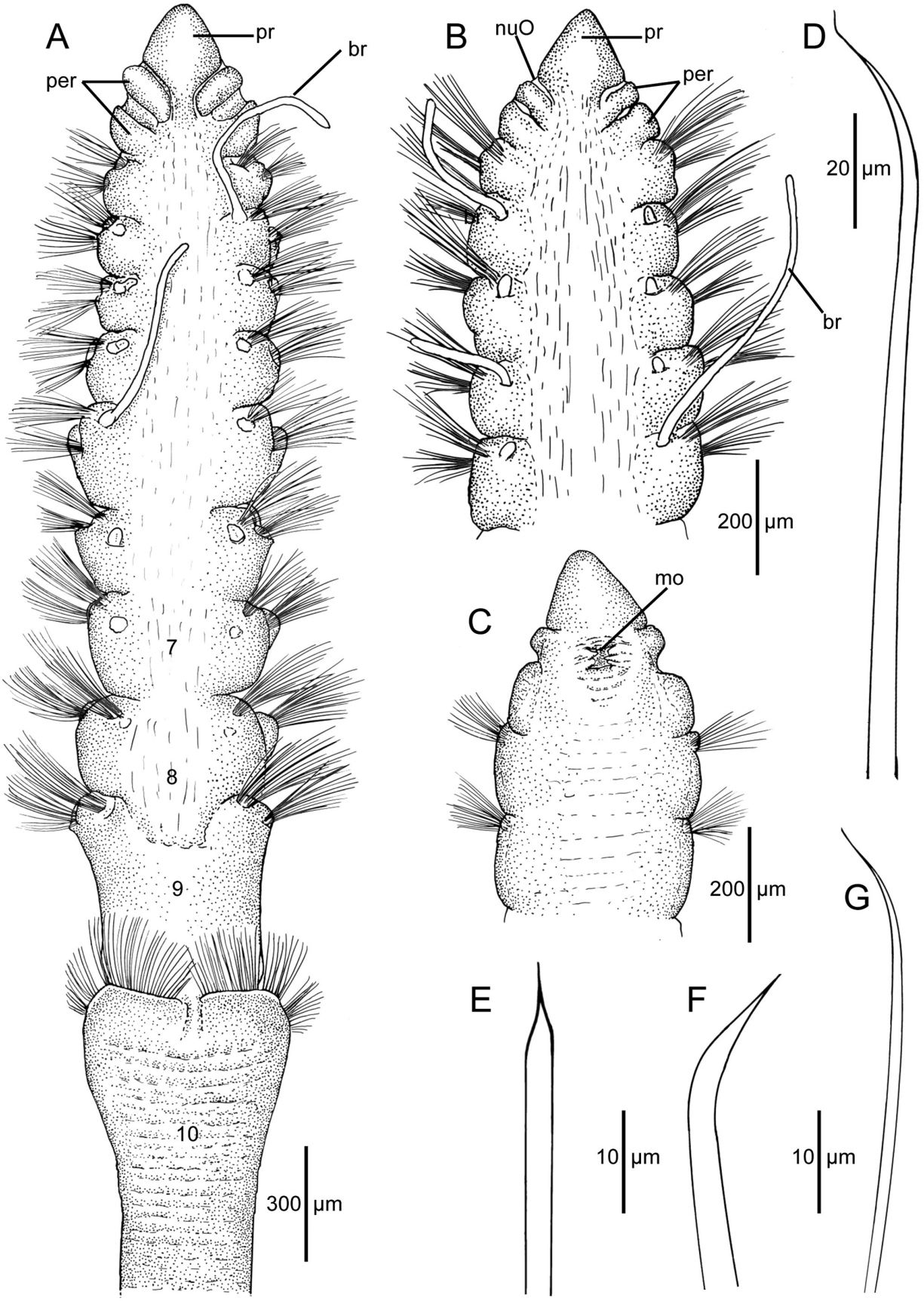

FIGURE 10. *Heterospio guiana* **n. sp**. A, anterior end (setiger 1–10), dorsal view; B, anterior end (setiger 1–5), dorsal view; C, anterior end, ventral view; D, neuropodial capillary, setiger 4; E–F, neuropodial subuluncini, setiger 12; G, neuropodial capillary setiger 12. A, C, paratype (LACM-AHF Poly 13268); B, D–G, holotype (LACM-AHF Poly 13269).

Branchiae or their stubs present on setigers 2–7 or 8 (Fig. 10A), not observed on setiger 9; when present, most branchiae long, thin, rounded in cross section, tapering to rounded tip; branchiae with narrow ciliated groove; internal blood vessel extends along entire length. Juveniles with branchiae observed only on setigers 2–4.

All parapodia biramous with setae near anterior edge of each segment. Thoracic setigers with dense fascicles in dorso-lateral locations on each segment (Fig. 11A, C); thoracic notosetae with numerous capillaries (ca. 50–60) in dense fascicles consisting of five or more curved setal rows; neurosetae similarly arranged with capillaries even more numerous (~75+) becoming thicker, almost spinous (Figs. 10D, 11C). Abdominal setigers from setiger 10 with setae arranged in long double rows almost entirely encircling body, with narrow dorsal, ventral, and lateral gaps approximating position of parapodia. Setiger 10 with all capillaries arranged in two rows; from setiger 11 anterior row of setae of noto- and neuropodia mostly thicker mucronate or subuluncinate spines (Figs. 10E–F, 11D), with posterior row consisting of thin capillaries (Figs. 10G, 11D); simple blunt-tipped spines not observed.

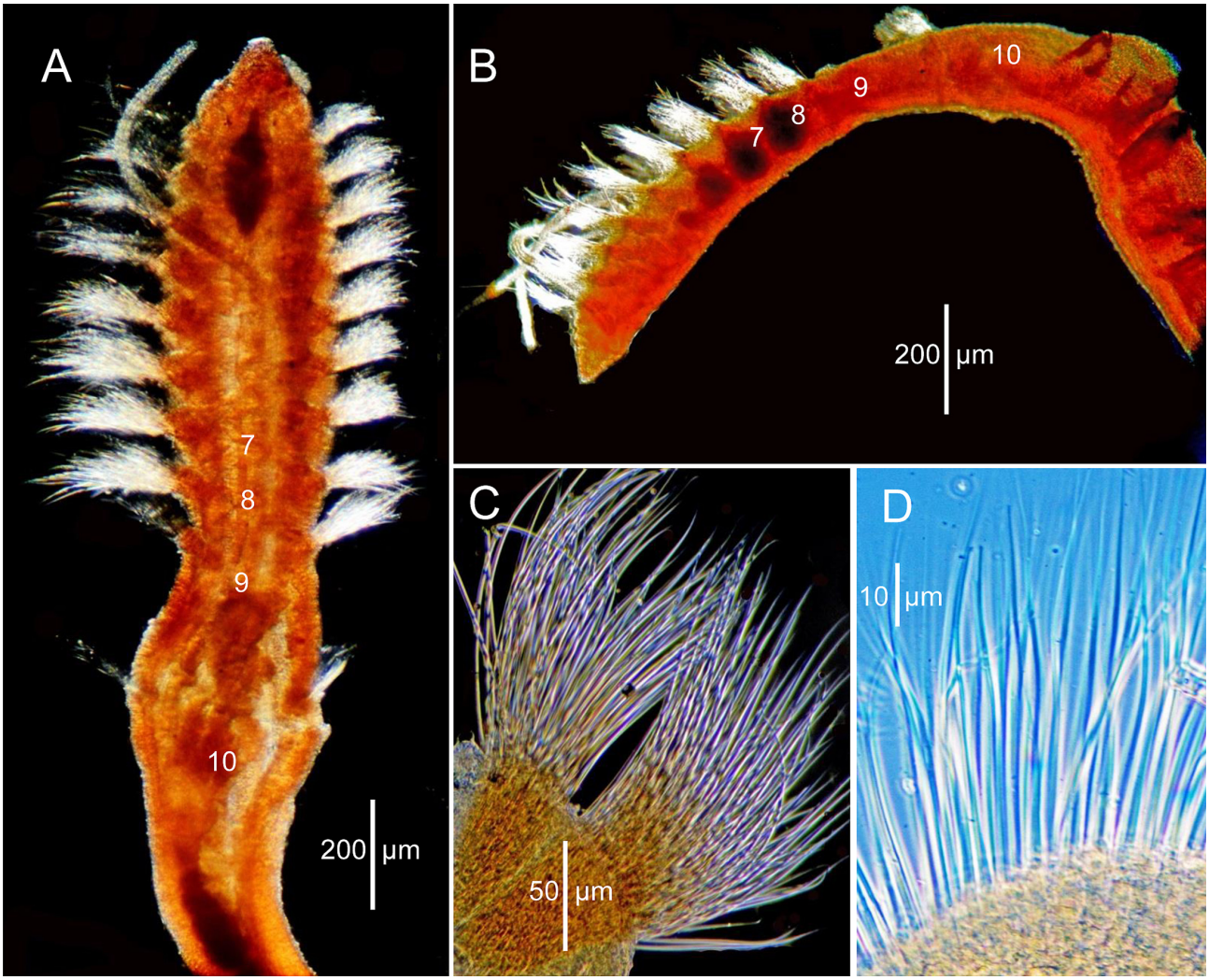

FIGURE 11. *Heterospio guiana* **n. sp**. A, anterior end, dorsal view; B, anterior end, left lateral view; C, setiger 4, anterior view; D, notopodial subuluncini and capillaries, setiger 12. A, holotype (LACM-AHF Poly 13268); B–D, paratype (LACM-AHF Poly 13269).

Posterior region not present among fragments.

Methyl Green staining. Posterior dorsal areas of prostomium and peristomial lobes retain stain; rest of body lacking distinct pattern.

Remarks. *Heterospio guiana* **n. sp**. most closely resembles the Iceland material described by Parapar *et al.* (2014) as *H. longissima sensu* Hartman and *H. paulolanai* **n. sp**. from off Brazil. However, as discussed above, Hartman's material is described herein as two different species, both of which are different than the one described by Parapar *et al.* (2014). One difference between *H. longissima sensu* Parapar *et al.* and *H. guiana* **n. sp**. is that there

are only seven pairs of branchiae on *H. guiana* **n. sp**. instead of eight; however, the missing pair may simply not be visible as scars or fully developed on the Suriname specimens. The main differences, however, between the two species are: (1) setiger 9 of *H. guiana* **n. sp**. is three times the length of setiger 8 instead of only twice the length, (2) dense fascicles of thick capillaries, which are most numerous on the neuropodia, occur on the thoracic parapodia of setigers 1–9 in *H. guiana* **n. sp**. rather than fewer capillaries in fan-shaped fascicles, and (3) abdominal setiger 10 of *H. guiana* **n. sp.** has encircling rows of capillaries whereas the Icelandic specimens have an anterior row of subuluncini and a posterior row of capillaries; subuluncini do not begin until setiger 11 on *H. guiana* **n. sp**.

Heterospio guiana **n. sp**. is also similar to *H. paulolanai* **n. sp**. The two species differ in that in *H. guiana* **n. sp**. setiger 9 is three times longer than setiger 8, branchiae occur on setigers 2–7, the mouth is a simple opening between 6–8 small lateral lobes, and setigers 11–12 have aristate spines in the anterior row of setae and capillaries in the second, whereas in *H. paulolanai* **n. sp**. setiger 9 is 2.5 times longer than setiger 8, branchiae occur on setigers 2–8, the mouth is a transverse slit between two large lateral lobes, setiger 11 has aristate spines and capillaries, and setiger 12 has acicular spines in the first setal row and subuluncini and capillaries in the second row.

Etymology. Named for the location of this species in the Guiana region of South America.

Distribution. Off northeastern South America, Suriname, in upper continental slope depths, 520–550 m.

Heterospio southwardorum new species

Figure 12

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Material examined. NE Atlantic Ocean, Bay of Biscay, off Bilbao, Spain, R/V *Sarsia*, Cruise 5, **Sta. 5-56**, 19 Jul 1967, coll. A. & E. Southward, EBS, 43.717°N, 03.797°W, 641 m, **holotype (**LACM-AHF 13283).

Description. A moderately sized species, holotype **(**LACM-AHF 13283) incomplete with 13 setigers, 21.3 mm long, 0.43 mm wide across thoracic segments, 0.37 mm wide across middle abdominal segment. Thorax with eight crowded segments followed by elongate setiger 9. Setigers 1–7 twice as wide as long; setiger 8 slightly longer, about as wide as long; setiger 9 greatly elongated, as long as setigers 1–8 combined. Abdominal setigers 10–13 long, narrow, encompassing about 16 mm of total length of holotype. Color in alcohol opaque white to light tan; pigment entirely absent.

Pre-setiger region short, as long as first two thoracic setigers (Fig. 12A–B). Prostomium flattened, disk-like, broadly rounded anteriorly (Fig. 12A–B); eyespots absent; nuchal organs elongate slits anterior to anterior peristomial ring (Fig. 12A). Peristomium with two rings; first ring narrow, dorsally visible posterior to nuchal organs, not continuing ventrally; second ring large, similar in size and shape to following setigers, interrupted by broad dorsal crest that merges with setiger 1 (Fig. 12A), entire on ventral surface, interrupted by mouth (Fig. 12B). Dorsal tentacles not present, but scars evident in notch between peristomial rings. Mouth a triangular-shaped opening surrounded laterally by thickened lobes (Fig. 12B); proboscis not everted.

Branchiae or their stubs present on setigers 2–7 (Fig. 12A); intact branchiae short, oval-shaped. All parapodia biramous with setal fascicles arising from near anterior edge of segment. Thoracic region with eight short setigers (Fig. 12A), each slightly wider than long; setiger 8 slightly longer than those preceding. Setiger 9 elongated, as long as setigers 1–8 combined. All thoracic setigers slightly flattened dorsally with notopodia of setigers 1–7 weakly inflated and elevated over dorsum; notopodia of setigers 8–9 with thickened lobes from which setae arise; neuropodia of setigers 1–9 with short, postsetal lobes (Fig. 12B), most evident on setigers 1–7. Abdominal segments from setiger 10 rounded in cross section with parapodia on anterior borders as transverse ridge encircling body, producing cinctures or rows of setae similar to those of some cirratulids; these ridges interrupted dorsally, ventrally, and laterally denoting location of noto- and neuropodia.

All thoracic notopodia of setigers 1–9 with 12–16 long capillaries in spreading fascicles; capillaries of neuropodia more numerous, with 25–30 arranged in tight, dense fascicle. Setae of noto- and neuropodia of following setigers in two transverse rows; setigers 10–11 all capillaries, rows with distinct dorsal and lateral gaps; setiger 12 with all capillaries in notopodia and a few acicular spines in anterior row of neuropodia; setiger 13 with cinctures of 10–12 spines in anterior row and 25–30 capillaries (Fig. 12C) in posterior row; capillaries with thin fine tip; spines flattened, tapering to narrow pointed tip, none with aristate tip (Fig. 12D).

Posterior bulbous section not present.

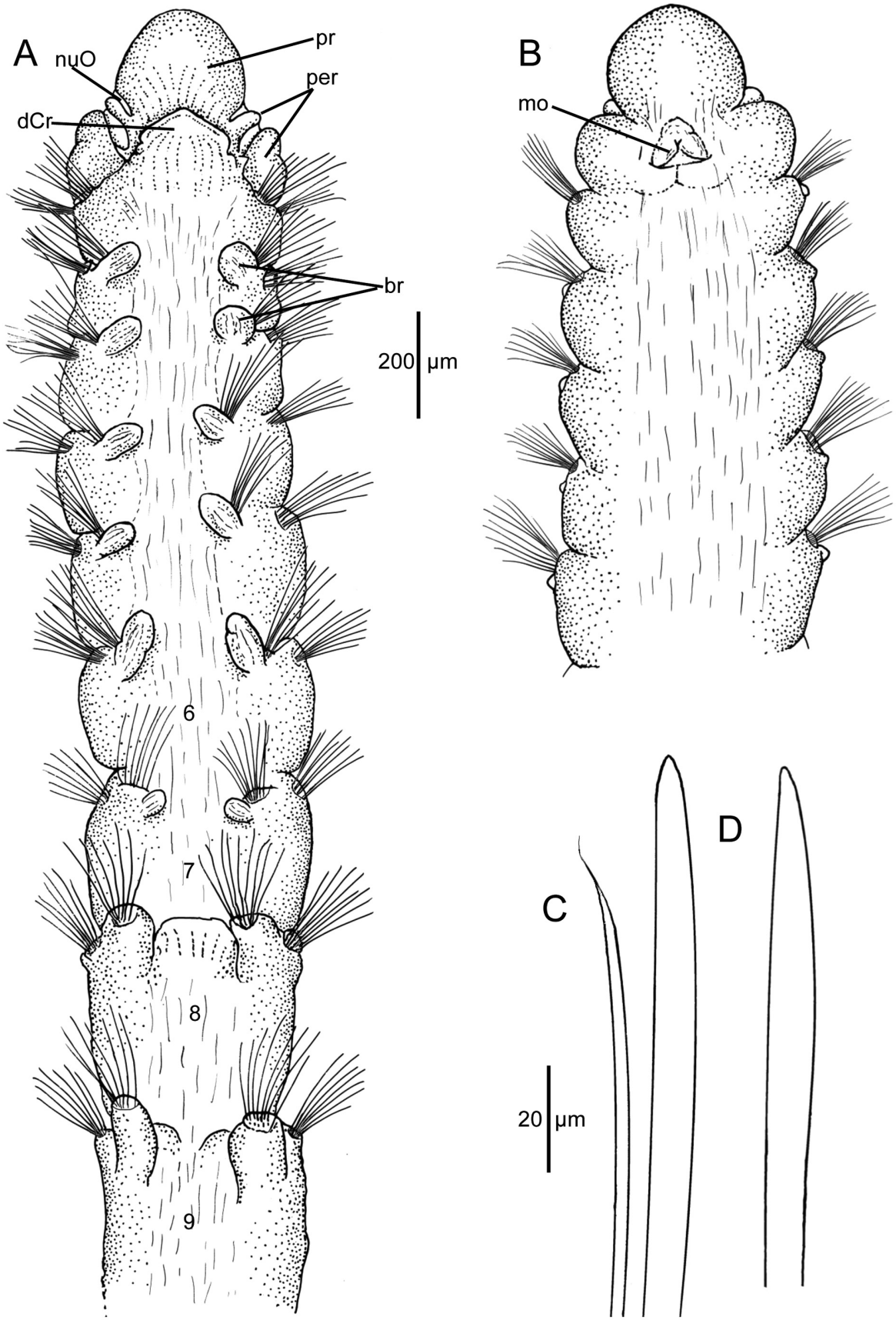

FIGURE 12. *Heterospio southwardorum* n. sp. Holotype (LACM-AHF Poly 13283): A, anterior end (setiger 1–9), dorsal view; B, anterior end (setiger 1–5), ventral view; C, capillary neuroseta, setiger 13; D, acicular spines, setiger 13.

Methyl Green staining. No pattern, stain not concentrated anywhere along body.

Remarks. *Heterospio southwardorum* **n. sp**. is most similar to *H. mediterranea*. Both species have a broad disk-like prostomium, two peristomial rings, dorsal peristomial crest, and in both species setiger 9 is the first elongate segment, being as long as setigers 1–8 combined. The two species differ in that in *H. southwardorum* **n. sp**. the first peristomial ring is narrow and separated from the prostomium by the nuchal groove, branchiae are present on setigers 2–7, capillary setae are present on setigers 10–11, with acicular spines first present on setigers 12–13, and subuluncini are absent. In contrast, *H. mediterranea* has both peristomial rings of an equivalent size, branchiae are present on setigers 2–8, and capillary setae are present on setigers 10–12, with acicular spines and subuluncini first present from setiger 13. See Table 1 for further comparison of *H. southwardorum* **n. sp**. with its congeners.

Etymology. This species is named for the late Drs. Alan and Eve Southward, prominent marine zoologists who directed the R/V *Sarsia* cruise in the Bay of Biscay during which this species was collected. Dr. Eve Southward was a deep-sea biologist and an authority on annelids of the family Siboglinidae.

Distribution. North Atlantic Ocean, Bay of Biscay off Spain, 641 m.

Species of *Heterospio* from the South Atlantic Ocean

Heterospio paulolanai new species

Figure 13

urn:lsid:zoobank.org:act:9D2C1C8E-4088-4EA7-B564-EAFB7B64AA2E

Material examined. **South Atlantic Ocean, Brazil, offshore São Paulo, *Súeste* IV, Sta. 6672**, coll. 14 Nov 1985, 24.735°S, 45.917°W, 69 m, mud and shell gravel, **holotype** (MZUSP 5588).

Description. Holotype (MZUSP 5588) only specimen, incomplete with 12 setigers, long, narrow, 27 mm long, 1.0 mm wide across thoracic setigers, 0.8 mm wide across abdominal segments. Specimen with some segments (setigers 1, 9, and 11) damaged, partially dissected by a previous worker. Thoracic region with nine setigers, 1–8 short, 9 transitional, about 2.5 times as long as setiger 8 (Fig. 13A). Thoracic segments with defined dorso-lateral setal fascicles transitioning to abdominal segments with setae arising from broad cincture-like fascicles with rows of setae mostly surrounding anterior margin of each segment, but with wide dorsal and ventral gaps. Abdominal segments 10–12 very long, each longer than entire thoracic region. Color in alcohol brown.

Pre-setiger region triangular in shape, about as long as first two thoracic setigers (Fig. 13A–B). Prostomium rhomboid-shaped, tapering to rounded tip (Fig. 13A); eyespots absent, nuchal organs narrow slits laterally at posterior junction of prostomium and peristomium (Fig. 13A). Peristomium with two dorsolateral rings apparent dorsally and laterally, separated by groove from which dorsal tentacles arise medially; no tentacles present, but scars evident in grooves. Peristomium incomplete dorsally, interrupted by posterior extension of prostomium merging with dorsal surface, dorsal crest lacking. Ventral surface of peristomium broad a single broad surface, anteriorly encompassing mouth, merging posteriorly with broad ventral surface of thoracic segments (Fig. 13B). Mouth a transverse slit consisting of simple opening between two large lateral lobes and simple anterior and posterior lips (Fig. 13B).

Branchiae or their stubs present on setigers 2–8 (Fig. 13A), not observed on setiger 9 possibly due to damage from an earlier dissection; most branchiae when present long, thin, rounded in cross section, tapering to rounded tip; branchiae with narrow ciliated groove; internal blood vessel extends along entire length.

All parapodia biramous with setae emerging from near anterior edge of each segment (Fig. 13A–B). Thoracic setigers with notches from which dense setal fascicles in dorsolateral locations arise on each segment; postsetal lamellae not observed, but short elevated ridge present on posterior margin of notch from which thoracic neurosetae arise; thoracic notosetae with numerous capillaries (25+) in dense fascicle with distinct rows not defined; neurosetae similarly arranged with capillaries even more numerous (~60+). Abdominal setigers from setiger 10 with setae arranged in long double rows nearly surrounding body, with relatively wide dorsal and ventral gaps. Setiger 10 with all capillaries arranged in two rows; setiger 11 with anterior row of aristate spines (Fig. 13C) and posterior row consisting of thickened capillaries (Fig. 13D); setiger 12 with anterior row of acicular spines (Fig. 13E) and posterior row of thick, curved, pointed subuluncini (Fig. 13F).

Posterior region not present.

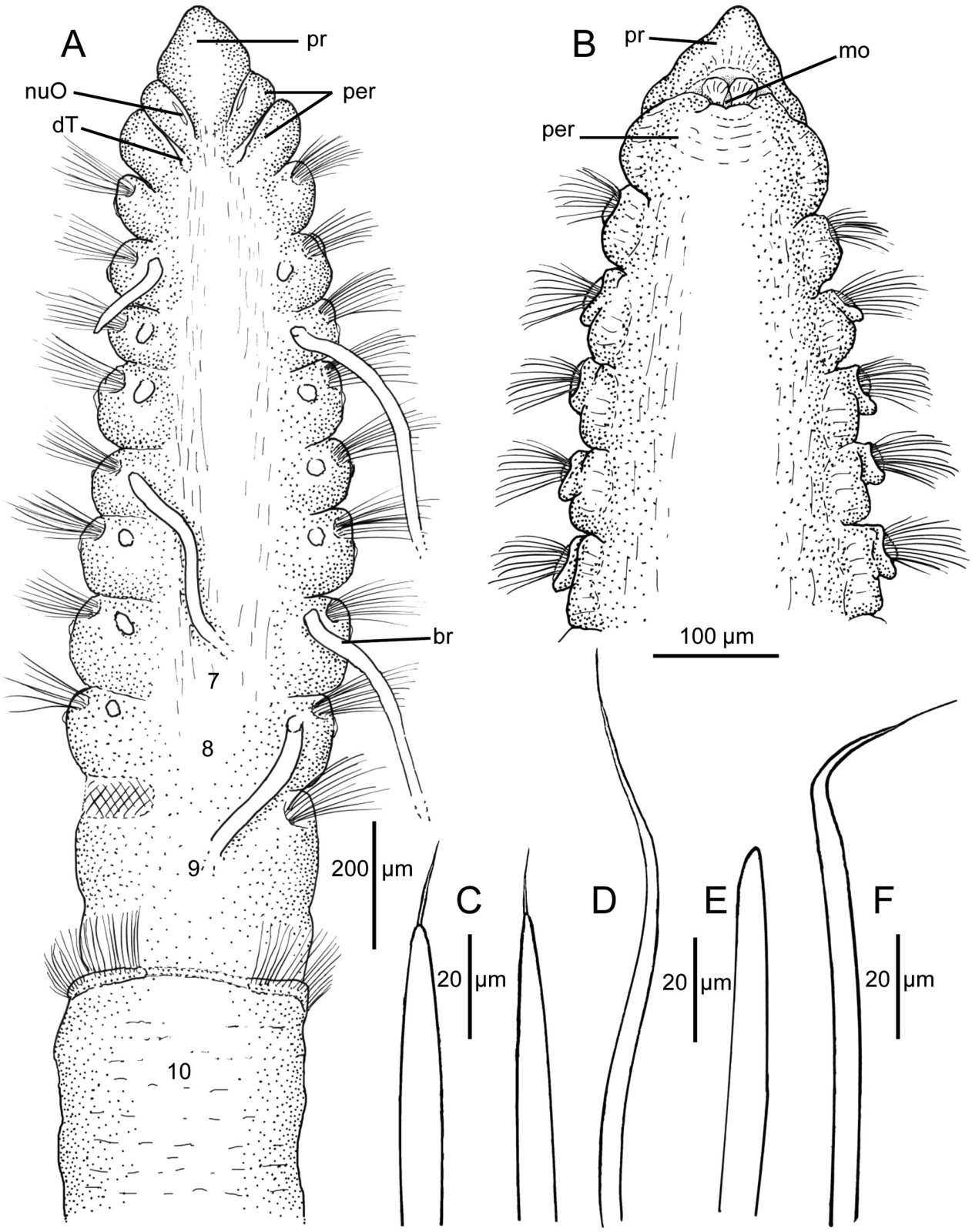

FIGURE 13. *Heterospio paulolanai* **n. sp**. Holotype (MZUSP 5588): A, anterior end (setiger 1–10), dorsal view; B, anterior end (setiger 1–5), ventral view; C, neuropodial aristate spines, setiger 11; D, neuropodial capillary seta, setiger 11; E, neuropodial acicular spine, setiger 12; F, neuropodial subuluncinus, setiger 12.

Methyl Green staining. Methyl Green producing prominent pattern on pre-setiger and anterior thoracic segments. Stain concentrates on posterior and lateral margins of prostomium and both peristomial rings on dorsal and lateral surfaces. Stain also concentrates laterally on setigers 1–5 producing dark-green parapodia. Rest of body lacking distinct pattern.

Remarks. *Heterospio paulolanai* **n. sp**. belongs to a group of *Heterospio* having a narrow conical prostomium, two peristomial rings, 7–8 pairs of branchiae, and setiger 9 as the first elongate segment about 2–3 times longer than setiger 8. Of these, *H. paulolanai* **n. sp**. is most similar to *H. aruba* **n. sp**., *H. guiana* **n. sp**., and *H. sinica* in having all capillaries on setiger 10 and following setigers with at least a few aristate spines. However, *H. aruba* **n. sp**. and *H. paulolanai* **n. sp**. also have acicular spines that are lacking in *H. guiana* **n. sp**. and *H. sinica*. *Heterospio aruba* **n. sp**. differs from *H. paulolanai* **n. sp**. in having prominent postsetal lamellae on thoracic neuropodia, an oral opening that is a narrow transverse slit with no obvious lobes or surrounding papillae, and a distinct ventral ridge that extends from the mouth posteriorly over the peristomium and first seven setigers. In contrast, *H. paulolanai* **n. sp**. has no obvious thoracic neuropodial lamellae, an oral opening bordered by two large lateral lobes, and no ventral ridge.

Etymology. This species is named for the late Professor Paulo da Cunha Lana, prominent Brazilian authority on annelids. Prof. Lana was host of the sixth International Polychaete Conference held in Curitiba, Brazil (Aug 2–7, 1998) and later elected the ninth President of the International Polychaetology Association (2010–2013).

Distribution. Off southeastern Brazil, 69 m.

Species of *Heterospio* from the Pacific Ocean and Adjacent Seas

Heterospio alata new species

Figures 14–15

urn:lsid:zoobank.org:act:928F46F1-0540-4698-AD4D-D0A209AC23F8

Material examined. (*16 specimens*) **South China Sea, off Brunei, Island of Borneo**, **Site CA1,** R/V *Emma*, coll. J.A. Blake, Chief Scientist, BC, **Sta. 55**, 01 Jun 2011, 5.728°N, 114.246°E, 1150 m, **holotype** (MCZ 163704); 1 **paratype** (MCZ 163705); **Sta. 10**, 06 Jun 2011, 5.865°N, 114.209°E, 1453 m (1, MCZ 163706); **Sta. 44**, 02 Jun 2011, 5.472°N, 114.153°E, 1294 m, 1 **paratype** (MCZ 163707); **Sta. 46**, 02 Jun 2011, 5.801°N, 114.303°E, 1234 m, 2 **paratypes** (MCZ 163708); **Sta. 48**, 02 Jun 2011, 5.758°N, 114.257°E, 1219 m, 3 **paratypes** (MCZ 163709); **Sta. 49**, 02 Jun 2011, 5.740°N, 114.233°E, 1199 m, 1 **paratype** (MCZ 163710); **Sta. 53**, 01 Jun 2011, 5.679°N, 114.193°E, 1212 m 1 **paratype** (MCZ 163711); **Sta. 54**, 09 Jun 2011, 5.703°N, 114.220°E, 1171 m (1 juv, MCZ 163712); **Sta. 58**, 01 Jun 2011, 5.727°N, 114.272°E, 1127 m 1 **paratype** (MCZ 163713); **Sta. 59**, 31 May 2011, 5.433°N, 114.162°E, 1114 m (1 juv, MCZ 163714).—**Site CA2**, R/V *Emma*, coll. P.A. Neubert, Chief Scientist, BC, **Sta. TU3**, 24 Jun 2011, 19.898°N, 113.747°E, 1267 m, 1 **paratype** (MCZ 163715); **Sta. TU5**, 24 Jun 2011, 5.231°N, 113.747°E, 1224 m, 1 **paratype** (MCZ 163716).

Description. A moderately sized species, most specimens incomplete, one small specimen complete in two parts. Body elongate, narrow, anterior crowded segments slightly narrower than thicker elongate abdominal segments; posterior fragments with bulbous posterior end. Holotype (MCZ 163704) an anterior fragment with 16 setigers, 14.8 mm long, 0.22m wide across thorax; 0.24 wide across abdomen; paratype (MCZ 163708): 13 setigers, 11.6 mm long, 0.24 across thorax; 0.29 across abdomen; small paratype (Sta. 49): 15 setigers, 5.8 mm long, 0.13 mm wide across thorax, and 0.15 mm across abdomen. One small paratype (MCZ 163708) complete, in two parts with 24 setigers: 14.4 mm long, 0.12 mm wide across thorax; 0.15 mm wide across abdominal setigers (includes nine thoracic, 11 abdominal, and a bulbous posterior section with four setigers with hooks). Color in alcohol light tan; pigment entirely absent.

Pre-setiger region triangular in shape, short, about as long as first two thoracic setigers (Figs. 14A–C, 15B). Prostomium pear-shaped or triangular, tapering to narrow rounded tip; eyespots absent, nuchal organs narrow slits along posterior margin (Fig. 14C). Peristomium with a single large achaetous ring, complete ventrally, but interrupted dorsally by narrow dorsal crest extending from prostomium to border of setiger 1 (Figs. 14A, C, 15B). Dorsal tentacles absent; scars not clearly evident, but likely in notch between dorsal crest and anterior borders of peristomium. Mouth arising ventrally at posterior margin of prostomium, consisting of narrow vertical slit between four lateral lobes (Fig. 14B); proboscis sometimes present as rounded lobes.

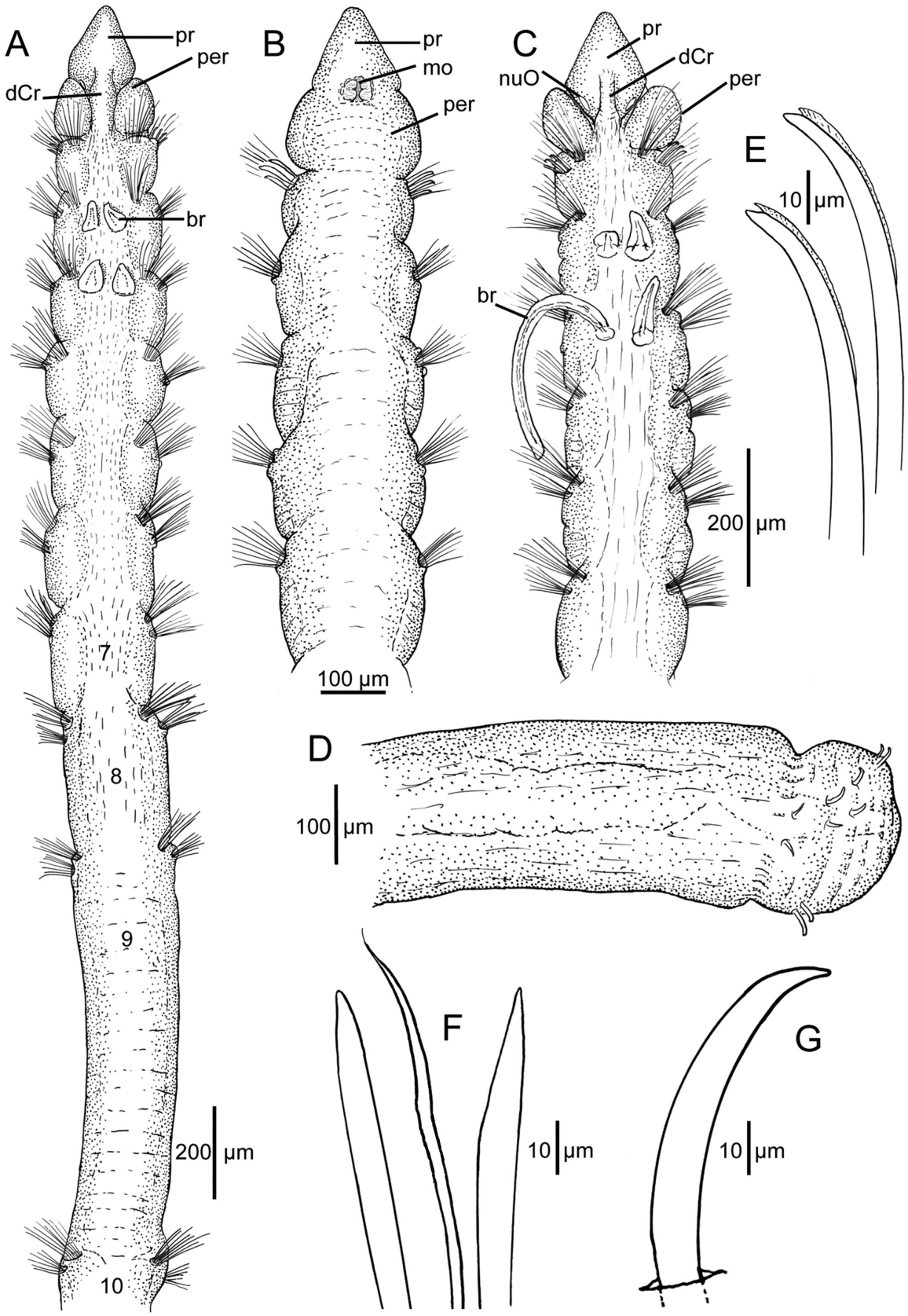

FIGURE 14. *Heterospio alata* **n. sp**. A, anterior end (setiger 1–10), dorsal view; B, anterior end (setiger 1–5), ventral view; C, anterior end (setiger 1–6), dorsal view; D, posterior end, left lateral view; E, neuropodial hooked spines, setiger 1; F, acicular spines and capillary (setiger 11); G, hook from posterior bulbous section. A–B, holotype (MCZ 163704); C–G, paratype (MCZ 163716).

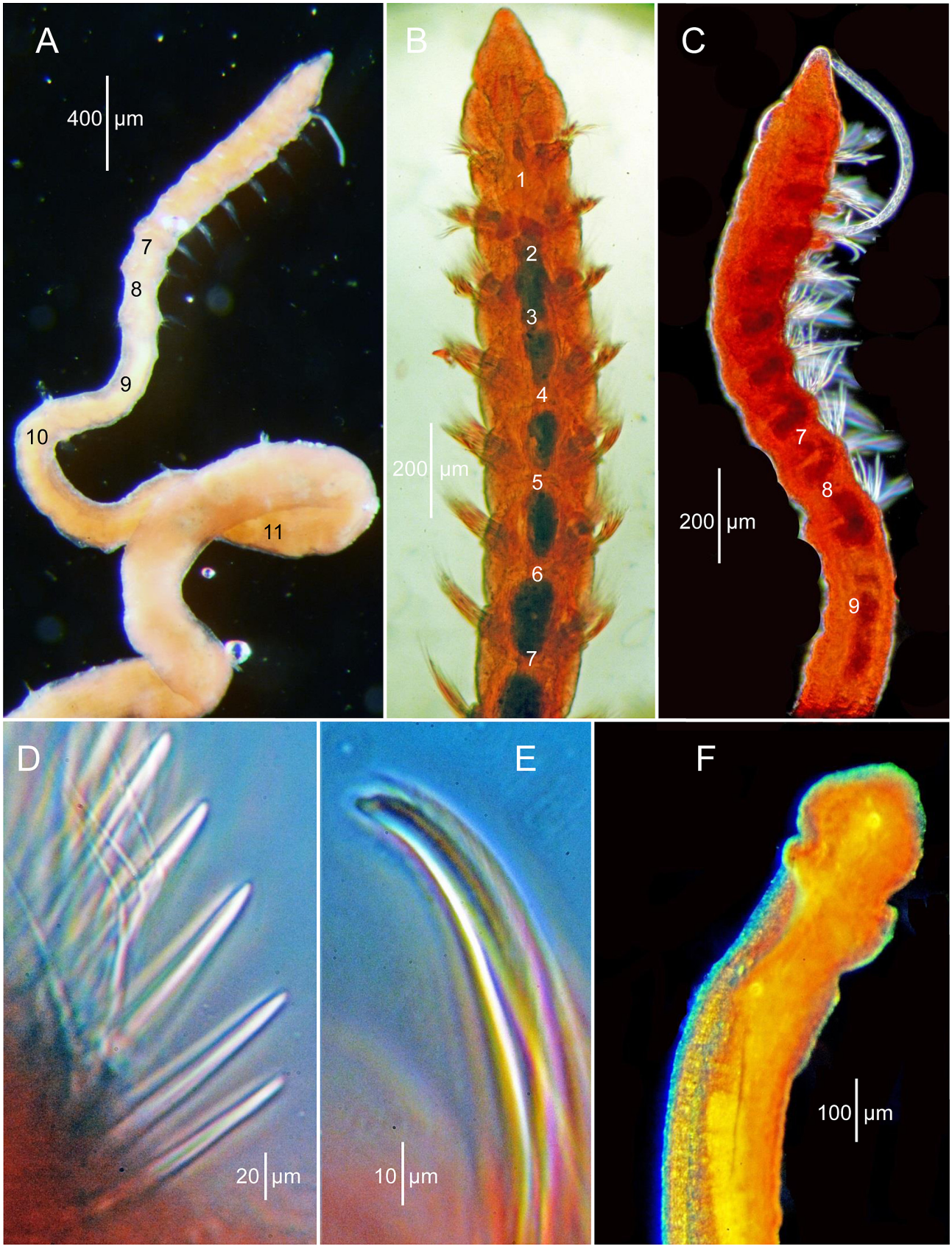

FIGURE 15. *Heterospio alata* **n. sp**. A, anterior and middle segments (setiger 1–11), lateral view; B, anterior end (setiger 1–7), dorsal view; C, anterior end (setiger 1–9), left lateral view; D, neuropodial acicular spines and capillaries, setiger 11, E, neuropodial hook from setiger 1; F, posterior end, left lateral view. A, F, paratype (MCZ 163707); B, holotype (MCZ 163704); C, paratype (MCZ 163710); D–E, paratype (MCZ 163708).

Thoracic region defined by eight short crowded setigers followed by elongate setiger 9 about as long as setigers 1–7 (Fig. 14A). Transition from thoracic segments with defined dorsolateral setal fascicles to abdominal segments denoted by setae arising from broad cincture-like rows mostly surrounding anterior margin of each segment occurs at setiger 11.

Branchiae or their stubs present on setigers 2–3 (Fig. 14A, C) not observed on subsequent segments; most branchiae when present short, thick, but with a few longer, thin, rounded in cross section, tapering to rounded tip (Fig. 15A, C).

All parapodia biramous with setae emerging from near anterior edge of each segment. Thoracic setigers 1–10 with dense fascicles of setae in dorsolateral locations on each segment; thoracic notosetae numerous capillaries in dense fascicles consisting of five or more curved rows; neurosetae of setiger 1 with about six curved bidentate spines (Fig. 14E) and an equivalent number of capillaries; neurosetae of setigers 2–10 numerous capillaries. Bidentate hooks of setiger 1 curved, tapering to pointed tip; apical tooth an extension of a flange or crest occurring along convex side of shaft and extending over curved tip or main tooth (Figs. 14E, 15E). Abdominal setigers from setiger 11 with parapodia as low ridges bearing setae arranged in long double rows almost entirely surrounding body; with dorsal, ventral, and lateral gaps approximating separate noto- and neuropodia; anterior row with about 12–15 acicular spines (Figs. 14F, 15D) per noto- or neuropodium; posterior row with numerous capillaries (Fig. 14F); acicular spines flattened, tapering to narrow tip (Figs. 14F, 15D); aristae not evident on any spines.

Posterior region a short rounded bulbous section, about as long as wide, distinctly set off from elongate abdominal segments by a groove (Figs. 14D, 15F); bearing four setigers each with a pair of curved hooks with pointed tips (Figs. 14G, 15E).

Methyl Green staining. No pattern.

Remarks. *Heterospio alata* **n. sp**. is the third of four species of the genus to be reported with neuropodial hooked spines on setiger 1. The first was *H. catalinensis* (Hartman, 1944) from southern California in shelf depths (Hartman 1944, 1957). The second species was *Heterospio* sp. A reported by Uebelacker (1984) from the Gulf of Mexico. The fourth is *Heterospio bidentata* **n. sp**. described from abyssal depths of eastern Australia (see below). Of these, *H. catalinensis* and *H.* sp. A have unidentate spines on setiger 1, whereas *H. bidentata* **n. sp**. and *H. alata* **n. sp**. both have bidentate spines. In *H. bidentata* **n. sp**. the apical tooth is a distinct secondary tooth arising directly from the shaft; whereas in *H. alata* **n. sp**. the apical "tooth" is an extension of a flange or crest that occurs along the convex side of the shaft and extends over the curved tip or main tooth of the hook providing the bidentate appearance. This type of hook is remarkably similar to the "*alate*" hooks found in some species the cirratulid genus *Caulleriella* (see Blake 2021b).

Other characters more or less limited to *H. alata* **n. sp**. include having only two pairs of branchiae on setigers 2–3, a single peristomial ring interrupted dorsally by a narrow dorsal crest, and the shift to cincture-like rows of noto- and neurosetae including acicular spines not occurring until setiger 11 rather than the more typical setiger 10.

Biology. *Heterospio alata* **n. sp**. was relatively rare throughout the two survey sites. Most of the specimens occurred at the CA1 survey site at Stations 46, 48, and 55 in sediment having 99% fine sediments (silt + clay) with the following grain size and TOC results by percent: Sta. 46: sand (1%), silt (79%), clay (20%), TOC (1%); Sta. 48: sand (4%), silt (73%), clay (26%), TOC (4%); Sta. 55: sand (1%), silt (52%), clay (47%), TOC (4.7%). One specimen (MCZ 163708) had eggs measuring 122–152 µm in diameter.

Etymology. The epithet *alata* is from the Latin *alatus* for wing, in reference to the apical tooth on the neuropodial hooks of setiger 1 that appears as an extension of a flange that occurs along the convex side of the shaft on the hook.

Distribution. South China Sea, off Brunei, Island of Borneo, 1114–1453 m.

Heterospio bidentata new species

Figures 16–17

urn:lsid:zoobank.org:act:F02FC7F2-9427-4C87-B909-EF789C240339

Material examined. **Continental slope off Queensland, Eastern Australia, Coral Sea Marine Park,** R/V *Investigator*, Sta. 134, coll. 14 June 2017, Brenke sledge, start 23.750°S, 154.572°E, 2093 m to end 28.774°S, 154.546°E, 2156 m, **holotype** (AM W.52715).

Description. A moderately sized species, holotype (AM W.52715) only available specimen, incomplete, with 14 setigers, 10 mm long, 0.20 mm wide across thoracic setigers. Body long, narrow, threadlike, divided into thoracic region with crowded segments and abdominal region with elongate cylindrical segments; posterior segments missing. Thoracic parapodia weakly swollen, elevated over dorsal and ventral surfaces (Fig. 16A–C); abdominal parapodia reduced; cylindrical, dorsal and ventral surfaces smooth, lacking grooves or ridges. A thin membrane observed on some abdominal setigers suggesting remnants of an adhering tube. Color in alcohol light tan; pigment absent.

Pre-setiger region narrow, about as long as first 2.5 setigers (Fig. 16A–C). Prostomium elongate, weakly diamond-shaped, tapering anteriorly to rounded tip, posteriorly extending over peristomium to anterior margin of setiger 1 as a dorsal crest (Fig. 16A–B); eyes absent, nuchal organs not observed. Peristomium with two lateral grooves, producing two rings apparent laterally, but not crossing dorsal and ventral surfaces (Fig. 16A–C); dorsally interrupted by dorsal crest; dorsal tentacles absent, scars not apparent. Ventrally, mouth a semi-circular opening on first peristomial ring, with seven short lobes on anterior lip, none on posterior lip (Fig. 16C). Branchiae present on setigers 2–5 as short stubs or scars dorsal to notosetae (Fig. 16A–B).

Thoracic region consisting of six short setigers, each about as wide as long and a seventh setiger about 1.5 times longer than setiger 6 (Fig. 16A–B); setigers 1–7 slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum; similarly inflated ventrally; setiger 8 greatly elongate, as long as first six thoracic segments, setiger 9 equally as long as setiger 8, setigers 8–14 comprising available elongate middle body or abdominal setigers, each about 15 times longer than short thoracic setigers, cylindrical with parapodia reduced, not conspicuous.

All parapodia biramous with setal fascicles arising from anterior edge of segments. All thoracic notopodia with 8–12 capillaries; thoracic neuropodia of setiger 1 with five curved bidentate spines (Fig. 16D–E) and 3–4 capillaries; setigers 2–7 with 6–8 capillary noto- and neurosetae. Elongate setiger 8 with capillaries, transitioning to acicular spines in both noto- and neuropodia on setiger 9, setae arranged in short fan-shaped fascicles consisting of two rows of setae with acicular spines in anterior row and capillaries in posterior row; parapodia of setigers 9–13 lateral with noto-and neuropodia close together leaving broad dorsal and ventral gaps, not producing encircling cinctures. Thoracic neuropodial bidentate spines of setiger 1 strongly curved, with thick blunt-tipped main fang on concave side of shaft surmounted by thin apical tooth on convex side (Fig. 16D–E). Abdominal acicular spines with thick, weakly curved shaft tapering to narrow pointed tip (Fig. 16F–H); aristate setae and subuluncini not observed.

Far posterior segments and pygidium unknown.

Methyl Green staining. Methyl Green imparts a distinctive pattern in which the pre-setiger region and dorsal and ventral surfaces of the thoracic setigers are heavily stained (Fig. 17). The stain is concentrated in numerous large glandular cells that occur in those areas.

Remarks. *Heterospio bidentata* **n. sp**. is only the fourth species of the genus reported to have curved neuropodial spines in setiger 1 and the second with bidentate hooks. Two species reported with unidentate hooks are *H. catalinensis* (Hartman, 1944) from southern California in shelf depths (Hartman 1944, 1957) and *Heterospio* sp. A reported by Uebelacker (1984) from the Gulf of Mexico. *Heterospio bidentata* **n. sp**. and *H. alata* **n. sp**., both described in the present study, are the first having bidentate hooks in the neuropodia of setiger 1.

In *H. bidentata* **n. sp**. the apical tooth is a distinct secondary tooth arising directly from the shaft; whereas in *H. alata* **n. sp**. the apical "tooth" is an extension of a flange or crest that occurs along the convex side of the shaft and extends over the curved tip or main tooth of the hook providing the bidentate appearance. See earlier remarks for *H. alata* **n. sp**.

Heterospio bidentata **n. sp**. is further unusual among species of the genus in having the transition from defined tight setal fascicles to paired rows of setae with spines occurring on setiger 9. In most species, this transition occurs on setiger 10; in the other species with bidentate hooks, *H. alata* **n. sp.**, the transition occurs at setiger 11. In addition, the rows of spines and capillaries on setigers 9–13 of *H. bidentata* **n. sp**. are short and limited to the lateral sides of individual segments, leaving wide dorsal and ventral gaps instead of producing the encircling cinctures that characterize most species of the genus.

Etymology. The epithet is from *bidens*, Latin for two-toothed, in reference to the bidentate neuropodial hooks present on setiger 1 of this species.

Distribution. Abyssal Plain off Queensland, Eastern Australia, Coral Sea, 2093–2156 m.

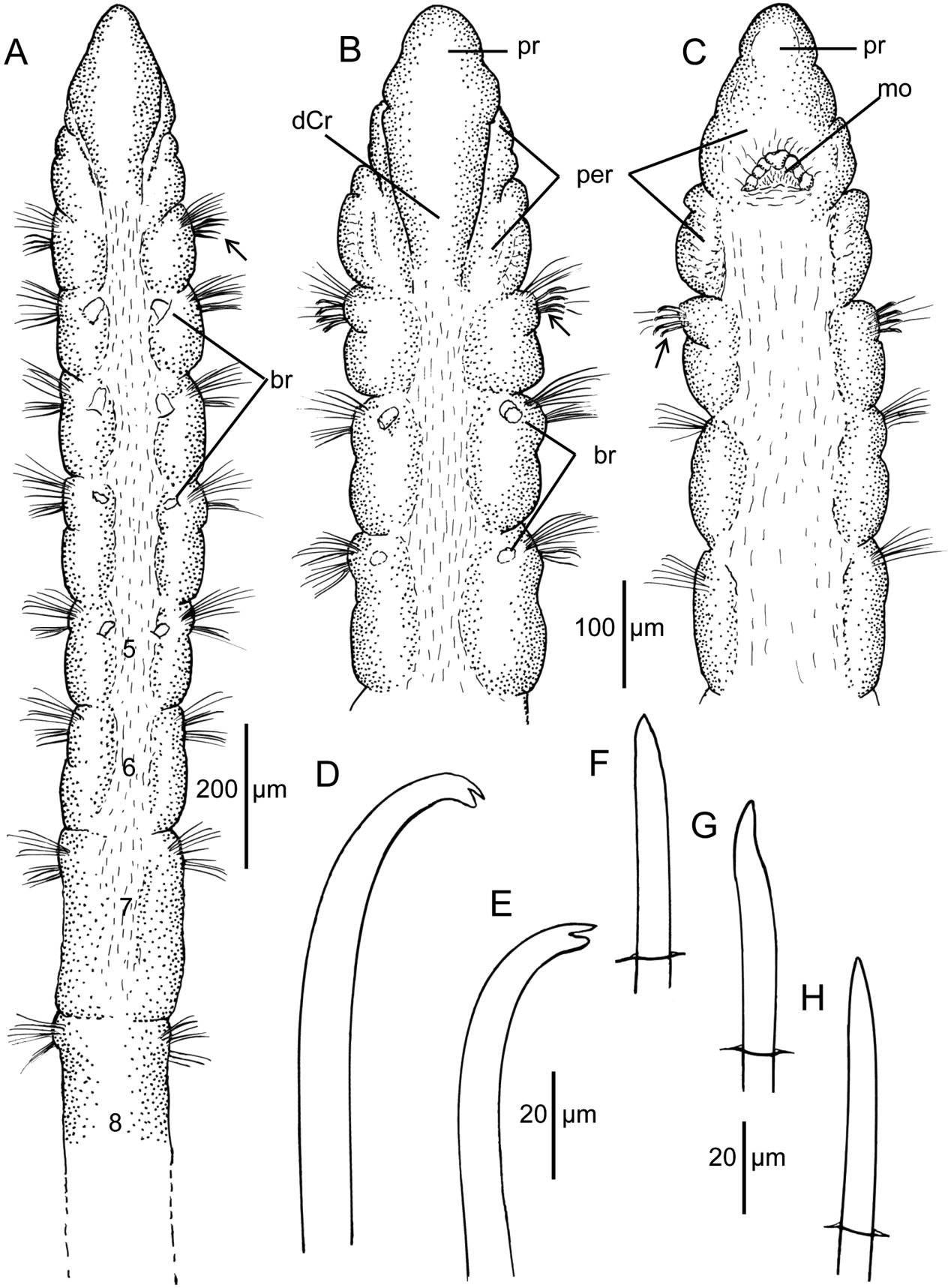

FIGURE 16. *Heterospio bidentata* **n. sp**. Holotype (AM W.52715): A, anterior end (setiger 1–8), dorsal view; B, anterior end (setiger 1–3), dorsal view; C, anterior end (setiger 1–3), ventral view; D–E, neuropodial acicular bidentate hooks from setiger 1; F–H, acicular spines from setiger 12. Arrows denote location of neuropodial hooks on setiger 1.

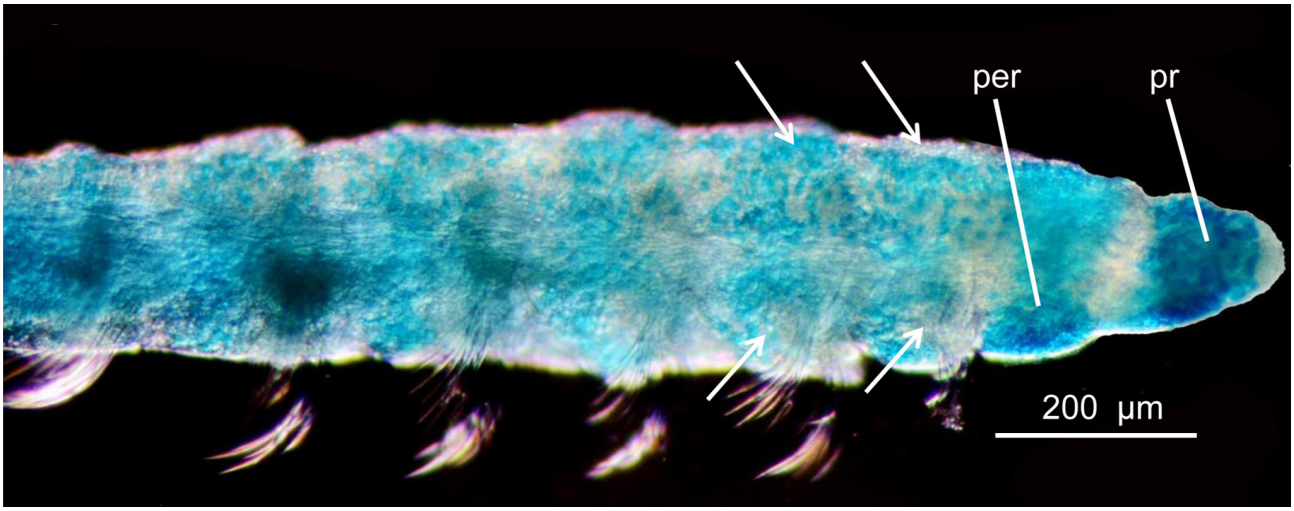

FIGURE 17. *Heterospio bidentata* **n. sp**. Holotype (AM W.52715): Anterior end (setiger 1–6) with Methyl Green stain. Arrows denote concentrations of MG.

Heterospio brunei new species

Figures 18–20

urn:lsid:zoobank.org:act:A2AD64EA-ED3D-4758-8613-38C3BEE33DA3

Material examined. (*12 specimens*) **South China Sea, off Brunei, Island of Borneo**, **Site CA2**, R/V *Emma*, coll. P.A. Neubert, Chief Scientist, BC, **Sta. DA3**, 03 Jul 2011, 5.421°N, 113.492°E, 1772 m **holotype** (MCZ 163717); **Sta. DA4**, 01 Jul 2011, 5.438°N, 113.517°E, 1851 m, 2 juvs (MCZ 163718); **Sta. JA1**, 30 Jun 2011, 5.473°N, 113.611°E, 1888 m, 1 juv (MCZ 163719); **Sta. JA3**, 3 Jul 2011, 5.49°N, 113.581°E, 1922 m, 1 **paratype** (MCZ 163720); **Sta. ME3**, 26 Jun 2011, 5.343°N, 113.643°E, 1665 m, 1 **paratype** (MCZ 163721); **Sta. ME7**, 4 Jul 2011, 5.369°N, 113.624°E, 1725 m, 1 **paratype** (MCZ 163722); **Sta. ME11**, 25 Jun 2011, 5.347°N, 113.553°E, 1719 m, 1 **paratype** (MCZ 163723); **Sta. ME14**, 26 Jun 2011, 5.422°N, 113.651°E, 1792 m, 2 **paratypes** (MCZ 163724).—**Site CA1**, R/V *Emma*, coll. J.A. Blake, Chief Scientist, BC, **Sta. 14**, 06 Jun 2011, 5.757°N, 114.097°E, 1675 m, 1 **paratype** (MCZ 163725); **Sta. WH-Jokit-NE**, 06 Jun 2011, 5.891°N, 114.199°E, 1400 m, 1 **paratype** (MCZ 163726).

Description. Body long, narrow, threadlike, divided into thoracic region with setigers 1–8 crowded and setiger 9 first elongate, about two times longer than setiger 8 (Figs. 18A, 19A), abdominal region with elongate cylindrical segments, and posterior region terminating in bulbous pre-pygidial region bearing four setigers with hooks. No intact complete specimens, however, holotype (MCZ 163717) recognized as complete in two parts, with 23 total setigers: a 12-setiger anterior fragment and an 11-setiger posterior fragment including a 4-setiger posterior bulbous section; both fragments together 24.0 mm long, anterior setigers 0.23 mm wide, middle abdominal setigers 0.27 mm wide. Other specimens incomplete anterior fragments: 14-setiger female paratype (MCZ 163721) with eggs (147–182 µm average diameter), 13.8 mm long, 0.26 mm wide across anterior setigers, 0.31 mm wide across abdominal setigers; 13-setiger paratype (MCZ 163724) 9.89 mm long, 0.22 mm wide across anterior setigers, 0.31 mm wide across abdominal setigers; at least three additional posterior fragments available. Color in alcohol opaque white to light tan; at least two specimens darker, likely due to retention of Rose Bengal from sample sorting procedure.

Pre-setiger region short, about as long as next 2.5 segments. Prostomium triangular, tapering anteriorly to narrow, rounded tip (Figs. 18A–B, 19A); eyespots absent; nuchal organs narrow slits dorsolateral on weakly swollen posterior border of prostomium (Fig. 18A). Peristomium in two parts; a narrow, swollen, anterior ring merged with posterior margin of prostomium and separated from a larger second ring by a groove with medial notches (Fig. 18A); no dorsal crest; ventrally second ring continuing across venter; mouth a wide transverse opening at posterior border of prostomium, with a row of short lobes on anterior lip and four narrow lobes on posterior lip (Fig. 18B); pharynx a short, rounded lobe everted on some specimens. Dorsal tentacles not observed.

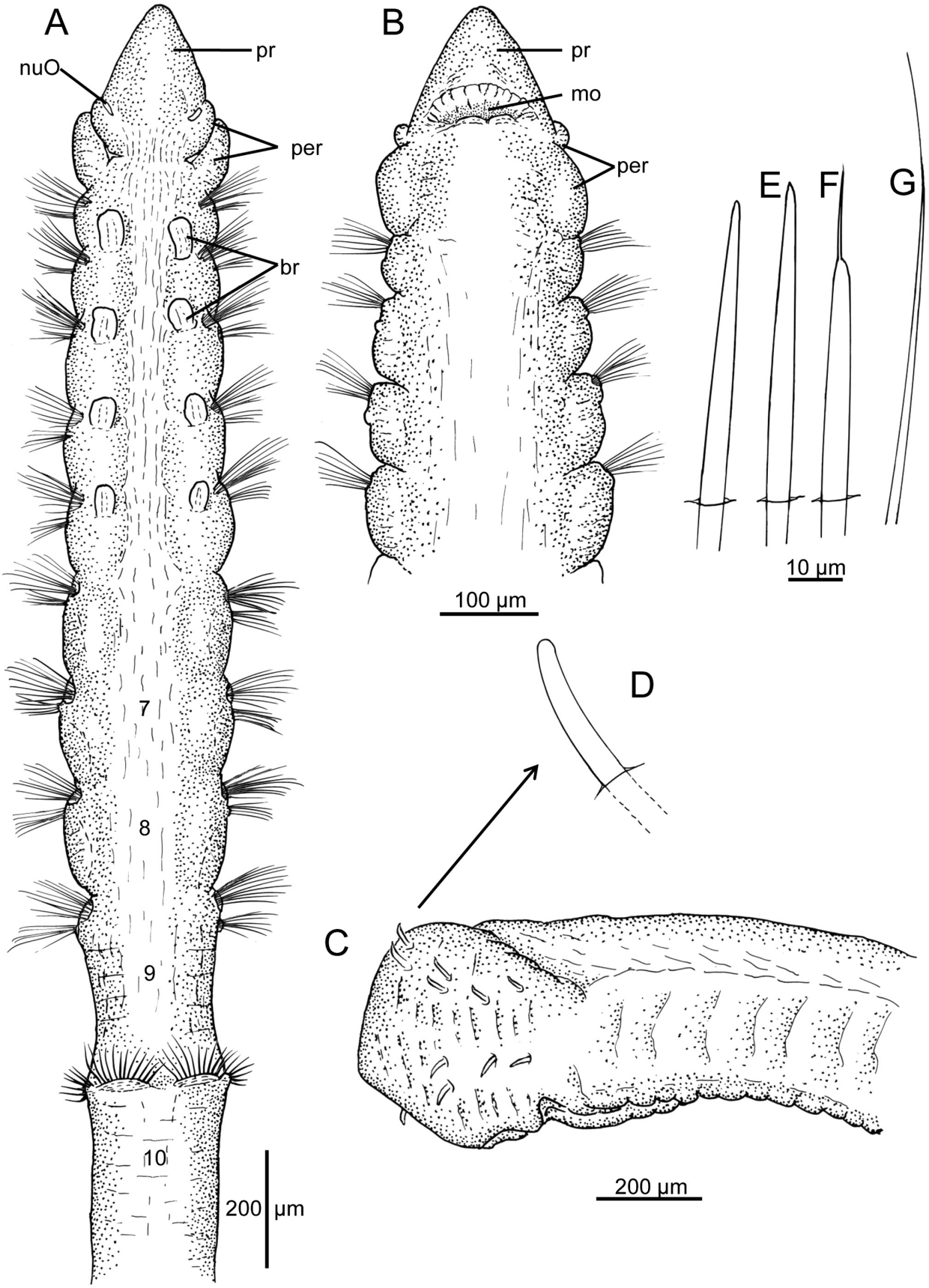

FIGURE 18. *Heterospio brunei* **n. sp**. A, anterior end (setiger 1–10), dorsal view; B, anterior end (setiger 1–4), ventral view; C, posterior end, left lateral view; D, notopodial hook from posterior end; E, neuropodial acicular spines, setiger 10; F, neuropodial aristate spine, setiger 10; G, neuropodial capillary, setiger 10. A, C–G holotype (MCZ 163717); B, paratype (MCZ 163720).

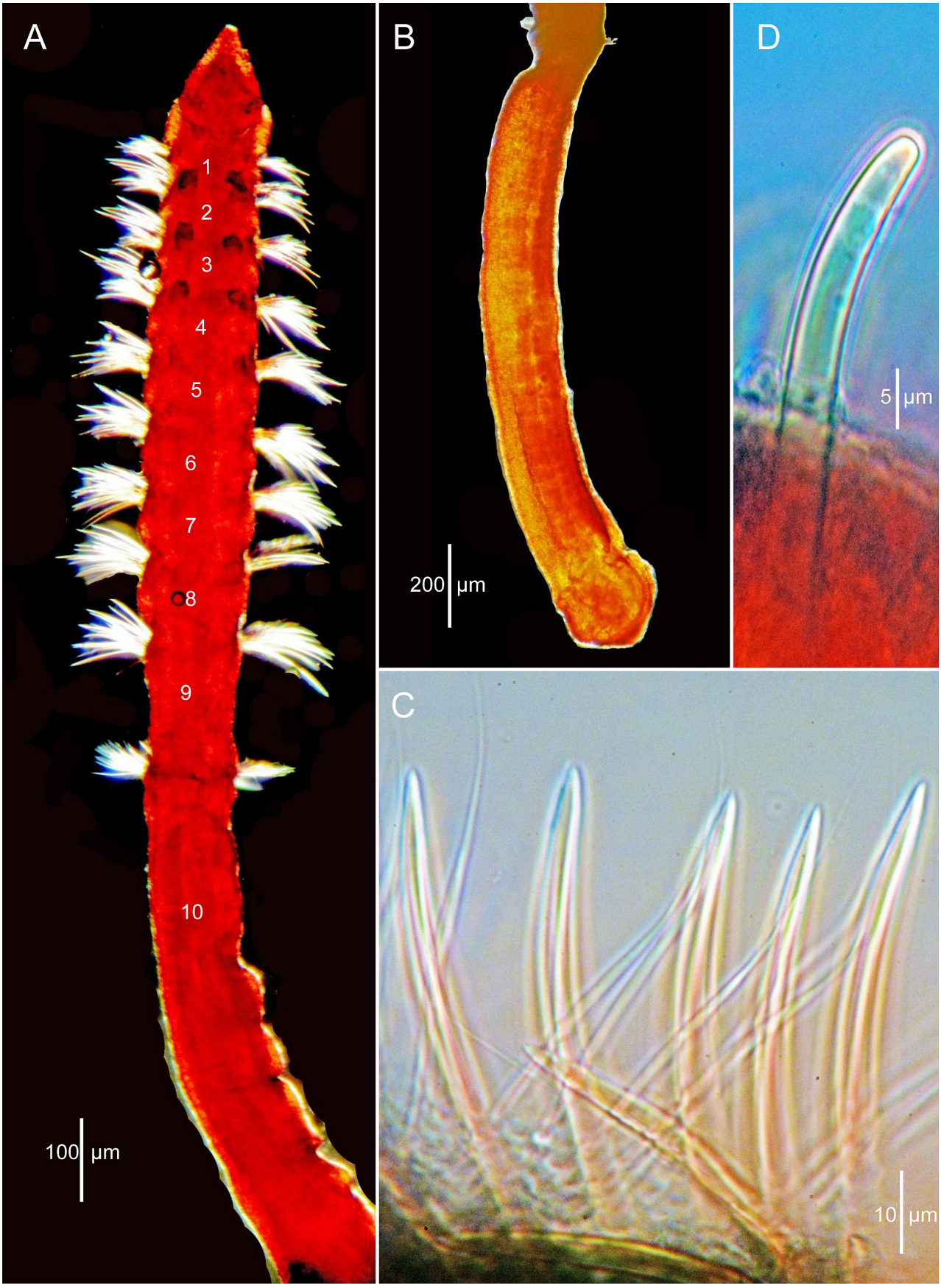

FIGURE 19. *Heterospio brunei* **n. sp**. Holotype (MCZ 163717): A, anterior end (setiger 1–10), dorsal view; B, posterior end right lateral view; C, notopodial acicular spines and capillaries, setiger 10; D, notopodial hook from posterior section. A–C stained with Shirlastain A.

Branchiae present on setigers 2–5 on all specimens except juveniles (Figs. 18A, 19A); most branchiae short, stubby, a few longer ones basally thick, tapering to rounded tip; prominent stubs or branchial scars typically present if long branchiae not evident; no evidence of branchiae or scars after setiger 5. Smallest juveniles with branchiae on setigers 2–3.

Thoracic region consisting of eight short setigers, each about as wide as long and a ninth transitional setiger about twice as long setiger 8 (Figs. 18A, 19A). All thoracic setigers slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum; similarly inflated ventrally.

All parapodia biramous with setal fascicles arising from anterior edge of segment. All thoracic noto- and neuropodia of setigers 1–9 with 12–15 long capillaries in spreading fascicles arising from a rounded torus (Fig. 18A). Elongate abdominal setigers from setiger 10 with numerous (25+) acicular spines in both noto- and neuropodia arranged in long, transverse fascicles producing setal cinctures similar to those found on the cirratulid genus *Chaetozone* (Fig. 18A). Cinctures with about 25–30 acicular spines in each noto- and neuropodium in tight anterior row followed by numerous thin capillaries in posterior row. Cinctures with lateral and dorsal gaps between fascicles, with 50–60 spines on a side. Most spines from setiger 10 acicular with thick, weakly curved shaft tapering to narrow tip (Figs. 18E, 19C); a few spines in setigers 11–12 with thin arista on tip (Fig. 18F); posterior row all capillaries (Figs. 18G, 19C); aristate spines not observed in more posterior setigers. Holotype with spines on all setigers from 10–19.

Posterior bulbous section with at least four parapodia (Figs. 18C, 19B), each with 1–2 acicular spines in each ramus. Each spine curved, with blunt tip (Figs. 18D, 19D).

Methyl Green staining. Distinctive pattern on pre-setiger region and anterior thoracic setigers (Fig. 20).

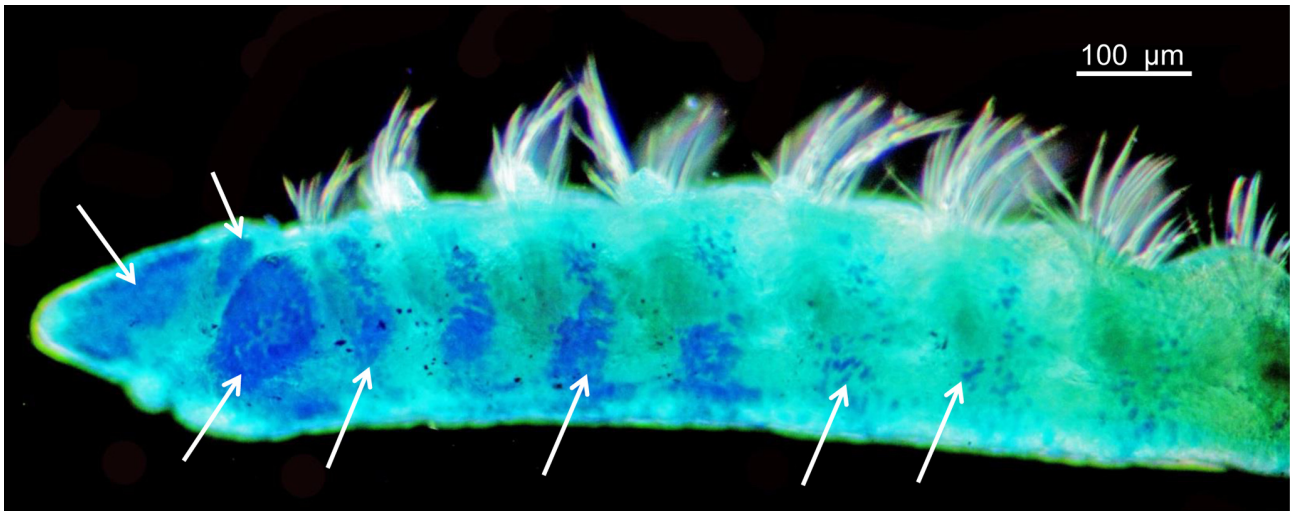

FIGURE 20. *Heterospio brunei* **n. sp**. Paratype (MCZ 163720): anterior end (setiger 1–8), in left lateral view showing MG staining pattern. Arrows denote prominent MG concentrations areas on prostomium, peristomium, and anterior setigers.

Remarks. With branchiae from setigers 2–5 and setiger 9 transitional, about 2–3 times longer than setiger 8, *Heterospio brunei* **n. sp**. is most similar to *H. peruana* (off Peru) and *H. hartmanae* **n. sp**. (North Atlantic), all from lower continental slope and abyssal depths. Both *H. brunei* **n. sp**. and *H. hartmanae* **n. sp**. have a wide transverse oral opening at the posterior border of the prostomium with a row of numerous short lobes on the anterior lip and a few larger lobes on the posterior lip; the oral morphology was not reported for *H. peruana*.

The main differences between these species appear to be in the nature of the spines on the abdominal parapodia and the nature of the peristomium. *Heterospio brunei* **n. sp**. has numerous simple acicular spines from setiger 10 to the end of abdominal section, the few aristate spines are limited to setigers 11 and 12. *Heterospio peruana* has aristate spines and subuluncini from setiger 10 but simple acicular spines are not reported; *H. hartmanae* **n. sp**. has only acicular spines, no aristate spines or subuluncini are present. All three species have two peristomial rings, but they are of very unequal size in *H. brunei* **n. sp.** with the anterior ring being very narrow and the second ring very wide, whereas they are subequal in size in *H. hartmanae* **n. sp**. and *H. peruana*.

Biology. Sediment grain size at all stations where *Heterospio brunei* **n. sp**. occurred contained fine sediments (97–99% silt + clay) with few sand-sized particles; total organic carbon (TOC) ranged from 0.9–3.5% at these same stations (Blake *et al.* unpublished data).

Etymology. The species is named for the country off which the survey was conducted.
Distribution. South China Sea, off Brunei, Island of Borneo, 1400–1922 m.

Heterospio catalinensis (Hartman, 1944)

Figures 21–22

Longosoma catalinensis Hartman, 1944: 322, pl. 27, figs. 1–3; 1957: 336, pl. 43, fig. 8.
Heterospio catalinensis Hartman 1969: 205–206, figs. 1–4. Vargas *et al.* 1985: 335; Maurer *et al.* 1988: 47. **Not** Fauchald *et al.* 2009: 786.

Material examined. (*44 specimens*) **Pacific Ocean, Allan Hancock Pacific Expeditions. Off California, Santa Catalina Island, off Long Point, R/V *Velero III* Sta. 900-38,** coll. 18 Nov 1938, dredged, 33.41°N, 118.354°W, 73 m, rock, brachiopods, and sponges, det. Olga Hartman, **holotype** (LACM-AHF Poly 582).—**Southern California Bight**, **off San Clemente Island**, 1.8 miles from East End Light, **R/V *Velero IV* Sta. 4045-56,** coll. 05 Apr 1956, Hayward grab, 33.311°N, 118.281°W, 104 m, (2, LACM-AHF Poly 13295); **off Santa Catalina Island**, 4 miles from Long Point Light, **R/V *Velero IV* Sta. 2144-52,** coll. 07 Aug 1952**,** Orange peel grab, 33.403°N, 118.358°W, 82 m, fine black sand, (1, LACM-AHF Poly 13296); **Orange County, off Newport Beach,** 1 mile from end of Balboa Pier, **R/V *Velero IV* Sta. 2745-54,** coll. 15 May 1954, Campbell grab, 33.597°N, 117.901°W, 14.6 m, gray sand, (1, LACM-AHF Poly 13297); **San Diego County, off Oceanside**, 0.25 miles from Oceanside Pier, **R/V *Velero IV* Sta. 4761-56**, coll. 08 Dec 1956, Hayward grab, 33.197°N, 117.392°W, 9.1 m, black silt, (6, LACM-AHF Poly 13298); **San Diego County, off Del Mar**, 1.95 miles from Del Mar Stack, **R/V *Velero IV* Sta. 5772-58**, coll. 01 Aug 1958, Hayward grab, 32.987N, 117.291°W, 23.7 m, olive green silty sand (1, LACM-AHF Poly 13299); **Orange County, off San Juan Capistrano**, 0.75 miles from San Juan Capistrano Pier, **R/V *Velero IV* Sta. 4774-56**, coll. 10 Dec. 1956, Hayward grab, 33.49°N, 117.663°W, 11.9 m, black & dark green very fine sand, oily & H_2S (2, LACM-AHF Poly 13300); **San Diego County, 0.7 miles from Cardiff by the Sea Tower**, **R/V *Velero IV* Sta. 4759-56,** coll. 08 Dec 1956, Hayward grab, 33.031°N, 117.296°W, 36. 5 m, very fine green sand (16, LACM-AHF Poly 13302); **Off Santa Catalina Island**, 47 miles from Jewfish Point, **R/V *Velero IV* Sta. 2122-52,** coll. 19 Jun 1952, Orange peel grab**,** 33.318°N, 118.294°W, 87.8 m, (2, LACM-AHF Poly 13303); **San Diego County, off Oceanside**, 0.25 mile from Oceanside Pier, **R/V *Velero IV* Sta. 4761-**56, coll. 08 Dec 1956, Hayward grab, 33.197°N, 117.392°W, 9.1 m, black silt, (3, LACM-AHF Poly 13304); S**an Diego County, off Oceanside,** 7.6 miles from Oceanside Pier, **R/V *Velero IV* Sta. 4867-57**, coll. 20 Feb 1957, Hayward grab**,** 33.293° N, 117.482 W, 11.9 m (5, LACM-AHF Poly 13305).—**Southern California Bight Survey,** E Santa Barbara Channel, Santa Barbara County, **Sta. Bight 03-4047**, coll. ABC Laboratories, 24 Jul 2003, van Veen grab, 34.39548°N, 119.66218°W, 24.7 m, soft bottom (1, LACM-AHF Poly 13291); Los Angeles County, off Malibu, Nicholas Canyon Beach, **Sta. Bight 03-4069**, coll. City of Los Angeles Environmental Monitoring, 31 Jul 2003, van Veen grab, 34.036°N, 118.917°W, 15.5 m, soft bottom (1, LACM-AHF Poly13292); E Santa Barbara Channel, Ventura County, off Emma Wood State Beach, **Sta. Bight 03-4043**, coll. ABC Laboratories, 23 Jul 2003, van Veen grab, 34.284°N, 119.355°W, 18.2 m, soft bottom, (1, LACM-AHF Poly 13293); Ventura County, SE of San Miguel Island, **Sta. Bight 03-4421**, coll. Channel Islands National Marine Sanctuary, 21 Aug 2003, van Veen grab, 33.988°N, 120.38°W, 95 m, soft bottom, (1, LACM-AHF Poly 13294).

Description. A moderately sized species, all specimens incomplete; however one posterior fragment available. Body elongate, anterior eight segments crowded, dorsoventrally flattened, each about three times as wide as long; setiger 9 first elongate segment (Fig. 21A), becoming more cylindrical; abdominal segments 10–13 long, narrow and cylindrical in cross section; one posterior fragment with an elongate bulbous posterior end. Holotype (LACM-AHF Poly 582) an 11-setiger anterior fragment, 15 mm long, 1.2 mm wide across thoracic segments; a 12-setiger anterior fragment (LACM-AHF Poly 13294) 20.1 mm long, 0.9 mm wide across setiger 4 (Fig. 21A–B); a 13-setiger anterior fragment (LACM-AHF Poly 13298) 11 mm long, 1.2 mm wide across thorax (Fig. 22A). Color in alcohol light tan; pigment entirely absent.

Pre-setiger region triangular in shape, relatively short, about as long as first two thoracic setigers (Fig. 21A). Prostomium conical, tapering to narrow rounded tip, dorsally merging posteriorly with peristomium and continuing to border of setiger 1 (Fig. 21A); eyespots absent, nuchal organs narrow slits along posterior margin. Peristomium large, ventrally entire, dorsally separated into two rings by two curved grooves from which dorsal tentacles arise

(Fig. 21A); one of two dorsal tentacles attached on one specimen (Fig. 22A: LACM-AHF Poly 13298); dorsal tentacles large, thick, with prominent folds and a deep ventral groove (Fig. 22A). Ventrally, mouth from margin of prostomium, consisting of narrow vertical slit between four large lateral lobes and single ventral row of 4–5 short lobes (Fig. 22B); proboscis everted on several specimens as a short inflated lobe.

Thoracic region defined by eight short crowded setigers followed by an elongate setiger 9 about four times as long as setigers 6–8 combined (Fig. 21A). Transition from thoracic segments with defined dorsolateral setal fascicles to abdominal segments denoted by setae arising from broad cincture-like rows mostly surrounding anterior margin of each segment occurs at setiger 10 (Fig. 21A).

Branchiae or their stubs present on setigers 2–9 (Fig. 21A); most branchiae when present long, thin, rounded in cross section, tapering to rounded tip; weakly moniliform (Figs. 21A, 22A).

All parapodia of thoracic and abdominal regions biramous with setae emerging from near anterior edge of each segment; two posteriormost setigers of posterior bulbous region with only notosetae. Thoracic notopodia reduced to low inconspicuous mounds with setae arising from notch; neuropodia with a low rounded postsetal lamella on setigers 1–8 (Fig. 21B). Thoracic setigers 1–9 with dense fascicles of capillary setae in dorsolateral locations on each segment; thoracic notosetae numerous capillaries in dense fascicles consisting of five or more curved rows; neurosetae of setiger 1 with about 6–10 curved elongate and narrow acicular spines preceded by at least two rows of capillaries (Figs. 21A–B, 22A); neurosetae of setigers 2–9 numerous capillaries. Hooks of setiger 1 unidentate, weakly sigmoid, with tip sharply curving to narrow blunted tip (Figs. 21D, 22C). Abdominal setigers from setiger 10 with parapodia as low ridges bearing setae arranged in long double rows almost entirely surrounding body; with small dorsal, ventral, and lateral gaps approximating separate noto- and neuropodia; setigers 10–12 with numerous capillaries in both rows. Setiger 13 with anterior row of subuluncinate spines tapering to tapering tip, some appearing aristate (Figs. 21E, 22D); posterior row of setae with numerous capillaries. Posterior fragment with three parapodia anterior to bulbous posterior section; these parapodia possibly representing setigers 18–20 have only two rows of capillaries without any spinous setae.

Posterior region an elongate bulbous section, about 3.5 times longer than wide, distinctly set off from elongate abdominal segments (Figs. 21C, 22B); with six setigers, each with a pair of curved hooks with pointed tips (Figs. 21F–I, 22D–F); first four of these posterior setigers with noto- and neuropodial spines, last two with only notopodial spines.

Methyl Green staining. Stain concentrated dorsolaterally on peristomial rings, and laterally anterior and posterior to each set of noto- neuropodial setal fascicles from setiger 1 to at least setiger 12; branchiae and neuropodial lamellae not retaining stain.

Remarks. *Heterospio catalinensis* (as *Longosoma*) was the second species of the genus to be described after Ehlers (1874, 1875) described *H. longissima* and the first reported to have acicular spines in the neuropodia of setiger 1 (Hartman 1944). To date, including the present study, four species of *Heterospio* have been reported with neuropodial spines on setiger 1: *H. catalinensis* (Hartman 1944, 1957; Southern California), *H.* sp. A (Uebelacker 1984; Gulf of Mexico), *H. alata* **n. sp**. (South China Sea), and *H. bidentata* **n. sp**. (Coral Sea off E. Australia). Of these *H. catalinensis* and *H.* sp. A from shallow shelf depths have unidentate spines in setiger 1, whereas *H. alata* **n. sp**. and *H. bidentata* **n. sp**. have bidentate spines on setiger 1 and are both deep-water species.

Despite *H. catalinensis* having been described relatively early in *Heterospio* history by Hartman (1944), and from southern California where numerous surveys have taken place, there have been few subsequent reports of the species, apart from Hartman herself in 1957 and 1969. The reports of the species from Costa Rica by Vargas *et al.* (1985) and Maurer *et al.* (1988) did not provide any additional morphological observations. The present account, therefore, is the first to include updated morphological observations for the species in the 65 years since Hartman (1957).

Fauchald *et al.* (2009) referred Uebelacker's 1984 report of *Heterospio* sp. A from the Gulf of Mexico to *H. catalinensis*; however, we disagree with this assignment. *Heterospio catalinensis* and *H.* sp. A are similar, but differ in the following respects: *H. catalinensis* has branchiae on setigers 2–9, low, rounded neuropodial postsetal lamellae occur on setigers 1–8, setiger 9 is the first elongate setiger, about four times as long as setiger 8, and the modified neuropodial hooks on setiger 1 are long and have a sharply curved tip; *H.* sp. A in contrast, has branchiae on setigers 2–6 (or 7), neuropodial postsetal lamellae are not reported, setiger 8 is the first elongate setiger and about twice as long as setiger 7, and the modified neuropodial spines of setiger 1 are hirsute with a bluntly rounded apex rather

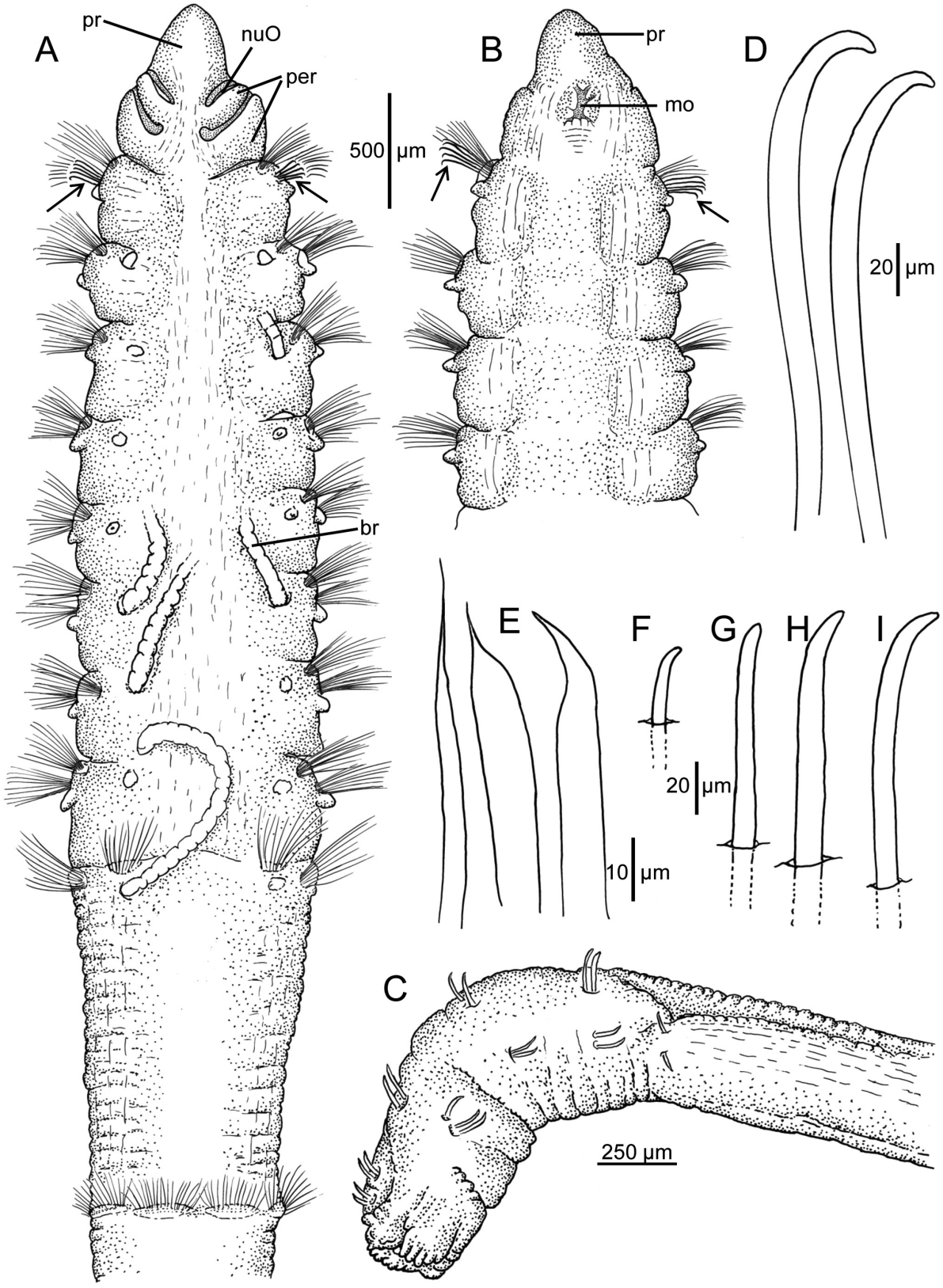

FIGURE 21. *Heterospio catalinensis* (Hartman, 1944). A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior fragment, right lateral view; D, acicular hooks, neuropodia setiger 1; E, capillary and acicular spines, setiger 13; F–I, hooks from posterior bulbous section: F, 1st posterior setiger, G, 2nd posterior setiger, H, 3rd posterior setiger; I, 4th posterior setiger. A–B (LACM-AHF Poly 13294); C, E–I (LACM-AHF Poly 13298); D, (LACM-AHF Poly 13300). Arrows indicate location of neuropodial spines on setiger 1.

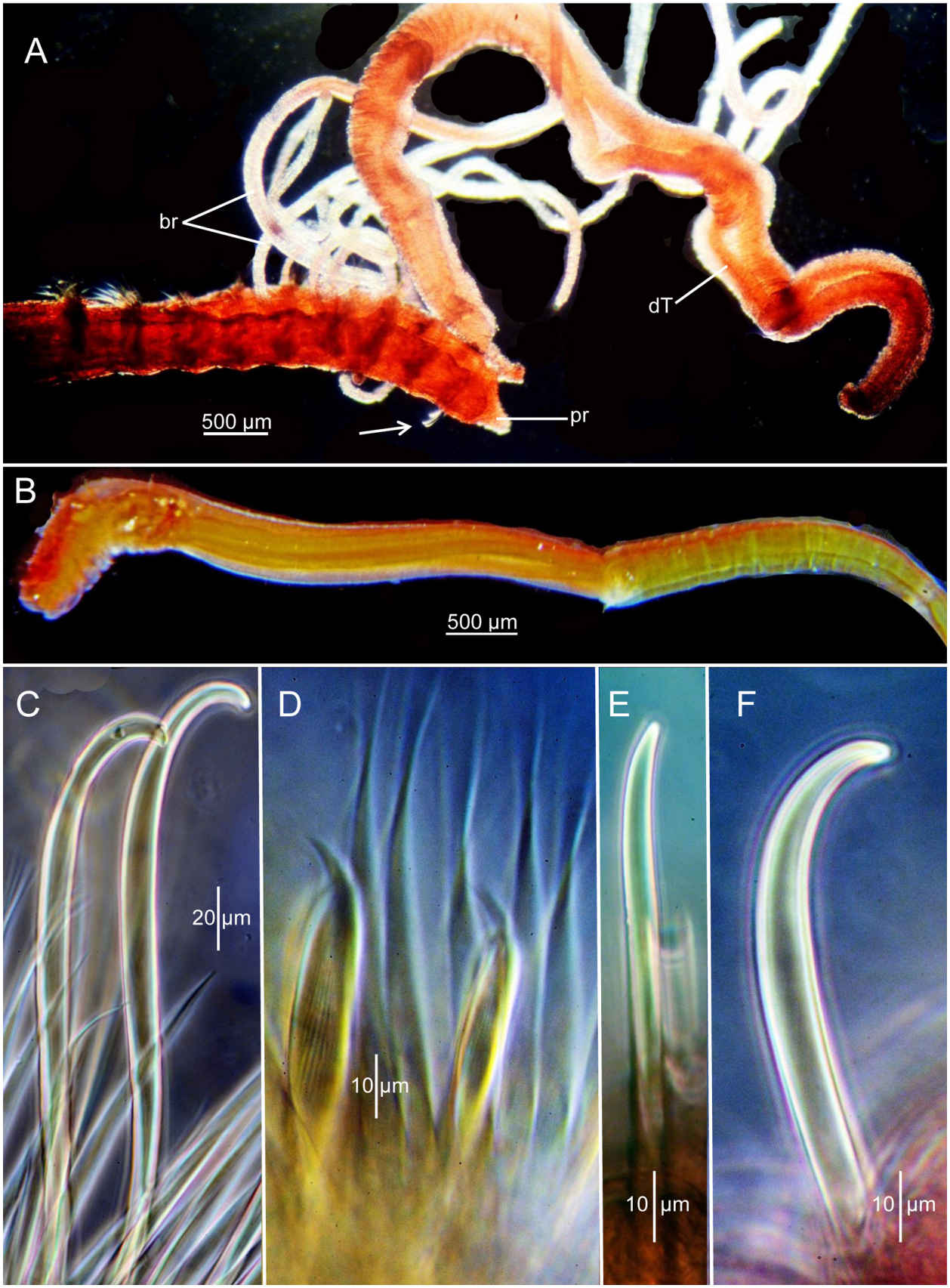

FIGURE 22. *Heterospio catalinensis* (Hartman, 1944). A, anterior end, right lateral view; B, posterior end, right lateral view; C, acicular hooks, neuropodia setiger 1; D, aristate hooks and subuluncini from setiger 13; E–F, acicular hooks posterior bulbous section. A–B, D–F: LACM-AHF Poly 13298, C: LACM-AHF Poly 13300. Arrows indicate location of neuropodial spines on setiger 1.

than sharply curved. Based on the present study of *H. catalinensis* and Uebelacker's (1984) description of *H.* sp. A, both species have only capillaries on abdominal setigers 10–12 with spines first present from setiger 13. Hartman (1957) was the first to report subuluncini in *H. catalinensis* but did not indicate on which abdominal setigers they occurred. Here we report the presence of subuluncini on setiger 13 in *H. catalinensis*, while Uebelacker (1984) reported both acicular and subuluncinate spines, also from setiger 13, on *H.* sp. A. Given the morphological differences and disjunct geographic locations between *H. catalinensis* and *H.* sp. A, the Gulf of Mexico specimens most likely represent a separate undescribed species rather than *H. catalinensis* as listed by Fauchald *et al.* (2009).

Records of *H. catalinensis* from the Gulf of California in 1550–1590 m by Mendez (2006, 2007) are likely not this species because of their much greater collection depth.

Biology. *Heterospio catalinensis* is widely distributed offshore southern California and although the original collection reports it being dredged from bottoms with rock, brachiopods, and sponges (Hartman 1944) other more recent records from grab samples are from soft bottoms consisting of fine sands.

Distribution. Southern California, 9–104 m; Costa Rica, Gulf of Nicoya, 20–46 m.

Heterospio ehlersi new species

Figures 23–24

urn:lsid:zoobank.org:act:5E6FB9FA-CD55-4473-83B1-E1F506B3DCA2

Material examined. **South China Sea, Gulf of Thailand**, Unocal Thailand Survey, **Sta. BWC-1-D-1**, 8.958ºN, 101.332ºE, 60–70 m, coll. 03 May 1991, Battelle Ocean Sciences, **holotype** (LACM-AHF Poly 13289).

Description. Holotype (LACM-AHF Poly 13289) only specimen, long, narrow, threadlike; complete with 26 setigers including nine thoracic, 14 abdominal, and three in posterior bulbous section; 10 mm long, 0.25 mm wide across thoracic setigers, and 0.4 mm wide across abdominal setigers. Thoracic region with setigers 1–8 short and crowded, setiger 9 first elongate, as long as 2.5 preceding setigers (Figs. 23A, 24A). Abdominal region with elongate cylindrical segments, each about as long as entire thoracic region, terminating in posterior bulbous section bearing at least three parapodia with hooks (Fig. 24B–C). Color in alcohol opaque white.

Pre-setiger region short, about as long as first three segments (Fig. 23A). Prostomium triangular, tapering anteriorly to narrow, rounded tip (Figs. 23A–B, 24A); eyespots absent; nuchal organs narrow slits dorsolateral on border with peristomium (Fig. 23A). Peristomium a single ring, interrupted dorsally by thick dorsal crest extending from posterior border of prostomium over setiger 1 to anterior border of setiger 2 (Fig. 23A); grooves on either side of dorsal crest likely site where dorsal tentacles arise, but these not present. Ventrally, peristomium entire, interrupted by mouth between prostomium and peristomium (Fig. 23B); mouth a transverse groove with shallow vestibule on anterior border and narrow posterior lip with short lobes (Fig. 23B); pharynx not observed.

Branchiae present on setigers 2–4 either intact or as stubs; when present, branchiae long, thin, crenulated, with internal blood vessel.

Thoracic region consisting of eight short setigers, each about three times as wide as long and a ninth transitional setiger about 2.5 times as long as setiger 8 (Figs. 23A, 24A). All thoracic setigers slightly flattened dorsally with parapodia weakly inflated and elevated over dorsum; ventral similarly inflated, but with broad ventral ridge extending over setigers 1–8 (Fig. 23B).

All parapodia biramous with setal fascicles arising from anterior edge of segment. All thoracic noto- and neuropodia of setigers 1–9 with 12–15 long capillaries in spreading fascicles arising from a rounded torus. Elongate abdominal setigers from setiger 10 to about 20 with widely spaced noto- and neuropodia; distinct dorsal, lateral and ventral gaps producing four sets of setae; continuous encircling cinctures not present until last few abdominal setigers (20–23) where reduced gaps result in cinctures of both spines and capillaries. Spines in anterior row numbering about 15–20 per noto- or neuropodium on most abdominal setigers, last few setigers with up to 25 spines per podium; numerous capillaries in posterior row in all abdominal setigers. Acicular spines curved or straight, tapering to narrow tip (Fig. 23D); aristate spines and subuluncini not observed.

Posterior bulbous section about as long as wide (Fig. 24B), with three parapodia each with 1–2 acicular spines per ramus. Each spine curved, with blunt tip (Figs. 23E, 24C).

Methyl Green staining. Dorsal peristomial ring retains stain, otherwise no pattern.

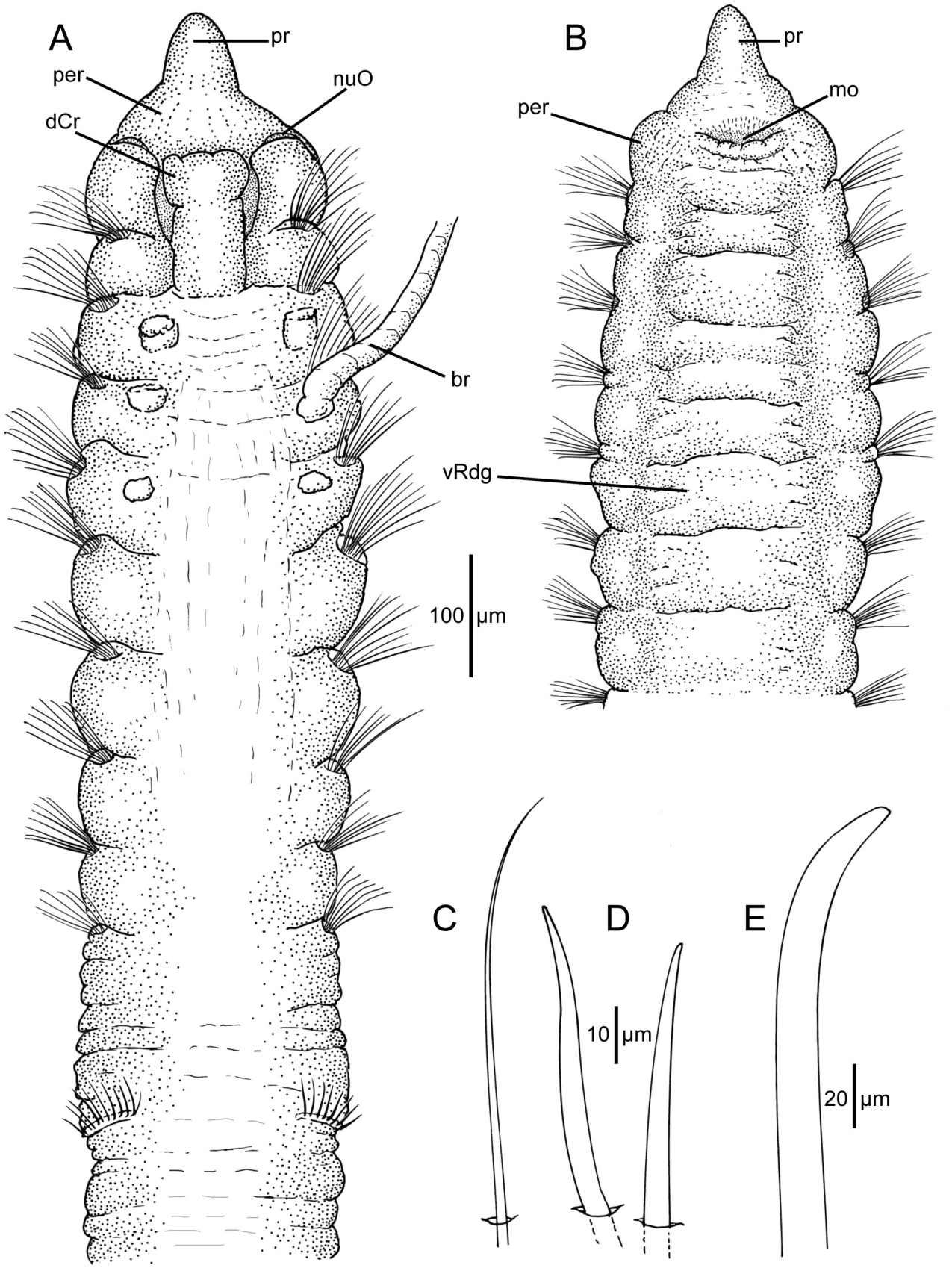

FIGURE 23. *Heterospio ehlersi* **n. sp**. Holotype (LACM-AHF Poly 13289): A, anterior end, dorsal view; B, anterior end, ventral view; C, capillary from setiger 10, posterior row; D, acicular spines from setiger 10; E, notopodial hook from bulbous posterior end.

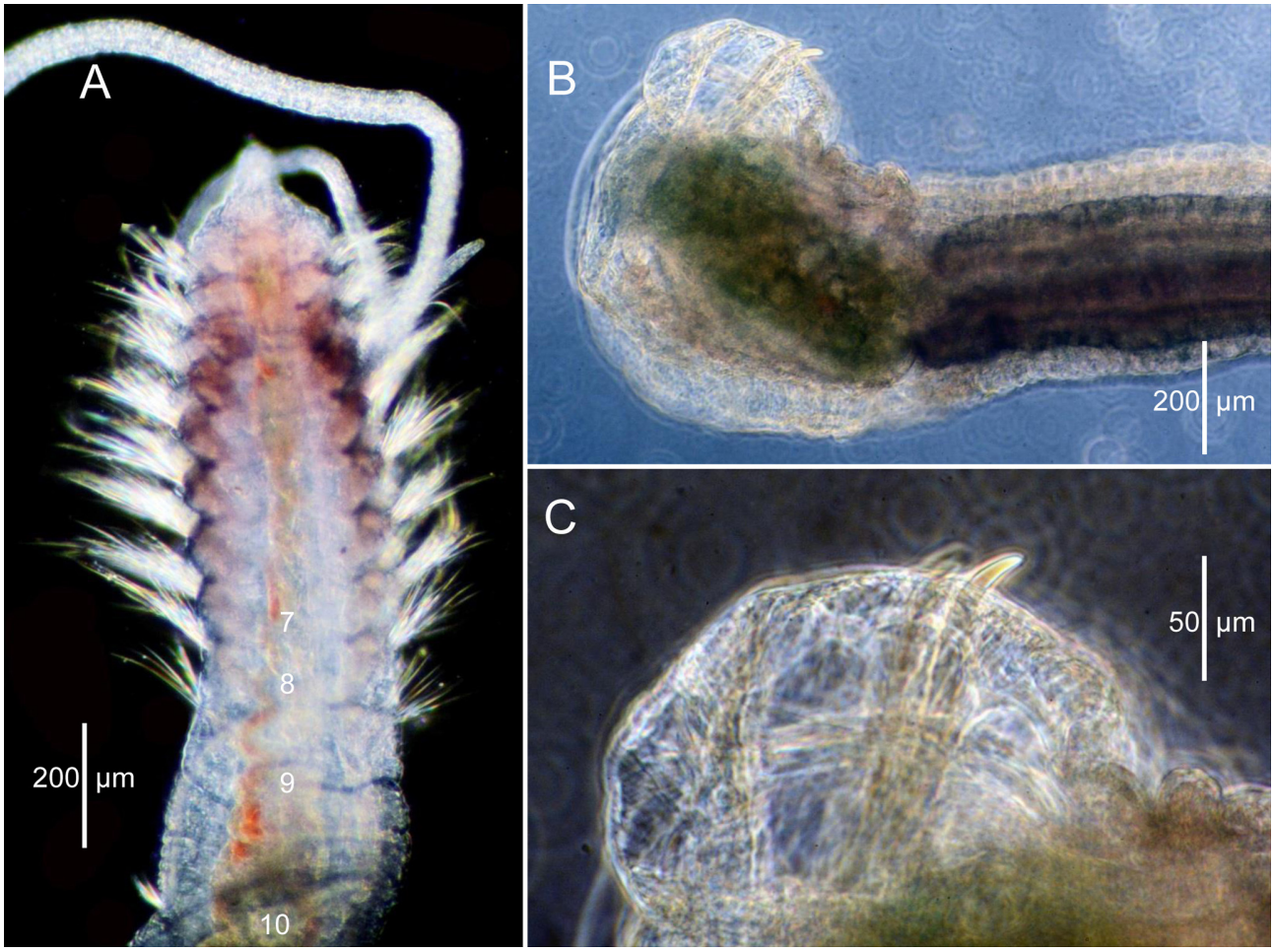

FIGURE 24. *Heterospio ehlersi* **n. sp**. Holotype (LACM-AHF Poly 13289): A, anterior end, dorsal view; B, bulbous posterior end right lateral view; C, bulbous posterior end with detail of notopodial hook. Stained with Shirlastain A.

Remarks. Among shallow-water species of *Heterospio* that lack neuropodial spines on setiger 1, have five or fewer pairs of branchiae, and have setiger 9 as the first elongate setiger, *H. ehlersi* **n. sp**. from the South China Sea mostly closely resembles *H. africana* **n. sp**. from off Mozambique. They differ in that *H. ehlersi* **n. sp**. has branchiae from setigers 2–4, one peristomial ring, and acicular spines from setiger 10 to the end of the abdominal region, whereas *H. africana* **n. sp**. has branchiae from setigers 2–6, two peristomial rings, only capillaries on setiger 10. and following setigers with both subuluncini and acicular spines.

Heterospio ehlersi **n. sp**. also closely resembles *H. brunei* **n. sp**., a deep-water species from off Borneo, also in the South China Sea, having a reduced number of branchial pairs, with setiger 9 as the first elongate segment, and with acicular spines present from setiger 10. They differ in that *H. ehlersi* **n. sp**. has one peristomial ring instead of two, branchiae on setigers 2–4 instead of 2–5, and an oral opening with short lobes on the posterior lip instead of short lobes on both the anterior and posterior lips. In addition, the nature of the broad ventral ridge observed on *H. ehlersi* **n. sp**. is unique among known species of the genus.

Etymology. This species is named for Professor Ernst Heinrich Ehlers (1835–1925), prominent German zoologist and polychaete systematist. He was a Professor at the University of Göttingen where he identified and named the genus *Heterospio* and the type-species, *H. longissima*, in 1874.

Distribution. South China Sea, Gulf of Thailand, 60–70 m.

***Heterospio knoxi* new species**
Figure 25
urn:lsid:zoobank.org:act:F9CDB736-A633-4022-BB10-0E60017B0E19

Longosoma sp. Knox 1960: 1131.

Material examined. **Pacific Ocean, New Zealand, North Island, Hawke Bay**, coll. Aug 1956, Desmond Hurley, cone grab, 39.388978°S, 177.080489°E, 13–61 m, **holotype** (LACM-AHF Poly 13320); 1 **paratype** (LACM-AHF Poly 13290).

Description. A large species, both specimens incomplete, but in excellent condition. Holotype (LACM-AHF Poly 13320) with 13 setigers, 26.5 mm long, 1.4 mm wide across thoracic setiger 5; paratype (LACM-AHF Poly 13290) with 12 setigers, 19.6 mm long, 1.3 mm wide across setiger 5. Body long, narrow, divided into thoracic region with first eight setigers crowded and setiger 9 first elongate segment, as long as setigers 6–8 combined (Fig. 25A–B). Thoracic setigers 1–9 dorsoventrally flattened, with low mid-dorsal ridge extending from setiger 3 to 8 (Fig. 25A); mid-ventral ridge present from setiger 3 to anterior border of setiger 9 (Fig. 25B). Abdominal region with elongate cylindrical segments; posterior region not present. Color in alcohol opaque white to light tan.

Pre-setiger region short, about as long as setigers 1and 2 (Fig. 25A–B). Prostomium triangular, tapering anteriorly to narrow, rounded tip, posteriorly merging with anterior peristomial ring and continuing posteriorly as a caruncle-like dorsal crest overlying second peristomial ring and mid-dorsum of setigers 1–2 (Fig. 25A); eyespots absent; nuchal organs narrow slits between posterior lateral border of prostomium and first peristomial ring. Peristomium entire ventrally, divided into two parts dorsally and laterally; these sections include a narrow, anterior ring separated from prostomium by a curved groove that includes the nuchal organs and a posterior ring separated from the first by a curved groove from which the dorsal tentacles arise (Fig. 25A); tentacles not present on either specimen. Ventral surface of peristomium relatively smooth; mouth a narrow vertical slit with two lateral lobes and posterior lip formed by anterior border of peristomium (Fig. 25B). Branchiae from setigers 2–9; thin when present; others broken or as stubs (Fig. 25A). Individual branchiae with short moniliform-like sections; with internal blood vessel.

All parapodia biramous with setal fascicles arising from anterior edge of segment. All thoracic noto- and neuropodia of setigers 1–9 with 40–50 long capillaries in spreading fascicles arising from a cuplike notch; neuropodia with a thickened postsetal lamella or posterior lateral flange-like enlargement on posterior side of setal fascicle (Fig. 25B). Elongate abdominal setigers from setiger 10 with parapodia modified into elongate ridges bearing setae that mostly encircle entire body, leaving only minute dorsal, ventral, and lateral gaps to denote individual noto- and neuropodia (Fig. 25A–B); when spines present, resulting armature resembles that of some cirratulid polychaetes of the genus *Chaetozone.* Setigers 10–11 with setae all capillaries, those of anterior row thicker and larger than those of posterior row; setiger 12 with anterior row of thicker setae, mostly subuluncini with thickened shaft and thick tapering tip, and a few acicular spines (Fig. 25C–D) and posterior row of slender capillaries; setiger 13 with subuluncini replaced by aristate and acicular spines in about equal numbers in anterior row (Fig. 25E–F) and with posterior row of thin capillaries (Fig. 25G).

Remarks. These two specimens of *Heterospio* (as *Longosoma*) were donated to the late Dr. Olga Hartman during a visit by the late Dr. George Knox to the Allan Hancock Foundation in 1959; their observations on these specimens and comparison with Dr. Hartman's *H. catalinensis* were reported by Knox (1960). The two specimens were originally part of a collection of 27 specimens collected in Aug 1956 from 12 stations in Hawke Bay, consisting of fine sands and muds. Coordinates given here were taken from a mid-point of the Bay since the exact station for these specimens is unknown; however, among the collections of the National Institute of Water & Atmospheric Research Ltd (NIWA), Wellington, New Zealand, nine stations are listed with specimens from this survey. These range in depth from 13 to 61 m ($\overline{x} = 36 \pm 12.34$); the data indicate that most of the 12 specimens listed have been dry and are in poor condition (G. Reid, personal communication).

Heterospio knoxi **n. sp**. from New Zealand, with branchiae from setigers 2–9, two peristomial rings, setiger 9 being the first elongate setiger, and aristae acicular spines in some abdominal parapodia, most closely resembles *H. sinica* from the East China Sea (Wu & Chen 1966). The two species differ in that *H. knoxi* **n. sp**. has a distinct caruncle-like dorsal crest that extends from the prostomium over the peristomium to the middle of setiger 2, and both aristate and acicular spines are present in setiger 13. In contrast, *H. sinica* has no peristomial dorsal crest and setigers 13–17 have aristate spines but no acicular ones. See Table 1 for additional information.

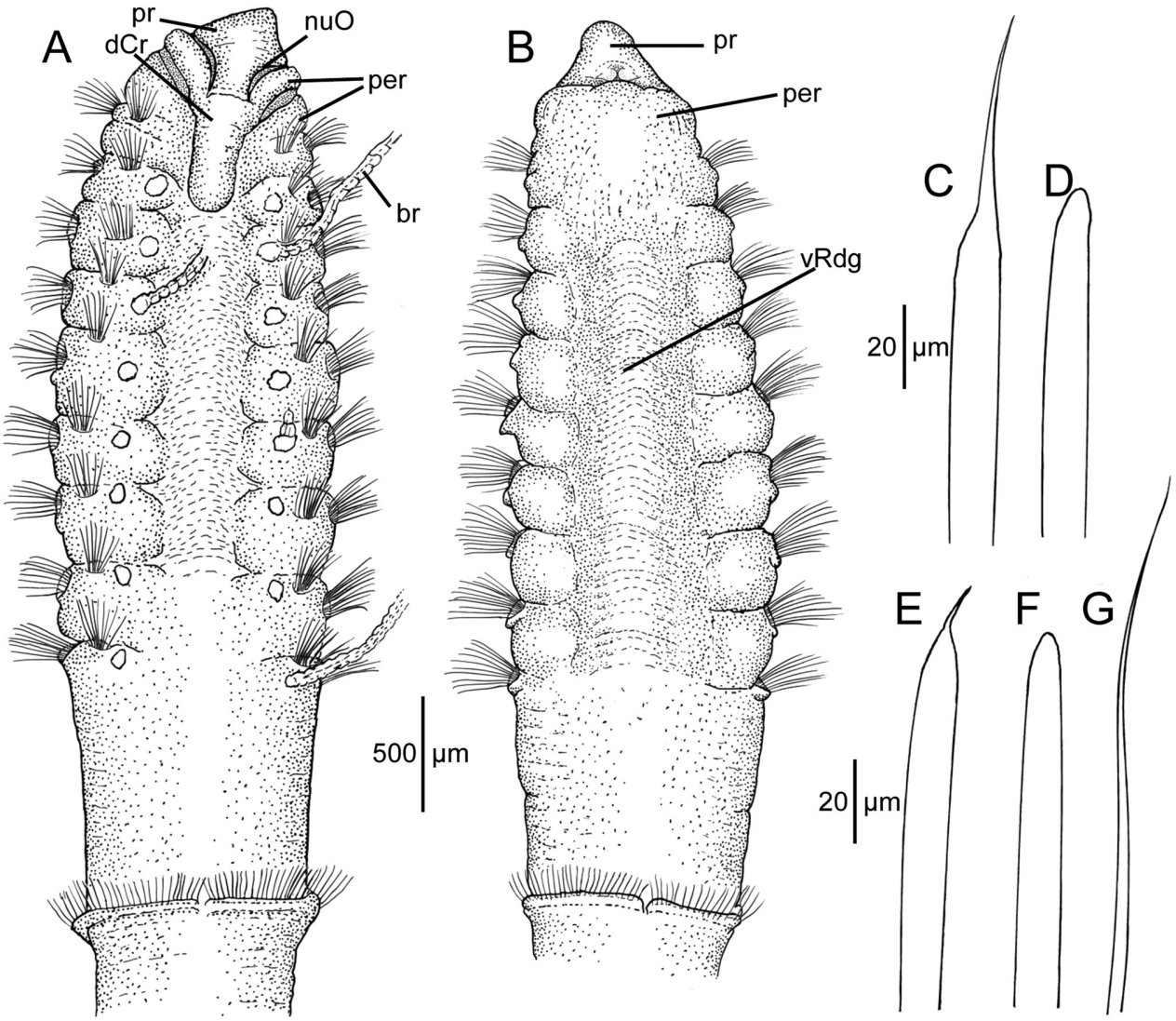

FIGURE 25. *Heterospio knoxi* **n. sp**. A, anterior end, dorsal view; B, anterior end, ventral view; C–D, subuluncini (C) and acicular spine (D) from setiger 12; E–G, aristate spine (E), acicular spine (F) and capillary (G) from setiger 13, A, E–F, holotype (LACM-AHF Poly 13320); B–D, paratype (LACM-AHF Poly 13290).

Methyl Green staining. Anterior half of prostomium and branchiae not stained; stain concentrated on both peristomial rings, dorsal crest and on parapodia, best seen ventrally; rest of body staining uniformly, destaining readily.

Biology. The holotype has oocytes in the coelom measuring 145–160 µm in diameter. The habitat of Hawke Bay, New Zealand, where these specimens were collected was reported to consist of grey sands to fine muddy sands with seafloor temperatures ranging from 13.0–13.3°C (Knox 1960).

The report of *Heterospio* sp. by Estcourt (1967) from Marlborough Sound, South Island, NZ, as a dominant species in shallow subtidal benthic assemblages, may be the same as *H. knoxi* **n. sp**.

Etymology. This species is named for the late Professor George A. Knox (1919–2008), of the University of Canterbury, Christchurch, New Zealand. Professor Knox was a marine ecologist and noted authority on polychaete systematics who identified *Heterospio* (as *Longosoma)* in New Zealand and recognized its unusual characteristics (Knox 1960).

Distribution. New Zealand, North Island, Hawke Bay, 13–61 m.

Heterospio peruana Borowski, 1994

Heterospio peruana Borowski, 1994: 131–136, figs. 1, 2A–G.

Material examined. **Pacific Ocean, SEPBOP, off Western South America, Peru-Chile Trench**, R/V *Anton Bruun*, Cruise 11, Sta. 95, coll. 15 Oct 1965, R.J. Menzies, 08.517°S, 81.667°W, Menzies trawl, 4332–4423 m, 1 specimen in two parts (LACM-AHF Poly 13306).

Description. A single incomplete specimen in two parts, not in good condition; anterior fragment with 12 setigers, 12.5 mm long and a posterior fragment with two segmental setigers and intact bulbous posterior end with five setigers with hooks.

Pre-setiger region with conical, broadly rounded prostomium and two peristomial rings, incomplete dorsally; without dorsal crest; nuchal organs in groove between prostomium and first peristomial ring; dorsal tentacles not present.

Thoracic segments flattened dorsally, rounded ventrally. Thoracic setigers 1–8 short, about twice as wide as long; setiger 9 first elongate segment, about twice as long as setiger 8. Setiger 10 first abdominal segment, as long as entire thoracic region; setigers 11 and 12 equally as long as setiger 10. Branchiae on setigers 2–5 reduced to scars or stubs on this specimen.

All setigers biramous. Thoracic parapodia as rounded pads without postsetal lamellae; with noto- and neuropodia well separated, bearing 20–30 thin capillaries in tight well-defined fascicles. Parapodia of abdominal setigers 10–12 as transverse low ridges, with setae in two rows mostly surrounding body; first row with numerous thickened spinous setae and second row with thin capillaries. Spinous setae of setiger 10 mostly aristate or subuluncini-like with an elongated tapering point. Spines of setiger 12 with those of notopodia mostly aristate, and those of neuropodia mostly acicular.

Bulbous posterior end with five setigers bearing large curved hooks in each ramous.

Methyl Green staining. Not tested due to poor condition of specimen.

Remarks. These fragments from the Peru-Chile Trench agree well with the original account by Borowski (1994) from the abyssal plain of the Peru Basin, except that the abdominal neurosetae tend to be more acicular rather than aristate or subuluncini as in the notopodia.

By having branchiae on setigers 2–5 and setiger 9 as the first elongate segment, ca. 2–2.5 times as long as the shorter thoracic setigers*, Heterospio peruana* most closely resembles *H. hartmanae* **n. sp**. from the North Atlantic Ocean and *H. brunei* **n. sp**. from the South China Sea. All three of these widely separated species are from abyssal or lower continental slope depths.

In *H. hartmanae* **n. sp**. the abdominal spines in the cinctured abdominal segments are mainly simple spines with narrow rounded tips; only a few have pointed tips and none are aristate. In contrast, the acicular spines of cinctured segments in *H. peruana* are illustrated by Borowski (1994) as distinctly aristate or subuluncinate-like capillaries where the extended tip is thicker than the smoothly tapering tip of typical capillaries. In the present study aristate spines have been observed, but also acicular spines in some abdominal neuropodia. *Heterospio brunei* **n. sp**. has a few aristate spines in the first one or two abdominal setigers, but most are acicular throughout. *H. hartmanae* **n. sp**. and *H. peruana* have two prominent peristomial rings, whereas *H. brunei* **n. sp**. has only one.

Distribution. Abyssal Plain, DISCOL manganese nodule site, Peru Basin, 4125–4188 m (Borowski 1994); Peru-Chile Trench, 4423 m (This study).

Species of *Heterospio* from the Indian Ocean and Adjacent Seas

Heterospio africana new species

Figures 26–27

urn:lsid:zoobank.org:act:0BF6D8E4-55B9-4A24-BC45-A2A0D2585828

Material examined. East Africa, off Mozambique, International Indian Ocean Expedition, R/V *Anton Bruun*, Cruise 7, **Sta. AB 372 H**, coll. 19 Aug 1964, Olga Hartman, Campbell Grab, 24.900ºS, 34.923ºE, 55 m, sand and mud, **holotype** (LACM-AHF Poly 13288).

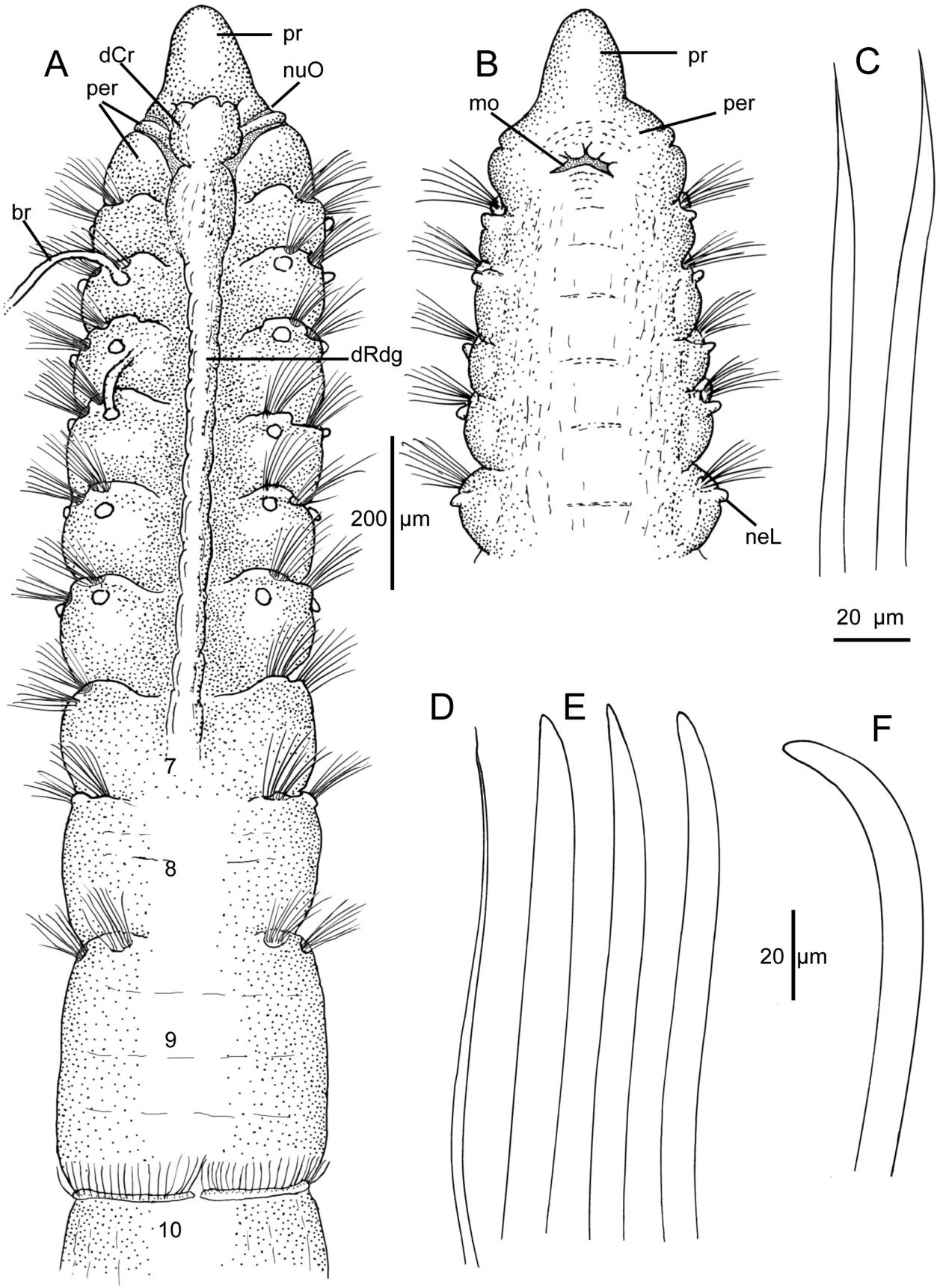

FIGURE 26. *Heterospio africana* **n. sp**. Holotype (LACM-AHF Poly 13288): A, anterior end, dorsal view; B, anterior end, ventral view; C, subuluncini, setiger 13; D, capillary seta from setiger 10; E, acicular spines from setiger 14; F, notopodial hooked seta from posterior bulbous section.

Description. Holotype (LACM-AHF Poly 13288) complete, 16.6 mm long, 0.25 mm wide across thoracic setigers and 0.41 mm wide across abdominal setigers; with 27 setigers, including 9 thoracic, 14 abdominal, and 4 in posterior bulbous section. Body long, thin, with most abdominal setigers each about as long as entire thoracic region. Thoracic region generally dorso-ventrally flattened, cylindrical in cross section. Dorsal surface of thoracic region with narrow dorsal ridge extending from peristomium to end of setiger 7 (Fig. 26A); venter relatively smooth with no ventral ridge or groove (Fig. 26B). Color in alcohol opaque white.

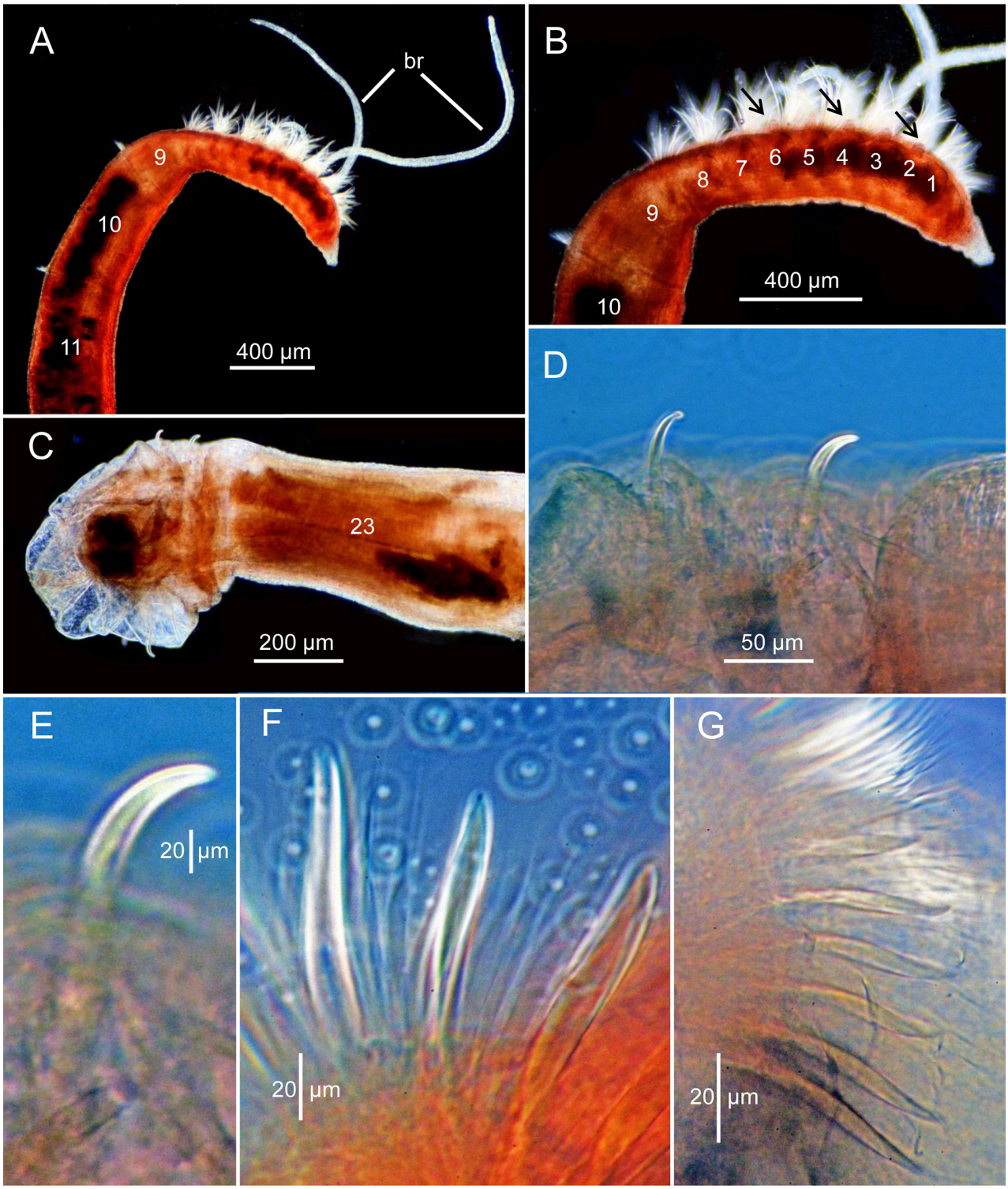

FIGURE 27. *Heterospio africana* **n. sp**. Holotype (LACM-AHF Poly 13288): A–B, anterior end, right lateral view; C, bulbous posterior section attached to setiger 23, right lateral view; D, two notopodial hooks from bulbous posterior section; E, detail of posterior hook; F, notopodial acicular spines from setiger 15; G, neuropodial acicular spines from setiger 16. Stained with Shirlastain A. Arrows on Figure 2B point to branchial stubs on the right side of setigers 2, 4, and 6.

Pre-setiger region triangular as long as first three setigers (Fig. 26A). Prostomium conical, smoothly rounded on tip (Fig. 26A–B); eyes absent; nuchal organs narrow grooves on posterior lateral margins at border with peristomium (Fig. 26A). Peristomium divided into the two rings by dorsolateral grooves from which dorsal tentacles arise in other species, but tentacles not attached in holotype. First ring very narrow; second ring as large as following setiger 1 (Fig. 26A). Peristomium interrupted dorsally by prominent dorsal crest on setiger 1 and continuing posteriorly as a narrow dorsal ridge to near end of setiger 7 (Fig. 26A). Ventrally, peristomium smooth, with oral opening a transverse slit bordered anteriorly by four lobes and posteriorly by a single curved lower lip (Fig. 26B); proboscis not observed.

Branchiae present on setigers 2–6 (Fig. 26A), with no evidence of scars or stubs on setiger 7 or later even when stained with MG or Shirlastain A; branchiae when present long, thin, rounded in cross section, tapering to rounded tip; branchiae with narrow ciliated groove; internal blood vessel extends along entire length.

All parapodia of thoracic and abdominal setigers biramous with setal fascicles arising from near anterior border of each segment; at least three of four setigers of posterior region biramous; last likely only with notosetae. Thoracic region with eight short setigers, each about twice as wide as long; with setiger 8 slightly longer, about half again as long as setiger 7; setiger 9 first elongated setiger, about 2.5 times longer than setiger 7. Setiger 10 first abdominal setiger, about as long as setigers 1–8 combined; subsequent abdominal setigers 11–23 each of a similar length, about as long as entire thoracic region (Fig. 27A). Thoracic notopodia through setiger 9 with notosetae arising as tight fascicles from simple grooves or notches; neuropodia of setigers 1–8 with a short postsetal lamella (Fig. 26B). Abdominal parapodia from setiger 10 with parapodia as narrow ridges or rows encircling each segment, with narrow dorsal, ventral, and lateral gaps separating noto- and neurosetae (Fig. 26A).

All thoracic noto- and neuropodia of setigers 1–9 with numerous long capillaries in tightly packed, spreading fascicles, of 25 to 30 or more long capillaries (Figs. 26A, 27A–B). Abdominal setigers 10–11 with two rows of capillaries, mostly encircling body; capillaries of first row thicker than thin capillaries of second row (Fig. 26D). Setigers 12–13 with subuluncini (Fig. 26C) and a few acicular spines in first row and thin capillaries in second row. Setigers 14–20 with acicular spines in first row (Fig. 26E) and thin capillaries in second row; rarely with aristate spines among the acicular spines. Acicular spines weakly curved, narrowing to narrow blunted tip (Figs. 26E, 27F–G). Far posterior setigers 21–23 with subuluncini replacing acicular spines in first row and thin capillaries in second row. Posterior bulbous section with four parapodia each with distinctly curved hooks (Figs. 26F, 27D–E); first three of these setigers biramous with two hooks; fourth setiger with only a single notopodial hook.

Posterior bulbous section as long as wide, heavily wrinkled, with parapodia best observed in anterior half (Fig. 27C); posterior half with large folds surrounding anal opening.

Methyl Green staining. No pattern.

Remarks. In *Heterospio africana* **n. sp**., the large peristomial crest continues along the surface of the first seven setigers as a narrow, but prominent mid-dorsal ridge. Such a prominent ridge has not been observed in other species. In addition, while *H. africana* **n. sp**. is one of several species to have setiger 9 as the first elongate setiger, about 2.5 times the length of setiger 8, it is the only species with branchiae limited to setigers 2–6. Species with branchiae from setiger 2–7 and a similarly long setiger 9 include *H. guiana* **n. sp**. and *H. paulolanai* **n. sp**.; however, both of these species lack a dorsal peristomial crest.

Etymology. The species is named for its occurrence off the SE coast of Africa.

Distribution. East Africa, off Mozambique, 55 m.

Heterospio antonbruunae new species

Figure 28

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Material examined. (*3 specimens*) **Indian Ocean, Mozambique Channel between SW Africa and Madagascar**, **International Indian Ocean Expedition**, Cruise 7, R/V *Anton Bruun*, **Sta. 363G**, 05 Aug 1964, Campbell grab, 23.633°S, 43.40°E, 1350 m, **holotype** (LACM-AHF Poly 13321), 1 **paratype** (LACM-AHF 13285); **Sta. 363L**, 06 Aug 1964, Campbell grab, 23.283°S, 43.50°E, 84l m, 1 **paratype** (LACM-AHF Poly 13284).

Description. All specimens incomplete, each with 11 setigerous segments. Holotype (LACM-AHF Poly 13321) 19.1 mm long and 0.26 mm wide across anterior segments; paratypes of similar lengths. Body long, thin and fragile,

generally cylindrical in cross section, with distinct evidence of tearing at posterior ends; without longitudinal grooves or ridges along dorsal and ventral surfaces. Segmental boundaries denoted entirely by location of parapodia and setal fascicles. Color in alcohol opaque white; pigment entirely absent.

Pre-setiger region short, as long as first two thoracic setigers (Fig. 28A–B). Prostomium oval, as long as wide, distinctly rounded on anterior margin, merged with peristomium mid-dorsally (Fig. 28B), ventrally bordered by anterior margin of mouth; eyespots absent; nuchal organs indistinct, narrow posterior lateral grooves anterior to first peristomial ring. Peristomium divided into two rings by dorsolateral grooves from which dorsal tentacles arise in other species (Fig. 28B), but tentacles not present on these specimens; location of paired grooves produce prominent mid-dorsal crest between them extending to anterior margin of setiger 1 (Fig. 28B). Mouth located mid-ventrally between prostomium and peristomium, consisting of a large oval opening surrounded by numerous short lobes (Fig. 28C); pharynx observed internally on holotype or inflated externally on paratypes.

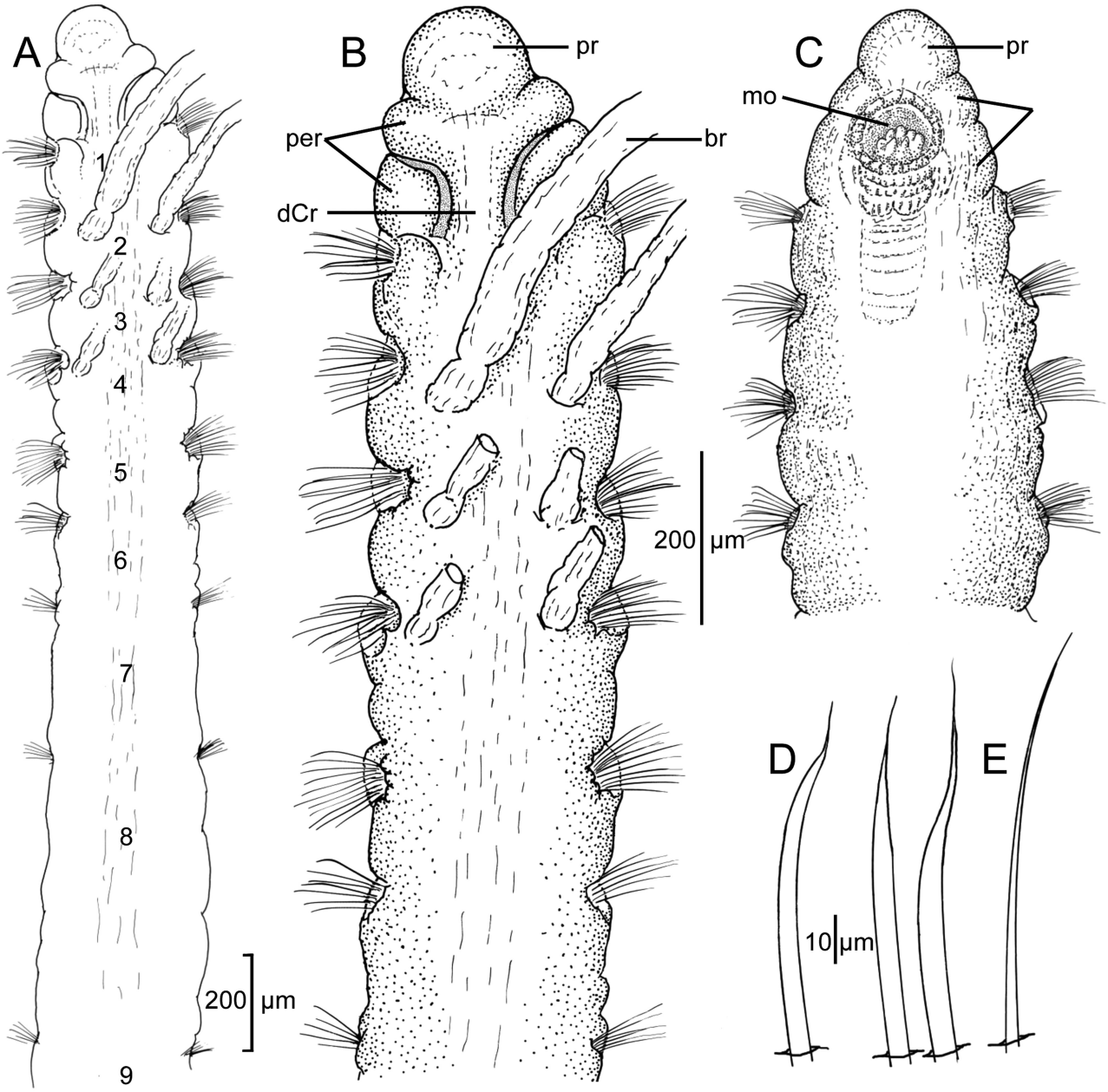

FIGURE 28. *Heterospio antonbruunae* **n. sp**. A, diagram of first nine setigers of holotype, dorsal view; B, first seven setigers of holotype, dorsal view; C, first four setigers of holotype, ventral view; D, three large neuropodial spinous-like capillaries from anterior row of setiger 11; E, thin neuropodial capillary from second row of setiger 11. A–B. holotype (LACM-AHF Poly 13321); C–E, paratype (LACM-AHF Poly 13285).

Branchiae present on setigers 2–4 (Fig. 28A–B); branchiae long, thin, rounded in cross section, tapering to rounded tip; branchiae with narrow ciliated groove; internal blood vessel extends along entire length.

All parapodia biramous with setal fascicles arising from near anterior border of each segment (Fig. 28B–C). Thoracic region of holotype and one paratype (LACM-AHF Poly 13285) with six short setigers, each slightly wider than long (Fig. 28A–B); segments from setiger 7 becoming progressively longer: setiger 7 first elongate setiger, about 1.5 x as long as setiger 6 (Fig. 28A); setiger 8 about 3.5 x as long as setiger 6 (Fig. 28A), followed by a very elongate setiger 9 about as long as entire anterior region from prostomium to end of setiger 8. Paratype (LACM-AHF Poly 13284) with setiger 6 first elongate, about 1.5 x as long as setiger 5. All thoracic parapodia including setiger 9 with setae arising from swollen notches; postsetal lamellae not observed. Abdominal parapodia from setiger 10 with parapodia as narrow ridges or rows extending along sides of each segment, with gaps between noto- and neurosetae. Nature of more posterior parapodia unknown.

Thoracic notopodia of setigers 1–9 with numerous long capillaries in tightly packed, dense spreading fascicles, 75 or more capillaries on setigers 1–6, number of capillaries reduced on setigers 7–9; setigers 10–11 with two rows of setae, both rows with capillaries on setiger 10; setiger 11 with thin capillaries in posterior row (Fig. 28E) and thicker, spinous-like setae in anterior row, thick basally and tapering to fine point (Fig. 28D), not appearing to be either mucronate spines or subuluncini.

More posterior segments and posterior end not present.

Methyl Green staining. Narrow transverse line across venter on anterior thoracic setigers, otherwise no pattern.

Remarks. In addition to *Heterospio antonbruunae* **n. sp**. from the Mozambique Channel in 854–1350 m, three other described species have branchiae on setigers 2–4, a broadly rounded prostomium, and the first elongate setiger anterior to setiger 9: *H. angolana* from 105 m off West Africa (Bochert & Zettler 2009); *H. bathyala* **n. sp**. from off the SE USA in 796–1509 m, and *H. reducta*, originally described from lower slope depths of 2335 m in the Mediterranean by Laubier *et al.* (1974) and variously reported from shallower bathyal depths off Ireland (Amoureux 1982; this study) and Iceland (Parapar *et al.* 2014). Of these four*, H. angolana* is the only one from shallow shelf depths and differs from the other three in having a single peristomial ring instead of two. Of the three deep-water species, *H. antonbruunae* **n. sp**. is most similar to *H. bathyala* **n. sp**. in having a broadly rounded prostomium and branchiae from setigers 2–4. The two species differ in that setiger 6 or 7 is the first elongate setiger in *H. antonbruunae* **n. sp**. instead of setiger 8 and the mouth opening *of H. bathyala* **n. sp**. has only 4–6 large lobes surrounding the mouth instead of many small ones. There are also acicular spines on setigers 12–14 of *H. bathyala* **n. sp**., however, these setigers are not yet known for *H. antonbruunae* **n. sp**. See Table 1 for further comparative observations.

Etymology. This species is named for the R/V *Anton Bruun*, the primary research vessel for the International Indian Ocean Expedition surveys of 1963–1965.

Distribution. Continental slope off Madagascar, Mozambique Channel, 854–1350 m.

Heterospio indica Parapar, Vijapure, Moreira & Sukumaran, 2016

Figure 29

Heterospio indica Parapar, Vijapure, Moreira & Sukumaran, 2016: 4–14, figs. 1–8.
Heterospio longissima: Rosenfeldt 1989: 231, fig. 7. **Not** Ehlers, 1874, 1875. *Fide* Parapar *et al.* (2016).
Heterospio longissima: Hartman 1974a: 232; 1974b: 625**;** Wehe & Fiege 2002: 60; **Not** Ehlers, 1874, 1875.

Material examined. (*2 specimens*) **Indian Ocean, International Indian Ocean Expedition**, R/V *Anton Bruun*, Cruise 4B, **Arabian Sea, Off Pakistan, S of Karachi, off mouth of Indus River**, **Sta. 230B,** coll. 15 Nov 1963, John Ryther, Menzies Trawl, 23.517ºN, 66.917ºE, 88 m, sand, green clay, mud, (1, LACM-AHF Poly 13286).—R/V *Anton Bruun*, Cruise 4B, **Arabian Sea off Madhavpur, India, Sta. 210A**, coll. 16 Nov. 1963, John Ryther, Gulf of Mexico shrimp trawl, 21.117°N, 69.8°E to 21.15°N, 69.8°E, 34–37 m, (1, LACM-AHF Poly 13287).

Description. Both specimens incomplete, each with 12 setigers. Body long, narrow, with evidence of tearing at posterior end; without longitudinal grooves or ridges along dorsal and ventral surfaces. Segmental boundaries denoted entirely by location of parapodia and setal fascicles. Body with nine anterior thoracic setigers with first eight crowded, each about five times wider than long (Fig. 29A–B), followed by an elongated setiger 9 about three times longer than each of first eight setigers. Following three abdominal segments each about as long as entire

thoracic region. Largest specimen (LACM-AHF Poly 13286) 25 mm long and 1.1 mm wide across setiger 6; second specimen (LACM-AHF Poly 13287) smaller, 8.3 mm long and 0.5 mm wide. Color in alcohol opaque white; pigment entirely absent.

Pre-setiger region triangular in shape, about as long as first three thoracic setigers (Fig. 29A–B). Prostomium conical, wide basally, tapering to broadly rounded tip (Fig. 29A–B); eyespots absent, nuchal organs narrow slits along posterior-lateral margin. Peristomium with two rings, separated by groove extending across ventral surface (Fig. 29B), interrupted dorsally by dorsal crest extending from prostomium to setiger 1 (Fig. 29A); no dorsal tentacles present, but scars evident in medial notch in dorsal groove between peristomial rings. Mouth arising on first peristomial ring, located between two large lateral lobes and a single posterior lobe or lip (Fig. 29B); proboscis not emergent on either specimen.

Branchiae present on setigers 2–9 on both specimens (Fig. 29A); most reduced to scars or stubs, but when present, branchiae long, thin, rounded in cross section, tapering to rounded tip; branchiae with narrow ciliated groove; internal blood vessel extending along entire length.

All parapodia biramous with setal fascicles arising from near anterior edge of each segment. All thoracic setigers slightly flattened dorsally with parapodia weakly inflated dorsally and bearing setal fascicles in tight bundles. Neuropodia with prominent digitate postsetal lobe on all nine thoracic setigers (Fig. 29B). Abdominal setigers round in cross section and bearing setae in two transverse rows encircling anterior border of each segment. Abdominal parapodia from setiger 10 as narrow transverse and elongate lobes, encircling anterior margin of setigers 10–12; noto- and neuropodia with distinct dorsal and ventral gaps between setal fascicles; lateral gaps between noto- and neuropodia narrower.

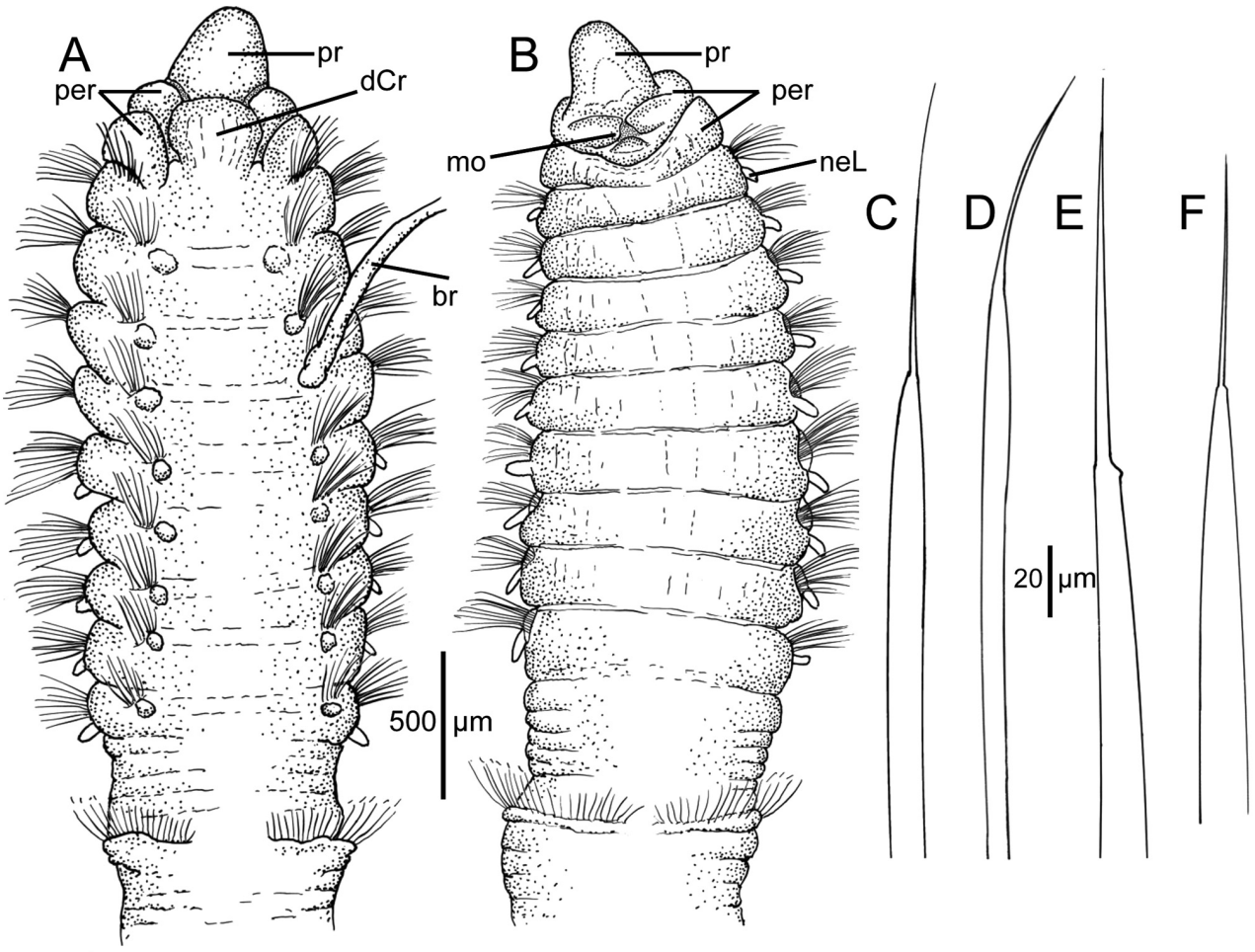

FIGURE 29. *Heterospio indica* Parapar *et al.* 2016 (LACM-AHF Poly 13286). A, anterior end, dorsal view; B, anterior end, ventral view; C–F, spinous neurosetae from setiger 12.

All thoracic notopodia of setigers 1–9 with 50–75 long capillaries in dense spreading fascicles; neuropodia with

similar numbers of capillaries in dense fascicles. Noto- and neuropodia of setiger 10 with thin capillaries arranged in two transverse rows with distinct dorsal and lateral gaps (Fig. 29A–B). Setigers 11–12 with anterior row containing thick spinous setae and posterior row with thin capillaries; spinous setae all with thick shaft, tapering to long, arista-like tip (Fig. 29C–F); these resembling different forms of subuluncini and aristate spines rather than capillaries as stated in Parapar *et al.* (2016). The few simple acicular spines present may be ones where tip has broken off.

Posterior region not present among fragments.

Methyl Green staining. Body staining uniformly; most of prostomium not staining, otherwise no pattern.

Remarks. The present specimens from shallow water in the Arabian Sea were originally referred to *H. longissima* by Hartman (1974a–b) and are here redescribed and referred to the recently described *H. indica* by Parapar *et al.* (2016) from the west coast of India. Although not mentioned by Parapar *et al.* (2016), a distinct dorsal peristomial crest and prominent neuropodial postsetal lamellae on thoracic setigers 1–9 were illustrated by these authors and occur in the present specimens. The only other species to have such prominent postsetal lamellae is *H. aruba* **n. sp**. described from shallow water in the Caribbean Sea (see above). The two species differ in that *H. indica* has both peristomial rings prominent on the ventral surface and the small oval mouth opening is surrounded by two large lateral lobes and a single posterior lobe; in contrast, *H. aruba* **n. sp.** has a smooth ventral surface lacking peristomial rings and the mouth is a simple transverse slit not surrounded by prominent oral lobes. In addition, *H. aruba* **n. sp**. lacks a dorsal peristomial crest instead of having one. *Heterospio aruba* **n. sp**. has branchiae on setigers 1–8 instead of 1–9; however, these specimens are smaller than recorded for *H. indica* and it is possible an additional branchia might develop with further growth. Although few specimens are available, it appears as if the neuropodial postsetal lamellae of *H. aruba* **n. sp**. are short over the first 1–3 setigers and then become longer over setigers 4–8 and then short again on setiger 9. In contrast, the neuropodial postsetal lamellae of *H. indica* are of a similar length over all nine setigers.

Parapar *et al.* (2016) described the spinous setae as different types of capillaries; however our interpretation is that these setae resemble the different kinds of subuluncini and aristate spines reported from species of *Heterospio* here and elsewhere.

Distribution. Arabian Sea, off Pakistan and W India 34–88 m (this study); W India 2.5–22 m (Parapar *et al.* 2016).

Discussion

Systematic Relationships

Although the name *Heterospio* suggests an affinity with Spionidae, morphological and molecular results indicate a close relationship to cirratuliform polychaetes (Blake & Maciolek 2019; Rouse *et al.* 2022). Morphologically, the nature of the pre-setiger region, long filiform branchiae, and arrangement of abdominal setae into cinctures are similar to those of cirratulids. In addition, the hooked setae found in the neuropodia of *Heterospio alata* **n. sp**. are of the "*alate*" type, previously known only from the cirratulid genus *Caulleriella* (Blake 2021b). However, the extremely long abdominal segments and bulbous posterior region with curved hooks are entirely unique features that define *Heterospio* species and distinguish them from other polychaetes.

Rouse *et al.* (2022) used 18S rDNA sequences from two species, *H. catalinensis* and *H. indica*, and demonstrated that *Heterospio* was a well-supported sister-taxon to the Cirratulidae, Acrocirridae, and Flabelligeridae, confirming a similar assessment of a similarity to cirratuliforms by Blake & Maciolek (2019) based on morphology and a COI sequence from *H. indica* made by Parapar *et al.* (2016). The two species that provided DNA data are from relatively shallow habitats on the continental shelf. Given that most of the now known 23 species of *Heterospio* are relatively rare and from offshore habitats >250 m, it is unlikely that a phylogenetic analysis of relationships within the genus based on DNA will be forthcoming anytime soon.

Systematic Problems

The main problem identified in the present study is with the identity of *Heterospio longissima*, the type-species of the genus originally reported by Ehlers' (1874, 1875) from upper continental slope depths (837 m) SW of Ireland. The type is considered to be lost and to date there have been no confirmed specimens collected that agree with Ehlers' (1874, 1875) original description. Instead, an alternate concept of the species reported by Hartman (1965) has been used globally to identify *H. longissima*. In the present study, we have re-examined Hartman's original

materials and identified significant differences between her published description and the actual specimens. We have, therefore, referred Hartman's original materials to two separate new species, *H. hartmanae* **n. sp**. and *H. guiana* **n. sp**., neither of which agree with either Ehlers' or Hartman's concept of *H. longissima*.

Surveys in the general vicinity of Ehlers' collecting site have yielded confusing and contradictory results. Amoureux (1982, 1987) reported but did not describe specimens he identified as *Heterospio longissima*. In addition, he reported *H. reducta*, a species originally described from the Mediterranean from some of the same samples as his *H. longissima*. We also found specimens of *H*. cf. *reducta* from off Ireland in one of our samples (MCZ 100580) in about 980 m. Parapar *et al.* (2014) described specimens from off Iceland that he identified as *H. longissima sensu* Hartman, 1965. However, given that we have determined that Hartman's description was in error and the Parapar *et al.* description does not agree with Hartman's erroneous description, it is likely that those specimens represent an undescribed species. To date, no specimens that agree with Ehlers' original account have been reported anywhere in the North Atlantic. An examination of the specimens identified as *H. longissima* by Amoureux (1982) would therefore be of considerable interest to locate and examine.

Morphology

The major characters traditionally used to characterize species of *Heterospio* include: (1) the number of branchiae, (2) the position of the first elongated segment and its length relative to both the preceding segment and the following one, (3) the presence or absence of modified neurosetae on setiger 1, and (4) the kinds of setae in the abdominal segments, including where they occur or change. Setae include capillaries, acicular spines, aristate spines, and subuluncini. As part of the present study, other characters not typically observed have proven to be important. A discussion of these and the more traditional characters follows. Table 1 provides a summary of the main morphological characters required to identify the known species of *Heterospio*.

Number of setigerous segments. Prior to this study, the only complete specimen of *Heterospio* was the fragmented holotype of *H. peruana* Borowski, 1994 that was of composed of three parts and included 22 setigers (nine thoracic, eight abdominal, and five posterior setigers). Complete specimens have been discovered in five of our new species: *Heterospio hartmanae* **n. sp**. (27 setigers: nine thoracic, 15 abdominal, three posterior); *H. dibranchiata* **n. sp**. (27 setigers: nine thoracic, 15 abdominal, three posterior); *H. alata* **n. sp**. (24 setigers: nine thoracic, 11 abdominal, four posterior); *H. ehlersi* **n. sp**. (26 setigers: nine thoracic, 14 abdominal, three posterior); *H. africana* **n. sp**. (27 setigers: nine thoracic, 14 abdominal, four posterior). These results suggest that the final adult segment configuration consists of about 24–27 setigers.

Thoracic or anterior region. The thoracic region includes the pre-setiger region and the following 8–9 setigerous segments that have defined setal fascicles located on the dorso-lateral anterior margins of each setiger. These setal fascicles differ from those of abdominal segments where the setae arise in rows that may encircle the segment in cinctures in a manner similar to those of some cirratulids of the genus *Chaetozone*. The transition from the more consolidated setal fascicles to the cincture-like fascicles defines the boundary between thoracic and abdominal segments. In most species, the first nine setigers constitute the thoracic region with setiger 10 being the first abdominal segment.

Pre-setiger region. The pre-setiger area includes the prostomium with nuchal organs, peristomium with dorsal tentacles, and the ventral oral opening. The prostomium is typically described as conical, but in fact there are two different forms: (1) triangular or conical, tapering to a narrow apex and (2) broadly rounded and flattened to nearly disk-like. The difference between these two prostomial shapes is striking, yet has not been emphasized in previous descriptions despite *Heterospio longissima*, the type-species (Ehlers 1875), and both *H. mediterranea* and *H. reducta* (Laubier *et al.* 1974) being originally illustrated with a broadly rounded prostomium. In the present study, *H. antonbruunae* **n. sp**., *H. bathyala* **n. sp**., *H*. cf. *reducta*, and *H. southwardorum* **n. sp**. have prostomia that are broadly rounded and flattened or disk-like.

The nature of the mouth or oral opening has not been reported in any previous description apart from noting an emergent sac-like proboscis on some specimens (Borowski 1994; Parapar *et al.* 2014, 2016). In the present study, we have examined the ventral side of the pre-setiger region of each species. When the pharynx is not everted, a wide range of morphology of the mouth is evident, from a wide transverse slit to a narrow vertical or narrow triangular opening or large oval opening. The oral opening is surrounded by lobes of various sizes on the anterior, posterior, or lateral sides. In *H. dibranchiata* **n. sp**., two larger lobes lateral to the oral opening were at first mistaken for an everted proboscis when seen in lateral view. The diverse nature of oral morphology in *Heterospio* warrants further investigation as a useful taxonomic character.

TABLE 1. Morphological Characteristics of the Known Species of *Heterospio*.

Species/ Character	Prostomium	Peristomium	First elongate setiger	Branchiae	Neuro-podial postsetal lamellae/ lobes	Neuro-podial hooks Setiger 1
longissima	Broadly rounded ant margin	1 ring w/o dorsal crest	Set 9, as long as set 1–8	Set 2–9	Absent	Absent
alata **n. sp.**	Triangular, tapering to narrow tip	1 ring, w/ dorsal crest	Set 9, as long as set 1–6	Set 2–3	Absent	Present, w/ 2 teeth "alate"
africana **n. sp.**	Conical, rounded on tip	2 rings, first very narrow; w/ large dorsal crest	Set 9, ca. 2.5x as long as set 8	Set 2–6	Present; short lobe set 1–6	Absent
angolana	Broadly rounded	1 ring	Set 6–8 each progressively longer; set 9 1st long body seg	Set 2–4	Present, low lobes, set 1–5	Absent
aruba **n. sp.**	Conical, tapering to narrow rounded tip	2 rings, incomplete dorsally & ventrally	Set 9, as long as set 6–8	Set 2–8	Present, short lobes, set 1–9	Absent
antonbruunae **n. sp.**	Short, as long as wide; broadly rounded	2 rings, incomplete dorsally & ventrally	Set 7, ca.2x as long as 6; set 8 ca. 4x longer than 6	Set 2–4	Absent	Absent
bathyala **n. sp.**	Flattened, disk-like, broadly rounded anteriorly	2 rings, 1st narrow; 2nd large; w/ dorsal crest	Set 8, as long as set 1–4; set 9 20x longer than 1–7	Set 2–4	Absent	Absent
bidentata **n. sp.**	Pear-shaped, tapering to rounded tip	2 rings; w/ dorsal crest	Set 7, ca. 2x times longer than 6; set 8 as long as set 1–6; set 9 similar lengths.	Set 2–5	Absent	Present, bidentate
brunei **n. sp.**	Conical, tapering anteriorly to narrow, rounded tip	2 rings incomplete dorsally, complete ventrally	Set 9, ca 2x as long as set 8	Set 2–5	Absent	Absent
canariensis **n. sp.**	Triangular, broad broadly rounded tip,	2 rings, 1st narrow, forming anterior lip of mouth; 2nd larger, bulbous w/ dorsal crest continuing to middle set 3	Set 9, ca. as long as set 5–8	Set 2	Absent	Absent
catalinensis	Conical, w/ narrow rounded tip	2 rings, 1st narrow, 2nd larger, dorsally complete	Set 9, ca. long as set 1–4	Set 2–9	Present; short lobe set 1–8	Present, acicular
dibranchiata **n. sp.**	Triangular, tapering to narrow tip	1 ring, incomplete, separated by dorsal crest & ventral ridge	Set 7–9 each progressively longer than set 6: set 7 (2 x), set 8 (3.5 x) & set 9 (ca. 9 x)	Set 2–3	Absent	Absent

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TABLE 1. (Continued)

Species/ Character	Prostomium	Peristomium	First elongate setiger	Branchiae	Neuro-podial postsetal lamellae/ lobes	Neuro-podial hooks Setiger 1
ehlersi **n. sp.**	Triangular, tapering to rounded tip	1 ring, incomplete dorsally, separated by dorsal crest	Set 9, ca. 2.5 x as long as set 8	Set 2–4	Absent	Absent
guiana **n. sp.**	Triangular, tapering to narrow tip	2 thick rings	Set 9, ca. 3 x longer than set 8	Set 2–7(8)	Absent	Absent
hartmanae **n. sp.**	Pear-shaped, tapering to narrow, rounded tip	2 thick rings	Set 9, ca. 2.5 x longer than set 8	Set 2–5	Absent	Absent
indica	Triangular, broadly rounded on tip	1 ring, w/ dorsal crest	Set 9, ca. 2x longer than set 8	Set 2–9	Present, prominent lobe set 1–9	Absent
knoxi **n. sp.**	Triangular, narrowly rounded on tip	2 rings complete dorsally; w/ dorsal crest; ventrally entire	Set 9, ca 3x longer than set 8	Set 2–9	Present, set 1–9, low flange post to fascicle	Absent
mediterranea	Broadly rounded, disk-like	2 large rings	Set 9, ca. as long as set 1–8	Set 2–8	Absent	Absent
paulolanai **n. sp.**	Pear-shaped, tapering to narrow rounded tip	2 rings, incomplete dorsally, merged ventrally	Set 9, ca. 2.5 x as long as set 8	Set 2–8 (?9)	Present low ridge post to fascicle	Absent
peruana	Conical, broadly rounded on tip	2 rings, incomplete dorsally	Set 9, 2–3.5 x as long as set 8	Set 2–5	Absent	Absent
reducta	Triangular w/ broadly rounded tip	2 rings, 1st narrow, 2nd larger, w/ low crest; entire across venter	Set 8, as long as set 1–7	Set 2–4	Absent	Absent
sinica	Conical, tapering to rounded tip	2 rings, 1st narrow	9, ca. as long as set 1–5	Set 2–9	Absent	Absent
southwardorum **n. sp.**	Broadly rounded, disk-like	2 rings, 1st narrow w/ nuchal organ on ant border; entire across venter	9, as long as set 1–8	Set 2–7	Present, short lobe set 1–7	Absent

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TABLE 1. (Continued)

Species/ Character	Setae setiger 10 or first abdominal setiger	Setae of subsequent abdominal setigers	Oral morphology	Posterior region	Distribution	Reference
longissima	Capillaries	Set 11–12 capillaries	2 transverse lobes ant to mouth	Unknown	N Atlantic, Off SW Ireland, 837 m	Ehlers 1874, 1875
alata **n. sp.**	Capillaries	Ac spines in 1st row; capillaries in 2nd row	Narrow vertical slit between 4 lateral lobes	Bulbous, w/ 4 set, each with curved hooks	South China Sea, off Borneo, 1114–1453 m	This study
africana **n. sp.**	Capillaries	Set 11–12, 2 rows of caps; set 12–13 w/ subuluncini in 1st row, caps in 2nd; 14–20 w/ ac spines 1st row, caps 2nd.	Narrow transverse slit; w/ 4 lobes on anterior border and simple posterior lip; pharynx not observed	Bulbous w/4 set, each with curved hooks	East Africa, off Mozambique, 55 m	This study
angolana	Capillaries	Set 11 capillaries; Set 12–15 ant row subuluncini, post row pointed ac spines	Unknown; sac-like proboscis	Unknown	SE Atlantic, off Angola, 105 m	Bochert & Zettler 2009
aruba **n. sp.**	Capillaries	Set 11–13 aristate spines 1st row; capillaries 2nd row. Few simple ac spines with aristate from set 13	Simple narrow transverse slit; proboscis not observed	Unknown	Caribbean Sea, off Island of Aruba, 30 m	This study
antonbruunae **n. sp.**	Capillaries	Set 11 capillaries 1st row, spinous capillaries 2nd row	Large oval opening surrounded by small lobe; internal pharynx observed	Unknown	Indian Ocean, Mozambique Channel, 854–1350 m	This study
bathyala **n. sp.**	Set 9–11 w/ caps in 2 rows	Set 12–14 ac spines in 1st row, capillaries in 2nd row	4–6 short lobes surround oral opening	Bulbous, w/ 2–3 set, each w/ curved hooks	SE USA, off Carolinas, 796–1509 m	This study
bidentata **n. sp.**	Set 9 w/ ac. spines in both noto- and neuropodia	Setigers 9–14 w/ ac spines in 1st row of cinctures; capillaries in second row	Mouth a semi-circular opening on 1st peristomial ring, w/ 7 short lobes on ant border	Unknown	Queensland, Eastern Australia, 2093–2156 m	This study
brunei **n. sp.**	Set 10 w/ ac spines in both noto- & neuropodia	Set 10–19 w/ ac spines in 1st row & capillaries in 2nd row	mouth a wide transverse opening w/ short lobes on ant & post lips	Bulbous, w/ 4 set each w/ 1–2 acicular spines in each ramus	South China Sea, off Borneo, 1400–1922 m	This study

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TABLE 1. (Continued)

Species/ Character	Setae setiger 10 or first abdominal setiger	Setae of subsequent abdominal setigers	Oral morphology	Posterior region	Distribution	Reference
canariensis **n. sp.**	Ac spines in both noto- & neuropodia	Set 10–13 w/ ac spines in 1st row & caps in 2nd row	Mouth a transverse slit w/ 6 lobes on ant lip & smaller lobes on post lip, merging w/ ventral ridge extending over set 1–5	Bulbous, oval-shaped, w/ 3 set, each ramus w/ 1–2 hooked spines	E North Atlantic. off Canary Islands, 2351–2988 m	This study
catalinensis	Caps & few subuluncini in neuropodia	Set 10–13 (?) in cinctures; caps and subuluncini	Mouth not reported; proboscis a smooth sac	Bulbous, elongate, with 4–5 set each ramus w/ hooked spines	Southern California, ca. 75 m	Hartman, 1944, 1957, 1969; This study
dibranchiata **n. sp.**	Capillaries	Set 11–12: 1st row ac spines, 2nd row caps; Set 13–24: 1st row ac spines; 2nd row aristate-like subuluncini.	Mouth narrow vertical slit bordered anteriorly by 3 short narrow lobes, laterally by 2 large lobes & posteriorly by 7–9 lobes	Bulbous w/ terminal anus; w/ 3 set, each w/ 1–2 hooked spines in each ramus	Gulf of Mexico, off Louisiana 241–955 m	This study
ehlersi **n. sp.**	Ac spines in both noto- & neuropodia	Set 11-23 w/ ac spines in 1st row & caps in 2nd row	Mouth a transverse opening with a row of short lobes on posterior lip	Bulbous ca. as wide as long; w/ 3 setigers each with 1–2 hooked spines	South China Sea, Gulf of Thailand 60–70 m	This study
guiana **n. sp.**	Capillaries	Set 11–12: w/ aristate spines in 1st row; caps in 2nd row	Simple opening between 6–8 lateral lobes; proboscis sac-like, emergent on few specimens	Unknown	Off NE South America, Suriname, 520–550 m	This study; Hartman 1965 as *H. longiissima* (in part)
hartmanae **n. sp.**	Ac spines in 1st row; caps in 2nd row	Set 11–24:w/ ac spines in 1st row; caps in 2nd row	Transverse opening w/ 7–8 short lobes on ant lip & 3–4 narrow lobes on post lip; pharynx when everted short rounded sac	Bulbous, w/ 3 set each w/ 2 ac spines in each ramus	W North Atlantic, off eastern North America, 2470–4950 m	This study; Hartman 1965 as *H. longiissima* (in part)
indica	Caps w/ setae of 1st row thicker than those of 2nd row	Set 11–13: 1st row w/ subuluncini; 2nd row w/ thin caps	2 large lateral lobes & a single posterior lobe or lip	Bulbous, w/ 5 set each bearing 2–4 acicular hooks	Arabian Sea, W coast of India, 2.5–22 m	Parapar *et al.* 2016; This study

.....continued on the next page

TABLE 1. (Continued)

Species/ Character	Setae setiger 10 or first abdominal setiger	Setae of subsequent abdominal setigers	Oral morphology	Posterior region	Distribution	Reference
knoxi **n. sp.**	Caps w/ setae of 1st row thicker than those of 2nd row	Set 10–11 w/ caps in both rows; setiger 11 w/ subuluncini and acicular spines in first row; set 12–13 w/ aristate and acicular spines	Elongate slit w/2 large lateral lobes; posterior lip smooth	Unknown	New Zealand, 12–117 m	Knox 1960; This study
mediterranea	Capillaries	Set 11–12, caps; set 13 w/ subuluncini and ac spines in 1st row, caps, in 2nd row	Unknown	Unknown	Mediterrean Sea off Marseille Fr, & Spain, 100–350 m;	Laubier, *et al*. 1974
paulolanai **n. sp.**	Capillaries	Set 11 w/ ant row aristate spines & post row caps. Set 12 w/ ant row ac spines & post row of subuluncini.	Mouth a transverse slit opening between 2 large lateral lobes and simple ant and post lips.	Unknown	Off NE Brazil, 69 m	This study
peruana	1st row subuluncini; 2nd row caps	Set 11–12 (?13+) w/ aristate spines (+ few ac spines) in 1st row; 2nd row caps	Unknown; everted proboscis sac-like	Bulbous, w/ 5 set with curved hooks	Off Peru 4125–4188 m; 4423 m	Borowski 1994; This study
reducta	Set 9, caps	Set 10–12, caps in both rows	Unknown; everted proboscis sac-like	Unknown	Mediterranean Sea, 1200–1800m, 2335 m; off SW Ireland, 500–1400 m; off Iceland, 270–922 m	Laubier, *et al*. 1974; Amoureux 1982; Langeneck *et al*. 2017; Parapar *et al*. 2014; This study
sinica	Set 10–12, 1st row subuluncini; 2nd row caps	Set 13–17, ant row, w/ aristate spines; post row caps	Unknown; proboscis a pouch	Unknown	East China Sea, 30 m	Wu & Chen 1966
southwardorum **n. sp.**	Set 10–11 w/ caps in 2 rows	Set 12 w/ caps in notopodia & few ac spines in 1st row of neuropodia; set 13 w/ ac spines 1st row & caps in 2nd row of noto- and neuropodia	Mouth a triangular-shaped opening surrounded laterally by thickened lobes; proboscis not everted	Unknown	N Atlantic, Bay of Biscay off Spain, 641 m	This study

Abbreviations: abd, abdominal; ac, acicular, ant, anterior; ca., about; caps, capllaries; post, posterior; seg, segment; set, setiger(s); w/, with; w/o, without.

The peristomium typically exhibits one or two lobes or rings dorsally and laterally, with these usually not continuing onto the relatively smooth venter that extends posteriorly from the posterior lip of the mouth. Dorsally, the first peristomial ring is typically narrower than the second, with the nuchal grooves located on the anterior edge of the ring or posterior margin of the prostomium. The first ring is separated from the second by a groove that typically ends in a medial notch from which the dorsal tentacles emerge. Both *H. dibranchiata* **n. sp**. and *H. alata* **n. sp**. have only a single large peristomial ring. In these species, the nuchal organs are grooves on the posterior margin of the prostomium anterior to the peristomial ring. In several species a mid-dorsal crest is present extending from the prostomium posteriorly over anterior setigers to varying degrees. In *H. alata* **n. sp**., *H. bidentata* **n. sp**., and *H. dibranchiata* **n. sp**., the dorsal crest appears to be an extension of the prostomium, similar to a spionid caruncle that continues posteriorly over the peristomium and merges with setiger 1, but often extends more posteriorly. In *H. canariensis* **n. sp**., the dorsal crest extends from the prostomium posteriorly onto setiger 2. In *H. aruba* **n. sp**. and *H. canariensis* **n. sp**., a ventral ridge extends from the posterior lip of the mouth posteriorly over five or more setigers. Details of these characteristics of the pre-setiger region have not been emphasized in previous descriptions.

Although dorsal tentacles were rarely attached to the specimens examined, there do appear to be differences among species in their structure. For example, the dorsal tentacles of *Heterospio bathyala* **n. sp**. are long, relatively thin and weakly lobed along their length, and only slightly larger in diameter than the branchiae (Fig. 6A, E). In contrast, the dorsal tentacles of *H. catalinensis* are large, thickened along their length, and have a deep ciliated groove; they are considerably larger than the branchiae (Fig. 22A). These differences in the size and configuration of dorsal tentacles among species suggest different feeding strategies. Unfortunately, the dorsal tentacles are usually lost during collection and preservation and living specimens have never been observed.

Thoracic setigers. The anterior or thoracic setigers of *Heterospio* species typically consist of eight or nine segments that are initially short and wider than long; the last one to three of these segments becomes longer in different species-specific patterns and begins to resemble the elongate abdominal segments. For example, in *H. aruba* **n. sp**., *H. brunei* **n. sp**., *H. guiana* **n. sp**., *H. hartmanae* **n. sp**., and *H. paulolanai* **n. sp**. the ninth setiger is the first noticeably elongate segment but it is only two to three times longer than setiger 8. In *H. canariensis* **n. sp**. the ninth setiger is also the first elongate segment, but it is as long as setigers 1–5 combined; in *H. southwardorum* **n. sp**. the ninth setiger is as long as the first 1–8 setigers combined, and in *H. alata* **n. sp**. the ninth setiger is as long as setigers 1–7. A different segmental pattern occurs in *H. bathyala* **n. sp**. where setiger 8 is the first elongate setiger and is about as long as setigers 1–6 combined and setiger 9 is very long, about 20x as long as setigers 1–7 combined. In *H. dibranchiata* **n. sp**., setigers 1–6 are short and setigers 7–9 become progressively longer than each of the first six setigers: setiger 7 is 2x longer; setiger 8 is 3.5x longer, and setiger 9 is about nine times longer than each of setigers 1–6.

Thoracic parapodia are relatively simple with notosetae usually emerging directly from the body wall. Neuropodia appear to be better developed, they are usually a cushion-like pad from which setae emerge. In some species a short postsetal lobe or lamella is present; these are especially well-developed in *H. aruba* **n. sp**. and *H. indica*. Apart from four species that have uni- or bidentate hooks in the neuropodia of setiger 1, all thoracic setae are capillaries. These may be relatively simple spreading fascicles of 15–20 capillaries or dense fascicles of 50 or more depending on the species.

Branchiae have been observed on all species described to date and first occur from setiger 2 slightly medial to and near the base of the notopodia and emergence of notosetae. Among the species known to date, the following branchial patterns have been observed: **one pair** *H. canariensis* **n. sp**.; **two pairs** *H. alata* **n. sp**. and *H. dibranchiata* **n. sp**.; **three pairs** *H. antonbruunae* **n. sp**., *H. angolana*; *H. bathyala* **n. sp**., *H. ehlersi* **n. sp**. and *H. reducta*; **four pairs** *H. brunei* **n. sp**., *H. bidentata* **n. sp**., *H. hartmanae* **n. sp**., and *H. peruana*; **five pairs** *H. africana* **n. sp**.; **six pairs** *H. southwardorum* **n. sp**., **seven pairs** *H. aruba* **n. sp**., *H. guiana* **n. sp**., *H. paulolanai* **n. sp**, and *H. mediterranea*; **eight pairs** *H. longissima*; *H. catalinensis*, *H. indica*, *H. knoxi* **n. sp**., and *H. sinica*. It is also likely that *H. paulolanai* **n sp**. has eight pairs of branchiae; however damage to setiger 9 on the holotype precludes confirmation that branchiae might be present on that segment. When present, branchiae are long and filamentous, often crenulated or nearly moniliform and have a central blood vessel. However, most elongate or intact branchiae are usually missing, but are denoted by scars, short stubs, or short developing branchiae. Branchial scars are easily observed when the specimen is stained with Shirlastain A or MG.

Abdominal region. The actual transition from thoracic to abdominal setigers does not begin until the parapodia change from narrow podia and setal fascicles to paired elongate rows of setae that emerge from ridges and extend as longitudinal cinctures around each segment. Initially, these paired rows of setae may exhibit large gaps dorsally

between the notopodia and ventrally between the neuropodia, and also laterally between the noto- and neuropodia. These gaps tend to be reduced in more posterior abdominal setigers as spines replace the capillaries. In cinctures having rows of spines that surround the body, these cinctures resemble those found in cirratulid polychaetes of the genus *Chaetozone* (Blake & Magalhães 2019).

Abdominal segments are usually many times longer than the entire thoracic region. However, individual abdominal segments do not appear to have fixed lengths and likely are capable of considerable stretching, probably due to the numerous transverse muscle bands that are present on most of the segments. Living specimens have not been observed, however, to confirm such behavior.

Abdominal setae include capillaries, acicular spines, aristate spines, and subuluncini. The presence or absence of these various types of setae are important systematic characters. However, in some species there may be a transition from capillaries, e.g., on setiger 10, to spines by setiger 12 or 13, which means that if one only has specimens with up to 11 setigers and only capillaries are present, it is not possible to know if additional segments would yield other kinds of setae. Unfortunately, this is the situation with the type-species, *H. longissima*, and *H. reducta*, both widely reported in the literature.

Posterior region. The posterior region of *Heterospio* consists of a long narrow asetigerous section extending from the last abdominal setiger and attached to a compact bulbous enlargement organized into 3–5 separate setigers and containing curved hooks. These setigers usually have two or up to three hooks in each of the noto- and neuropodia; Borowski (1994) noticed that the last or terminal setiger of *H. peruana* had only notopodial hooks. The hooks are short and thickened, terminating in a pointed or rounded tip and directed anteriorly. The pygidium or anal opening is on the posterior end and sometimes recessed between two rounded lobes.

Biology

Little is known concerning the biology of *Heterospio*, largely due to the lack of living specimens as well as the fragmented nature of most specimens that have been studied to date.

Habitat. *Heterospio* species appear to be deep-burrowing worms that are found in sediments having well-mixed high sand and silt inventories. Regardless of where collected, species of *Heterospio* are not common and are considered rare (Blake & Maciolek 2019). One exception to this generality is in the Marlborough Sounds of New Zealand where Estcourt (1967) recorded *Heterospio* sp. as one of the most frequently encountered polychaetes. In our data, one of our new species, *Heterospio dibranchiata* **n. sp**., while rare, was widely distributed at sites ranging from 241–955 m off Louisiana in the Gulf of Mexico. The species was among the top ten numerical dominants at one location at 955 m where 10 of the 39 specimens were collected.

On the Atlantic slope and rise, *Heterospio bathyala* **n. sp**. was limited to Stations 11 (off Cape Fear, NC) and 14 (off Charleston, SC) along the 800 m isobath. These locations were adjacent sites having complex local bottom currents influenced by the Gulf Stream (Blake & Grassle 1994); both sites were thought to be depositional with well-mixed sediments having roughly equivalent amounts of sand, silt, and clay (Blake & Grassle 1994). It is noteworthy that apart from one additional specimen, this species did not occur at any of the other five sites in the 600–1500 m depth range sampled off the Carolinas in the same program (Blake *et al.* 1987).

Heterospio hartmanae **n. sp**. (as *H. longissima* in Hartman 1965 and Hartman & Fauchald 1971) was routinely collected at abyssal sites along the Gay-Head Bermuda Transect, but also occurred at a few lower continental slope and rise sites in the ACSAR surveys in the U.S. South Atlantic region (Blake & Grassle 1994). The species occurred at two of the four 3000 m stations off the Carolinas: Sta. 13 off Cape Fear, NC, and Station 16 off Charleston, SC, where the species was the fourteenth most abundant species (Blake & Grassle 1994).

Burrowing and feeding. Borowski (1994) observed that specimens of his abyssal species, *H. peruana*, were recovered from depths of 5–20 cm in the sediment, thus forming deep burrows. Borowski (1994) observed a mucoid sheath on one specimen; we observed adhering tube fragments in *H. bidentata* **n. sp**.; these observations may suggest tube formation.

Jumars *et al.* (2015) suggested that the enlarged posterior end of *Heterospio* might provide these worms with the ability to burrow backward more often than burrowing forward. However, the bulbous posterior end more than likely serves as an anchoring device because the paired hooks are directed anteriorly and could serve to hold the worm in place, but could also assist in moving the worm deeper into the sediment. As noted in the morphology section, the numerous narrow annular rings on the elongated segments suggest that these segments are capable of considerable stretching and contraction. How this capability actually works in burrowing and other activities is not known.

Parapar *et al.* (2016) confirmed that palps (i.e., dorsal tentacles) were present in *H. indica*; in this study, we have

confirmed that dorsal tentacles are definitely present in *H. bathyala* **n. sp**. (Fig. 6A–B) from off the Carolinas, *H. catalinensis* off southern California, and *H. dibranchiata* **n. sp**. from the Gulf of Mexico. Jumars *et al.* (2015: A149) suggested that if palps were present, *Heterospio* species are likely discretely mobile and potentially subsurface deposit feeders similar to cirratulids. In the present study we have observed dorsal tentacles in three species of which those of *H. bathyala* **n. sp**. and *H. dibranchiata* **n. sp**. while larger than the branchiae, are relatively thin as in cirratulids providing support to the deposit feeding strategy suggested by Jumars (2015). However, the dorsal tentacles of *H. catalinensis* are large, thickened, and with a prominent ciliated groove, suggesting a possible interface feeding strategy as in spionids.

Reproduction and development. Nothing is known concerning reproduction in *Heterospio*. Uebelacker (1984) found large eggs and sperm in specimens she examined from the Gulf of Mexico and we have observed large oocytes of 152 µm in largest diameter in *H. alata* **n. sp**., 145–160 µm in *H. knoxi* **n. sp**., and up to 182 µm in *H. brunei* **n. sp**. The presence of large eggs suggests a direct or lecithotrophic type of development.

Examination of several small complete specimens and juveniles suggests that the final number of segments is developed early and between the thoracic, abdominal, and posterior sections approximately 24 to 27 total setigers are developed. Initially, most of the abdominal segments, while long, are of a similar length. This suggests that with growth, the existing segments become larger and longer rather than additional segments being added.

Bathymetry

The depth distributions of all known species of *Heterospio* are plotted in Table 2. The 23 taxa can be roughly divided into continental shelf species, 0–250 m (10); upper and middle continental slope species, 250–2000 m (9); and lower continental slope and abyssal species, 2000–5000 m (5). Thus, species of *Heterospio* can be found over all depth ranges, but with most (14) collected in deep-water 250 m or deeper off the continental shelf. The three species with the shallowest depth records are *H. indica* (2–22 m), *H. aruba* **n. sp**. (30 m), and *H. sinica* (30 m). Only two species have been found in abyssal depths >3000 m: *H. hartmanae* **n. sp**. from the North Atlantic Ocean and *H. peruana* from the Eastern Pacific Ocean off South America.

Heterospio reducta is plotted twice in Table 2 to emphasize the distinct differences in depth and geographic distribution recorded for the original deep-sea type collection from the Mediterranean Sea and later accounts from the northeast Atlantic Ocean. These disjunct geographic and bathymetric records suggest that more than one species is involved. This possibility is further supported by the fact that because no single specimen having more than 12 setigers has ever been reported, the far posterior sections of these specimens remains unknown and their identity cannot be confirmed.

Geographic Distribution

The distribution of all 23 known species of *Heterospio* are shown on a map with each species plotted by their type locality (Figure 30). These results show that the known species are distributed more or less uniformly with North America, South America, Africa, and Europe each having four species; two from Australia and New Zealand, and the remaining five from Asia and India. Five additional undescribed species currently referred to known species or with provisional designations are recorded but not plotted from off Iceland (2), the Gulf of Mexico (1), Peru (1), Japan (1), and the Andaman Sea (1).

In general, specimens of *Heterospio* are rarely collected. Exceptions are where numerous samples are collected as part of large monitoring or reconnaissance surveys. For example, (1) 55 specimens of *H. hartmanae* **n. sp**. were collected as part of the deep-water transects from New England to Bermuda in the 1960s and as part of the ACSAR program off the U.S. Atlantic coast 1980s, (2) 27 specimens of *H. bathyala* **n. sp**. from off SE USA, were collected, also as part of the ACSAR program; (3) 40 specimens of *H. dibranchiata* **n. sp**. were collected as part of oil platform surveys in the Gulf of Mexico in 2008, and (4) 28 specimens of two species, *H. alata* **n. sp**., and *H. brunei* **n. sp**. from SE Asia off Brunei as part surveys of the oil and gas industry in 2011. We were able to examine 44 specimens of *H. catalinensis*, a species first described in 1944 from southern California and subsequently discovered in various surveys in the region. Other species are rare and represented by single or only a few specimens.

Despite 20 years of surveys of the continental shelf, slope, and abyssal depths (550–3400 m) off northern California not a single specimen of *Heterospio* was identified from the 292 0.25m^2-box core samples (Hilbig & Blake 2000; Blake *et al.* 2009; Blake *et al.* unpublished data). Similarly, no specimens of *Heterospio* have been reported to date from anywhere in Antarctic and Southern Ocean regions or in the Clarion-Clipperton Zone, a vast expanse in the abyssal Pacific Ocean rich in manganese nodules.

TABLE 2. Bathymetric distributions of the known species of *Heterospio*.

Species/Depth range (m)	0–50	50–100	100–250	250–500	500–1000	1000–2000	2000–3000	3000–4000	4000–5000
indica									
catalinensis									
knoxi **n. sp.**.									
aruba **n. sp**.									
sinica									
africana n**. sp**.									
ehlersi **n. sp.**									
paulolanai **n. sp.**									
angolana									
mediterranea									
dibranchiata **n. sp.**									
cf. *reducta*—NE Atl.									
guiana **n. sp.**									
southwardorum **n. sp.**									
longissima									
bathyala **n. sp.**									
antonbruunae **n. sp.**									
alata **n. sp.**									
reducta—Med. Sea									
brunei **n. sp.**									
bidentata **n. sp.**									
canariensis **n. sp.**									
hartmanae **n. sp.**									
peruana									

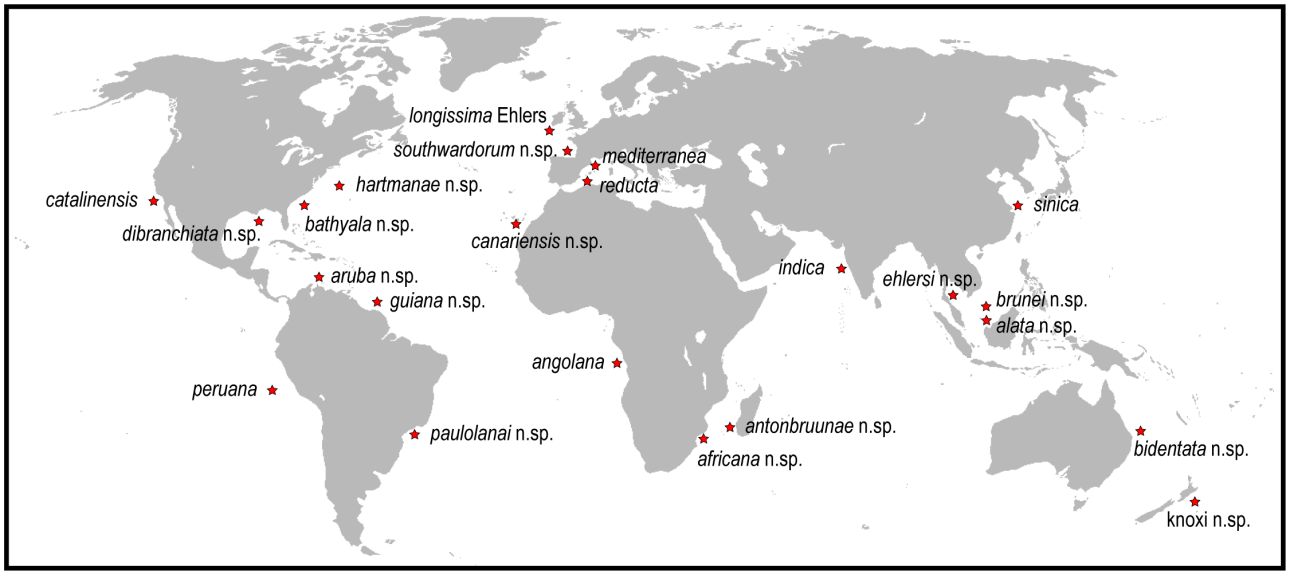

FIGURE 30. Map showing the distribution of all 23 known species of *Heterospio* based on their type locality.

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Samples from the Gulf of Mexico were collected as part of surveys around two oil platforms and associated pipelines off Louisiana (2008–2010) managed by the first author and funded by Total E&P USA. The field work off Brunei included two separate surveys in 2011. The first survey was led by the first author as part of a project for Total E&P Deep Offshore Borneo B.V.; the second survey was led by Dr. Pamela Neubert as part of a project for Petronas Carigali Brunei Ltd.

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Specimens from the Indian Ocean from the IIOP project and the Peru-Chile Trench as part of the SEPBOP project were provided by Ms. Leslie Harris of the LACM. Ms. Harris also provided a specimen from the Gulf of Thailand identified by the late Mr. R. Eugene Ruff and two specimens from New Zealand that had been provided to the late Dr. Olga Hartman by the late Dr. George Knox. Observations on the New Zealand specimens by these workers were reported by Knox (1960).

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