

New species of *Microspio* Mesnil, 1896 (Annelida: Spionidae), with additions to the description of *M. pigmentata* (Reish, 1959) and comparative notes on all members of the genus

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Abstract.—Three new species of *Microspio* were found in collections from a range of depths including shallow water in Bermuda, the continental shelf off Massachusetts, and deep water in the South China Sea off Brunei. *Microspio fischeri*, new species, is associated with shallow water sponges in Bermuda where it is a prey species of a predatory syllid; it is characterized by the medial placement of the first pair of branchiae as well as unusual notopodial capillaries in anterior chaetigers and enlarged notopodial lobes in posterior chaetigers. *Microspio lydonia*, new species, from the continental shelf on the east coast of the United States is distinguished from *M. pigmentata* (Reish, 1959) from the west coast by differences in the structure of the nuchal organs and hooded hooks, pigmentation, and Methyl Green staining patterns. Additions to the description of *M. pigmentata* include illustration of the nuchal organs and dorsal ciliary bands. *Microspio ariena*, new species, from deep water in the South China Sea off Brunei has enlarged branchiae with large glands that stain deeply with Methyl Green on a few anterior chaetigers, followed by much smaller branchiae on additional chaetigers. The three new species bring the total of described species in the genus to twenty-one, although some species remain problematic. A table comparing important characteristics of all 21 known species of *Microspio* is included.

Keywords: Bermuda, continental slope, deep-water, Polychaeta, North Atlantic, South China Sea, sponge association

The spionid polychaete genus *Microspio* addition of the new species in this paper Mesnil 1896 comprises a small group of (Table 1)¹. The genus was established by species, with 18 accepted prior to the Mesnil (1896) to include two species: *Spio*

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¹ Two species were erroneously included in the chapter on Spionidae in the Handbook of Zoology (Blake et al. 2020:83). *Microspio africana* (Rullier, 1964), also listed in that chapter as a *Spio*, had been transferred to the genus *Dispio* by Intes & Le Loeuff (1977). *Microspio gracilis*, which was described as a *Prionospio* by Hartmann-Schröder (1962), was transferred to *Microspio* by Blake (1983) but was considered incertae sedis by Maciolek (1990). It is most likely a juvenile form but has both noto- and neuropodial hooks, which eliminates *Microspio* as a possible genus.

Table 1.—Type localities, depths, and characteristics of *Micropsia* species. Information taken from original descriptions or additional publications as indicated. Abbreviations: af = anterior fragment, ch(s) = chaetiger(s), L = length, NR = not recorded, W = width.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Noto-chaetae/lamella on chaetiger I	Hooks start chaetiger	No. hooks per fascicle	No. teeth	Branchiae	Sabre chaetae	Comment
<i>ariena</i>	South China Sea	1150	L: 1.5 W: 0.4 Chs: 13; af	Bilobed (?)	Not apparent, even with stain	Possibly on ch 2, obvious from ch 3; 2 rows per chaetiger	Yes/Yes	11	4	3	Large on chs 2-6/7, small or missing thereafter	Absent, but 1-3 thin inferior-most ventral chaetae	Branchial glands elongated, banana-like
<i>atlantica</i> (Langerhans, 1880)	Madeira (off Portugal)	NR (from fish basket)	L: 10 W: NR Chs: 28-30	Bilobed	Extend posteriorly through ch 2, posterior tips slightly curved ^a	Two rows of ciliated cells with 6 cells in each ^a	No/Yes	9	1-2	3 (in profile)	Develop first on ch 3 ^a . Ch 2 to 20-22; absent last 8-10 chaetigers; completely free	NR	Larval development and additional characters described by Hamnerz (1956)
<i>elegantula</i> Blake, 1984	New Zealand (Wellington Harbour)	Intertidal	L: 8 W: 0.8 Chs: 82	Rounded, slightly incised	None described or figured	Single row ciliated patches on dorsum between branchial bases	Yes/Yes	11	6-7	Multi (5): main tooth, long apical pair, plus short apical pair	Extend nearly to last chaetiger, glandular	None	Pigment on palps, prostomium, interramal chs 1-18

Table 1.—Continued.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Noto-chaetae/lamella on chaetiger 1	Hooks start chaetiger	No. hooks per fascicle	No. teeth	Branchiae	Sabre chaetae	Comment
<i>fischeri</i>	Bermuda	Low intertidal, wading depth	L: 2 W: 0.3 Chs: 22–24	Bilobed	Two oval or U-shaped areas from posterior margin of prostomium to middle ch 2; indistinct, seen only after staining; surrounded by semi-circle of ciliated cells extending across ch 2	Present between bases of branchiae, particularly visible on median chaetigers	No/No	9	3 (usually 2)	2	Straplike through chs 14–18, then smaller or absent posteriorly	1–2 per podium from chs 9–10	First pair branchiae medial. Posterior notopodial lobes large, glandular. Associated with sponge <i>Ircinia</i> sp.
<i>granulata</i> Blake & Kudenov, 1978	NSW, Australia	Botany Bay	L: 10 W: 1.5 Chs: 31	Bilobed	Short medial band and long lateral curved band	Present from ch 3 to 13–20, connect branchiae; small band elongated on posterior chaetigers ^b	No/Yes, (plus additional lobe ^b)	9	8–9 (fide Blake & Kudenov); 5–6 in type and 3–5 in smaller specimens ^b	3	Straplike from ch 2, first pair as long as second pair continue nearly to end of body; free from branchia	From chs 15–17 ^b	Large specimen with occipital tentacle (papilla). Anterior capillaries distally hirsute (bristled). Ventral epidermal glands present. Redescribed by Meifner & Götting (2015).
<i>hartmannae</i> Blake, 1983	Argentina (southern)	18–26	L: 3.5 W: 0.3 Chs: 34	Broadly rounded, entire	Curved lateral ciliated ridges, surround large field of cilia on chs 2–3	Present from ch 3–6	Yes/Yes	11	4–5	3 (one above the other)	Slightly shorter on ch 2, each broad and glandular	Single, from chs 12–13	Anterior with scattered, indistinct pigment spots.

Table 1.—Continued.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Notochaetae/lamella on chaetiger 1	Hooks start chaetiger	No. hooks per fascicle	No. teeth	Branchiae	Sabre chaetae	Comment
<i>kussakini</i> Chlebovitsch, 1959	Kurile Islands, NW Pacific	Intertidal	L: 13 W: 1.0 Chs: 47	Narrow, bluntly rounded slightly expanded laterally	Indistinct, U-shaped area to ch 2	Not visible	Yes/Yes	9 (18-23) ⁸	7-10 ⁶	2	First pair short, others equal length; fused with lamellae anteriorly, separate posteriorly	Three, stout, in hook-bearing chaetigers	Holotype & paratype redescribed by Bick & Meifner (2011)
<i>lydomia</i>	W North Atlantic, Georges Bank	130-255	L: 44 W: 1.0 Chs: 16	Straight, slightly flared	U-shaped, extending to posterior margin of ch 2	Present mid-segment from ch 3	Yes/Yes	10	5 initially, increase to 26	Multi (6-7; 3 (or 2) single + 2 pairs)	Ch 2 to end, except last 2-3 chaetigers	Absent, but with 2-3 thin chaetae in inferior-most position	Posterior notopodial capillaries very long, stiff. Neuropodial capillaries 2x length of hooks.
<i>maori</i> Blake, 1984	New Zealand	Intertidal	L: 17 W: 0.5 Chs: 75	Narrow, conical or slightly expanded	NR	Present from ch 2, extend between branchiae	Yes/Yes	17-19	2-3 initially, increase to 9-12	2	Long, straplike anteriorly, shorter posteriorly. Basally fused to lamellae throughout. Extend nearly to last chaetiger	2-3 capillaries in posterior chaetigers, not described as sabre chaetae	Irregular black spots on posterior chaetigers and pygidium. All four pygidial cirri ventral.

Table 1.—Continued.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Notochaetae/lamella on chaetiger I	Hooks start chaetiger	No. hooks per fasciole	No. teeth	Branchiae	Sabre chaetae	Comment
<i>meznikowitana</i> (Claparède, 1869)	Gulf of Naples	Found low water in France ^d	L: 11 W: 0.5 Chs: 36	Slightly incised	Lateral bands on either side of prostomium; at metamorphosis, reach 3 rd segment (posterior margin of ch 2) ^d	Nototrochs persist in metamorphosed juvenile ^d	No/Yes ^d	8 (other authors ^d report 11)	2-5	3 ^d	Ch 2 to next-to-last segment. Develop first on chs 2, 3, 4; at 23 chaetigers, branchiae on segments 2-8 ^a	Character not mentioned	Type of genus; spermatophores studied by Claparède & Meznikow (1868); larval development studied by Cazaux (1971).
<i>microcera</i> (Dorsey, 1977)	San Clemente Island, California	Intertidal -3	L: 8 W: 0.5 Chs: 42	Bilobed	Short medial band and long lateral curved band	Pair of comma-shaped bands per chaetiger from ch 3-ca. 15	No/Yes	8-10	6, reduced to 2-3 posteriorly	3 (side-by-side pair above main tooth)	First pair shorter than second, extend nearly to last chaetiger, glandular, robust on chs 2-5	None (Maciolek 1990); present in all hook-bearing chaetae ^b tigers ^b	Anterior capillaries hirsute. Two pairs ventral epidermal glands until ch 11. Redescribed by Maciolek (1990).
<i>minuta</i> (Hartmann-Schröder, 1962)	Chile	Rhizoids of <i>Macrocystis</i>	L: 2.5 W: 0.4 Chs: 26, af	Bilobed	Cannot be determined on type; prominent curved pair on Galapagos specimen ^e	Cannot be determined on type; double row of patches from ch 3 on Galapagos specimen ^e	No/No	9	2-4	2 (original) ^{3e}	From ch 2 nearly to end; free from lamella except at base.	Single	Redescribed from Galapagos specimen; medial dorsal pigment suggests post-larval form (Blake 1983).

Table 1.—Continued.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Notochaetae/lamella on chaetiger 1	Hooks start chaetiger	No. hooks per fasciole	No. teeth	Branchiae	Sabre chaetae	Comment
<i>moorei</i> (Gravier, 1911)	South Shetland Islands	10	L: 16 W: 1 Chs: 50	Rounded, somewhat rectangular, not incised	NR	Ridge between gills on each segment	No/Yes	15	10	2	From ch 2, free from lamellae	Character not mentioned	Genus (<i>Mesospio</i>) referred to <i>Microspio</i> by Foster (1971); characters discussed by Blake (1983)
<i>multidentata</i> Zhou, Ji & Li, 2009	East China Sea	Intertidal	L: 12 W: 1.3 Chs: 55, af	Weakly rounded (slight flare)	NR	NR	No/Yes	26-27	Increase to 26	Multi (5): main tooth, long apical pair, plus short apical pair	Chs 2-24/55 (paratypes 24/44; 27/39; 24/33); glandular	None	Posterior capillaries very long, needlelike.
<i>occipitalis</i> Hartmann-Schröder, 1983	Australia, southern coast	?shallow	L: 4.9 W: 0.34 Chs: 31	Broadly rounded, weakly incised	Curved; nuchal pits surround prostomial caruncle on ch 2	Present from ch 2, extend between branchiae	No/Yes	9	4-5	3 (in profile)	Straplike, long anteriorly; becoming shorter; on nearly all chaetigers; fused only at base with lamella	1-2, from ch 11, long, become notopodial lamellae and on medial dorsum	With occipital tentacle. Pigment spots at base of notopodial lamellae and on medial dorsum
<i>paradoxa</i> Blake, 1983	Galápagos Islands	17-18	L: 3 W: 0.3 Chs: 20, af	Bilobed	NR	NR	No/No	9	?	3	Broad, extend to end of 20-chaetiger fragment, glandular	Present on some segments with thick capillaries	Chs 4-6 with thick capillaries in U-shaped row; chs 7-10 with hirsute capillaries

Table 1.—Continued.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Notochaetae/lamella on chaetiger 1	Hooks start chaetiger	No. hooks per fasciole	No. teeth	Branchiae	Sabre chaetae	Comment
<i>pigmentata</i> (Reish, 1959)	Southern California	4–27	L: 15 W: 1.5 Chs: 80	Broadly rounded	U-shaped, extending to base of ch 2 ^f	Widely separated double rows of patches across dorsum ^f	Yes/Yes	11–12	30	Multi (6–8: 2 (or 3) single plus posteriorly; 2–3 pairs)	Elongate anteriorly, smaller, rounded posteriorly; continuing to last 10 chaetigers	0–2 ^f	Strongly pigmented on anterior end. Posterior capillaries very long, stiff. Caps. with hooks not much longer than hooks.
<i>profunda</i> Maciolek, 1990	W Atlantic, Tongue of the Ocean, Bahamas	1760–3600	L: 4 W: 1 Chs: 19, af	Bilobed	NR	NR	Yes/Yes	10–11	8	3 (side-by-side pair above main tooth)	Long, tapered anteriorly; continuing nearly to last chaetiger	None	Posterior capillaries very long, stiff
<i>rolasiana</i> Augener, 1918	W Africa, Gulf of Guinea, Ilha de Rolas	NR	L: 3 W: NR Chs: 27–29	Straight or slightly rounded	NR	NR	Uncertain, possibly Yes/Yes	11	2–3	3 (in profile)	Free at base, ch 2 to posterior, may be absent in far posterior	NR	Questionable. Plate VII, Figs. 206, 207 appear to be a larval form but Augener said some specimens were adults and valid as a separate species

Table 1.—Continued.

Species	Type locality	Type depth (m)	Maximum reported size (mm)	Anterior edge of prostomium	Nuchal organs	Dorsal ciliated bands	Notochaetae/lamella on chaetiger 1	Hooks start chaetiger	No. hooks per fascicle	No. teeth	Branchiae	Sabre chaetae	Comment
<i>spinosa</i> Blake, 1996	Santa Maria Basin, California	90–150	L: 7.5 W: 0.5 Chs: 44	Broadly rounded	Lateral to caruncle, continue as dorsolateral ciliated patches on anterior chaetigers	On ch 3, patches posterior to caruncle, then bands across dorsum between branchial bases	No/No	11	5–8	2, becoming unidentate in posterior	From ch 2 through middle chaetigers; thick, grooved	From ch 9–11	Strongly pigmented on anterior end. Posterior capillaries very long, stiff.
<i>tetrabanchia</i> Maciolek, 1990	W North Atlantic, SE U.S.A.	584–807	L: 1.5 W: 0.3 Chs: 33	Bluntly rounded	Small, oval, extend to ch 1	Character not mentioned but figured as single row of patches between branchial bases	Yes/Yes	9–10	6 (usually 4–5)	3 (one above the other)	Elongate; 4 pairs, on chs 2–5	2–3 per fascicle	

References: ^a Hannerz (1956), ^b Meißner & Götting (2015), ^c Bick & Meißner (2011), ^d Cazaux (1971), ^e Blake (1983), ^f this study.

mecznikowianus Claparède, 1869 and *Spio atlanticus* Langerhans, 1880, with the main character separating the two genera being the first occurrence of branchiae on chaetiger 1 in *Spio* and chaetiger 2 in *Microspio*. No additional species were described in the genus until Augener described a species from West Africa in 1918 (*M. rolasiana* Augener, 1918). Gravier (1911) described *Mesospio moorei*; this genus was later synonymized with *Microspio* by Foster (1971).

Söderström (1920:247) rejected the idea that the first occurrence of branchiae, the length of the first branchiae, or the fusion or lack of fusion of the branchiae with the dorsal lamellae were relevant systematic characters and synonymized *M. mecznikowiana* and *M. atlantica*, making *M. mecznikowiana* the type species of the genus. He (op. cit.) instead used the number of longitudinal dorsal ciliary bands to distinguish the two genera, with *Spio* having four such bands (i.e., two pairs) per segment and *Microspio* having two (i.e., one pair). Bick et al. (2010), however, pointed out the presence of only one pair of these bands in at least one species accepted as *Spio* (*S. goniocephala* Thulin, 1957). Although Hannerz (1956) tended to reject the separation of *Spio* and *Microspio* based on any of the proposed characters, he observed a few unusual features in the morphology and development of *M. atlantica* that suggested a separate genus for this species might actually be justified; he resurrected the species from its synonymy with *M. mecznikowiana* and left the genera as they stood.

Problems with the definition of *Microspio* and assignment of species to it are apparent in a few of the species assigned to the genus. Developmental studies by Hannerz (1956, for *M. atlantica*) and Simon (1967, for *S. setosa*) demonstrated that the first pair of branchiae do not appear in those species until the animal is fully developed, with branchiae first appearing

from chaetiger 2 in *S. setosa* and chaetiger 3 in *M. atlantica*, whereas the mature adults have branchiae from chaetigers 1 and 2, respectively. When Claparède described *M. mecznikowiana*, he mentioned the presence of rudimentary, nipple-like gills on chaetiger 1, contradicting his own statement that gills begin on chaetiger 2 (Claparède 1869:64–65). Cazaux (1971) followed the development of *M. mecznikowiana* through the 23-chaetiger stage; he documented branchiae first appearing as small buds on chaetigers 2, 3, and 4 when the worm was at the 17-chaetiger benthic stage and on chaetigers 2–8 in the 23-chaetiger juvenile. Thus, either chaetiger 2 is the final as well as first occurrence of the first pair of branchiae in this species or, if *M. mecznikowiana* follows the same pattern as *M. atlantica* and *S. setosa*, branchiae may later appear on chaetiger 1. *Microspio mecznikowiana* has been reported in many ecological studies (e.g., Çınar et al. 2014, Mikac 2015) but has not been redescribed in recent times, so this issue is unresolved. *Microspio rolasiana* Augener, 1918 was described from newly settled individuals, some of which Augener decided were adults but may not have developed a full complement of branchiae; this species has not been reported since the original description. Using SEM, Meißner & Götting (2015: Fig. 10B, C) were able to see an extra lobe associated with chaetiger 1 in *Microspio granulata* Blake & Kudenov, 1978; they speculated that one interpretation of this lobe is that it could be a branchial remnant.

Based on the confusion surrounding the first appearance and size of the anterior branchiae, Foster (1971) regarded *Microspio* as a subgenus of *Spio*, saying further that they should perhaps be synonymized. However, misunderstanding does not preclude validity and is not a sound basis for synonymy (Blake & Kudenov 1978). Recent authors treating *Microspio* as a separate genus include Blake & Kudenov (1978), Blake (1983, 1984, 1996), Maciolek

(1990), Bick & Meißner (2011), and Meißner & Götting (2015). Given the lack of any phylogenetic investigations, morphological or molecular, into the relationship of these genera, the separation of genera is followed here.

The majority of *Microspio* species have been described from intertidal or shallow subtidal depths (Table 1); only three species (*M. profunda* Maciolek, 1990, *M. spinosa* Blake, 1996, and *M. tetrabanchia* Maciolek, 1990) have been described from locations deeper than 100 m; those were from 584–807 m, 90–150 m, and 1760–3600 m, respectively. The three new species found in the present collections come from a range of depths, including shallow water in Bermuda, the continental slope (150 m) off Massachusetts, USA, and deep water (1150 m) in the South China Sea off Brunei.

Materials and Methods

Collections of polychaetes from offshore the U.S.A. Atlantic coast were made in the 1980s during the Georges Bank Benthic Infauna Monitoring Program (GBMP, aka BIMP) conducted for the U.S. Department of the Interior, Bureau of Land Management (BLM), now the Bureau of Ocean Energy Management (BOEM) and the deep-water U.S. Atlantic Continental Slope & Rise Program (ACSAR, aka ASLAR) also conducted for BOEM (at the time called the Minerals Management Service or MMS). Specimens from off Brunei in the South China Sea were collected as part of deep-water baseline studies conducted for Total E&P Deep Offshore Borneo B.V. in 2011. Collection of the material from Bermuda was made by hand in shallow water near the Bermuda Biological Station (see Fischer & Fischer 1995 for details). Specimens of *M. pigmentata* (Reish, 1959) were borrowed from the Los Angeles County Museum, Allan Hancock Foundation collections.

In the field, samples were sieved on either a 300- μ m-mesh or a 500- μ m-mesh sieve, preserved in 10% formalin, and later transferred to 70% ethyl alcohol (EtOH). Specimens were examined with light microscopy using a high-quality Wild M-5 stereomicroscope and a Zeiss research compound microscope equipped with phase contrast optics. Measurements were made using an ocular micrometer. Photographs were taken with a Nikon D7100 camera mounted on the stereo- and compound microscopes. Some specimens were stained with Shirlastain A to highlight surficial morphology; other specimens were stained with a saturated solution of Methyl Green (MG) in 70% EtOH to elucidate staining patterns, which are usually associated with glandular structures that preferentially retain this stain. The MG stain dissipates completely in fresh EtOH, although some morphological features may retain the stain for several days or even weeks. Line drawings were made in pencil using a drawing tube (camera lucida) on the Zeiss or sometimes by tracing photographs. Sketches were scanned and imported into Adobe Illustrator where vector line drawings were made. Plates were prepared using Adobe Power Point and Adobe Photoshop software.

This work has been registered in ZooBank with the registration number urn:lsid:zoobank.org:pub:D24F8834-3230-469D-A2CD-759B018EF8AB.

Abbreviations of sampling programs and institutions referred to in this paper:

ACSAR	Atlantic Continental Slope & Rise (<i>aka</i> ASLAR)
AHF	Allan Hancock Foundation
ASLAR	Atlantic Slope and Rise (<i>aka</i> ACSAR)
BOEM	Bureau of Ocean Energy Management
BLM	Bureau of Land Management
BIMP	Benthic Infauna Monitoring Program (<i>aka</i> GBMP)
CAMP	California Monitoring Program

GBMP	Georges Bank Monitoring Program (<i>aka</i> BIMP)
LACM	Los Angeles County Museum
MCZ	Museum of Comparative Zoology, Harvard University
MMS	Minerals Management Service
USNM	Smithsonian Institution, National Museum of Natural History

Results

Microspio Mesnil, 1896

Microspio Mesnil, 1896; type-species: *Spio mecznikowianus* Claparède, 1869 (type by subsequent designation [Söderström 1920]).

Mesospio Gravier, 1911; type-species: *Mesospio moorei* Gravier, 1911, by monotypy. Fide Foster 1971.

Diagnosis.—Prostomium anteriorly rounded to deeply incised, frontal or lateral horns always absent; eyespots present or absent; occipital antenna present or absent. Nuchal organ with median and lateral ciliary bands extending to chaetiger 2 or 3, sometimes an oval or U-shaped ciliated groove. Longitudinal metameric dorsal ciliated organs present or absent. Transverse ciliary bands connecting bases of branchiae on some segments. Branchiae present from chaetiger 2, restricted to anterior region or continuing to posterior end of body; completely free or partly fused with bases of notopodial postchaetal lamellae. Ventral epidermal glands present or absent. Notochaetae capillaries of various types; notopodial spines present or absent; neurochaetae include capillaries and hooded hooks, hooks bi-, tri-, or multidentate; ventral sabre chaetae present or absent. Pygidium with 2–4 anal cirri.

Remarks.—Bick & Meißner (2011) discussed characters important in the description of *Spio* and *Microspio* species; they emphasized the need to include new characters such as the shape of the nuchal

organs and dorsal ciliary bands in any revision. Meißner et al. (2011, 2015) refined the diagnosis of *Microspio* to include characterization of the nuchal organs and metameric dorsal bands; the wording of the present diagnosis differs slightly from that given in Blake et al. (2020), primarily with reference to these ciliary patterns. It also includes the potential for inferior sabre chaetae being absent, as well as the branchiae being completely free from the notopodial postchaetal lamellae as described by early authors (Mesnil 1896) and as seen, for example, in the middle and posterior chaetigers of *Microspio elegantula* Blake, 1984 and *M. granulata* Blake & Kudenov, 1978 as figured in Meißner et al. (2015). This feature is difficult to see in the anterior region of very small specimens; it is usually clearer in middle and posterior regions; sometimes the branchiae may be (partly) fused in anterior chaetigers and free in posterior chaetigers, as in *M. lydonia*, new species, described below. Table 1 includes a summary of described characters for currently accepted *Microspio* species.

Microspio fischeri, new species Figs. 1–3

ZooBank LSID.—urn:lsid:zoobank.org:act:4CE1500E-17D7-4069-A1C5-2B2BF7A34C76

Material examined.—North Atlantic Ocean, Bermuda, SW of St. George's, near Ferry Point, coll. A. Fischer, 16 Jun 1994, 21.746°N, 64°42.827'W, intertidal, associated with *Ircinia* sp. (sponges), holotype (MCZ 162298); 6 paratypes (MCZ 162299).

Description.—A very small species, complete specimens measuring 0.3 mm wide and 2.0 mm long for 22–24 chaetigers. Color in alcohol: chalk white. Body slightly tapered in far posterior region; regenerating specimen with posterior segments much smaller than preceding chaetigers. Prostomium deeply incised

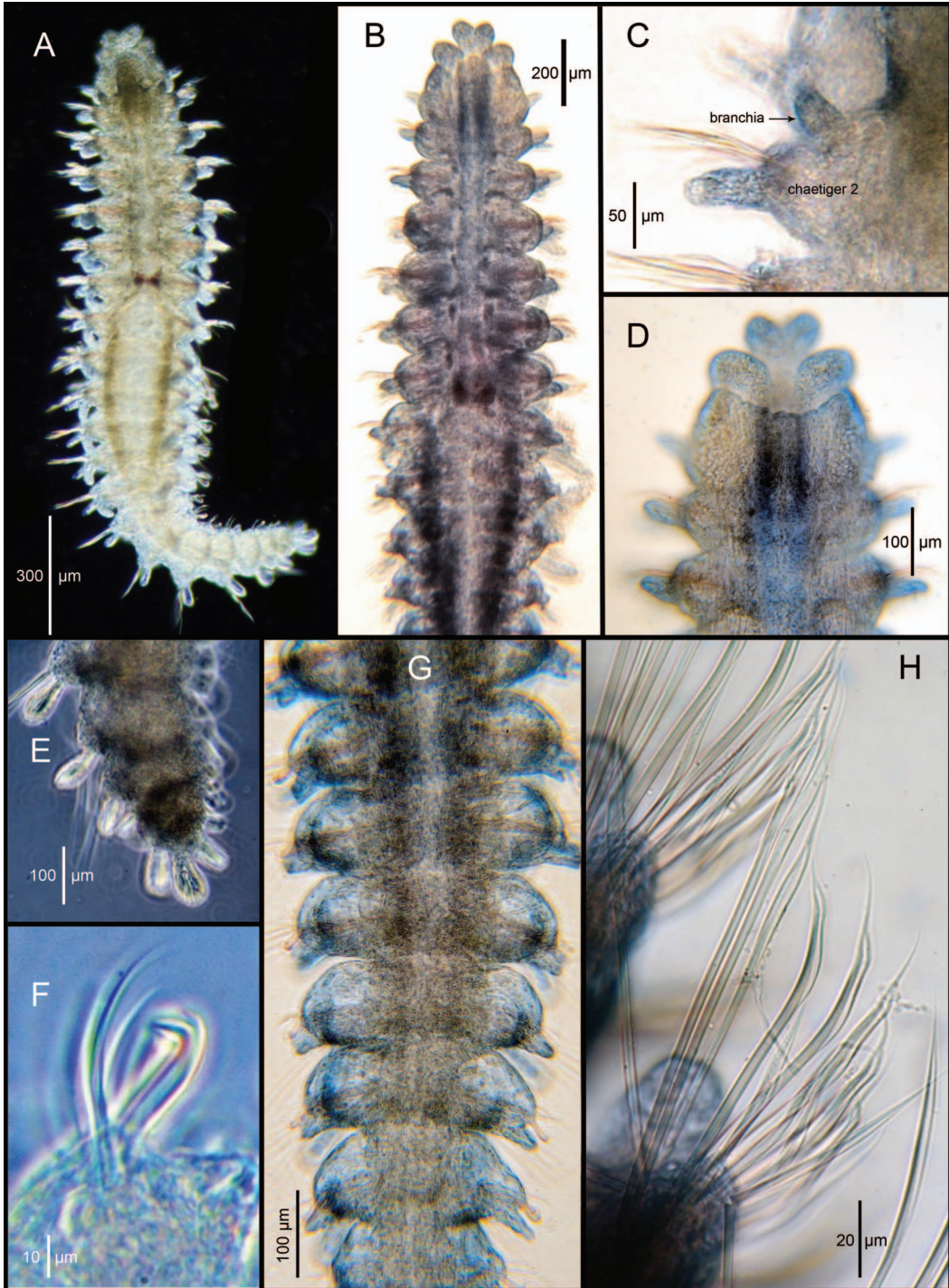


Fig. 1. *Microspio fischeri*. A, C, D–F, H: Holotype (MCZ 162298); B, G: Paratype (MCZ 162299). A, entire worm, dorsal view. B, ventral view. C, anterior end, dorsal view, chaetigers 1 and 2, left side. D, anterior end, ventral view, peristomium and chaetigers 1–3. E, pygidium. F, neuropodial hooded hook. G, middle and posterior chaetigers, ventral view. H, notochaetae, chaetiger 4, anterior view.

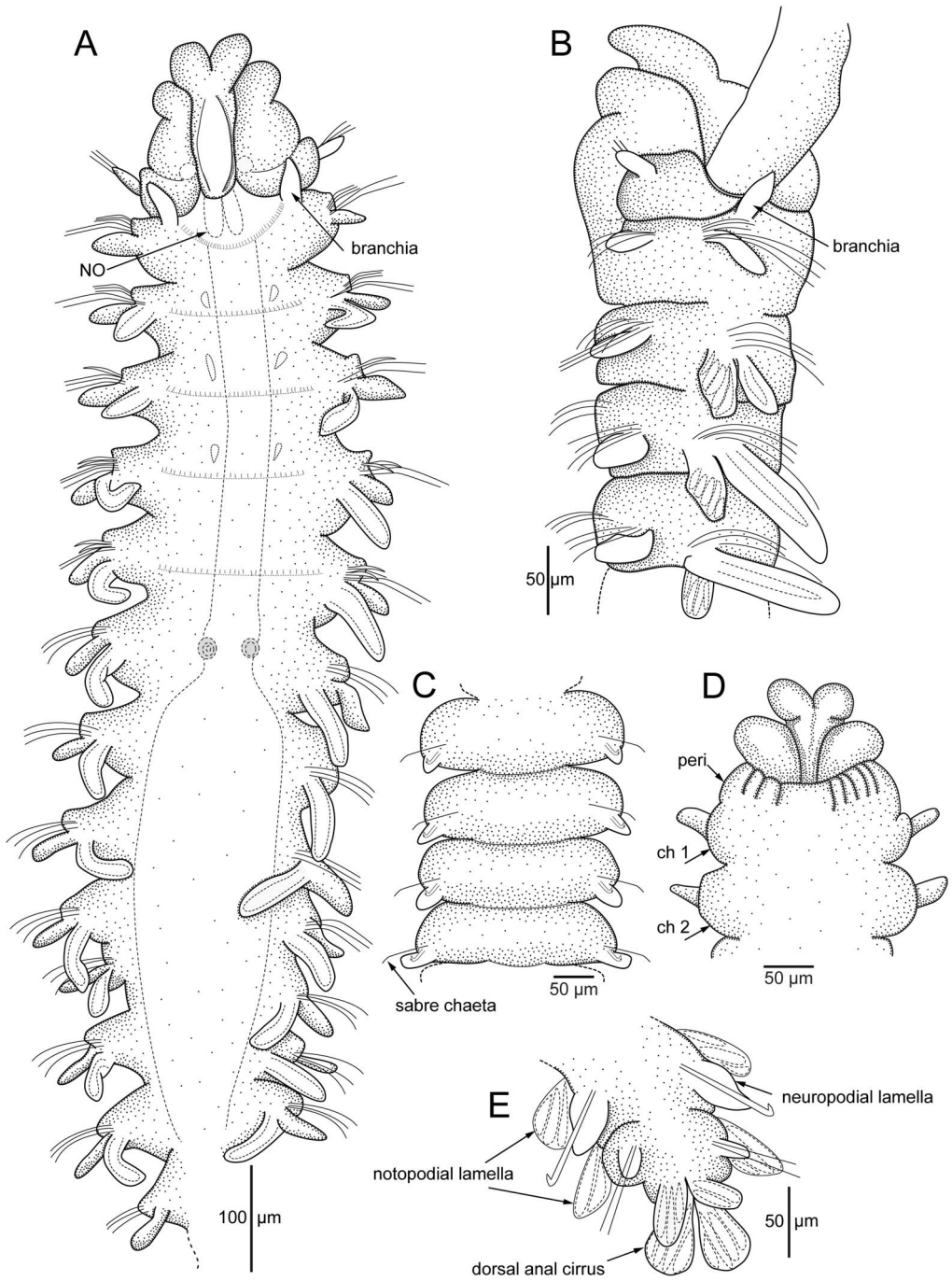


Fig. 2. *Microspio fischeri*. Holotype (MCZ 162298). A, dorsal view. B, anterior end, lateral view. C, chaetigers 13–16, ventral view. D, anterior end, ventral view. E, pygidium, ventral view. Abbreviations: ch = chaetiger, NO = nuchal organ, peri = peristomium.

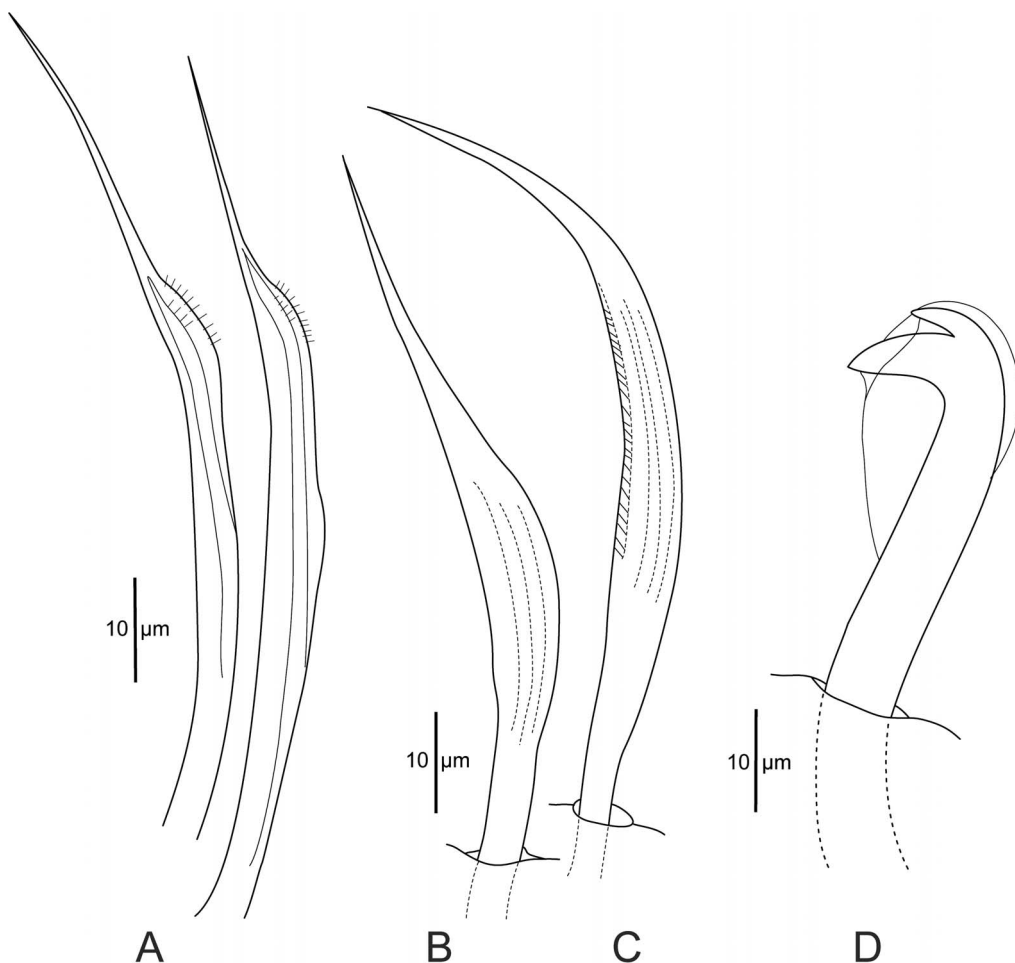


Fig. 3. *Microspio fischeri*. A–D: Holotype (MCZ 162298). A, notopodial chaetae from chaetiger 7. B, neuropodial chaeta, posterior row, chaetiger 4. C, neuropodial chaeta, anterior row, chaetiger 4. D, neuropodial hooded hook.

anteriorly, forming rounded anterior lobes (Figs. 1A, B, D, 2A), medial portion with straight sides, posterior portion narrow elevated caruncle extending to middle of chaetiger 2; occipital tentacle absent; eyespots absent. Palps with groove, without sheath or papillae, with rounded tip, extending for roughly one-half the body length. Nuchal organs oval or U-shaped, from posterior margin of caruncle to middle of chaetiger 2, indistinct, seen only after staining, surrounded by curved row of ciliated cells extending between branchial bases (Fig. 2A). Transverse dorsal

ciliated bands present between bases of branchiae from chaetiger 3, particularly visible on median chaetigers, continuing throughout posterior segments. Longitudinal dorsal metameric ciliary bands or patches not observed. Venter without epidermal glands. Internal gut narrow and straight to chaetiger 7; then separated from wider intestine with two glandular structures on either side that retain Shir-lastain A (Figs. 1A, B, 2A); wider intestine narrowing toward end of body. Peristomium surrounding prostomium dorsally,

fused with chaetiger 1 ventrally but not dorsally (Figs. 1B, D, 2A, B, D).

Chaetiger 1 weakly distinguished from chaetiger 2 on venter (Figs. 1D, 2D), segments distinct thereafter (Fig. 1B). Chaetiger 1 reduced, lacking notopodium, neuropodium small, with a few short, fine capillary chaetae (Figs. 1A, C, 2A, B). Notopodial postchaetal lamellae from chaetiger 2 small at first, oval, rounded on distal margin (Fig. 2B); lamellae gradually becoming larger along anterior and middle chaetigers and noticeably large and club-shaped in far posterior chaetigers (Figs. 1A, E, 2E); all notopodial postchaetal lobes glandular, especially in posterior chaetigers. Notopodial prechaetal lobes inconspicuous bump in anterior chaetigers, absent in middle and posterior chaetigers. Neuropodial postchaetal lamellae small, oval on first two chaetigers, becoming larger, square-shaped through middle region (Fig. 2B), glandular in posterior chaetigers; no neuropodial prechaetal lobes. Neuropodia appearing increasingly swollen posteriorly, most obvious in ventral view starting around chaetiger 6–9 (Fig. 1B); swollen area anterior to chaetae, which are positioned in posterior portion of podium in these segments (Figs. 1G, 2C). Branchiae from chaetiger 2; first pair small, triangular, upright, well separated medially from notopodial lobe (Figs. 1A, C, 2A, B); from chaetiger 3, branchiae at base of notopodial lamellae, short, rounded at first, rapidly becoming larger, strap-like, through chaetigers 14–18, then becoming smaller or absent in far posterior chaetigers (Figs. 1A, 2A, B). Branchiae close to but do not appear fused with notopodial postchaetal lamellae.

Anterior notopodial chaetae all capillaries, arranged in two rows; anterior row of chaetiger 2 with three chaetae, these shorter, curved, limbate, moderately granulated; posterior row with three chaetae, these longer, straight, alimbate. Chaetiger 3 with one short, granular limbate chaeta and three longer limbate chaetae. Noto-

chaetae of chaetigers 4–8 include 5–10 capillaries, each broadly limbate with long, fine aristate tips, limbation of these chaetae long, thickened and undulating, with a few small protruding fibrils below the arista (Figs. 1H, 3A); these chaetae in two rows with 2–3 shorter aristate capillaries in first row and with up to seven long chaetae in second row. Posterior notochaetae long thin capillaries with only narrow limbation. Anterior neuropodial chaetae include ca. five short, thin capillaries on chaetiger 1; from chaetiger 2, capillaries in two rows, anterior row shorter, with broad limbation and fine aristate tips. Neurochaetae of chaetigers 4–6 arranged in ventral group of three in slightly curved row, separate from additional dorsal group of 3–4 broad, thickened chaetae with narrow tapered tip (Figs. 2B, 3B). Chaetigers 7–8 also with broad, limbate capillaries but these smaller than in preceding chaetigers. Neuropodial hooded hooks from chaetiger 9, usually 2 per fascicle, sometimes 1 or 3, absent from last 1–3 chaetigers; hooks bidentate, with small pointed apical tooth surmounting main fang (Figs. 1F, 3D); hood bulbous, entirely surrounding apex, with opening from which fang emerges; shaft straight, then curving at point of emergence from neuropodium. Hooks accompanied by 0–2 fine straight capillaries. Ventral sabre chaetae present from chaetiger 9–10, golden in transmitted light, curved, usually single but may be two per podium.

Pygidium with four anal cirri; oval to paddle-like, highly glandular, dorsal cirri larger than ventral cirri (Figs. 1E, 2E).

Methyl Green staining pattern.—Body destains fairly rapidly; stain is retained briefly on anterior-most ends of peristomium. Posterior parapodial lamellae and anal cirri initially stain deeply but rapidly lose the stain. Venter picks up stain on chaetigers 4–5 but this is also rapidly lost. No indication of ventral epidermal glands.

Remarks.—*Microspio fischeri* has three morphological characters that make it

unique among *Microspio* species: 1) the almost medial location of the first pair of branchiae, which are well separated from the notopodial lamellae; 2) the enlarged, glandular, and club-shaped notopodial postchaetal lamellae of posterior chaetigers; and 3) the unusual aristate capillary chaetae of some anterior notopodia, some of which have thickened undulating liminations.

Microspio fischeri shows some similarity to *M. paradoxa* Blake, 1983, described from 17–18 m water depth in the Galápagos Islands, in that both species have modified capillaries in several anterior chaetigers. In *M. fischeri*, the notochaetae of chaetigers 4–8 include broadly limbate capillaries with long, fine aristate tips; the limination is long, thickened, and undulating. In *M. paradoxa*, the posterior row of notochaetae in chaetigers 7–10 includes capillaries with a wide limination that is notched or open, which is unique in Spionidae (Blake 1983); *M. paradoxa* differs further from other *Microspio* species by having the notochaetae of chaetigers 4–6 in a U-shaped arrangement. In *M. paradoxa*, the neurochaetae of chaetigers 4–6 are thicker than those of chaetigers 3 and 7, whereas in *M. fischeri*, the neurochaetae of chaetigers 4–6 are arranged in a ventral group of three in a slightly curved row, separate from an additional dorsal group of 3–4 broad, thickened chaetae with a narrow tapered tip; chaetigers 7–8 also have broad, limbate capillaries but these are smaller overall than in preceding chaetigers.

Several species, including *M. granulata*, *M. microcera*, and *M. minuta*, have a bilobed prostomium, lack notochaetae on chaetiger one, and have hooks starting on chaetiger 9, but differ from *M. fischeri* in other characters such as the number of teeth on the hooks, as well as the placement of the first pair of branchiae (see Table 1).

Biology.—The discovery of a new *Microspio* species in Bermuda was part of a

research project on the biology of the bioluminescent syllid *Odontosyllis enopla* Verrill, 1900 conducted by Albrecht and Ursula Fischer in 1994. Apart from the spectacular bioluminescence associated with the syllid, nothing was known about the biology of the species, including their fate after swarming and spawning until the results by Fischer & Fischer (1995). The authors were able to study the diet of post-swarming adults in the laboratory, including specimens transported to Germany from the collection site in Bermuda. Fischer & Fischer (1995:242) state: "We offered a variety of potential diets to post-swarming worms: artificial fish food; the sponges *Ircinia*, *Chondrilla*, and *Tedania* and the excavating sponge, *Cliona* sp.; hydrozoans (e.g., *Myrionema amboinense* Pictet); colonies of encrusting bryozoans; the ascidian *Botrylloides*; and a number of polychaetes (cirratulids, terebellids, spionids, and decapitated nereids). Of all of these food items only spionids and, in a few cases, small terebellid polychaetes were accepted as food." The preferred prey was a spionid, later identified as a new species of *Microspio*, which was found in large numbers inhabiting sponges of the genus *Ircinia* in Bermuda.

In a communication to one of us (JAB) in November 1994, Dr. A. Fischer described the *Microspio* collecting site as shallow sublittoral with moderate current, and a rough coral gravel substrate at the fringe of a *Thalassia* sea grass bed. The brown sponges (*Ircinia* sp.) were growing upright between gravel and sea grass. Dr. Fischer described the *Microspio* specimens as very numerous in these sponges; they were residing in sediment-covered mucoid tubes oriented perpendicular to the surface of the sponge. When the sponges collected were removed from seawater and became stressed and fouling, the worms left the sponges in great numbers, probably due to oxygen stress. After collection, the worms proved to be hardy, and Dr. Fischer was able to transport them to his laboratory in

Germany where further feeding experiments were performed with the syllids.

Associations of spionids and sponges appear to be rare and all reported taxa are genera and species of the *Polydora* complex (Martin & Britayev 1998, 2018). All five known species of *Polydorella* live on the surface of sponges where they construct tubes (Williams 2004, Radashevsky 2015). A few polydorid species are known to burrow and build tubes directly into the sponge from which they extend their palps and feed in the overlying water. The best known example is *Polydora colonia* Moore, 1907, which builds tubes in the sponge *Microciona prolifera* and other species. First described from near Woods Hole, Massachusetts, the species has since been widely collected globally, apparently because the host sponges colonize the hulls of ships, which transport the worms to distant ports (Blake 1971, David & Williams 2012, Blake et al. 2020). *Polydora spongicola* Berkeley & Berkeley, 1950 has been collected from several different sponge species and is known from Canada to southern California (Woodwick 1963) and the north-western Pacific (Radashevsky 1993). *Carazziella spongilla* Sato-Okoshi, 1998 constructs tubes within the sponge *Spongilla alba*, in a brackish water lake in Japan. *Microspio fischeri* is thus the first non-polydorid species of Spionidae to be reported as an inhabitant of sponges.

Etymology.—This species is named in honor of Dr. Albrecht Fischer, who collected the organisms and made them available to us for study.

Distribution.—Shallow sublittoral; known only from the type locality in Bermuda, associated with the sponge genus *Ircinia*.

Microspio pigmentata (Reish, 1959)

Fig. 4

Material examined.—Eastern Pacific Ocean, California. Orange County, Lower Newport Bay, Newport Harbor, Sta. NB-

14, 33°36'31.17"N, 117°54'11.72"W, 13 ft., gray mud, coll. D. J. Reish, 26 Jan 1951, 11 paratypes, (LACM-AHF Poly 606).—San Diego Bay, id. L. Harris, 14 May 2020, St. NB-DS/R.2, 40 m, 2 specimens (LACM-AHF Poly 12727).—Santa Maria Basin, coll. Battelle: off Purisima Point, CAMP 1-2, Sta. R-5, rep. 2, Jan 1987, 34°42.69'N, 154 m, 1 specimen (LACM-AHF Poly 12724); CAMP 2-5, Sta. R-5, rep. 1, May 1988, 34°42.69'N, 154 m, 1 specimen (LACM-AHF Poly 12725). CAMP 3-4, Sta. R-8, Rep 2, May 1989, 34°55.30'N, 120°45.90'W, 90 m, 1 voucher specimen id. Susan Williams (LACM-AHF Poly 12723). CAMP 1-3, Sta. PJ-7, May 1987, 34°55.79'N, 120°48.60'W, 123 m, 1 specimen (LACM-AHF Poly 12726).

Additions to description.—Nuchal organs with medial ciliary bands adjacent to posterior prostomium extending to chaetiger 2, then turning laterally, with small gap between this and second, lateral band (Fig. 4A, B). From chaetiger 3, dorsum with two transverse rows of ciliated patches; one row extending between branchial bases; second row widely separated from first, near segmental groove (Fig. 4C). Single pair of longitudinal dorsal metameric ciliated organs visible after staining on chaetigers 10—end of 27-chaetiger fragment, largest on chaetiger 20–25 (Fig. 4D).

Venter with dark pigment spots on midline of several segments.

Methyl Green staining pattern.—Prostomium stains deeply, especially in middle region where pigment is concentrated, posterior tip destains rapidly. Ventral peristomium retains stain evenly on posterior half, speckled on anterior half. Nuchal organs and transverse ciliary rows do not stain. Small glands in branchiae and both notopodial and neuropodial lamellae stain deeply. Dorsum with numerous small, stained spots in most chaetigers, weakly organized into transverse rows; venter also with stained spots concentrated along midline in anterior chaetigers where pig-

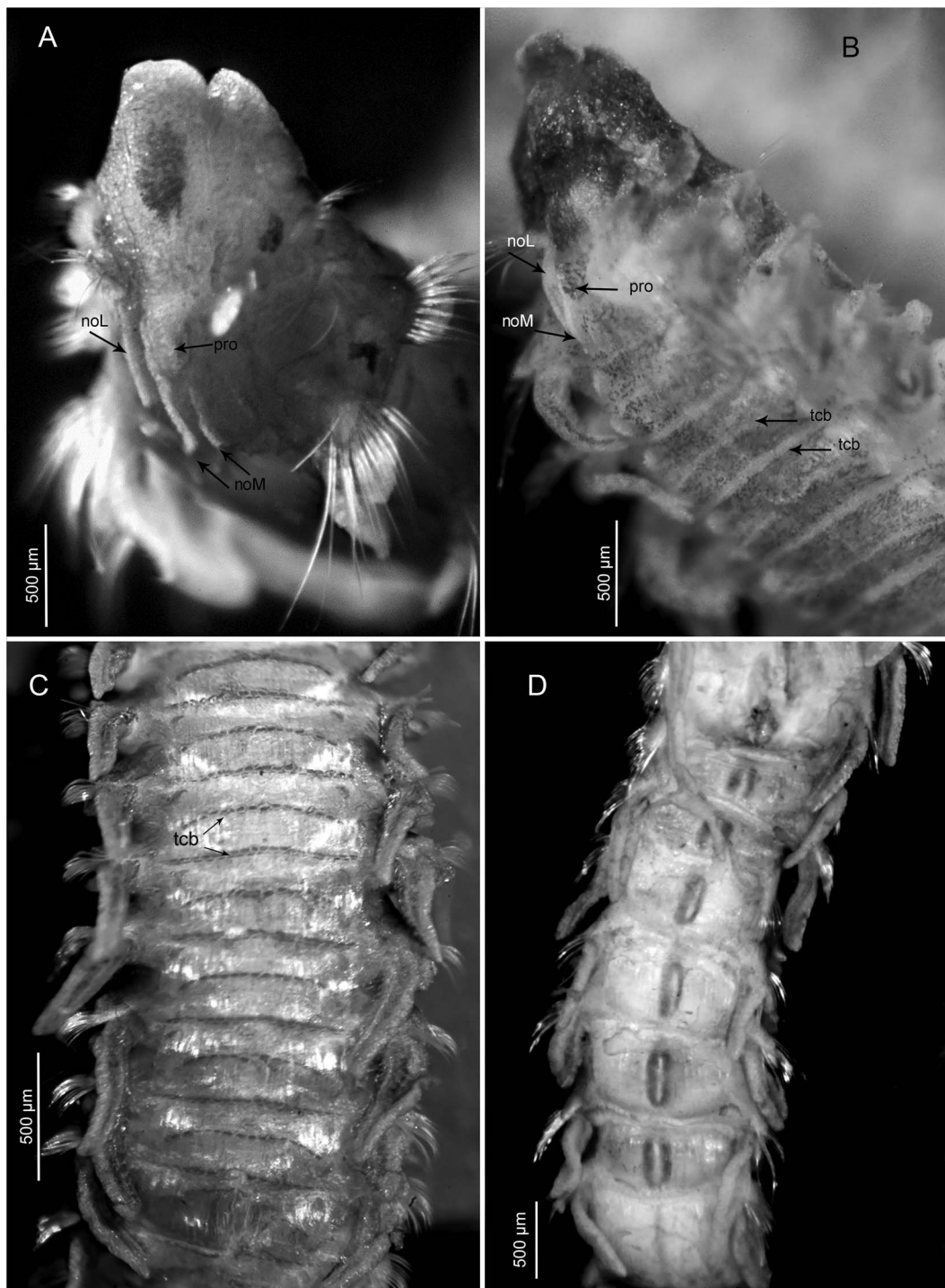


Fig. 4. *Microspio pigmentata* (Reish, 1959) A, C, D, specimen collected in eastern Pacific, San Diego, California, May 2020 (LACM-AHF Poly 12727). B, paratype LACM-AHF Poly 606. A, B, anterior end, dorsolateral view. C, D, middle posterior chaetigers, with Shirlastain A (C) and after stain had dissipated overnight (D). Abbreviations: noL = nuchal organ, lateral band, noM = nuchal organ, medial band, pro = prostomium, tcb = transverse ciliary band.

ment is densest, become diffuse posteriorly, no indication of ventral epidermal glands.

Remarks.—Neither Reish (1959) nor Maciolek (1990) mentioned nuchal organs, transverse dorsal ciliated bands, or metameric longitudinal bands in their descriptions; examination of the paratypes and additional fresh material allowed these characters to be described. The nuchal organs are for the most part typical for the genus, although the medial band is alongside the prostomial caruncle rather than posterior to it. The double, widely separated, transverse ciliary bands are unusual in that they appear as isolated patches rather than a continuous row, and other *Microspio* species have a single rather than double row (see Table 1).

Microspio lydonia, new species

Figs. 5, 6

ZooBank LSID.—urn:lsid:zoobank.org:act:C3624AEA-DB0C-45DE-8133-B1A229529C81

Microspio pigmentata Maciolek (1990), in part.—Not Reish (1959).

Material examined.—Western North Atlantic, off Massachusetts, Georges Bank, head of Lydonia Canyon, Sta. 7, 40°28.7'N, 67°42.7'W, Cruise M2, coll. M. Rawson, Lamont-Doherty, Chief Scientist, R/V *Oceanus*, 11 Nov 1981, ca. 150 m, rep. 3, Holotype (USNM 1655928) and 4 paratypes (USNM 1655929); rep. 5, 1 paratype (USNM 1655930). coll. G. Hampson, WHOI, Chief Scientist. Cruise M3, R/V *Endeavor*, 17 Feb 1982, 152 m, rep. 1, 2 paratypes plus posterior fragment from a 3rd specimen (USNM 1655931); rep. 3, 7 specimens (6 lost) (USNM 1655932); rep. 5, 4 paratypes (USNM 1655933). Cruise M4, R/V *Cape Henlopen*, 13 May 1982, 40°28.8'N, 67°43.2'W, 130 m, rep. 3, 1 specimen (USNM 1655934). Sta. 7A, Cruise M12, R/V *Gyre*, 5 Jun 1984, 40°32.2'N, 67°44.2'W, 167 m, rep. 4, 1 specimen (USNM 1655935). Sta. 8,

Cruise M12, R/V *Gyre*, 5 Jun 1984, 40°27.1'N, 67°37.4'W, 152 m, rep. 4, 1 specimen (USNM 1655936).—Georges Bank, head of Oceanographer Canyon, Sta. 9, 40°26.7'N, 68°09.8'W, Cruise M1, R/V *Eastward*, Jul 1981, ca. 145 m, rep. 3, 1 specimen (USNM 1655937); Cruise M3, R/V *Endeavor*, 13 Feb 1982, 145 m, rep. 4, 2 specimens (partly dried out) (USNM 1655938); Cruise M4, R/V *Cape Henlopen*, 16 May 1982, 144 m, rep. 6, 3 specimens (USNM 1655939); Cruise M8, R/V *Gyre*, 19 May 1983, 143 m, rep. 1, 2 specimens (USNM 1655940); Cruise M9, R/V *Gyre*, 19 Jul 1983, 144 m, rep. 3, 1 specimen (USNM 1655941); Cruise M12, R/V *Gyre*, 8 Jun 1984, 144 m, rep. 1, 2 specimens (USNM 1655942), rep. 4, 1 specimen (USNM 1655943), rep. 6, 1 specimen (USNM 1655944).—Georges Bank, Sta. 12, 40°22.2'N, 68°30.2'W, ca. 105 m, Cruise M1, R/V *Eastward*, Jul 1981, rep. 2, 2 specimens (USNM 1655945); Cruise M2, R/V *Oceanus*, 12 Nov 1981, rep. 3, 1 specimen (USNM 1655946); Cruise M3, R/V *Endeavor*, 12–13 Feb 1982, 105 m, rep. 2, 1 specimen (USNM 1655947). Sta 17, 40°34.9'N, 67°11.1'W, Cruise M3, R/V *Endeavor*, 18 Feb 1982, 145 m, rep. 6, 1 specimen (USNM 1655948). Sta. 18, 40°33.5'N, 67°13.7'W, Cruise M3, R/V *Endeavor*, 17–18 Feb 1982, 145 m, rep. 1, 2 specimens (USNM 1655949); rep. 6, 3 specimens (USNM 1655950); Cruise M4, R/V *Cape Henlopen*, 13 May 1982, 150 m, rep. 2, 3 specimens (USNM 1655951); rep. 3, 1 specimen (USNM 1655952).—US North Atlantic ACSAR Program, Sta. 11, 40°01.3'N, 70°55.1'W, coll. R. Petrecca, WHOI, Chief Scientist, Cruise North-1, Leg 2, R/V *Cape Hatteras*, 8 Dec 1984, rep. 1, 253 m, 3 specimens (USNM 1655953); rep. 2255 m, 6 specimens (USNM 1655954). Cruise North-2, coll. G. Hampson, WHOI, Chief Scientist, R/V *Oceanus*, 4 May 1985, rep. 3250 m, 5 specimens (one with posterior) (USNM 1655955).

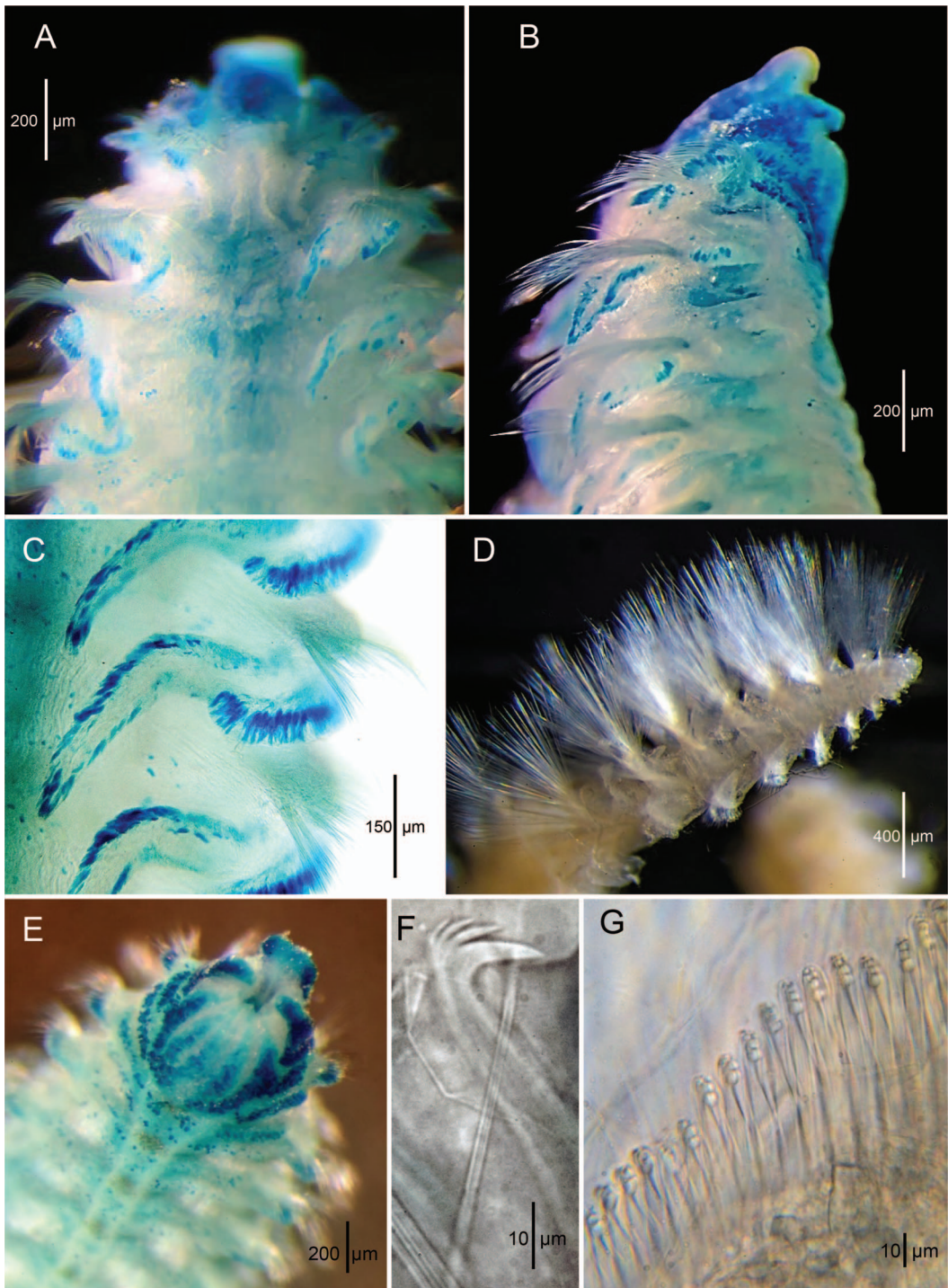


Fig. 5. *Microspio lydonia*. A, B, E: Holotype (USNM 1655928). C: specimen from Sta 18 (USNM 1655950). D, F, G: Paratype (USNM 1655931). A, anterior end, dorsal view. B, anterior end, lateral view. C, branchiae and notopodial lamellae chaetiger 5-7. D, posterior end. E, peristomium, ventral view. F, G, hooded hooks. A-C, E, stained with Methyl Green.

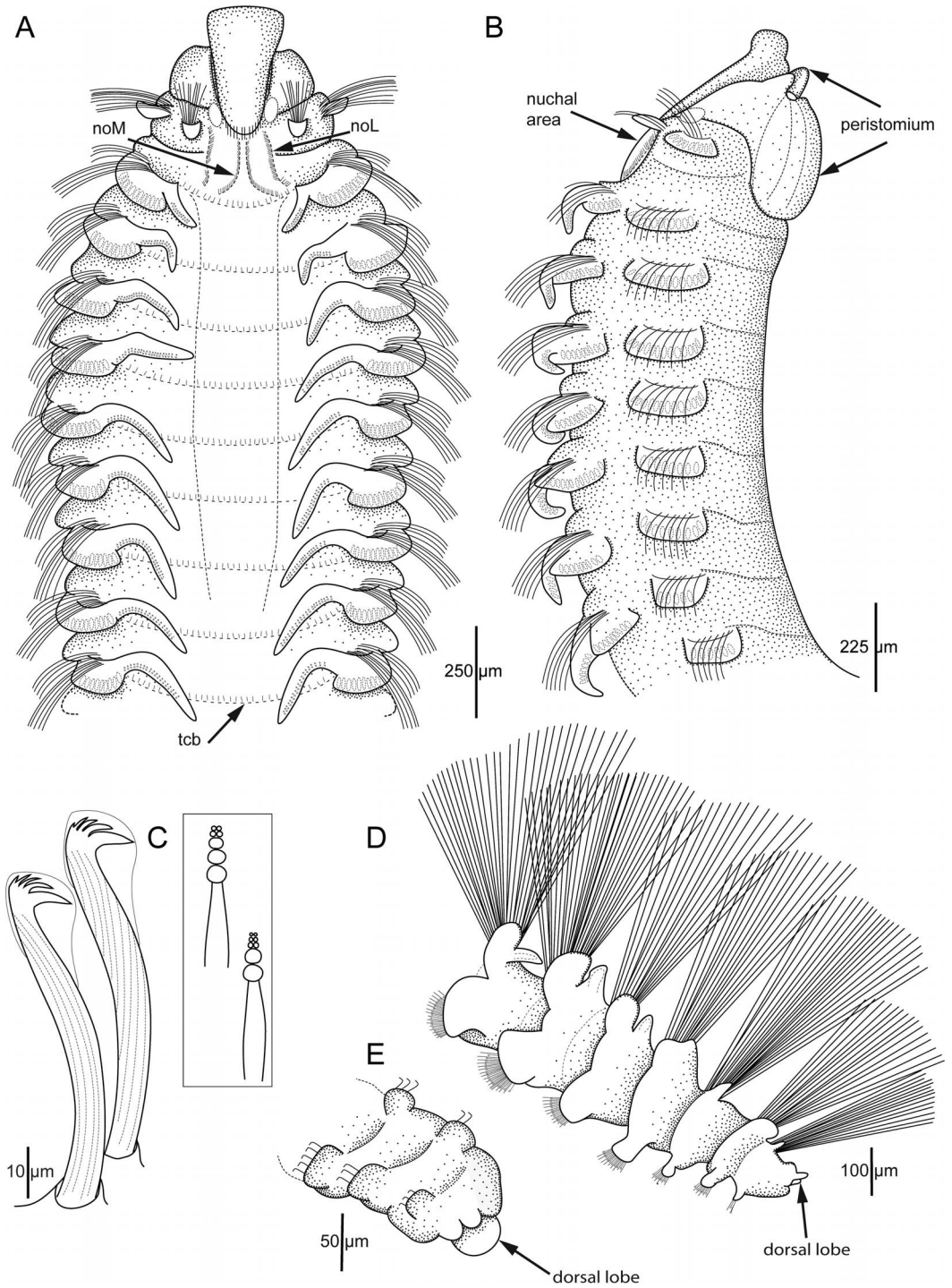


Fig. 6. *Microspio lydonia*. A: specimen from GB Sta. 18 (USNM 1655949), B: specimen from GB Sta. 12 (USNM 1655946), C, D: paratype from GB Sta. 7 (USNM 1655931), E: specimen from North Sta. 11 (USNM 1655955). A, anterior end, dorsal view. B, anterior end, lateral view. C, hooks, insets showing arrangement of teeth not to scale. D, posterior end, lateral view. E, pygidium, ventral view, smaller specimen. Abbreviations: noL = nuchal organ, lateral band; noM = nuchal organ, medial band; tcb = transverse ciliary band.

Description.—Holotype incomplete, 1 mm wide, 4 mm long for 16 chaetigers; other specimens 0.8–1 mm wide, 2.5–3.0 mm long for 11–16 chaetigers. Color in alcohol white, one specimen with very faint circular pigment mid-prostomium, two specimens with faint brownish pigment spots mid-venter on six to eight anterior chaetigers.

Prostomium rectangular, slightly flared anteriorly (Figs. 5A, 6A); no occipital tentacle; eyespots 0–4, if present, brown spots in trapezoid arrangement. Palps present on one small specimen, extending lengthwise through widest anterior region, other palps lost. Peristomium forming low collar on dorsal side, inflated, puckered on ventral side (Fig. 5A, B, 6A, B). Nuchal organ with medial bands from posterior margin of prostomium extending longitudinally to middle of chaetiger 2, then turning laterally, small gap between medial and lateral band, which also extends to middle of chaetiger 2, may turn slightly laterally at the end (Figs. 5A, 6A). Chaetiger 1 with cilia obscuring posterior margin of prostomium, visible with MG staining (Figs. 5A, 6A); from chaetiger 2, dorsum with transverse ciliary bands extending between branchial bases (Fig. 6A). Longitudinal dorsal metameric ciliary bands or patches not observed.

Chaetiger 1 with both notopodial and neuropodial postchaetal lamellae and chaetae: notopodium with small, rounded, slightly oval, glandular lamella and about 15–20 capillary chaetae; neuropodial lamellae broader than notopodial lamellae, with about 20 capillary chaetae. From chaetiger 2, notopodial lamellae broad, glandular, largest in anterior and mid-body chaetigers (Figs. 5C, 6A, B), then becoming smaller, oval, in posterior segments, very small in far posterior chaetigers (Figs. 5D, 6E); no prechaetal notopodial lamellae. Neuropodial lamellae glandular, rectangular with broad, rounded distal edge through midbody, then becoming smaller through posterior chae-

tigers (Figs. 5D, 6B, D). Branchiae from chaetiger 2, first pair about same size or slightly smaller than those following (Figs. 5A, 6A), continuing throughout posterior segments, except for last 2–3 chaetigers; basally fused to notopodial lamellae (Figs. 5C, 6A), longest through mid-body region, then becoming very small, short posteriorly, increasingly separate from lamellae.

Anterior notopodial and neuropodial chaetae capillaries in two rows, anterior row shorter than posterior row, 20–30 chaetae per fascicle. Neuropodial hooded hooks from chaetiger 10, initially 5–6 per fascicle, increasing up to 26 in posterior chaetigers, then abruptly decreasing to 2–5 in last few chaetigers; with anterior row of curved capillary chaetae up to twice the length of hooks and 2–3 thin, inconspicuous chaetae in inferiormost position of fascicle; hooks multidentate, with main fang surmounted by usually 3 (sometimes 2) large single teeth and by 2 (sometimes 3) pairs of smaller apical teeth (Figs. 5F, G, 6C); shaft of hooks slightly curved, appearing striated. Posterior notopodial chaetae long, fine, stiff capillaries numerous in last 10–12 chaetigers (Figs. 5D, 6D).

Pygidium on smallest specimens with rounded dorsal lobe (Fig. 6E), larger specimen with two tiny dorsal lobes (Figs. 5D, 6D).

Methyl Green staining pattern.—Dorsal prostomium stains deeply in middle region with a dense speckled pattern; posterior prostomium usually clear but often with a few small spots medial and posterior to eyes, cilia across base visible with staining (Fig. 5A). Anterior prostomium mostly clear of stain on dorsal surface; lateral tips stain on ventral surface as a continuation of stain along the lateral edge of prostomium (Fig. 5E). Dorsal and lateral peristomium stain in dense pattern, similar to prostomium (Fig. 5B). Ventral peristomium stains in stripes along posterior half, with lateral stripes going over top and down into the gullet (Fig. 5E). Ventral portion of chaetiger 1 stains, paralleling

ventral peristomial stained pattern. Small glands in palps, branchiae, and both notopodial and neuropodial lamellae stain deeply. Dorsum and venter both with transverse rows of small stained spots along length of body, these stain more deeply in anterior (especially just posterior to nuchal organs) and mid-body.

Pigmentation.—Of the 60+ specimens examined, 6–10 had eyespots, four had brown pigmented spots on the mid-line of the venter, and two had a bit of brown pigment laterally (between the parapodia) on some anterior segments starting with chaetiger 3. Only one specimen had a faint round patch on the middle of the prostomium.

Remarks.—*Microspio lydonia* is very similar to *M. pigmentata* (Reish, 1959) and was identified as such in an earlier paper (Maciolek 1990). Characters shared in common include unusual multidentate hooded hooks and a posterior region with extremely long, stiff capillary chaetae. Maciolek (1990) redescribed *M. pigmentata* (Reish, 1959) based on the holotype from California and additional material from several locations along the east coast of the U.S.A.; her Fig. 8 is based on one of several specimens from Florida, which was considered identical to the holotype. At that time, some differences among the specimens from various locations, especially Georges Bank, were noted but not considered to be of taxonomic importance; these and additional differences are now given more weight, particularly given the geographic separation between the original *M. pigmentata* and *M. lydonia*. These differences include size, pigmentation, the structure of the nuchal organs and transverse ciliary bands, the number and arrangement of teeth on the hooks, the number of hooks per chaetiger, and the structure of the pygidium.

Microspio lydonia is a smaller species than *M. pigmentata*; it measures roughly half the width for the same length/number of chaetigers. *Microspio pigmentata* is

strongly pigmented, with a circular patch of brown pigment in the middle of the prostomium and between the noto- and neuropodia of one to several anterior segments. Reish (1959) also described dorsal pigment medially on chaetigers 2–6 (or up to chaetiger 12), and dark ventral pigment spots were seen on the material examined in this study. Only a few specimens of *Microspio lydonia* had any pigment on the dorsal surface and that was very faint; a few specimens had light brown spots on the mid-line of the venter.

The nuchal organs of *M. lydonia* originate at the posterior end of the prostomium and there is one row of transverse cilia per segment, whereas in *M. pigmentata* the medial ciliary band first runs alongside the prostomium and there are two dorsal ciliary bands per segment. *Microspio lydonia* exhibits a striped MG staining pattern on the ventral side of the peristomium; in comparison, the ventral peristomium of *M. pigmentata* retains stain in the posterior portion, but this is solid or speckled, not striped.

The multidentate hooks of *M. lydonia* usually have three, sometimes only two, single teeth surmounted by one or two pairs of very small apical teeth. The hooded hooks of the *M. pigmentata* holotype were described by Reish (1959) as having two large single teeth surmounted by a pair of smaller teeth and a third small tooth at the apex; Maciolek (1990) reported hooks with two single and three pairs of teeth as clearly seen on the holotype as well as on the specimens from Florida and North Carolina, thus differing from the three single teeth and apical pairs in *M. lydonia*. Up to 30 hooks per fascicle are present in the posterior chaetigers of *M. pigmentata*, whereas *M. lydonia* has slightly fewer, up to 26 per fascicle. Both *M. lydonia* and *M. pigmentata* have extremely long capillary chaetae in the far posterior chaetigers, but these may be more numerous in *M. lydonia*. With only three posterior ends available, the charac-

ter of the pygidial lobe in *M. lydonia* was difficult to confirm, but it appears to have poorly developed cirri, if any, which differs from *M. pigmentata*, which has four anal cirri.

All of these differences point to the conclusion that the Georges Bank material represents a different species; material from the Gulf of Mexico and southeastern U.S.A. previously reported as *M. pigmentata* (Johnson 1984, Maciolek 1990) should be reevaluated.

In addition to the current material examined, 71 lots of material from the MMS GBMP and ACSAR programs are accessioned at the USNM (Accessions 359235 and 364005) as *Microspio* cf. *pigmentata*, but this material was not available for reexamination for this study. However, the material on hand is from several of the same stations, so it is with some confidence that we suggest that the *Microspio* in those lots is the same as this newly described species.

Etymology.—The species name refers to Lydonia Canyon, where much of the material was collected. The canyon itself was named for NOAA's Coast and Geodetic Survey vessel, the *Lydonia*, one of the four ships that conducted surveys of the area between the years 1930 and 1932.

Distribution.—Northwestern North Atlantic, off Massachusetts, 130–255 m.

Microspio ariena, new species
Figs. 7–8

ZooBank LSID.—urn:lsid:zoobank.org:act:F5C8ACA5-0A33-49AE-B6B9-19F86BEB57C1

Material examined.—South China Sea, off Brunei. coll. J. A. Blake, Chief Scientist. Site CA1, R/V *Emma*, Sta. 55, 01 Jun 2011, 05°43.652'N, 114°14.768'E, 1150 m, holotype (MCZ 162300).

Description.—A small species, holotype incomplete, 0.4 mm wide, 1.5 mm long for 13 chaetigers. Color in alcohol white, no pigment. Prostomium with anterior edge

difficult to discern, may be oriented ventrally, may have medial incision with slightly inflated tips, posterior end extending to posterior of chaetiger 1; no eyespots, no occipital tentacle (Figs. 7A, D, 8A). Peristomium forming low dorsal collar, fused with chaetiger 1 ventrally but not dorsally. Nuchal organs not obvious, even with MG or Shirlastain A. Transverse dorsal ciliated bands short, indistinct on chaetiger 2, obvious from chaetiger 3 through end of fragment; two rows per chaetiger, cilia oriented in opposite directions in fixed specimen (Fig. 8A). Longitudinal dorsal metameric ciliary bands or patches not observed. Dorsum with small tear-shaped glands mid-chaetiger. Venter without epidermal glands. Chaetiger 1 with very small, oval to slightly pointed, notopodial lamella and 4–6 notopodial capillaries (Fig. 8A), neuropodium with slightly larger lamella and 10–12 capillary chaetae (Figs. 7A, D, 8A). Chaetigers 1 and 2 distinct dorsally and ventrally. Notopodial postchaetal lamellae glandular, small rounded rectangles from chaetiger 2, becoming smaller, slightly oval in posterior chaetigers. Neuropodial lamellae small, gently rounded rectangles throughout, slightly glandular. Branchiae from chaetiger 2, large, elliptical, densely packed with large elongate glands, largest on chaetigers 3–6, smaller on 7, missing on chaetigers 8–11, small, digitiform on chaetigers 12–13 (last two of fragment) (Figs. 7A, B, D, 8A, B); fusion of branchiae with base of lamellae not clear, fused at base, if at all.

Capillary chaetae in two rows from chaetiger 2 in both noto- and neuropodia; anterior row slightly curved, shorter than posterior row, capillaries slightly bilimbate, not granulated or striated. Hooded hooks from chaetiger 11, straight, tridentate with two small teeth side-by-side over large tooth, appearing bidentate in profile (Figs. 7E, 8C); hooks numbering four per fascicle, with a few accompanying capillaries that greatly exceed hooks in length.

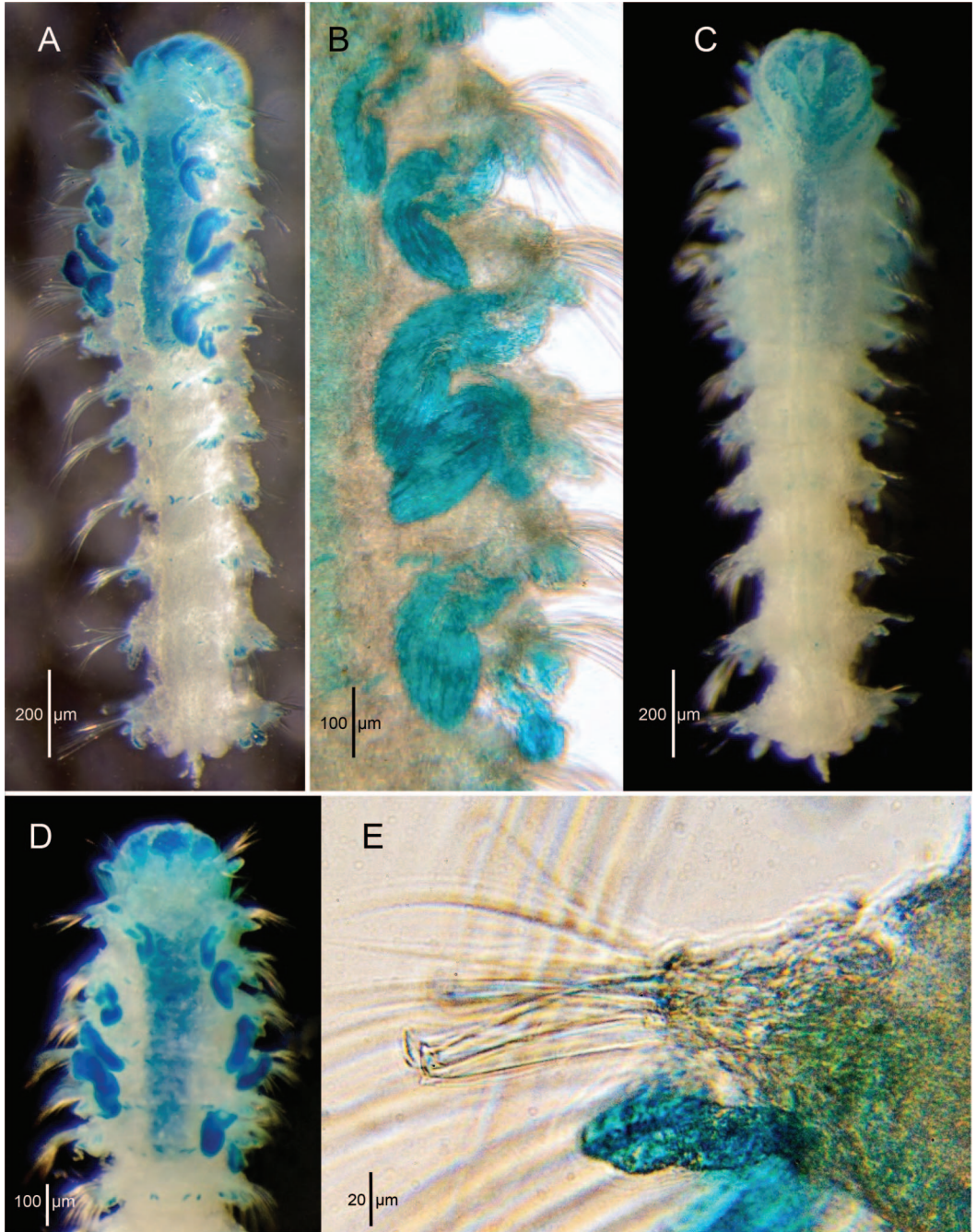


Fig. 7. *Microspio ariena*. Holotype (MCZ 162300). A, dorsal view. B, close-up of branchiae on right side. C, ventral view. D, anterior end, dorsal view. E. neuropodium with chaetae and lamella, ventral view. A–E stained with Methyl Green.

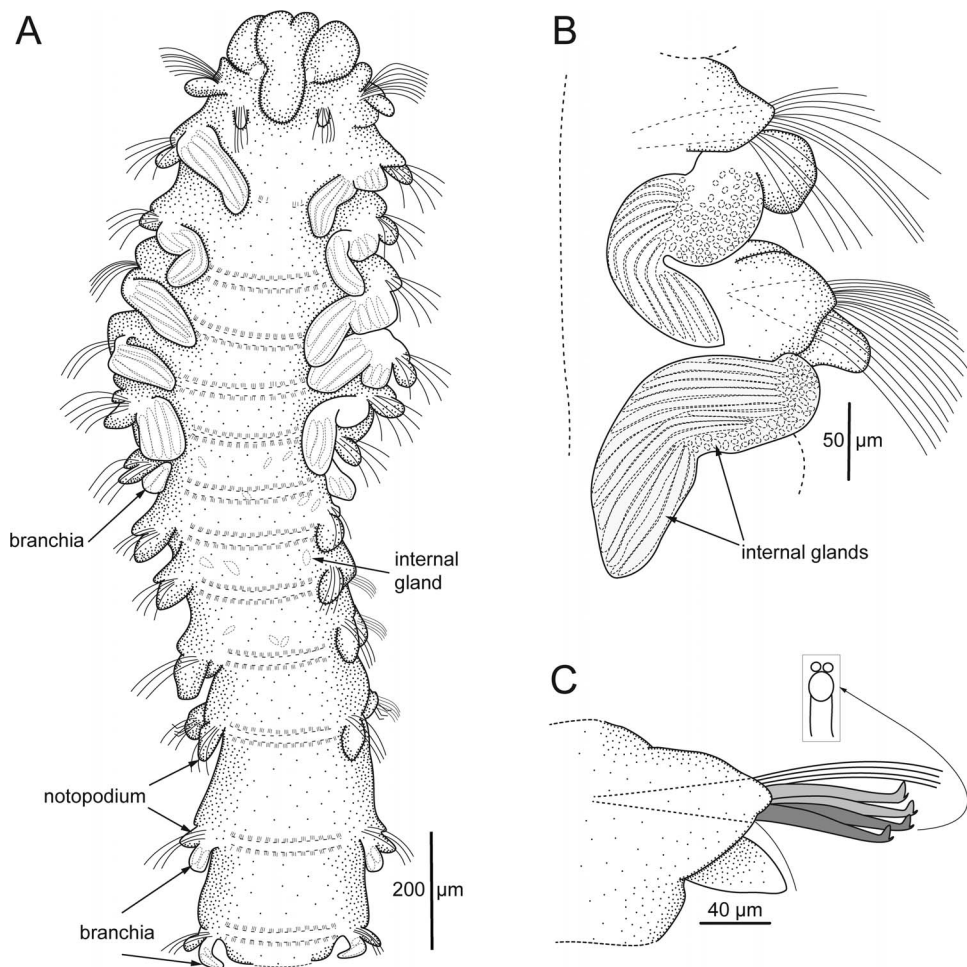


Fig. 8. *Microspio ariena*. Holotype (MCZ 162300). A, dorsal view. B, branchiae on chaetigers 3 and 4. C, ventral view of posterior parapodium with hooks, inset not to scale.

Sabre chaetae absent, 1–3 delicate neuropodial chaetae in inferiormost position from chaetiger 9.

Posterior and pygidium unknown.

Methyl Green staining pattern.—Prostomium stains dorsally, darkest in middle area; peristomium stains dorsally and ventrally, becoming irregularly spotted ventrally as destaining occurs. Branchiae and notopodial lamellae stain heavily in anterior chaetigers; in chaetigers 8–13, notopodial lamellae with a few glands that stain lightly. Neuropodial lamellae stain lightly throughout. Dorsal surface with 1–

4 small elongate or tear-shaped glands mid-chaetiger. Venter stains lightly in anterior region, with irregular and widely scattered spots. Internal gut stains posteriorly to chaetiger 7 (where anterior branchiae end).

Remarks.—*Microspio ariena* is most similar to *Microspio profunda* Maciolek, 1990 from 1760–3600 m off New England, Delaware, and the Bahamas. The two species have a similar prostomial shape, i.e., slightly bilobed, although this feature is more pronounced in *M. profunda* than in *M. ariena*; both lack eyes and an

occipital tentacle and have notopodia and notopodial capillaries on chaetiger 1. The hooded hooks are slender and similarly tridentate in both species, but number up to eight in *M. profunda* and only up to four in the anterior fragment of *M. ariena*. The two species differ in the shape of the branchiae, which are long and straplike along the entire body in *M. profunda* but are large, elliptical, and heavily glandular in the anterior region and very small in later chaetigers in *M. ariena*. The branchiae differ considerably in shape among the three deep-water species, being long and tapered in the anterior chaetigers of *M. profunda* and *M. tetrabranchia*, but shorter and elliptical as well as heavily glandular in *M. ariena*. The absence of branchiae from chaetigers 8–11 in *M. ariena* is unusual for this genus; no branchial scars were noted on those chaetigers but having only one specimen for study precludes understanding whether this is a consistent feature of the species.

Etymology.—Latin *ariena*, meaning *fruit of the plantain* or *banana*; used as a noun in apposition, the specific name refers to the elongate glands in the branchiae that resemble a hand of bananas.

Distribution.—Known only from the type locality in the South China Sea, off Brunei; 1150 m.

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