Zootaxa 4930 (1): 001–123
https://www.mapress.com/j/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4930.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:97110C21-173C-4552-96AC-4B5DC987FF1C

ZOOTAXA

4930

New species and records of Orbiniidae (Annelida, Polychaeta) from continental shelf and slope depths of the Western North Atlantic Ocean

JAMES A. BLAKE[1,2]

[1]*Aquatic Research & Consulting, 24 Hitty Tom Road, Duxbury, MA 02332. USA.*
[2]*Department of Invertebrate Zoology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138 USA.* *jablake9@gmail.com;* *https://orcid.org/0000-0001-8217-9769*

Magnolia Press
Auckland, New Zealand

Accepted by J. Williams: 20 Jan. 2021; published: 17 Feb. 2021

JAMES A. BLAKE

New species and records of Orbiniidae (Annelida, Polychaeta) from continental shelf and slope depths of the Western North Atlantic Ocean

(*Zootaxa* 4930)

123 pp.; 30 cm.

17 Feb. 2021

ISBN 978-1-77688-186-4 (paperback)

ISBN 978-1-77688-187-1 (Online edition)

FIRST PUBLISHED IN 2021 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/j/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract

Twenty-four species of Orbiniidae, 12 new to science, are reported from continental shelf and slope (deep-sea) habitats of the western North Atlantic. The majority of new material was collected during reconnaissance and monitoring surveys along the entire U.S. Atlantic coast from New England to the Carolinas that were intended to understand the potential impacts of oil and gas exploration in poorly known offshore environments. Additional materials from shallow water and shelf habitats off New England and New York as part of other projects are also included. New collections of *Califia schmitti* (Pettibone, 1957), *Leitoscoloplos acutus* (Verrill, 1873), *L. fragilis* (Verrill, 1873), *L. obovatus* Mackie, 1987, *L. robustus* (Verrill, 1873), *Scoloplos intermedius* (Hartman, 1965), *Orbinia swani* (Pettibone, 1957), *Phylo felix* (Kinberg, 1866), *P. norvegicus* (Sars, 1872), *P. ornatus* (Verrill, 1873), and *Questa trifurcata* (Hobson, 1970) provide additional morphological details, variability, and extended geographic and bathymetric distributions of previously known species. New species include *Leitoscoloplos pustulus* **n. sp.**, *Scoloplos papillatus* **n. sp.**, *S. pettiboneae* **n. sp.**, *S. pseudoarmiger* **n. sp.**, *S. verrilli* **n. sp.**, *Leodamas cuneatus* **n. sp.**, *L. mucronatus* **n. sp.**, *L. notoaciculatus* **n. sp.**, *Phylo paraornatus* **n. sp**.,

Orbiniella acsara **n. sp.**, *O. armata* **n. sp**., and *O. mimica* **n. sp**. Juveniles of some species of *Leitoscoloplos* and *Scoloplos* were found to resemble known species of the meiofaunal orbiniid genus *Schroederella* Laubier, 1962. As such, *S. berkeleyi* Laubier, 1971 is referred to synonymy with *Leitoscoloplos acutus*. More importantly, the genus *Schroederella* was found to be pre-occupied by *Schroederella* Enderlein, 1921 in the Insecta, Diptera, family Helomyzidae. *Gesaschroederella* **nomen nov**. is therefore proposed as a replacement name for the polychaete homonym.

Key words: New England, North Carolina, South Carolina, deep-sea, *Califia*, *Leodamas*, *Leitoscoloplos*, *Orbinia*, *Orbiniella*, *Phylo*, *Questa*, *Schroederella*, *Scoloplos*

Introduction

Orbiniid polychaetes are often characteristic of nearshore benthic communities along continental margins; however, they are rarely encountered in deep-sea habitats. Blake (2017, 2020) reviewed most of the key literature on orbiniids, updated the definitions of most genera, and collectively reported on 59 species, including 36 new species, many of which were from deep-water or poorly known habitats. Blake (2020) noted that there have been few reports on lower slope and abyssal orbiniids and, when collected, most species are rare. To date, out of the more than 237 known species of Orbiniidae, including species treated in the present study, only about 58 occur in depths greater than 500 m and only about 14 occur deeper than 3000 m.

Extensive reconnaissance and monitoring surveys conducted in 1980–2010 along the U.S. Atlantic coast from New England to the Carolinas yielded large collections of polychaetes, including orbiniids. In the nearshore and continental shelf habitats some species of *Leitoscoloplos* and *Scoloplos* were sufficiently abundant to characterize certain benthic assemblages. In the continental slope and rise depths, however, most orbiniids were relatively rare given the large number of samples collected. Exceptions to these generalizations include the genera *Microrbinia* and *Orbiniella*, whose small meiofaunal-sized species are often sufficiently abundant to characterize local benthic assemblages. In the present study approximately 8,180 specimens were examined yielding 24 species, of which 12 are new to science. Taxa are ordered in the text following the convention of Hartman (1957) and Blake (2017, 2020). The following taxa are included this study:

*Leitoscoloplos acutus (*Verrill, 1873)
Leitoscoloplos fragilis (Verrill, 1873)
Leitoscoloplos obovatus Mackie, 1987
Leitoscoloplos pustulus **n. sp.**
Leitoscoloplos robustus (Verrill, 1873)
Scoloplos intermedius (Hartman, 1965)
Scoloplos papillatus **n. sp.**
Scoloplos pettiboneae **n. sp.**
Scoloplos pseudoarmiger **n. sp.**
Scoloplos verrilli **n. sp.**
Leodamas cuneatus **n. sp.**
Leodamas mucronatus **n. sp.**
Leodamas notoaciculatus **n. sp.**
Califia schmitti (Pettibone, 1957)
Orbinia swani Pettibone, 1957
Phylo felix (Kinberg, 1866)
Phylo norvegicus (Sars, 1872)
Phylo ornatus (Verrill, 1873)
Phylo paraornatus **n. sp.**
Microrbinia linea Hartman, 1965
Orbiniella acsara **n. sp.**
Orbiniella armata **n. sp.**
Orbiniella mimica **n. sp.**
Questa trifurcata (Hobson, 1970)

Materials and methods

Materials examined as part of this study. The majority of specimens examined as part of this study were collected by the author and colleagues as part of offshore surveys funded by the U.S. Department of the Interior′s former Minerals Management Service (MMS), now the Bureau of Ocean Energy Management (BOEM). These studies were intended to provide a baseline and be used to evaluate the potential impact of oil and gas exploration and development on Georges Bank off New England (1981–1985) and along the U.S. Atlantic Continental Slope and Rise (ACSAR) from the Canadian boundary to the Carolinas (1983–1987). Specimens from an additional MMS project in 1992 that focused on the continental slope off Cape Hatteras, North Carolina, are also included. Supplemental samples from Massachusetts Bay collected over several years (1992–1997) as part of the Massachusetts Water Resources Authority's (MWRA) long-term Harbor and Outfall Monitoring Program (HOM) associated with an ocean outfall are also included together with samples from the New Bedford Harbor (NBH) long-term monitoring program collected in 1999 for the U.S. Army Corps of Engineers (USACE) to document remediation of a U.S. EPA Superfund Site associated with PCB contamination. In addition, miscellaneous samples from the northeastern United States from Maine to New Jersey either collected by the author or accumulated from various environmental surveys are also included. All MMS collections are deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Other collections are deposited in the Museum of Comparative Zoology (MCZ), Harvard University. Type specimens of a few species reported in this study were examined during earlier visits to or loans from the USNM and Los Angeles Museum of Natural History (LACM). A few specimens were retained by the author (JAB) for additional study as part of another on-going project.

The sample coordinates were based on Loran-C time delays for the pre-1990 projects and later with GPS. In general, each sample was based on a unique set of coordinates, even if a replicate was collected from the same station. For the MWRA monitoring project each station had a set of reference coordinates. Once these were located, each replicate collected at the site was assigned these values. The navigation was checked for each replicate sample, however, and if the vessel drifted more than 0.01 nmi. (ca. 18 m) off station, then the reference coordinates were reacquired. Similarly, collection of samples during the Georges Bank monitoring on the continental shelf was based on station-specific reference coordinates. Up to six replicate biology grab samples were collected as near to these coordinates as possible given weather conditions and capability of the survey vessels.

For most offshore sampling on the continental shelf, including the MWRA Massachusetts Bay and the MMS Georges Bank programs, a Kynar-coated 0.04-m^2 Ted Young grab was used for collection of the samples. For the deep-water MMS ACSAR and Cape Hatteras programs, a 0.25-m^2 Sandia Box core was used. The sample box was subdivided into 25 10 x 10 x 50 cm subcores from which the upper 10 cm of nine or ten subcores (0.09 or 0.10-m^2 surface area) were used for benthic biology. A few subcores from the ACSAR samples collected from off North Carolina were cut at 2, 5, and 10 cm depths and processed separately in order to provide data on benthic organisms living at the 0–2, 2–5, and 5–10 cm depth intervals (Blake 1994). The majority of samples were processed using fine-mesh sieves to separate the invertebrates from the sediments. The offshore MMS and MWRA samples were carefully processed using a 300-µm-mesh sieve. A 500-µm-mesh sieve was routinely used with other surveys. The use of fine-mesh sieves ensured that sufficient numbers of smaller specimens, including juveniles, were retained.

Morphological observations. Specimens were examined using a Wild M-5 stereomicroscope and a Zeiss RA research microscope equipped with phase contrast and Nomarski differential interference optics. Photomicrographs were taken with a Nikon D7100 camera mounted on both the stereo- and compound microscopes. For observation, specimens were first stained with a solution of Shirlastain A in water to highlight difficult-to-see surficial morphology. Some specimens were stained with a saturated solution of Methyl Green (MG) in 70% 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 and later transferred to Dura-Lar® matte film and inked.

Due to the large numbers of specimens and numerous juveniles in some collections, such as the MWRA materials from Massachusetts Bay and the MMS offshore surveys, it was possible to examine juveniles of various sizes of selected species of *Leitoscoloplos*, *Scoloplos*, and *Orbinia* in order to determine at what stage of development certain key characters such as branchiae, neuropodial uncini, subpodial lobes and/or flanges, interramal cirri, glandular patterns, and oral morphology first appeared. Detailed growth sequences were not developed; however, the collections are available in the event such information is required in future investigations.

Abbreviations used on figures: ac, acicula; acSp, acicular spine; an, anus; anC, anal cirrus; br, branchiae; bv,

blood vessel; cil, cilia; dOr, dorsal organ; eySp, eyespot; gL, glands; irC, interramal cirrus; irP, interramal process; lLmo, lower lip of mouth; mo, mouth; neL, neuropodial lobe; neP, neuropodium; noL, notopodial lobe; noP, notopodium; nuO, nuchal organ; per, peristomium; phrx, pharynx; pr, prostomium; prob, proboscis; pyg, pygidium; Set, setiger; subFl, subpodial flange; subPa, subpodial papilla; subPL, subpodial lobe; stPa, stomach papilla; uLmo, upper lip of the mouth; vC, ventral cirrus.

Systematic account

Family Orbiniidae Hartman, 1942

Type genus: *Orbinia* Quatrefages, 1866, designated by Hartman, 1942.

Diagnosis. (modified from Blake 2017). Body elongate, usually divided into a wide, dorsoventrally flattened thoracic region formed of firm, muscular segments and a posterior abdominal region rounded in cross-section and composed of soft, fragile segments bearing dorsally elevated parapodia, or abdominal parapodia not elevated; bodies usually with distinct body regions, or body regions indistinct. Prostomium of variable shapes, with anterior margin ranging from acutely pointed to bluntly rounded; 1–2 pair of eyespots sometimes present, but usually absent; paired nuchal organs present. Proboscis soft, eversible, saclike without armature, sometimes dendritically branched when everted. Peristomium composed of 1–3 achaetous rings; juveniles with two rings often with only one as adult. Paired cirriform and ciliated branchiae located mid-dorsally between notopodia, beginning either on or just posterior to thoracic region, continuing to posterior end; or branchiae entirely absent. Small dorsal sense organs sometimes present anterior and medial to branchiae in some thoracic and abdominal parapodia. Notopodia simple, with fingerlike postsetal lobes; sometimes divided or forked. Interramal cirri sometimes present between notopodia and neuropodia of posterior thoracic and/or abdominal segments. Neuropodia well developed in thoracic region, sometimes forming elevated ridges bearing numerous setae; one to many postsetal lamellae often present, sometimes continuing ventrally as additional subpodial or stomach papillae. Abdominal neuropodia extending laterally and dorsally, usually bilobed; ventral cirrus often present; ventral flange may be present. Lateral ciliated organ sometimes present between noto- and neuropodia. Notosetae include capillaries, flail setae, and furcate setae; modified spines sometimes present in abdominal notopodia. Thoracic neurosetae may include crenulated capillaries, blunt-tipped crenulated setae, crenulated or smooth uncini, and modified spines; or any combination of capillaries, uncini, and spines. Abdominal neurosetae include capillaries and flail setae; imbedded aciculae usually present, protruding on some genera. Multidentate swan hooks or bidentate hooks or crotchets known from two genera. Pygidium simple, collar-like, often with 2–4 long filamentous anal cirri.

Remarks. A few edits to the diagnosis of Blake (2017) serve to update minor details. However, this diagnosis essentially follows the more extensive family definition of Hartman (1957). With the inclusion of the genus *Questa*, orbiniids now contain a few species having bidentate hooks or crotchets similar to those found in some paraonids (Giere *et al.* 2008). The multidentate swan hooks found in *Proscoloplos* are a more complex manifestation of hooked setae. When present, furcate setae of orbiniids typically have two long tynes from which numerous thin needles or spines project into the space between forming a web. In species of *Questa*, however, two long, thick tynes have either one or two shorter and thinner basally attached prongs arising between them.

Subfamily Orbiniinae Hartman, 1957. Emended by Blake 2000.

Type genus. *Orbinia* Quatrefages, 1866, designated by Hartman 1957.

Diagnosis. (after Blake 2017). Body large, with distinct regions; parapodia lateral in thoracic region, typically shifted dorsally in abdominal region. Prostomium bluntly rounded to acutely pointed; nuchal organs present; eyespots present or absent. Peristomium with 1–2 achaetous rings, separated from prostomium. Noto- and neuropodial postsetal lamellae single, simple lobes to multiple lobes, sometimes branched; subpodial lobes and stomach papillae present or absent; interramal cirri present or absent. Setae including aciculae, capillaries, furcate setae, spines, uncini, modified spear-like setae, and flail setae. Branchiae typically present, rarely absent; branchiae usually single,

rarely branched; oval to flattened, with two longitudinal rows of cilia and typical orbiniid structure with two blood vessels connected by numerous capillaries; branchiae of abdominal region thinner, more elongate than on thorax. Pygidium with several long filamentous anal cirri, or cirri absent.

Inclusive genera. *Berkeleyia, Califia, Leitoscoloplos, Leodamas, Naineris, Orbinia, Phylo, Protoaricia,* and *Scoloplos*.

Remarks. The subfamily Orbiniinae contains most of the better-known genera and species of Orbiniidae.

Genus *Leitoscoloplos* Day, 1977

Type-species: *Haploscoloplos bifurcatus* Hartman, 1957, designated by Day 1977

Diagnosis. (after Blake 2017). Prostomium pointed, conical; peristomium typically with one achaetous ring, but with additional superficial annulae on some species. Branchiae lacking, or present from middle, to posterior thoracic, transitional, or abdominal setigers. Posterior thoracic setigers with 0–2 postsetal lobes and 0–2 subpodial lobes; abdominal setigers with 0–4 subpodial papillae; stomach papillae rare, interramal cirri present or absent. Thoracic neurosetae including only crenulated capillaries. Without abdominal neuropodial spines, with 2–3 imbedded aciculae present or absent. Notopodial furcate setae present or absent in abdominal segments.

Remarks. The genus *Leitoscoloplos* differs from *Scoloplos* in lacking spines or uncini in thoracic neuropodia. However, this classification is likely to change with further study because *Leitoscoloplos* species appear to contain several distinct groups. Blake (2017) divided the genus into five groups (A–E), based largely on the presence and distribution of branchiae, as a practical means to separate groups of species to facilitate their identification. Presently, the genus consists of 32 species (Blake 2020), four of which have been encountered in the present study; one new species, *L. pustulus* **n. sp**. has also been identified. The five species occur in Groups B (branchiae present from middle to posterior thoracic setigers) and Group C (branchiae present from transitional segments between thoracic and abdominal segments). Interestingly, no species in the so-called *L. kerguelensis* group were encountered (Group D, with branchiae first present from anterior abdominal setigers). It appears as if Group D is largely limited to the southern hemisphere and Pacific Ocean. Among species of *Leitoscoloplos* encountered in the present study, three are taxa with an interramal cirrus between the noto- and neuropodia of abdominal segments: *L. fragilis*, *L. obovatus*, and *L. robustus*. In addition, *L. pustulus* **n. sp**. has a short interramal process in the same location. Thus four of five species of *Leitoscoloplos* along the Atlantic coast of the US have a distinct interramal cirrus or process. Species of *Leitoscoloplos* having this feature are rare elsewhere.

Of the five species of *Leitoscoloplos* encountered in the present study, two, *L. obovatus* and *L. pustulus* **n. sp**., are from upper continental slope depths, while the other three species are well known and range from intertidal or shallow water to shelf depths of less than 100 m. The five species covered in this paper are:

1. *Leitoscoloplos acutus* (Verrill, 1873)
2. *Leitoscoloplos fragilis* (Verrill, 1873)
3. *Leitoscoloplos obovatus* Mackie, 1987
4. *Leitoscoloplos pustulus* **n. sp**.
5. *Leitoscoloplos robustus* (Verrill, 1873)

Leitoscoloplos acutus (Verrill, 1873)

Figures 1–3

Anthosoma acutum Verrill, 1873: 305–306.
Scoloplos acutus: Verrill 1881: 301, 305, 309; Procter 1933: 141, Fig. 32. Not Curtis 1969; Not Zhadan 1998.
Scoloplos armiger: Hartman 1944, pl. 18, fig. 5. Not O.F. Müller 1776.
Scoloplos (*Scoloplos*) *acutus*: Pettibone 1963: 293–294, fig. 74g.
Leitoscoloplos acutus: Maciolek-Blake *et al*. 1985: B-5; Blake *et al*. 1998: C-1, C-2; Blake 2017: 18.
Scoloplos (*Leitoscoloplos*) *acutus*: Trott: 2004: 280.
Schroederella berkeleyi Laubier, 1971: 1483–1486, fig. 1. **New synonymy**.

Material examined. (*2,726 specimens*). **Northeastern USA. Gulf of Maine, Damariscotta River Estuary**, Lowes Cove, coll. J.A. Blake, 26 Jul 1967, 43°59.658′W, 69°33.255′W, intertidal (7, MCZ 161514); West Side Seal Cove, coll. G. Noyes, 03 Aug 1966, 43°53.087′W, 69°34.147′W, 1–2 m (1, MCZ 161515); Cove north of Wiley Point, coll. D. Dorsey and V. Walker, 15 Aug 1966, 43°59.063′W, 69°33.047′W, 1 m (5, MCZ 161516); Oyster Creek, coll. D. Dorsey, 05 Aug 1966, 43°53.363′N, 69°30.615′W, 1–2 m (1, MCZ 161517).—**Connecticut, Long Island Sound,** USACE Dredged Material Disposal Site Survey, **Sta. NL1KE**, Rep. 2, 17 Feb 2000, 41°16.323′N, 72°03.877′W, 16 m (8, MCZ 161521); Rep. 3, 17 Feb 2000, 41°16.313′N, 72°03.894′W, 16 m (3, MCZ 161522). **Sta. NL2KE**, Rep. 1, 17 Feb 2000, 41°16.303′N, 72°03.143′W, 12 m (7, MCZ 161523); Rep. 2, 17 Feb 2000, 41°16.297′N, 72°03.155′W, 12 m (5, MCZ 161524); Rep.3, 17 Feb 2000, 41°16.312′N, 72°03.154′W, 12 m (5, MCZ 161525). **Sta. NLLRF**, Rep. 1, 17 Feb 2000, 41°16.688′N, 72°01.949′W, 16 m (8, MCZ 161526); Rep. 2, 17 Feb 2000, 41°16.710′N, 72°02.000′W, 16 (5, MCZ 161527); Rep. 3, 17 Feb 2000, 41°16.657′N, 72°01.908′W, 16 m (12, MCZ 161528). **Sta. NLRLC**, Rep. 1, 17 Feb 2000, 41°16.504′N, 72°04.492′W, 14 m (1, MCZ 161529); Rep. 3, 17 Feb 2000, 41°16.425′N, 72°04.464′W, 14 m (2, MCZ 161530). **Sta. NLSEA**, Rep. 2, 17 Feb 2000, 41°16.483'N, 72°04.887′W, 15 m (1, MCZ 161531). **Sta. WLW5H**, Rep.2, 19 Feb 2000, 40°59.265′N, 73°29.669′W, 34 m (1, MCZ 161532).—**Atlantic Ocean, off New Jersey**, 14 Aug 2008; Excalibur **Sta. 27B**, 40°21.5148, 73°54.3525′W, 21 m (2, MCZ 161534).—**Massachusetts, New Bedford Harbor, Long Term Monitoring Program, 1999 September–October Survey for USACE**: **Sta. 123**, 29 Sep 1999, Rep. 1, 41°40.016′N, 70°55.034′W, 2.5 m (2, MCZ 161535). **Sta. 128**, Rep. 1, 29 Sep 1999, 41°39.926′N, 70°55.041′W, 3 m (8, MCZ 161536). **Sta. 212**, 24 Sep 1999, 41°38.826′W, 70°54.906′W, 3.3 m (132, MCZ 161537). **Sta. 318**, 10 Oct 1999, 41°35.664′N, 70°52.283′W, 6.6 m (2, MCZ 161538). **Sta. 331**, 15 Sep 1999, 41°34.198′N, 70°55.707′W, 7.3 m (2, MCZ 161539).—**Massachusetts**, **Duxbury Bay**, coll. J.A. Blake, 02 Aug 1981, 42°2.15′N, 70°40.06′W, low intertidal (10, MCZ 161533).—**Massachusetts Bay**, **MWRA Harbor and Outfall Monitoring Program**. **1992 May Survey: Sta. FF-4**, 42°17.30′N, 70°25.49′W, 92 m (65, MCZ 161400). **Sta. FF-5**, 42°08.00′N, 70°25.35′W, 64 m (5, MCZ 161401). **Sta. FF-9**, 42°18.75′N, 70°39.40′W, 51 m (25, MCZ 161402). **Sta. WH3**, 42°23,39′N, 70°49.84′W, 36 m (292, MCZ 161403). **1992 August Survey**: **Sta. NF-1**, 42°20.35′N, 70°50.51′W, 42 m (5, MCZ 161404); **Sta. NF-2**, 42°20.31′N, 70°49.69′W, 26 m, (4, MCZ 161405). **Sta. NF-5**, 40°25.62′N, 70°50.03′W, 28 m (4, MCZ 161406). **Sta. NF-7,** 42°24.60′N, 70°48.89′W, 32 m (33, MCZ 161407); **Sta. NF-8**, 42°24.00′N, 70°51.81′W, 28 m (5, MCZ 161408). **Sta. NF-11**, 42°23.39′N, 70°50.25′W, 31 m (23, MCZ 161409). **Sta. NF-12**, 42°23.40′N, 70°49.83′W, 33 m (33, MCZ 161410). **Sta. NF-13,** 42°23.40′N, 70°49.35′W, 33 (1, MCZ 161411). **Sta. NF-14**, 42°23.20′N, 70°49.36′W, 32 m (13, MCZ 161412); **Sta. NF-1**5, 42°22.93′N, 70°49.67′W, 32 m (17, MCZ 161413). **Sta. NF-16**, 42°22.70′N, 70°50.26′W, 29 m (31, MCZ 161414). **Sta. NF-19**, 42° 22.30'N 70° 48.30'7W, 32 m (23, MCZ 161415). **Sta. NF-20**, 42°22.69′N, 70°50.69′W, 27 m (10, MCZ 161416). **Sta. FF-1**, Rep. 2, 42°27.94′N, 70°37.31′W, 68 m (5, MCZ 161417). **Sta. FF-4**, Rep. 1, 42°17.30′N, 70°25.50′W, 86 m (7, MCZ 161418); Rep. 2, (5, MCZ 161419). **Sta. FF-5**, Rep. 1, 42°08.00′N, 70°25.35′W, 61 m (10, MCZ 161420); Rep. 3, (5, MCZ 161421). **Sta. FF-6**, Rep. 1, 41°53.90′N, 70°24.20′W, 33 m (2, MCZ 161422); Rep. 2 (2, MCZ 161423); Rep. 3 (4, MCZ 161424). **Sta. FF-7**, Rep. 3, 41°57.50′N, 70°16.00′W, 37 m (1, MCZ 161425). **Sta. FF-9**, Rep. 1, 42°18.75′N, 70°39.40′W, 48 m (14, MCZ 161426). **Sta. FF-10**, Rep. 1, 42°24.84′N, 70°52.72′W, 27 m (45, MCZ 161427); Rep. 2 (30+, MCZ 161428); Rep. 3 (53, MCZ 161429). **Sta. FF-11**, Rep. 1, 42°39.50′N, 70°30.00′W, 86 m (4, MCZ 161430); Rep. 2 (2, MCZ 161431). **Sta. FF-12**, Rep. 1, 42°23.40′N, 70°53.98′W, 22 m (67, MCZ 161432); Rep. 2 (65, MCZ 161433), **Sta. FF-13**, Rep. 1, 42°19.19′N, 70°49.38′W, 19 m (2, MCZ 161434); Rep. 2 (2, MCZ 161435); Rep. 3 (23, MCZ 161436). **Sta. FF-14**, Rep. 1, 42°25.00′N, 70°39.29′W, 69 m (4, MCZ 161437); Rep. 2 (2, MCZ 161438); Rep. 3 (15, MCZ 161439). **1995 August Survey: Sta. FF-1A**, 42°33.84′N, 70°40.55′W, 32 m (10, MCZ 161440). **Sta. FF-4**, 42°17.30′N, 70°25.50′W, 87 m (~20, MCZ 161441). **Sta. FF-9**, 42°18.75′N, 70°39.40′W, 49 m (31, MCZ 161442). **Sta. FF-10**, 42°24.84′N, 70°52.72′W, 27 m (50+, MCZ 161443). **Sta. FF-11**, 42°39.50′N, 70°30.00′W, 87 m (37, MCZ 161444). **Sta. FF-12**, 42°23.40′N, 70°53.98′W, 22 m (25+, MCZ 161445); **Sta. FF-13**, Rep. 1, 42°19.19′N, 70°49.38′W, 19 m (50+, MCZ 161446). **Sta. FF-14**, 42°25.00′N, 70°39.29′W, 77 m (40, MCZ 161447). **1996 August Survey**: **Sta. NF-14**, 42°23.20′N, 70°49.36′W, 33 m (7, MCZ 161448). **Sta. NF-15**, 42°22.93′N, 70°49.67′W, 32 m (10, MCZ 161449); **Sta. NF-18**, 42°23.80′N, 70°49.31′W, 35 m (7, MCZ 161450). **Sta. NF-19**, 42°22.30′N, 70°48.30′W, 32 m (5, MCZ 161451). **Sta. NF-24**, Rep. 1, 42°22.83′N, 70°48.10′W, 37 m, (27, MCZ 161452); Rep. 2 (22, MCZ 161453); Rep. 3 (35, MCZ 161454). **Sta. MF-2**, 42°20.31′N, 70°49.69′W, 30 m (27, MCZ 161455). **Sta. MF-5**, 42°25.62′N, 70°50.03′W, 36 m (6, MCZ 161456). **Sta. MF-7**, 42°24.60′N, 70°48.89′W, 33 m (17, MCZ 161457). **Sta. MF-8**, 42°24.00′N, 70°51.81′W, 30 m (53, MCZ 161458). **Sta. MF-9**, 42°23.99′N, 70°50.69′W, 29 m (42, MCZ 161459).

Sta. MF-10, 42°23.57′N, 70°50.29′W, 35 m (38, MCZ 161460). **Sta. MF-12**, Rep. 1, 42°23.40′N, 70°49.83′W, 34 m (37, MCZ 161461); Rep. 2 (31, MCZ 161462); Rep. 3 (39, MCZ 161463). **Sta. MF-16**, 42°22.70′N, 70°50.26′W, 29 m (14, MCZ 161464). **Sta. MF-20**, 42°22.69′N, 70°50.69′W, 28 m (35, MCZ 161465). **Sta. MF-21**, 42°24.16′N, 70°50.19′W, 33 m (22, MCZ 161466). **Sta. MF-22**, 42°20.87′N, 70°48.90′W, 36 m (22, MCZ 161467). **Sta. FF-1A**, Rep. 1, 42°33.84′N, 70°40.55′W, 32 m (2, MCZ 161468); Rep. 2 (3, MCZ 161469); Rep. 3 (15, MCZ 161470). **Sta. FF-4**, Rep. 1, 42°17.30′N, 70°25.50′W, 87 m (7, MCZ 161471); Rep. 2 (6, MCZ 161472); Rep. 3 (3, MCZ 161473). **Sta. FF-5**, Rep. 1, 42°08.00′N, 70°25.35′W, 61 m (13, MCZ 161474); Rep. 2 (3, MCZ 161475); Rep. 3 (7, MCZ 161476). **Sta. FF-9**, Rep. 1, 42°18.75′N, 70°39.40′W, 49 m (5, MCZ 161477); Rep. 2 (3, MCZ 161478); Rep. 3 (8, MCZ 161479). **Sta. FF-10**, Rep. 1, 42°24.84′N, 70°52.72′W, 27 m (41, MCZ 161480); Rep. 2 (28, MCZ 161481); Rep. 3 (35, MCZ 161482). **Sta. FF-11**, Rep. 1, 42°39.50′N, 70°30.00′W, 87 m, (3, MCZ 161483); Rep. 2, (10, MCZ 161484); Rep. 3, (10, MCZ 161485). **Sta. FF-12**, Rep. 1, 42°23.40′N, 70°53.98′W, 22 m, (56, MCZ 161486); Rep. 2, (44, MCZ 161487); Rep. 3 (40, MCZ 161488). **Sta. FF-13,** Rep. 1, 42°19.19′N, 70°49.38′W, 19 m (83, MCZ 161489); Rep. 2 (38, MCZ 161490); Rep. 3 (116, MCZ 161491). **Sta. FF-14**, Rep. 1, 42°25.00′N, 70°39.29′W, 77 m (6, MCZ 161492); Rep. 2 (15, MCZ 161493); Rep. 3 (13, MCZ 161494). **1997 August Survey**: **Sta. MF-**2, 42°20.31′N, 70°49.69′W, 30 m (2, MCZ 161495). **Sta. MF-5,** 42° 25.62′N, 70° 50.03′W, 36 m (4, MCZ 161496). **Sta. MF-9**, 42°23.99′N, 70°50.69′W, 29 m (22, MCZ 161497). **Sta. MF-10,** 42°23.97′N, 70°50.29′W, 35 m (34, MCZ 161498). **Sta. MF-12**, Rep. 1, 42°23.40′N, 70°49.83′W, 34 m (20, MCZ 161499); Rep. 2 (32, MCZ 161500); Rep. 3 (40, MCZ 161501). **Sta. MF-16,** 42°22.70′N, 70°50.26′W, 29 m (32, MCZ 161502). **Sta. MF-20**, 42°22.69′N, 70°50.69′W, 28 m **(**19, MCZ 161503). **Sta. MF-21**, 42°24.16′N, 70°50.19′W, 33 m (13, MCZ 161504). **Sta. MF-22,** 42°20.87′N, 70°48.90′W, 36 m (38, MCZ 161505). **Sta. FF-9**, Rep. 1, 42°18.75′N, 70°39.40′W, 49 m (3, MCZ 161506); Rep. 2 (5, MCZ 161507); Rep. 3 (4, MCZ 161508). **Sta. FF-10**, Rep. 1, 42°24.84′N, 70° 52.72′W, 27 m (9, MCZ 161509); Rep. 2 (46, MCZ 161510). **Sta. FF-12**, Rep. 1, 42°23.40′N, 70°53.98′W, 22 m (50, MCZ 161511); Rep. 2 (32, MCZ 161512); Rep. 3 (34, MCZ 161513).—**Off Massachusetts, Georges Bank**, **MMS Benthic Infauna Monitoring Program**, coll. G.W. Hampson, Chief Scientist. **Sta. 11**: Cruise M4, Rep 1, 16 May 1982, 40°30.8′N, 68°33.7′W, 83 m (2, USNM 1620840); Cruise M5, Rep. 2, 28 Jul 1982, 40°30.8′N, 68°33.7′W, 77 m (2, USNM 1620841); Cruise M6, Rep. 5, 26 Nov 1982, 40°30.8′N, 68°33.7′W, 83 m (1, USNM 1620842); Cruise M11, Rep. 1, 02 Feb 1984, 40°30.8′N, 68°33.7′W, 86 m (1, USNM 1620843); Rep. 3 (3, USNM 1620844). **Sta. 13**: Cruise M1, Rep. 4, Jul 1981, 40°29.5′N, 70°12.6′W, 65 m (1, USNM 1620845); Cruise M2, Rep. 3, 9 Nov 1981, 40°29.2′N, 70°12.4′W, 60 m (2, USNM 1620846); Cruise M3, Rep. 1, 11 Feb 1982, 40°29.2′N, 70°12.4′W, 69 m (1, USNM 1620847); Rep. 5 (1, USNM 1620848); Cruise M5, Rep. 5, 28 Jul 1982, 40°29.5′N, 70°12.6′W, 62 m (1, USNM 1620849); Cruise M6, Rep. 5, 27 Nov 1982, 40°29.3′N, 70°12.4′W, 67 m (1, USNM 1620850); Rep. 6 (1, USNM 1620851); Cruise M8, Rep. 1, 21 May 1983, 40°29.3′N, 70°12.5′W, 70 m (1, USNM 1620852); Cruise M12, Rep. 1, 03 Jun 1984, 40°29.5′N, 70°12.6′W, 70 m (1, USNM1620853). **Sta. 18**: Cruise M3, Rep. 6, 18 Feb 1982, 40°33.5′N, 67°13.7′W, 145 m (8, USNM 1620854).

Other material examined. Massachusetts, Craigsville Beach, Centerville, Barnstable County, coll. W.J. Wall, 26 Jun 1969, intertidal, holotype of *Schroederella berkeleyi* Laubier, 1971 (USNM 44946).

Description. A moderate-sized species, typically about 20–22 mm long with 75–80 setigers; specimen from Georges Bank (USNM 1620847) complete, long and narrow, with 125 setigers, 25 mm long and about 1.5 mm wide across middle of thorax; recorded up to 40 mm long by Pettibone (1963). Body elongate, with thoracic region dorsoventrally flattened, with individual segments short and narrow, 6–8 times wider than long (Figs. 1A, 2A); individual segments separated by narrow transverse groove. Abdominal segments also narrow, crowded without obvious annulations; posterior segments crowded (Fig. 2E). Body with no longitudinal grooves or ridges; abdominal segments with a light-colored thin line along venter. Color in alcohol light tan.

Pre-setiger region triangular, relatively short, about as long as first two or three setigers. Prostomium thickened basally, narrowing to pointed apex (Fig. 1A–B); nuchal organs oval slits on posterior lateral margin; eyespots absent. Peristomium a single short smooth achaetous ring (Fig. 1A), weakly divided ventrally due to upper and lower lips of mouth. Upper lip of mouth with two rounded medial lobes and 2–3 smaller lateral lobes (Fig. 1B); lower lip of mouth bordered with about 7–8 smaller lobes (Fig. 1B). Proboscis when everted with 1–3 lobes.

Thorax with 14–16 setigers with abrupt transition to abdominal segments (Figs. 1A, 2A). Boundary between thorax and abdomen best observed by elongation of neuropodia and decrease in number of neurosetae. Thoracic notopodial lobes more or less triangular in shape, digitiform, narrowing apically arising from narrow base (Figs. 1D, 2B); neuropodial lobes also digitiform, shorter than notopodial lobe, arising from broadly rounded base (Figs. 1D,

2B). Abdominal notopodia elongate, narrow, digitiform (Figs. 1E, 2C). Abdominal neuropodia thickened, becoming relatively short in middle and posterior segments, each narrowing to pointed apical lobe and with subterminal ventral cirrus on lateral margin (Figs. 1E, 2C); with elongate, narrow subterminal flange ventral to neuropodium; subpodial papillae absent (Figs. 1E, 2C). Interramal cirrus or protuberance entirely absent.

Branchiae typically from setiger 10–13, initially thoracic branchiae small and short, becoming full size by about setigers 14–15 (Fig. 1A). Anterior branchiae triangular, tapering to rounded apex; branchiae of abdominal segments becoming weakly asymmetrical with bulge on inner margin (Figs. 1E, 2C); each branchia with transverse folds and cilia on inner margin (Fig. 2C, arrows).

Notosetae including camerated capillaries and furcate setae; up to 20–30 capillaries in 2–3 irregular rows in thoracic notopodia or largest specimens reduced to 10–15 long, thin capillaries in abdominal segments accompanied by 1–3 furcate setae (Fig. 2D). Thoracic neurosetae all capillaries with about 45–55 setae in 4–5 rows; abdominal neurosetae including 2–7 capillaries with barbs along one edge and 1–2 short protruding aciculae, these minute, with rounded apex (Fig. 1E inset). Furcate setae of abdominal notopodia with unequal tynes, each tyne with a flattened rounded apex within which an opening and narrow channel can be observed with light microscope; narrow elongate fibrils present between tynes (Fig. 1F); flail setae absent.

Pygidium with lateral, dorsal, and ventral lobes surrounding anal opening; with two long, thin anal cirri arising dorsolateral (Figs. 1C, 2F).

Variability. Apart from small juveniles, the morphology presented here is consistent over the range of sizes considered to represent adults. In the very largest specimens, however, a rounded, rudimentary subpodial flange may be present on the last thoracic setiger and/or the first abdominal setiger. This rudimentary flange transitions into the larger subpodial flange that develops on anterior abdominal segments and that continues on all abdominal neuropodia.

Juvenile morphology. Juveniles of this species that were present with the adults were initially thought to be similar to *Schroederella berkeleyi* Laubier, 1971, a species established for small meiofaunal orbiniids from an intertidal sand beach in Massachusetts (Laubier 1971). However, examination of the holotype of *S. berkeleyi* and numerous juveniles in the new collections suggests that the juveniles represent part of a growth sequence for *Leitoscoloplos acutus*. Juveniles from Massachusetts Bay (MCZ 161433, MCZ 161464, and MCZ 161511) were examined in detail.

Specimens elongate, usually coiled in preservation and somewhat contracted (Fig. 3A–E). Complete specimens ranged from 2.1 mm long with 21 setigers (Fig. 3A) to 3.7 mm long with 48 setigers (Fig. 3F); posterior pre-pygidial segments crowded due to active growth zone. Thoracic setigers through middle abdominal setigers all about same width, narrowing in far posterior segments. Color white to light tan.

Prostomium long, triangular, acutely pointed; eyespots absent; nuchal organs not observed. Peristomium with a single achaetous ring vaguely separated laterally and ventrally by weakly developed lines, but not into two separate rings. Anterior lip of mouth with two large lobes; posterior lip with five or six small lobes forming a posterior border.

Thorax with 7–9 setigers in smallest juveniles (21–28 setigers and 2.1–2.5 mm long); thorax with 11–13 setigers in larger juveniles (40–48 setigers and 3.0–3.7 mm long); thoracic setigers each shorter than abdominal segments. Branchiae from setigers 10–11, short, minute at first, becoming longer in anterior abdominal segments. Thoracic notopodia initially short, papillate, increasing in length, becoming digitiform by about setiger 6–7; abdominal notopodia long and narrow. Thoracic neuropodia initially papillate, becoming longer and digitiform by about setigers 7–8; abdominal neuropodia with thickened base, apically separated into two lobes, initially equivalent in size and shape; larger juveniles with inner lobe becoming longer as in adults. Neuropodia with short, narrow subpodial flange with smooth border. Subpodial papillae and interramal cirri absent.

Thoracic notosetae of small juveniles with 4–6 camerated capillaries in a single row, increasing to about 15–16 capillaries in larger juveniles, most in one row, a few in a second posterior row; abdominal notosetae 3–4 camerated capillaries; furcate setae observed only on larger 45–48-setiger juveniles in far posterior segments. Thoracic neurosetae consisting of 12–15 capillaries arranged in two rows, increasing to 20–25 capillaries in two rows in larger juveniles. Abdominal neurosetae with 2–3 capillaries, these smooth, barbs not observed; a short, thin, sharply pointed acicula present.

Pygidium with two anal cirri; short and thick in small juveniles (Fig. 3C–D), long and thin in 40-setiger juveniles (Fig. 3E).

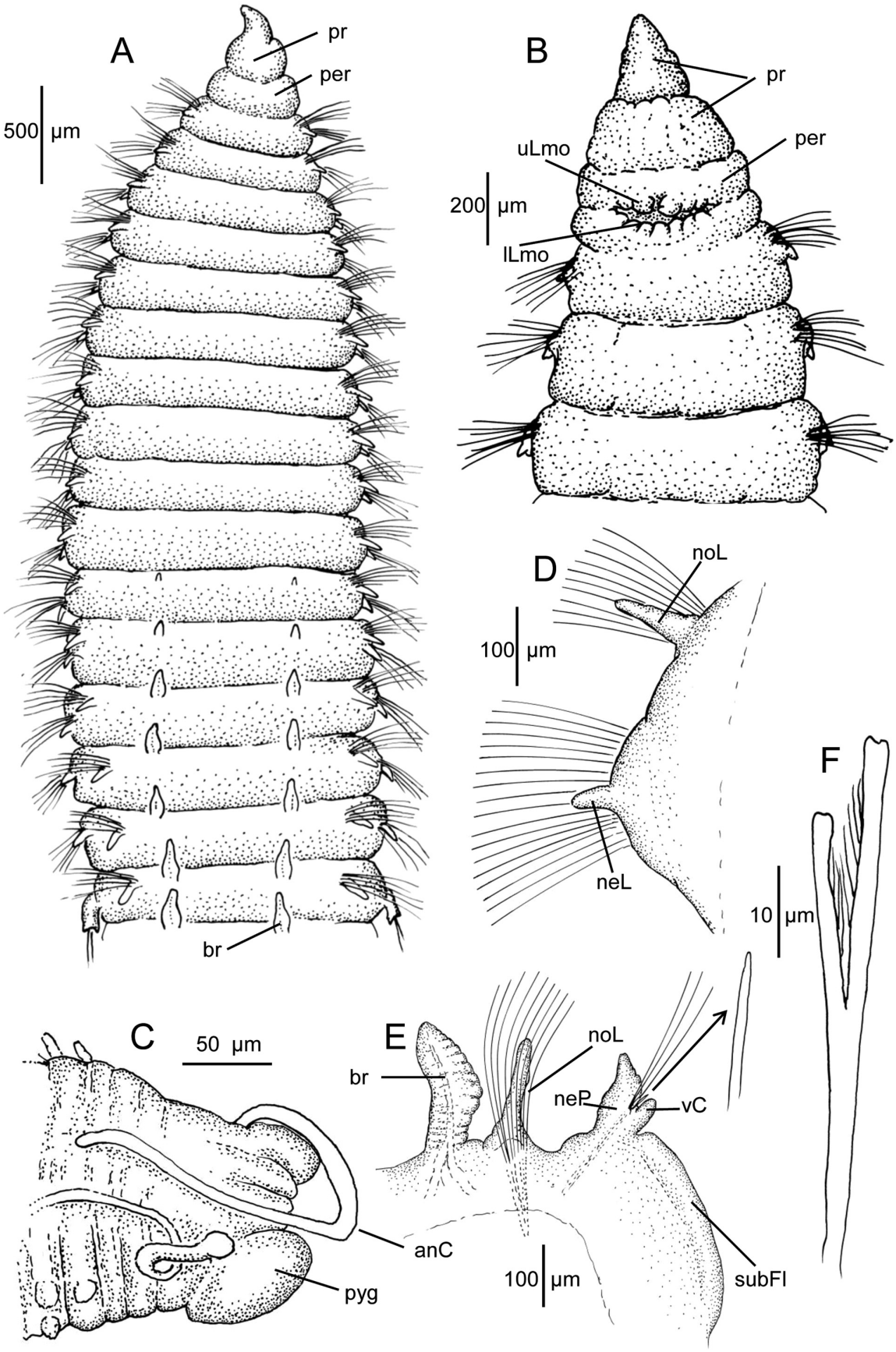

FIGURE 1. *Leitoscoloplos acutus* (Verrill, 1873). A, anterior end, dorsal view; B, anterior segments, ventral view; C, posterior end, dorsolateral view; D, middle thoracic setigers, posterior view; E, posterior abdominal setiger, anterior view; F, furcate seta. A, D–F (USNM 1620848); B (MCZ 161458); C (MCZ 161418).

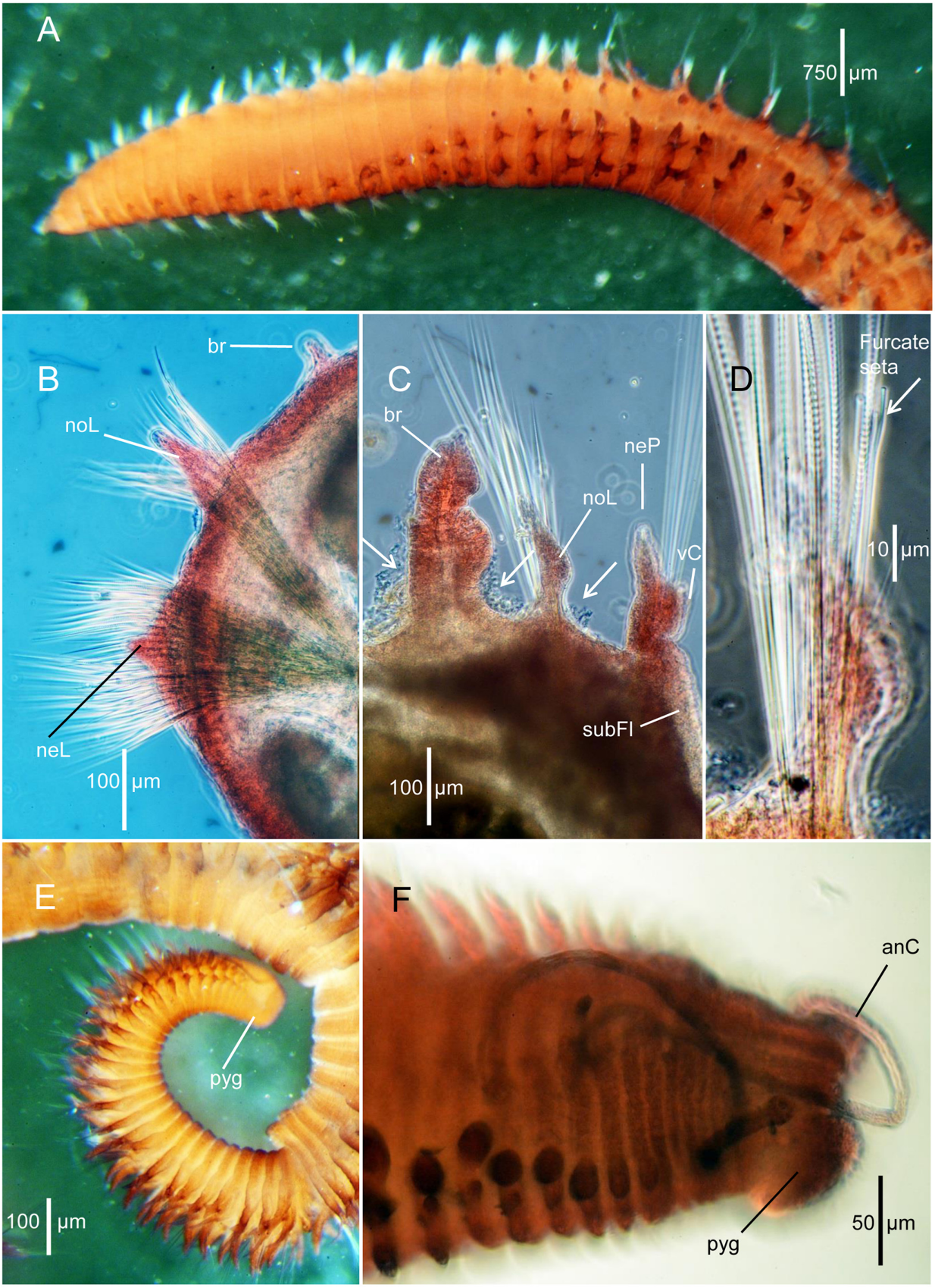

FIGURE 2. *Leitoscoloplos acutus* (Verrill, 1873). A, anterior half of large specimen, dorsolateral view; B, middle thoracic setiger, anterior view; C, middle abdominal setiger, posterior view; D, fascicle of abdominal notosetae with capillaries and furcate seta; E, posterior setigers, left lateral view; F, posterior end, dorsolateral view. A, E (MCZ 161445); B (USNM 1620847); C–D (USNM 1620841); F (MCZ 161419). All stained with Shirlastain A.

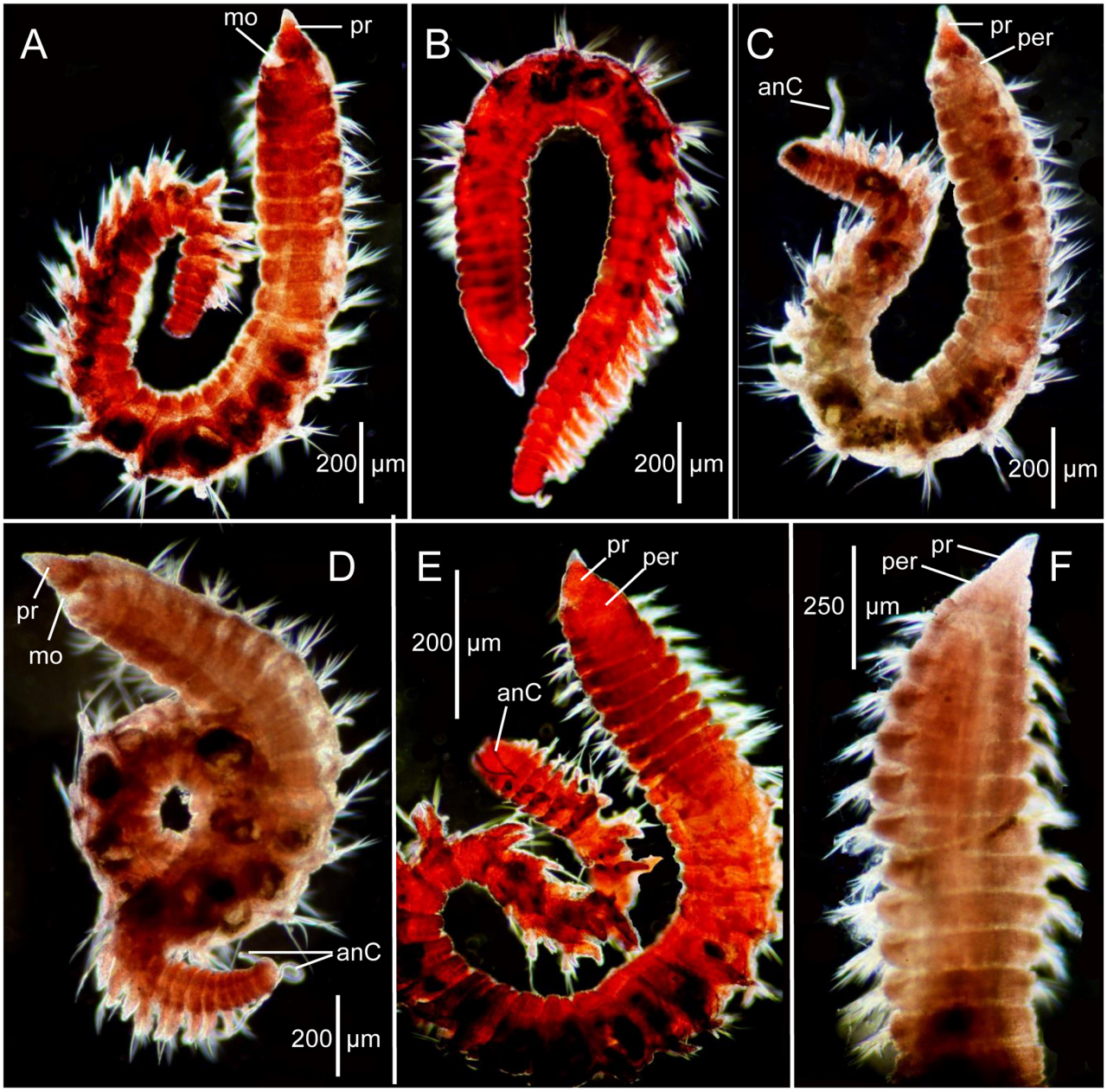

FIGURE 3. *Leitoscoloplos acutus* (Verrill, 1873). Juveniles: A, 21 setigers; B, 26-setigers; C, 28 setigers; D, 28 setigers; E, 40 setigers; F, 48 setigers, anterior end. A–D (MCZ 161432); E (MCZ 161464); F (MCZ 161511). All stained with Shirlastain A.

Remarks. *Leitoscoloplos acutus*, although first described by Verrill (1873) from Vineyard Sound, has never been fully described and illustrated from New England waters. The present paper is the first to provide such detail for the species. The species is common and typically found in sediments with mixed sand and silt.

Leitoscoloplos acutus is most similar to *L. pugettensis* (Pettibone, 1957), a widely distributed species along the North American Pacific coast from British Columbia to Central America (Mackie 1987; Blake 1996; Dean & Blake 2015). Both species lack extra subpodial lobes or papillae and have a prominent subpodial flange ventral to the abdominal neuropodia. *L. pugettensis,* however, although similar, is a much larger species, up to 200 mm long and with more than 200 setigers. The largest specimens of *L. acutus*, in contrast, are about 40 mm long with ca. 150 setigers; the largest specimens in the present study (more than 2700 specimens) are about 25 mm long with 125 setigers. The number of thoracic setigers in *L. pugettensis* is 14–20 with branchiae from setigers 13–18 or the penultimate segment based number of thoracic setigers; whereas in *L. acutus*, the number of thoracic setigers ranges from 14–16 with the branchiae occurring more anteriorly from setigers 9–13.

Curtis (1969), working in the Canadian Arctic (Ellesmere Island, 81°N), evaluated a growth sequence of speci-

mens of *Scoloplos* collected at depth of 10 m. He provided data suggesting that *Leitoscoloplos acutus* represented a developmental phase of *S. armiger* where neuropodial uncini and subpodial papillae were entirely absent in small specimens having a width of 0.5 mm and fully present in specimens with a width of 2 mm; intermediate sizes had differing stages in the acquisition of these characters. However, there was no descriptive data provided to confirm the identity of either species he studied and given the much greater diversity of orbiniids recently revealed, it is unlikely that Curtis (1969) was dealing with either *L. acutus* or *S. armiger*.

There were hundreds of juveniles present in the collections due to the use of 300-µm-mesh sieves in the offshore monitoring surveys. Examination of juvenile morphology of various sizes confirmed a consistent agreement with the adults. Although a full growth sequence has not been developed, the samples are archived and available if such an analysis is required in the future. As part of the examination of juveniles, a comparison with the holotype of *Schroederella berkeleyi* suggests that the specimen agrees with juveniles of *Leitoscoloplos acutus* and is here referred to synonymy. There is nothing in the original account of *S. berkeleyi* that sets it aside as either a separate genus or species within the Orbiniidae. It should be noted that the only other possible synonyms locally would be either *L. fragilis* or *L. robustus*. However, none of the juveniles of *L. acutus* exhibit interramal cirri/processes or subpodial papillae which have been observed on smaller specimens of those species (see account of juvenile morphology for *L. fragilis*, below).

Zhadan (1998) reported two *Scoloplos* species from the White Sea, North Sea, Barents Sea, and East Greenland as *S. armiger*, the type species of the genus, and *S. acutus* previously known only from North America. Zhadan based her identification of *S. acutus* on observations that smaller specimens (<1.75 mm wide) lacked hooks or uncini in thoracic neuropodia and subpodial papillae in posterior thoracic and abdominal neuropodia, whereas specimens larger than 1.75 mm wide had these characters. However, she did not have a full size range of specimens from the type locality in New England (USA). In the present study no specimens were found with either thoracic uncini or subpodial papillae in the neuropodia at any stage of development and are thus referred to the genus *Leitoscoloplos*. A comparison of these U.S. Atlantic specimens of *L. acutus* with *Scoloplos verrilli* **n. sp**., the only local New England species of *Scoloplos* having characteristics similar to the larger *S. acutus* specimens reported by Zhadan (1998), indicates that her specimens represent a different species. *Leitoscoloplos actus* reported here have a long, smooth subpodial neuropodial flange on abdominal segments; in contrast, *S. verrilli* **n. sp**. has a short glandular neuropodial flange. Further, specimens of *S. verrilli* **n. sp**. that are smaller than the largest specimens of *L. acutus* have both thoracic neuropodial uncini and neuropodial subpodial papillae. Recent investigations of *S. armiger* from the North Sea have shown that shallow and subtidal populations are both ecologically and reproductively isolated from one another (Kruse & Reise 2003; Kruse *et al*. 2003, 2004). Results from molecular sequence data support these observations that shallow and subtidal North Sea populations likely represent separate species (Bleidorn *et al*. 2006). Additionally, these authors determined that Norwegian specimens from near the type locality of *S. armiger* represented yet a third species. To date, these three taxa have not been described or compared with regard to their morphology.

Biology. Mature females of *Leitoscoloplos acutus* with internal eggs of various sizes arranged segmentally in middle abdominal setigers were collected in May 1992 in Massachusetts Bay, suggesting a late spring spawning. Adult females 25 mm long and 1.5 mm wide from Station FF-4 (MCZ 161400) had large eggs that ranged from 106 to 204 µm in diameter. The eggs have a smooth cytoplasm and clear germinal vesicle. These data suggest that mature eggs will likely exceed 210 µm in diameter, indicating direct development or a brief lecithotrophic larval development similar to that of the related species *L. pugettensis* (Pettibone, 1957) reported by Blake (1980) from California.

Sediment grain size at stations 11 and 13 on Georges Bank, where *Leitoscoloplos acutus* was most prevalent, consisted of 60–95% fine sands and reduced amounts of silt-sized particles, whereas at Station 13A, where the related species *L. obovatus* occurred, the sediments were fine grained, consisting of 80–90% silt and clay (Maciolek-Blake *et al*. 1985: Appendix J). These data suggest that closely related deposit-feeding polychaete species may be spatially partitioned by the nature of sediments in their habitat. Specimens of *L. acutus* were often observed with large sand grains in their guts, reflecting the nature of the sandy sediments where they were found, whereas this was not the case for *L. obovatus*, which inhabits fine-grained sediments. In Massachusetts Bay, *L. acutus* is abundant at several MWRA nearfield stations that have sediments consisting of fine-grained sands with lesser amounts of silt (Blake *et al*. 1998); 30 or more specimens in one 0.04 m^2 grab sample was a common occurrence at several stations.

Distribution. Maine to New Jersey, intertidal to offshore in mixed sand/silt sediments; Massachusetts Bay, 22–92 m; Georges Bank, 65–145 m. Pettibone (1963) recorded the species from the Canadian Arctic to Chesapeake Bay, 6–180 m, but this wider distribution is not confirmed in the present study.

Leitoscoloplos fragilis (Verrill, 1873)

Figures 4–5

Anthostoma fragile Verrill, 1873: 598–599.
Scoloplos fragilis: Verrill 1881: 301; Hartman 1942: 60–61, figs. 113-115; Brown 1982: 213–227.
Scoloplos (Scoloplos) fragilis: Pettibone 1963: 290–292, fig. 76a–f.
Haploscoloplos fragilis: Hartman 1944: 340, pl. 14, fig. 5, pl. 18, fig. 6; 1945: 30, pl. 6, fig. 5; 1951: 76–78, pl. 21, figs. 1–3; 1957: 271–272, p. 25, figs. 1–3; Trott 2004: 280.
Leitoscoloplos fragilis: Taylor 1984: 1.19–1.21, fig. 1.18a–g; Mackie 1987: 15–16, fig. 16; Blake *et al*. 2001: Appendix, 9-1; Fauchald, Granados-Barba & Solís-Weiss 2009: 763; Blake 2017: 18.

Material examined. (*1,239 specimens*) **Northeastern USA**, **Maine, Damariscotta River Estuary**, Upper Dodge Cove, coll. V. Walker, 05 Aug 1966, 43°59.658′N, 69°33.255′W, intertidal (18, MCZ 161580).—**Massachusetts**, **Woods Hole**, coll. G. Sene Silva, 08 Aug 2005, intertidal (1, MCZ 161581).—**Massachusetts, New Bedford Harbor, Long-term Monitoring Program, 1999 September-October Survey**: (**Upper Harbor**): **Sta. 105-1**, 14 Sep 1999, 41°36.407′N, 70°53.983′W, 6.4 m (1, MCZ 161540); **Sta. 108-3**, 06 Oct 1999, 41°40.496′N, 70°54.955′W, 1 m (3, MCZ 161541); **Sta. 111-1**, 05 Oct 1999, 41°40.42′N, 70°54.9′W, 1 m (1, MCZ 161542); **Sta. 120-1**, 18 Nov 1999, 41°13′N, 70°55.08′W, 1 m (5, MCZ 161543); **Sta. 121-3**, 18 Nov 1999, 41°40.154′N, 70°55.003′W, 1.4 m (5, MCZ 161544); **Sta. 125-3**, 29 Sep 1999, 41°40.01′N, 70°55.098′W, 3 m (2, MCZ 161545); **Sta. 130-3**, 01 Oct 1999, 41°39.848′N, 70°55.086′W, 1.8 m (2, MCZ 161546); **Sta. 134-1**, 01 Oct 1999, 41°39.756′N, 70°55.032′W, 2.3 m (46, MCZ 161547); **Sta. 135-3,** 01 Oct 1999, 41°39.753′N, 70°54.936′W, 1.7 m (40, MCZ 161548); **Sta. 139-1**, 29 Sep 1999, 41°39.675′N, 70°55.104′W, 1.4 m (71, MCZ 161549); **Sta. 140-3**, 01 Oct 1999, 41°39.685′N, 70°54.977′W, 3.3 m (30, MCZ 161550); **Sta. 147**, 28 Sep 1999, 41°39.594′N, 70°54.91′W, 1.7 m (2, MCZ 161551); **Sta. 150-3**, 28 Sep 1999, 41°39.513′N, 70°55.087′W, 3.4 m (13, MCZ 161552); **Sta. 154-2**, 28 Sep 1999, 41°39.415′N, 70°55.050′W, 3.4 m (3, MCZ 161553). (**Lower Harbor**): **Sta. 202-1**, 06 Oct 1999, 41°39.323′N, 70°55.032′W, 4.7 m (30, MCZ 161554); **Sta. 207-1**, 22 Sep 1999, 41°38.984′N, 70°55.270′W, 1.7 m (147, MCZ 161555); **Sta. 208-2**, 23 Sep 1999, 41°38.981′N, 70°55.022′W, 1.3 m (35, MCZ 161556); **Sta. 212-2**, 24 Sep. 1999, 41°38,826′N, 70°4.906′W, 3.3 m (2, MCZ 161557); **Sta. 216-2**, 22 Sep 1999, 41°38.660′N, 70°55.023′W, 2.2 m (10, MCZ 161558); **Sta. 218-1**, 27 Oct 1999, 41°38.663′N, 70°54.527′W, 9.5 m (26, MCZ 161559); **Sta. 220-2**, 22 Sep 1999, 41°38.507′N, 70°55.141′W, 11.1 m (31, MCZ 161560); **Sta. 222-1**, 23 Sep 1999, 41°38.501′N, 70°54.641′W, 3.1 m (79, MCZ 161561); **Sta. 224-3**, 22 Sep 1999, 41°38.338′N, 70°55.269′W, 10 m (37, MCZ 161562); **Sta. 226-1**, 21 Sep 1999, 41°38.336′N, 70°54.809′W, 3.5 m (39, MCZ 161563); **Sta. 227-3**, 21 Sep 1999, 41°38.330′N, 70°54.537′W, 3 m (71, MCZ 161564); **Sta. 231-1**, 21 Sep 1999, 41°38.166′N, 70°54.874′W, 4.1 m (21, MCZ 161565); **Sta. 235-3**, 20 Sep 1999, 41°38.011′N, 70°55.035′W, 8.8 m (17, MCZ 161566); **Sta. 237-1**, 24 Sep 1999, 41°38.006′N, 70°54.541′W, 6 m (1, MCZ 161567); **Sta. 240-3**, 20 Sep 1999, 41°37.873′N, 70°54.91′W, 10 m (28, MCZ 161568); **Sta. 242**, 20 Sep 1999, 41°37.67′N, 70°54.416’′W, 5.8 m (9, MCZ 161569); **Sta. 245-3**, 19 Sep 1999, 41°37.67′N, 70°54.780′W, 3.4 m (43, MCZ 161570); **Sta. 249-1**, 19 Sep 1999, 41°37.52′N, 70°54.67′W, 2.4 m (17, MCZ 161571); **Sta. 250-3**, 19 Sep 1999, 41°37.51′N, 70°54.42′W, 8.5 m (10, MCZ 161572). (**Outer Harbor**): **Sta. 306-3**, 14 Sep 1999, 41°37.15′N, 70°52.237′W, 2.8 m (12, MCZ 161573); **Sta. 310-1**, 14 Sep 1999, 41°36.407′N, 70°53.983′W, 6.4 m (1, MCZ 161574).—**Connecticut**, **Noank**, coll. J.A. Blake, 3 May 1966, 41°19.48′N, 71°59.05′W, intertidal (1, MCZ 161582); **Mystic**, coll. J.A. Blake, 21 Dec 1965, 41°20.8′N, 71°58.29′W, intertidal (1, MCZ 161579).—**New York, Long Island Sound**, **off Eastchester**, **Sta. IG 25**, coll. P.L. Neubert, 28 Oct 1999, 40°52.45′N, 73°45.15′W, 23 m (18, MCZ 161585); **Sta. IG 26**, 28 Oct 1999, 40°52.20′N, 73°45.66′W, 13 m (115, MCZ 161586); **off Throgs Neck**, **Sta. TN6A**, coll. P.L. Neubert, 40°48.6848′N, 73°48.6204′W, 4 m (150, MCZ 161583); **Sta. TN12A**, 40°48.7949′N, 73°47.1572′W, 16 m (45, MCZ 161584).

Description. Specimen from New Bedford Harbor (NBH) (MCZ 161559) complete, 3.5 cm long, 1.0 mm wide across thorax with 145 setigers, similar to largest specimens reported by Mackie (1987) from Nantucket, Massachusetts, of 3.9 cm long, 1.9 mm wide across thorax with 150 setigers. Pettibone (1963) reports larger specimens up 15

cm long, 3 mm wide, and with up to 250 setigers. Body elongate, with thoracic segments short, dorsoventrally flattened, about 4.5 times as wide as long (Fig. 4A). Thoracic segments of largest specimens with low transverse ridge across dorsum and venter between parapodia. Anterior abdominal segments becoming longer, about 1.5 times as wide as long in anterior segments; middle and posterior abdominal segments crowded, very short. Larger specimens with shallow mid-ventral groove present from middle abdominal segments to near posterior end. Color in alcohol light tan.

Pre-setiger region triangular, elongate, as long as first two setigers (Fig. 4A–B). Prostomium conical, tapering to pointed tip; nuchal organs curved slits on posterior lateral margin; eyespots absent (but see juvenile morphology below). Peristomium a single smooth achaetous ring dorsally, ventrally encompassing mouth with upper lip formed of two large lobes and lower lip with curved row of eight or more narrow elongate lobes (Fig. 4B). Proboscis not observed but recorded as a multilobed sac when everted (Pettibone 1963).

Thorax with 14–16 setigers (13–16 recorded by Mackie 1987) with abrupt transition to abdominal segments with elongation of neuropodia and decrease in number of neurosetae. Thoracic notopodial postsetal lobes short, triangular in shape along most of thorax (Fig. 4C), becoming longer in last 1–2 thoracic setigers (Fig. 4D); all notopodial postsetal lamellae arising directly from body wall. Thoracic neuropodial postsetal lobes short, papillate, arising from broadly rounded base (Fig. 4C); last 1–3 thoracic neuropodia with extra postsetal lobe and 1–2 short subpodial papillae resulting in last 1–3 thoracic setigers with three short lobes (Fig. 4D). Abdominal notopodia becoming longer, fingerlike in middle and posterior segments (Fig. 4E–F). Abdominal neuropodia longer and thickened in middle and posterior segments each narrowing to long narrow apical lobe with a short subterminal lateral cirrus; extra subpodial papillae retained only on first 3–4 abdominal neuropodia (Fig. 4E), papillae then merging with subpodial flange and continuing over middle and posterior abdominal setigers as large, subpodial flange with 2–3 distinct lobes (Fig. 4F). Prominent fingerlike interramal cirrus present on last 1–2 thoracic setigers (Fig. 4D), continuing on anterior and middle abdominal setigers (Fig. 4E), reduced to low interramal mound or process in posterior neuropodia (Fig. 4F).

Branchiae from setiger 14 or posterior thoracic segment on Connecticut specimens and larger specimens from New Bedford Harbor, but recorded from abdominal segments by Pettibone (1963) and Mackie (1987); first branchiae on Connecticut and NBH specimens minute, papilliform, becoming full size by about setigers 25–27 or anterior abdominal segments. Anterior branchiae triangular, tapering to rounded apex (Fig. 4D); branchiae of middle and posterior abdominal segments becoming longer and narrow apex more pointed (Fig. 4E–F); all branchiae with transverse folds and cilia on inner and outer margins.

Notosetae all camerated capillaries; furcate and flail setae not observed; capillaries of thoracic segments numbering about 40 in 3–4 irregular rows in thoracic notopodia, reduced to about 15–20 in abdominal segments. Thoracic neurosetae all camerated capillaries with about 50 in 3–4 rows; abdominal neurosetae including 3–7 long stiff capillaries with barbs along one edge and 1–2 imbedded aciculae, none observed protruding.

Pygidium with two thin lateral anal cirri (Fig. 5B–C).

Variability. The adult specimens encountered here differ from the accounts by Pettibone (1963) and Mackie (1987) in having branchiae from the last one or two thoracic setigers instead of the first abdominal setiger. In addition, the interramal cirrus is typically first present on posterior thoracic segments together with extra subpodial lobes. The interramal cirri are best observed by staining with Shirlastain A; they are more-or-less limited to the last thoracic and middle abdominal setigers. The cirri are reduced to a short, rounded process on small specimens and difficult to see.

Juvenile morphology. Juveniles were present in samples from the Throgs Neck (TN) (MCZ 161583) and NBH (MCZ 161564) collections. Several of these specimens were examined in an effort to determine at what size the characters that distinguish *L. fragilis* from local congeners were present. However, unlike the 300-µm-mesh sieve used to collect the *L. acutus* juveniles from Massachusetts Bay, the sieve size used to separate the fauna from the TN and NBH sediment was 500-µm mesh. As a result, there were fewer juveniles in these samples. However, the smallest sizes observed of *L. fragilis* were similar to those of *L. acutus*.

All juveniles have an acutely pointed prostomium; body segments are crowded, especially in posterior setigers. A 28-setiger juvenile from TN is 2.1 mm long with nine thoracic setigers and branchiae from setiger 10 (Fig. 5A). Low interramal processes are present on anterior abdominal setigers; these are the anlage of interramal cirri. At this stage, the prostomium is short and triangular. A 32-setiger NBH juvenile is 2.9 mm long with 11 thoracic setigers with branchiae from setiger 12 (Fig. 5B, E). At this stage, the prostomium has elongated. The characteristic

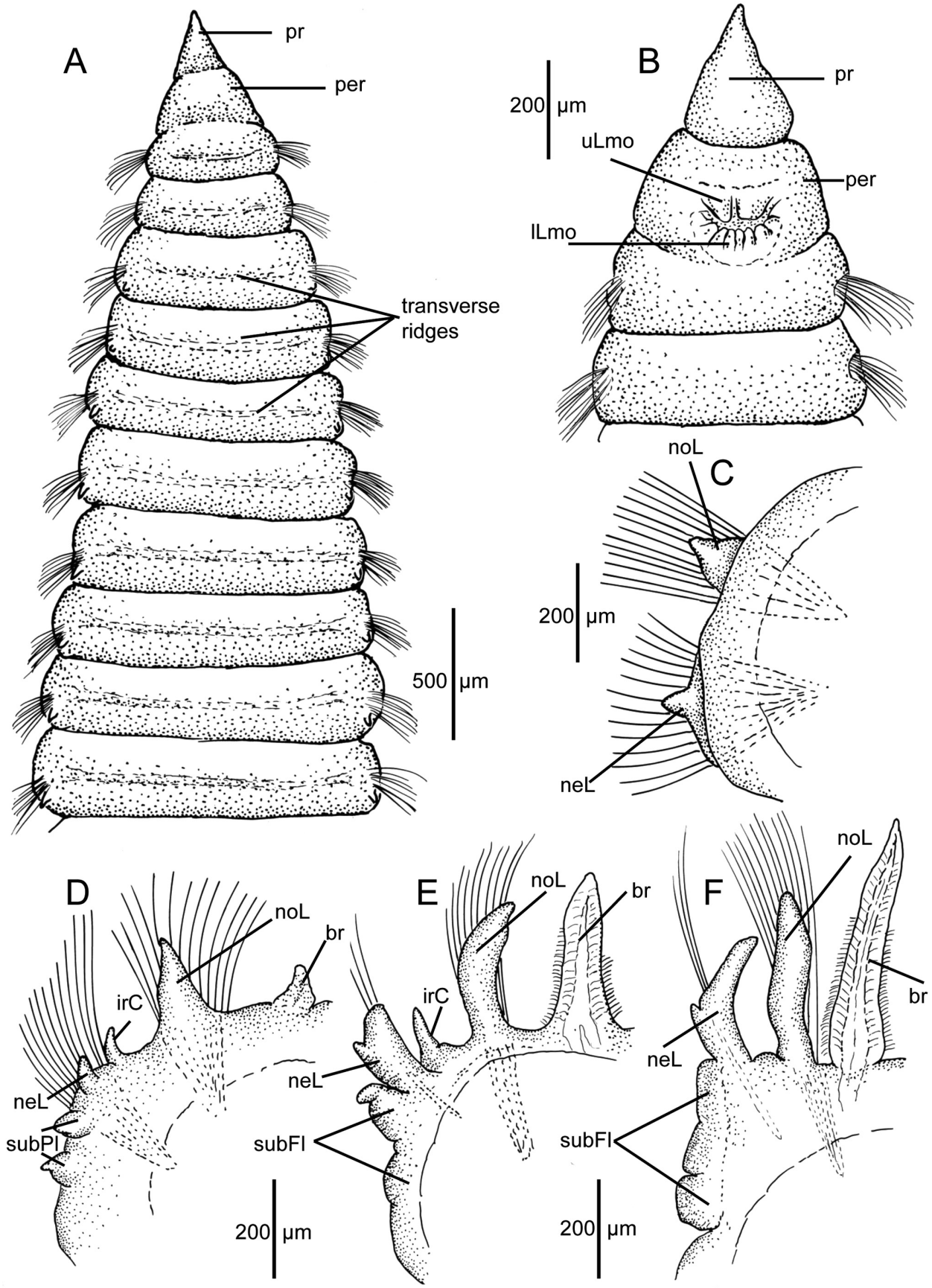

FIGURE 4. *Leitoscoloplos fragilis* (Verrill, 1873). (MCZ 161582): A, anterior end, dorsal view; B, anterior end, ventral view; C, thoracic setiger 11, posterior view; D, thoracic setiger 16, posterior view; E, setiger 25, posterior view; F, posterior setiger, posterior view.

interramal cirri are observed on a few anterior abdominal setigers as low mounds; in middle and posterior neuropodia short subpodial flanges are irregular in shape due to weakly developed subpodial lobes; posterior setigers are crowded and the characteristic lobed subpodial flange is evident (Fig. 5E). A 40-setiger NBH juvenile is 3.27 mm long with 12 thoracic setigers and branchiae from setiger 13 (Fig. 5C). A few interramal cirri were observed in middle thoracic setigers (Fig. 5D) and the neuropodia of the same segments were observed to have an irregular subpodial flange due to the presence of a superior subpodial papilla and medial notch. The prostomium has become longer and more pointed. Interestingly, a pair of eyespots was observed on the prostomium of the latter specimen and others of the same size (Fig. 5F). Such eyespots were not observed on adults. The pygidium of all juveniles consisted two lobes each bearing a long anal cirrus (Fig. 5B, F). Only camerated capillaries were observed in the noto- and neuropodia of these juveniles.

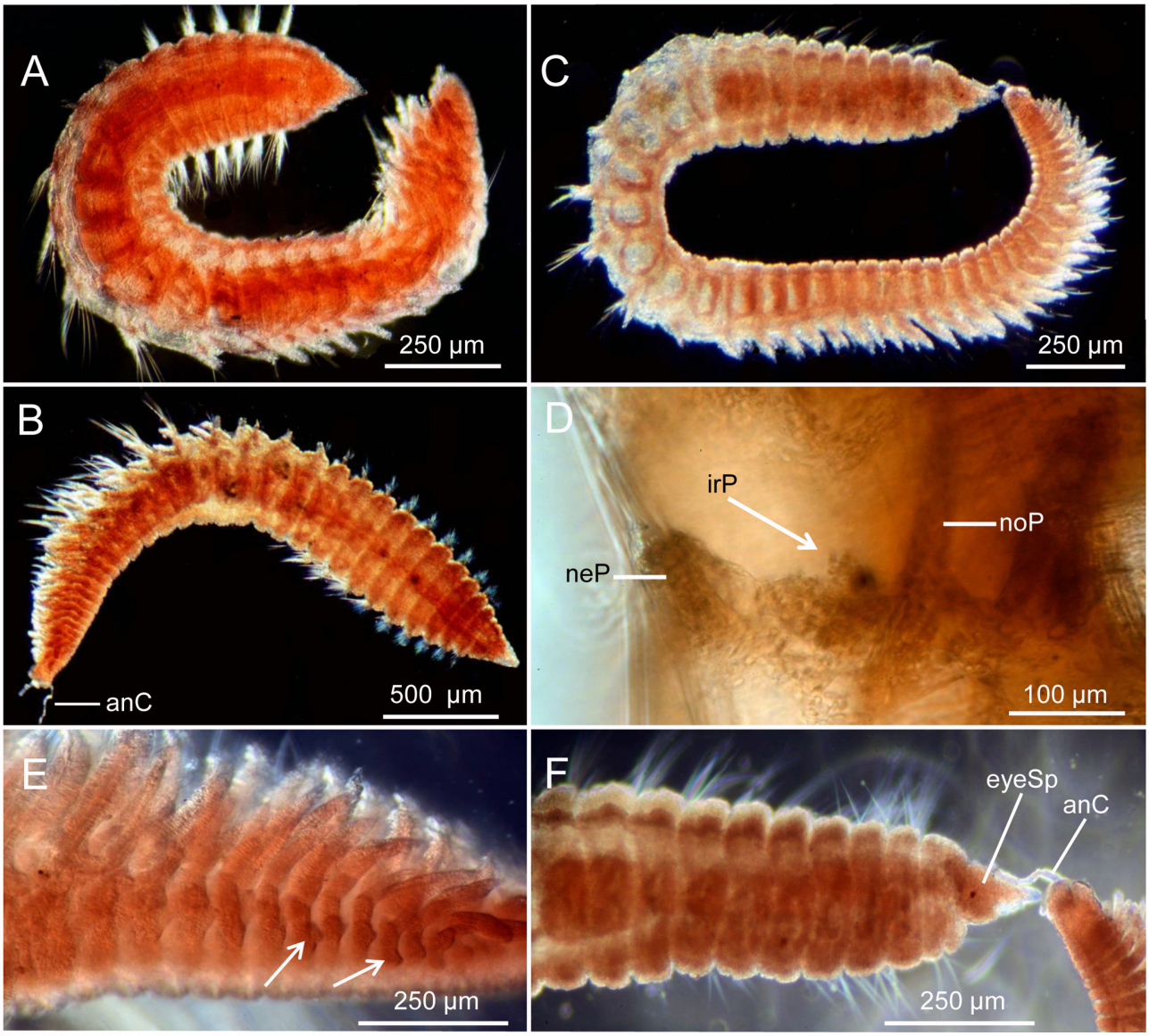

FIGURE 5. *Leitoscoloplos fragilis* (Verrill, 1873). Juveniles: A, 28-setiger juvenile, dorsolateral view; B, 32-setiger juvenile, dorsolateral view; C, 40-setiger juvenile, lateral view; D, same, abdominal setiger with interramal cirrus; E, far posterior setigers, lateral view; F, anterior and posterior ends, with pygidium. A (MCZ 161584); B (MCZ 161567). All stained with Shirlastain A.

Remarks. *Leitoscoloplos fragilis* is most similar to *L. robustus* with which it sometimes occurs. The bilobed subpodial flanges of abdominal segments differ from those of *L. robustus*, which has relatively smooth subpodial flanges (see comments below for *L. robustus*).

The juveniles and adults reported here indicate that the fewest number of thoracic setigers observed is nine on a

28-setiger specimen with branchiae from 10; the largest juvenile reported is a 40-setiger specimen with 12 thoracic setigers and branchiae from setiger 13. The larger adults reported here are up to 150 setigers, 12 cm long and with a thorax of 14–16 setigers and branchiae from the posteriormost thoracic setigers. The characteristic interramal cirri were present, if only rudimentary, on the smallest juveniles collected and the lobed appearance of the subpodial flange was obvious on the 40-setiger juvenile. These results indicate that the most important characters required to identify *L. fragilis* are evident early in development.

Biology. Brown (1982) described some aspects of the distribution and biology of *L. fragilis* on a tidal flat in Delaware, USA. The species lives in the upper 15 cm of sediments having sand-size particles (1.36–1.44 mean phi Ø). Salinity at the site ranged from 28–30 PSU and a wide range of water temperatures from 2.0°C in December to 28°C in August. At the study site, a wave-swept sand bar, the species occurred on slopes, ridges, and troughs with the highest densities on slopes. At least three age classes were found, with reproductive maturity occurring after two years; the smallest specimens occurred in the August or mid-summer samples. Gametogenesis and reproductive biology were not investigated; egg diameters were not provided and cocoons with eggs or larvae were not observed.

In New Bedford Harbor, Massachusetts, the highest densities of *L. fragilis* occurred in lower portions of the Upper Harbor and throughout the Lower Harbor at stations having high sand and gravel content of 50% or greater (Blake *et al*. 2001).

Distribution. Eastern Canada to Florida; Gulf of Mexico; intertidal to shallow subtidal.

Leitoscoloplos obovatus Mackie, 1987

Figures 6–7

Haploscoloplos fragilis intermedius Hartman, 1965: 128 (in part). *Fide* Mackie 1987.
Leitoscoloplos cf. *fragilis*: Maciolek-Blake *et al.* 1985: Appendix B-5. **Not** Verrill 1873.
Leitoscoloplos sp. A: Maciolek-Blake *et al*. 1985: B-5, D-19.
Leitoscoloplos obovatus Mackie, 1987: 18–19, Fig. 19.

Material examined. (97 *specimens*) **Northeastern USA, off New England, Gay-Head Bermuda Transect**, R/V *Atlantis* **Sta. S1-3**, 24 May 1961, 39°58.4′N, 70°40.317′W, 300 m, **holotype** (AHF-Poly 1450).—**Georges Bank**, **Benthic Infauna Monitoring Program**, coll. G.W. Hampson, Chief Scientist. **Sta. 13A**: Cruise M4, R/V *Cape Henlopen*, Rep. 6, 18 May 1982, 40°30.00′N, 70°00.5′W, 83 m (3, USNM 1620855); Cruise M5, R/V *Oceanus*, Rep. 1, 28 Jul 1982, 40°30.00′N, 71°00.5′W, 74 m (7, USNM 1620856); Rep. 4 (4, USNM 1620857); Rep. 6 (3, USNM 1620858); Cruise M6, R/V *Oceanus*, Rep. 2, 28 Nov. 1982, 40°30.00′N, 71°00.5′W, 78 m (3, USNM 1620859); Rep. 3 (6, USNM 1620860); Cruise M8, R/V *Gyre*, Rep. 1, 21 May 1983, 40°30.00′N, 71°00.5′W, 80 m (2, USNM 1620861); Rep. 2 (3, USNM 1620862); Rep. 3 (4, USNM 1620863); Rep. 5 (1, USNM 1620864); Rep. 6 (4, USNM 1620865); Cruise M9, R/V *Gyre*, Rep. 1, 20 Jul 1983, 40°30.0′N, 71°00.5′W, 80 m (1, USNM 1620866); Rep. 4 (4, USNM 1620867); Rep. 5 (1, USNM 1620868); Cruise M10, R/V *Oceanus*, Rep. 1, 13 Nov. 1983, 40°30.0′N, 71°00.5′W, 80 m (2, USNM 1620869); Rep. 2 (3, USNM 1620870); Rep. 4 (1, USNM 1620871); Rep. 5 (1, USNM 1620872); Rep. 6 (1, USNM 1620873); Cruise M11, R/V *Oceanus*, Rep. 1, 01 Feb 1984, 40°30.00′N, 71°00.5′W, 80 m (3, USNM 1620874); Rep. 2 (1, USNM 1620875); Rep. 3 (1, USNM 1620876); Rep. 4 (3, USNM 1620877); Rep. 5 (2, USNM 1620878); Cruise M12, R/V *Gyre*, Rep. 1, coll. 02 Jun 1984, 40°30.0′N, 71°00.5′W, 80 m (1, USNM 1620879); Rep. 2 (1, USNM 1620880); Rep. 3 (5, USNM 1620881); Rep. 4 (1, USNM 1620882); Rep. 5 (2, USNM 1620883); Rep. 6 (2, USNM 1620884).—**Southeastern USA, US South Atlantic ACSAR program,** coll. J.A. Blake, Chief Scientist. **off Cape Hatteras, North Carolina. Sta. 9**: Cruise SA-4, R/V *Cape Hatteras*, Rep. 1, 24 May 1985, 35°28.41′N, 74°47.44′W, 640 m (1, USNM 1620885). **Off Cape Fear, North Carolina**, **Sta. 11**: Cruise SA4, R/V *Cape Hatteras*, Rep. 1, 22 May 1985, 33°04.86′N, 76°25.13′W, 800 m (2, USNM 1620886); Cruise SA-5, R/V *Gyre*, Rep. 1, 23 Sep 1985, 33°94,83′N, 76°25.1′W, 796 m (6, USNM 1620887); Cruise SA-6, R/V *Cape Hatteras*, Rep. 1, 22 Nov 1985, 33°04.95′N, 76°25.15′W, 804 m (1, USNM 1620888); Rep. 2, 22 Nov. 1985, 33°04.94′N, 76°25.06′W, 807 m (1, USNM 1620889); Rep. 3, 22 Nov 1985, 33°04.84′N, 76°25.06′W, 807 m (2, USNM 1620890). **Off Charleston, South Carolina, Sta. 14**: Cruise SA-4, R/V *Cape Hatteras*, Rep. 2, 20 May 1983, 32°23.64′N, 77°01.1′W, 802 m (1, USNM 1620891); Cruise SA-5, R/V *Gyre*, Rep. 2, 19 Sep 1985, 32°23.72′N, 77°01.24′W, 799 m (1, USNM 1620892); Cruise SA-6, R/V *Cape Hatteras*, Rep. 1, 18 Nov 1985, 32°23.73′N, 77°01.10′W, 799 m (2, USNM 1620893).—**Off New England, US North Atlantic ACSAR program**,

coll. G.W. Hampson, Chief Scientist. **Sta. 12**: Cruise NA-2, R/V *Oceanus*, Rep. 1, 04 May 1985, 39°54.31′N, 70°55.04′W, 551 m (2, USNM 1620894); Cruise NA-4, R/V *Gyre*, Rep. 1, 30 Nov 1985, 39°54.28′N, 70°55.12′W, 560 m (2, USNM 1620895); Rep. 2, 30 Nov 1985, 39°54.28′N, 70°55.12′W, 559 m (2, USNM 1620896); Cruise NA-6, R/V *Gyre*, Rep. 3, 30 Jul 1986, 39°54.24′N, 70°55.09′W, 563 m (2, USNM 1620897).

Description. Holotype small, incomplete, with 21 setigers, 4 mm long, 0.40 mm wide across thorax (Mackie 1987). Many specimens complete, but coiled, difficult to measure; one large complete specimen from Georges Bank (USNM 1620861) with 80 setigers, 12.5 mm long, 0.6 mm wide across thoracic region (Fig. 6B). Body elongate, about same width along most of body, narrowing in far posterior setigers. Body generally cylindrical in cross section with thoracic segments short, about five times wider than long. Abdominal segments shorter, but still wider than long with dorsal surface becoming flattened with parapodia and branchiae shifted dorsally; ventral surface rounded. A shallow, narrow ventral groove present along entire body from middle thoracic segments; groove appearing as a light line when body stained with Shirlastain A. Dorsal grooves and ridges absent. Color in alcohol opaque white.

Pre-setiger region triangular, about as long as first two-and-a-half setigers (Fig. 6A–C). Prostomium triangular, narrowing to pointed apex; nuchal organs narrow curved slits on posterior lateral margin (Fig. 6A); eyespots absent. Peristomium a single ring, smooth dorsally (Fig. 6B), ventrally forming upper and lower lips of mouth (Fig. 6C); upper lip formed by two thickened lobes separated medially by short papilla; lateral and ventral lips of mouth formed by ten or more lobes; proboscis, when everted formed of three or more filaments or lobes.

Thorax of most specimens with 11 setigers abruptly transitioning to abdominal segments (Fig. 6A–B); small specimens with 9 or 10 thoracic setigers. Transition to abdominal segments best observed by elongation and thickening of neuropodia and commensurate reduction in number of neurosetae. A prominent interramal cirrus first appearing on tenth thoracic setiger, continuing between noto- and neuropodia along entire body (Figs. 6B; 7C–D); in addition, one or two extra subpodial papillae appear ventral to neuropodial lobe on thoracic setigers 10–11 (Fig. 7B); these continuing over anterior abdominal segments (Fig. 7C), one lobe typically located on a short subpodial neuropodial flange. In addition, 1–3 small stomach papillae also occurring on posterior thoracic and anterior abdominal setigers (Figs. 6A (arrows); 7B–C), with an occasional one occurring on middle abdominal segments.

Branchiae typically first present on setiger 11, or last thoracic setiger (Fig. 6B); narrow and short at first, becoming longer in middle and posterior abdominal segments (Fig. 7B–D), but not noticeably longer than notopodial postsetal lobes; branchiae of middle and posterior abdominal segments becoming asymmetrical with enlargement typically directed laterally (Fig. 7D). Each branchia with a central blood vessel and transverse folds and cilia on inner and lateral margins.

Notosetae including camerated capillaries and furcate setae; about 30 capillaries in two rows in thoracic notopodia, reduced to 10–15 long, thin camerated capillaries (Fig. 7F); in abdominal notopodia, capillaries accompanied by 0–2 furcate setae. Thoracic neurosetae all capillaries with about 60 setae in three rows; abdominal neurosetae include 3–5 capillaries and 1–2 short protruding aciculae, these minute, with pointed tip. Capillaries of abdominal neuropodia appearing weakly jointed along length with oblong lobes only observed at 1000x in light microscope (Fig. 7G). Furcate setae of abdominal notopodia with unequal tynes, each tyne with a rounded apex; narrow elongate fibrils present between tynes; shaft of furcate setae with cross bars or low ribs along length (Fig. 7E). Flail setae absent.

Pygidium with two or three thickened lobes surrounding anal opening and two long dorsolateral cirri (Fig. 6D).

Remarks. More than 70 newly collected specimens encountered at a single location, Sta. 13A on Georges Bank, the so-called "mud patch" (Maciolek-Blake *et al*. 1985); additional specimens from upper continental slope stations off New England and the Carolinas also identified. Collection includes a range of sizes from juveniles to mature adults.

The specimens of *Leitoscoloplos obovatus* reported here represent only the second account of the species. Mackie (1987) described *L. obovatus* from specimens previously reported as *Haploscoloplos fragilis intermedius* by Hartman (1965) from a 300 m site southeast of Georges Bank. Other specimens reported by Hartman as this subspecies from deeper slope depths (ca. 1400 m) were raised to full species status by Mackie (1987) and referred to the genus *Scoloplos* (*S. intermedius* is treated separately in this paper, see below). The majority of specimens reported here are from outer shelf depths on Georges Bank located near the original collection site reported by Hartman (1965) and Mackie (1987).

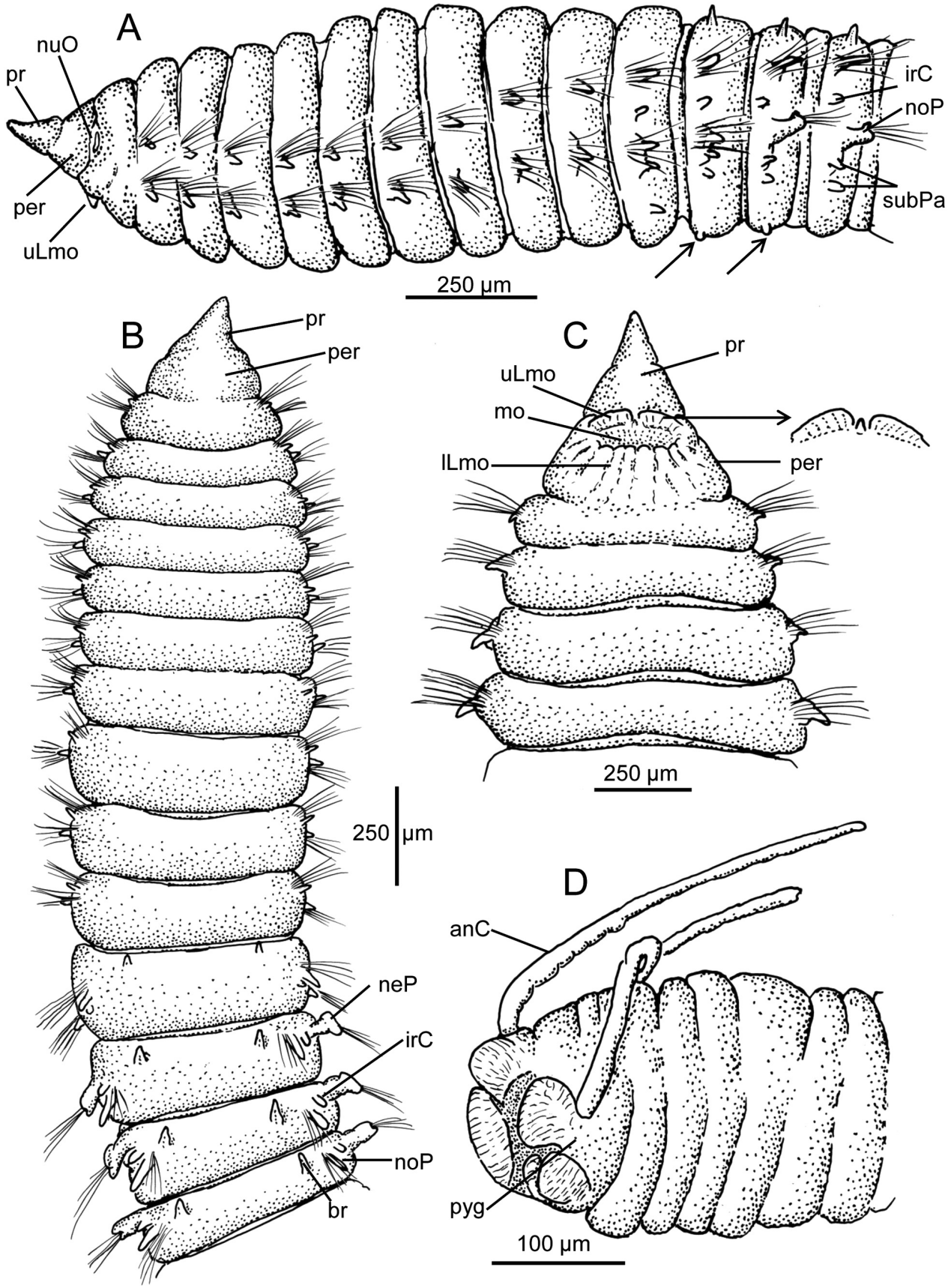

FIGURE 6. *Leitoscoloplos obovatus* Mackie, 1987. A, anterior end, left lateral view; B, anterior end, dorsal view; C, anterior end, ventral view; D, pygidium, right lateral view. A, C–D (USNM 1620879); B (USNM 1620869).

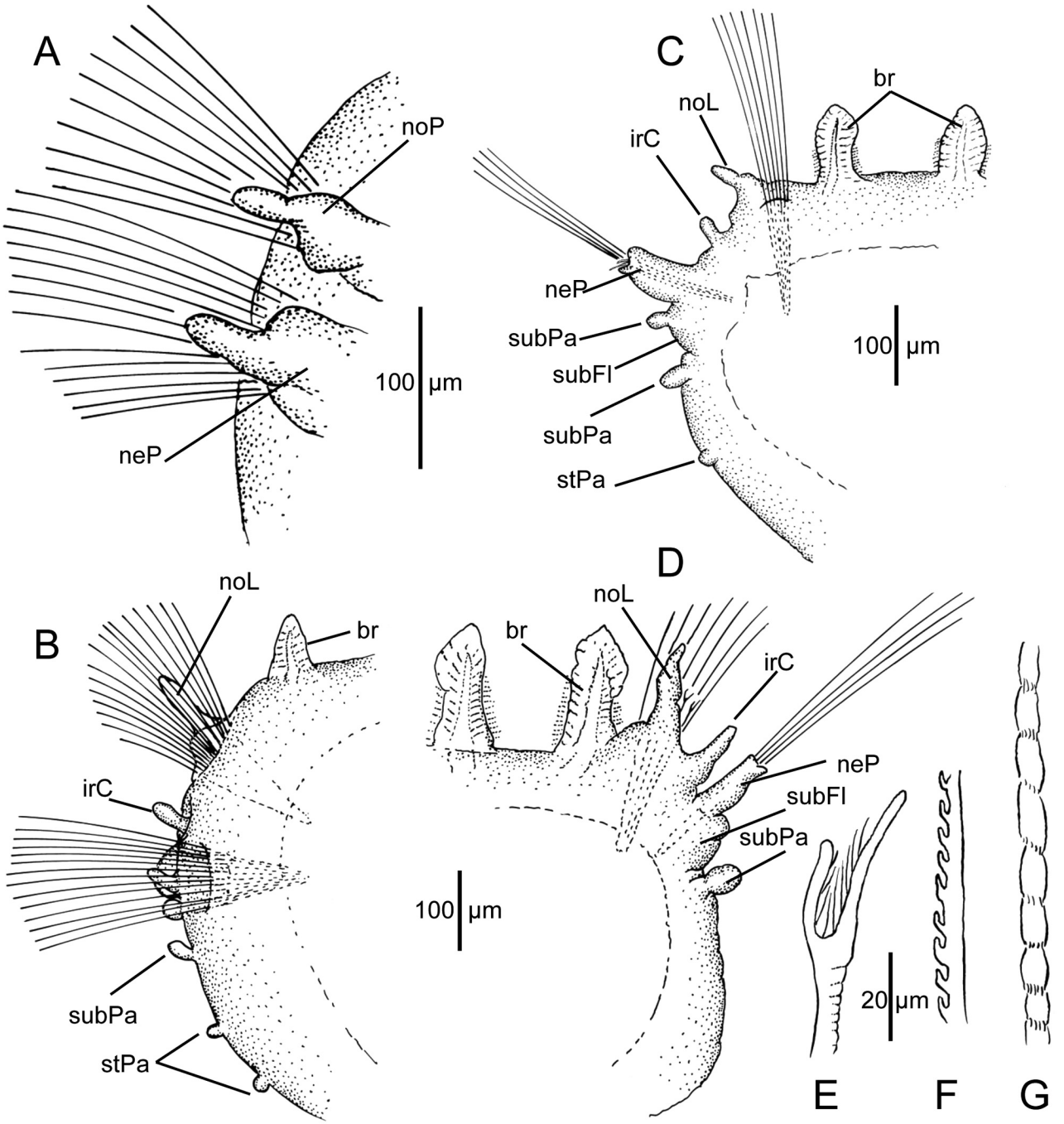

FIGURE 7. *Leitoscoloplos obovatus* Mackie, 1987. A, thoracic setiger 6, posterior view; B, thoracic setiger 11, anterior view; C, anterior abdominal setiger, anterior view; D, middle abdominal setiger, posterior view; E, furcate seta; F, detail of notopodial capillary seta . A (USNM 1620875); B–G (USNM 1620871).

Leitoscoloplos obovatus is unusual within the genus in having an interramal cirrus in posterior thoracic and all abdominal setigers, 1–3 subpodial papillae in posterior thoracic and most abdominal setigers, and 2–6 small stomach papillae in posterior thoracic and anterior abdominal setigers. Mackie (1987) had only four small incomplete specimens, each with fewer than 40 setigers; the present collection includes more than 70 specimens, many complete, with up to 80–100 setigers. The new materials confirm Mackie's (1987) observation that the small sessile papillae on the venter are in actuality stomach papillae; although sparse and inconspicuous, they do form partial rows on the venter.

In addition to *L. obovatus*, only five other species of *Leitoscoloplos* have interramal cirri: *L. fragilis* (Verrill, 1873), *L. mackiei* Eibye-Jacobsen, 2002, *L. multipapillatus* Hernández-Alcántara & Solís-Weiss, 2014, *L. panamen-*

sis (Monro, 1933b), and *L. robustus* (Verrill, 1873). *Leitoscoloplos pustulus* **n. sp**. has a short interramal process, but not distinct cirri. Of these, only *L. multipapillatus* has stomach papillae. However, rather than being sparse as in *L. obovatus*, the stomach papillae of *L. multipapillatus* are formed into prominent rows that produce a conspicuous ventral fringe in posterior thoracic and anterior abdominal setigers.

Biology. Large, elongate eggs were observed in one Georges Bank specimen (USNM 1620882) with 3–4 eggs per individual swollen segment in the anterior abdomen; individual eggs measured about 190 µm in average diameter. These results from a June 1984 sample indicate a summer spawning and the large eggs suggest either a direct or lecithotrophic mode of development. A specimen collected in May 1985 from off Cape Hatteras (USNM 1620885) contained large eggs that were partially extruded from the body, indicating they were being discharged. These eggs measured 192–236 µm in diameter, again implying a direct mode of development.

Sediment grain size at Station 13A, the only location on Georges Bank where *L. obovatus* occurred, has fine-grained sediments consisting of 80–90% silt and clay (Maciolek-Blake *et al*. 1985). The site is locally termed the "Mud Patch."

Distribution. Off northeastern USA, in shelf and upper slope depths, 80–550 m; off southeastern USA, upper slope depths, ca. 640–800 m.

Leitoscoloplos pustulus new species

Figures 8–9

urn:lsid:zoobank.org:act:8D316141-7EAB-4B75-BA31-3FD44EC29D0E

Leitoscoloplos nr. *acutus*: Hilbig 1994: 942. **Not** Verrill 1873.

Material examined. (*289 specimens*) **Southeastern USA, off Cape Hatteras, North Carolina, US South Atlantic ACSAR program**, coll. J.A. Blake, Chief Scientist. **Sta. 9**: Cruise SA-3, R/V *Gyre*, Rep. 1, 22 Jul 1984, 35°28.30′N, 74°47.70′W, 579 m, **holotype** (USNM 1620901), 60 **paratypes** (USNM 1620902); Rep. 2, 22 Jul 1984, 35°28.40′N, 74°47.50′W, 614 m, 43 **paratypes** (USNM 1620903); Rep. 3, 22 Jul 1984, 35°28.30′N, 74°47.60′W, 598 m, 28 **paratypes** (USNM 1620904). Cruise SA-4, R/V *Cape Hatteras*, Rep. 1, 24 May 1985, 35°28.41′N, 74°47.44′W, 640 m (20, USNM 1620905); Rep. 2, 24 May 1985, 35°28.41′N, 74°47.56′W, 603 m (35, USNM 1620906); Rep. 3, 24 May 1985, 35°28.28′N, 74°47.52′W, 623 m (26, USNM 1620907). Cruise SA-5, R/V *Gyre*, Rep. 1, 25 Sep 1985, 35°28.41′N, 74°47.46′W, 629 m (~30, USNM 1620908); Rep. 2, 25 Sep 1985, 35°28.41′N, 74°47.47′W, 629 m (32, USNM 1620909); Rep. 3, 25 Sep 1985, 35°28.27′N, 74°47.61′W, 629 m (14, USNM 1620910).

Description. Holotype complete, with 105 setigers, 13.2 mm long, 0.7 mm wide across middle of thoracic region. Body elongate, with thoracic region narrow at first, becoming wider and dorsoventrally flattened in middle and posterior segments, with individual segments short and wide, about 4–6 times wider than long near transition to abdominal segments. Individual thoracic segments separated by narrow transverse groove from about setiger 6, becoming more distinct and broader from about setiger 10 (Fig. 8A). Abdominal segments short and wide at first, becoming even shorter and crowded posteriorly. Abdominal segments with a biannulate appearance and an expanded intersegmental area posterior to elevated parapodia. Middle and posterior abdominal segments short, crowded, about twice as wide as long. Shallow mid-ventral groove present from anterior segments to near posterior end. Color in alcohol light tan.

Pre-setiger region triangular, short, about as long as setiger 1 and part of setiger 2 (Figs. 8A–B, 9B). Prostomium triangular, narrowing to pointed apex (Figs. 8A–B, 9B); nuchal organs narrow curved slits on posterior lateral margin (Fig. 9B), observed with difficulty; eyespots absent. Peristomium a single short smooth achaetous ring dorsally and laterally (Fig. 8A); ventrally forming upper and lower lips of mouth (Fig. 8B). Mouth surrounded by several thickened lobes (Fig. 8B); proboscis when everted with no more than three lobes.

Thorax of holotype and larger paratypes typically with 14 setigers, rarely 15, with abrupt transition to abdominal segments (Figs. 8A, 9A). Boundary between thorax and abdomen indicated by elongation of neuropodia and decrease in number of neurosetae. Thoracic notopodial lobes arising from narrow base, triangular in shape, narrowing apically (Fig. 8C); neuropodia digitiform, shorter than notopodial lobe, arising from broadly rounded base surrounding neuropodial lobe (Fig. 8C); entire neuropodium recessed into a notch on body wall. Abdominal notopodia elongate, narrow, digitiform, tapering to narrow rounded tip (Fig. 8D), becoming narrower in posterior setigers (Fig. 8E). Short, rounded interramal protuberance or process present between noto- and neuropodial bases, best observed

on anterior abdominal parapodia (Fig. 8D) but also present in middle abdominal segments, albeit observed with difficulty. Abdominal neuropodia thickened, relatively short in middle and posterior segments, each divided into two apical lobes, with dorsal lobe longest (Fig. 8D–E); each neuropodium with elongate, bulbous, fleshy subterminal flange (Fig. 8D); flange often with distinct large blister-like rounded protuberance on lateral or posterior margins, best developed in middle abdominal segments (Figs. 8E, 9C, arrows). Many specimens with large hole or opening on flange, suggesting the protuberance had erupted. Contents of blisters variable, appearing glandular rather than reproductive in nature. Neuropodium of setiger 14 on holotype with extra rounded lobe below setae; this becoming larger and transitioning to subpodial flange on abdominal setigers 15–16. Otherwise, no extra subpodial papillae or stomach papillae observed along body of any specimens.

Branchiae typically from setiger 11–12, usually 12 (holotype); initial thoracic branchiae small, becoming full size by about setigers 13–15 (Fig. 8A). All branchiae relatively short; anterior branchiae triangular, tapering to narrow papillate rounded apex (Fig. 8D); branchiae of middle and posterior abdominal segments generally thicker, tapering to wider rounded apex (Fig. 8E); each branchia with transverse folds and cilia on inner and lateral margins (Fig. 8D–E).

Notosetae camerated capillaries and furcate setae; about 30 capillaries in two rows in thoracic notopodia reduced to 10–15 long, thin camerated capillaries in abdominal segments accompanied by 0–2 furcate setae. Thoracic neurosetae all capillaries with about 60 setae in three rows; abdominal neurosetae include 2–7 capillaries with few barbs along one edge (Fig. 8E inset) and 1–2 short protruding aciculae, these minute, with pointed tip (Fig. 8D inset). Furcate setae of abdominal notopodia with unequal tynes, each tyne with a rounded and notched apex within which an opening and narrow channel extending into the tyne can be observed with light microscope; narrow elongate fibrils present between tynes (Fig. 8F); flail setae absent.

Pygidium a rounded lobe surrounding anal opening surmounted by two lobes from which two long, thin anal cirri arise (Fig. 9D).

Variability. The most unusual features of *Leitoscoloplos pustulus* **n. sp.** are the rounded, blister-like swellings on the neuropodial subpodial flanges of abdominal segments. These are typically present on all of the large specimens and may be limited to a few segments or prominent in one form or another along most of the abdominal region. Small swellings are usually clear or filled with large cells; large swellings are dark and appear to be filled with granular material, possibly ingested sediment that has somehow entered the subpodial flanges from the intestinal tract. There is no evidence that the flanges are modified for gamete storage and release or as brood chambers. A large number of the flanges were observed to be open and empty suggesting the contents had been discharged.

An extra thoracic neuropodial lobe or papilla was observed on the last thoracic setiger in most specimens examined. Over the next two abdominal segments, this lobe or papilla is transformed into the subpodial flange of the neuropodia. There are no other extra lobes or papillae evident along the body.

Remarks. Specimens of *Leitoscoloplos pustulus* **n. sp**. from off Cape Hatteras were originally identified as *L.* cf. *acutus*, a widely reported species in nearshore shelf depths along the Atlantic coast of the U.S. and Canada (see above). *Leitoscoloplos pustulus* **n. sp**., however, differs from *L. acutus* in having instead of lacking an interramal process between the abdominal noto- and neuropodia, having an inflated subpodial flange often with a prominent rounded blister or swelling instead of smooth, narrow flanges without swellings, and in having, instead of lacking, an extra neuropodial lobe on the last thoracic setiger that clearly transitions into the abdominal subpodial flange over subsequent abdominal neuropodia.

Biology. Eggs were observed on several paratypes. These ranged from 40–100 μm in diameter. Unusually dense assemblages of benthic infaunal invertebrates occurred in the continental slope sediments off Cape Hatteras, North Carolina, at Station 9 at 600 m where *L. pustulus* **n. sp**. was discovered (Blake & Hilbig 1994). Infaunal densities ranged from 24,055 to 61,244 (mean = 46,255) individuals per m^2 in nine samples taken at Station 9 in 1984 and 1985.

High sedimentation rates and organic carbon flux have been recorded from the slope off Cape Hatteras and may account for the high infaunal productivity in the area. Most of the dominant infaunal organisms are species more typical of coastal habitats rather than deep-sea species that dominate other areas of the U.S. Atlantic continental slope. A parallel investigation regarding the nature of organic matter in the Cape Hatteras sediments revealed a mixture of both marine and terrestrially derived carbon (Rhoads & Hecker 1994).

Etymology. The epithet is from the Latin, *pustula* for bubble or blister, referring to the nature of the abdominal subpodial flanges which often bear a blister-like swelling on the lateral or posterior margin.

Distribution. Off Cape Hatteras, North Carolina, 579–640 m.

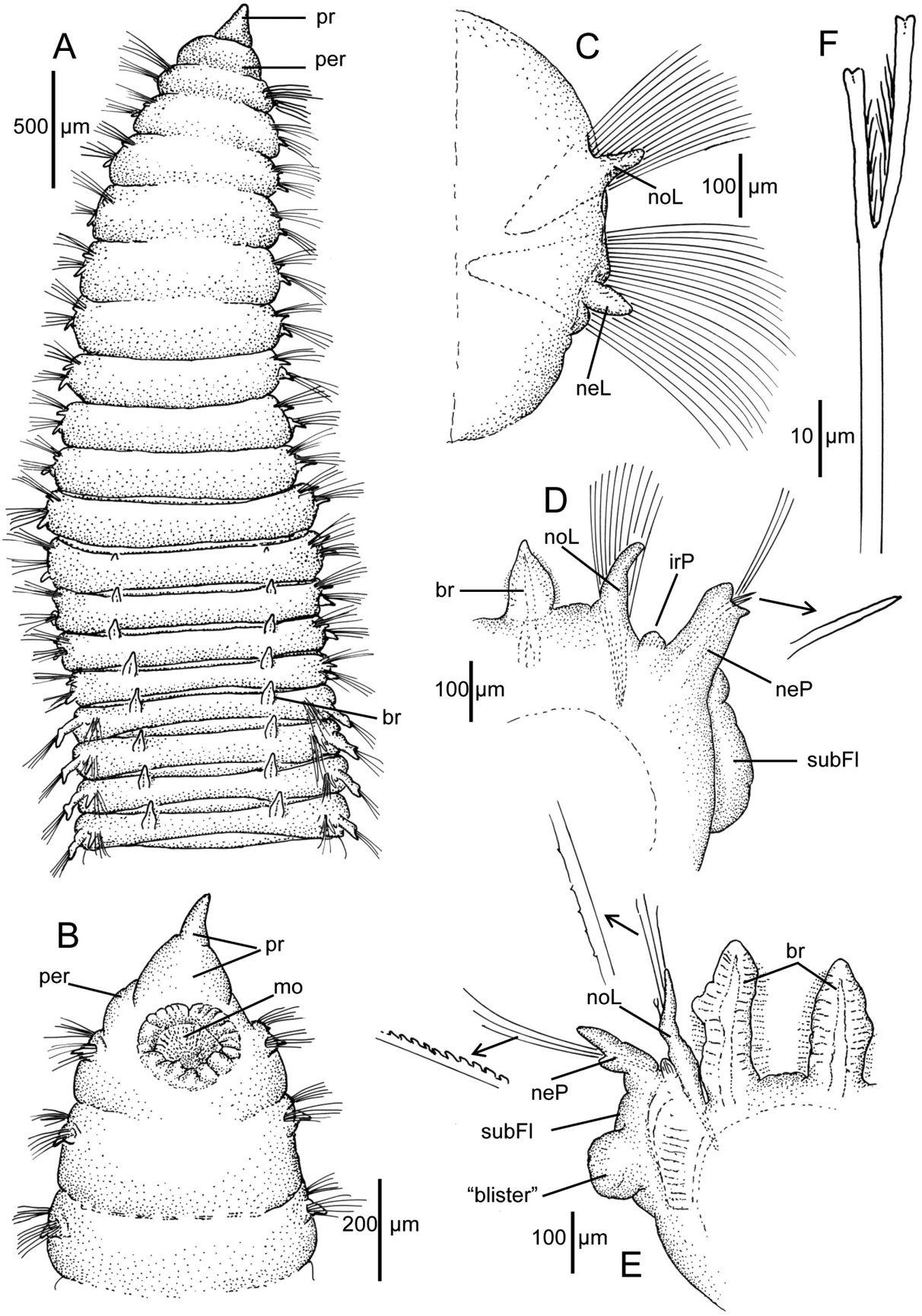

FIGURE 8. *Leitoscoloplos pustulus* **n. sp**. Paratypes (USNM 1620902): A, anterior end, dorsal view; B, anterior end, ventral view; C, middle thoracic setiger, posterior view; D, anterior abdominal setiger, posterior view; E, posterior abdominal setiger, posterior view; F, furcate seta.

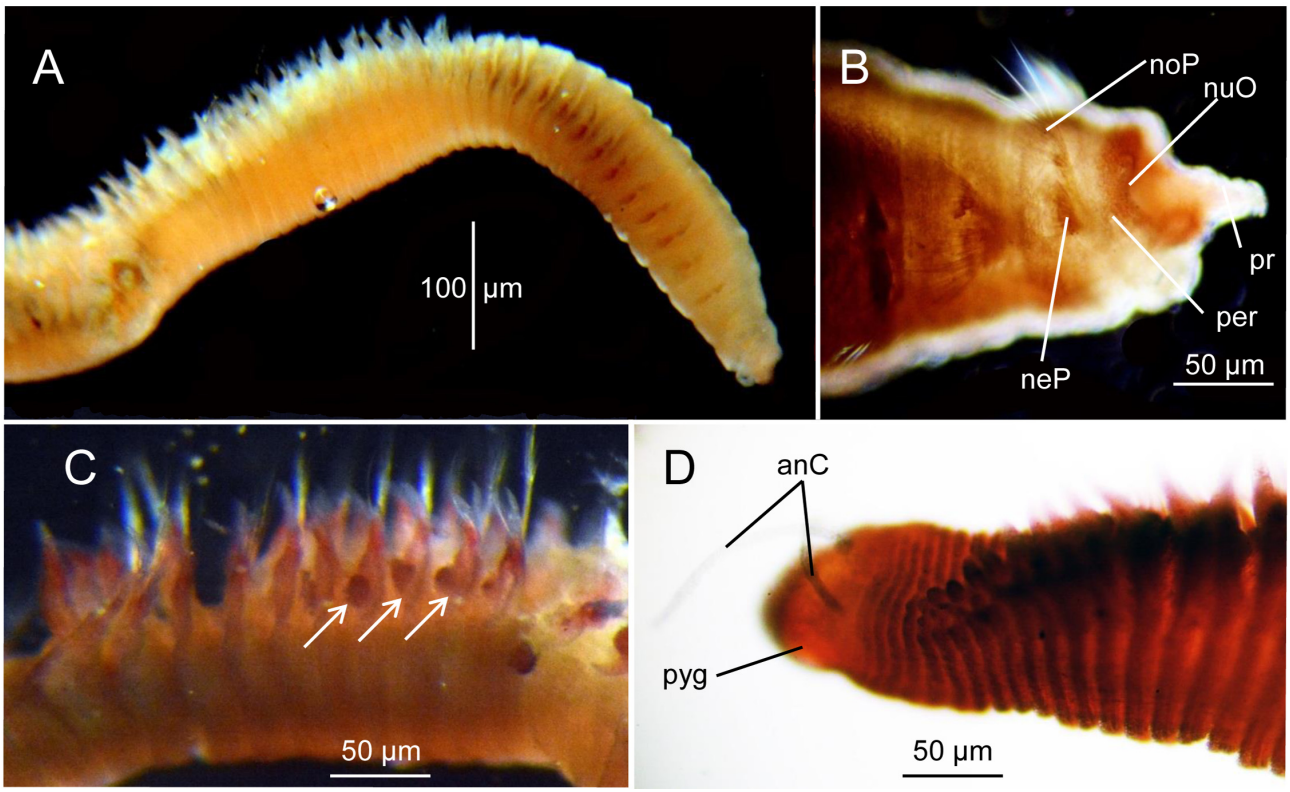

FIGURE 9. *Leitoscoloplos pustulus* **n. sp**. Holotype (USNM 1620901): A, anterior end, right lateral view; B, pre-setiger region and first 2–3 setigers, right lateral view; C, middle of body in right lateral view, arrows point to bulbous neuropodial flanges; D, pygidium right lateral view. All stained with Shirlastain A.

Leitoscoloplos robustus **(Verrill, 1873)**

Figures 10–11

Anthosoma robustum Verrill, 1873: 49, 54, 71, 134, 303, pl. 14, fig. 76.
Scoloplos robustus: Verrill 1881: 301, 317; Andrews 1891: 292; Sumner, *et al*. 1913: 624.
Scoloplos robusta: Webster & Benedict 1884: 724.
Scoloplos bustoris Eisig, 1914:422–423; Hartman 1942: 58–60, figs. 111–112; Horn & Bookhout 1950: 1, pls. 1–4. *Fide* Hartman 1957.
Haploscoloplos tortugaensis Monro, 1933a: 261–263, fig. 10a–d. *Fide* Mackie 1987.
Scoloplos rufa Treadwell, 1941: 1, figs. 1–6. *Fide* Hartman 1956.
Haploscoloplos bustoris: Hartman 1945: 30. *Fide* Hartman 1957.
Haploscoloplos robustus Hartman 1951: 78, pl. 21, figs. 4–6; 1956: 258, 268, 290; 1957: 272, pl. 25, figs 4–6; Day 1973: 91; Trott 2004: 280.
Scoloplos (*Scoloplos*) *robustus*: Pettibone 1963: 288–290, fig. 76g.
Leitoscoloplos robustus: Taylor 1984 1.17–1.19, fig. 1.16a–f; Mackie 1987: 16–18, fig. 17; Fauchald, Granados-Barba & Solís-Weiss 2009: 763; Blake 2017: 18.

Material examined. (*145 specimens*) **Northeastern USA, Gulf of Maine, Damariscotta River Estuary**, Lowes Cove, coll. G. Noyes, 7 Aug 1966, 43°56.012′N, 69°34.688′W, intertidal (5, MCZ 161587); upper end Pleasant Cove, coll. V. Walker, 19 Aug 1966, 43°54.956′N, 69°35.844′W, intertidal (21, MCZ 161588); Cove inside of Little Point, coll. D. Dorsey and V. Walker, 12 Aug 1966, 44°01.196′N, 69°32.823′W, 1–2 m (3, MCZ 161589); Seal Cove, coll. D. Dorsey and G. Noyes, 03 Aug 1966, 43°53.161′N, 69°34.119′W, 1–2 m (4, MCZ 161590); Peter's Island, coll. V. Walker, 01 Sep 1966, 43°54.504′N, 69°33.764′W, 1–2 m (16, MCZ 161591); Middle Pleasant Cove, coll. D. Dorsey and V. Walker, Sep 1966, 43°55.259′N, 69°35.167′W, 1–2 m (66, MCZ 161592); Long Cove, coll. D. Dorsey and V. Walker, 04 Aug 1966, 43°54.299′N, 69°33.859′W, 1 m (5, MCZ 161594).—**Connecticut, Long Island Sound,** US EPA Dredged Material Disposal Site Survey, **Sta. NLLRF**, Rep. 2, 17 Feb 2000, 41°16.710′N,

72°02.000′W, 16 m (1, MCZ 161596).—**New York, Long Island Sound, off Northport,** pipeline survey, **Sta. IG-01**, coll. P.L. Neubert, 27 Oct 1999, 40°55.75′N, 73°20.73′W, 3 m (1, MCZ 161682). **Eastchester Bay, off Locust Point**, pipeline survey, **Sta. LP 2**, Rep. 1, coll. P.L. Neubert, 14 Jul 2000, 40º49.201′N, 73º48.016′W, 4.5 m (14, MCZ 161593).—**Off New Jersey,** Atlantic Ocean, August 2008; Excalibur pipeline survey, **Sta. 39B**, coll. P.L. Neubert, 40°16.4468′N, 73°42.6671′W, 28 m (1, MCZ 161595).—**Massachusetts, New Bedford Harbor, Long-term Monitoring Program, 1999 September-October Survey**. **Sta. 208-2**, 23 Sep 1999, 41°38.981′N, 70°55.022′W, 1.3 m (1, MCZ 161575); **Sta. 306-3**, 14 Sep 1999, 41°37.15′N, 70°52.237′W, 2.8 m (1, MCZ 161576).—**Off Massachusetts, Georges Bank**, **Benthic Infauna Monitoring Program**, coll. G.W. Hampson, Chief Scientist. **Sta. 4**: Cruise M6, R/V *Oceanus*, Rep. 2, 25 Nov 1982, 40°50.7′N, 68°00.2′W, 65 m (2, USNM 1620911); Cruise M10, R/V *Oceanus*, Rep. 2, 14 Nov 1983, 40°50.7′N, 68°00.2′W, 67 m (1, USNM 1620912). **Sta. 10**: Cruise M1, R/V *Eastward*, Jul 1981, Rep. 5, 40°,42.0′N, 68°36.0′W, 62 m (1, USNM 1620913); Cruise M3, R/V *Endeavor*, Rep. 5, 12 Feb 1982, 40°42.0′N, 68°35.1′W, 62 m (1, USNM 1620914); Cruise M4, R/V *Cape Henlopen*, Rep. 2, 16 May 1982, 40°42.0′N, 68°35.2′W, 62 m (1, USNM 1620915); Cruise M5, R/V *Oceanus*, Rep. 6, 28 Jul 1982, 40°42.0′N, 68°35.3′W, 56 m (1, USNM 1620916); Cruise M8, R/V *Gyre*, Rep. 4, 20 May 1983, 40°42.0′N, 68°35.2′W, 62 m (1, USNM 1620917); Rep. 5, (4, USNM 1620918). **Sta. 11**: Cruise M2, R/V *Oceanus*, Rep. 2, 12 Nov 1981, 40°30.8′N, 68°33.5′W, 80 m (1, USNM 1620919); Rep. 5 (1, USNM 1620920); Cruise M3, R/V *Endeavor,* Rep. 1, 12 Feb 1982, 40°30.8′N, 68°33.6′W, 86 m (1, USNM 1620921); Rep. 2 (1, USNM 1620922); Cruise M4, R/V *Cape Henlopen*, Rep. 3, 16 May 1982, 40°30.8′N, 68°33.7′W, 83 m (2, USNM 1620923); Cruise M6, Rep. 3, R/V *Oceanus*, 26 Nov 1982, 40°30.8′N, 68°33.7′W, 83 m (1, USNM 1620924); Cruise M8, R/V *Gyre*, Rep.4, 20 May 1983, 40°30.8′N, 68°33.7′W, 84 m (1, USNM 1620925); Cruise M11, R/V *Oceanus*, Rep. 1, 14 Nov 1983, 40°30.8′N, 68°33.7′W, 86 m (1, USNM 1620926); Cruise M12, R/V *Gyre*, Rep. 6, 3 Jun 1984, 40°30.8′N, 68°33.7′W, 86 m (2, USNM 1620927).

Description. A large species, specimens from Georges Bank (USNM 1620918) up to 9.5 cm long, 3.5 mm wide across thoracic setigers, with 280 setigers (one complete); smaller specimens from Maine up to 17.5 mm long, 1 mm wide across thoracic setigers, with 125 setigers (complete specimen). Body elongate, with thoracic segments and anteriormost abdominal segments dorsoventrally flattened, with individual segments short, about 4–5 times wider than long; individual segments separated by narrow transverse groove (Figs. 10A, 11A). Individual thoracic and anterior abdominal segments with thin, transverse ridge extending between parapodia and entirely across dorsal and ventral surfaces producing a biannulate appearance (Fig. 11A–C). Abdominal segments becoming longer with a narrow intersegmental ring anterior to larger segmental ring continuing ventrally between neuropodia. Middle and posterior segments about twice as wide as long. Shallow mid-ventral groove present from middle abdominal segments to near posterior end. Color in alcohol light tan.

Pre-setiger region triangular, elongate, as long as first 2½ setigers (Fig. 10A–C). Prostomium conical, tapering to pointed tip; nuchal organs curved slits on posterior lateral margin (Fig. 10A); eyespots absent. Peristomium a single smooth achaetous ring dorsally (Fig. 10A–B), ventrally encompassing mouth with upper lip formed of two large lobes and lower lip with curved row of ten or more narrow elongate lobes (Fig. 10C). Proboscis with one or more lobes when everted.

Thorax on larger specimens with 22–25 setigers with abrupt transition to abdominal segments. Boundary between thorax and abdomen indicated by elongation of neuropodia and decrease in number of neurosetae. Thoracic notopodial postsetal lobes short, weakly triangular in shape, narrowing apically, arising directly from body wall (Fig. 10D–E). Abdominal notopodia becoming longer, digitiform in middle and posterior segments (Fig. 10F–G).Thoracic neuropodial postsetal lobes short, stubby, arising from broadly rounded base (Fig. 10D); last 1–3 thoracic neuropodia with extra postsetal lobe and usually a short subpodial papilla resulting in one or two final thoracic setigers with three short lobes on largest specimens (Fig. 10E). Abdominal neuropodia thickened, becoming relatively short in middle and posterior segments, each narrowing to pointed apical lobe bearing subterminal ventral cirrus on lateral margin (Fig. 10F); extra postsetal lobes or subpodial papillae appearing to merge into subpodial flange over first 3–4 abdominal setigers (Fig. 10F); subsequent middle and posterior abdominal setigers with large, thickened, subterminal flange ventral to neuropodium (Fig. 10G); subpodial papillae absent on abdominal segments. Prominent interramal cirrus present on anterior abdominal setigers (Fig. 10F); narrow, conical or fingerlike at first, continuing for about 75 setigers, then reduced to short ciliated patch and/or protuberance in middle setigers (Fig. 10G); entirely absent in posterior setigers.

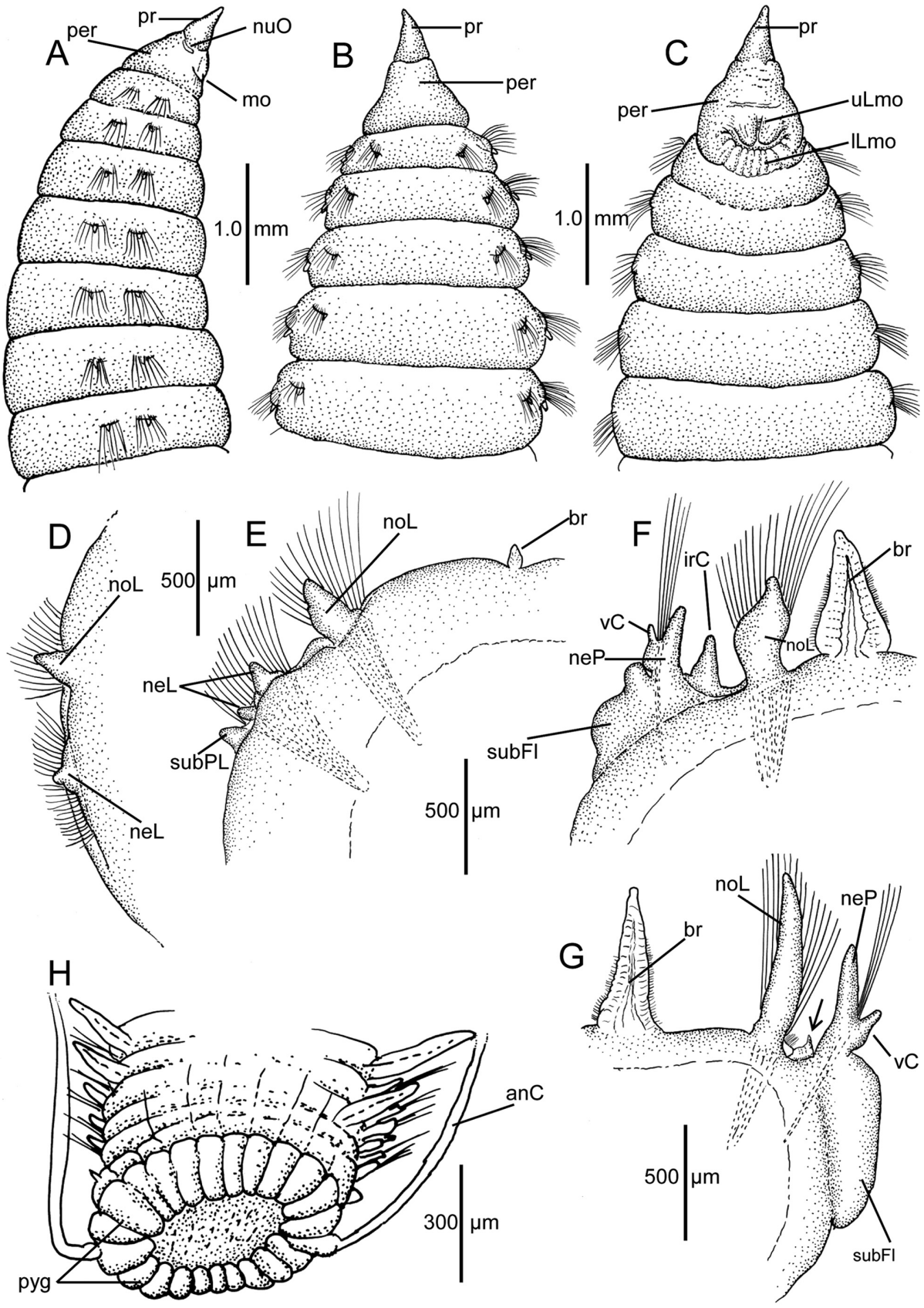

FIGURE 10. *Leitoscoloplos robustus* (Verrill, 1873). A, anterior end, right lateral view; B, anterior end, dorsal view; C, anterior end, ventral view; D, setiger 10, posterior view; E, thoracic setiger 23, posterior view; F, abdominal setiger 29, posterior view; G, posterior abdominal setiger, posterior view, arrow denotes interramal cirrus; H, pygidium, dorsal view. A–G (USNM 1620918); H (USNM 1620927).

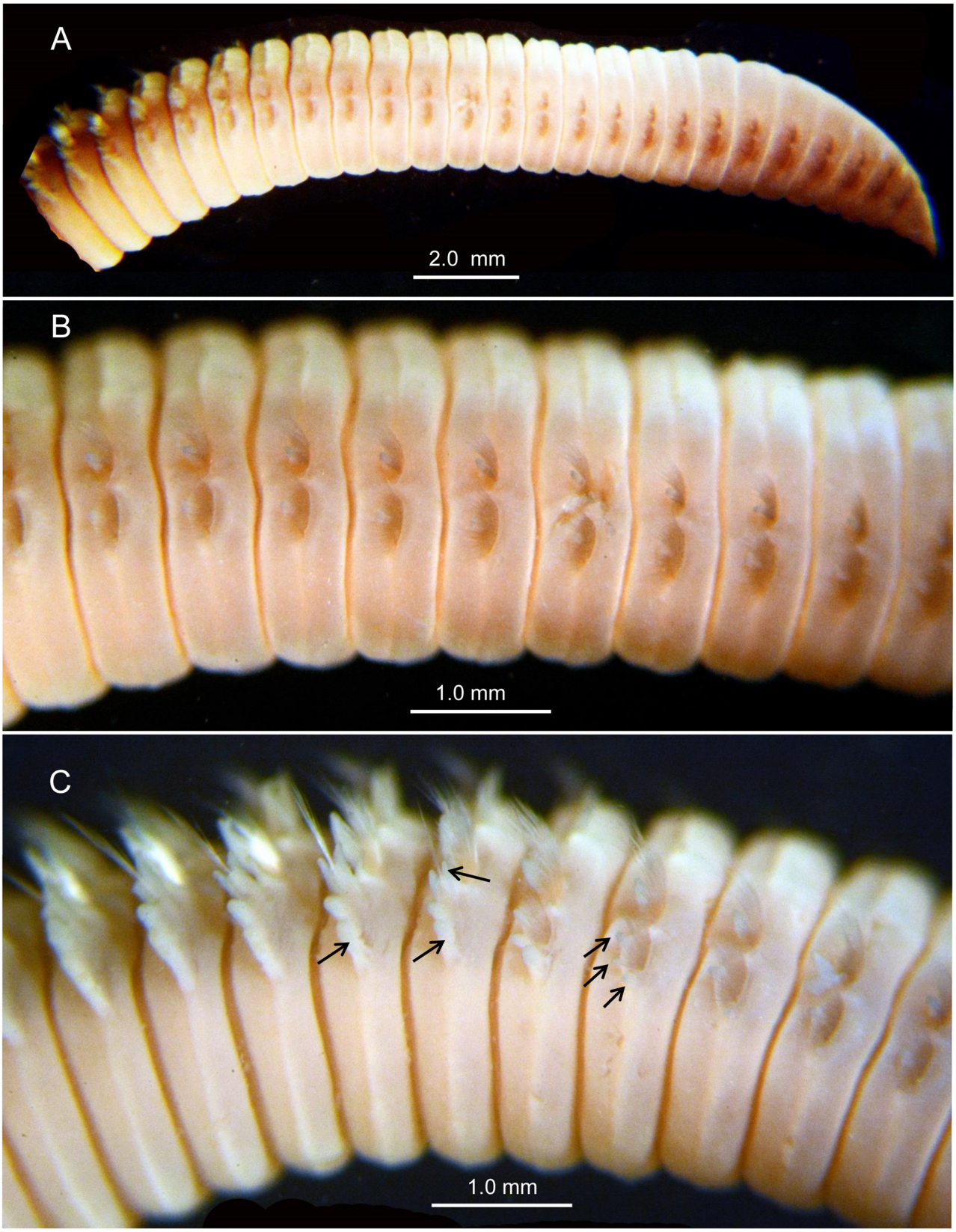

FIGURE 11. *Leitoscoloplos robustus* (Verrill, 1873). A, anterior end, right lateral view; B, thoracic setigers of same; C, anterior abdominal setigers of same. (USNM 1620913). Arrows denote interramal cirri and subpodial papillae. All stained with Shirlastain A.

Branchiae typically from setiger 20–23, usually 22; initial thoracic branchiae short, papilliform (Fig. 10E), becoming full size by about setigers 25–27 or anterior abdominal segments (Fig. 10F). Anterior branchiae triangular, tapering to rounded apex; branchiae of middle and posterior segments becoming narrower and longer (Fig. 10G); each branchia with transverse folds and cilia on inner and outer margins.

Notosetae all camerated capillaries; furcate and flail setae not observed; capillaries of thoracic notopodia numbering about 50 in 4–5 irregular rows, reduced to about 25 in abdominal segments. Thoracic neurosetae all camerated capillaries with about 75–100 in 5–6 rows; abdominal neurosetae 8–9 long stiff capillaries with barbs along one edge and 1–3 imbedded aciculae, none observed protruding.

Pygidium consisting of numerous lobes surrounding anal opening; with two thin anal cirri attached laterally (Fig. 10H).

Variability. Smaller specimens with 14–19 thoracic setigers and branchiae from setigers 13–17 have been recorded (Mackie 1987; specimens from Maine in the present study). However, the nature of the extra postsetal lobes in the last thoracic neuropodia and relatively smooth form of the abdominal subpodial flanges of the neuropodia are similar to those of the larger specimens.

Remarks. *Leitoscoloplos robustus* is the largest known species of the genus (Pettibone 1963; Mackie 1987). Pettibone (1963) reported specimens having 300 setigers, a length of 37.5 cm and a thoracic width of 10 mm. The largest specimen measured in this study had 280 setigers and was 9.5 cm long and 3.5 mm wide across thoracic setigers. It is likely that larger specimens are in the Georges Bank samples, but most specimens were coiled upon preservation, including one that was complete and could not be accurately measured.

Leitoscoloplos robustus differs from the closely related *L. fragilis* in that the latter species has extra subpodial papillae in abdominal segments that continue posteriorly along most of the body and that typically divide the subpodial flange into separate lobes. In contrast, *L. robustus* has no abdominal subpodial papillae or lobes after the first 2–3 abdominal setigers and the borders of the subpodial flanges are therefore smooth and entire along most of the body. In addition, *L. robustus* has prominent neuropodial ventral cirri in abdominal setigers that is reduced or inconspicuous in *L. fragilis*.

Although similar morphologically, the distinction between *L. fragilis* and *L robustus* among specimens from the eastern U.S. was supported in a molecular analysis by Bleidorn (2009). In the same analysis, *L. robustus* specimens from Maine and Florida were shown to exhibit only minor genetic differences.

Distribution. Eastern Canada to Florida, intertidal to 86 m; northern Gulf of Mexico, Florida, intertidal to 10 m.

Genus *Scoloplos* de Blainville, 1828

Type species: *Lumbricus armiger* Müller, 1776, by monotypy.
Synonym: *Scolaricia* Eisig, 1914. Type-species: *Scolaricia typicus* Eisig, 1914, by monotypy. *Fide* Day 1973.

Diagnosis. (Emended). Prostomium pointed, usually prolonged; single achaetous peristomial ring. Branchiae first present from middle or posterior thoracic setigers or from abdominal setigers (8–26). Posterior thoracic setigers with 0–2 postsetal lobes and 0–2 subpodial lobes, never more than four lobes of both types combined; not forming ventral fringes. Thoracic neurosetae including blunt, inconspicuous uncini, few or many in distinct rows; accompanied by few to many crenulated capillaries; furcate setae usually present; heavy spear-like spines and bristle-topped setae absent. Abdominal neuropodia with imbedded, non-projecting acicula. Abdominal noto- and or neuropodial flail setae present or absent.

Remarks. Specimens of *Scoloplos* having thoracic neuropodial uncini or hooks and extra neuropodial postsetal or subpodial lobes have for the most part been identified as *S. armiger* (Müller, 1776), resulting in the species being identified from wide geographic areas and thus considered cosmopolitan (Hartman 1957; Pettibone 1963; Hartmann-Schröder 1971, 1996; Blake 1996). Accounts of *S. armiger* among European investigators, however, suggest that several species are involved. For example, McIntosh (1910) described specimens that have only a few thoracic neuropodial uncini or spines; whereas Hartmann-Schröder (1971, 1996) described specimens with numerous thoracic neuropodial uncini. Supporting the view that European *S. armiger* may represent a suite of species, recent investigations have demonstrated that different populations in shallow and subtidal locations in the North Sea are ecologically and reproductively isolated from one another (Kruse & Reise 2003; Kruse *et al*. 2003, 2004). Results

from molecular sequence data also support these observations (Bleidorn *et al*. 2006). Additionally, these authors determined that specimens from the type locality in Norway represented yet a third species. These results suggest that at least three cryptic species are likely present among northern European specimens collectively identified as *S. armiger*. Bleidorn *et al*. (2006, 2009) also provided molecular results on some orbiniids from California in the eastern Pacific identified locally as *S. armiger* that might represent additional undescribed species. To date, none of these various species have been described or redescribed, including specimens from the type locality.

Previous studies along the U.S. Atlantic coast have reported species of *Scoloplos* as *S. armiger*, the widely reported European species, and *S. acmeceps*, an eastern Pacific species (Pettibone 1963; Maciolek-Blake *et al*. 1985; Trott 2004). The present morphological study of *Scoloplos* specimens from shelf and slope depths along the U.S. Atlantic coast suggest that several distinct species are present, none of which are either *S. armiger* or *S. acmeceps*. Three basic morphotypes are evident: (1) specimens with rows of numerous thoracic neuropodial uncini or hooks and with no extra postsetal or subpodial lobes; (2) specimens with thoracic neuropodial uncini reduced to a single row or a few isolated ventral spines and with extra postsetal and/or subpodial lobes; (3) specimens with 3–4 rows of numerous thoracic neuropodial uncini and with extra postsetal and/or subpodial lobes. Within these three basic morphotypes, there is considerable additional morphology available to separate individual species. These include differences in (a) the pre-setiger morphology with details of the upper and lower lips of the mouth, (b) the shape and form of the thoracic noto- and neuropodia, (c) the presence and form of subpodial flanges with or without internal glands, (d) the shape of the branchiae along the body, (e) the presence or absence of an interramal process or cirrus, (f) the presence or absence of notopodial furcate setae, (g) details of the intersegmental areas, and (h) pygidial morphology. These characters and other aspects of the following five species identified from shelf and slope depths along the U.S. Atlantic coast are reported:

1. *Scoloplos intermedius* (Hartman, 1965)
2. *Scoloplos papillatus* **n. sp**.
3. *Scoloplos pettiboneae* **n. sp**.
4. *Scoloplos pseudoarmiger* **n. sp**.
5. *Scoloplos verrilli* **n. sp**.

Scoloplos intermedius (Hartman, 1965)

Figures 12–14

Haploscoloplos fragilis intermedius Hartman, 1965: 128, pl. 28, fig. a; Hartman & Fauchald 1971: 91 (in Part). *Fide* Mackie 1987.
Scoloplos intermedius: Mackie 1987: 23–24, fig. 23.
Scoloplos sp. 1: Blake *et al*. 1987: C-4; Maciolek *et al*. 1987a: D-4; Maciolek *et al*.; 1987b: D-3; Hilbig 1994: 942.
Scoloplos sp. 2: Blake *et al*. 1987: C-4; Hilbig 1994: 942.

Material examined. (*119 specimens*) **Northeastern USA, off New England, Gay-Head Bermuda Transect**, R/V *Atlantis*, **Sta. F-1**, 24 May 1961, 39°47′N, 70°45′W, 1500 m, **holotype** (LACM-AHF Poly 0686).—**US North Atlantic ACSAR program**, **off New England**, coll. G.W Hampson, Chief Scientist. **Sta. 3**: Cruise NA-2, Rep. 1, 26 Apr 1985, 41°01.34′N, 66°20.21′W, 1340 m (1, USNM 1620941); Cruise NA-3, Rep. 2, 03 Jul 1985, 41°01.38′N, 66°20.22′W, 1330 m (3, USNM 1620942). **Sta. 9**: Cruise NA-2, Rep. 1, 03 May 1985, 39°50.43′N, 70°01.58′W, 1235 (1, USNM 1620943). Cruise NA-4, Rep. 1, 27 Nov 1985, 39°50.42′N, 70°01.65′W, 1224 m (1, USNM 1620944); Rep. 3, 27 Nov 1985, 39°50.39′N, 70°01.65′W, 1239 m (1, USNM 1620945); Cruise NA-5, Rep. 3, 03 May 1986, 39°50.39′N, 70°01.62′W, 1238 m (1, USNM 1620946); Cruise NA-6, Rep. 2, 28 Jul 1986, 39°50.41′N, 70°01.62′W, 1230 m (2, USNM 1620947). **Sta. 10**: Cruise NA-2, Rep. 1, 03 May 1985, 39°48.11′N, 70°05.26′W, 1210 m (2, USNM 1620948); Rep. 3, 03 May 1985, 39°48.12′N, 70°05.24′W, 1210 m (1, USNM 1620949); Cruise NA-4, Rep. 1, 27 Nov 1985, 39°48.09′N, 70°05.29′W, 1222 m (1, USNM 1620950); Rep. 3, 30 Nov 1985, 39°48.38′N, 70°54.96′W, 1244 m (1, USNM 1620951). **Sta. 13**: Cruise NA-4, Rep. 1, 29 Nov 1985, 39°48.37′N, 70°55.12′W, 1244 m (1, USNM 1620952); Cruise NA-6, Rep. 2, 30 Jul 1986, 39°48.25′N, 70°54.95′W, 1273 m (1, USNM 1620953). **Sta. 15**: Cruise NA-2, Rep.1, 05 May 1985, 39°40.08′N, 70°54.26′W, 2150 m (1, USNM 1620954).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR program**, coll. R.M. Petrecca, Chief Scientist. **Sta.**

2: Cruise Mid-1, Rep. 1, 01 Apr 1984, 38°35.78′N, 72°53.65′W, 2013 m (1, USNM 1620955); Cruise Mid-2, Rep. 2, 03 Aug 1984, 38°35.74′N, 72°53.68′W, 2014 m (1, USNM 1620956); Rep. 3, 03 Aug 1984, 38°35.76′N, 72°53.81′W, 2004 m (1, USNM 1620957); Cruise Mid-3, Rep. 1, 02 Dec 1984, 38°35.75′N, 72°53.67′W, 2010 m (1, USNM 1620958); Cruise Mid-5, Rep. 1, 05 Aug 1985, 38°35.68′N, 72°53.79′W, 2010 m (1, USNM 1620959); Cruise Mid-6, Rep. 2, 13 Nov 1985, 38°35.65′N, 72°53.70′W, 2024 m (1, USNM 1620960). **Sta. 3**: Cruise Mid-1, Rep. 1, 05 May 1984, 38°36.88′N, 72°51.41′W, 2055 m (1, USNM 1620961); Rep. 2, 05 May 1984, 38°36.88′N, 72°51.34′W, 2055 m (1, USNM 1620962); Cruise Mid-2, Rep. 3, 03 Aug 1984, 38°36.84′N, 72°51.46′W, 2056 m (2, USNM 1620963); Cruise Mid-5, Rep. 1, 05 Aug 1985, 38°36.79′N, 72°51.54′W, 2050 m (1, USNM 1620964). **Sta. 5**: Cruise Mid-1, Rep. 2, 04 May 1984, 38°50.53′N, 72°33.10′W, 2065 m (2, USNM 1620965); Cruise Mid-3, Rep. 3, 05 Dec 1985, 38°50.47′N, 72°33.07′W, 2070 m (1, USNM 1620966); Cruise Mid-5, Rep. 1, 03 Aug 1985, 38°50.44′N, 72°33.18′W, 2077 m (1, USNM 1620967); Rep. 3, 03 Aug 1985, 38°50.42′N, 72°33.24′W, 2080 m (2, USNM 1620968); Cruise Mid-6, Rep. 1, 11 Nov 1985, 38°50.49′N, 72°33.17′W, 2084 m (1, USNM 1620969). **Sta. 6**: Cruise Mid-2, Rep. 1, 01 Aug 1984, 39°05.65′N, 72°02.97′W, 2084 m (1, USNM 1620970). **Sta. 9**: Cruise Mid-2, Rep. 1, 06 Aug 1984, 38°17.24′N, 73°14.51′W, 2109 m (1, USNM 1620971). **Sta. 10**: Cruise Mid-1, Rep. 2, 07 May 1984, 38°51.80′N, 73°19.96′W, 2095 m (1, USNM 1620972). **Sta. 11**: Cruise Mid-1, Rep. 1, 07 May 1984, 38°40.16′N, 72°56.82′W, 1515 m (1, USNM 1620973); Rep. 3, 07 May 1984, 38°40.22′N, 72°56.27′W, 1520 m (1, USNM 1620974); Cruise Mid-2, Rep. 3, 05 Aug 1984, 38°40.25′N, 72°56.24′W, 1504 m (2, USNM 1620975); Cruise Mid-3, Rep. 1, 04 Dec 1984, 38°40.13′N, 72°56.27′W, 1540 m (1, USNM 1620976); Rep. 3, 04 Dec 1984, 38°40.14′N, 72°56.35′W, 1520 m (2, USNM 1620977); Cruise Mid-4, Rep. 1, 17 May 1985, 38°40.10′N, 72°56.43′W, 1510 m (3, USNM 1620978); Rep. 3, 17 May 1985, 38°40.11′N, 72°56.44′W, 1510 m (3, USNM 1620979); Cruise Mid-5, Rep. 1, 06 Aug 1985, 38°40.12′N, 72°56.45′W, 1505 m (2, USNM 1620980); Rep. 2, 06 Aug 1985, 38°40.12′N, 72°56.47′W, 1502 m (2, USNM 1620981); Rep. 3, 06 Aug 1985, 38°40.14′N, 72°56.46′W, 1502 m (3, USNM 1620982). Cruise Mid-6, Rep. 1**,** 38°40.13′N, 72°56.48′W, 1504 m (1, USNM 1620983). **Sta. 13**: Cruise Mid-1, Rep. 1, 02 Apr 1984, 37°53.33′N, 73°45.09′W, 1613 m (3, USNM 1620984); Rep. 2, 02 Apr 1984, 37°53.38′N, 73°45.10′W, 1613 m (1, USNM 1620985); Rep. 3, 02 Apr 1984, 37°53.36′N, 73°45.10′W, 1613 m (1, USNM 1620986); Cruise Mid-2, Rep. 1, 07 Aug 1984, 37°53.35′N, 73°45.01′W, 1614 m (2, USNM 1620987); Cruise Mid-3, Rep. 1, 30 Nov 1984, 37°53.32′N, 73°45.10′W, 1615 m (2, USNM 1620988); Rep. 2, 30 Nov 1984, 37°53.35′N, 73°45.00′W, 1615 m (4, USNM 1620989); Rep. 3, 30 Nov 1984, 37°53.29′N, 73°45.11′W, 1612 m (1, USNM 1620990); Cruise Mid-4, Rep. 1, 19 May 1985, 37°53.26′N, 73°45.25′W, 1615 m (3, USNM 1620991); Rep. 2, 19 May 1985, 37°53.29′N, 73°45.30′W, 1607 m (2, USNM 1620992); Cruise Mid-5, Rep. 1, 09 Aug 1985, 37°53.26′N, 73°45.21′W, 1607 m (3, USNM 1620993); Rep. 2, 09 Aug 1985, 37°53.27′N, 73°45.28′W, 1605 m (3, USNM 1620994); Cruise Mid-6, Rep. 1, 16 Nov 1985, 37°53.31′N, 73°45.30′W, 1609 m (3, USNM 1620995); Rep. 3, 16 Nov. 1985, 37°53.23′N, 73°45.27′W, 1607 m (1, USNM 1620996). **Sta. 14**: Cruise Mid-1, Rep. 3, 02 Apr 1984, 37°53.79′N, 73°44.78′W, 1503 m (6, USNM 1620997); Cruise Mid-4, Rep. 3, 19 May 1985, 37°53.82′N, 73°44.76′W, 1490 m (3, USNM 1620998); Cruise Mid-5, Rep. 1, 10 Aug 1985, 37°53.79′N, 73°44.78′W, 1490 m (3, USNM 1620999); Rep. 2, 10 Aug 1985, 37°53.79′N, 73°44.79′W, 1490 m (2, USNM 1621000); Rep. 3, 10 Aug 1985, 37°53.80′N, 73°44.74′W, 1490 m (2, USNM 1621001); Cruise Mid-6, Rep. 1,15 Nov. 1985, 37°53.69′N, 73°44.69′W, 1515 m (2, USNM 1621002); Rep. 2, 15 Nov. 1985, 37°53.80′N, 73°44.74′W, 1494 m (1, USNM 1621003).—**Southeastern USA, US South Atlantic ACSAR program**, coll. J.A. Blake, Chief Scientist. **off Cape Lookout, North Carolina, Sta. 2**: Cruise SA-3, Rep. 1, 15 Jul 1984, 34°15.00′N, 75°43.70′W, 1002 m (2, USNM 1621004). **Sta. 3**: Cruise SA-3, Rep. 3, 14 Jul 1984, 34°15.10′N, 75°40.30′W, 1189 m (2, USNM 1621005). **Sta. 4**: Cruise SA-2, Rep. 1, 20 May 1984, 34°11.70′N, 75°38.60′W, 2064 m (1, USNM 1621006); Rep. 2, 20 May 1984, 34°11.90′N, 75°38.70′W, 2029 m (1, USNM 1621007); Rep. 3, 20 May 1984, 34°11.50′N, 75°39.00′W, 1969 m (3, USNM 1621008); Cruise SA-3, Rep. 1, 13 Jul 1984, 34°12.10′N, 75°38.60′W, 2066 m (3, USNM 1621009); Rep. 2, 14 Jul 1984, 34°10.41′N, 75°39.10′W, 2005 m (2, USNM 1621010); Rep. 3, 14 Jul 1984, 34°11.17′N, 75°38.98′W, 2006 m (1, USNM 1621011); Cruise SA-4, Rep. 1, 23 May 1985, 34°11.29′N, 75°38.67′W, 2015 m (1, USNM 1621002); Rep. 2, 23 May 1985, 34°11.22′N, 75°38.44′W, 2015 m (1, USNM 1621013); Rep. 3, 23 May 1985, 34°11.29′N, 75°38.67′W, 2015 m (3, USNM 1621014). Cruise SA-5, Rep. 1, 24 Sep 1985, 34°11.27′N, 75°38.63′W, 2032 m (1, USNM 1621015). **Off Charleston, South Carolina**, **Sta. 14**: Cruise SA-4, Rep. 1, 20 May 1985, 32°23.64′N, 77°01.13′W, 805 m (1, USNM 1621016).

Description. A small to moderately sized species, all specimens except juveniles incomplete. Holotype 11 mm long, 0.80 mm wide across thorax with 37 setigers (Mackie 1987); new collections with four specimens having

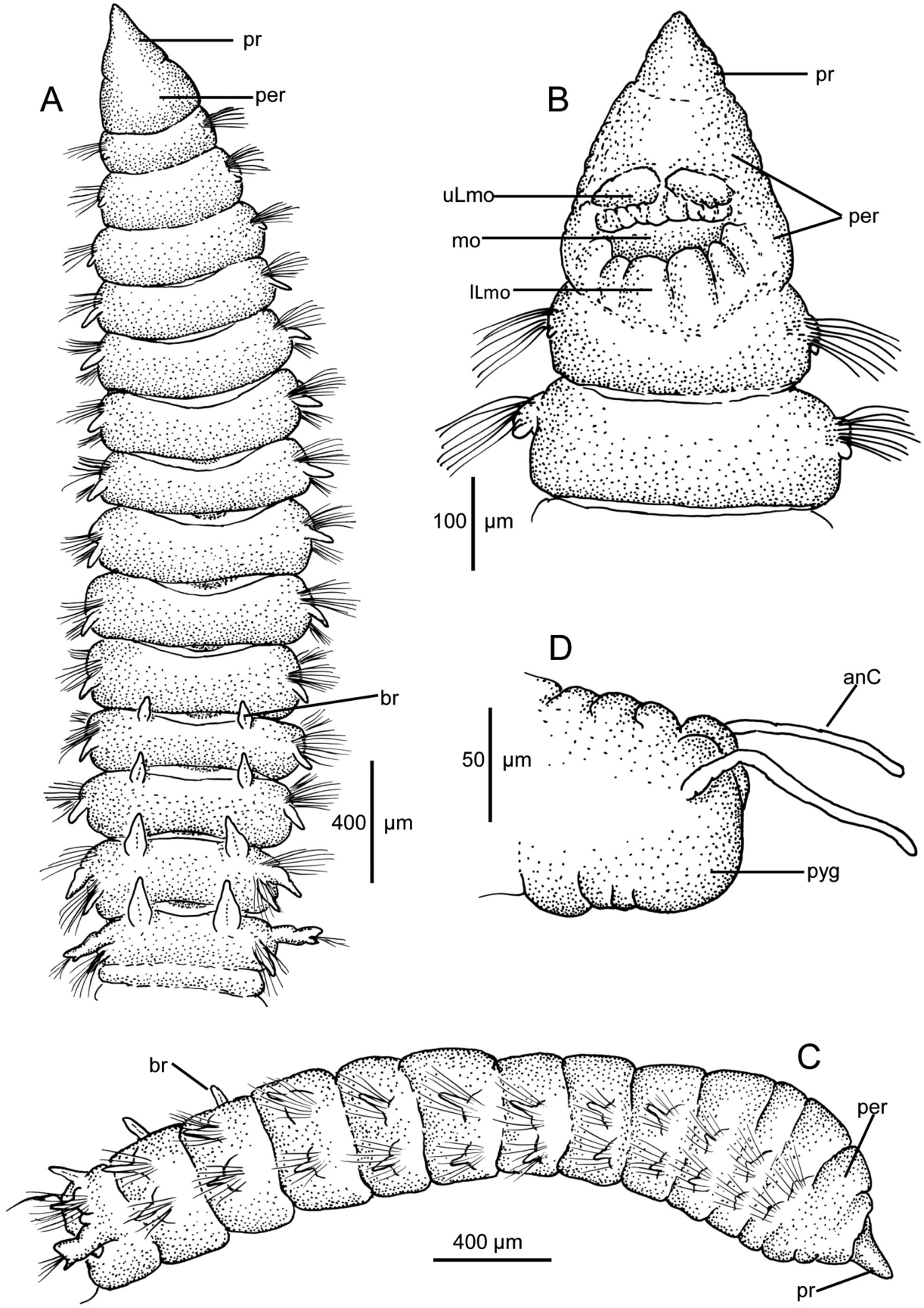

FIGURE 12. *Scoloplos intermedius* (Verrill, 1873). A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end, right lateral view; D, pygidium, left lateral view. A (USNM 1620973); B (USNM 1620993); C (USNM 1620974); D (USNM 1620967).

50 or more setigers, 12–15 mm long, and 1–1.2 mm wide across thorax: USNM 1620962: 14 mm long, 1.2 mm wide, 50 setigers, 12 thoracic setigers, and branchiae from setiger 11; USNM 1620942: 13 mm long, 1.1 mm wide, 52 setigers, 13 thoracic setigers, and branchiae from setiger 12; USNM 1620995: 15 mm long, 1.2 mm wide, 54 setigers, 13 thoracic setigers, and branchiae from setiger 10; USNM 1620960: 12 mm long, 1.0 mm wide, 55 setigers, 13 thoracic setigers and, branchiae from setiger 10.

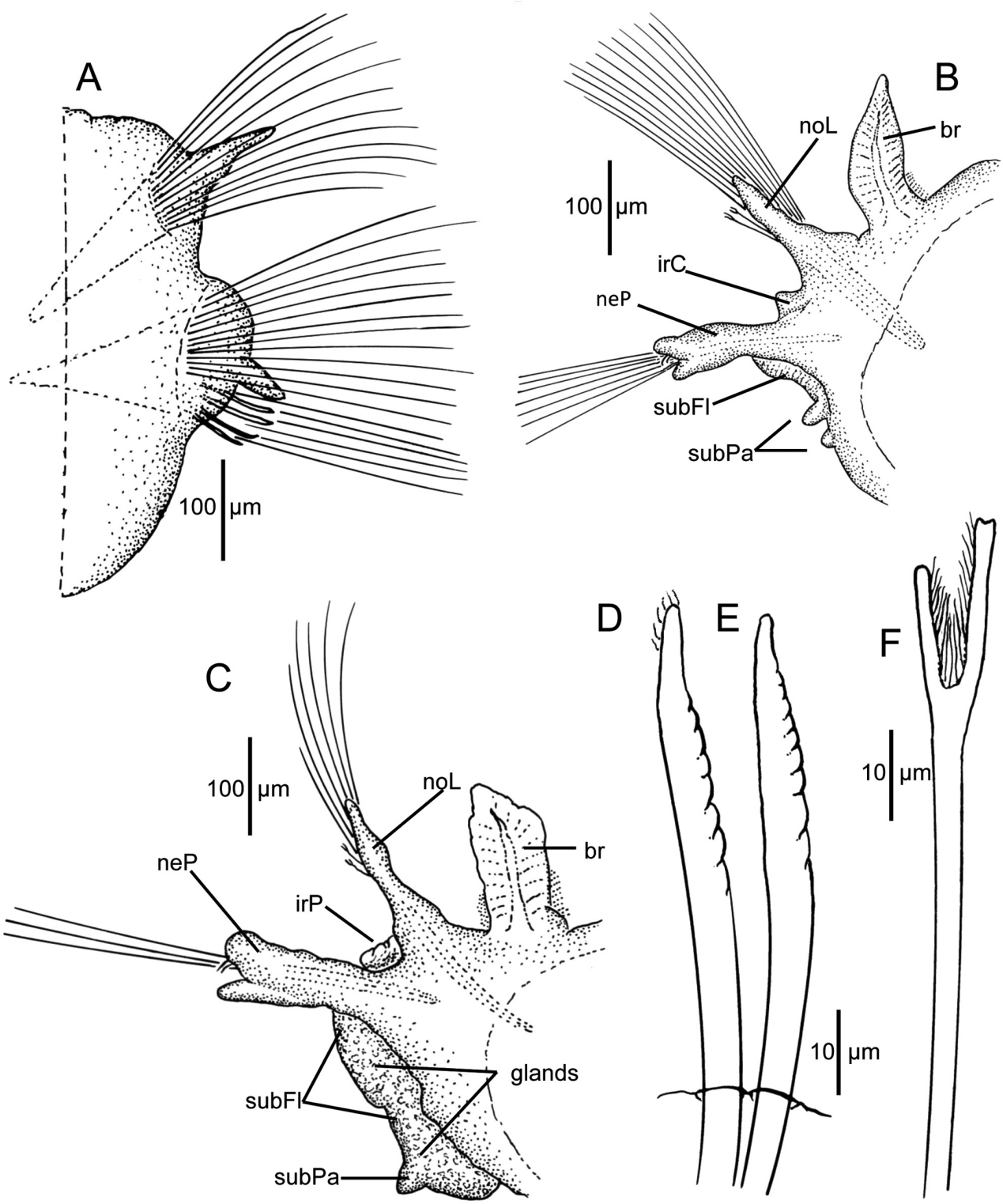

FIGURE 13. *Scoloplos intermedius* (Verrill, 1873). A, thoracic setiger 7, anterior view; B, anterior abdominal setiger, posterior view; C, middle abdominal setiger, posterior view; D–E, thoracic neuropodial uncini; F, furcate seta. (USNM 1620993).

Thoracic setigers numbering 11–13 in larger specimens; 6–10 in juveniles. Thoracic segments short, dorsoventrally flattened, 5–6 times wider than long (Fig. 12A) with middle thoracic segments often with weak mid-dorsal groove. Abdominal segments ventrally rounded, dorsally flattened with elevated parapodia; anterior and middle abdominal setigers with intersegmental grooves of venter narrow, bordered with flattened bands on anterior and posterior sides; parapodia located between bands of two segments producing a triannulate appearance; posterior parapodia more crowded, with intersegmental bands not apparent. Shallow ventral groove present along entire body on most specimens; dorsal grooves and ridges absent. Transition from thorax to abdomen denoted by elongation of neuropodium, with split apex developing over 1–2 successive segments (Fig. 12A, C). Color in alcohol light tan. Subpodial flanges of middle and posterior abdominal neuropodia often with internal glands but these not pigmented as in other species.

Pre-setiger region triangular in shape, as long as first 2–3 setigers (Fig. 12A–C). Prostomium conical, tapering to pointed tip; nuchal organs vertical curved slits on posterior lateral margin; eyespots absent. Peristomium longer than first setiger, with a single smooth annular ring dorsally (Fig. 12A), surrounding mouth on ventral side, forming upper and lower lips (Fig. 12B); upper lip of mouth with two large protruding lobes anterior to several small rounded lobes; lower lip of mouth with six large, elongate lobes (Fig. 12B).

Thoracic notopodia triangular, tapering to narrow digitiform postsetal lobe, short at first, then becoming longer, narrow in middle and posterior thoracic segments (Fig. 13A). Thoracic neuropodia with digitiform postsetal lobe arising from a broadly rounded base, lobes short at first, becoming long and fingerlike (Fig. 13A–C). Transition to abdominal segments abrupt, with neuropodium becoming larger, elongate, and apically divided into two lobes separated by a notch from which setae arise (Fig. 13B–C); medial lobe thick, rounded; ventral lobe narrower, shorter, rounded apically. Interramal cirrus present in anterior abdominal setigers as short conical lobe (Fig. 13B), reduced to thick variously developed process in posterior setigers (Fig. 13C). Each abdominal neuropodium with narrow subpodial flange; with 1–2, rarely 3, subpodial papillae on anterior abdominal segments with one papilla usually arising from basal margin of subpodial flange (Fig. 13B); single papilla continuing through middle abdominal setigers (Fig. 13C), absent in posterior setigers. Subpodial flanges of middle and posterior abdominal setigers with numerous internal glands (Fig. 13C), but these not darkly pigmented as on related species.

Branchiae from posterior thoracic setiger 10–12 (Fig. 12A, C); branchiae elongate, generally triangular in shape, tapering to narrow papillate tip (Fig. 13B); branchiae of middle and posterior setigers becoming broader, and irregular in shape (Fig. 13C), rarely asymmetrical. Each branchia ciliated along lateral and medial margins.

Thoracic notosetae numerous, thick, long, camerated capillaries arranged in 4–5 rows. Thoracic neurosetae arranged in about five rows with similar appearing camerated capillaries and 3–6 uncini concentrated in lower part of setal fascicle; uncini observed on all thoracic setigers of larger specimens; juveniles with irregular number of uncini not observed on all thoracic setigers. Individual uncini with shafts smooth on convex side tapering to narrow, rounded tip; concave side of shaft flattened, bearing low transverse ribs along most of shaft (Fig. 13D–E); tip of shaft sometimes with hood formed of emergent fibrils (Fig. 13D). Abdominal notosetae thin, camerated capillaries and 1–2 furcate setae. Furcate setae with unequal tynes (Fig. 13F), long tyne with blunted tip and an apical notch; shorter tyne with rounded tip; each tyne with a row of thin needles extending into center toward other tyne. Abdominal neurosetae with up to 4–5 thin smooth capillaries, barbs not observed in light microscope, and 1–2 curved aciculae, sometimes protruding, with rounded tip. Flail setae not observed.

Pygidium observed only on a few juveniles as a pair of rounded lobes surrounding anal opening and with two thin anal cirri arising dorsally (Fig. 12D, 14E).

Juvenile morphology. Although none of the samples contained large numbers of specimens, sufficient numbers of juveniles were present to document some aspects of their morphology and the stage in development when certain key characters of adults become present. Specimens from NA-6, Sta. 9 (USNM 1620947) and Mid-4, Sta. 11 (USNM 1620978) were studied in some detail.

A 15-setiger juvenile from NA-6, Sta. 9 (USNM 1620947) is 1.3 mm long and 150 μm wide across thoracic setigers (Fig. 14A). The body is relatively thick throughout with six distinctive thoracic setigers and nine crowded abdominal setigers. Branchiae are present on setigers 14 and 15 (Fig. 14A). The pre-setiger region appears to be fully developed. The prostomium is adult-like in being triangular and tapering to a narrow, rounded apex (Fig. 14A–B); nuchal organs were not observed. The peristomium consists of a single ring that is relatively smooth dorsally and surrounds the mouth ventrally. At this stage the upper lip of the mouth has only two weakly developed lobes and the ventral lip is a single ridge lacking lobes. The specimen had been feeding however, as silt particles were pres-

ent in the gut. Parapodia are generally well developed; thoracic postsetal lobes are only short papillae; abdominal notopodia are short thick lobes; abdominal neuropodia are short and thick, with no evidence of the bilobed nature of adults. An interramal cirrus is present on the last setiger. All notosetae are camerated capillaries, furcate setae were not observed; thoracic neurosetae include camerated capillaries and 2–4 hooks or uncini bearing a row of transverse barbs or ridges along the shaft; abdominal neurosetae include 2–3 long capillaries. The pygidium is a rounded lobe with two short papillae that are anlage of anal cirri (Fig. 14A).

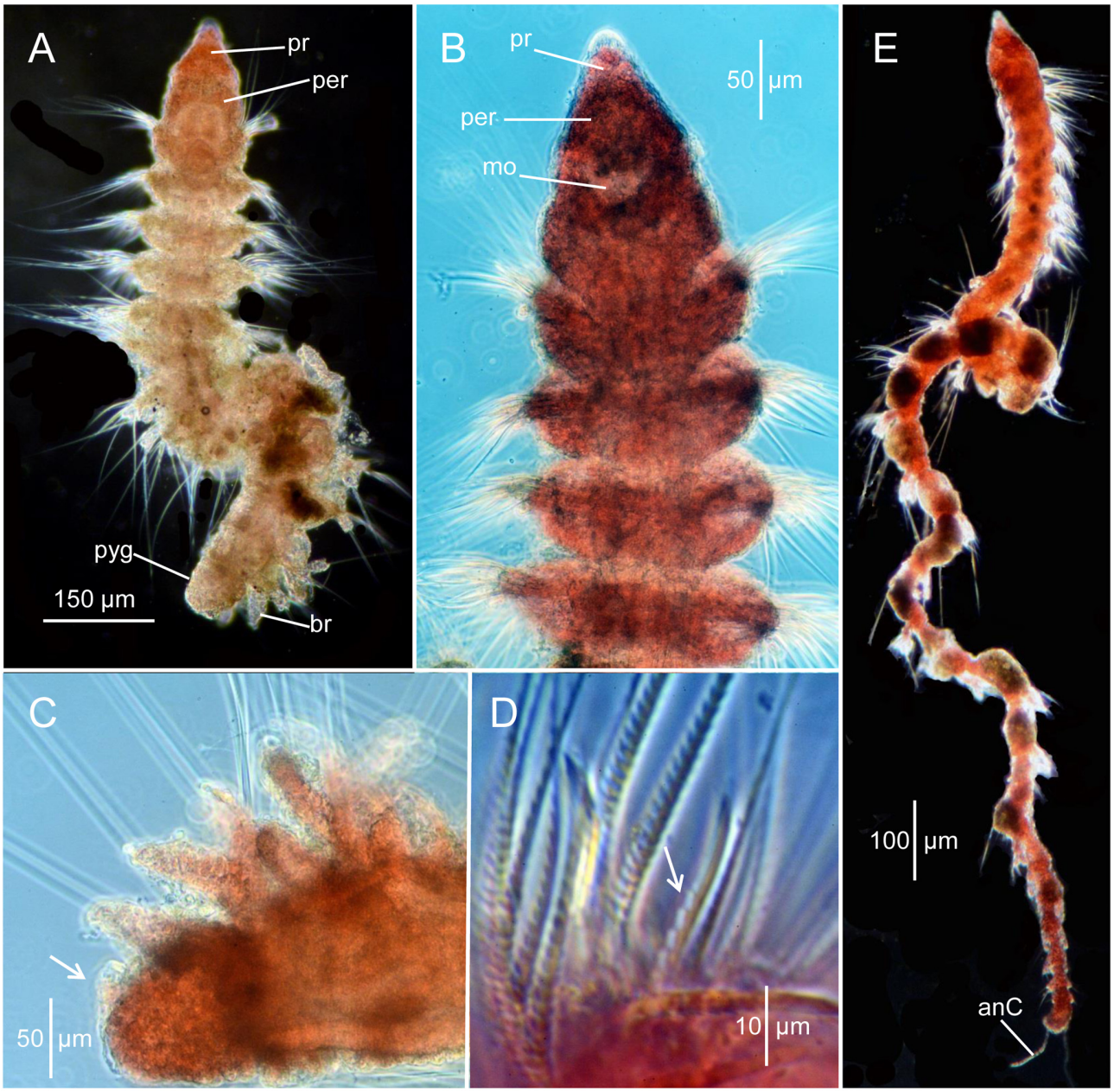

FIGURE 14. *Scoloplos intermedius* (Verrill, 1873). Juveniles: A, 15-setiger juvenile; B, same, anterior end, ventral view; C, same posterior end right lateral view; D, thoracic neurosetae; E, 31-setiger pre-adult. A–C (USNM 1620947); D–E (USNM 16209478). All stained with Shirlastain A.

A 31-setiger pre-adult from Sta. Mid-4, Sta. 11 (USNM 1620978) is 3.2 mm long and about 150 µm wide anteriorly and 120 µm wide in middle segments (Fig. 14E). The body is long and thin, with middle segments that are up to twice as long as wide and appear weakly moniliform and distended guts due to ingested sediments. There are six thoracic setigers and branchiae are present from setiger 15. The first interramal cirri were observed on setiger 8 as short triangular lobes. The pre-setiger region is about the same as with the smaller specimen from NA-6. Thoracic notosetae include about 15 camerated capillaries; abdominal notosetae include 5–10 camerated capillaries and

a single furcate seta was observed. Thoracic neurosetae include about 25 capillaries and 2–4 hooks or uncini with transverse barbs across the shafts (Fig. 14D); abdominal neurosetae include a few long capillaries and 1–2 short, pointed aciculae. The pygidium bears two long anal cirri (Fig. 14E).

Variability. In adults, the shape of the interramal cirrus varies from a short, rounded or triangular-shaped lobe to an elongate cirrus. Except for always being shorter than either the noto- or neuropodium, there is no consistency in this character even within specimens from the same sample. The thoracic neuropodial uncini are generally consistent in morphology among specimens except for the apical hood which can be either absent or worn.

Remarks. This species was originally described as *Haploscoloplos fragilis intermedius* by Hartman (1965) from deep-water collections off New England collected by the late Dr. Howard Sanders. Additional materials were reported by Hartman & Fauchald (1971) from the same general area. Mackie (1987), as part of a revision of the genus *Leitoscoloplos*, determined that upper slope (ca. 300 m) and lower slope (ca. 1500 m) specimens reported by Hartman (1965) as *H. fragilis intermedius* represented two different species. Mackie (1987) described the upper slope specimens as a new species, *L. obovatus* (see above). He also determined that the specimens reported by Hartman from the deeper slope locations represented a species of *Scoloplos* and raised the subspecies to full species status, *S. intermedius*.

The new collections of *S. intermedius* reported here are from middle and lower continental slope depths from along the entire U.S. Atlantic continental margin from near the Canadian boundary to the Carolinas. *Scoloplos intermedius* is the only North Atlantic species of the genus known to have an interramal cirrus and the only species from the Western North Atlantic to occur in deep water (1200–2100 m). *Scoloplos papillatus* **n. sp**. (see below) from off Cape Hatteras, North Carolina is an upper slope depths (600–800 m) species that lacks interramal cirri.

Scoloplos intermedius is most similar to *S. similis* Mackie, 1987 from off South Africa in shelf depths (124 m) by having an interramal cirrus between the noto- and neuropodia of the last thoracic and anterior abdominal setigers and subpodial papillae that continue along most of the abdominal segments. The two species differ in that *S. intermedius* has 11–13 thoracic setigers and branchiae from setigers 10–12, whereas *S. similis* has 15 thoracic setigers and branchiae from setiger 12. Both species have subpodial papillae and subpodial flanges; however, the subpodial flanges of *S. intermedius* are thick and glandular in abdominal setigers and with a subpodial papilla. In contrast the subpodial flanges of *S. similis* are short and separated from the neuropodium by a distinct notch; internal glands in the subpodial flanges were not reported by Mackie (1987). Furcate notosetae are present in abdominal segments of *S. intermedius* but were not present in the three specimens of *S. similis* examined by Mackie (1987).

Juveniles described here indicate that the interramal cirrus and thoracic neuropodial uncini develop early, while the final number of thoracic setigers and position of the branchiae develop later. Interestingly, the nature of the presetiger region of the smallest juveniles closely resembles that of adults.

Distribution. Continental slope off the U.S. Atlantic coast, New England to North Carolina, 1210–2109 m.

Scoloplos papillatus new species

Figures 15–17

urn:lsid:zoobank.org:act:DF1B8B75-38BE-4841-8452-13DCF90DD7AB

Material examined. (*36 specimens*) **Southeastern USA, off Cape Hatteras, North Carolina, MMS Cape Hatteras Survey,** coll. J.A. Blake, Chief Scientist, R/V *Endeavor.* **Sta. CH-3**: Aug 1992, 35°37.08′N, 74°46.12′W, 812 m, **holotype** (USNM 1621017) and 17 **paratypes** (USNM 1621018). **Sta. SA-9**: Sep. 1992, 35°28.36′N, 74°41.26′W, 620 m, 18 **paratypes** (USNM 1621019).

Description. A large, elongate species; thoracic segments dorsoventrally flattened, often with middle thoracic segments swollen dorsally, likely from location of internal retracted pharynx; abdominal segments ventrally rounded, dorsally flattened with elevated parapodia. Shallow ventral groove present along entire body on most specimens; dorsal grooves and ridges absent. Holotype complete, coiled, with 182 setigers, 45 mm long, 1.8 mm across thorax; with 17 thoracic setigers and branchiae from setiger 14 (Fig. 17A). Large incomplete paratype (USNM 1621018), with 180 setigers, 37 mm long, 2.1 mm wide across thorax; with 18 thoracic setigers and branchiae from setiger 14 (Fig. 17B). Transition from thorax to abdomen abrupt, denoted by appearance of elongate and enlarged neuropodia, simple at first, becoming longer and with apex split over successive segments. Thoracic segments short, about five times wider than long. Color in alcohol light tan; dorsum of abdominal segments between branchiae with 1–3 medial dorsal brown pigment spots in intersegmental swelling (Fig. 17D arrows), this distinctive pigment conspicu-

ous on large specimens; large subpodial flanges of middle and posterior abdominal neuropodia often with darkly pigmented internal glands.

Pre-setiger region relatively short, slightly wider than long, triangular, overall as long as first two setigers (Fig.15A). Prostomium conical, tapering to pointed tip; nuchal organs vertical curved slits on posterior lateral margin; eyespots absent. Peristomium slightly longer than first setiger, with a single smooth annular ring dorsally (Fig. 15A), surrounding mouth ventrally, forming upper and lower lips; upper lip in two parts each with numerous narrow lobes (Fig. 15B–C); lower lip with an equivalent number of narrow lobes.

Anterior thoracic notopodia with digitiform postsetal lobe, short at first (Fig. 15D), then becoming longer, narrow in posterior thoracic segments (Fig. 15E); each notopodial lobe arising from a thick base. Thoracic neuropodia initially with a shorter, thick postsetal lobe arising from a broadly rounded base (Fig. 15D); posterior thoracic neuropodia developing short postsetal lobe and a short subpodial papilla ventral to neuropodium (Fig. 15E). Transition to abdominal segments abrupt, with fewer noto- and neurosetae. Abdominal notopodial postsetal lobes becoming narrow and elongate along rest of body (Fig. 16A–C); abdominal neuropodia narrow, divided apically into two parts separated by notch; medial lobe long, pointed; ventral lobe shorter, rounded apically, directed laterally, appearing as ventral cirrus (Fig. 16A–C). Interramal cirrus absent. Each abdominal neuropodium with narrow subpodial flange (Figs. 16B–C, 17E); with one subpodial papilla on anterior abdominal segments (Figs. 16A, 17C). Subpodial flanges of middle and posterior abdominal setigers with numerous internal glands; these darkly pigmented on many specimens (Fig. 16C).

Branchiae from posterior thoracic setiger 13 or 14 (Fig. 15A); branchia short, narrow at first, becoming leaflike, longer, and full size by first abdominal segment; each anterior branchiae broad, tapering to narrow papillate tip (Fig. 16A); a few anterior abdominal branchiae bifid, with a second apical papilla (Fig. 16A inset). Branchiae of middle and posterior setigers becoming longer, triangulate, rarely asymmetrical (Fig. 16B–C). Each branchia ciliated along lateral and medial margins.

Thoracic notosetae numerous thick, long, camerated capillaries arranged in 4–5 rows. Thoracic neurosetae arranged in about five rows with similar appearing camerated capillaries and 5–10 uncini alternating with capillaries in second row; uncini occurring over first 7–10 setigers, becoming reduced to 3–4 uncini in lower part of setal fascicle; then either absent or not observed in later thoracic setigers. Individual uncini with shafts smooth on convex side, tapering to narrow, rounded tip; concave side of shaft flattened, bearing paired transverse knobs or barbs along most of shaft (Fig. 15F–G). Abdominal notosetae thin, camerated capillaries and 1–2 furcate setae. Furcate setae with unequal tynes, each tyne with blunted tip and apical notch; shaft with rows of transverse barbs or ridges; tynes with a row of thin needles extending medially (Figs. 15H, 17G). Abdominal neurosetae with up to 4–5 thin capillaries, each with short barbs along one edge and 1–2 curved aciculae, sometimes protruding, with rounded tip (Fig. 16A insets). Flail setae not observed.

Pygidium short, with about ten narrow dorsal lobes, two large lateral lobes, and a single large ventral lobe surrounding anal opening; with two short dorsal anal cirri arising dorsally (Figs. 16D, 17F).

Remarks. Among species of *Scoloplos* along the U.S. Atlantic coast having a reduced number of uncini in thoracic neuropodia, *S. papillatus* **n. sp**. from upper slope depths is most similar to *S. verrilli* **n. sp.**, (see below) a common species in New England near-shore shelf sediments. The two species are similar in size (up to 42–45 mm long) and number of setigers (about 180–200). *S. papillatus* **n. sp**. has 17–18 thoracic setigers whereas *S. verrilli* **n. sp**. has 16–17 thoracic setigers; both species have branchiae from setigers 13–14. Obvious differences are in the development of extra podial lobes in posterior thoracic setigers: *S. papillatus* **n. sp**. develops both a subpodial lobe and subpodial papillae ventral to the neuropodium, whereas *S. verrilli* **n. sp**. develops a second postsetal lobe on the neuropodium and a subpodial lobe. There also appear to be differences in the nature of the upper lip of the mouth: in *S. papillatus* **n. sp**., the upper lip is divided into two parts, each of which has numerous narrow lobes; in *S. verrilli* **n. sp**., the upper lobe is formed into two large, relatively smooth lobes that do not appear to be further divided. The most conspicuous difference between the two species, however, is that *S. papillatus* **n. sp**. has 1–3 medial brown pigment spots in dorsal intersegmental swelling in abdominal segments, whereas in *S. verrilli* **n. sp**. the intersegmental areas are neither swollen nor pigmented.

Scoloplos papillatus **n. sp**. is also similar to *S. californiensis* Blake, 2020 from deep water off California and *S. sparsaciculus* Blake, 2020 from deep water in the South China Sea in having a reduced number of uncini in the thoracic neuropodia. Both of the two latter species have an extra subpodial lobe, but this is only present in anterior abdominal segments, whereas *S. papillatus* **n. sp**. also has an extra subpodial lobe on posterior thoracic setigers.

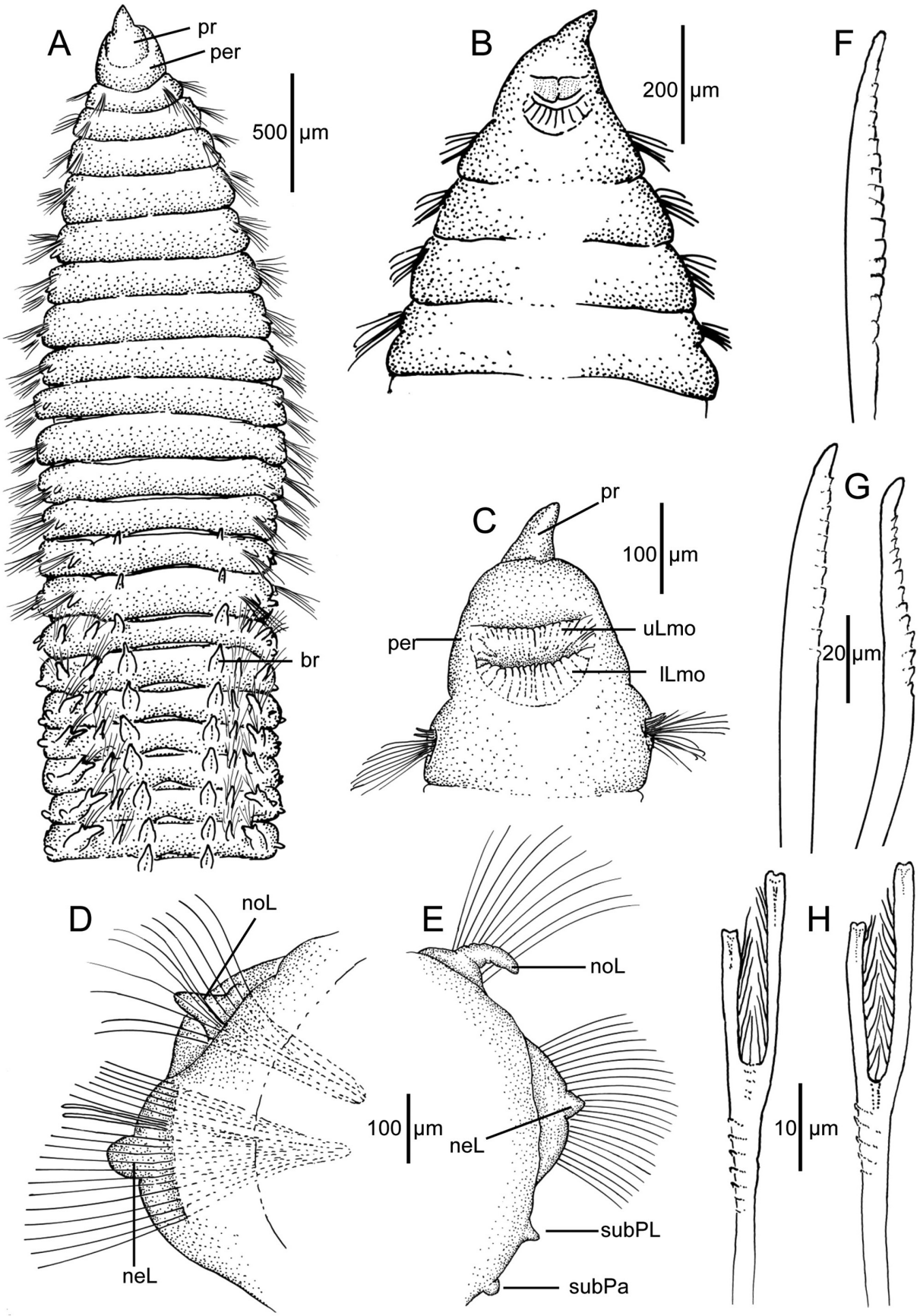

FIGURE 15. *Scoloplos papillatus* **n. sp**. Paratype (USNM 1621019): A, anterior end, dorsal view; B, anterior end, ventral view; C, pre-setiger region, ventral view; D, thoracic setiger 7, anterior view; E, thoracic setiger 15, posterior view; F–G, thoracic neuropodial uncini; H, furcate setae.

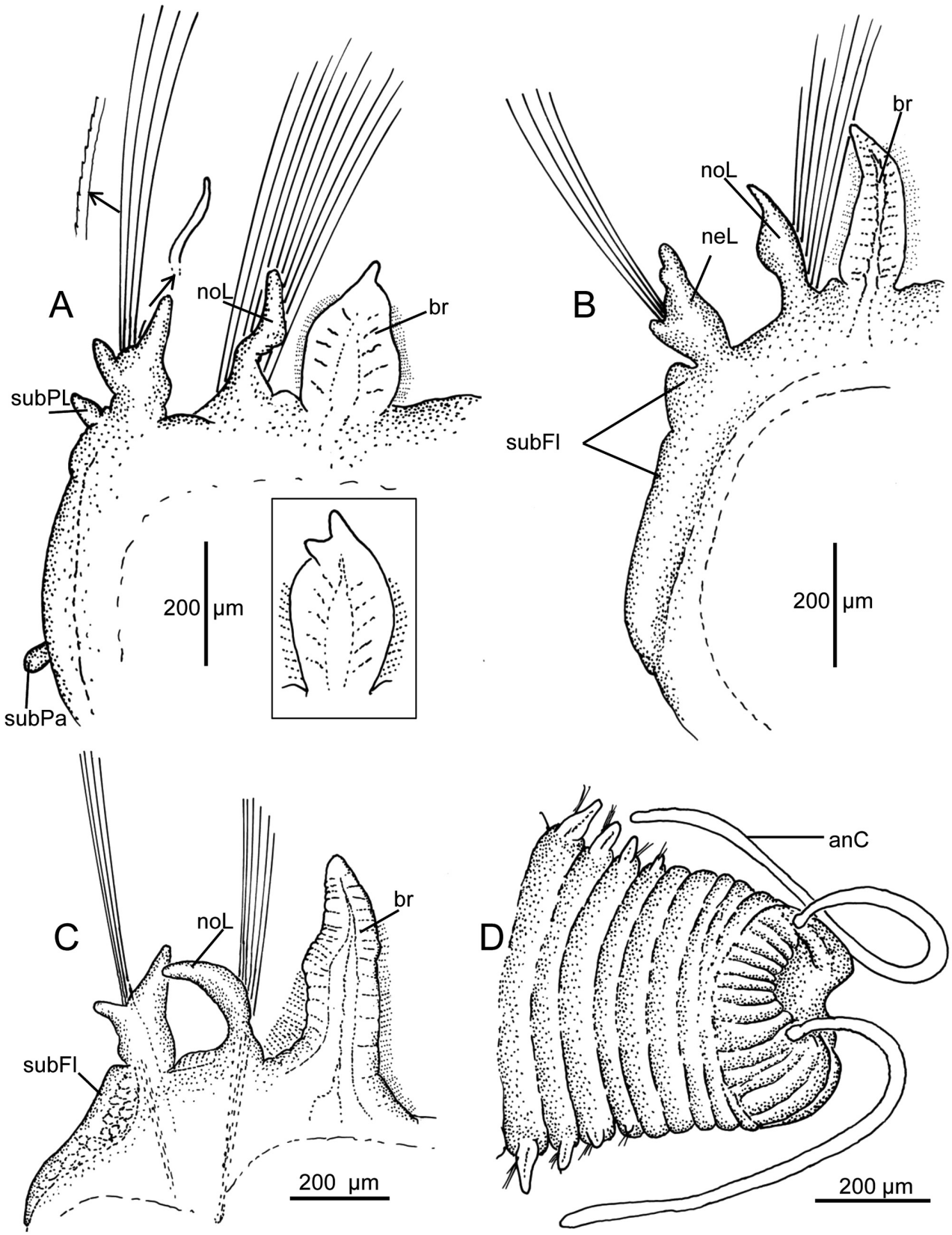

FIGURE 16. *Scoloplos papillatus* **n. sp**. A, anterior abdominal setiger, posterior view with inset showing separate branchia with bifid tip; B, middle abdominal setiger, posterior view; C, far posterior abdominal setiger, posterior view; D, posterior end with pygidium, dorsal view. A–C, paratype (USNM 1621018); D, holotype (USNM 1621017).

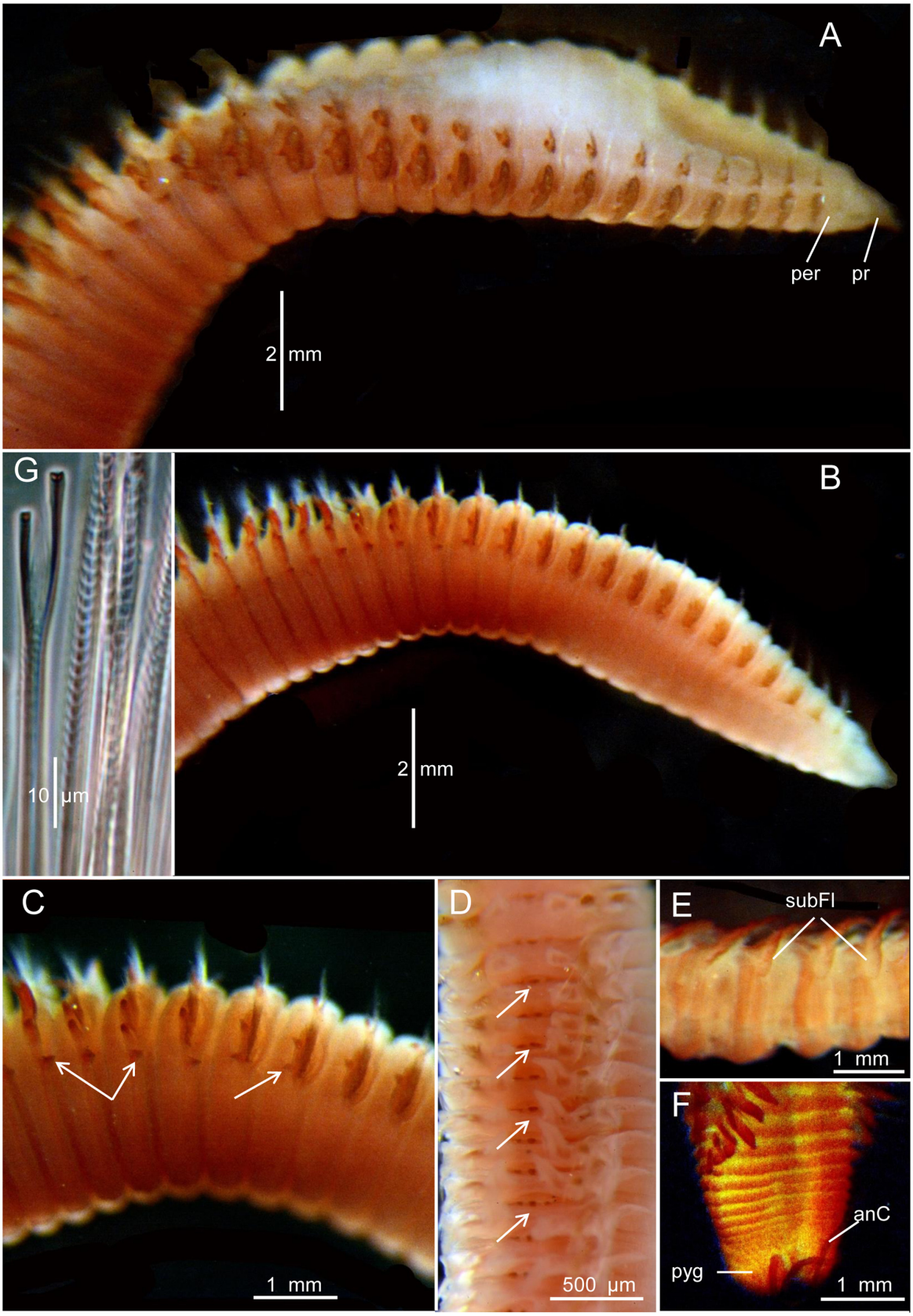

FIGURE 17. *Scoloplos papillatus* **n. sp**. A, anterior end of holotype, dorsolateral view; B, anterior end of paratype ventrolateral view; C, furcate notoseta and camerated capillaries, abdominal setiger; D, anterior abdominal segments dorsal view with pigmented interramal swellings denoted with arrows; E, middle abdominal segments, lateral view; F, posterior end and pygidium. A, D–F, holotype, (USNM 1621017); B–C, G paratype, (USNM 1621018). A–F stained with Shirlastain A.

S. papillatus **n. sp**. has 17–18 thoracic setigers and branchiae from setigers 13–14, whereas *S. californiensis* has 12 thoracic setigers and branchiae from setigers 11–12.

Biology. The upper continental slope off Cape Hatteras, North Carolina, where *Scoloplos papillatus* **n. sp**. was discovered is unusual in having high infaunal densities of 24,055 to 61,244 (mean = 46,255) individuals per m^2 (Blake & Hilbig 1994). The fauna is dominated by polychaetes such as *Scalibregma inflatum* Rathke, 1843, *Cossura longocirrata* Webster & Benedict, 1887, and *Aricidea quadrilobata* Webster & Benedict, 1887, species that are more typical of shelf depths. Rhoads & Hecker (1994) found that organic matter in the Cape Hatteras sediments is a mixture of both marine and terrestrially derived carbon that is more typical of continental shelf sediments, suggesting that the high percentage of refractory organic matter favors the survival of preadapted shelf species over those from adjacent slope environments.

Etymology. Latin, for *papilla*, a nipple or bud, referring to the subpodial papillae that occur on upper and lower margins of the subpodial flanges of this species.

Distribution. Off Cape Hatteras, North Carolina, upper continental slope, 620–812 m.

Scoloplos pettiboneae new species

Figures 18–20

urn:lsid:zoobank.org:act:A50E6B37-2447-41C9-95C9-BD6B9A5F901A

Scoloplos acmeceps: Maciolek-Blake *et al*. 1985: B-5; Blake *et al*. 1998: C-1, C-2. **Not** Chamberlin 1919a.

Material examined. (*132 specimens*) **Northeastern USA, Georges Bank, Benthic Infauna Monitoring Program (1981–1985)**, coll. G.W. Hampson, Chief Scientist. **Sta. 5-11**: Cruise M3, R/V *Endeavor*, Rep. 1, 16 Feb 1982, 40°39.2′N, 67°46.6′W, 81 m, **holotype** (USNM 1621020). **Sta. 5-**1: Cruise M-14, R/V *Gyre*, Rep. 4, 26 Nov 1985, 40°39.44′N, 67°46.03′, 76 m (1 juvenile, USNM 1622338). **Sta. 5-3**: Cruise M4, R/V *Cape Henlopen*, Rep. 1, 14 May 1982, 40°39.8′N, 67°46.1′W, 84 m, 1 **paratype** (USNM 1621021). **Sta. 5-4**: Cruise M4, R/V *Cape Henlopen*, Rep. 4, 14 May 1982, 40°39.5′N, 67°46.5′W, 80 m (4, USNM 1621022). **Sta. 5-5**: Cruise M2, R/V *Oceanus*, Rep. 4, 19 Nov 1981, 40°39.3′N, 67°46.2′W, 81 m, 1 **paratype** (USNM 1621023); Cruise M6, R/V *Oceanus*, Rep. 3, 23 Nov 1982, 40°39.3′N, 67°46.2′W, 79 m, 2 **paratypes** (USNM 1621024). **Sta. 5-18**: Cruise M2, R/V *Oceanus*, Rep. 4, 18 Nov 1981, 40°39.6′N, 67°47.6′W, 80 m, 1 **paratype** (USNM 1621025); Cruise M3, R/V *Endeavor*, Rep. 6, 15 Feb 1982, 40°39.6′N, 67°47.6′W, 82 m (11, USNM 1621026). **Sta. 5-29**: Cruise M3, R/V *Endeavor*, Rep. 1, 15 Feb 1982, 40°39.5′N, 67°50.4′W, 85 m (1, USNM 1621027); Cruse M4, R/V Cape *Henlopen*, Rep. 5, 24 Nov 1982, 40°39.5′N, 67°50.4′W, 83 m, 1 **paratype** (USNM 1621028). **Sta. 5-25**: Cruise M1, R/V *Eastward*, Rep. 6, Jul 1981, 40°39.4′N, 67°46.9′W, 80 m (3, USNM 1621029); Cruise M4, R/V *Cape Henlopen*, Rep. 5, 19 May 1982, 40°39.5′N, 67°49.0′W, 82 m (4, USNM 1621030). **Sta. 3**: Cruise M3, R/V *Endeavor*, Rep. 3, 18 Feb 1982, 66°53.7′N, 66°46.5′W, 97 m, 8 **paratypes** (USNM 1621031); Cruise M4, R/V *Cape Henlopen*, Rep. 1, 12 May 1982, 40°53.7′N, 66°46.5′W, 90 m (7, USNM 1621032); Rep. 3, 4 **paratypes** (USNM 1621033); Cruise M5, R/V *Oceanus*, Rep. 1, 24 Jul 1982, 40°34.3′N, 67°45.3′W, 92 m, 8 **paratypes** USNM 1621034); Rep. 3 (14, USNM 1621035); Cruise M6, Rep. 3, 22 Nov 1982, 40°34.3′N, 67°45.3′W, 98 m, 10 **paratypes** (USNM 1621036); Rep. 5, 10 **paratypes** (USNM 1621037). **Sta. 6**: Cruise M6, R/V *Oceanus*, Rep. 1, 22 Nov 1982, 40°34.3′N, 67°45.3′W, 98 m (3, USNM 1621038). **Sta. 12**: Cruise M2, R/V *Oceanus*, Rep. 4, 12 Nov 1981, 40°22.2′N, 68°30.2′W, 105 m (5, USNM 1621039). **Sta. 13**: Cruise M5, R/V *Oceanus*, Rep. 5, 28 Jul 1982, 40°29.5′N, 70°12.6′W, 62 m (5, USNM 1621040). **Sta. 18**: Cruise M2, R/V *Oceanus*, Rep. 3, 18 Nov 1981, 40°33.5′N, 67°13.7′W, 150 m, 8 **paratypes** (USNM 1621041).—**Massachusetts Bay, MWRA Harbor and Outfall Monitoring Program. 1992 August Survey: Sta. NF-17**, 42°22.88′N, 70°48.89′W, 29 m (10, MCZ 161599). **1996 August Survey: Sta. NF-19**, 42°22.30′N, 70°48.30′W, 32 m (7, MCZ 161600). **Sta. NF-24**, Rep. 1, 42°22.83′N, 70°48.10′W, 37 m (1, MCZ 161601). **Sta. MF-4**, 42°24.93′N, 70°48.39′W, 36 m (1, MCZ 161602). **Sta. MF-7**, 42°24.60′N, 70°48.89′W, 33 m (1, MCZ 161603). **Sta. MF-8**, 42°24.00′N, 70°51.81′W, 30 m (5, MCZ 161604). **Sta. MF-9**, 42°23.99′N, 70°50.69′W, 29 m (2, MCZ 161605). **Sta. MF-20**, 42°22.69′N, 70°50.69′W, 28 m (1, MCZ 161606). **Sta. FF-1A**, Rep. 2, 42°33.84′N, 70°40.55′W, 32 m (1, MCZ 161607). **Sta. FF-9**, Rep. 2, 42°18.75′N, 70°39.40′W, 49 m (2, MCZ 161608). **1997 August Survey**: **Sta. MF-12**, Rep. 3, 42°23.40′N, 70°49.83′W, 34 m (1, MCZ 161609). **Sta. FF-9**, Rep. 2, 42°18.75′N, 70°39.40′W, 49 m (1, MCZ 161610); Rep. 3 (1, MCZ 616611). **Sta. FF-12**, Rep. 2, 42°23.40′N, 70°53.98′W, 22 m (1, MCZ 161612).

Comparative material examined. **California, Tomales Bay**, Pelican Point, coll. 15 Aug 1952, Pacific Marine Station, intertidal, 4 specimens of *Scoloplos acmeceps* Chamberlin, 1919a (JAB).

Description. A moderate to large species; thorax broad, with segments about five times wider than long; generally flattened across both dorsal and ventral surfaces; abdominal segments ventrally rounded, dorsally flattened, with elevated parapodia; middle and posterior segments numerous, short, and crowded. Shallow ventral groove present on few thoracic segments or absent; dorsal longitudinal grooves and ridges absent. Holotype complete, with 115 setigers, 30.1 mm long, 0.8 mm wide across thorax; with 17 thoracic segments and branchiae from setiger 14. Paratype (USNM 1621037) with 102 setigers, 20 mm long, 0.7 mm across 17-setiger thorax; branchiae from setiger 13. Color in alcohol light tan. Middle thoracic setigers and a few anterior abdominal setigers with transverse band of glands across middle of dorsal and ventral surfaces of individual segments (Figs. 18A, 19A–B); these glands retaining pink color of Rose Bengal applied during the benthic sorting process and staining darkly with Shirlastain A. Subpodial flanges of abdominal segments also stain prominently due to dense concentrations of internal glands (Figs. 18E–F; 19C).

Pre-setiger region elongate, triangular, about as long as first three setigers (Figs. 18A–C, 19A). Prostomium long, narrowing to acutely pointed apex (Fig. 18A–C); nuchal organs elongate grooves on posterior lateral margins (Fig. 18C); eyespots absent. Peristomium a single ring, shorter than first setiger, smooth on dorsal surface, ventrally with a row of short lobes forming the posterior lip of mouth; dorsal lip a smooth surface without lobes (Fig. 18B–C); proboscis rarely everted, one paratype (USNM 161682) with proboscis with three thick rounded lobes.

Thoracic notopodia triangular, short at first, with postsetal lobe becoming longer in posterior thoracic segments (Fig. 18D); each notopodial lobe arising from a thick base. Thoracic neuropodia fleshy, enlarged and rounded, with short nipple-like postsetal lobe (Fig. 18D–E); subpodial papillae absent. Transition from thorax to abdomen generally abrupt due to appearance of elongated neuropodium with fewer setae and development of two unequal apical neuropodial lobes (Fig. 18E). Interramal cirri absent, but short interramal process or protuberance present between noto- and neuropodia of abdominal segments (Fig. 18E). Last one or two thoracic neuropodia with a subpodial lamella that transitions into prominent subpodial flange of abdominal segments.

Branchiae from posterior thoracic setiger, usually setiger 13 or 14 in larger specimens (Fig. 18A); branchiae narrow, short at first, becoming longer but still narrow, with rounded apex through middle abdominal segments (Fig. 18E); branchiae of posterior segments also narrow, but tapering to somewhat pointed apex (Fig. 18F); all branchiae heavily ciliated on medial and lateral margins (Fig. 18E–F).

Thoracic notosetae numerous thick, long, camerated capillaries arranged in 3–4 rows. Thoracic neurosetae arranged in up to five rows with first three rows consisting of numerous short uncini and posterior rows of camerated capillaries (Fig. 18D). Individual uncini with shafts tapering to rounded tip; concave side of shaft with rows of barbs (Figs. 18G–I, 19D–E); convex side of shaft with narrow thickened hood on some uncini (Figs. 18G–H, 19E); this hood prominent on some setae. Abdominal notosetae thin, camerated capillaries and 1–2 furcate setae. Furcate setae with unequal tynes; each tyne with blunted tip and apical notch, with row of thin needles extending medially (Figs. 18J, 19F). Abdominal neurosetae with up to 4–5 thin capillaries each with short barbs along one edge and 1–2 curved aciculae, sometimes protruding, with rounded tip. Flail setae not observed.

Pygidium short, with two rounded dorsal lobes, two large lateral lobes and a single large ventral lobe surrounding anal opening; with two long, thin anal cirri arising dorsally (Fig. 19G).

Juvenile morphology. Juveniles of this species were initially thought to belong to the genus *Schroederella*, originally established for small interstitial or meiofaunal orbiniids found in intertidal sand beaches (Laubier 1962, 1971; Badalamenti & Castelli 1991, but see above for *L. acutus*). However, several of the distinctive characters of *Scoloplos pettiboneae* **n. sp.** were found on these juveniles, thus establishing their identity as this species. Study of the juveniles allowed some aspects of juvenile morphology to be documented; however, a complete growth sequence was not established. A specimen from Georges Bank (USNM 1622338) was examined in detail and is described here.

Specimen long, narrow, threadlike, complete with 41 setigers, 5.5 mm long, 0.25 mm wide across thoracic region (Fig. 20A). Color light tan, with distinct glandular bands present dorsally on anterior setigers (Fig. 20A).

Prostomium long, triangular, acutely pointed (Fig. 20A–B); eyespots absent; nuchal organs not observed. Peristomium with two achaetous rings, not well separated from one another (Fig. 20A–B); anterior dorsal border with prostomium weakly sculpted; ventrally obscured by upper lip of mouth. Upper lip of mouth with two large lobes; lower lip with broad border, lobes not well developed at this stage (Fig. 20B).

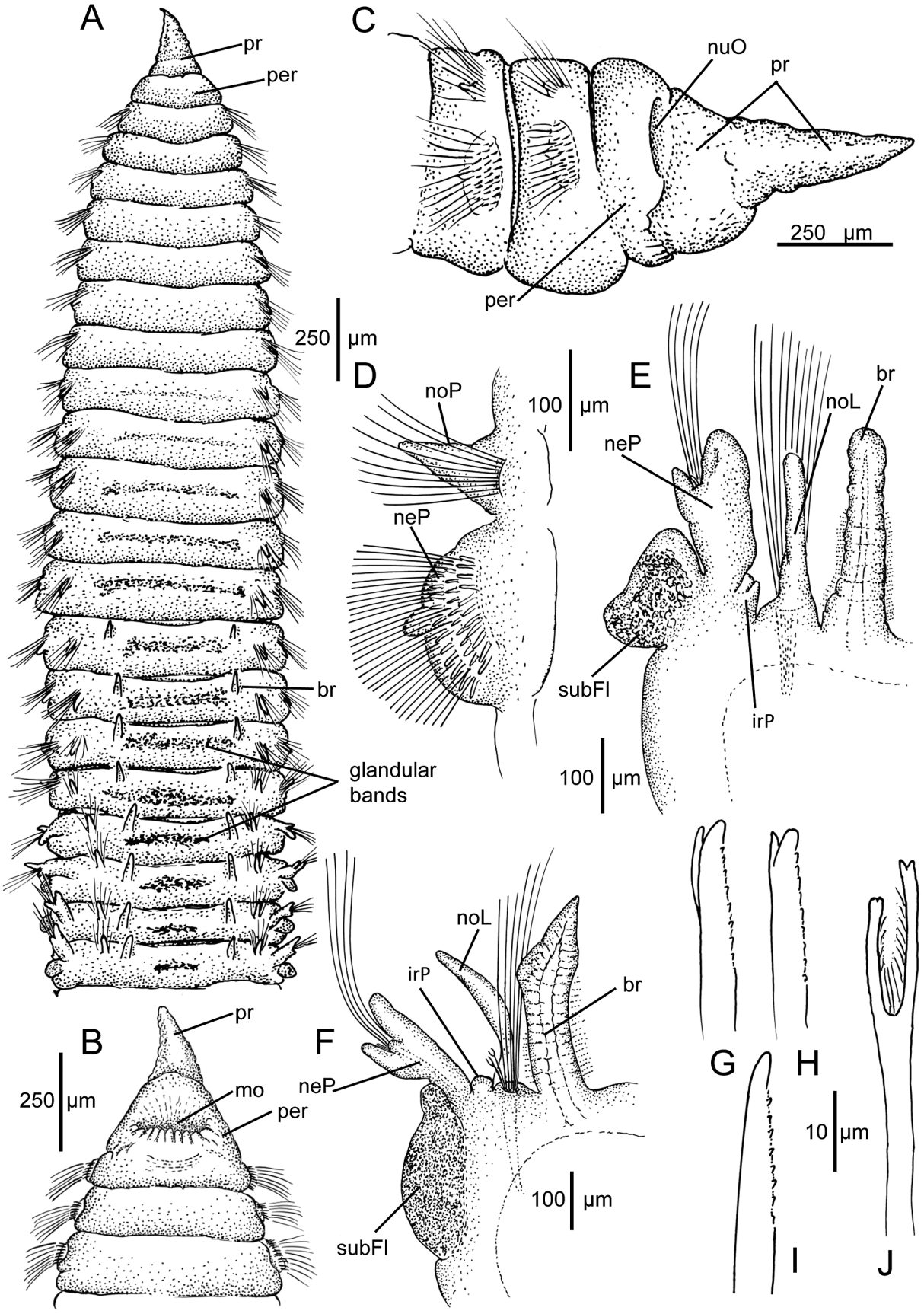

FIGURE 18. *Scoloplos pettiboneae* **n. sp**. Paratypes (USNM 1621021): A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end, right lateral view; D, thoracic setiger 10, anterior view; E, anterior abdominal setiger, posterior view; F, posterior abdominal setiger, anterior view; G–I, thoracic neuropodial uncini; J, furcate seta.

Thorax with nine setigers, slightly wider than abdominal segments through setiger 7, then narrowing, entire body thin and fragile throughout. Branchiae from setiger 10, narrow, arising near base of notopodia. Thoracic setigers short, about three times wider than long (Fig. 20A–B); abdominal segments becoming long, narrow (Fig. 20C), then short again in far posterior setigers.

Thoracic notopodia initially short, papillate, increasing in length and becoming digitiform by about setiger 4–5; abdominal notopodia long and narrow. Thoracic neuropodia similar to notopodia; abdominal neuropodia with thickened base with two apical lobes, ventral lobe longer, narrower than dorsal lobe (Fig. 20D). Neuropodia with short, glandular subpodial flange (Fig. 20D). Subpodial papillae absent. Interramal processes not evident at this stage, but some parapodia with rounded folds between abdominal noto- and neuropodia.

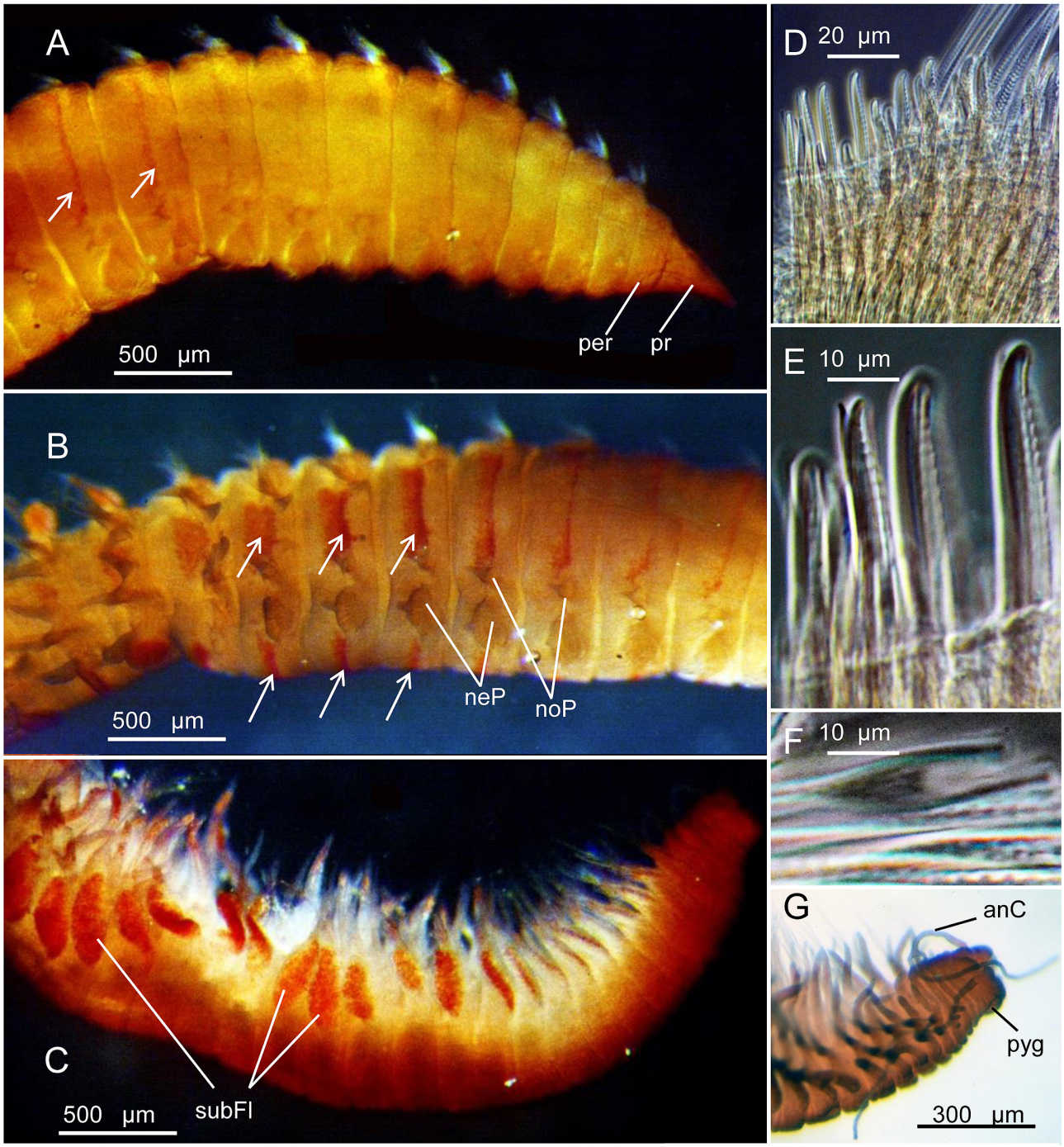

FIGURE 19. *Scoloplos pettiboneae* **n. sp.** A, anterior end, right lateral view (arrows denote glandular bands); B, same, transition from thorax to abdomen (arrows denote glandular bands); C, posterior abdominal segments; D, rows of thoracic neuropodial uncini; E, details of thoracic neuropodial uncini; F, abdominal notopodial furcate seta and capillaries; G, far posterior setigers and pygidium. A–C, G, holotype (USNM 1621020); D–F, paratype (USNM 1621021). A–C, G stained with Shirlastain A.

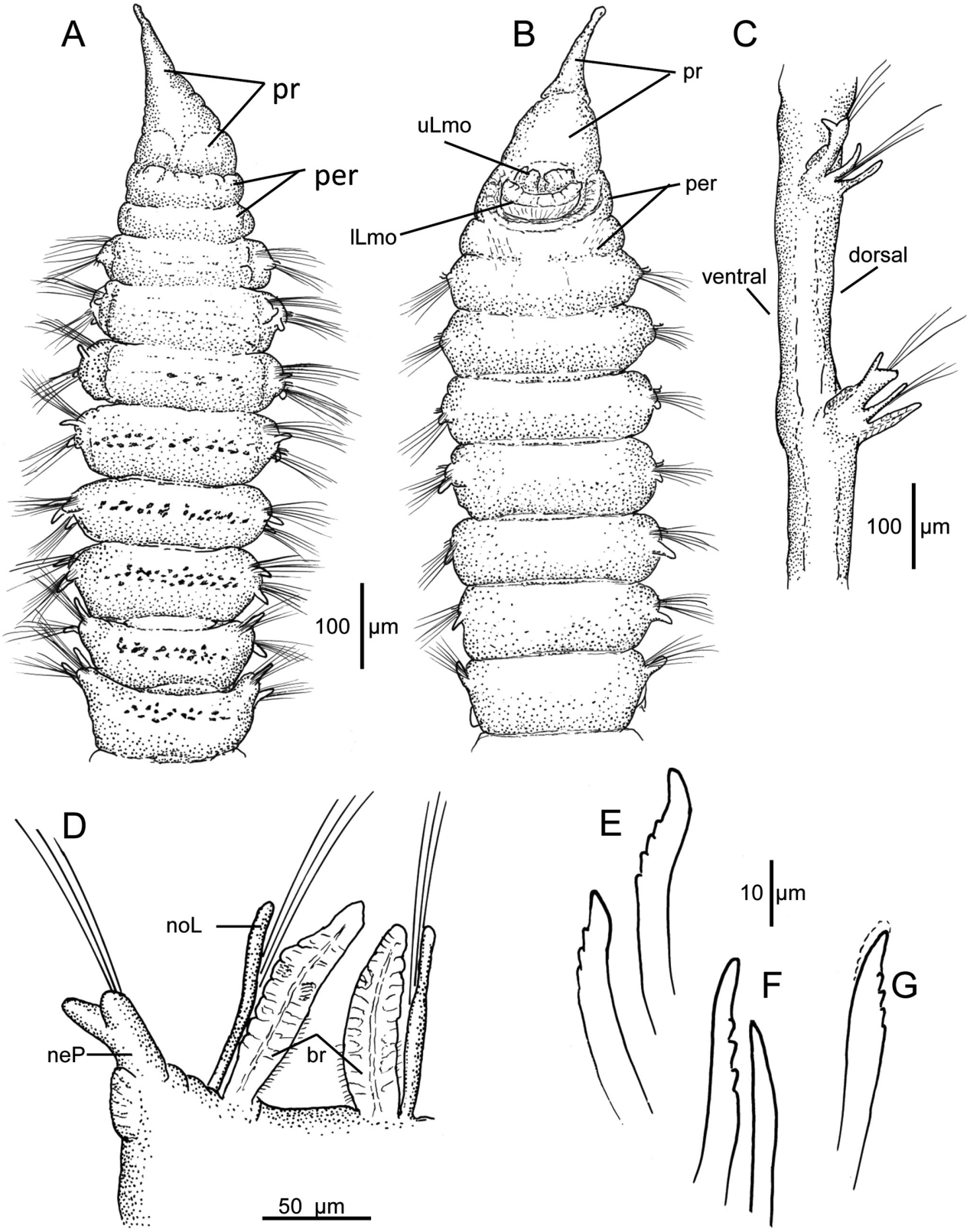

FIGURE 20. *Scoloplos pettiboneae* **n. sp.** Juvenile morphology (USNM 1622338): A, anterior end, dorsal view; B, anterior end, dorsal view; C, middle abdominal setiger, lateral view; D, setiger 30 (abdominal), posterior view; E–G, thoracic neuropodial uncini.

Thoracic notosetae 4–6 camerated capillaries; abdominal notosetae 3–4 camerated capillaries and one furcate seta. Thoracic neurosetae consisting of two rows of 3–4 uncini and 6–10 long, camerated capillaries. Uncini with 3–4 short ribs on concave side of shaft, shaft tapering to narrow rounded apex (Fig. 20E–G); some uncini lacking ribs (Fig. 20F); uncini not observed on last 2–3 thoracic setigers. Abdominal neurosetae with 2–3 capillaries, these smooth, barbs not observed; a short thin sharply pointed acicula present.

Pygidium with two anal cirri.

Variability. Larger specimens typically have 16–17 thoracic setigers and branchiae from setigers 13 or 14. However, smaller specimens such as a complete paratype (USNM 1621037) have 56 setigers, is 7.0 mm long with 11 thoracic setigers and branchiae from setiger 10. The juvenile reported above measures 5.5 mm long with 9 thoracic setigers and branchiae from setiger 10.

All specimens, juvenile or adult, have an unusually long, narrow, pointed prostomium; distinct glandular bands across the dorsum; short, glandular subpodial flanges; and at least some evidence of interramal processes in abdominal setigers. Ventral bands of glands are prominent in adults but are not well developed in juveniles. The juvenile has two peristomial rings that are merged in the adults. This same pattern where the two peristomial rings of postlarvae and juveniles merge and produce a single peristomial ring in adults has been reported for species of *Naineris* (Okuda 1946; Blake 1980, 2000; Giangrande & Petraroli 1991). This is the first report of such a peristomial change in a species of *Scoloplos*.

Remarks. *Scoloplos pettiboneae* **n. sp.** is a distinctive species along the U.S. Atlantic coast in having an unusually long, narrowly pointed prostomium and the absence of any extra subpodial lobes or papillae associated with the posterior thoracic or abdominal setigers. The species has a short interramal dorsal process or protuberance, but no cirrus, between the noto- and neuropodia of abdominal segments and has prominent dorsal and ventral glandular bands on the middle and posterior thoracic setigers and dorsal patches that continue on to a few anterior abdominal segments; these glands and associated bands stain with Rose Bengal and Shirlastain A. *Scoloplos pettiboneae* **n. sp.**, like many other orbiniids, has prominent subpodial flanges, but in this species the flanges are thin and short, with numerous glands that stain with Rose Bengal and Shirlastain A and that appear as flaps along anterior and posterior abdominal segments.

Scoloplos pettiboneae **n. sp.** is most similar to *S. acmeceps* Chamberlin, 1919a from the U.S. Pacific coast. Several specimens of *S. acmeceps* from low intertidal sediment in Tomales Bay, California, were examined and compared with *S. pettiboneae* **n. sp.** *Scoloplos acmeceps* is a larger species with up to 200 segments and 150 mm long according to Hartman (1957). The Tomales Bay specimens are shorter, with about 180 segments and 50 mm long. They exhibit thin glandular bands dorsally and ventrally across the thorax as in *Scoloplos pettiboneae* **n. sp.**, but the bands are not as prominent and do not retain stain. In addition, the subpodial flanges of *S. acmeceps*, while thin, are not glandular and do not retain stain. The short interramal process observed in *S. pettiboneae* **n. sp.** is not present on the Tomales Bay specimens of *S. acmeceps* and is not reported or illustrated by Hartman (1957). Interestingly, the last thoracic segment (19) of the Tomales Bay specimens is transitional in having a semicircular subpodial flange that continues as the more elongate flanges of the abdominal segments. This is the same pattern described here for *S. pettiboneae* **n. sp.** and has not been previously reported for *S. acmeceps* and further supports the similarity between the two species.

Etymology. This species is named for the late Dr. Marian H. Pettibone, in recognition of her studies of the polychaete fauna of New England and revisionary work on the Orbiniidae.

Distribution. Off New England, Massachusetts Bay 29–45 m; Georges Bank, 62–150 m.

Scoloplos pseudoarmiger **new species**

Figures 21–24

urn:lsid:zoobank.org:act:F61D4F4C-B4C4-486F-8234-64EF1EE566C8

Scoloplos armiger: Maciolek-Blake *et al*. 1985: B-5; Blake *et al*. 1998: C-1, C-2 (in part). **Not** Müller 1776.

Material examined. (*21 specimens*) **Northeastern USA, Georges Bank**, **Benthic Infauna Monitoring Program (1981–1984)**, coll. G.W. Hampson, Chief Scientist. **Sta. 10**: Cruise M12, R/V *Gyre*, Rep. 6, 03 Jun 1984, 40°42.0′N, 68°35.3′W, 66 m, **holotype** (USNM 1620928). **Sta. 1**: Cruise M4, R/V *Cape Henlopen*, Rep. 1, 12

May 1982, 41°13.0′N, 67°15.3′W, 58 m, 1 **paratype** (USNM 1620929). Cruise M5, R/V *Oceanus*, Rep. 6, 22 Jul 1982, 41°13.0′N, 67°15.3′W, 53 m (1, USNM 1620930); Cruise M8, R/V *Gyre*, Rep. 3, 15 May 1983, 41°13.0′N, 67°15.3′W, 57 m, 1 **paratype** (USNM 1620931); Cruise M10, R/V *Oceanus*, Rep. 3, 15 Nov. 1983, 41°13.0′N, 67°15.3′W, 55 m (1, USNM 1620932). **Sta. 4**: Cruise M6, Rep. 6, 22 Nov 1982, 40°50.7′N, 68°00.2′W, 65 m (1, USNM 162939); Cruise M8, R/V *Gyre*, Rep. 3, 19 May 1983, 40°50.7′N, 68°00.2′W, 66 m, 1 **paratype** (USNM 1620933); Cruise M11, R/V *Oceanus*, Rep. 1, 02 Feb 1984, 40°50.7′N, 68°00.2′W, 67 m (1, USNM 1620934); Cruise M12, R/V *Gyre*, Rep. 4, 04 Jun 1984, 41°13.0′N, 67°15.3′W, 55 m, 1 **paratype** (USNM 1620935). **Sta. 10**: Cruise M2, R/V *Oceanus*, Rep. 5., 12 Nov. 1981, 40°42.0′N, 68°35.3′W, 60 m,1 **paratype** (USNM 1620936); Cruise M12, R/V *Gyre*, Rep. 4, 03 Jun 1984, 40°42.0′N, 68°35.3′W, 66 m, 1 **paratype** (USNM 1620937). **Sta. 5-29**: Cruise M6, R/V *Oceanus*, Rep. 2, 24 Nov 1982, 40°39.5′N, 67°50.4′W, 81 m, 1 **paratype** (USNM 1620938).—**Massachusetts Bay**, **MWRA Harbor & Outfall Monitoring Program. 1996 August Survey: Sta. NF 13**, Rep. 1, 42°23.40′N, 70°49.35′W, 33 m (1, MCZ 161613).

Description. A moderate to large, elongate species; thoracic segments dorsoventrally flattened, abdominal segments ventrally rounded, dorsally flattened, with elevated parapodia; abdominal segments flattened dorsally, rounded ventrally. Shallow mid-dorsal groove present in thoracic segments; narrow mid-ventral groove present along most of body. Holotype complete, with 172 setigers, 31.3 mm long and about 0.8 mm wide across dorsum of thorax; thorax with 20 setigers and branchiae from setiger 16 (Fig. 23B). Other specimens with 16–20 thoracic segments and branchiae from setigers 13–16 (Fig. 21A). Smaller specimens (<25 mm long) with fewer thoracic setigers and earlier start of branchiae. Transition from thorax to abdomen gradual, with last defined thoracic setiger lacking uncini; subsequent setigers transitioning with neuropodium becoming enlarged and reduced number of capillaries. Body segments uniannulate in thoracic region, becoming biannulate in abdominal segments, with each parapodium separated from following one by a wide intersegmental band (Fig. 23F). Color in alcohol light tan; subpodial flanges of most abdominal neuropodia glandular, darkly pigmented (Figs. 22C–D, 23F).

Pre-setiger region narrow, triangular, as long as first three setigers (Figs. 21A–C, 23A–B, D). Prostomium long, divided into anterior and posterior sections (Fig. 21A–C), with narrow anterior section tapering to pointed tip, separated laterally and ventrally from larger posterior section bearing nuchal organs as semi-circular slits on posterior lateral margin and anterior to mouth ventrally (Fig. 21B–C); eyespots absent. Peristomium a single ring, with lateral groove (Fig. 21B), about as long as first setiger; smooth dorsally, surrounding mouth ventrally, forming upper and lower lips (Fig. 21C); upper lip of mouth with two thickened transverse lobes; lower lip with about seven narrow elongate lobes. Holotype with proboscis everted, consisting of two rounded lobes (Fig. 23B, D). Lower lip of mouth extending mid-ventrally onto setiger 1 (Fig. 21C).

Anteriormost 3–4 thoracic notopodia with no apparent postsetal lobe; from about setiger 5–6 a short, broadly triangular but low postsetal lobe appears (Fig. 22A), continuing to about setiger 13–14, thereafter lobe lengthening, becoming digitiform, arising from narrow base (Fig. 22B), continuing onto abdominal setigers. Thoracic neuropodia with low, broadly rounded base; first 3–4 thoracic neuropodia with no apparent postsetal lobe; from about setiger 5, a short semi-circular papillate lobe appears (Fig. 22A) that begins lengthening and transitioning to a short digitiform lobe over subsequent segments; posterior thoracic setigers with a narrow digitiform postsetal lobe arising from a broad, rounded base. Last 1–3 thoracic neuropodia developing 1–3 extra subpodial lobes or papillae (Figs. 22B, 23E arrows); thoracic neuropodial postsetal lobe thickening and elongating in anterior neuropodia becoming incorporated into abdominal neuropodium; second thoracic postsetal lobe retained ventral to abdominal neuropodium, transforming into subpodial flange over subsequent segments (Fig. 22C); 1–2 additional ventral-most postsetal lobes or papillae retained as subpodial papillae over a few anterior abdominal neuropodia (Fig. 22C). Abdominal neuropodia becoming thicker, apically divided into two parts separated by notch from which setae emerge (Fig. 22C–D); medial lobe longer, pointed; lateral lobe shorter, rounded apically. Each abdominal neuropodium with short, rounded subpodial flange; one subpodial papilla ventral to flange on 5–10 anterior abdominal segments (Fig. 22C). Subpodial flanges of most abdominal setigers relatively short, thickened, with numerous internal glands; these glands darkly pigmented on most specimens (Figs. 22D, 23F, 24D). Interramal cirrus absent, but patch of sensory cilia present between noto- and neuropodia along most of abdomen (Figs. 22C–D, 24D arrows).

Branchiae first present from posterior thoracic setigers 13–16; branchiae short at first, triangular, becoming longer and full size by first abdominal segment (Fig. 21A); each anterior branchia broad, tapering to narrow rounded tip (Fig. 22B–C); subsequent branchiae longer, triangular, asymmetrical (Figs. 22D, 24D). Each branchia thickly ciliated along lateral and medial margins (Figs. 22B–D, 24D arrows).

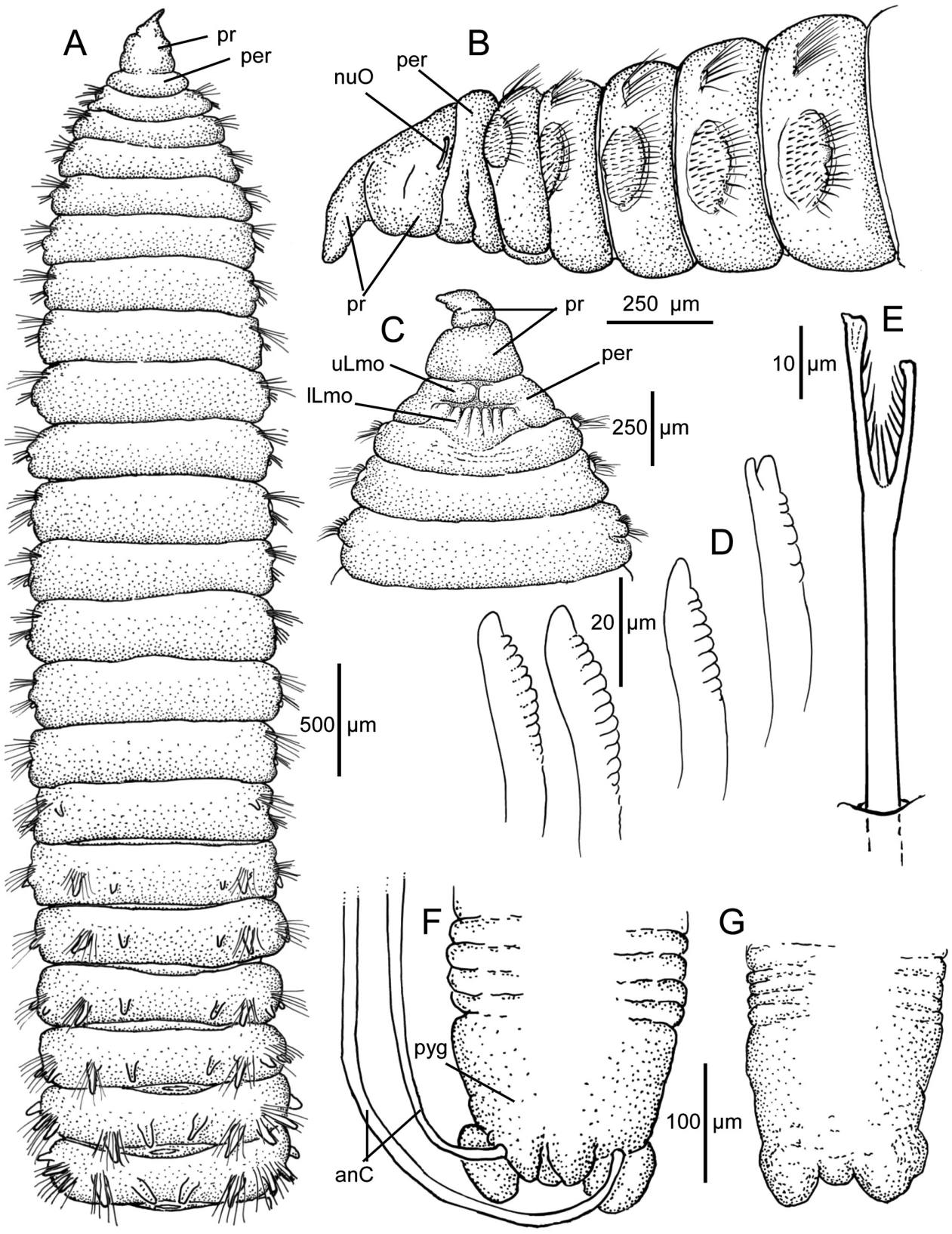

FIGURE 21. *Scoloplos pseudoarmiger* **n. sp.** A, anterior end, dorsal view; B, anterior left lateral view; C, anterior end, ventral view; D, thoracic neuropodial uncini; E, furcate seta; F, pygidium, dorsal view; G, pygidium, ventral view. A–D (USNM 1620929); E–G (USNM 1620935).

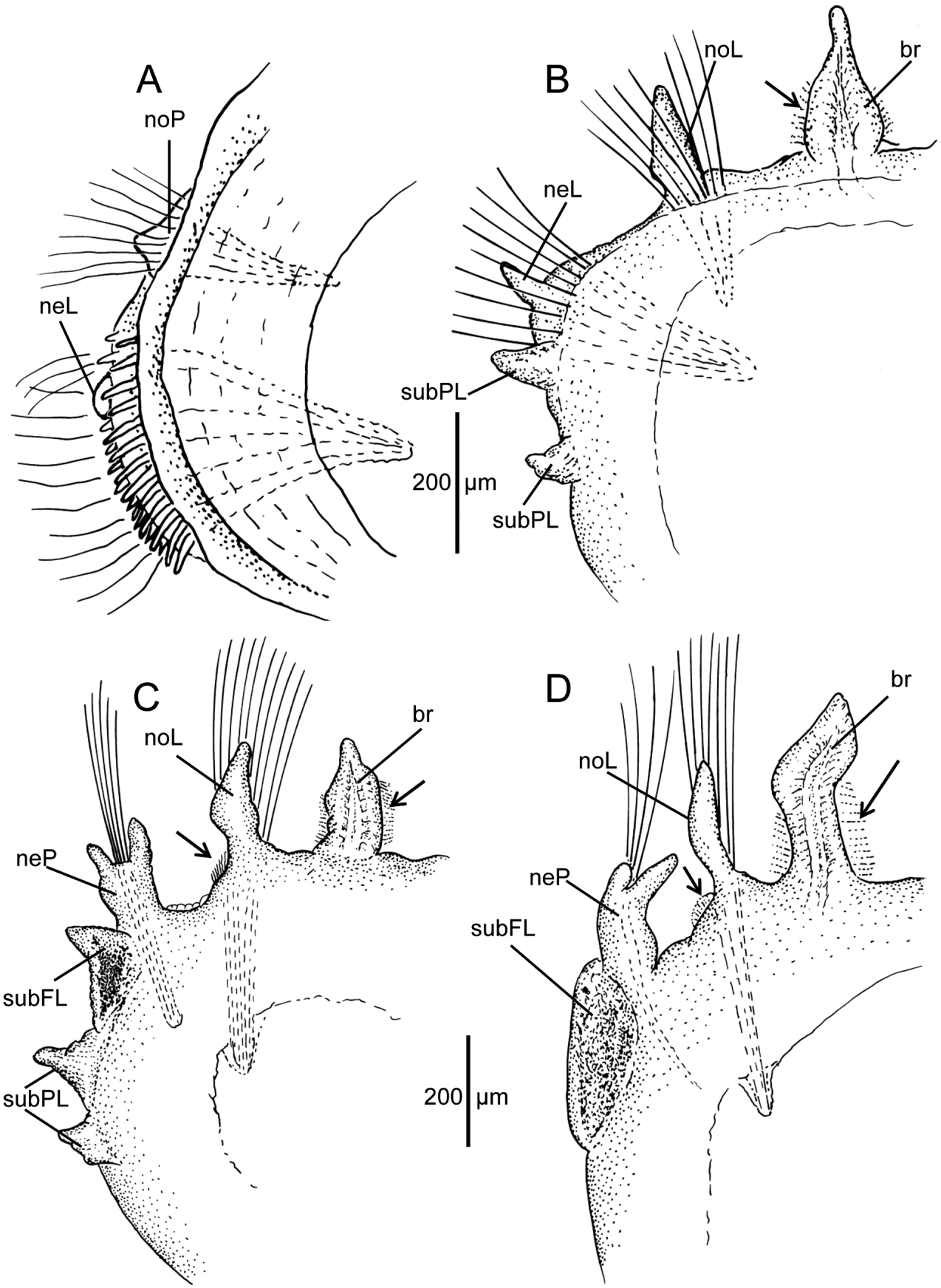

FIGURE 22. *Scoloplos pseudoarmiger* **n. sp.** Paratype (USNM 1620929): A, thoracic setiger 7, anterior view; B, thoracic setiger 14, anterior view; C, anterior abdominal setiger 25; D, middle abdominal setiger, ca. setiger 40.

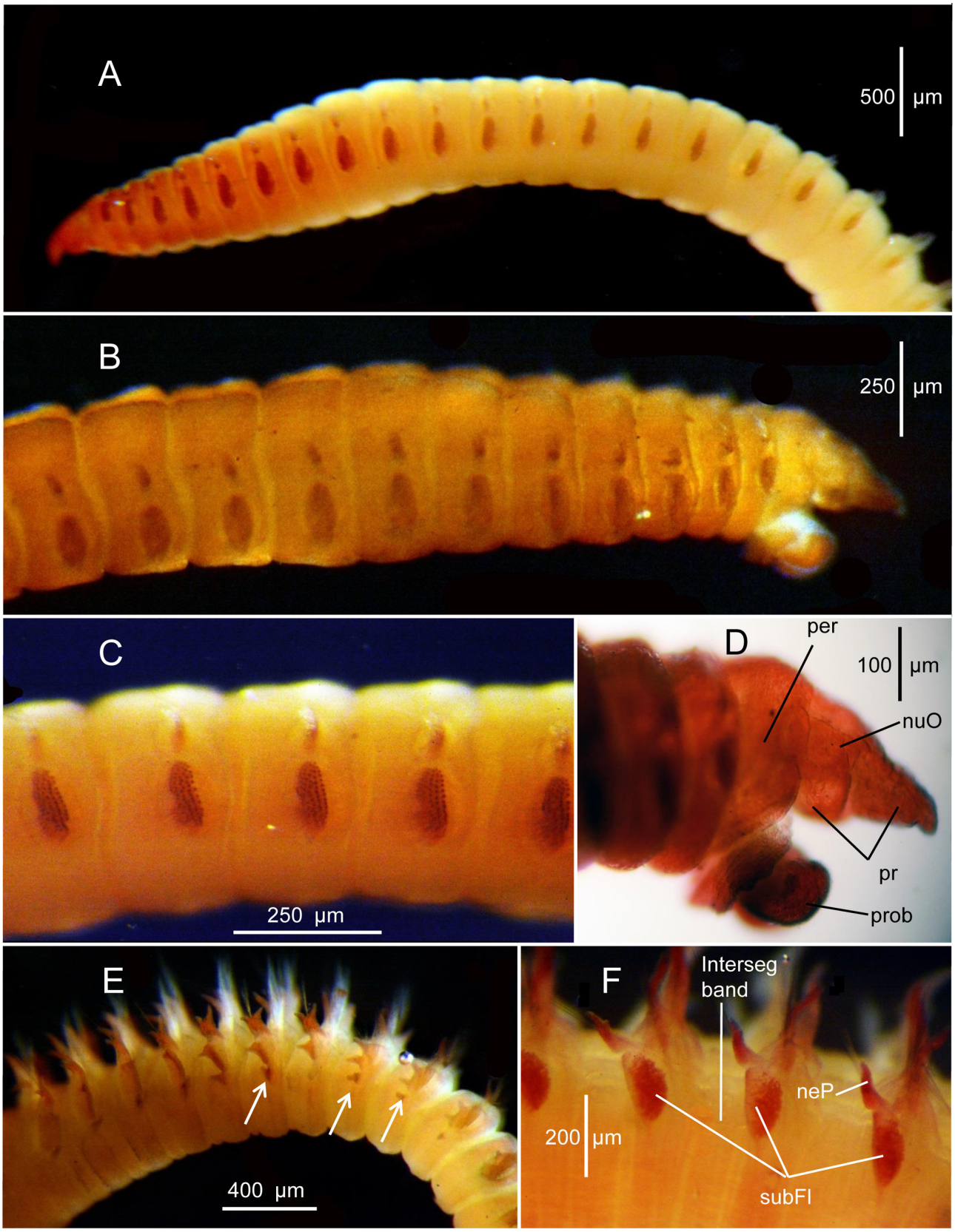

FIGURE 23. *Scoloplos pseudoarmiger* **n. sp.** A, anterior end, paratype, left lateral view; B, anterior end, holotype, right lateral view; C, middle thoracic setigers, paratype; D, pre-setiger region, and setigers 1–2 of holotype, right lateral view; E, transitional area between thorax and abdomen, right lateral view (arrows denote subpodial lobe); F, abdominal parapodia, right lateral view with subpodial flanges noted. A, C, F, paratype (USNM 1620929); B, D, holotype (USNM 1620928); E, (USNM 1620938). All stained with Shirlastain A.

Thoracic notosetae long camerated capillaries arranged in 2–3 rows. Thoracic neurosetae arranged in four rows of numerous uncini and a fifth row of camerated capillaries; about 10 or more uncini in each row (Figs. 21B, 22A, 23C); uncini occurring on all thoracic setigers except last, being transitional to abdominal setigers. Individual uncini with shafts smooth on concave side, tapering to narrow, rounded tip; some uncini with distinct hood behind smooth tip; convex side of shaft flattened, bearing rows of transverse ribs (Figs. 21D, 24A–C). Abdominal notosetae thin capillaries and 1–2 furcate setae; capillaries with camerated shafts; furcate setae with unequal tynes, each tyne with blunted tip and apical notch; tynes each with row of thin needles extending medially (Fig. 21E). Abdominal neurosetae with up to 5–6 thin capillaries, each mostly smooth but some with short barbs along one edge, and 1–2 curved aciculae, sometimes protruding, with rounded tip. Flail setae not observed.

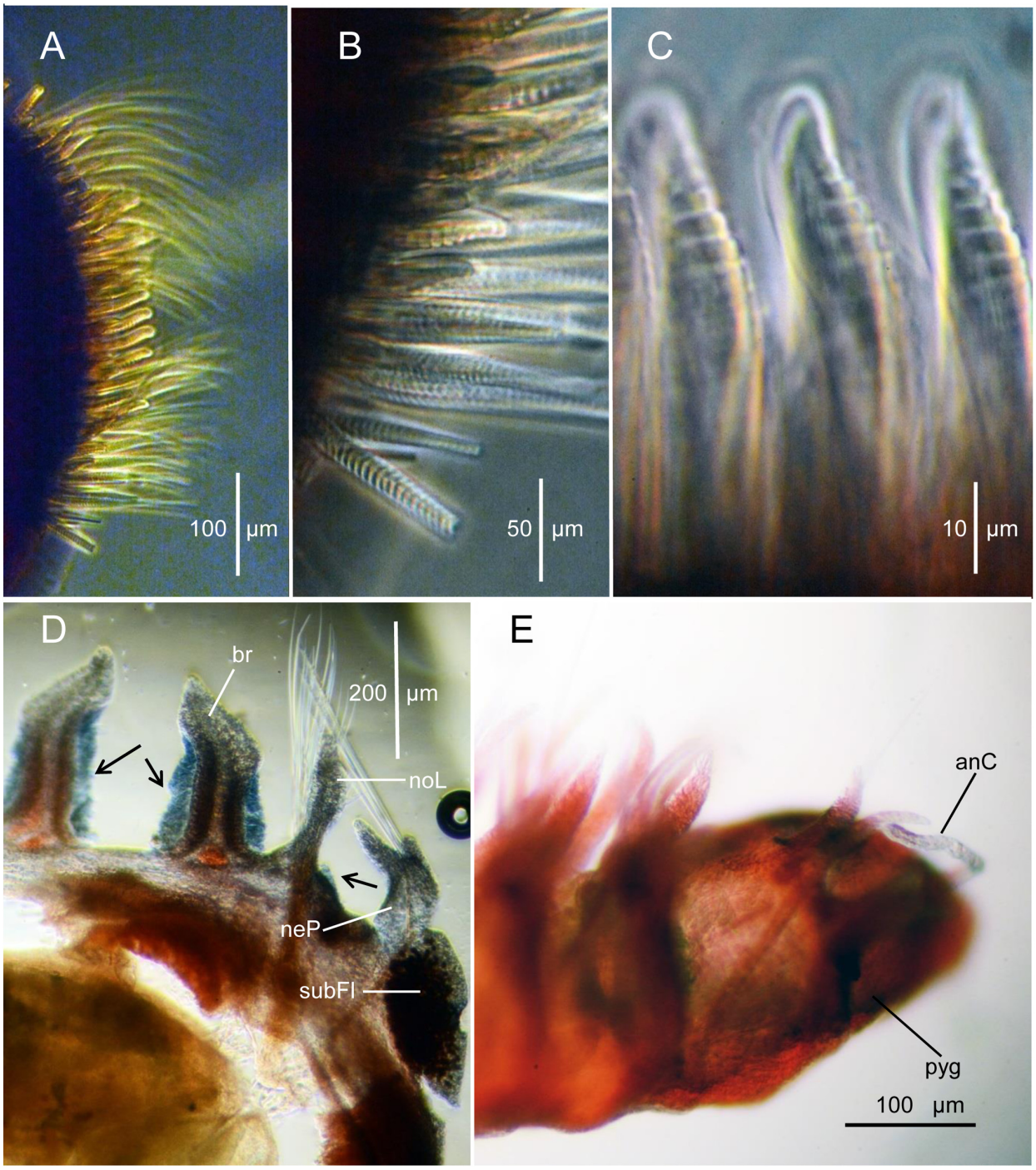

FIGURE 24. *Scoloplos pseudoarmiger* **n. sp.** A, rows of thoracic neuropodial uncini, setiger 6; B, close up of same; C, three uncini showing transverse ribs across shaft; D, abdominal setiger, posterior view (arrows denote cilia); E, pygidium. A–D, paratypes (USNM 1620929); E, holotype (USNM 1620928). D–F stained with Shirlastain A.

Pygidium short, with two short dorsal lobes, two large lateral lobes, and one short, rounded ventral lobe (Fig. 21F–G); all lobes surrounding anal opening; two long, narrow anal cirri arising dorsally (Figs. 21F, 24E).

Remarks. *Scoloplos pseudoarmiger* **n. sp**. belongs to a group of *Scoloplos* species with numerous rows of uncini in the thoracic neuropodia and extra subpodial lobes or papillae in posterior thoracic and anterior abdominal neuropodia. In this respect, *S. pseudoarmiger* **n. sp**. is the only species of the genus to have this combination of characters along the U.S. Atlantic coast. According to Hartmann-Schröder (1971, 1996) and Zhadan (1998) northern European specimens of *S. armiger* belong in this category. However, McIntosh (1910) describes *S. armiger* specimens from Britain as having few thoracic neuropodial uncini. As noted earlier, recent field investigations have demonstrated that at least two species of *Scoloplos* that are ecologically and reproductively isolated from one another occur in the North Sea (Kruse & Reise 2003; Kruse *et al*. 2003, 2004). These results from the North Sea were supported by Bleidorn *et al*. (2006) using molecular data that also identified a third species from Norway near the type-locality of *S. armiger*. To date, however, none of these three potential European species have been redescribed and separated from one another with morphological data. In the present study, *S. pettiboneae* **n. sp**., *S. pseudoarmiger* **n. sp**., and *S. verrilli* **n. sp**. represent a similar group of three closely related nearshore and shelf species that are easily separated from one another by distributional patterns and different morphologies.

Scoloplos pseudoarmiger **n. sp**., in having multiple rows of uncini in thoracic neuropodia, is most similar morphologically to northern European specimens of *S. armiger sensu* Hartmann-Schröder (1996) and Zhadan (1998). At this time, however, there is insufficient information to know if the two European reports represent the same species. However, the majority of specimens reported by Zhadan (1998) were from Arctic and sub-Arctic habitats whereas Hartmann-Schröder (1996) reported specimens from north of Germany and the North Sea. The present records of *S. pseudoarmiger* **n. sp**. are from shelf depths in temperate latitudes. Important characters from these reports of *S. armiger* are compared with *S. pseudoarmiger* **n. sp**. in Table 1.

TABLE 1. Comparison of some characters of *Scoloplos armiger sensu* Hartmann-Schröder (1971, 1996) and Zhadan (1998) with *Scoloplos pseudoarmiger* **n. sp.**

Character	*S. armiger*	*S. pseudoarmiger* n. sp.
No. segments	>200	>170
No. thoracic setigers	>22 (H-S); 18 (Zh)	>20
First occurrence of branchiae	9–17 (H-S); 13–14 (Zh)	13–16
Prostomium	Large, triangular, entire, narrowing to pointed tip	Large, with narrow pointed anterior part separated laterally and ventrally from larger posterior part anterior to mouth
Peristomium	A smooth ring	With ventrolateral groove
Occurrence of extra subpodial lobes	Post 1–5 th setigers; a nt 1–7 abd setigers	# Post 1–3 th setigers; ant 1–5 abd setigers, transforms into subpodial flange
Occurrence of subpodial papillae	Post 1–2 th setigers; ant 1–7 abd setigers	Post 1–3 th setigers; ant 5–10 abd setigers
Nature of abdominal subpodial flange	Elongate, smooth border	Short, rounded; with numerous internal pigmented glands
Morphology of thoracic neuropodial uncini	In 2–4 rows; thick, blunt tipped, with transverse ribs along shaft; some reported with (Zh) or without (H-S) hood on convex side of apex	In four rows; thick, blunt tipped, with transverse ribs along shaft; some with hood on convex side of apex
Interramal cilia abdominal segments	Present	Present
Nature of oral lips	Not reported	Upper lip with 2 lobes; lower lip with 7–8 narrow lobes
Segmental annulations	Not reported	Th segments uniannulate; abd segments bi-annulate (wide intersegmental band)

Abbreviations: abd, abdominal; ant, anterior; No, number; post, posterior; th, thoracic; H-S, Hartmann-Schröder; Zh, Zhadan.

Based on the information presented in Table 1, *Scoloplos armiger* and *S. pseudoarmiger* **n. sp**. have similar numbers of setigerous segments, numbers of thoracic setigers, and first branchiae from posterior thoracic setigers. *Scoloplos pseudoarmiger* **n. sp**. differs from the two European reports of *S. armiger* in details of the prostomium, peristomium, distribution of the subpodial lobes and papillae over thoracic and abdominal setigers, and morphology of the abdominal subpodial flanges. While details of the upper and lower lips of the mouth and segmental annulation patterns along the body may be important, they were not reported for the European species.

The first extra subpodial lobe that occurs in posterior thoracic setigers of *S. pseudoarmiger* **n. sp**. is shown in the present study to represent a transitional phase in the development of the subpodial flange ventral to the abdominal neuropodia. The resulting flanges are short and oval in shape and have numerous pigmented internal glands. The subpodial flange of the European reports of *S. armiger* is more elongate and lacks internal glands.

Etymology. The epithet is from *pseudo*, Greek for false combined with *armiger*, the most common species name in the genus *Scoloplos*. According to Wikipedia, "an *armiger* in heraldry is a person entitled to use a heraldic achievement (e.g., bear arms, an 'armour-bearer') either by hereditary right, grant, matriculation, or assumption of arms." According to Webster, *armiger* means (1) squire, (2) one entitled to bear heraldic arms. The term is from Medieval Latin.

Distribution. Massachusetts Bay, 33 m; Georges Bank, 53–93 m.

Scoloplos verrilli new species

Figures 25–27

urn:lsid:zoobank.org:act:72DA560F-2F73-4C2A-9D8D-D7BBE81DBA43

Scoloplos (*Scoloplos*) *armiger*: Pettibone 1963: 292–293, fig. 76 h–I; Trott 2004: 280. **Not** Müller, 1776.
Scoloplos armiger: Blake *et al*. 1998: C-1, C-2 (in part). **Not** Müller, 1776.

Material examined. (*88 specimens*) **Northeastern USA, Massachusetts Bay**, **MWRA Harbor and Outfall Monitoring Program. 1995 August Survey**: **Sta. FF-13**, 42°19.19′N, 70°49.38′W, 19 m, **holotype** (MCZ 161633) and 4 **paratypes** (MCZ 161634). **Sta. FF-9**, 42°18.75′N, 70°39.40′W, 49 m, 11 **paratypes** (MCZ 161631**). Sta. FF-10**, 42°24.84′N, 70°52.72′W, 27 m (1, MCZ 161632).—**1992 August Survey**: **Sta. NF-1**, 42°20.35′N, 70°50.51′W, 42 m (2, MCZ 161614). **Sta. NF-5**, 40°25.62′N, 70°50.03′W, 28 m (2, MCZ 161615). **Sta. NF-6**, 42°24.30′N, 70°49.99′W, 31 m (2, MCZ 161616). **Sta. NF-7**, 42°24.60′N, 70°48.89′W, 32 m (5, MCZ 161617). **Sta. NF-11,** 42°23.39′N, 70°50.25′W, 31 m (1, MCZ 161619). **Sta. NF-12**, 42°23.40′N, 70°49.83′W, 33 m (6, MCZ 161620). **Sta. NF-13**, 42°23.40'N, 70°49.35'W, 33 m (1, MCZ 161621). **Sta. NF-15**, 42°22.93′N, 70°49.67′W, 32 m (3, MCZ 161622). **Sta**. **NF-19**, 42°22.30′N, 70°48.30′W, 32 m (5, MCZ 161623). **Sta. FF-4**, Rep. 2, 42°117.30′N, 70°25.50′W, 48 m (MCZ 161624). **Sta. FF-9**, Rep. 1, 42°18.75′N, 70°39.40′W, 48 m (9, MCZ 161625). **Sta. FF-9**, Rep. 2, 42°18.75′N, 70°39.40′W, 48 m (9, MCZ 161626). **Sta. FF-10**, Rep. 3, 42°24.84′N, 70°52.72′W, 27 m (2, MCZ 161618). **Sta. FF-12**, Rep. 1, 42°23.40′N, 70°53.98′W, 22 m (1, MCZ 161627); Rep. 2, 2 **paratypes** (MCZ 161628); Rep. 3, 4 **paratypes** (MCZ 161629). **Sta. FF-13**, Rep. 1, 42°19.19′N, 70°49.38′W, 19 m (9, MCZ 161630).—**1996 August Survey**: **Sta. MF-02**, 42°20.331′N, 70°49.69′W, 30 m (3, MCZ 161647). **Sta. MF-07**, 42°24.60′N, 70°48.89′W, 33 m (2, MCZ 161648). **Sta. MF-08**, 42°24.00′N, 70°51.81′W, 32 m (3, MCZ 161649). **Sta. MF-09**, 42°23.99′N, 70°50.69′W, 29 m (3, MCZ 161650). **Sta. MF-10**, 42°23.57′N, 70°50.69′W, 35 m (2, MCZ 161651). **Sta. MF-14**, 42°22.70′N, 70°50.26′W, 29 m (1, MCZ 161652). **Sta. MF-20**, 42°22.69′N, 70°50.69′W, 28 m, 4 **paratypes** (MCZ 161653). **Sta. MF-22**, 42°20.87′N, 70°48.90′W, 36 m (1, MCZ 161654). **Sta. NF-15**, 42°22.93′N, 70°49.67′W, 32 m; (1, MCZ 161655). **Sta. NF-19**, 42°22.30′N, 70°48.30′W, 32 m (4, MCZ 161656). **Sta. NF-24**, Rep. 1, 42°22.83′N, 70°48.10′W, 37 m (1, 161657); Rep. 2, 12 **paratypes** (MCZ 161658). Rep. 3, 19 **paratypes** (MCZ 161659). **Sta. FF-5**, Rep. 3, 42°08.0084′N, 70°25.35′W, 61 m (1, MCZ 161635). **Sta. FF-9**, Rep. 1, 42°18.75′N, 70°39.40′W, 49 m (2, MCZ 161636); Rep. 2 (4, MCZ 161637). **Sta. FF-10**, Rep. 1, 42°24.84′N, 70°52.72′W, 27 m (5, MCZ 161638); Rep. 2, 4 **paratypes** MCZ 161639); Rep. 3 (1, MCZ 161640). **FF-Sta. 12**, Rep. 1, 42°23.40′N, 70°49.83′W, 22 m, 15 **paratypes** (MCZ 161641); Rep. 2 (5, MCZ 161642); Rep. 3 (5, MCZ 161643). **Sta. FF-13**, Rep. 1, 42°19.19′N, 70°49.38′W, 19 m (3, MCZ 161644); Rep. 2, 5 **paratypes** (MCZ 161645); Rep. 3 (3, MCZ 161646).—**1997 August Survey**: **Sta. FF-9**, Rep. 1, 42°18.75′N, 70°39.40′W, 49 m (2, MCZ 161660). **Sta. FF-10**, Rep. 1, 42°24.84′N, 70°52.72′W, 27 m (5, MCZ 161661). **Sta. FF-12**, Rep. 1, 42°23.40′N, 70°49.83′W, 22 m (3, MCZ 161662); Rep. 2 (5, MCZ 161663); Rep. 3 (3, MCZ 161664). **Sta. MF-2**, 42°20.31′N, 70°49.69′W, 29 m (1, MCZ 161665). **Sta. MF-**

9, 42°23.99′N, 70°50.69′W, 35 m (2, MCZ 161666). **Sta. MF-10**, 42°23.57′N, 70°59.29′W, 34 m (5, MCZ 161667). **Sta. MF-12**, Rep. 3 42°23.40′N, 70°49.83′W, 34 m (2, MCZ 161668). **Sta. MF-20**, 42°23.69′N, 70°50.69′W, 28 m, 1 **paratype** (MCZ 161669).

Description. A large species; holotype complete, partially coiled, 175 setigers, 42 mm long and 0.8 mm wide across thorax; paratype (MCZ 161634) with ca. 200 setigers, 42.2 mm long, 1.3 mm across thorax; both with 17 thoracic setigers and branchiae from setiger 14. Other large specimens with 16–17 thoracic setigers and branchiae from setigers 13–14. Thoracic segments dorsoventrally flattened, often with 6–8 anterior thoracic segments swollen dorsally due to location of internal retracted pharynx; Thoracic segments short, about six times wider than long (Fig. 25A), transitioning to abdominal segments at least 2½ times longer than thoracic segments (Fig. 27A–B). Transition from thorax to abdomen denoted by appearance of elongate, enlarged neuropodium, simple at first, becoming longer and with apex split over successive segments. Color in alcohol light tan; subpodial flanges of middle and posterior abdominal neuropodia with a few internal glands retaining stain red with Rose Bengal and reddish brown with Shirlastain A.

Pre-setiger region triangular, wider than long, as long as first 2½ setigers (Fig. 25A–C). Prostomium conical, tapering to pointed tip (Figs. 25A–C; 27A–B); nuchal organs semi-circular slits on posterior lateral margin (Fig. 25C); eyespots absent. Peristomium as long as first setiger, with a single smooth annular ring dorsally (Fig. 25A), surrounding mouth ventrally, forming upper and lower lips (Fig. 25B); upper lip of mouth with two narrow transverse curved lobes; ventral lip of mouth with 8–10 narrow elongate lobes. Proboscis with three long, narrow lobes seen when everted (Fig. 27B).

Anterior thoracic notopodia with digitiform postsetal lobe, base arising directly from body wall; lobe triangular, short at first (Fig. 26A), then becoming longer, narrow in posterior thoracic segments (Fig. 26B). Thoracic neuropodia with broad base, bearing medial postsetal lobe, short and rounded at first (Fig. 26A), then becoming conical in shape in posterior thoracic setigers; posterior thoracic neuropodia from setigers 14–15 developing a second short postsetal lobe and a short subpodial papilla (Fig. 26B). Transition to abdominal segments abrupt, with neuropodia becoming thick, elongate and with fewer neurosetae (Figs. 25A, 26C); notopodial postsetal lobes becoming narrow and elongate along rest of body (Figs. 26C–E, 27E). Abdominal neuropodia of anterior and middle setigers elongate, narrow, divided into two parts separated by notch (Fig. 26C–D); medial lobe long, pointed; ventral lobe shorter, rounded apically, directed laterally; ventral lobe lost in far posterior neuropodia that taper to a pointed tip (Fig. 26E). Interramal cirrus absent, but distinct low, rounded interramal swelling bearing cilia present at base of notopodium (Fig. 26B–E). Abdominal neuropodia with narrow subpodial flange throughout (Figs. 26D–E, 27E); anteriormost abdominal neuropodia with subpodial flange transitioning from second postsetal lobe of thoracic neuropodia (Fig. 27C); a single subpodial papilla retained on a few anterior abdominal segments. Subpodial flanges of middle and posterior abdominal setigers with few large internal pigmented glands.

Branchiae from thoracic setiger 13 or 14; branchiae short, triangular at first (Figs. 25A, 26B), becoming longer, leaflike; branchiae full size by first abdominal segment (Fig. 26C). Branchiae of middle and posterior setigers elongate, narrow, weakly asymmetrical (Figs. 26D–E, 27E). Each branchia thickly ciliated along lateral and medial margins (Figs. 26C–E, Fig. 27E).

Thoracic notosetae numerous thick, long, camerated capillaries arranged in 2–3 rows. Thoracic neurosetae with about four rows of capillaries and a few hooked uncini first occurring as a group in ventral most part of fascicle and then over subsequent setigers extending dorsally as single curved row of 7–8 uncini between third and fourth row of capillaries (Fig. 25D). Uncini difficult to observe among more numerous capillaries, always shorter and observed in ventral part of fascicle. Uncini best observed in first 7–10 setigers, becoming reduced to 3–4 uncini in lower part of setal fascicle; either absent or not observed in posterior thoracic setigers. Individual uncini with shafts smooth on convex side, tapering to narrow, rounded tip; concave side of shaft flattened, bearing barbs along most of shaft (Fig. 25E). Abdominal notosetae thin, camerated capillaries and 1–2 furcate setae. Furcate setae with unequal tynes; long tyne with blunted tip and apical notch; shorter tyne with narrow rounded tip; each with row of thin needles extending medially (Fig. 25F–G). Abdominal neurosetae with up to 4–6 thin capillaries, each with short barbs along one edge, and 1–2 narrow curved aciculae, sometimes protruding, with rounded tip (Fig. 26D inset). Flail setae not observed.

Pygidium short, with two dorsal lobes each subdivided into 2–3 parts and two large ventrolateral lobes surrounding anal opening; with two long anal cirri arising dorsally (Figs. 26F, 27D).

Remarks. *Scoloplos verrilli* **n. sp**. was commonly collected in Massachusetts Bay as part of the long-term monitoring program associated with an offshore outfall. The species differs from *S. pettiboneae* **n. sp**. and *S. pseu-*

doarmiger **n. sp**., which are also present offshore Massachusetts, in having only a few uncini in thoracic neuropodia instead of numerous uncini in multiple rows. Along the U.S. Atlantic coast, *S. verrilli* **n. sp**. from off New England is most similar to *S. papillatus* **n. sp**., which occurs in upper slope sediments off North Carolina. Details regarding the differences between these two species were reviewed in the account for *S. papillatus* **n. sp**. (see above).

Scoloplos armiger sensu Pettibone (1963) is believed to be the same as *S. verrilli* **n. sp**. because she noted that only a few spines, together with numerous capillaries, were present in thoracic neuropodia. However, her account suggests that other species were likely present in her material as well.

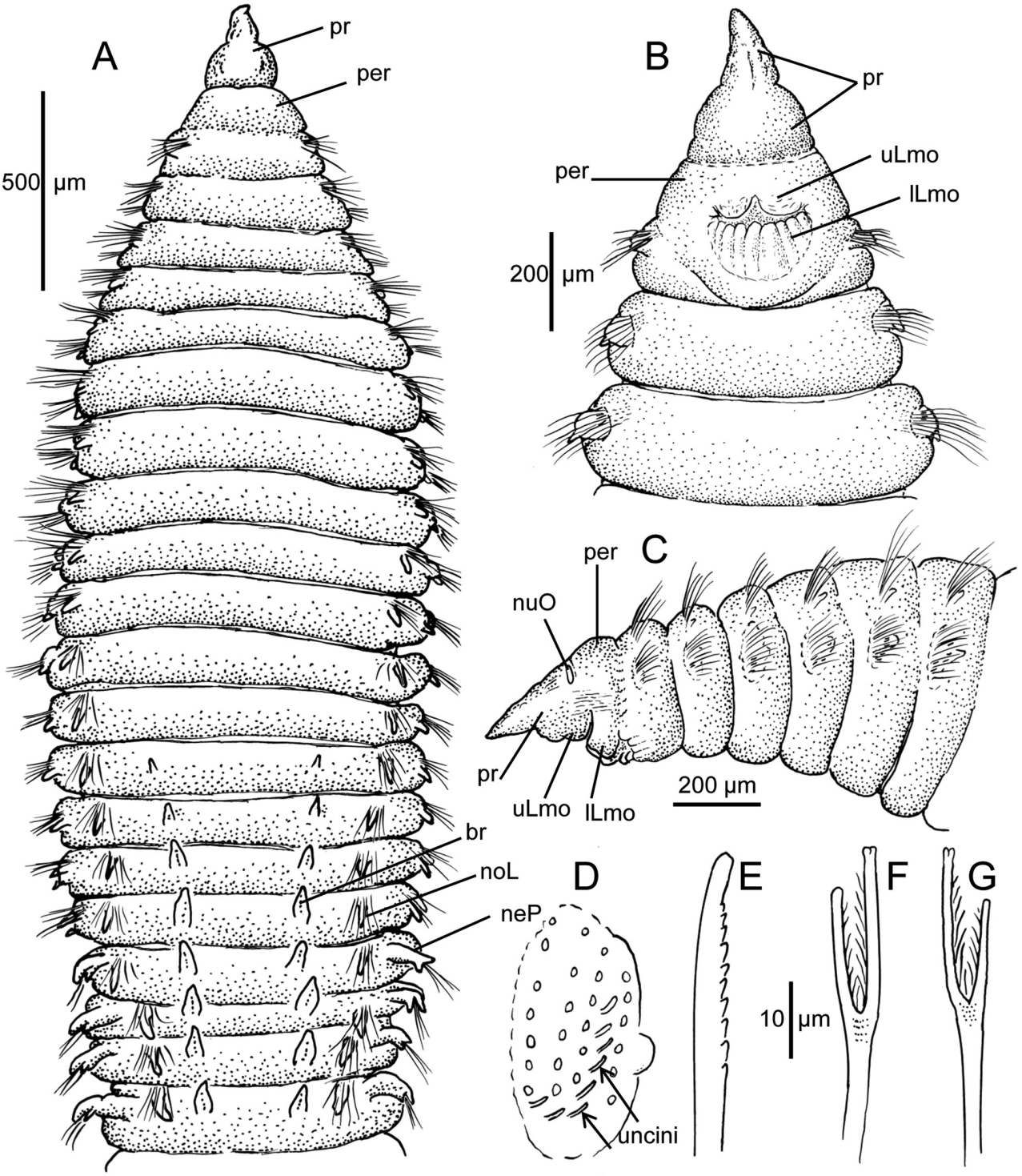

FIGURE 25. *Scoloplos verrilli* **n. sp.** Paratypes (MCZ 161628): A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end, left lateral view; D, diagram of thoracic setiger and rows of capillaries and uncini (not to scale); E, thoracic neuropodial uncinus; F, G, furcate setae.

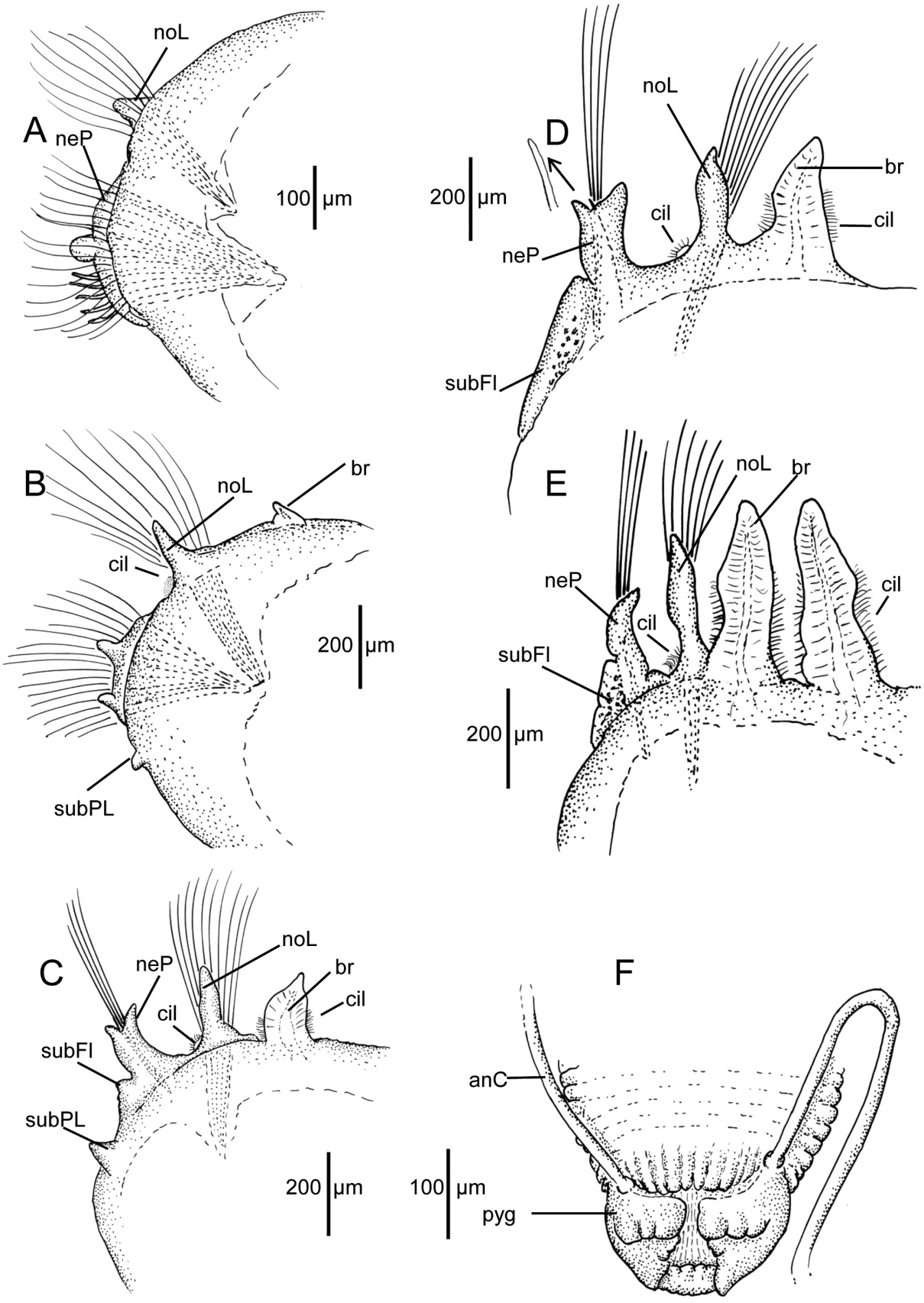

FIGURE 26. *Scoloplos verrilli* **n. sp.** Paratypes (MCZ 161628): A, thoracic setiger 5, anterior view; B, thoracic setiger 15, posterior view; C, anterior abdominal setiger 20, posterior view; D, middle abdominal setiger, posterior view; E, far posterior abdominal setiger, posterior view; F, pygidium, dorsal view.

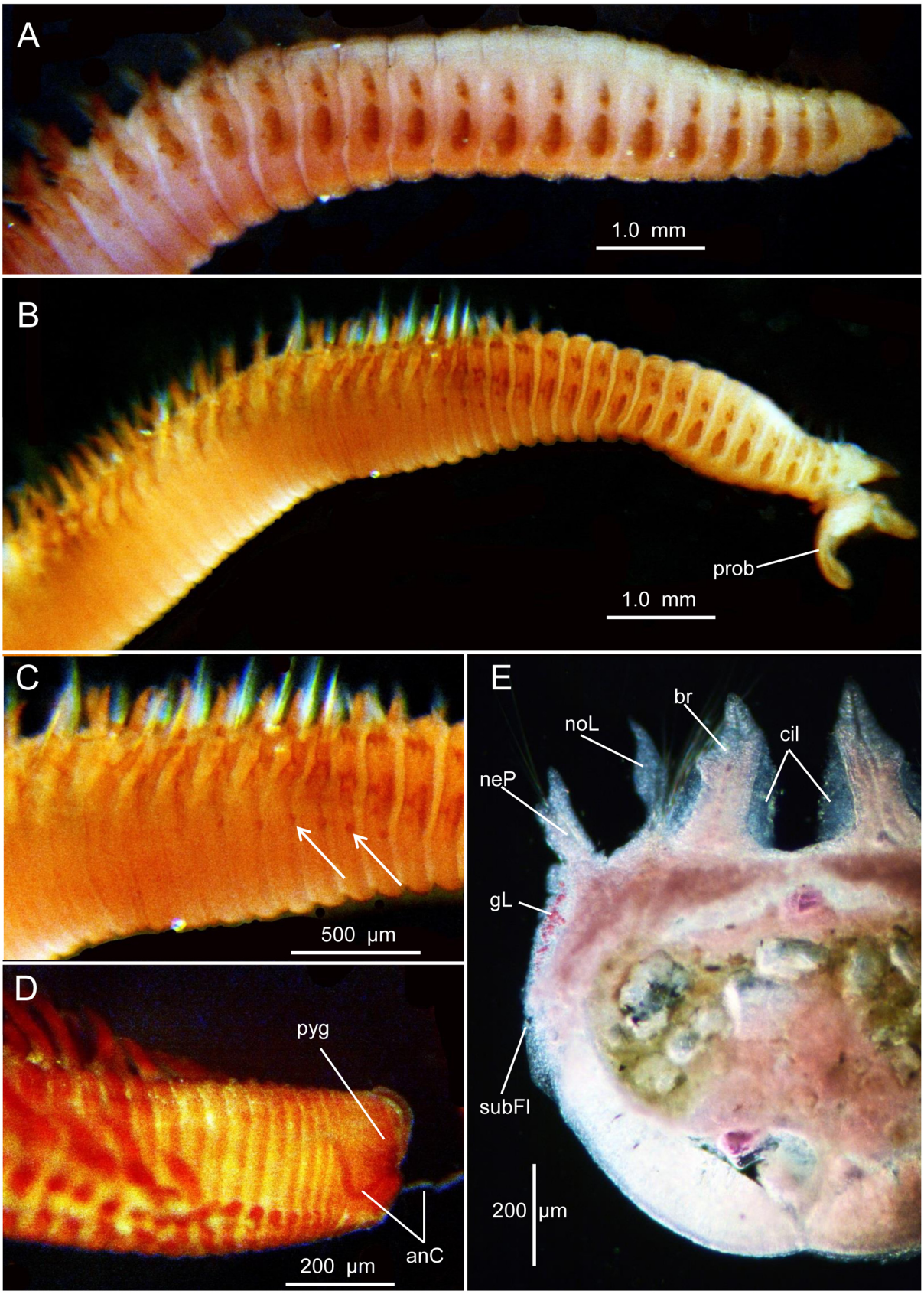

FIGURE 27. *Scoloplos verrilli* **n. sp.** A, holotype, anterior end, right lateral view; B, paratype, anterior end, right lateral view; C, paratype, detail of thoracic-abdominal transition, arrows denote subpodial lobes; D, holotype, pygidium, left lateral view; E, middle abdominal setiger, posterior view. A, D, holotype (MCZ 161633); B–C, E, paratype (MCZ 161634). All stained with Shirlastain A.

Etymology. This species is named for Professor Addison Emery Verrill, eminent 19th century zoologist at Yale University. Professor Verrill's surveys and subsequent publications on the marine invertebrates of offshore New England included descriptions of numerous polychaetes including orbiniids. Currently three common species of *Leitoscoloplos* and one species of *Phylo* that occur along the U.S. Atlantic coast were originally described by Verrill (1873).

Distribution. Massachusetts Bay, 19–51 m.

Genus *Leodamas* Kinberg, 1866

Type-species: *Leodamas verax* Kinberg, 1866, by monotypy.
Synonym: *Branchethus* Chamberlin, 1919b. **Type-species:** *Branchethus latum* Chamberlin, 1919b, by monotypy. *Fide* Hartman 1957.

Diagnosis. (after Blake 2017). Prostomium pointed on anterior margin, usually prolonged; most species with a single achaetous peristomial segment; immature adults of some species with two achaetous peristomial segments and adults of at least one species with vague indication of two achaetous segments. Branchiae single or multiple branches, either from anterior thoracic setigers 4–7 or from posterior thoracic setigers or first abdominal setigers. Posterior thoracic setigers with 0–2 postsetal lobes and 0–2 subpodial lobes, never more than four lobes of both types combined; lobes not forming ventral fringes. Thoracic neuropodial uncini large, conspicuous, arranged in one to many distinct vertical rows, with accompanying capillaries few or entirely lacking; heavy spear-like spines and bristle-topped setae absent. Abdominal neuropodia with projecting aciculae, either thin and inconspicuous or large and curved apically. Abdominal noto- or neuropodial flail setae present or absent.

Remarks. Blake (2017) redefined *Leodamas* and referred 29 species to the genus; two additional species were subsequently qdescribed by Sun *et al.* (2018) from the East China Sea and Blake (2020) from the South China Sea. Blake (2017) divided the species into two groups: (Group A) species with branchiae from an anterior thoracic setiger (4–7) and thoracic neuropodial uncini typically in three or more rows and (Group B) species with branchiae from a posterior thoracic or anterior abdominal setiger (12–29) and with thoracic neuropodial uncini typically in 1–2 rows. The species assigned to Group B were previously referred to the genus *Scoloplos*, but redefined as a separate group of *Leodamas* species by Blake (2017). Only species belonging to Group A were found in the present study.

Based on Blake (2017, 2020) and Sun *et al*. (2018), 21 species of *Leodamas* are known, of which only four have been reported from depths greater than 500 m. In the present study, three additional species have been found: (1) *L. cuneatus* **n. sp.** in lower slope depths of New England and mid-Atlantic sites off New Jersey and Delaware, (2) *L. mucronatus* **n. sp.** from upper slope depths off South Carolina, and (3) *L. notoaciculatus* **n. sp.** from inner shelf depths off New Jersey. The two deep-water species have unusual pre-setal morphology.

Leodamas cuneatus new species

Figures 28–29
urn:lsid:zoobank.org:act:5650CFB0-06EA-4527-B0A1-AC0C167C54C8

Leodamas sp. 1: Maciolek *et al*. 1987b: D-3.

Material examined. **Off New England, US North Atlantic ACSAR Program**, coll. G.W. Hampson, Chief Scientist. **Sta. 5**: Cruise NA-2, Rep. 1, 20 Apr 1985, 40°05.07′N, 67°29.78′W, 2060 m, **holotype** (USNM 1622267). **Sta. 11**: Cruise NA-1, 3 Dec 1984, Rep. 2, 40°01.29′N, 70°55.04′W, 255 m, 2 **paratypes** (USNM 1622268).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR Program**, coll. R.M. Petrecca, Chief Scientist. **Sta. 11**: Cruise Mid-3, Rep. 2, 04 Dec 1984, 38°40.14′N, 72°56.31′W, 1520 m (1, USNM 1622269).

Description. A moderately sized species, holotype nearly complete with 90 setigers, about 30 mm long and 1.4 mm across thorax; larger of two juvenile paratypes (USNM 1622268) complete with 39 setigers, 3.7 mm long, 0.43 mm wide across thorax. Thorax of holotype with 14 setigers and branchiae from setiger 5; larger paratype with eight thoracic setigers and branchiae from setiger 5. Thoracic segments slightly wider than abdominal segments. Thoracic segments flattened dorsally and ventrally; abdominal segments also flattened dorsally, but rounded ventrally, with parapodia shifted dorsally. Thoracic setigers short, about 5 times wider than long; individual thoracic segments

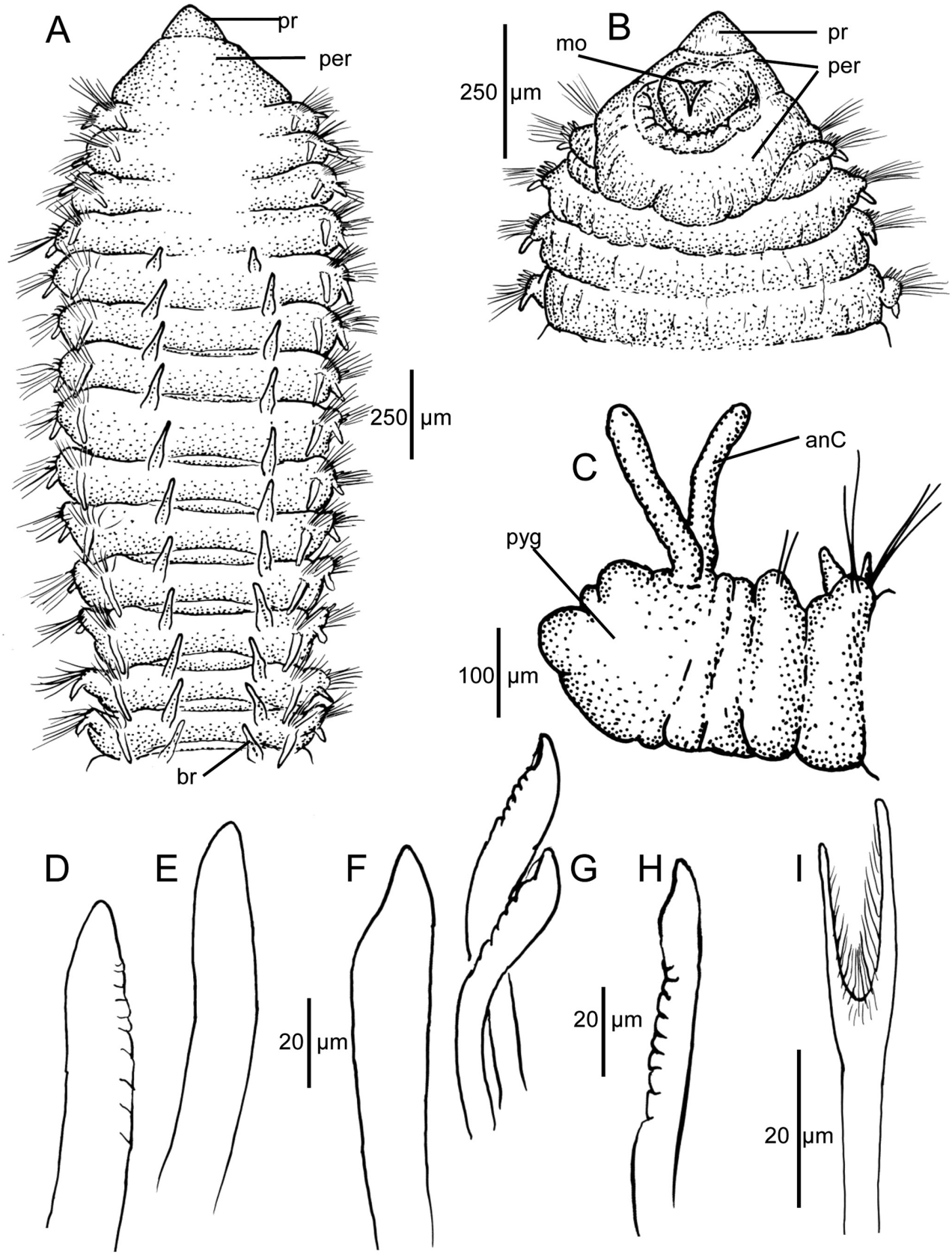

FIGURE 28. *Leodamas cuneatus* **n. sp.** A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end and pygidium, right lateral view; D–F, heavy thoracic neuropodial uncini of first row; G, uncini of rows 2 and 3; H, uncinus of row 4; I, notopodial furcate seta. A–C, holotype (USNM 1622267) ; D–I, paratype (USNM 1622268).

separated dorsally by prominent intersegmental ridge (Fig. 28A), ridges less prominent ventrally; in abdominal segments intersegmental area expanding across segments and with parapodial ridge individual segments visibly biannulate. Color in alcohol opaque white.

Pre-setiger region triangular, wedge-shaped, merged dorsally with setiger 1 (Fig. 28A–B). Prostomium short, broadly triangular, narrowing to pointed tip (Fig. 28A–B); nuchal organs not observed; eyespots absent. Peristomium smooth dorsally, not divided by annular rings; ventrally surrounding mouth and forming upper and lower lips (Fig. 28B); upper lip a smooth circular ring; ventral lip with about 10 short lobes; proboscis partially everted on holotype. Peristomium thickened on ventral side posterior to mouth, extending over setiger 1 (Fig. 28B).

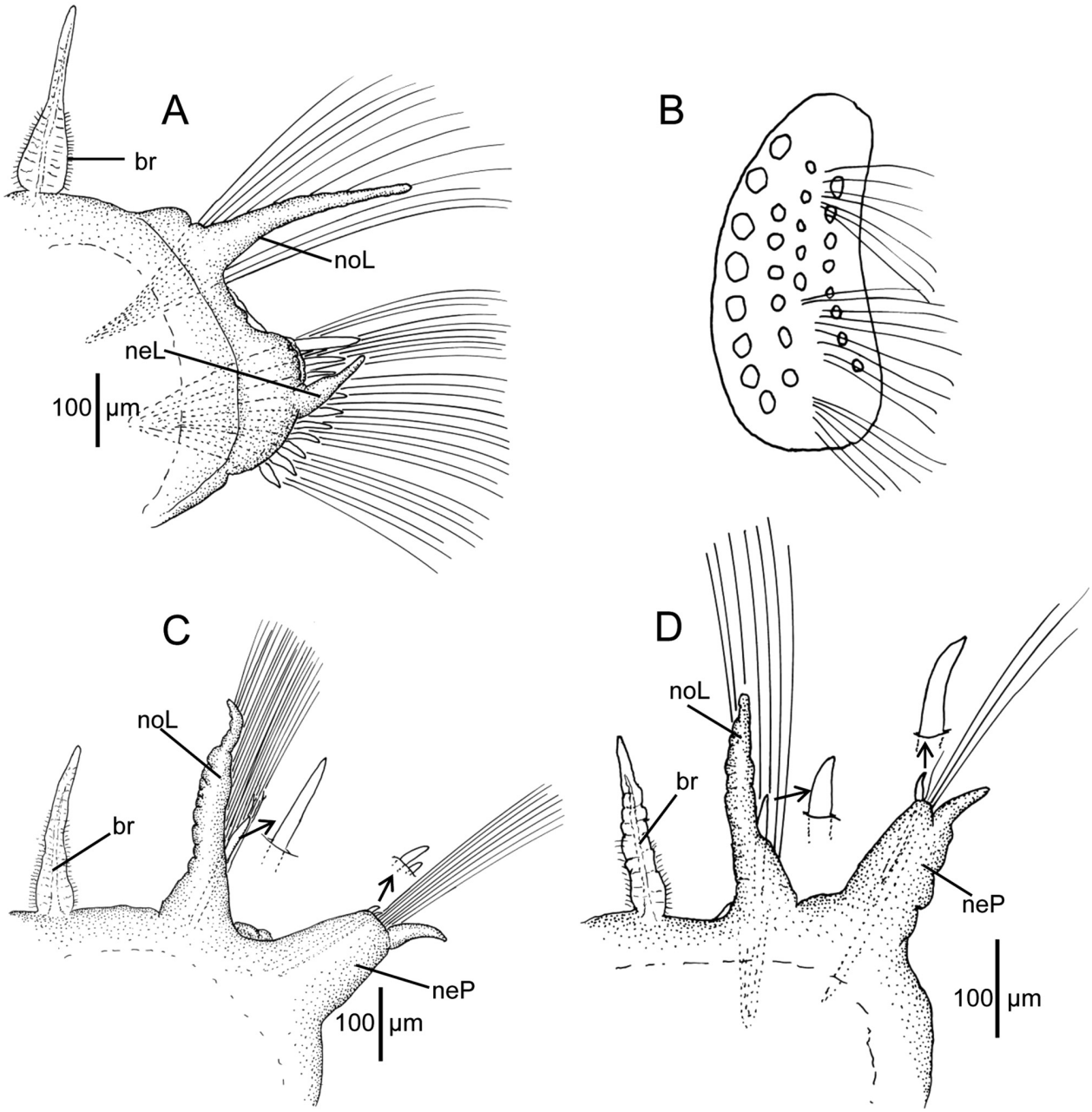

FIGURE 29. *Leodamas cuneatus* **n. sp.** Holotype (USNM 1622267): A, thoracic setiger 11, posterior row; B, diagram of location of thoracic neuropodial uncini and capillaries (not to scale); C, abdominal setiger 24, posterior view (insets not to scale); D, abdominal setiger from mid-body, posterior view (insets not to scale).

Thoracic notopodia with single long, tapering digitiform postsetal lobe (Fig. 29A). Thoracic neuropodia enlarged, rounded, with digitiform postsetal lobe arising from middle of rounded neuropodial base, lobe shorter than that of notopodium (Fig. 29A). Transition to abdominal segments identified by narrowing and elongation of neuropodium and fewer capillary neurosetae. Abdominal notopodia similar to those of thorax with long, digitiform

postsetal lobe (Fig. 29C–D). Abdominal neuropodia with long, narrow subterminal lateral digitiform lobe, continuing to near posterior end (Fig. 29C–D). Interramal cirrus absent, but low thickened ridge present between noto- and neuropodia of anterior abdominal setigers.

Branchiae from setiger 5, with first pair short, widest basally (Fig. 28A); subsequent thoracic and anterior abdominal branchiae elongate, widest basally, tapering to narrow apex (Figs. 28A, 29A, C–D); middle and posterior abdominal branchiae more or less narrow along entire length; all branchiae with lateral cilia along at least half their length.

Thoracic notosetae all camerated capillaries; first 2–3 setigers with 15–20 notosetae, increasing to 30–40 over subsequent thoracic segments, then reduced to 2–3 by setiger 14. Thoracic neuropodia with up to 20 uncini or spines accompanied by capillaries arising in 3–4 groups. Uncini arranged in up to four vertical rows (Fig. 29B) with 8–9 spines of first row largest (Fig. 28D–F), with weakly developed ridges along one edge (Fig. 28D) or entirely smooth (28E–F); spines of second and third rows smaller, with distinct ribs along one edge and subterminal notch (Fig. 28G); spines of last row narrowest with distinct ribs along one edge (Fig. 28H); thoracic neuropodial capillaries arranged in 3–4 poorly defined groups. Abdominal notosetae including camerated capillaries, 1–3 furcate setae, and a single large acicular spine (Fig. 29C–D insets); furcate setae with unequal tynes, with narrow tips and with thin fibrils along each edge extending inward toward opposite tyne (Fig. 28I). Abdominal neurosetae including capillaries and 1–2 emerging acicular spines (Fig. 29C–D insets); capillaries numbering 7–10 at first, reduced to 3–4 in middle and posterior setigers. Flail setae not observed.

Pygidium rounded, with two thick anal cirri, only observed on both juvenile paratypes (Fig. 28C).

Remarks. *Leodamas cuneatus* **n. sp**. is a distinctive species in having a broad wedge-shaped pre-setiger region that gives the worm the appearance of having a foreshortened anterior end; although short, the prostomium is clearly pointed, not blunt on the tip. In addition, there is a range of large to small spines with and without ribs along the shaft in the thoracic neuropodia. Species of *Leodamas*, by definition, typically have well-developed emergent acicular spines in abdominal neuropodia. However, in *L. cuneatus* **n. sp**. there are also emergent spines in abdominal notopodia. Based on morphology, this species has no close relatives.

Etymology. The epithet *cuneatus* is derived from *cuneus*, Latin for wedge, in reference to the unusual wedge-shaped pre-setiger region of this species.

Distribution. U.S. Atlantic continental slope, New England to off Delaware, in slope depths, 255–2060 m.

Leodamas mucronatus new species

Figures 30–33

urn:lsid:zoobank.org:act:E8FEAF96-8C12-4148-B100-300C30D828A1

Scoloplos (*Leodamas*) sp. 3: Blake *et al.* 1987: 71, C-4, D-8; Blake & Grassle 1994: 855.

Material examined. **Southeastern USA, off Charleston, South Carolina, US South Atlantic ACSAR program**, coll. J.A. Blake, Chief Scientist. **Sta. 14A**: Cruise SA-5, R/V *Gyre*, Rep. 1, 20 Sep 1985, 32°32.25′N, 77°15.24′W, 600 m, 2 **paratypes** (USNM 1622270); Rep. 2, 20 Sep 1985, 32°32.26′N, 77°15.29′W, 605 m, **holotype** (USNM 1622271), 6 **paratypes** (USNM 1622272).

Description. An elongate, threadlike species, consistently narrow along entire body, narrowest in far posterior segments; not exhibiting any enlargement or thickening of thoracic segments (Fig. 32A). Holotype complete with 110 setigers, 13.5 mm long and 0.7 mm wide across thoracic setigers. Paratype (USNM 1622270) incomplete with 80 setigers, 14 mm long, 0.7 mm wide. Holotype and paratypes with 19 thoracic setigers and branchiae from setiger 6 (Figs. 30A, 32A). Thoracic segments flattened dorsally, rounded ventrally; abdominal segments also flattened dorsally and rounded ventrally, with parapodia shifted dorsally. Thoracic setigers about 2.8 times wider than long (Figs. 30A, 32C); individual thoracic segments separated dorsally by a prominent intersegmental ridge (Figs. 30A, 32C); segments only weakly divided on venter; abdominal segments also short, about same width as thorax. Color in alcohol opaque white.

Pre-setiger region triangular, merged dorsally and ventrally with setiger 1 (Figs. 30A–B, 32C). Prostomium elongate, narrowing to acutely pointed tip (Figs. 30A–B, 32A, C); nuchal organs inconspicuous narrow slits on posterior lateral margin; eyespots absent. Peristomium smooth, merged with prostomium dorsally and ventrally and with setiger 1 dorsally (Fig. 30A); ventrally surrounding mouth, forming upper and lower lips (Fig. 30B); upper lip a smooth circular ring; ventral lip with 7–8 short lobes (Fig. 30B). Proboscis not everted on any specimen.

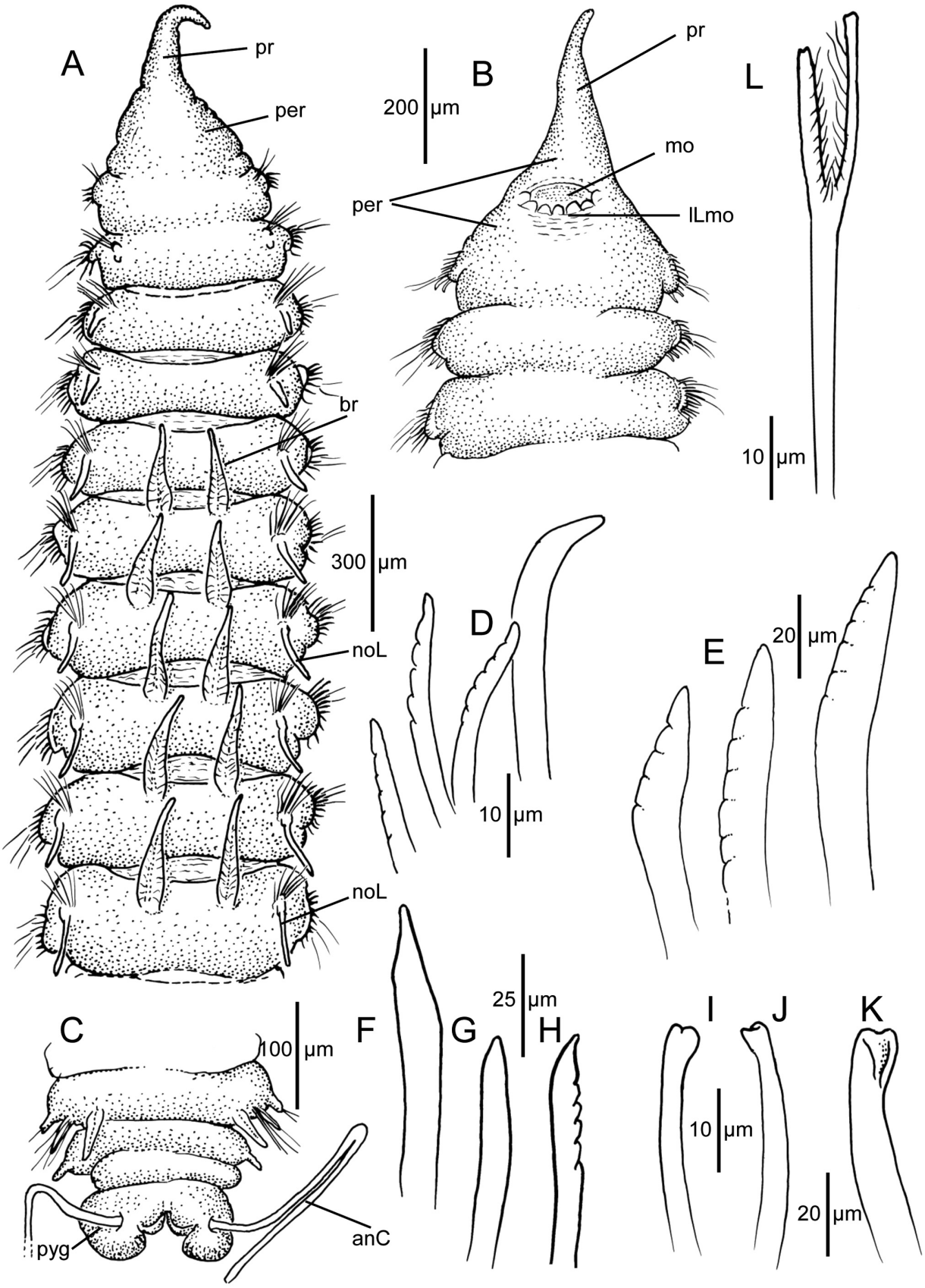

FIGURE 30. *Leodamas mucronatus* **n. sp.** Holotype (USNM 1622271): A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end with pygidium, dorsal view; D, smaller ribbed neuropodial uncini and larger smooth spine from setigers 1–2; E, large ribbed uncini from thoracic setigers 3–16; F–H, upper and lower uncini from setiger 18; I–K, abdominal neuropodial acicula; L, furcate seta.

Thoracic notopodia with postsetal lobes short, inconspicuous on setigers 1–2, thereafter becoming long, narrow, digitiform (Figs. 30A, 31A, 32D, 33A). Thoracic neuropodia initially short, inconspicuous, becoming longer, digitiform by about setiger 8–10 (Fig. 31A); from setiger 15, second long digitiform subpodial lobe developing ventral to neuropodium (Figs. 31B, 33D–E), continuing over remaining thoracic setigers and onto a few anterior abdominal setigers (Fig. 31C). Transition to abdominal segments identified by thickening and elongation of neuropodium and fewer capillary neurosetae. Abdominal notopodia similar to those of thorax with long, digitiform postsetal lobe (Fig. 31C–D). Abdominal neuropodia with rounded apex and long, narrow subterminal lateral lobe or ventral cirrus (Fig. 31C–D). Interramal cirrus absent, but abdominal parapodia with a low thickened ridge between noto- and neuropodia accompanied by small patch of sensory cilia in some middle and posterior setigers (Fig. 31D).

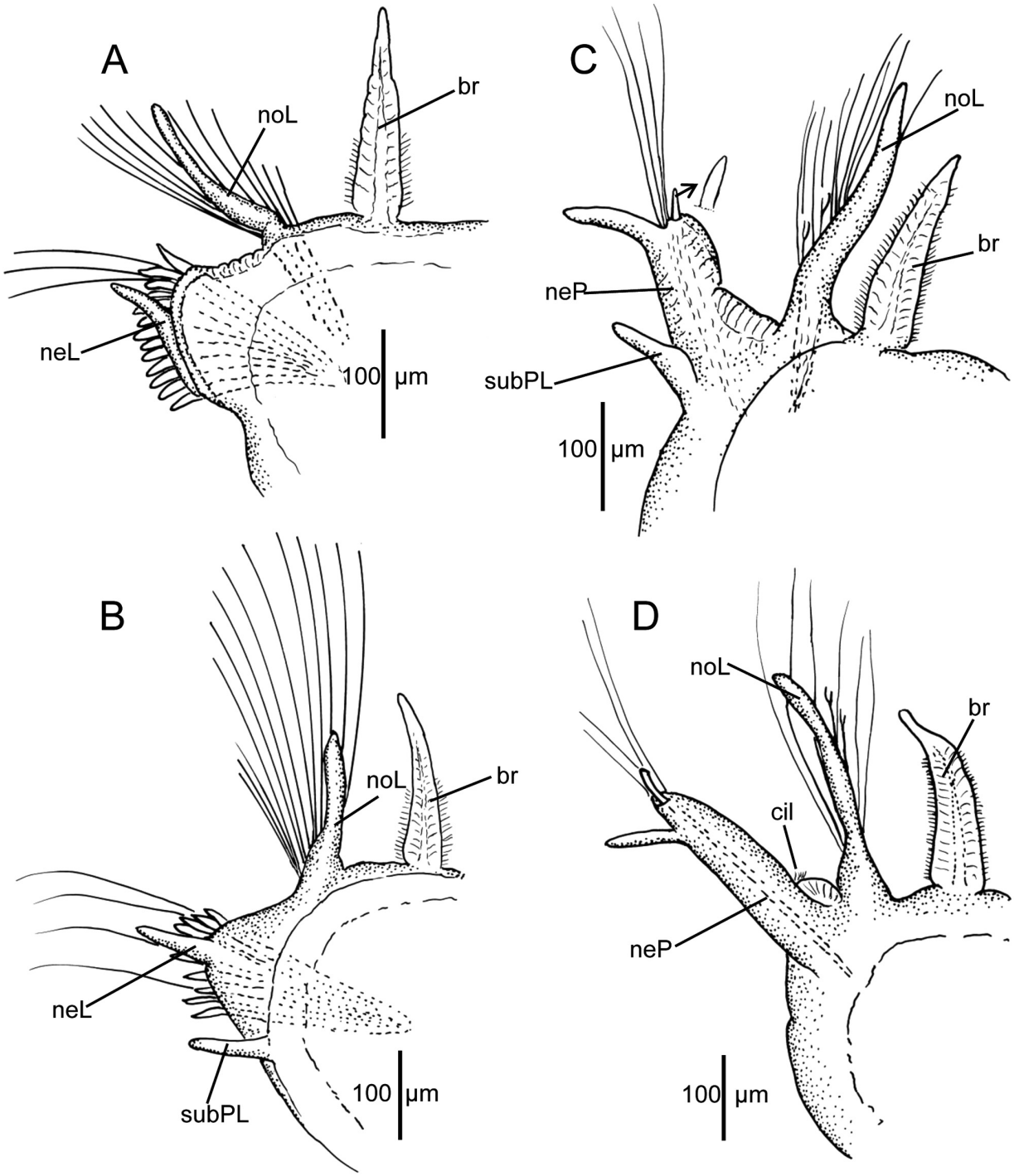

FIGURE 31. *Leodamas mucronatus* **n. sp.** Paratype (USNM 1622272): A, thoracic setiger 10, posterior view; B, thoracic setiger 16, posterior view. Holotype: (USNM 1622271): C, Abdominal setiger 30, posterior view (inset of acicula not to scale); D, far posterior setiger, posterior view.

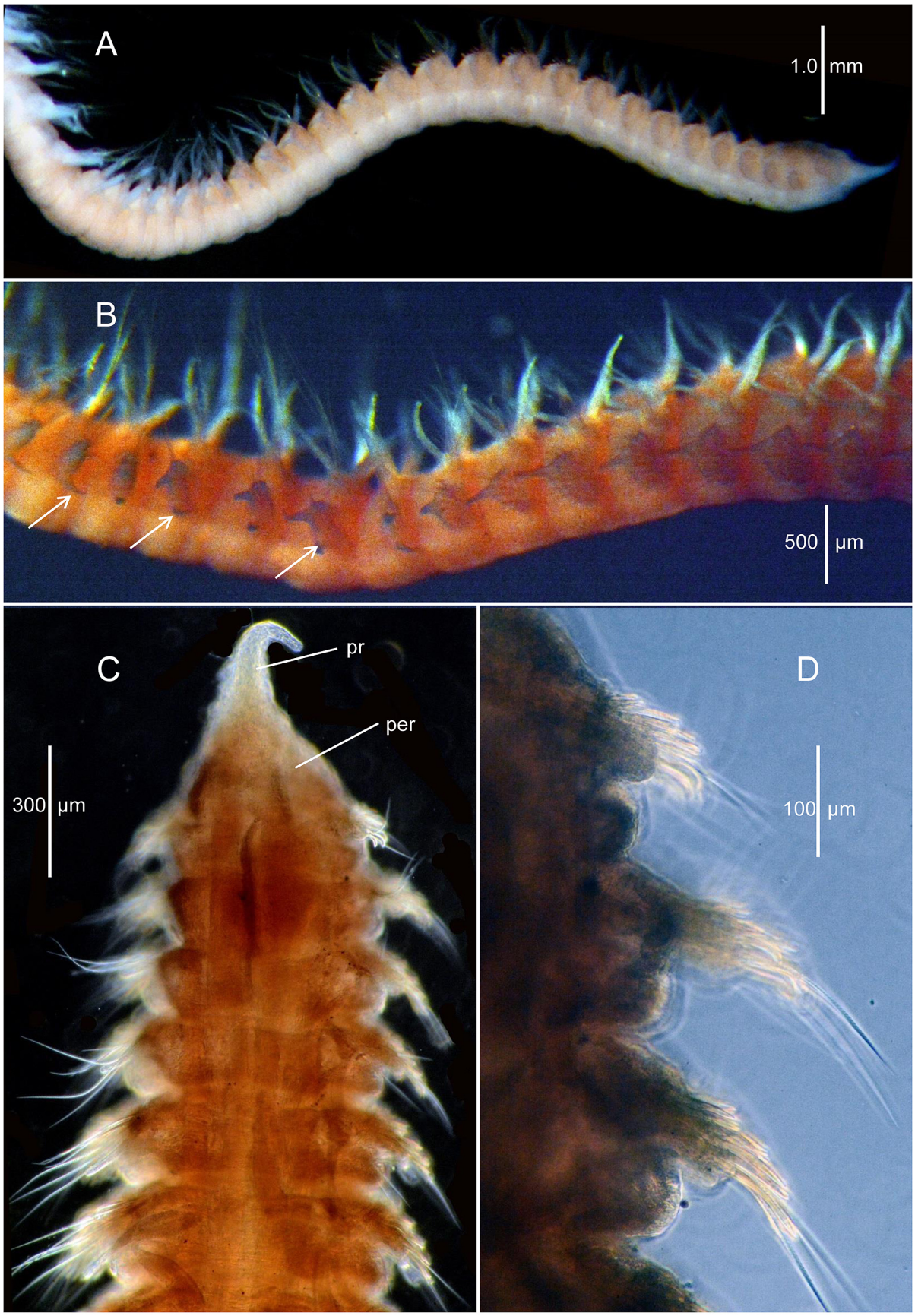

FIGURE 32. *Leodamas mucronatus* **n. sp.** Paratype (USNM 1622272): A, anterior one-fourth of body, right lateral view; B, transition from thorax to abdominal segments, right lateral view, arrows denote subpodial lobes; C, anterior end, dorsal view; D, setigers 1–3, ventral view of neuropodial uncini.

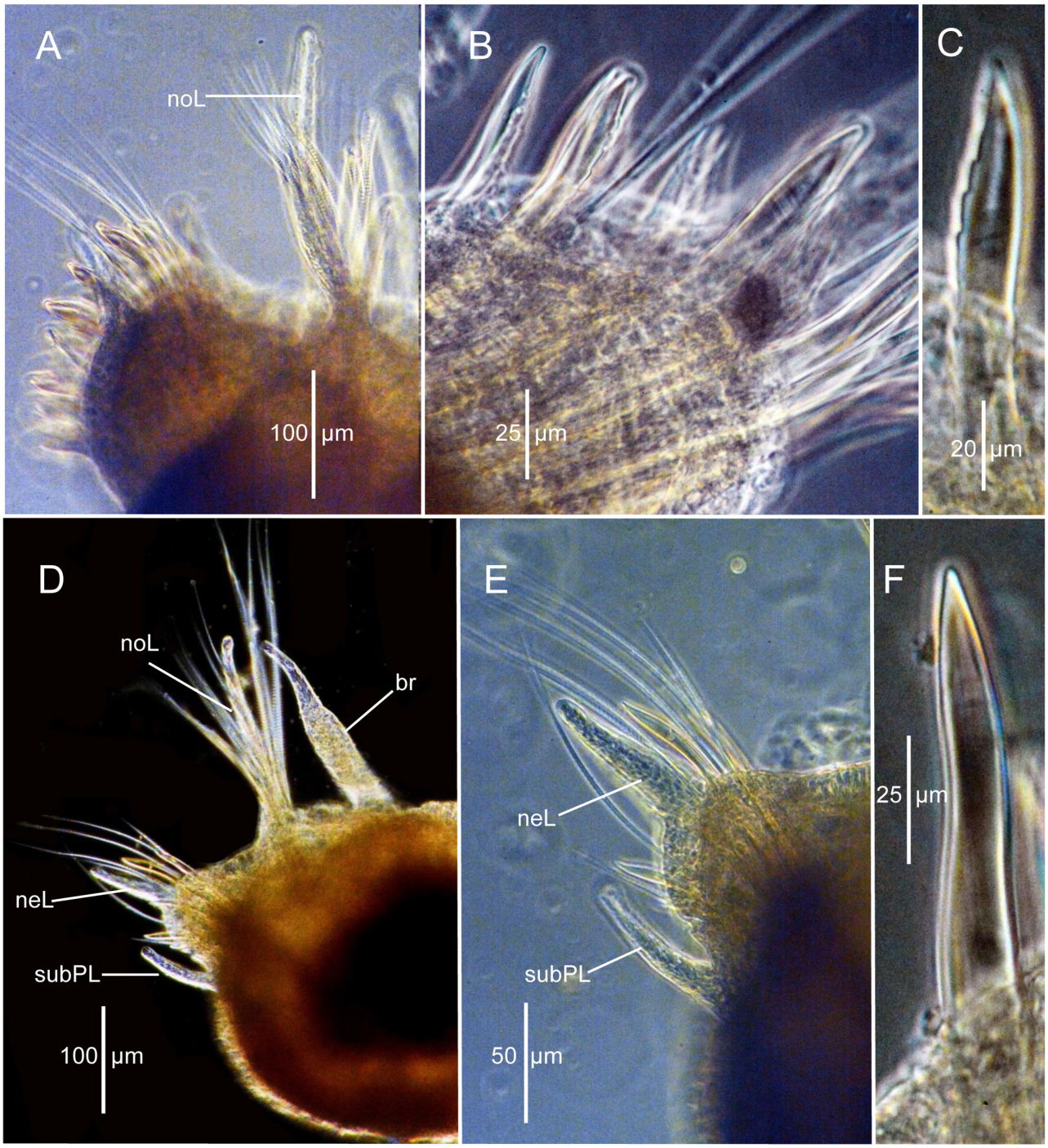

FIGURE 33. *Leodamas mucronatus* **n. sp.** Paratype (USNM 1622272): A, middle thoracic setiger, B, neuropodial uncini, thoracic setiger 15; C, detail of barbed uncini; D, thoracic setiger 18, anterior view; E, same, close-up of neuropodium; F, detail of spine from setiger 18. All stained with Shirlastain A.

Branchiae from setiger 6, elongate from first pair, widest basally (Fig. 30A), continuing along entire length of body (Figs. 31A–D, 33D); all branchiae with medial and lateral cilia along at least half their length.

Thoracic notosetae all camerated capillaries; first 2–3 setigers with 2–5 notosetae, increasing to 15–18 over subsequent thoracic segments. Thoracic neurosetae few capillaries and numerous uncini; uncini arranged in up to four vertical rows with capillaries limited to single tuft of 3–5 setae dorsal to last 1–2 rows of uncini and a few arising from last row of uncini. Uncini of setigers 1–2 narrow ribbed uncini on first 1–3 rows and 2–5 larger smooth curved uncini in last row (Fig. 30D); subsequent thoracic neuropodia of setigers 3–16 with large ribbed spines in all rows (Figs. 30E, 33B–C); setigers 17–18 with spines reduced to 2–3 per neuropodium, upper two spines large, smooth

(Figs. 30F–G, 33F), lowermost smaller, with weakly developed ribs (Fig. 30H). Abdominal notosetae including capillaries and 1–3 furcate setae. Furcate setae with unequal tynes, blunted on tips and with thin fibrils along each edge extending inward toward opposite tyne (Fig. 30L). Abdominal neurosetae including 3–4 relatively stiff capillaries, either smooth or with short barbs along one edge, and 1–2 emergent aciculae, each with an unusual, expanded tip with a notched apex (Fig. 30I–J), seen in some views as cavity (Fig. 30K). Flail setae not observed.

Pygidium with two lobes lateral to anal opening and with two elongate thin anal cirri (Fig. 30C).

Remarks. *Leodamas mucronatus* **n. sp**., in having branchiae from an anterior thoracic setiger and thoracic neuropodial uncini in three or more vertical rows, belongs to *Leodamas* Group A as defined by Blake (2017). *Leodamas mucronatus* **n. sp**. differs from other species in Group A by having a long, narrow, threadlike body and a triangular pre-setiger region that tapers to a long, acutely pointed prostomium. In addition, the elongate digitiform subpodial lobe on posterior thoracic and anterior abdominal setigers is unique in the genus. Other species have larger, more robust bodies and prostomia that are shorter and not acutely pointed. If present, extra neuropodial lobes are short, not elongate.

Etymology. The epithet is from *mucro*, Latin for a sharp point, referring to the long, pointed prostomium that is characteristic for this species.

Biology. Station 14A off Charleston at 600 m is an erosional current-swept area of sand waves with sediments having sand content of 91–94% (Blake & Grassle 1994). The site is dominated by polychaetes having long, thin bodies similar to *L. mucronatus* **n. sp**. The most abundant polychaete at the site is an as-yet-undescribed species of Cirratulidae in the genus *Caulleriella* (Blake & Grassle 1994: Table 6).

Distribution. Continental slope off Charleston, South Carolina, 600–605 m.

Leodamas notoaciculatus new species

Figures 34–35

urn:lsid:zoobank.org:act:D44B4EEC-F005-44B5-ADF3-C5782E2D2EDB

Material examined. **Atlantic Ocean, off New Jersey**, coll. P.A. Neubert, Chief Scientist, 12 Aug 2008; Excalibur pipeline survey, **Sta. 45B**, 40°11.5618′N, 73°40.4949′W, 38 m, **holotype** (MCZ 161598).

Description. A small species, holotype complete, 2.5 mm long, 0.4 mm wide across thorax for 40 setigers. Body widest across thoracic setigers, gradually narrowing along abdominal segments (Fig. 35A). With nine thoracic setigers and branchiae from setiger 5 (Fig. 34A). Thoracic segments generally flattened, about five times wider than long; dorsum with narrow intersegmental grooves enlarged and elevated medially (Fig. 34A), grooves continuing on anterior abdominal setigers; venter with similar grooves and medial enlargement, but not as prominent (Fig. 34B). Abdominal segments about twice as wide as long along most of body, not as flattened as those of thorax and more rounded on venter; posterior setigers crowded. Color in alcohol opaque white.

Pre-setiger region oval, with large peristomium overlapping setiger 1 and part of setiger 2 dorsally and merging with setiger 1 ventrally (Fig. 34A–B). Prostomium relatively short, triangular; eyespots absent; nuchal organs not observed. Peristomium a single ring, with lateral folds and relatively smooth dorsal crest (Figs. 34A, 35A); ventrally surrounding mouth and forming upper and lower lips. Upper lip with two lateral and one medial lobe, not well defined; ventral lip a thick rim not divided into separate lobes (Fig. 34B). Proboscis not everted.

Thoracic notopodia with no postsetal lobes on setigers 1–2; a pair of long, thin, digitate postsetal lobes fully developed from setiger 3 (Fig. 34A); these continuing onto abdominal segments and along entire body. Thoracic neuropodia of setigers 1–6 with no visible postsetal lobe or lamellae; short, rounded, papillate postsetal lobe from setiger 7 (Fig. 34A), becoming longer and digitate by setiger 9. Transition to abdominal segments identified by loss of thoracic neuropodial uncini and thickening and elongation of neuropodium. Abdominal neuropodia initially a short thickened digitate lobe, entire apically; middle abdominal setigers developing short medially directed lobe; subpodial lobes absent; subpodial flanges short, closely adhering. Interramal cirri absent.

Branchiae from setiger 5, elongate, widest basally, tapering to narrow tip (Fig. 34A); subsequent thoracic and anterior abdominal branchiae elongate, widest basally, tapering to narrow apex (Figs. 34A, 35A), similar along entire length of body; all branchiae with lateral cilia along at least half their length.

Thoracic notosetae including long camerated capillaries (Figs. 34A, 35A–B) and 1–2 emergent acicular spines; capillaries numbering up to 5–8 in notopodia; acicular spines short, pointed (Fig. 34I). Thoracic neurosetae including 10–12 prominent uncini arranged into two rows (Fig. 35B–C) and 3–4 capillaries on posterior margin; uncini of

first row of setigers 1–3 thinner, less robust than on following setigers; these uncini with 4–6 transverse rows of ribs along shaft (Fig. 34D); uncini of second row and all rows on setigers 4–9 larger, more robust, some with a distinct groove along concave margin and bordered with transverse ribs (Fig. 34E–F); some uncini smooth, lacking ribs (Fig. 34G). Abdominal notosetae including 3–7 capillaries, 1–2 emergent aciculae, and 1–2 furcate setae. Aciculae similar to those of thoracic notopodia; furcate setae with two unequal tynes, each tapering to pointed tip, with thin fibrils along inner margin extending inward toward opposite side (Fig. 34J). Abdominal neurosetae including 3–5 thin capillaries and 1–2 emergent aciculae, each acicula narrow, with narrow rounded tip (Fig. 34H). Flail setae not observed.

Pygidium with numerous elongate lobes surrounding anal opening; with two unusually long, thin anal cirri, these as long as one-third of entire body length (Figs. 34C, 35A).

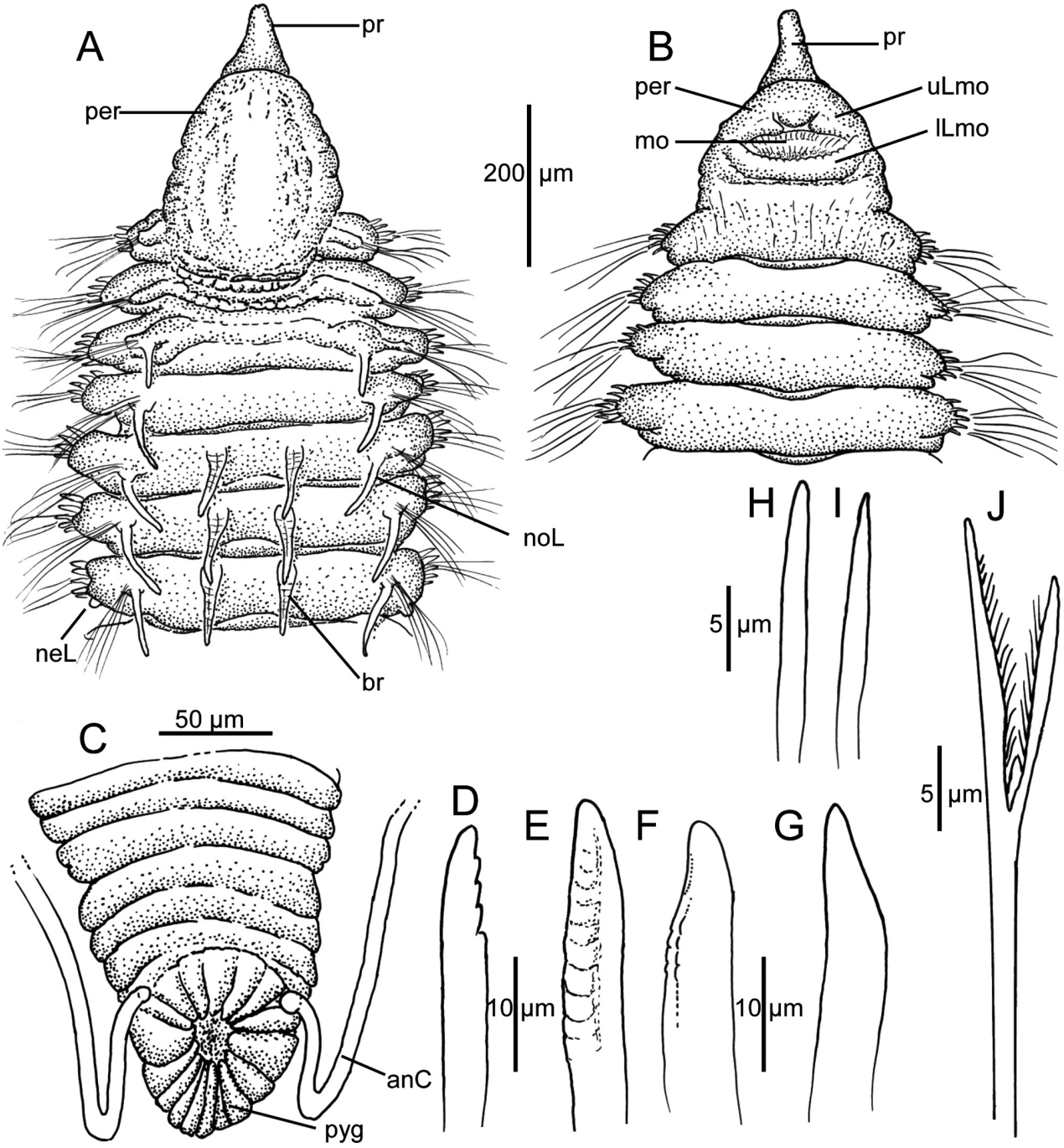

FIGURE 34. *Leodamas notoaciculatus* **n. sp.** Holotype (MCZ 161598): A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end, dorsal view; D–G, neuropodial uncini from thoracic setigers: setiger 1 (D), setiger 3 (E), setiger 5 (F); setiger 7 (G); H, abdominal neuropodial acicula; I, thoracic notopodial acicula; J, abdominal notopodial furcate seta.

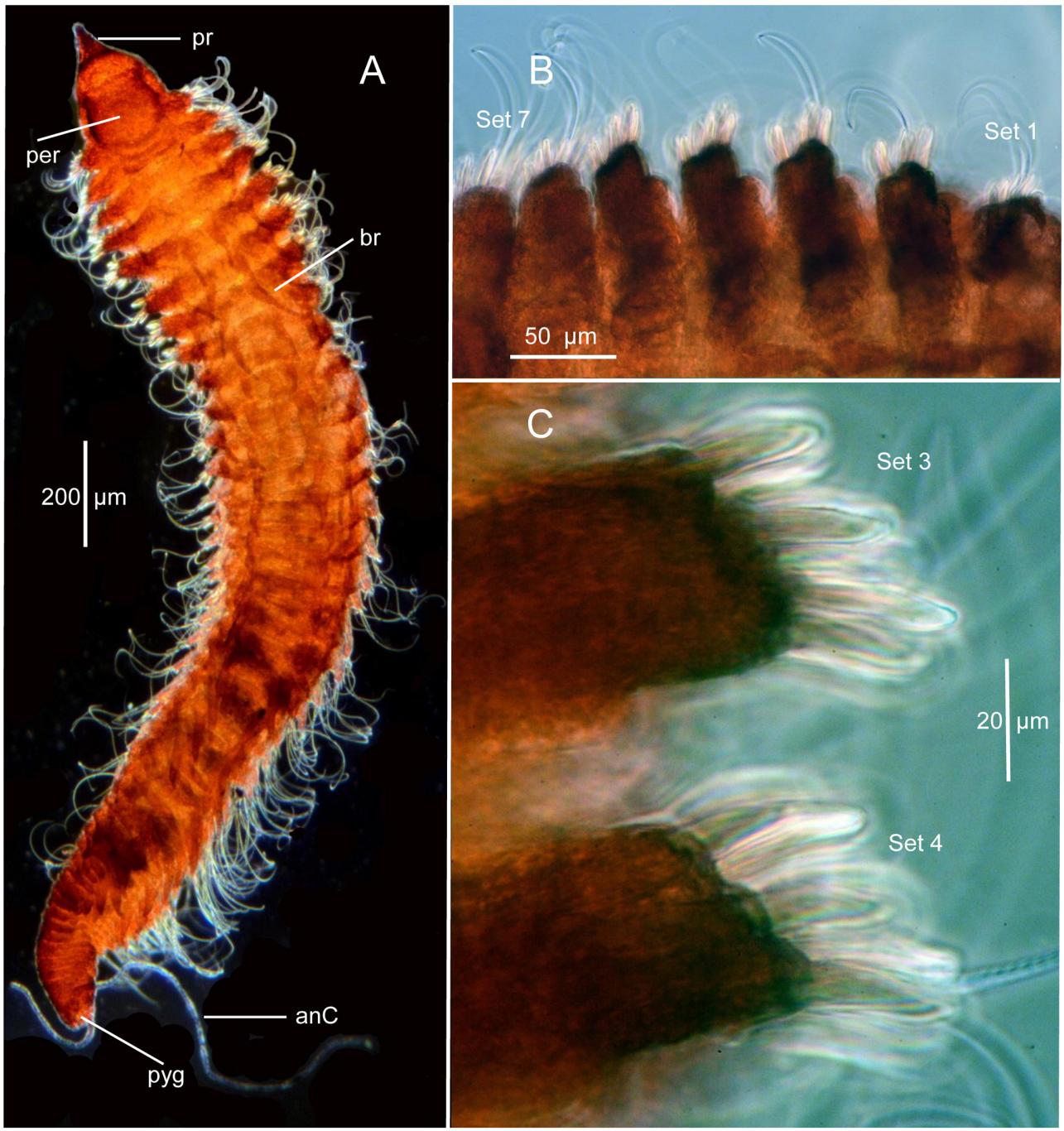

FIGURE 35. *Leodamas notoaciculatus* **n. sp**. Holotype (MCZ 161598): A, entire worm, dorsal view; B, setigers 1–7, dorsal view of neuropodial uncini; C, setigers 3–4, dorsal view of neuropodial uncini. All stained with Shirlastain A.

Remarks. The single available specimen of *Leodamas notoaciculatus* **n. sp.** is likely a juvenile but has several unique characters not found heretofore in the genus: (1) the pre-setiger region is large, oval-shaped, and longer than the first five setigers, (2) setigers 1–2 entirely lack notopodial postsetal lobes; then long, digitate fully developed postsetal lobes appear on setiger 3 and continue along the entire body, (3) the furcate setae have unequal tynes that terminate in narrow, pointed tips. Most orbiniids have furcate setae with blunt-tipped tynes. While the presence of emergent and prominent aciculae in abdominal neuropodia is typical in the genus, *L. notoaciculatus* **n. sp.** also has emergent aciculae in both the thoracic and abdominal notopodia.

Based on the review presented by Blake (2017) and more recent species described by Sun *et al.* (2018) and Blake (2020) there are no close relatives to *L. notoaciculatus* **n. sp**. The lack of specimens of this species is surprising given the long timeframe of benthic studies along the US Atlantic coast. However, the species was collected

from sediments having high sand content and these non-depositional sediments are not routinely sampled as part of offshore monitoring and reconnaissance programs.

Biology. Sediment grain size at Station 45B where *Leodamas notoaciculatus* **n. sp**. was collected consisted of 98% coarse sand, 0.7% silt, and 1.3% clay. The site was dominated by filter feeding amphipods and the polychaete *Polygordius jouinae* Ramey *et al*., 2006.

Etymology. The epithet is derived from the Greek, *noto* for back or dorsum, and the Latin *acicula* for pin, referring to the notopodial acicula found in this species.

Distribution. U.S. Atlantic continental shelf, off New Jersey, 38 m.

Genus *Califia* Hartman, 1957 Emended

Type-species: *Califia calida* Hartman, 1957, by monotypy.

Diagnosis. Prostomium pointed on anterior margin. Peristomium consisting of a single achaetous ring. Transition from thorax to abdomen abrupt due to distinct change in neuropodia. Branchiae from setiger 8–10; each branchia simple, lanceolate, may be lacking in most of abdominal region. Thoracic setae all capillaries; abdominal setigers 1–3 (rarely 4) with dense fascicles of thickened uncini in neuropodia and none to a few capillaries; subsequent thoracic neuropodia usually with all capillaries; one species with a few thin uncini and capillaries continuing to end of thorax. Neuropodial uncini of setigers 1–3 with shafts either smooth or with ribs; tip of shaft with distinct sheath, often frayed, appearing bristled in light microscopy. Neuropodia with or without postsetal lobe; subpodial lobes absent. Abdominal segments lacking interramal and ventral cirri. Abdominal setae including capillaries, furcate setae, and flail setae; no uncini. Pygidium a rounded lobe with two anal cirri.

Remarks. *Califia* is a small genus with only five known species (Blake 2017, 2020). Species of *Califia* are characterized by having heavy spines or uncini in the first three thoracic neuropodia and few transitional spines in setiger 4 (or typically, spines lacking). One species, *C. bilamellata* Blake, 2017, has a few thin thoracic neuropodial uncini with ribs along the shaft and capillaries continuing from setiger 4 to the end of the thorax. The heavy spines provide setigers 1–3 with a different appearance relative to the subsequent thoracic segments that have only capillaries or only a few similar spines. Pettibone (1957) noted that a few transitional spines were sometimes present among the capillaries of the unmodified setiger 4 of *C. schmitti* (Pettibone, 1957); Blake (2017) observed extra spines on setigers 4–5 of the holotype of *C. chilensis* Hartman, 1967 and transitional spines have been observed in setiger 4 of *C. calida* by Blake (1996, 2020). However, the presence and number of extra neuropodial spines after setiger 3 is variable. In the present study, numerous specimens of *C. schmitti* were collected as part of the ACSAR program in slope depths off the U.S. Atlantic coast. One specimen was observed with extra spines on setiger 4 (Fig. 37C).

Califia schmitti (Pettibone, 1957)

Figures 36–37

Scoloplos (*Scoloplos*) *schmitti* Pettibone, 1957: 164, fig. 3; 1963: 287–288, fig. 74d.
Califia schmitti: Hartman 1959: 364; 1965: 127–128; Hartman & Fauchald 1971: 91; Blake *et al*. 1987: C-4; Maciolek *et al*. 1987a: D-4; Maciolek *et al*. 1987b: D-3; Hilbig 1994: 942.
Califia calida: Taylor 1984: 1-21 to 1-23, Figs. 1-21 to 1-22. **Not** Hartman 1957.

Material examined. (*97 specimens*) **Off New England, US North Atlantic ACSAR program**, coll. G.W. Hampson, Chief Scientist. **Sta. 3**: Cruise NA-2, Rep. 2, 26 Apr 1985, 41°01.34′N, 66°20.21′W, 1340 m (3, USNM 1622214); Rep. 3, 26 Apr 1985, 41°01.28′N, 66°20.25′W, 1345 m (1 juv., USNM 1622215); Cruise NA-4, Rep. 2, 22 Nov 1985, 41°01.42′N, 66°20.32′W, 1334 m (1 juv., USNM 1622216); Rep. 3, 22 Nov 1985, 41°01.45′N, 66°20.35′W, 1330 m (1, USNM 1622217); Cruise NA-6, Rep. 1, 25 Jul 1986, 41°01.55′N, 66°20.12′W, 1345 m (1, USNM 1622218). **Sta. 8**: Cruise NA-2, Rep. 2, 28 Apr 1985, 41°10.27′N, 67°37.22′W, 2180 m (2, USNM 1622219); Cruise NA-5, Rep. 2, 29 Apr 1986, 41°10.19′N, 67°37.29′W, 2165 m (1 juv., USNM 1622220). **Sta. 9**: Cruise NA-4, Rep. 1, 27 Nov 1985, 39°50.42′N, 70°01.65′W, 1224 m (1, USNM 1622221); Rep. 3, 27 Nov 1985, 39°50.39′N, 70°01.65′W, 1239 m (1, USNM 1622222); Cruise NA-6, Rep. 1, 28 Jul 1986, 39°50.37′N, 70°01.72′W, 1233 m (2, USNM 1622223).

Sta. 10: Cruise NA-2, Rep. 1, 03 May 1985, 39°48.19′N, 70°05.26′W, 1210 m (1, USNM 1622224); Cruise NA-4, Rep. 3, 27 Nov 1985, 39°48.10′N, 70°05.33′W, 1219 m (2, USNM 1622225). **Sta. 13**: Cruise NA-1, Rep. 1, 15 Nov 1984, 39°54.32′N, 70°55.09′W, 558 m (1, USNM 1622226); Cruise NA-4, Rep. 3, 30 Nov 1985, 39°54.32′N, 70°55.12′W, 544 m (1, USNM 1622227).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR program**, coll. R.M. Petrecca, Chief Scientist. **Sta. 3**: Cruise Mid-1, Rep. 1, 05 May 1984, 38°36.3′88N, 70°51.41′W, 2055 m (1, USNM 1622228); Rep. 3, 05 May 1984, 38°36.86′N, 70°51.29′W, 2060 m (1, USNM 1622229). **Sta. 5**: Cruise Mid-1, Rep. 2, 08 May 1984, 38°50.54′N, 72°33.18′W, 2055 m (1, USNM 1622230); Cruise Mid-2, Rep. 1, 01 Aug 1984, 38°50.42′N, 72°33.03′W, 2089 m (1, USNM 1622231); Rep. 2, 01 Aug 1984, 38°50.42′N, 72°33.05′W, 2089 m (1, USNM 1622232); Rep. 3, 01 Aug 1984, 38°50.52′N, 72°33.96′W, 2074 m (4, USNM 1622233); Cruise Mid-4, Rep. 1, 16 May 1985, 38°50.46′N, 72°33.23′W, 2080 m (4, USNM 1622234); Cruise Mid-6, Rep. 2, 11 Nov 1985, 38°50.49′N, 72°33.127′W, 2079 m (1, USNM 1622235). **Sta. 6**: Cruise Mid-1, Rep. 3, 03 May 1984, 39°05.59′N, 72°03.00′W, 2090 m (1, USNM 1622236); Cruise Mid-3, Rep. 3, 28 Nov 1984, 39°05.65′N, 72°03.08′W, 2085 m (1, USNM 1622237). **Sta. 7**: Cruise Mid-1, Rep. 3, 06 May 1984, 38°27.34′N, 72°03.48′W, 2100 m (1, USNM 1622238); Cruise Mid-2, Rep. 3, 06 Aug 1984, 38°27.34′N, 72°03.48′W, 2100 m (2, USNM 1622239). **Sta. 8**: Cruise Mid-2, Rep. 3, 08 Aug 1984, 38°27.18′N, 73°04.78′W, 2159 m (1, USNM 1622240). **Sta. 9**: Cruise Mid-6, Rep. 3, 17 Nov 1985, 38°17.24′N, 72°14.51′W, 2104 m (1, USNM 1622241). **Sta. 11**: Cruise Mid-1, Rep. 1, 07 May 1984, 38°40.16′N, 72°56.82′W, 1515 m (1, USNM 1622242); Rep. 3, 07 Aug 1984, 38°40.22′N, 72°56.27′W, 1520 m (1, USNM 1622243). **Sta. 13**: Cruise Mid-1, Rep. 1, 02 Apr 1984, 37°53.33′N, 73°45.09′W, 1613 m (1, USNM 1622244); Cruise Mid-2, Rep. 1, 07 Aug 1984, 37°53.35′N, 73°45.01′W, 1614 m (1, USNM 1622245); Cruise Mid-3, Rep. 2, 30 Nov 1984, 37°53.29′N, 73°45.11′W, 1612 m (1, USNM 1622246); Cruise Mid-4, Rep. 1, 19 May 1985, 37°53.26′N, 73°45.25′W, 1615 m (1, USNM 1622247); Cruise Mid-6, Rep. 3, 16 Nov 1985, 37°53.23′N, 73°45.27′W, 1607 m (2, USNM 1622248). **Sta. 14**: Cruise Mid-1, Rep. 2, 02 Apr 1984, 37°53.79′N, 73°44.78′W, 1503 m (1, USNM 1622249); Cruise Mid-5, Rep. 3, 10 Aug 1985, 37°53.79′N, 73°44.79′W, 1490 m (1, USNM 1622250).—**Southeastern USA, U.S. South Atlantic ACSAR program,** coll. J.A. Blake, Chief Scientist. **Off Cape Hatteras, NC**, **Sta. 10**: Cruise SA-4, Rep. 3, 24 May 1985, 35°26.44′N, 74°41.30′W, 1985 m (1, USNM 1622251). **Hatteras Canyon, Sta. 6**: Cruise SA-1, Rep. 3, 19 Nov 1983, 34°48.53′N, 75°16.22′W, 2060 m (7, USNM 1622252); Cruise SA-2, Rep. 1, 25 May 1984, 34°49.90′N, 75°13.50′W, 1974 m (7, USNM 1622253); Rep. 2, 25 May 1984, 34°50.20′N, 75°13.40′W, 1979 m (9, USNM 1622254); Rep. 3, 25 May 1984, 34°49.90′N, 75°13.70′W, 1984 m (5, USNM 1622255); Cruise SA-3, Rep. 1, 20 Jul 1984, 34°49.80′N, 75°13.50′W, 2003 m (3, USNM 1622256). **Off Cape Lookout, NC**, **Sta. 2**: Cruise SA-3, Rep. 2, 15 Jul 1984, 34°15.00′N, 74°43.70′W, 1002 m (1, USNM 1622257). **Sta. 3**: Cruise SA-2, Rep. 2, 27 Mar 1984, 34°14.63′N, 75°40.17′W, 1513 m (7, USNM 1622258); Cruise SA-3, 15 Jul 1984, 34°15.10′N, 75°40.30′W, 1489 m (7, USNM 1622259). **Sta. 4**: Cruise SA-1, Rep. 1, 16 Nov 1983, 34°11.68′N, 75°39.54′W, 1860 m (3, USNM 1622260); Cruise SA-4, 23 May 1985, Rep. 2, 23 May 1985, 34°11.22′N, 75°38.44′W, 2051 m (2, USNM 1622261); Rep. 3, 23 May 1985, 34°11.29′N, 75°38.67′W, 2015 m (1, USNM 1622262); Cruise SA-6, Rep. 3, 24 Nov 1985, 34°11.23′N, 75°38.53′W, 2057 m (1, USNM 1622263). **Off Cape Fear, NC**, **Sta. 11**: Cruise SA-5, Rep. 3, 23 Sep 1985, 33°04.86′N, 76°25.12′W, 797 m (1, USNM 1622264); Cruise SA-6, Rep. 1, 22 Nov. 1985, 33°04.95′N, 76°25.15′W, 804 m (1, USNM 1622265). **Off Charleston, SC**, **Sta. 14**: Cruise SA-4, Rep. 3, 20 May 1985, 32°23.67′N, 76°01.17′W, 803 m (1, USNM 1622266).

Comparative material examined. (*19 specimens*) **Gulf of Mexico, off Louisiana, Virgo Platform Survey**, R/V *Brooks McCall*, coll. J.A. Blake, Chief Scientist: **Sta. V-1W**, 11 Nov 2008, 29°10.9217′N, 088°10.2920′W, 340 m (1, MCZ 161670). **Sta. V-2W**, 11 Nov 2008, 29°10.9205′N, 088°10.3563′W, 347 m (1, MCZ 161671). **Sta. V-1E**, 11 Nov 2008, 29°10.9167′N, 088°10.09.8484′W, 340 m (1, MCZ 161672). **Sta. V-2E**, 11 Nov 2008, 29°10.9147′N, 088°09.7865′W, 340 m (1, MCZ 161673). **Sta. V-3E**, 11 Nov 2008, 29°10.9240′N, 088°09.7202′W, 340 m (2, MCZ 161674). **Sta. V-1S**, 11 Nov 2008, 29°10.7201′N, 088°10.0711′W, 361 m (2, MCZ 161675).**Sta. V-2S**, 11 Nov 2008, 29°10.6701′N, 088°10.0716′W, 364 m (3, MCZ 161676). **Sta. V-3S**, 11 Nov 2008, 29°10.6119′N, 088°10.0718′W, 361 m (1, MCZ 161677). **Sta. V-1N**, 11 Nov 2008, 29°11.1133′N, 088°10.0726′W, 335 m (1, MCZ 161678). **Sta. V-2N**, 11 Nov 2008, 29°11.1637′N, 088°10.0756′W, 331 m (3, MCZ 161679). **Sta. V-3N**, 11 Nov 2008, 29°11.2189′N, 088°10.0730′W, 330 m (2, MCZ 161680**). Sta. V-4N**, 12 Nov 2008, 29°11.4926′N, 088°10.0801′W, 313 m (1, MCZ 161681).

Description. A moderate to large species; complete specimen (USNM 1622224) with 125 setigers, 22.7 mm long and 0.5 mm wide across thoracic segments. Larger specimens all incomplete; one (USNM 1622224) with 60

setigers, 15 mm long and 1.3 mm wide; Pettibone (1957) recorded an incomplete specimen with 50 setigers, 20 mm long and 2 mm wide. Thoracic setigers about six times as wide as long (Fig. 36A); abdominal segments short, crowded, about 20 times as wide as long. First three setigers thickened on larger specimens due to modified neuropodia; with shallow mid-ventral groove on first 4–6 setigers (Fig. 37A). Thoracic segments uniannulate except for mid-dorsal intersegmental area from about setiger 9 where mid-dorsal swelling becomes evident (Fig. 36A); abdominal segments bi- or triannulate, best developed on venter. Color in alcohol light tan; some specimens with mid-dorsal intersegmental areas with dark pigment from about setigers 9–10 and on a few anterior abdominal segments.

Pre-setiger region triangular, about as long as first two setigers (Fig. 36A–B). Prostomium short, conical, tapering to narrow apex (Fig. 36A–B); eyespots absent; nuchal organs inconspicuous narrow slits on posterior-lateral margins. Peristomium short, wider than long, smooth dorsally, with a single annular ring surrounding elongate mouth opening (Fig. 36B); lateral lips composed of 5–6 rounded lobes on either side and single narrow anterior and posterior oral lobes; oral apparatus extending posteriorly about half way onto setiger 1 (Figs. 36B, 37C).

Thorax on all large specimens with 13 setigers. Setigers 1–3 with short, papillate postsetal notopodial lamellae (Fig. 36D); neuropodia with similar but larger postsetal lobes (Fig. 36D). Subsequent thoracic segments with elongate, digitate noto- and neuropodial postsetal lamellae (Fig. 36G). Abdominal notopodia narrow, elongate (Fig. 36I); abdominal neuropodia dorsally elevated, apically expanded and divided into two short equal lobes between which capillary setae arise (Fig. 36I), usually in two separate fascicles; narrow acicula present, difficult to observe.

Branchiae from setiger 9, full-sized from first, overall relatively short and narrow (Fig. 36A); branchiae of abdominal segments generally wider (Fig. 36I), but not longer than those of thoracic setigers (Fig. 36G).

All thoracic notosetae dense fascicles of camerated capillaries. Setigers 1–3 with modified neurosetae, thus differing in superficial appearance from setiger 4 and following segments having only fascicle of capillaries (Figs. 36D, 37A–B); anomalous extra neuropodial spines on setiger 4 rarely observed; one specimen (USNM 1622218) with a full complement of modified neurosetae one side of setiger 4 but only capillaries on the other side (Fig. 37C). Thoracic neurosetae of setigers 1–3, rarely 4 of three types: (1) anterior row of 10 or more short, narrow ribbed uncini with adhering sheath, fragmenting apically into tattered bristles (Figs. 36E, 37E); (2) 1–2 rows of long, smooth heavy spines bearing narrow adhering sheath apically divided into bristles, bristles sometimes extending beyond end of seta (Figs. 36F, 37F–G); and (3) superior fascicle of thin camerated capillaries (Fig. 36D); subsequent thoracic setigers with dense fascicles of short and long camerated capillaries (Fig. 37D). Abdominal notosetae including long, camerated capillaries and 2–3 delicate furcate setae; flail setae absent. Furcate setae with unequal tynes each bearing thin row of needles projecting medially; shaft with transverse rows of barbs (Fig. 36H). Abdominal neurosetae 5–10 thin smooth capillaries; with 1–2 thin projecting aciculae.

Pygidium a rounded lobe with two long, thin anal cirri (Fig. 36C).

Remarks. Pettibone (1957) reported the absence of neuropodial postsetal lobes on the modified setigers 1–3; however, a short thickened papillate lobe is present in the new materials. *Califia schmitti* is most similar to *C. calida* Hartman, 1957 from the eastern Pacific, recently redescribed by Blake (2020). The two species are similar in most respects and differ only in minor details.

Blake (2020) reported *C. calida* with up to 14 thoracic setigers and branchiae from setigers 8–9; whereas in the present study, the largest specimens of *C. schmitti* from the U.S. Atlantic slope have 13 thoracic setigers and branchiae consistently from setiger 9. The neuropodial postsetal lamellae of setigers 1–3 in *C. calida* are large, spherical lobes, whereas those of *C. schmitti* are short and papillate. The notopodial furcate setae of *C. calida* have smooth shafts versus shafts with transverse rows of narrow barbs in *C. schmitti*. The nuchal organs of *C. calida* are conspicuous ciliated mounds versus narrow inconspicuous slits in *C. schmitti*. The most noticeable difference, however, is the nature of the mouth and surrounding peristomial lips. In *C. calida*, the mouth is as wide as long and surrounded by 4–5 lobes on the anterior margin and thickened lobes laterally and posteriorly. In *C. schmitti*, the mouth is elongate and narrow, with a single narrow anterior lobe and 5–6 lateral lobes. In both species the oral morphology extends about half-way on to setiger 1.

The specimens examined from the Gulf of Mexico off Louisiana agreed well with the Atlantic slope specimens. Thoracic setigers numbered 11–12 with branchiae consistently from setiger 9. Four specimens from off Florida and Texas reported as *C. calida* by Taylor (1984) agree with *C. schmitti* in having 13 thoracic setigers and branchiae from setiger 9, but were reported from much shallower depths.

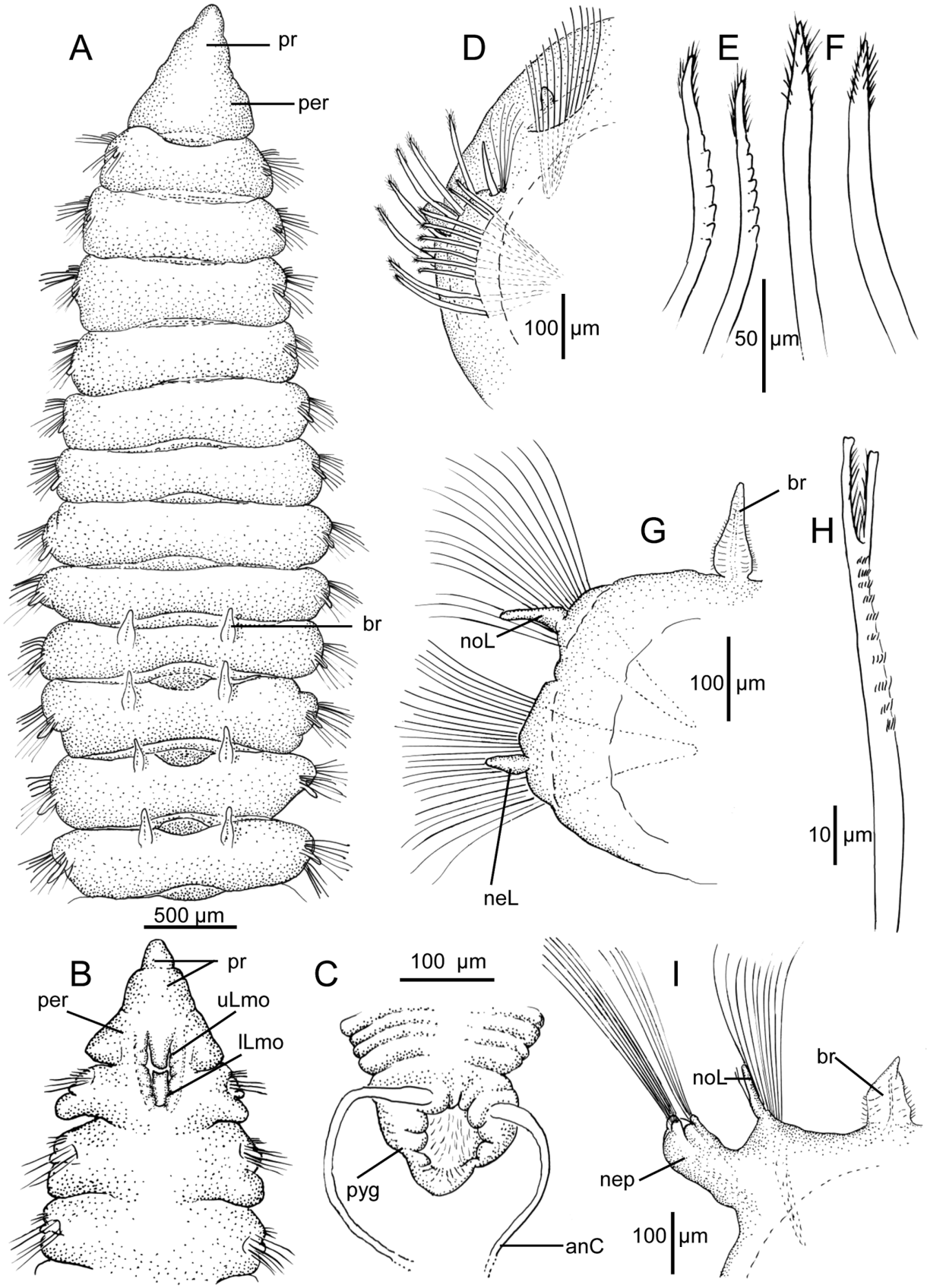

FIGURE 36. *Califia schmitti* (Pettibone, 1957). A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end, dorsal view; D, thoracic setiger 2, anterior view; E, modified neuropodial uncini from anterior row of setiger 2; F, modified neuropodial uncini from posterior row, setiger 2; G, thoracic setiger 9, posterior view; H, thoracic furcate seta from abdominal notopodium; I, anterior abdominal setiger, posterior view. A–B (USNM 1622218); C (USNM 1622224); D–I (USNM 1622247).

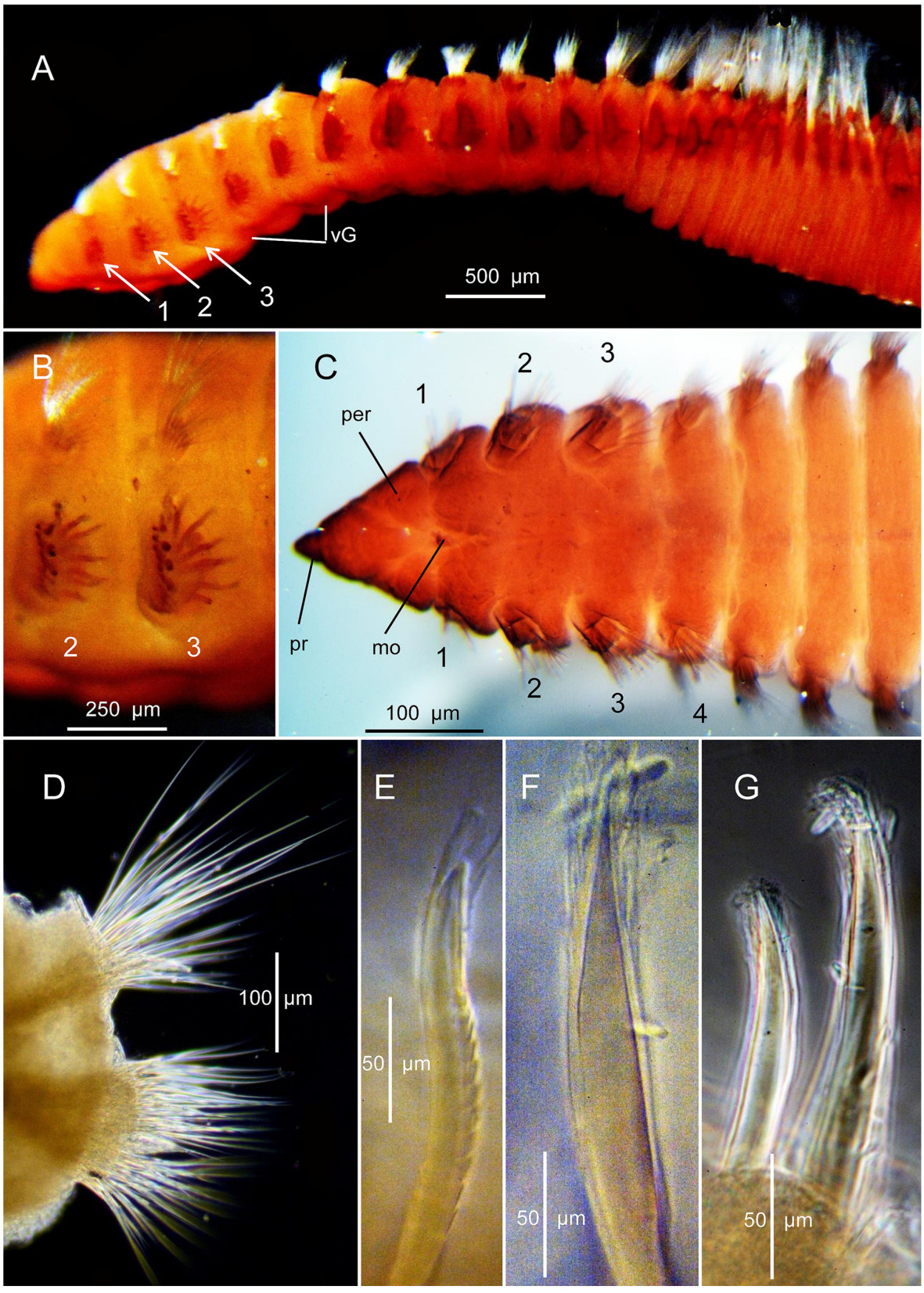

FIGURE 37. *Califia schmitti* (Pettibone, 1957). A, anterior end, left lateral view; B, same, detail of thoracic setigers 2–3; C, Anterior end, ventral view of first 7 setigers of specimen with modified neurosetae on setigers 1–4 on one side and setigers 1–3 on other side; D, thoracic setiger 9, anterior view; E, modified neuropodial uncini from anterior row of setiger 2; F–G, modified neuropodial uncini from posterior row, setiger 2. A–B (USNM 1622247); C, (USNM 1622217); D–G (USNM 1622247). All stained with Shirlastain A. Numbers identify setigers with modified neurosetae.

Biology. Out of 97 specimens from the U.S. Atlantic slope, 33 were collected from the Hatteras Canyon off North Carolina at a depth of 2000 m in sediments having high silt and clay inventories (Blake & Grassle 1994). The remaining 64 specimens were scattered over many stations and depths from New England to the Carolinas.

Distribution. Widespread along U.S. Atlantic continental slope; off New England to South Carolina, 544–2180 m; Gulf of Mexico, off Louisiana, 313–364 m.

Genus *Orbinia* Quatrefages, 1866

Aricia Savigny, 1820: 12, 35–36. Preoccupied. **Type-species**: *A. sertulata* Savigny, 1820, by monotypy.
Orbinia Quatrefages, 1866: 288. **Type-species**: *Aricia cuvieri* Audouin & Milne-Edwards, 1833 (=*Aricia sertulata* Savigny), designated by Hartman 1942.

Diagnosis. Prostomium conical, pointed; peristomium with one achaetous ring. Branchiae from thoracic setigers (5–20). Posterior thoracic segments with postsetal lobes (2–many) and subpodial lobes (3–many), usually forming ventral encircling fringe of five or more lobes. Thoracic neurosetae including blunt uncini, crenulated capillaries and rarely subuluncini; heavy spear-like or brush-tipped spines absent. Abdominal neuropodia with flail setae.

Remarks. Three species—*Orbinia swani* Pettibone, 1957, *O. riseri* (Pettibone, 1957), and *O. americana* Day, 1973—have been described and reported from the U.S. Atlantic coast. Each of these species was originally described from a single incomplete specimen. No specimens of *O. riseri* or *O. americana* were available in any of the new collections, but numerous specimens of *O. swani* were collected offshore on Georges Bank in the 1980s as part of the MMS long-term monitoring program. The specimens of *O. swani* include a range of sizes and a few complete specimens that provide additional details on the adult morphology as well as providing important information on morphological changes during growth.

Orbinia swani Pettibone, 1957

Figures 38–39

TABLE 2. Distribution and numbers of postsetal and subpodial lobes on specimens of *Orbinia swani* Pettibone, 1957 of different sizes and *O. americana* Day, 1973.

Specimens of *O. swani*	No th Set	No. set w/1 pst lobe	No. set w/2 pst lobes	No. set w/3 pst lobes	No. set w/4 pst lobes	No. set w/5 pst lobes
M-6, Sta. 5-12 (1st)	16	1–10	11–13	14–15	16–17	—
M-6, Sta. 5-12 (2nd)	17	1–10	11–15	16	17	—
M-4, Sta. 5-4	18	1–10	11–13	14–15	16–18	—
M-11, Sta. 5-28	21	1–10	11–14	15–16	17–18	19–21
M-10, Sta. 10	31	1	2	3	4	5–9
Holotype of *O. americana*	21	?	?	3	4	?

TABLE 2. (Continued)

Specimens of *O. swani*	No. set w/6 pst lobes	No. set w/7–12 pst lobes	No. set w/ & No. of subpod lobes	Br begin: Set	Th width (mm)
M-6, Sta. 5-12 (1st)	—	—	0	5	1.0
M-6, Sta. 5-12 (2nd)	—	—	0	5	1.0
M-4, Sta. 5-4	—	—	19 (1)	5	1.1
M-11, Sta. 5-28	—	—	18–19 (1); 20–25 (1–5)	5	1.2
M-10, Sta. 10	10–11	12–31	21–31 up to 22 on a side by set 25	5	2.2
Holotype of *O. americana*	?	18	7–22 up to 7 on a side	5	?

Abbreviations: Br, branchiae, pst, postsetal; set, setiger; subpod, subpodial; th, thoracic; w/, with.

Orbinia (*Orbinia*) *swani* Pettibone,1957: 161–162, fig. 1; 1963: 284, fig. 75 d–e.
Orbinia swani: Maciolek-Blake *et al*. 1985: B-5 (in part).
Scoloplos (?*Leodamas*) sp. A: Maciolek-Blake *et al*. 1985: B-5.

Material examined. **Northeastern USA. Maine, York Beach,** coll. 12 Jul 1953, E. Swan & N. Riser, **holotype** (USNM 28296).—**Georges Bank**, **Benthic Infauna Monitoring Program (1981–1984)**, coll. G.W. Hampson, Chief Scientist (*25 specimens*). **Sta. 1**: Cruise M-4, Rep. 6, 12 May 1982, 41°13.0′N, 67°15.3′W, 58 m (1, USNM 1622273); Cruise M-8, Rep. 3, 15 May 1983, 41°13.0′N, 67°15.3′W, 57 m (1, USNM 1622274); Cruise M-11, Rep. 4, Feb 1984, 41°13.0′N, 67°15.3′W, 55 m (1, USNM 1622275). **Sta. 2**: Cruise M-4, Rep. 2, 12 May 1982, 40°59.1′N, 66°55.9′W, 66 m (1, USNM 1622276); Cruise M-11, Rep. 5, 03 Feb 1984, 40°59.1′N, 66°55.8′W, 79 m (1, USNM 1622277). **Sta. 10**: Cruise M-10, Rep. 4, 14 Nov 1983, 40°42.0′N, 68°35.3′W, 66 m (1, USNM 1622278); Cruise M-11, Rep. 1, 02 Feb 1984, 40°42.0′N, 68°35.3′W, 66 m (1, USNM 1622279); Rep. 5, 02 Feb 1984, 40°42.0′N, 68°35.3′W, 66 m (2, USNM 1622280). **Sta. 12**: Cruise M-12, Rep. 2, 03 Jun 1984, 40°22.2′N, 68°30.2′W, 108 m (1, USNM 1622281). **Sta. 5-1**: Cruise M-2, Rep. 1, 19 Nov 1981, 40°39.5′N, 67°46.2′W, 81 m (1, USNM 1622282); Cruise M-4, Rep. 5, 14 May 1982, 40°39.5′N, 67°46.2′W, 80 m (1, USNM 1622283); Cruise M-8, Rep. 5, 17 May 1983, 40°39.5′N, 67°46.2′W, 81 m (1, USNM 1622284). **Sta. 5-2**: Cruise M-3, Rep. 1, 15 Feb 1982, 40°39.6′N, 67°45.8′W, 81 m (1, USNM 1622285). **Sta. 5-4**: Cruise M-4, Rep. 3, 14 May 1982, 40°39.5′N, 67°46.5′W, 80 m (1, USNM 1622286). **Sta. 5-9**: Cruise M-3, Rep. 3, 16 Feb 1982, 40°39.9′N, 67°46.7′W, 82 m (1, USNM 1622287); Cruise M-6, Rep. 3, 23 Nov 1982, 40°39.9′N, 67°46.7′W, 78 m (1, USNM 1622288). **Sta. 5-12**: Cruise M-6, Rep. 5, 23 Nov 1982, 40°39.6′N, 67°46.1′W, 80 m, (2, USNM 1622289). **Sta. 5-16**: Cruise M-4, Rep. 4, 16 May 1982, 40°40.16′N, 67°46.1′W, 70 m (1, USNM 1622290). **Sta. 5-20**: Cruise M-1, Rep. 6, Jul 1981, 40°38.5′N, 67°46.1′W, ~78 m (1, USNM 1622291); Cruise M-6, Rep. 6, 24 Nov 1982, 40°38.5′N, 67°46.1′W, 78 m (1, USNM 1622292). **Sta. 5-22**: Cruise M-2, Rep. 6, 20 Nov 1981, 40°39.5′N, 67°43.3′W, 80 m (1 USNM 1622293). **Sta. 5-28**: Cruise M-11, Rep. 3, 04 Feb 1984, 40°39.2′N, 67°46.6′W, 86 m (2, USNM 1622294).—**Atlantic Ocean, off Long Island,** Port Liberty pipeline survey, coll. P.A. Neubert, Chief Scientist. **Sta. 4**, 15 Feb 2012, 40°32.186′N, 073°42.150′W, 17 m (1, JAB).

Description. Holotype (USNM 28296) incomplete, with 58 setigers, 41 mm long, 2 mm wide across thorax; with 31 thoracic setigers, branchiae from setiger 5. Twenty-five newly collected specimens available from Georges Bank ranging from small to large with 16–31 thoracic setigers; all with branchiae from setiger 5. Only one specimen complete (USNM 1622294), with 151 setigers, 33.3 mm long and 1.1 mm wide across thorax; this specimen with 21 thoracic setigers and branchiae from setiger 5. Larger incomplete specimen (USNM 1622278) with 140 setigers, 60 mm long, 2.2 mm across thorax, with 31 thoracic setigers and branchiae from setiger 5. Smallest specimens with 16–19 thoracic segments. Description here based on larger specimens with up to 31 thoracic setigers. Difference with smaller specimens presented in Variability section. Color in alcohol light tan in larger specimens, opaque white in smaller or juvenile specimens; thoracic dorsal intersegmental glandular areas white.

Pre-setiger region and first three setigers enlarged, rounded dorsally (Figs. 38B, 39G–H), subsequent thoracic segments flattened dorsally (Fig. 38A) with parapodia elevated above mid-dorsal surface producing a dorsal channel between parapodia; venter of thoracic segments smooth, with weakly developed mid-ventral line or groove (Fig. 38C); intersegmental groove expanded mid-dorsally in middle and subsequent thoracic segments, appearing glandular (Fig. 38A). Thoracic segments about seven times wider than long (Fig. 38A, C). Abdominal segments crowded, weakly biannulate, short, rounded ventrally, flattened dorsally with parapodia shifted dorsally; dorsal and ventral grooves absent.

Prostomium triangular, narrow, tapering to acutely pointed tip (Figs. 38A–C, 39G–H); no eyespots; nuchal organs narrow slits on posterior lateral margin. Peristomium short, smooth, reduced dorsally, shorter than first setiger (Figs. 38A–C, 39G–H); ventrally forming upper and lower lips of mouth; anterior lips consisting of two thickened lobes; posterior lips consisting of several elongate lobes extending mid-ventrally on to setiger 1 (Fig. 38C); when everted, proboscis consisting of 3–4 lobes.

Thorax with up to 31 setigers in largest adults; smaller specimens or juveniles in present collections with as few as 16 setigers. Thoracic notopodia all similar with a triangular-shaped postsetal lobe. Abdominal notopodia becoming narrow and elongate. Thoracic neuropodia thick, elongate, oval-shaped, bearing rows of uncini and a few capillaries. On largest 31-setiger specimen, first setiger with single short postsetal lobe, increasing to two lobes on setiger 2, then up to 6–7 lobes by setigers 10–11 (Fig. 38D) and 12–13 postsetal lobes by setiger 25 (Fig. 38E); smaller specimens with a single postsetal lobe for up to 10 setigers (Fig. 39G–H), increasing gradually to about

six lobes in posterior thoracic setigers; postsetal lobes arranged in a row posterior to rows of uncini (Fig. 38D–E). Individual subpodial lobes or papillae first present from about setiger 21–22, increasing to about 20–22 on a side by setiger 25 (Fig. 38E), encircling venter as fringe and continuing on to few anterior abdominal setigers, then absent along rest of body. Abdominal neuropodia with elongate flange ventral to neuropodium, initially rounded apically and with single lobe derived from thoracic postsetal lobes (Fig. 38F); this transitioning into a short ventral cirrus located on dorsal margin of narrow subpodial flange (Fig. 38G); ventral cirrus and flange continuing along most of body. Interramal cirrus or process absent.

Branchiae from setiger 5 on all specimens (Fig. 38A); branchiae mid-dorsal, well-developed at first with broad base tapering apically (Fig. 38D–E); branchiae of abdominal setigers longer, triangular, heavily ciliated (Fig. 38F–G).

Thoracic notosetae all crenulated capillaries, initially numbering about 75–90 per fascicle, then reduced to about 25–30 in last few thoracic setigers. Abdominal notosetae including a fascicle of camerated capillaries and 2–4 furcate setae; furcate setae with blunt-tipped unequal tynes each with an apical notch (Fig. 39F); tynes with thin needles directed medially; shaft smooth, transverse rows of barbs not apparent. Thoracic neurosetae including conspicuous spinous uncini and a few capillaries arranged in 4–6 narrow rows with spines of each row alternating in position with spine of adjacent row. Uncini of first three rows narrow blunt-tipped spines with transverse ribs across shaft (Fig. 39A); uncini of subsequent neuropodia of rows 4–6 with large, recurved spines with prominent ribs along one edge and a few narrower ribbed spines (Fig. 39B–C), usually in ventral most part of fascicle; uncini of last 8–10 thoracic setigers on a 31-setiger specimen, large with expanded apex notched and with transverse ribs not apparent (Fig. 39D). Capillaries more numerous in setigers 1–3, then reduced to a single dorsal fascicle and 1–2 groups of a few capillaries near middle of neuropodium on following setigers. Abdominal neurosetae consisting of 10–15 long serrated capillaries and 1–2 thin flail setae. One or two minute imbedded aciculae also present, usually not emergent. Flail setae with row of barbs along one edge, apex with a thin arista (Fig. 39E).

Pygidium consisting of four large rounded lobes around anal opening; with two thin dorsolateral anal cirri (Fig. 39I).

Variability. There is considerable variability in the sequence of development and number of neuropodial postsetal lobes and subpodial papillae of *Orbinia swani* based on the size and stage of development of individual specimens. Some data are presented in Table 2, including a comparison with *O. americana*, which might actually be *O. swani* (see below). With increasing size, the number of postsetal lobes increases up to six in the largest specimens. Subpodial lobes or papillae do not appear until about 19 thoracic setigers are developed. With the development of 21 thoracic setigers, 1–5 subpodial lobes may be present. However, a fully developed subpodial fringe with about 22 papillae on a side is not apparent until 30–31 thoracic setigers are present. The difference in numbers and arrangement of these lobes and papillae are so different between juveniles and larger adults of this species that smaller specimens have most likely been mis-identified. In our collections some of the smaller specimens were originally referred to the genus *Leodamas* (Maciolek *et al*. 1985). Day (1973: 89) described a separate species from North Carolina with 21 thoracic setigers, *O. americana*, that was stated to differ from *O. swani* in having "… fewer thoracic segments, fewer foot-papillae and fewer stomach papillae."

The distribution of barbed and smooth thoracic neuropodial uncini or spines also appears to change with growth. All specimens appear to have narrow, elongate uncini with blunt tips and transverse rows of ribs on the shaft in setigers 1–3. From setiger 4, heavier recurved spines with expanded tips and rows of transverse barbs are the dominant spines, with the narrower uncini reduced to the lowermost locations in posterior rows. Heavier spines with expanded tips and transverse ribs on the convex side occur from about setiger 16 in smaller specimens and from setigers 10–31 in the largest specimens. In larger specimens, the transverse ribs disappear and the spines are more or less smooth on the convex surface; most of these smooth spines of posterior thoracic neuropodia have two subterminal grooves near the tip. In some views the lines of these grooves may appear to be flanges but are actually grooves on either side of a ridge. Thus, there are three different kinds of thoracic neuropodial uncini: (1) a thin elongate blunt-tipped spine with transverse ribs across the shaft; these are limited to setigers 1–3 and posterior or ventral sections of a few subsequent setigers; (2) larger recurved spines from setiger 4 that have blunt tips and prominent transverse ribs on the concave side of the shaft, and (3) large spines, sharply curved apically with ribs on the convex side of the curved tip or with the convex side lacking transverse ribs and divided by two longitudinal grooves.

Biology. Several specimens were observed with large eggs in, or associated with, the subpodial flanges. The largest eggs measured were 225–335 μm in diameter from a specimen at Sta. 5-22 (USNM 1622293). Large eggs of this diameter suggest direct development, likely with brood protection (Blake 1980).

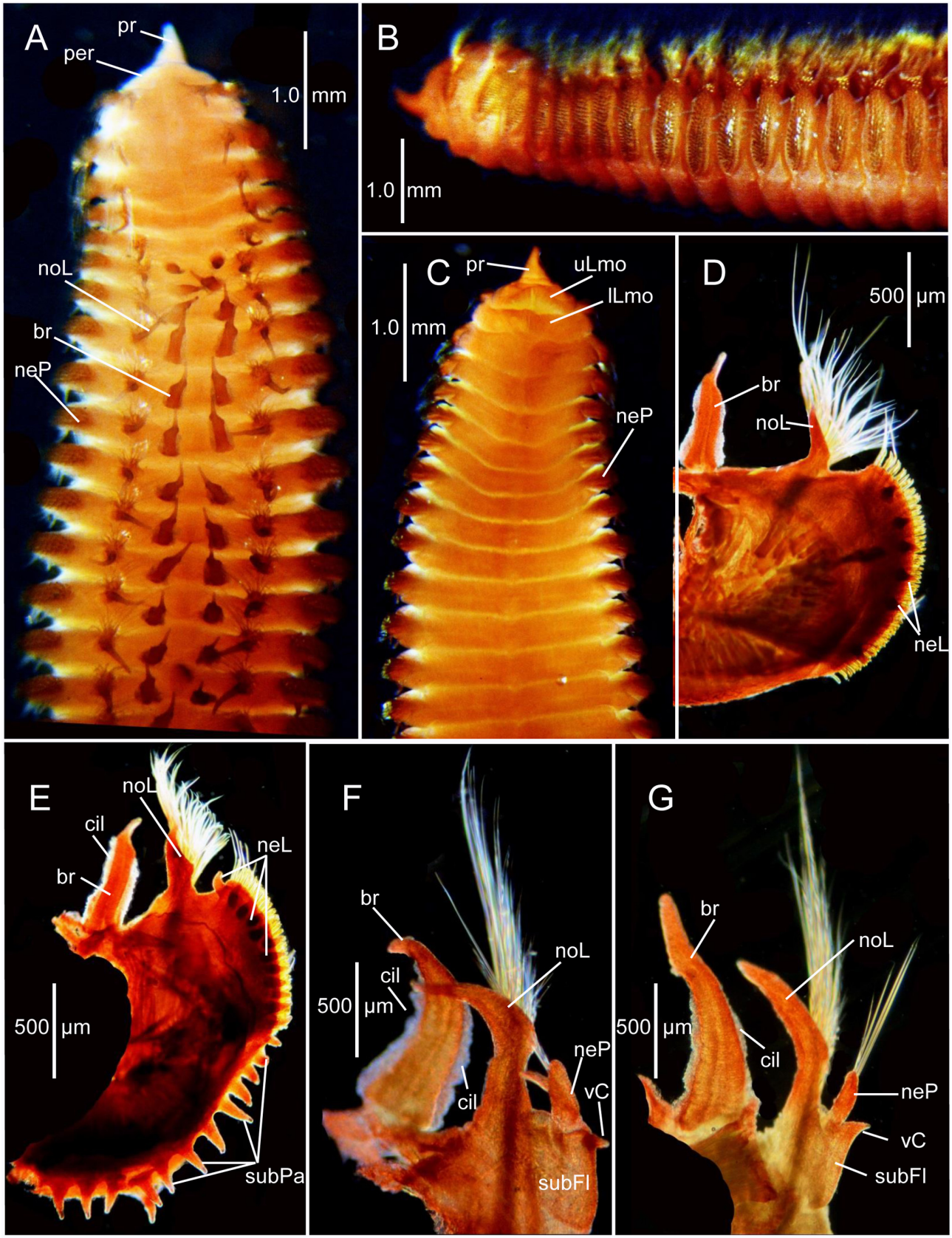

FIGURE 38. *Orbinia swani* (Pettibone, 1957). A, anterior end, dorsal view; B, anterior end, left lateral view; C, anterior end, ventral view; D, setiger 10, posterior view; E, setiger 25, posterior view; F, anterior abdominal setiger, posterior view; G, middle abdominal setiger, posterior view. A–C (USNM 1622287); E–G (USNM 1622278). All stained with Shirlastain A.

Sediments on Georges Bank where *Orbinia swani* was collected mainly consisted of >95% quartz sand with minor amounts of gravel, shell fragments, and echinoderm test fragments and minor amounts of silt and clay-size particles (Maciolek-Blake *et al*. 1985). Most specimens of *O. swani* from Georges Bank were observed to have large sand grains in their guts. Grain size at one sample from off Long Island having *O. swani* consisted of 99.6% sand.

Remarks. Pettibone (1957) described a large specimen from Maine with 31 thoracic setigers that served as the holotype and basis for the original description of *Orbinia swani*. The present collection from Georges Bank includes 21 specimens representing a range of sizes with 16–31 thoracic setigers. These collections demonstrate important differences between smaller specimens and the larger adults.

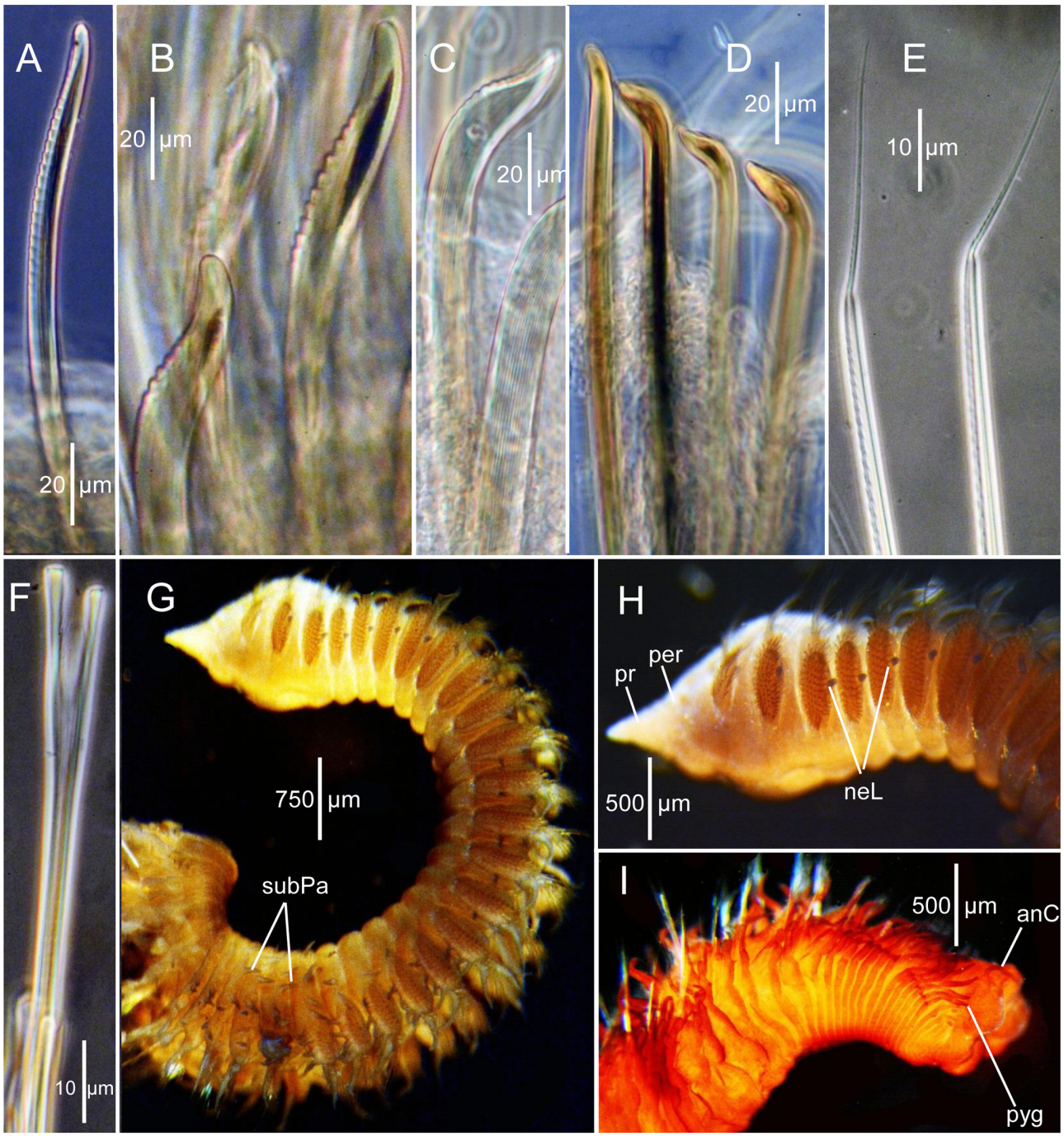

FIGURE 39. *Orbinia swani* (Pettibone, 1957). A, thoracic neuropodial uncinus, setiger 2, row 1; B–C, thoracic neuropodial uncini, setiger 2, rows 4–6; D, neuropodial uncini from posterior thoracic setiger; E, abdominal neuropodial flail setae; F, abdominal notopodial furcate seta; G, anterior half of specimen with 21 thoracic setigers, left lateral view; H, same, close-up view of pre-setiger and anterior 8 thoracic setigers, left lateral view; I, posterior segments and pygidium, left lateral view. A–F (USNM 1622278); G–I (USNM 1622294). G–I stained with Shirlastain A.

As noted in the Variability section above, several key morphological indicators change with growth. Since most species of *Orbinia* and *Phylo* have a conspicuous and well-developed fringe of subpodial or stomach papillae, smaller specimens that lack this morphology are difficult to correctly identify. However, *O. swani* differs from other species in having abdominal neuropodia with a single subpodial lobe that surmounts a narrow subpodial flange and continues along most of the abdominal segments. This feature is apparent in all specimens examined regardless of size. The smaller specimens, however, owing to the reduced number of postsetal lamellae and subpodial papillae, cannot be accurately identified as *O. swani*, unless a growth sequence is available. It is likely that other species have similar issues and some species have likely been described as separate species, when in effect they are juveniles of another species. Smaller specimens where the subpodial lamellae are absent or few in number might even be assigned to another genus such as *Leodamas* or *Scoloplos*.

Pettibone (1957), in her description *of O. swani*, did describe some differences with the thoracic neuropodial uncini but did not document their distribution along the body. She did not report the presence of flail setae in the abdominal neuropodia. However, flail setae are difficult to recognize as such and she likely assumed they were small capillaries rather than setae with the thin aristate tips described here.

Orbinia americana Day, 1973, described from off Beaufort, North Carolina, was based on a single specimen with 21 thoracic setigers. Day (1973) noted the similarity to *O. swani* but that his specimen had fewer thoracic neuropodial postsetal lobes and fewer subpodial lobes. This is a juvenile pattern and suggests that *O. americana* is likely a synonym of *O. swani*, but due to the COVID-19 pandemic and closure of museums, it was not possible to obtain the holotype for confirmation of the synonymy at this time.

Distribution. Maine intertidal; off Long Island, 17 m; Georges Bank, 55–86 m.

Genus *Phylo* Kinberg, 1866

Type-species: *Phylo felix* Kinberg, 1866, by monotypy.

Diagnosis. Prostomium pointed on anterior margin; peristomium with one achaetous ring. Branchiae first present from setiger 5–7. Posterior thoracic segments with several postsetal lobes and subpodial lobes (at least five of each type) together usually forming ventral fringe. Thoracic neurosetae including blunt uncini and crenulated capillaries; posterior thoracic segments with modified spear-like spines in neuropodia. Flail setae present or absent in posterior abdominal notopodia.

Remarks. Species of *Phylo* are characterized by having posterior segments of the thoracic region modified with long, pointed spines in the neuropodia. These spines provide species of *Phylo* with an obvious distinctness that makes them easy to identify. Twelve species of *Phylo* are considered valid (Read & Fauchald 2020a). Three known species, *P. felix*, *P. norvegicus* (M. Sars in G.O. Sars, 1872), and *P. ornatus* (Verrill, 1873) have been identified from shelf and slope samples in the present study. A fourth species, *Phylo paraornatus* **n. sp.**, has been discovered among specimens identified as *Orbinia swani* from the Georges Bank collections.

1. *Phylo felix* Kinberg, 1866
2. *Phylo norvegicus* (M. Sars in G.O. Sars, 1872)
3. *Phylo ornatus* (Verrill, 1873)
4. *Phylo paraornatus* **n. sp.**

Phylo felix Kinberg, 1866

Figure 40

Phylo felix Kinberg, 1866: 251–252; Hartman 1948: 105–106, pl. 15, fig. 10; 1953: 37–38; 1957: 262–265, pl. 23 (synonymy); 1966a: 10, pl. 2, fig. 4; Day 1973: 89; Maciolek-Blake *et al*. 1985: B-5; Blake 2017: 90–93, figs. 42–43 (synonymy).
Aricia formosa Hansen, 1882: 18, pl. 5, figs. 23–27; Augener 1934: 146–148. *Fide* Hartman 1957.
Aricia michaelseni Ehlers, 1897: 88–91, pl. 6, figs. 136–140; 1900: 12; 1901: 166. *Fide* Hartman 1948.—Not Monro 1930: 144–145, fig. 54; Okuda 1937: 101; Berkeley & Berkeley 1952: 96, figs. 194–196.
Orbinia (*Phylo*) *michaelseni*: Pettibone 1963: 282, fig. 75f.
Orbinia felix: Hobson & Banse 1981: 29.

Phylo felix heterosetosa Hartmann-Schröder, 1965: 192–194, figs. 176–177; Rozbaczylo 1985: 130. *Fide* Blake 2017.
Phylo kupfferi: Hartman 1967: 107–108 (in part); Rozbaczylo 1985: 130–131. Not Ehlers, 1874.
Phylo michaelseni: Rozbaczylo 1985: 131.
Orbinia (*Phylo*) *minima* Hartmann-Schröder & Rosenfeldt, 1990: 106–107, figs. 11–17. *Fide* Blake 2017.

Material examined. (*17 specimens*): **Northeastern USA, off New England, Georges Bank, Benthic Infauna Monitoring Program (1981–1984),** coll. G.W. Hampson, Chief Scientist. **Sta. 7A**: Cruise M-11, Rep. 5, 04 Feb 1984, 40°32.2′N, 67°44.2′W, 167 m (1, USNM 1622295). **Sta. 8**: Cruise M-2, Rep. 3, 11 Nov 1981, 40°27.1′N, 67°37.4′W, 152 m (1, USNM 1622296); Cruise M-5, Rep. 2, 23 Jul 1982, 40°27.1′N, 67°37.4′W, 140 m (1, USNM 1622297); Rep. 6, (1, USNM 1622298); Cruise M-6, Rep. 5, 22 Nov. 1982, 40°27.1′N, 67°37.4′W, 145 m (1, USNM 1622299); Rep. 6 (1, USNM 1622300); Cruise M-8, Rep. 6, 16 May 1983, 40°27.1′N, 67°37.2′W, 146 m (1, USNM 1622301); Cruise M-9, Rep. 5, 15 Jul 1983, 40°27.1′N, 67°37.4′W, 152 m (1, USNM 1622302); Cruise M-11, Rep. 2, 03 Feb 1984, 40°27.1′N, 67°37.4′W, 152 m (1, USNM 1622303); Rep. 5 (1, USNM 1622304); Cruise M-12, Rep. 1, 05 Jun 1984, 40°27.1′N, 67°37.4′W, 140 m (1, USNM 1622305). **Sta. 9**: Cruise M-8, Rep. 3, 19 May 1983, 40°26.7′N, 68°09.8′W, 143 m (1, USNM 1622306); Cruise M-12, Rep. 1, 08 Jun 1984, 40°26.7′N, 68°09.8′W, 144 m (1, USNM 1622307). **Sta. 16**: Cruise M-6, Rep. 3, 21 Nov. 1982, 40°34.2′N, 67°12.3′W, 138 m (1, USNM 1622308). **Sta. 18**: Cruise M-7, Rep., 09 Feb 1983, 40°33.5′N, 67°13.7′W, 147 m (1, USNM 1622309); Rep. 3 (1, USNM 1622310); Rep. 4 (1, juv. USNM 1622311). Cruise M-8, Rep. 4, 16 May 1983, 40°33.5′N, 67°13.7′W, 141 m (1, USNM 1622312).—**US North Atlantic ACSAR program**, coll. G.W. Hampson, Chief Scientist. Cruise NA-2, **Sta. 7**: Rep. 3, 28 Apr 1985, 40°27.44′N, 67°40.19′W, 558 m (1, USNM 1622313).

Description. A moderate to large species, a complete specimen from Chile with up to 240 setigers, 80 mm long and 2.9 mm wide; incomplete specimens up to 92 mm long (Blake 2017). Present specimens from Georges Bank smaller; complete specimen (USNM 1622309) with 87 setigers, 14 mm long and 1.0 mm wide; larger incomplete specimen (USNM 1622311) with 61 setigers, 21 mm long and 2.2 mm wide. Body elongate, with all segments short (Fig. 40A); thoracic segments about six times wider than long, flattened both dorsally and ventrally (Fig. 40B–C); abdominal segments strongly rounded on venter, flattened dorsally due to shift of parapodia to dorsum. Thoracic segments uniannulate; abdominal segments biannulate. No dorsal or ventral grooves along body. Branchiae from setiger 5. Present specimens light tan in alcohol.

Pre-setiger region short, wider than long (Fig. 40B–C). Prostomium triangular, narrow, tapering to pointed tip (Fig. 40A–C). eyespots absent; nuchal organs narrow paired slits at border of prostomium and peristomium. Peristomium a narrow ring, about as long as setiger 1 dorsally (Fig. 40A–B) but extending onto setiger 1 ventrally due to posterior lip of mouth. Mouth an elongate opening with two large lobes forming upper lip and numerous narrow lobes forming lower lip extending on to setiger 1 (Fig. 40C). Proboscis with 2–3 large inflated lobes when fully everted.

Thorax of present specimens with 15–18 setigers; one juvenile with 13 setigers. Thorax divided into anterior and posterior sections: anterior thorax consistently with 10 setigers; posterior thorax with large spines beginning on setiger 11 and continuing up to setiger 18 depending on specimen. Thoracic notopodia digitate, shortest in setigers 1–2, becoming long over subsequent thoracic setigers. Abdominal notopodia similarly elongate digitiform lobes. Interramal cirrus present between noto- and neuropodia of posterior thoracic setigers, continuing over abdominal setigers (Fig. 40I). Thoracic neuropodia thick, elongate, bearing up to five rows of uncini and capillaries (Fig. 40D). Setiger 1 with single neuropodial postsetal lobe, increasing up to 10 lobes by about setiger 12 (Fig. 40A, D), thereafter gradually decreasing to about 6–8 lobes by setiger 15. All neuropodial postsetal lobes short, conical, arranged in a row posterior to rows of neurosetae. Subpodial lobes or stomach papillae from about setiger 14, numbering 6–8 at first, then extending to ventral midline on both sides on setigers 16–18 (Fig. 40E); continuing on at least one anterior abdominal setiger, then entirely absent. Abdominal neuropodia elevated, divided apically into rounded inner lobe and narrow digitiform lateral lobe. First 1–2 abdominal segments with 2–3 extra lobes or ventral cirri ventral to neuropodium; these reduced to single ventral cirrus in all subsequent abdominal neuropodia.

Branchiae from setiger 5. Branchiae more medial in thoracic setigers and closer to notopodia in abdominal segments. Each branchia triangular in shape, narrowing to conical tip; all branchiae heavily ciliated (Fig. 40E, I).

Notosetae of anterior thoracic setigers in fascicles of 30–40 crenulated capillaries; posterior thoracic segments with capillaries reduced to about 15–20 per fascicle. Abdominal notosetae including 15–20 long thin capillaries with barbs or crenulations along one edge and 1–2 furcate setae; furcate setae with unequal blunt-tipped tynes connected by a web of numerous fine needles; shaft with transverse rows of ribs.

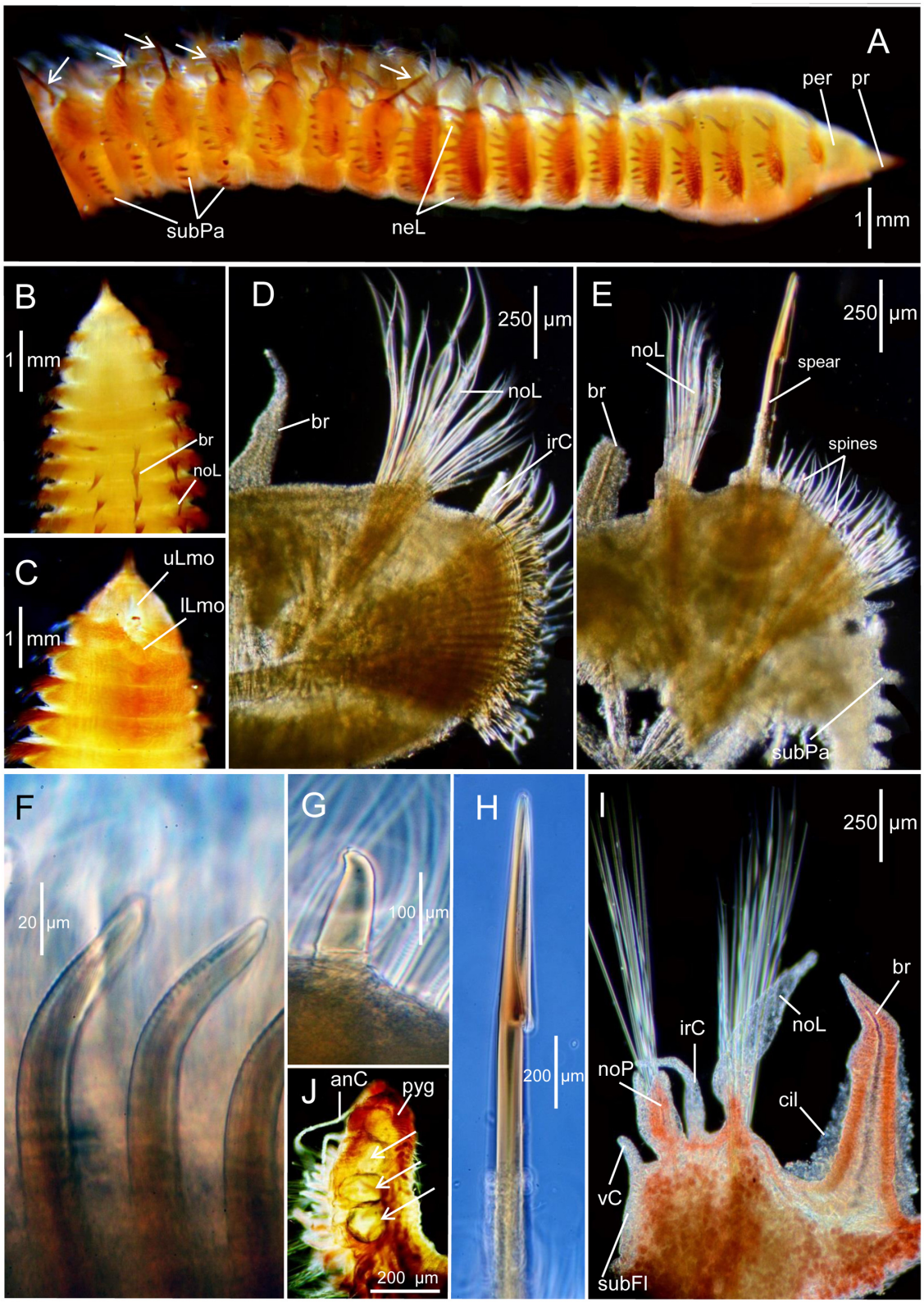

FIGURE 40. *Phylo felix* (Kinberg, 1866): A, anterior end, right lateral view (arrows denote spear-like notopodial spines); B, anterior end, dorsal view; C, anterior end, ventral view; D, thoracic setiger 9, anterior view; E, thoracic setiger 16, anterior view; F, thoracic neuropodial uncini, setiger 8; G, heavy curved neuropodial spine from first row on setiger 16; H, hastate or spear-like spine from uppermost position in neuropodium of setiger 16; I, abdominal setiger, anterior view; J, posterior end and pygidium (arrows denote sand grains in gut), left lateral view. A–G, H (USNM 1622307); J (USNM 1622309); I (USNM 1622301). Most stained with Shirlastain A.

Anterior thoracic neuropodial setigers 1–10 with 4–6 rows of uncini of two types: (1) 3–5 rows of large, heavy uncini, each with curved apex with transverse rows of ribs on convex side; tip of spine with a closely adhering sheath and (2) a posterior row of narrower crenulated spines. Posterior row of crenulated capillary setae accompanying uncini. Posterior thoracic setigers 11–18 with an anterior row of 5–6 large heavy smooth spines with a curved tip (Fig. 40G) and a single long hastate or spear-like spine in the uppermost position of first row (Fig. 40E, H); a few crenulated uncini also present together with crenulated capillaries. Abdominal neurosetae including 5–10 long capillaries, each with mostly smooth shafts and with short barbs along on edge; 1–2 minute imbedded aciculae also present. Flail setae absent.

Pygidium enlarged, swollen, turned dorsally, with a pair of long anal cirri (Fig. 40J).

Remarks. *Phylo felix* is a widely distributed species and the present specimens agree well with previous accounts (Blake 2017). One difference noted in the present collection is the presence of the emergent tips of a few thick relatively smooth, blunt-tipped spines accompanying the hastate spears in posterior thoracic setigers. Hartman (1957) illustrated these spines, mostly imbedded in the same location, ventral to the hastate spines; Blake (2017) illustrated these as entirely imbedded. Neither author provided details of these spines, however.

Biology. Some specimens had guts filled with large sand grains (Fig. 40J). Males with numerous sperm packets were observed; individual sperm have a short head and long tail.

Distribution. A widely reported species: Western North Atlantic, off New England, along outer shelf and shelf break on Georges Bank, 138–167 m and upper continental slope, 558 m; off North Carolina, 120–200 m. Southern Atlantic and SE Pacific: Brazil (type-locality), Uruguay, Argentina, Patagonia, Southern Chile, Straits of Magellan, intertidal to 424 m; Falkland Islands, intertidal to 361 m; Antarctic Peninsula and off Elephant Island, intertidal to 430 m. Eastern Pacific, southern California to Mexico, shallow subtidal.

Phylo norvegicus (M. Sars in G.O. Sars, 1872)

Figures 41–42

Aricia norvegica M. Sars in G.O. Sars, 1872: 408; 1873: 236, p. 16, figs. 1–8; McIntosh 1910: 506; Fauvel 1927: 17, fig. 75.
Phylo norvegica: Støp-Bowitz 1948: 66.
Phylo norvegicus: Hartman 1957: 261–262; 1959: 367; 1965: 130–131.
Orbinia (*Phylo*) *norvegica*: Pettibone 1963: 281–282, fig. 75c; Hartmann-Schröder 1974: 224; 1996: 295–296, fig. 131.
Orbinia sp. 1: Blake *et al*. 1987: C-4; Maciolek *et al*. 1987b: D-3; Hilbig 1994: 942.

Material examined. (*15 specimens*) **Off New England, US North Atlantic ACSAR program**, coll. G.W. Hampson, Chief Scientist. **Sta. 2**: Cruise NA-2, Rep. 2, 25 Apr 1985, 40°57.16′N, 66°13.70′W, 2100 m (1, USNM 1622314). **Sta. 3**: Cruise NA-1, Rep. 3, 09 Nov 1984, 41°01.41′N, 66°20.22′W, 1338 m (1, USNM 1622315). **Sta. 15**: Cruise NA-2, Rep. 1, 05 May 1985, 39°40.08′N, 70°54.26′W, 2150 m (1, USNM 1622316).—**Southeastern USA, U.S. South Atlantic ACSAR program,** coll. J.A. Blake, Chief Scientist. **Off Cape Hatteras, North Carolina**, **Sta. 10**: Cruise SA-4, Rep. 2, 24 May 1985, 35°26.34′N, 74°41.57′W, 1988 m (2, USNM 1622317). **Hatteras Canyon, Sta. 6**: Cruise SA-1, Rep. 4, 19 Nov 1983; 34°48.87′N, 75°15.94′W, 1950 m (1, USNM 1622318). **Off Cape Lookout, North Carolina**, **Sta. 1**: Cruise SA-2, Rep. 2, 26 Mar 1984, 34°15.81′N, 74°46.012′W, 583 m (1, USNM 1622319); Rep. 3, 27 Mar 1984, 34°156.81′N, 75°45.78′W, 593 m (1 juv., USNM 1622320); Cruise SA-3, Rep. 2, 15 Jun 1984, 34°15.20′N, 75°45.60′W, 599 m (1, USNM 1622321). **Sta. 2**: Cruise SA-2, Rep. 2, 27 Mar 1984, 34°14.46′N, 75°43.85′W, 1019 m (1, USNM 1622322). **Sta. 4**: Cruise SA-1, Epibenthic sled tow No. 1, 17 Nov 1983, 34°13.06′N, 75°39.04′W to 34°13.46′N, 78°37.68, 1910–2050 m (1, USNM 1622323). **Off Cape Fear, North Carolina**, **Sta. 11**: Cruise SA-5, Rep. 1, 23 Sep. 1985, 33°04.83′N, 76°25.17′W, 896 m (1, USNM 1622324). **Off Charleston, South Carolina**, **Sta. 14**: Cruise SA-5, Rep. 2, 19 Sep 1985, 32°23.73′N, 77°01.24′W, 799 m (1, USNM 1622325). **Sta. 15**: Cruise SA-5, Rep. 2, 18 Sep 1985, 32°11.94′N, 76°42.23′W, 1991 m (1, USNM 1622326).

Description. A large species, with 75 setigers and a length of 58 mm for an incomplete specimen (Hartmann-Schröder 1996). Present collection with all specimens incomplete; longest nearly complete (USNM 1622324) with 120 setigers, 55 mm long, 1.5 mm wide across thorax; a large anterior fragment (USNM 1622317) with 53 setigers, 24 mm long, 3 mm wide across thorax (Fig. 42A). Body elongate, with all segments short (Fig. 42A); thoracic segments about 10 times wider than long, flattened dorsally (Fig. 41A–B), rounded ventrally; abdominal segments

strongly rounded on venter, flattened dorsally due to parapodial shift dorsally. No dorsal or ventral grooves along body. Branchiae from setiger 6 (Fig. 41A). Present specimens light tan in alcohol with no other pigmentation.

Pre-setiger region short, wider than long; as long as first two setigers dorsally (Fig. 41A) but extending ventrally over setiger 1 due to nature of oral lips (Figs. 41B, 42B). Prostomium short, conical, tapering to rounded tip, with no obvious separation from peristomium (Figs. 41A–B, 42A–B); eyespots absent; nuchal organs narrow slits on posterior lateral margin, difficult to observe. Peristomium a single ring, triangular-shaped dorsally, distinctly separated from setiger 1 (Fig. 41A); ventrally forming large lateral swellings around mouth (Figs. 41B, 42 B); mouth with conical posterior oral lip arising from anterior margin of setiger 2 (Figs. 41B, 42B); anterior oral lips not developed, instead anterior margin of mouth a shallow vestibule (Fig. 41B). Proboscis observed partially everted as 1–3 narrow lobes within mouth; fully everted proboscis with 2–3 large, inflated lobes.

Thorax with 14–16 setigers and usually one transitional setiger. Thorax divided into anterior and posterior sections: anterior thorax with 1–12 setigers (Figs. 41A, 42A); posterior thorax with large spines beginning on setiger 13 continuing over setigers 14, 15 or 16 depending on specimen. Thoracic notopodia digitate, short at first (Fig. 41A, C), becoming long and narrow in middle and posterior thoracic setigers (Fig. 41A). Abdominal notopodia elongate digitiform lobes thickened basally, tapering to conical tip (Fig. 41D). Thoracic neuropodia thick, elongate, bearing six rows of uncini and capillaries. In largest specimens, setiger 1 with a single postsetal lobe, increasing to two lobes on setiger 2, four lobes on setiger 4, seven lobes on setigers 5–7, and nine lobes on setigers 11–12, thereafter decreasing in number with eight on setiger 13, five on setiger 15 and two on setiger 16. All neuropodial postsetal lobes short, stubby with a rounded tip (Figs. 41C, 42C). All postsetal lobes arranged in a row posterior to setae (Fig. 41C). Subpodial lobes or stomach papillae absent on thoracic and abdominal segments. Abdominal neuropodia elevated, divided apically into a rounded inner lobe and a pointed or digitiform lateral lobe (Figs. 41D, 42F). First 1–2 abdominal segments with 2–3 extra lobes or ventral cirri ventral to neuropodium; these reduced to a single cirrus in all subsequent abdominal neuropodia. Interramal cirri absent.

Branchiae from setiger 6 (Fig. 41A), one specimen (USNM 1622317) with a single small branchia on left side of setiger 5 and none on the right side. Branchiae near notopodia in both thoracic and abdominal segments. Each branchia triangular in shape with conical tip (Figs. 41C, 42C); some abdominal branchiae asymmetrical; all heavily ciliated (Figs. 41D).

Thoracic notosetae all crenulated capillaries in dense fascicle of 100 or more setae. Abdominal notosetae about 25 capillaries and 1–2 furcate setae initially, with numbers of capillaries reduced in 5–20 in middle and posterior setigers. Furcate setae with unequal tynes with rounded tips; each tyne with fine needles directed medially; shaft appearing smooth in light microscope (Fig. 41F). Thoracic neurosetae of setigers 1–12 numerous narrow spines in at least two anterior rows and four or more additional rows of long camerated capillaries (Fig. 41E); first row of spines continuing ventrally, then curving dorsally about one-third of distance up posterior side of neuropodium; these ventral spines longer and thicker than those of anterior rows; each spine tapering to a narrow pointed tip covered with a sheath extending well beyond tip of spine (Fig. 41E); shaft with transverse rows of minute ribs or barbs. From setiger 13, 4–5 large dark hastate or spear-like spines appearing in anterior row of neuropodia (Fig. 42E) with capillaries and sheathed spines still present but reduced in number. Most hastate spines imbedded with only spear-like point protruding; however, uppermost spine usually fully protruded (Fig. 42D–E). Imbedded oval-shaped gland ("glandular pouch" of Hartman 1957) present on posterior thoracic neuropodia, gland with distinct swollen aperture on surface in close proximity to uppermost hastate spine. Abdominal neurosetae consisting of 12–15 long capillaries, reduced to 4–5 capillaries in middle and posterior setigers; flail setae not observed; 1–2 minute imbedded aciculae also present, usually not emergent.

Pygidium not observed.

Remarks. *Phylo norvegicus* is most similar to *P. nudus* (Moore, 1911), a Pacific species, in lacking a ventral fringe of subpodial papillae or stomach papillae. The two species differ in that *P. nudus* has branchiae from setiger 5, an anterior thoracic region of setigers 1–11 and a posterior thoracic region of setigers 12–15, whereas *P. norvegicus* has branchiae consistently from setiger 6, an anterior thoracic region of setigers 1–12, and a posterior region of setigers 13–16. Further, the posterior modified spines of posterior thoracic setigers are distinctly hastate or spear-like in *P. norvegicus*, whereas the posterior spines of *P. nudus*, while expanded apically, are not hastate or spear-shaped.

Distribution. Northeastern Atlantic, North Sea, subtidal; Western North Atlantic, off New England to the Carolinas, continental slope, 583–2150 m.

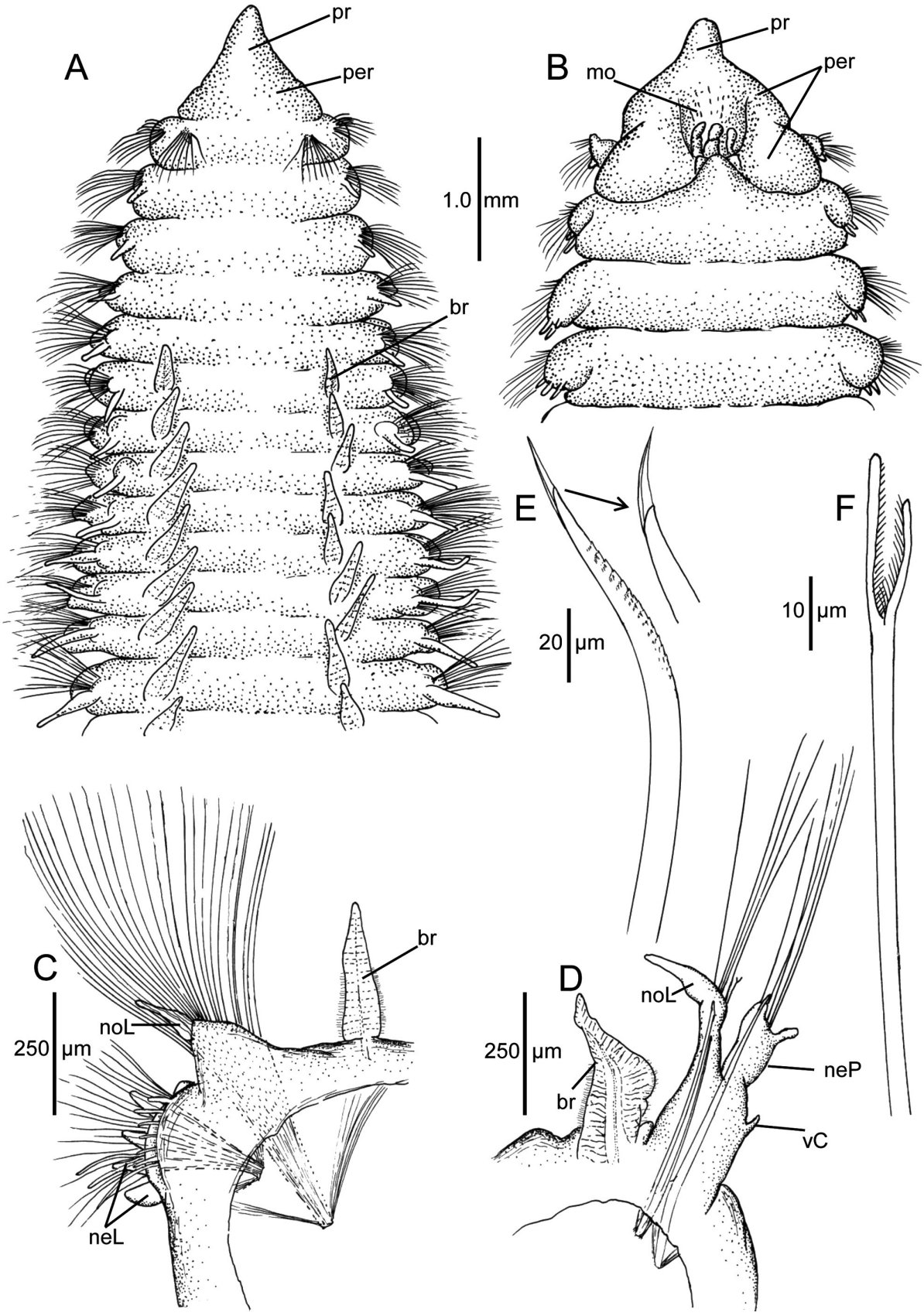

FIGURE 41. *Phylo norvegicus* (Sars, 1872). (USNM 1622317): A, anterior end, dorsal view; B, anterior end, ventral view; C, thoracic setiger 6, posterior view; D, abdominal setiger, posterior view; E, thoracic neuropodial uncinus (inset not to scale); F, notopodial furcate seta. A–C, I, J stained with Shirlastain A.

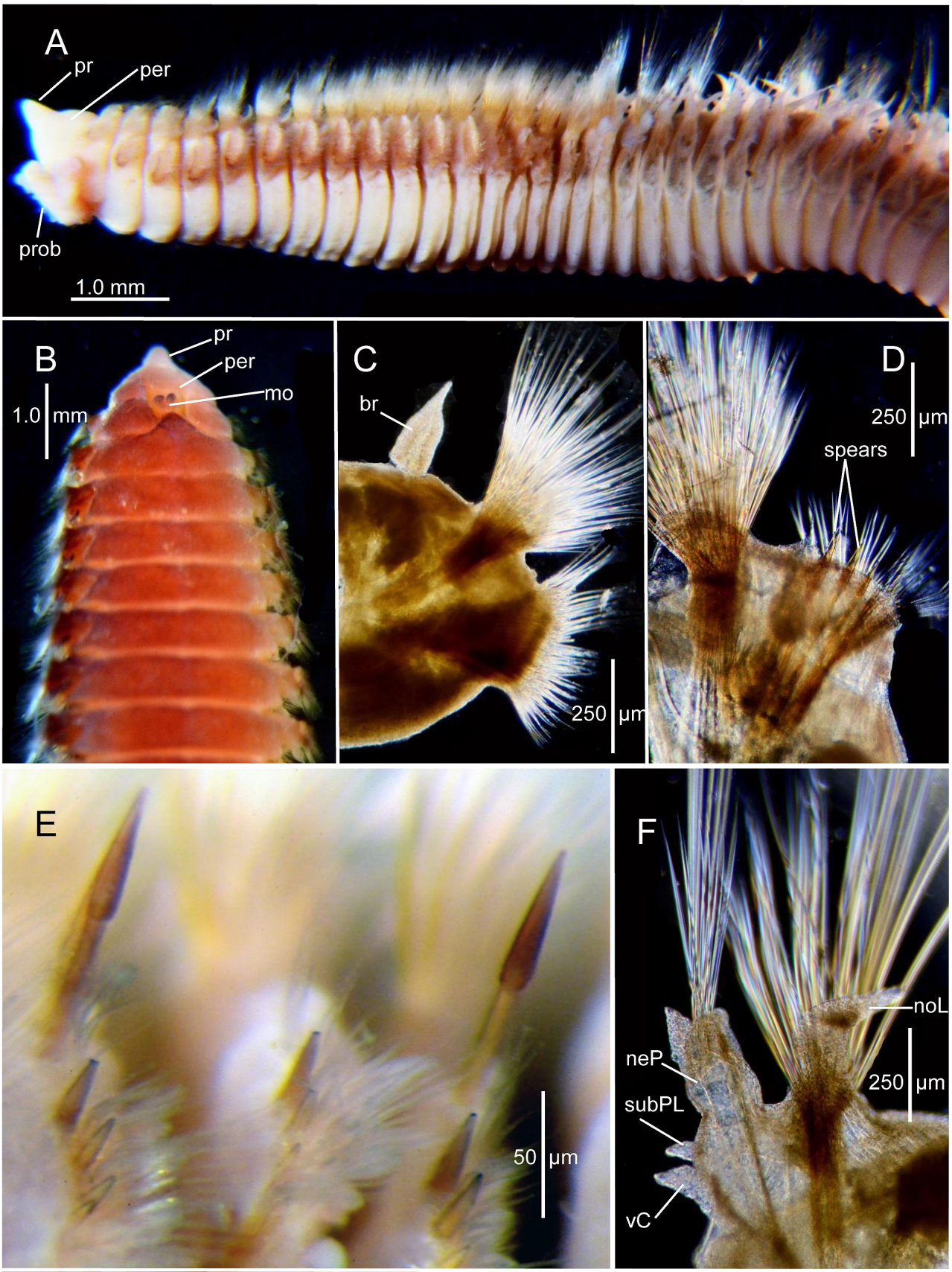

FIGURE 42. *Phylo norvegicus* (Sars, 1872). (USNM 1622317): A, anterior end, left lateral view; B, anterior end, ventral view; C, thoracic setiger 10, anterior view; D, anterior abdominal setiger 18, anterior view; E, setigers 13–15, showing spears; F, setiger 18, anterior abdominal setiger. All stained with Shirlastain A.

***Phylo ornatus* (Verrill, 1873)**
Figures 43–44

Aricia ornata Verrill, 1873: 596; Verrill & Smith 1874: 60, 71, 302–303; Webster & Benedict 1884: 724; Andrews 1891: 292; Sumner *et al.* 1913: 623.
Orbinia ornata: Hartman 1942: 61; 1944: 340, pl. 18, fig. 7, pl. 19, fig. 6 (as *Scoloplos armiger*); 1945: 28.
Phylo ornatus Hartman 1951: 79; 1957: 265, pl. 24, figs. 1–10.
Orbinia (*Orbinia*) *ornata*: Pettibone 1963: 285–286, fig. 75a–b.

Material examined. **Northeastern USA, Massachusetts**, Cape Cod Bay, coll. N.J. Maciolek, Jul 1975, 41°46′N, 70°14′W, ca. 12 m (2, MCZ 161597).

Description. A large species, recorded with up to 300 setigers, 250 mm long and 5 mm wide (Pettibone 1963); present specimens both incomplete, largest with 131 setigers, 60 mm long, and 4–5 mm wide across middle thoracic setigers. Recorded with 19–32 thoracic setigers, present specimens with 28–29 thoracic setigers; branchiae from setiger 5 (Fig. 43B). Body elongate, with thoracic segments more-or-less rectangular in cross section, about ten times wider than long; flattened dorsally, weakly rounded on venter; abdominal segments strongly rounded on venter, flattened across dorsum with parapodia dorsally elevated. A narrow mid-ventral line extends along most of body. All known specimens with branchiae from setiger 5. Present specimens light tan with no other pigmentation.

Pre-setiger region and first four setigers slightly elevated, rounded dorsally (Fig. 43A–B). Prostomium short, conical, tapering to rounded tip (Fig. 43A–B); eyespots absent; nuchal organs a narrow groove at junction with peristomium. Peristomium a narrow single ring dorsally; ventrally forming anterior and posterior lips of mouth, extending on to setiger 1. Anterior oral lips with two large rounded lobes; posterior lips formed by 5–6 weakly developed elongate lobes. When everted, proboscis consisting of two inflated lobes.

Present specimens with 28 and 29 thoracic setigers; Pettibone (1963) recorded specimens with 19–32 thoracic setigers; Hartman (1957) recorded 30 thoracic setigers (14 anterior and 16 posterior thoracic setigers based on presence of larger modified spines in posterior thoracic neuropodia). In present material, larger modified spines first present from setiger 15 in both. Thoracic notopodia all similar, triangular in posterior view (Fig. 44A–C) and digitate in lateral view (Fig. 43B, D). Abdominal notopodia elongate, digitiform lobes tapering to conical tip (Fig. 44D); some lobes with bifurcated tip. Thoracic neuropodia thick, elongate, bearing up to six rows of numerous uncini and groups of capillaries (Figs. 43A–D, 44A–C). First setiger with six rounded postsetal lobes; setiger 4 with nine short conical postsetal lobes (Fig. 44A); setiger 10 with 13 similar postsetal lobes, continuing for several more segments (Fig. 44B), then number of postsetal lobes decreasing to 3–4 on last thoracic setigers. All postsetal lobes arranged in a row posterior to rows of uncini. Subpodial lobes first present from setiger 12 with two lobes ventral to neuropodium (Fig. 43A, C); number of subpodial lobes increasing from three to about eight over setigers 15–20 (Fig. 44B–C), then increasing to about 35–40 on a side in two irregular rows through rest of thoracic region (Fig. 43D), continuing on to 5–6 abdominal setigers; these forming prominent ventral fringe encircling venter (Figs. 43D, 44C); individual subpodial lobes conical, tapering, with inflated tips (Fig. 44B–C). Abdominal neuropodia elevated, relatively short, divided apically into two lobes with lateral lobe long in anterior neuropodia and short in middle and posterior segments (Fig. 44D); a narrow, sometimes bulbous ventral flange present below neuropodium, but extra ventral cirri and subpodial lobes absent (Fig. 44D). Interramal cirri absent.

Branchiae from setiger 5 located mid-dorsally in thoracic setigers and widely separated from notopodium (Fig. 44B), but close to notopodium in abdominal segments (Fig. 44D). Each branchia triangular in shape, heavily ciliated.

Thoracic notosetae all crenulated capillaries, initially numbering about 25–30 per fascicle, increasing to about 45 setae per fascicle, and then reduced to about 30 in last few thoracic setigers. Abdominal notosetae about 18 capillaries and 1–2 furcate setae. Furcate setae with unequal tynes with blunt tips (Fig. 44H–I); each tyne with fine needles directed medially (Fig. 44I); shaft with transverse rows of barbs, but these difficult to see, likely worn. Thoracic neurosetae of setigers 1–14 including up to six rows of conspicuous spinous yellow uncini and a few capillaries; uncini with a curved shaft and blunt tip; shaft with transverse ribs (Fig. 44E). Each row of uncini alternating in position with spine of adjacent row. From setiger 15, uncini in first row larger, dark, with straight pointed shaft, rounded tip (Fig. 44F–G); position of uncini from setiger 15 also shifted, with most uncini arranged in six rows, but with first row of heavier spines extending dorsally toward notopodium (Fig. 43C–D). Abdominal neurosetae consisting of 5–8 long serrated capillaries; flail setae not observed. One or two minute imbedded aciculae also present, usually not emergent.

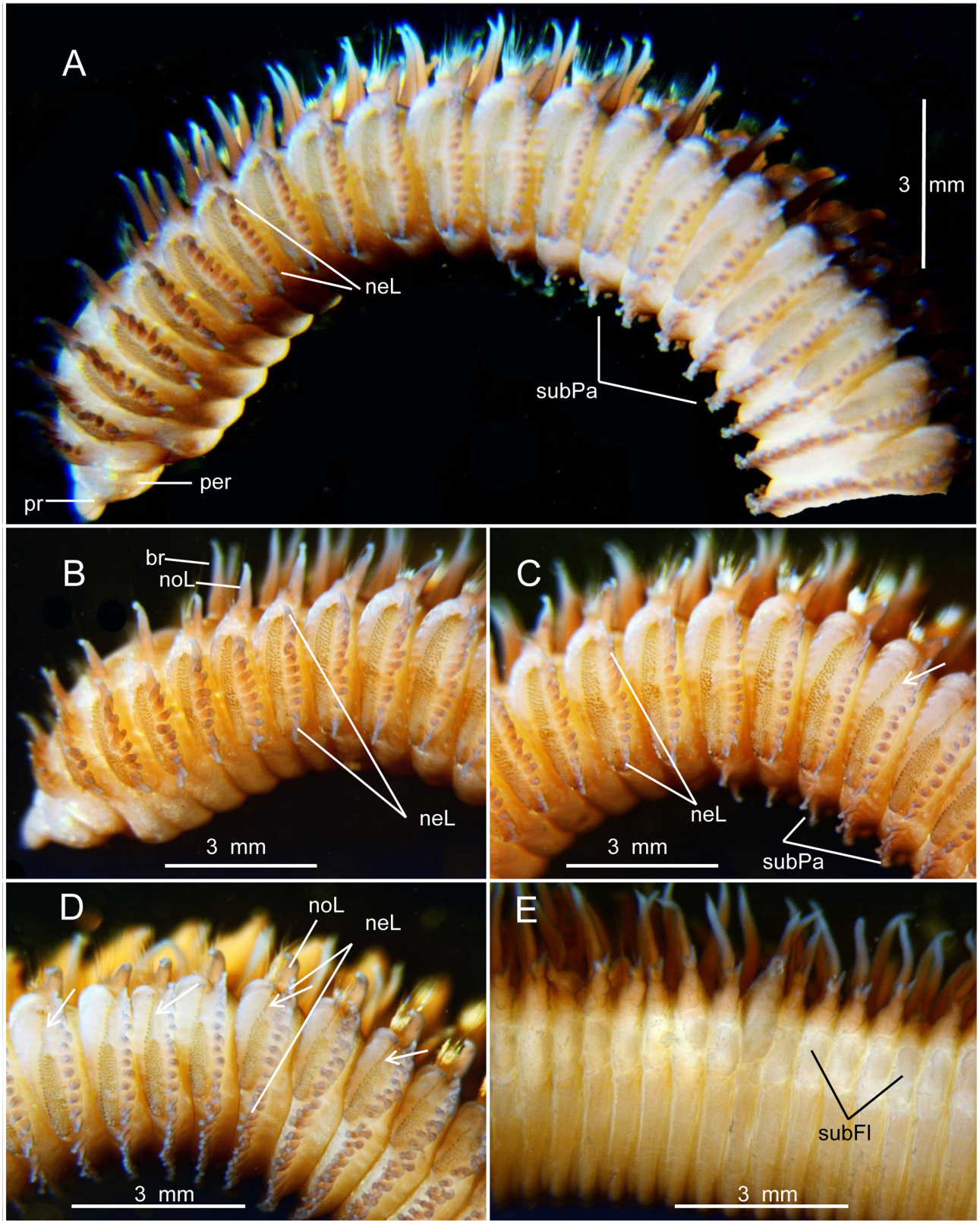

FIGURE 43. *Phylo ornatus* (Verrill, 1873). (MCZ 161597): A, anterior end, left lateral view; B, thoracic setigers 1–10; C, middle thoracic setigers; D, posterior thoracic setigers; E, middle abdominal setigers. Arrows indicate dorsal extension of anterior row of uncini. All stained with Shirlastain A.

Pygidium with a pair of long, thin dorsolateral cirri (Pettibone 1963).

Remarks. *Phylo ornatus*, unlike most species of *Phylo*, has specialized simple pointed neuropodial spines

that occur over 13 or more posterior thoracic segments; these are located on the first or anterior row of uncini. In contrast, *P. paraornatus* **n. sp**. has similar spines, but these are initially located in the upper part of the thoracic neuropodium and limited to the posterior row in the last 10 thoracic setigers. See further comments on these two species in the following account.

Distribution. Off Massachusetts to Florida; Gulf of Mexico. California records need to be confirmed. Intertidal to about 30 m.

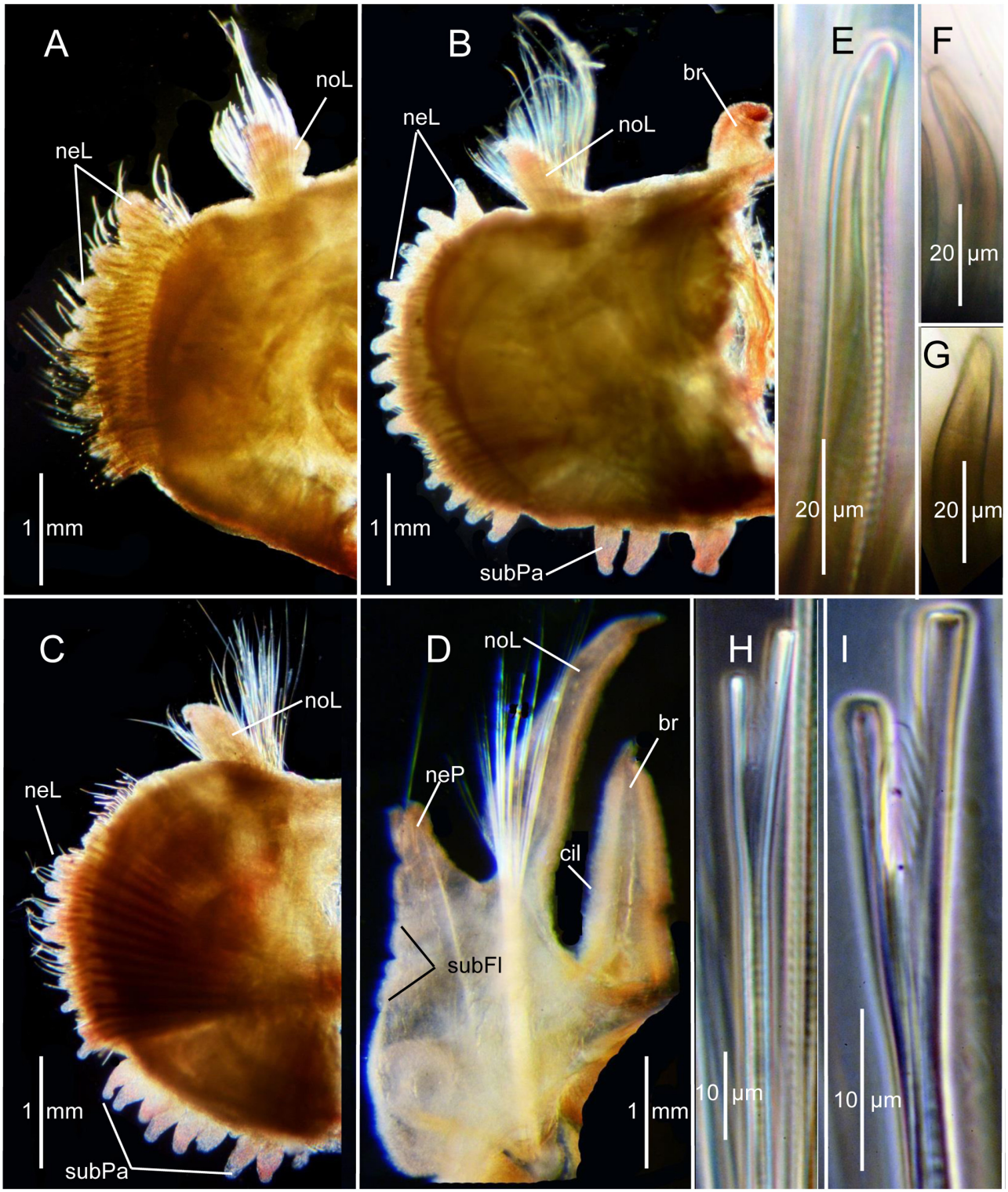

FIGURE 44. *Phylo ornatus* (Verrill, 1873). (MCZ 161597): A, thoracic setiger 4, posterior view; B, thoracic setiger 15, posterior view; C, thoracic setiger 20, posterior view; D, middle abdominal setiger, anterior view; E, thoracic neuropodial uncinus; F–G, posterior thoracic neuropodial spines; H–I, abdominal notopodial furcate setae. A–D stained with Shirlastain A.

***Phylo paraornatus* new species**
Figures 45–46
urn:lsid:zoobank.org:act:2C1F8283-BCA6-4224-B59C-B7F7FC4F4BAC

Orbinia swani: Maciolek-Blake *et al*. 1985: B-5 (in part).

Material examined. Northeastern United States, Georges Bank, **Benthic Infauna Monitoring Program (1981–1984)**, coll. G.W. Hampson, Chief Scientist. **Sta. 10**: Cruise M-12, Rep. 6, 4 Jun 1984, 40°42.0′N, 68°35.3′W, 66 m, **holotype** (USNM 1622327).

Description. Holotype only specimen available, incomplete (missing posterior end) and in two parts, with 79 setigers, 23 mm long and 2 mm wide. Body elongate, about same width throughout; thoracic segments with parapodia raised above dorsum, producing weak channel along dorsal surface. Individual thoracic segments short, rectangular, about eight times wider than long; separated by simple groove. Abdominal segments also short, but more cylindrical; intersegmental area thicker, producing annular ring or biannulate segments. Color in alcohol tan.

Pre-setiger region with peristomium and first three setigers expanded, rounded in profile (Fig. 45A–B). Prostomium long, narrow, acutely pointed Fig. 45A–B); eyespots absent; nuchal organs narrow groove at junction with peristomium. Peristomium a narrow single ring dorsally; ventrally forming anterior and posterior lips of mouth and together with mouth opening extending on to setiger 1. Anterior oral lips with two large rounded lobes; posterior border of mouth a thickened ridge extending onto setiger 1.

Holotype with 26 thoracic setigers; transition to abdominal segments marked by loss of thoracic spines and postsetal lobes together with change of large swollen neuropodium to narrow elevated lobe. Posterior thoracic segments from setiger 15 modified, with enlarged neuropodial spines in upper part of last setal row (Fig. 46D–F). Thoracic notopodia all similar with elongate, narrow, digitiform postsetal lobe. Thoracic neuropodia thickened, narrow, distinctly set off from intersegmental areas; each initially with three rows of uncini with a few capillaries in dorsal part of neuropodium (Fig. 46A–B); first two neuropodia with a few extra uncini in ventral part. Setiger 1 with a single digitate postsetal lobe, increasing to three on setiger 2, then up to six lobes by setiger 6 (Fig. 45A); maximally with eight lobes by setiger 18, then decreasing to four lobes by setiger 26 (Fig. 45C) or last thoracic segment. All postsetal lobes posterior to last row of uncini, each lobe thick with rounded apex (Fig. 46B). Subpodial lobes or stomach papillae first present from setiger 20 (Fig. 45B); number of subpodial lobes increasing to about 10 on a side in two irregular rows through rest of thoracic region and continuing onto four abdominal setigers (Fig. 45B–D); these forming a prominent ventral fringe but with a mid-ventral gap, along the mid-ventral line, thus fringe not entirely encircling venter. Individual subpodial lobes thickened basally, tapering to pointed apex (Fig. 45C). Abdominal neuropodia elevated but relatively short, with apex rounded with a single projecting lateral lobe. A single subpodial lobe present below neuropodium representing top of short, inconspicuous subpodial flange (Fig. 46H), continuing along entire body. Interramal cirri absent.

Branchiae from setiger 5 located mid-dorsally in thoracic setigers (Fig. 46A, D) and widely separated from notopodium, but closer to notopodium in abdominal segments (Fig. 46H). Each branchia triangular in shape, heavily ciliated.

Thoracic notosetae all long crenulated capillaries, numbering up to about 35–40 per fascicle (Fig. 46A, D), then reduced to about 20 in last few thoracic setigers. Abdominal notosetae about 10–12 capillaries and 1–3 furcate setae. Furcate setae with unequal tynes with blunt tips; each tyne with fine needles directed medially (Fig. 46I); shaft with transverse rows of barbs, but these worn and difficult to see. Thoracic neurosetae initially up to three rows of 10–12 conspicuous smooth yellow uncini with dark cores (Fig. 46C, G) and a few capillaries; uncini reduced to two rows by about setiger 18; individual uncini completely lacking transverse ribs, each with a weakly curved shaft and blunt tip (Fig. 46G). Each uncinus alternating in position with spine of adjacent row (Fig. 46B). From setiger 15, posterior row of uncini with upper 2–4 spines becoming larger, more pointed, and lighter in color (Fig. 46D–F); these continuing to posterior thoracic setigers. Uppermost of these larger spines believed to be most newly formed, enclosed in surrounding tissue appearing as a lobe (Fig. 46E–F). Abdominal neurosetae consisting of 4–8 long finely serrated flail setae with aristate tips (Fig. 46J). One or two minute imbedded aciculae also present, but usually not emergent and difficult to observe.

Pygidium not observed.

Remarks. *Phylo paraornatus* **n. sp**. and *P. ornatus* are unusual in the genus in having simple modified spines

that occur in 13 or more posterior thoracic segments instead of spear-like spines that are limited to only a few posterior thoracic segments. Both of these species occur off the U.S. Atlantic coast. The only other species of *Phylo* having more than nine setigers of posterior thoracic spines is *P. foetida* (Claparède, 1868) from the Mediterranean Sea. However, *P. foetida* has an interramal cirrus that is absent in both *P. ornatus* and *P. paraornatus* **n. sp**.

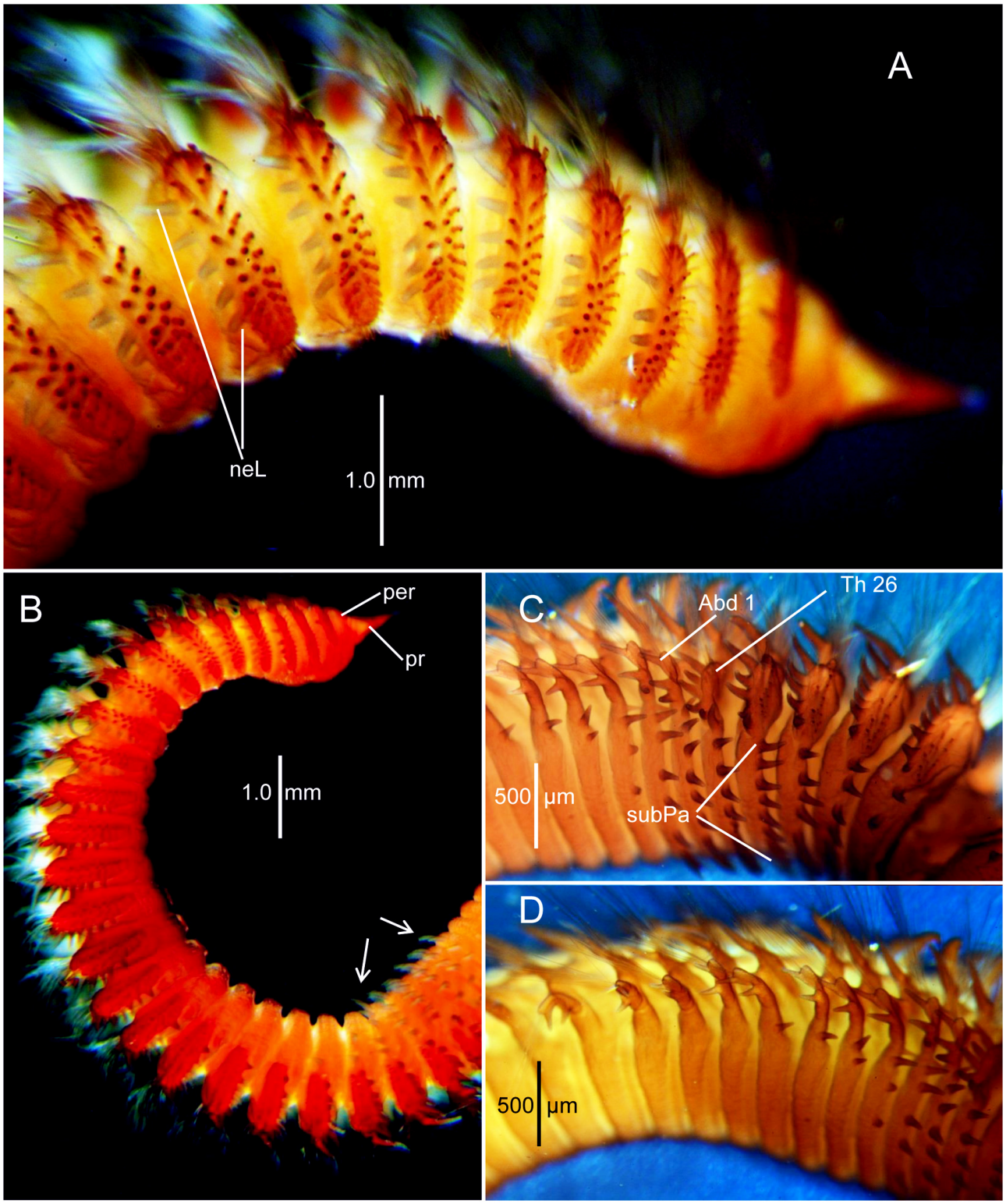

FIGURE 45. *Phylo paraornatus* **n. sp**. Holotype (USNM 1622327): A, anterior end, right lateral view; B, anterior 25 setigers, right lateral view, arrows denote subpodial papillae; C, transition between thoracic and abdominal setigers, right lateral view; D, anterior abdominal setigers, right lateral view. All stained with Shirlastain A.

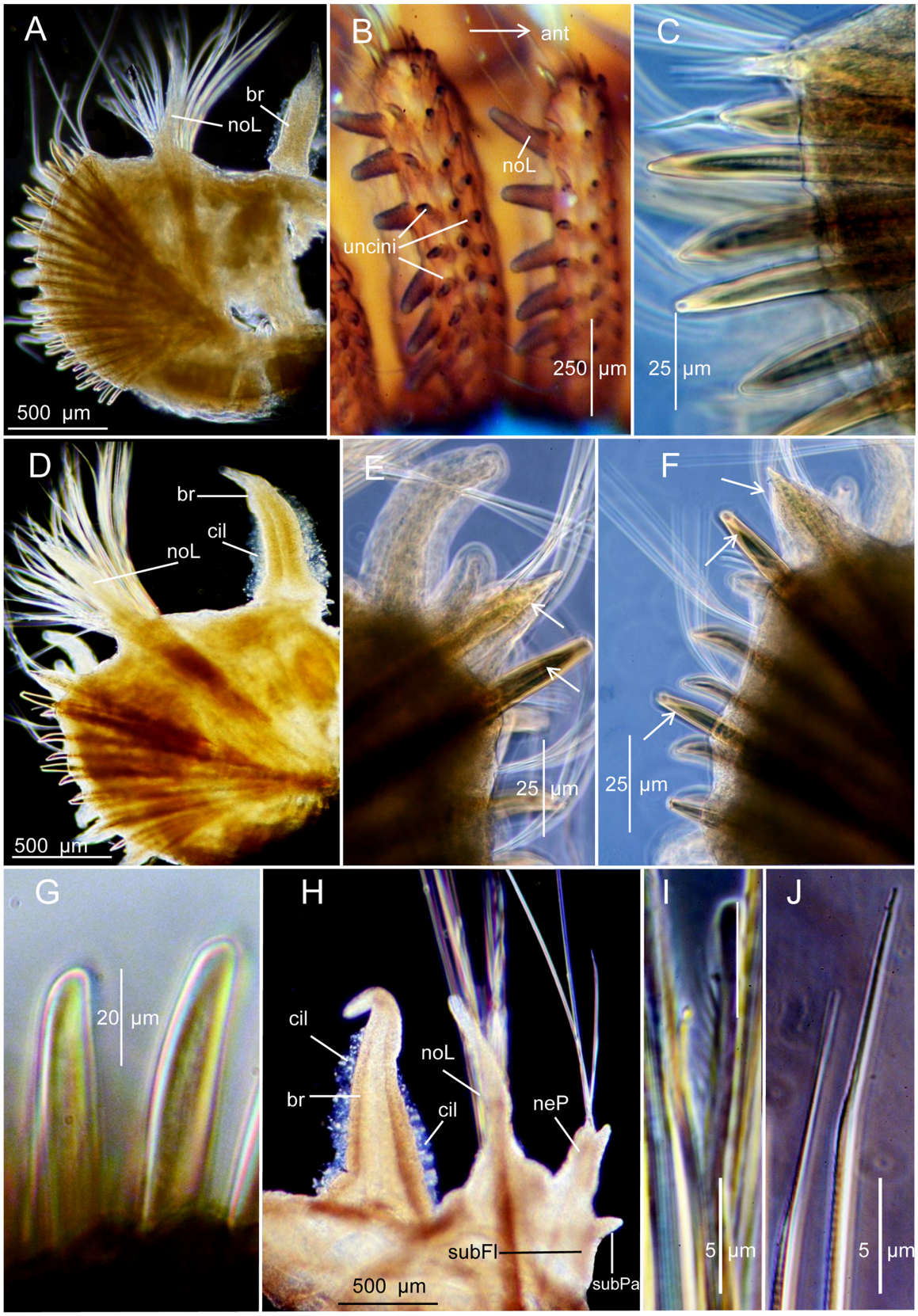

FIGURE 46. *Phylo paraornatus* **n. sp**. Holotype (USNM 1622327): A, thoracic setiger 7, posterior view; B, thoracic setigers 5–6, lateral view; C, thoracic setiger 7, anterior row of uncini; D, setiger 21, anterior view; E, same, detail, anterior view, showing modified spines (arrows); F, same, detail, posterior view showing modified spines (arrows); G, thoracic neuropodial uncini, setiger 3; H, middle abdominal setiger, posterior view; I, abdominal notopodial furcate seta; J, abdominal neuropodial flail setae. A–F, H stained with Shirlastain A.

There are several conspicuous differences between *P. ornatus* and *P. paraornatus* **n. sp**. In *P. ornatus*, the prostomium is short and conical, the subpodial or stomach papillae completely encircle the venter, thoracic neuropodial uncini have transverse ribs along the shaft, the modified spines occur from setiger 15 and are limited to the anterior row of uncini in thoracic neuropodia, and there is no subpodial papilla ventral to the abdominal neuropodium along the body. In contrast, in *P. paraornatus* **n. sp**. the prostomium is long and acutely pointed, the subpodial or stomach papillae are absent in a gap along the venter, thoracic neuropodial uncini are smooth and lack transverse ribs along the shaft, the modified spines occur from setiger 15 and are located at the top of the neuropodium or along the posterior row of uncini, and there is a single subpodial papilla ventral to the neuropodium that continues along the entire body.

Although *Phylo ornatus* and *P. paranoratus* **n. sp**. overlap geographically, the former is only known from nearshore habitats to a depth of about 30 m. Whereas *P. paraornatus* **n. sp**. occurs on the outer continental shelf at depths of 60 m or possible greater.

Etymology. The epithet is from *para*, Greek for near and *ornatus*, Latin for adorned, to indicate the similarity with the closely related species, *Phylo ornatus*.

Distribution. Off Massachusetts, on Georges Bank, 66 m.

Subfamily Microrbiniinae Blake, 2000

Type genus. *Microrbinia* Hartman, 1965. Designated by Blake 2000.

Diagnosis. (Emended). Body small, separation of body into thoracic and abdominal regions weakly defined or lacking; parapodia lateral throughout, not shifted dorsally in abdominal segments. Branchiae present or absent. Prostomium broad, bluntly rounded or more elongate and conical or acute; nuchal organs present. Peristomium with 2–3 achaetous rings, separated from prostomium, sometimes only vaguely defined dorsally, laterally, or ventrally. Noto- and neuropodial postsetal lamellae with short postsetal lobes or absent. Bases of podia separated throughout; setal tori reduced. Setae consisting of capillaries always present, blunt-tipped spines or uncini and swan hooks present or absent; furcate setae typically absent. Pygidium with anal cirri present or absent.

Inclusive genera. *Microrbinia, Orbiniella, Proscoloplos,* and *Pettibonella.*

Remarks. Only species of *Microrbinia* and *Orbiniella* were identified in this study. Three species of *Orbiniella* are new to science. Species of Microrbiniinae are in part defined on negative characters.

Genus *Microrbinia* Hartman, 1965

Type species: *Microrbinia linea* Hartman, 1965, by monotypy.

Diagnosis: (Emended) Body long, threadlike; thoracic region with a few short uniannulate segments gradually transitioning to elongate (biannulate) abdominal segments. Prostomium conical, tapering anteriorly; with paired nuchal organs; eyespots absent. Peristomium a single asetigerous ring. Noto- and neuropodia with well-developed postsetal lobes; branchiae absent; parapodia lateral to dorsolateral, some notopodia directed dorsally, but not shifted on to dorsal surface in abdominal segments. Branchiae absent. Setae serrated or camerated capillaries throughout; posterior notosetae including unusual long serrated spines with curved tips; furcate and flail setae absent. Pygidium with four anal cirri. Males with conical gland-like dorsal organs on a few anterior abdominal segments. Females with 1–2 large, elongate eggs in one or two swollen abdominal segments.

Remarks: The genus *Microrbinia* is monotypic with the only known species, *M. linea* occurring on the U.S. Atlantic continental slope. The species is unusual among orbiniids in having conical gland-like structures on the dorsal surface of some anterior abdominal segments. These appear to be associated with males; females have one or two elongate swollen segments containing large eggs, but none of the gland-like dorsal organs. The unusual serrated spinous notosetae that occur in middle and posterior abdominal segments have not been reported in other orbiniids. The threadlike nature of these worms suggests that they are meiofaunal organisms.

Microrbinia linea Hartman, 1965

Figures 47–48

Microrbinia linea Hartman, 1965: 129–130, pl. 24; Hartman & Fauchald 1971: 92; Maciolek *et al*. 1987a: D-4; Maciolek *et al*. 1987b: D-3; Blake *et al*. 1987: C-4; Blake 1993: 127–128, figs. 2–3; 1994: 921–925, Fig. 2; Blake & Grassle 1994: 850, 853, 855–861, 864–865; Hilbig 1994: 942.

Material examined (*3,371 specimens*). **Off New England, U.S. North Atlantic ACSAR program**, coll. G.W. Hampson, Chief Scientist. **Sta. 3**: Cruise NA-4, Rep. 2, 22 Nov 1984, 40°01.42′N, 66°20.32′W, 1334 m (2, USNM 1622339). **Sta. 5**: Cruise NA-1, Rep. 1, 05 Nov 1984, 40°05.16′N, 67°30.03′W, 2065 m (17, USNM 1622340); Rep. 2, 05 Nov 1984, 40°05.16′N, 67°30.01′W, 2070 m (23, USNM 1622341); Rep. 3, 05 Nov 1984, 40°05.29′N, 67°29.96′W, 2045 m (41, USNM 1622342); Cruise NA-2, Rep. 1, 29 Apr 1985, 40°05.07′N, 67°29.78′W, 2060 m (27, USNM 1622343); Rep. 2, 29 Apr 1985, 40°05.07′N, 67°29.78′W, 2065 m (21, USNM 1622344); Rep. 3, 29 Apr 1985, 40°05.07′N, 67°29.88′W, 2065 m (22, USNM 1622345); Cruise NA-3, Rep. 1, 04 Jul 1985, 40°05.11′N, 67°29.84′W, 2058 m (13, USNM 1622346); Rep. 2, 04 Jul 1985, 40°05.08′N, 67°29.85′W, 2060 m (10, USNM 1622347); Rep. 3, 04 Jul 1985, 40°05.03′N, 67°29.84′W, 2065 m (40, USNM 1622348); Cruise NA-4, Rep. 3, 25 Nov 1985, 40°05.07′N, 67°29.81′W, 2071 m (21, USNM 1622349); Cruise NA-5, Rep. 1, 29 Apr 1986, 40°05.06′N, 67°29.94′W, 2052 m (14, USNM 1622350); Rep. 2, 29 Apr 1986, 40°05.07′N, 67°29.87′W, 2072 m (21, USNM 1622351); Rep. 3, 30 Apr 1986, 40°05.01′N, 67°29.90′W, 2085 m (11, USNM1622352); Cruise NA-6, Rep. 1, 26 Jul 1986, 40°05.08′N, 67°29.79′W, 2063 m (22, USNM 1622353); Rep. 2, 26 Jul 1986, 40°05.03′N, 67°29.95′W, 2078 m (30, USNM 1622354); Rep. 3, 26 Jul 1986, 40°05.09′N, 67°29.67′W, 2055 m (33, USNM 16223455). **Sta. 6**: Cruise NA-2, Rep. 2, 29 Apr 1985, 40°05.03′N, 67°29.13′W, 2108 m (3, USNM 1622356); Cruise NA-4, Rep. 3, 25 Nov 1985, 40°05.09′N, 67°29.24′W, 2114 m (1, USNM 16223557). **Sta. 8**: Cruise NA-4, Rep. 1, 25 Nov 1985, 40°10.21′N, 67°37.24′W, 2184 m (2, USNM 1622358); Cruise NA-6, Rep. 3, 26 Jul 1986, 40°10.21′N, 67°37.28′W, 2188 m (1, USNM 1622359). **Sta. 9**: Cruise NA-1, Rep. 3, 12 Nov 1984, 39°50.53′N, 70°01.68′W, 1225 m (1, USNM 1622360); Cruise NA-6, Rep. 2, 28 Jul 1986, 39°50.41′N, 70°01.62′W, 1230 m (1, USNM 1622361); Rep. 3, 28 Jul 1986, 39°50.43′N, 70°01.69′W, 1221 m (1, USNM 1622362). **Sta. 10**: Cruise NA-1, Rep. 1, 12 Nov 1984, 39°48.22′N, 70°05.33′W, 1200 m (1, USNM 1622363); Rep. 2, 13 Nov 1984, 39°48.10′N, 70°05.29′W, 1234 m (4, USNM 1622364); Rep. 3, 15 Nov 1984, 39°48.09′N, 70°05.17′W, 1235 m (2, USNM 1622365); Cruise NA-2, Rep. 1, 03 May 1985, 39°48.11′N, 70°05.26′W, 1210 m (5, USNM 1622366); Rep. 2, 03 May 1985, 39°48.10′N, 70°05.21′W, 1212 m (2, USNM 1622367); Rep. 3, 03 May 1985, 39°48.12′N, 70°05.24′W, 1210 m (2, USNM 1622368); Cruise NA-4, Rep. 1, 27 Nov 1985, 39°48.09′N, 70°05.29′W, 1222 m (3, USNM 1622369); Cruise NA-5, Rep. 1, 03 May 1986, 39°48.06′N, 70°05.25′W, 1240 m (3, USNM 1622370); Rep. 2, 03 May 1986, 39°48.05′N, 70°05.52′W, 1270 m (1, USNM 1622371); Rep. 3, 03 May 1986, 39°48.09′N, 70°05.42′W, 1237 m (10, USNM 1622372); Cruise NA-6, Rep. 1, 28 Jul 1986, 39°48.06′N, 70°05.26′W, 1226 m (9, USNM 1622373); Rep. 3, 28 Jul 1986, 39°48.09′N, 70°05.25′W, 1228 m (8, USNM 1622374). **Sta. 12**: Cruise NA-5, Rep. 2, 06 May 1986, 39°54.27′N, 70°55.17′W, 548 m (1, USNM 1622375). **Sta. 13**: Cruise NA-1, Rep. 1, 09 Dec 1984, 39°48.45′N, 70°54.86′W, 1245 m (1, USNM 1622376); Cruise NA-6, Rep. 3, 30 Jul 1986, 39°48.25′N, 70°54.95′W, 1273 m (1, USNM 1622377). **Sta. 14**: Cruise NA-2, Rep. 1, 05 May 1985, 39°40.91′N, 70°54.17′W, 2095 m (3, USNM 1622378).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR program**, coll. Rosemarie Petrecca, Chief Scientist. **Sta. 6**: Cruise Mid-5, Rep. 2, 02 Aug 1985, 39°05.64′N, 72°03.24′W, 2080 m (1, USNM 1622379). **Sta. 12**: Cruise Mid-5, Rep. 3, 07 Aug 1985, 38°29.23′N, 72°42.22′W, 2495 m (1, USNM 1622380).—**Southeastern USA, U.S. South Atlantic ACSAR program,** coll. J.A. Blake, Chief Scientist. **Off Cape Lookout, North Carolina**, **Sta. 3**: Cruise SA-1, Rep. 2, 15 Nov 1983, 34°13.42′N, 75°39.45′W, 1690 m (9, USNM 1622381). **Sta. 4**: Cruise SA-1, Rep. 1, 16 Nov 1983, 34°11.68′N, 75°39.54′W, 1960 m (76, USNM 1622382); Rep. 2, 17 Nov 1983, 34°12.54′N, 75°39.03′W, 1940 m (52, USNM 1622383); Rep. 3, 17 Nov 1983, 34°11.77′N, 75°38.97′W, 1910 m (81, USNM 1622384); Cruise SA-2, Rep. 1, 20 May 1984, 34°11.70′N, 75°38.60′W, 2064 m (70, USNM 1622385); Rep. 2, 20 May 1984, 34°11.90′N, 75°38.70′W, 2029 m (95, USNM 1622386); Rep. 3, 20 May 1984, 34°11.50′N, 75°39.00′W, 1969 m (91, USNM 1622387); Cruise SA-3, Rep. 1, 13 Jul 1984, 34°12.10′N, 75°38.60′W, 2066 m (111, USNM 1622388); Rep. 2, 14 Jul 1984, 34°10.41′N, 75°39.10′W, 2005 m (62, USNM 1622389); Rep. 3, 14 Jul 1984, 34°11.17′N, 75°38.98′W, 2006 m (65, USNM 1622390); Cruise SA-4, Rep. 1, 23 May 1985, 34°11.20′N, 75°38.44′W, 2093 m (51, USNM 1622391); Rep. 2, 23 May 1985, 34°11.22′N, 75°38.44′W, 2051 m (53, USNM 1622392); Rep. 3, 23 May 1985, 34°11.29′N, 75°38.67′W, 2015 m (103, USNM 1622393); Cruise SA-5, Rep. 1, 24

Sep 1985, 34°11.27′N, 75°38.63′W, 2032 m (86, USNM 1622394); Rep. 2, 24 Sep 1985, 34°11.35′N, 75°38.74′W, 2000 m (50, USNM 1622395); Rep. 3, 24 Sep 1985, 34°11.22′N, 75°38.56′W, 2051 m (58, USNM 1622396); Cruise SA-6, Rep. 1, 24 Nov 1985, 34°11.17′N, 75°38.64′W, 2054 m (41, USNM 1622397); Rep. 2, 24 Nov 1985, 34°11.21′N, 75°38.61′W, 2049 m (35, JAB); Rep. 3, 24 Nov 1985, 34°11.23′N, 75°38.53′W, 2057 m (37, JAB). **Off Cape Fear**, **North Carolina**, **Sta. 11**: Cruise SA-4, Rep. 1, 22 May 1985, 33°04.86′N, 76°25.13′W, 800 m (99, USNM 1622398); Rep. 2, 22 May 1985, 34°04.92′N, 76°24.97′W, 802 m (116, USNM 1622399); Rep. 3, 22 May 1985, 33°04.87′N, 76°25.14′W, 799 m (61, USNM 1622400); Cruise SA-5, Rep. 1, 23 Sep 1985, 33°04.83′N, 76°25.19′W, 796 m (55, USNM 1622401); Rep. 2, 23 Sept 1985, 34°04.83′N, 76°25.17′W, 800 m (58, USNM 1622402); Rep. 3, 23 Sep 1985, 33°04.86′N, 76°25.12′W, 797 m (82, USNM 1622403); Cruise SA-6, Rep. 1, 22 Nov 1985, 33°04.95′N, 76°25.15′W, 804 m (79, USNM 1622404); Rep. 2, 22 Nov 1985, 33°04.94′N, 76°25.17′W, 804 m (113, USNM 1622405); Rep. 3, 22 Nov 1985, 33°04.84′N, 76°25.06′W, 807 m (76, USNM 1622406). **Sta. 12**: Cruise SA-4, Rep. 1, 22 May 1985, 33°00.31′N, 76°07.39′W, 1996 m (5, USNM 1622407); Rep. 3, 22 May 1985, 33°00.20′N, 76°07.25′W, 2000 m (2, USNM 1622408); Cruise SA-5, Rep. 1, 22 Sep 1985, 33°00.36′N, 76°07.27′W, 2004 m (1, USNM 1622409); Cruise SA-6, Rep. 1, 21 Nov 1985, 33°00.55′N, 76°07.45′W, 1992 m (4, USNM 1622410); Rep. 3, 21 Nov 1985, 33°00.38′N, 76°07.46′W, 1994 m (20, USNM 1622411). **Sta. 13**: Cruise SA-4, Rep. 1, 21 May 1985, 32°55.19′N, 76°49.78′W, 3015 m (7, USNM 1622412); Rep. 2, 21 May 1985, 32°55.78′N, 76°49.80′W, 3013 m (14, USNM 1622413); Rep. 3, 21 May 1985, 32°55.02′N, 76°49.47′W, 3015 m (17, USNM 1622414); Cruise SA-6, Rep. 1, 20 Nov 1985, 32°55.16′N, 75°50.25′W, 2999 m (59, USNM 1622415); Rep. 2, 20 Nov 1985, 32°55.22′N, 75°50.20′W, 3002 m (18, USNM 1622416); Rep. 3, 21 Nov 1985, 32°55.25′N, 75°50.08′W, 3006 m (14, USNM 1622417). **Off Charleston, South Carolina**, **Sta. 14A**: Cruise SA-5, Rep. 1, 20 Sep. 1985, 32°32.25′N, 77°15.24′W, 600 m (1, USNM 1622418). **Sta. 14:** Cruise SA-4, Rep. 1, 20 May 1985, 32°23.64′N, 77°01.13′W, 805 m (83, USNM 1622419); Rep. 2, 20 May 1985, 32°23.64′N, 77°01.19′W, 802 m (105, USNM 1622420); Cruise SA-5, Rep. 1, 19 Sep 1985, 32°23.67′N, 77°01.18′W, 796 m (36, USNM 1622421); Rep. 2, 19 Sep 1985, 32°23.72′N, 77°01.24′W, 799 m (64, USNM 1622422); Rep. 3, 19 Sep 1985, 32°23.63′N, 77°01.11′W, 799 m (85, USNM 1622423); Cruise SA-6, Rep. 1, 18 Nov 1985, 32°23.73′N, 77°01.10′W, 799 m (90, USNM 1622424); Rep. 2, 18 Nov 1985, 32°23.67′N, 77°01.09′W, 799 m (63, USNM 1622425); Rep. 3, 18 Nov 1985, 32°23.70′N, 77°01.06′W, 799 m (85, USNM 1622426). **Sta. 15**: Cruise SA-4, Rep. 3, 16 May 1985, 32°10.74′N, 76°42.93W, 2003 m (25, USNM 1622427); Rep. 2, 16 May 1985, 32°12.05′N, 76°42.18′W, 1991 m (38, USNM 1622428); Cruise SA-5, Rep. 1, 18 Sep 1985, 32°12.002′N, 76°42.23′W, 1988 m (18, USNM 1622429); Rep. 2, 18 Sep 1985, 32°11.99′N, 76°42.23′W, 1991 m (13, USNM 1622430); Rep. 3, 18 Sep 1985, 32°11.97′N, 76°42.19′W, 1991 m (23, USNM 1622431). **Sta. 16**: Cruise SA-4, Rep. 1, 15 May 1985, 31°35.23′N, 75°10.62′W, 3008 m (17, USNM 16224323); Rep. 3, 15 May 1985, 31°35.10′N, 75°10.36′W, 3008 m (23, USNM 1622433); Cruise SA-5, Rep. 1, 14 Sep 1985, 31°35.19′N, 75°10.39′W, 3009 m (10, USNM 1622434); Rep. 2, 16 Sep 1985, 31°35.14′N, 75°10.28′W, 3011 m (9, USNM 1622435); Rep. 3, 16 Sep 1985, 31°35.00′N, 75°10.46′W, 2999 m (10, USNM 1622436); Cruise SA-6, Rep. 1, 20 Nov 1985, 31°35.12′N, 75°10.34′W, 3029 m (25, USNM 1622437); Rep. 2, 20 Nov 1985, 31°35.10′N, 75°10.34′W, 3009 m (12, USNM 1622438); Rep. 3, 20 Nov 1985, 31°35.16′N, 75°10.22′W, 3012 m (15, USNM 1622439).

Description. A small, threadlike species; largest complete specimen (USNM 1622397) with 39 setigers, 8.4 mm long and 0.21 mm wide across thorax; another specimen (USNM 1622393) with 35 setigers, 6.5 mm long and 0.2 mm wide. Hartman (1965) reported largest specimens with about 35 setigers, 0.4 mm wide and 7.5–8.5 mm long. Over 3,100 specimens available in ACSAR collections representing a full range of sizes and reproductive modes. Body thin, cylindrical along entire length (Fig. 48E), with 6–7 short, uniannulate anterior thoracic setigers (Figs. 47A–B, 48A–B) followed by elongate, biannulate abdominal setigers with parapodia located at posterior margins (Figs. 47C–D, 48D, F). Dorsal and ventral longitudinal grooves or ridges absent. A few anterior abdominal setigers of presumed males with conical gland-like dorsal organs on individual segments (Figs. 47A, C, 48A, C–D). Females with one, rarely two, swollen middle abdominal segments bearing two long ova (Figs. 47D, F; 48 F) measuring between 233 and 321 μm in longest dimension (Blake 1993). Color in alcohol: opaque white.

Pre-setiger region long, narrow, about as long as first three setigers, merging with setiger 1 both dorsally and ventrally (Figs. 47A–C, 48A–B, E). Prostomium triangular, tapering to narrow conical tip; nuchal organs narrow slits on posterior lateral margins, difficult to observe; eyespots absent. Peristomium a single large smooth ring dorsally (Figs. 47A, 48A); ventrally forming anterior and posterior lips of mouth; each lip with 5–6 short lobes (Fig. 47B); everted proboscis not observed on any specimen.

Thoracic segments numbering 6–7, each relatively short, about three times wider than long and with narrow transverse intersegmental groove both dorsally and ventrally (Figs. 47A–B, 48A–B). Transition to abdominal segments denoted by a narrowing and elongation of individual segments and thickening and elongation of neuropodia (Figs. 47A, 48A). Abdominal segments with parapodia located at posterior margin preceded by intersegmental annular ring (Figs. 47A, 48A); some abdominal segments 5–6 times longer than wide (Figs. 47D, 48E), sometimes moniliform. Branchiae entirely absent.

Notopodia with either a short papilla or no visible postsetal lobe on setigers 1–2; thereafter prominent digitate notopodial postsetal lobe present, longest in posterior thoracic and anterior abdominal setigers (Figs. 47A, 48A). Neuropodia with a short digitate postsetal lobe in thoracic setigers, becoming long and thickened in abdominal setigers (Fig. 47B–C). Neuropodia of abdominal segments lateral, not shifted dorsally as in most orbiniids; prominently visible as thickened lateral lobes along body (Fig. 47C). Notopodia located in dorsal location along body (Fig. 47A).

Notopodia with a spreading fascicle of 6–10 camerated capillaries in thoracic setigers and anterior abdominal setigers; capillaries gradually replaced in middle and posterior abdominal setigers with 4–6 serrated spines; these with distinct serrations along one margin, tapering to a curved, pointed tip (Figs. 47E, 48H). Neurosetae of thoracic segments 4–5 camerated capillaries; these continuing over anterior abdominal setigers, then reduced to 1–3 smooth capillaries in middle and posterior abdominal setigers.

Pygidium a simple lobe bearing four thin anal cirri (Fig. 48E, G).

Remarks. *Microrbinia linea* is a small meiofaunal polychaete that is a dominant species in soft sediments on the U.S. Atlantic continental slope, especially off North and South Carolina. The species is unusual among orbiniids in having conical gland-like dorsal organs on the surface of some anterior abdominal segments. These structures appear to be associated with males; females have one or rarely two elongate swollen segments containing large eggs, but none of the dorsal gland-like structures.

Morphologically, *M. linea* can be recognized by the thin, threadlike body, in which six or seven short anterior setigers constitute the thorax; these transition to abdominal segments that are longer, biannulate, and sometimes moniliform, with the actual parapodia located on the posterior margin of individual segments. The neuropodia arise laterally in abdominal segments rather than being dorsally elevated as in larger orbiniids. The abdominal notopodia occur on the dorsal lateral surface. There are no branchiae. The unusual serrated spinous notosetae that occur in middle and posterior abdominal segments have not been reported in other orbiniids.

Biology. *Microrbinia linea* occurs along the entire U.S. Atlantic continental slope from off New England to South Carolina. The species was the top ranked dominant benthic invertebrate species at several sites off the Carolinas: Sta. 4 (2000 m) off Cape Lookout; Sta. 11 (800 m), Sta. 12 (2000 m), and Sta. 13 (3000 m) off Cape Fear; Sta. 14 (800 m) and Sta. 15 (2000 m) off Charleston (Blake & Grassle 1994). The species was also abundant at a few sites off New England but was not a dominant species (Maciolek *et al*. 1987b).

Blake (1994) provided data on vertical distribution in 10 x 10 x 10 cm cores that were cut to 0–2, 2–5, and 5–10 cm depth intervals from which the individual organisms were retained, counted, and identified. Raw numbers and percentages for these depth intervals for *Microrbinia linea* at Station 4 (2000 m) were: 0–2 cm: 65 (25%), 2–5 cm: 186 (71.5%), and 5–10 cm: 9 (3.5%). Thus 96.5% of all specimens of *M. linea* occurred in the upper 5 cm with the majority in the 2–5 cm depth interval. These results suggest that *M. linea* is a subsurface deposit feeder, but due to its small size is more or less limited to the upper 5 cm.

Due to the large numbers of specimens of *M. linea* available from seasonal collections on the North Carolina slope, Blake (1993) was able to assess some aspects of reproduction and size frequency of specimens from Sta. 4 off Cape Lookout at 2000 m. As part of this study, the unusual conical, gland-like dorsal organs on anterior abdominal segments of some specimens were observed. A histological examination revealed them to be glandular in nature, but no distinct pore or opening through either the structure or the integument was observed. This structure was prevalent in males and likely plays some role in copulation. Females lacked these structures.

Out of 577 individuals examined, 253 were found either with gametes or some evidence of sexuality. Of these, 201 were males (79.4%) and 52 were females (20.6%). Mature females bear two large eggs in a single segment (Figs. 47E, 48F) or rarely a second segment. The eggs are elongate (200–364 x 75–152 μm) and with a germinal vesicle in a finely granulated cytoplasm (Fig. 47F). The largest eggs were found in July 1984 (mean = 369 x 119 μm) and May 1985 (mean = 321 x 136 μm). Males were observed with gametes at all stages of spermiogenesis. Mature sperm are 8–10 μm long and long-headed. The highest percentages of mature males were observed in July and September, while females were most prevalent in May, September, and November (Blake 1993).

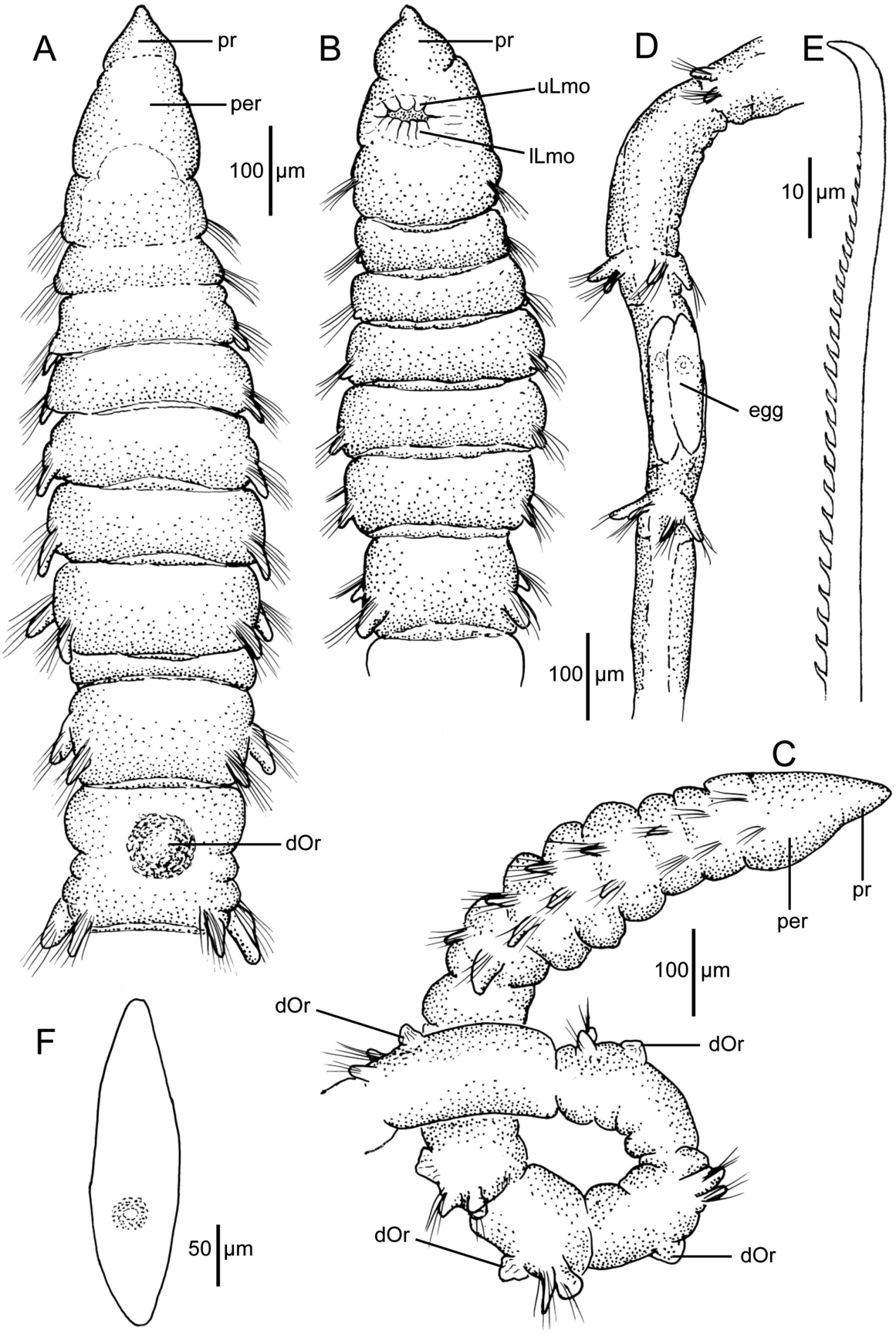

FIGURE 47. *Microrbinia linea* Hartman, 1965. A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior end, right lateral view; D, middle abdominal setigers with eggs; E, abdominal notopodial serrated spine; F, egg. A–B, E (USNM 1622397); C–D, F (USNM 1622388; after Blake 1993).

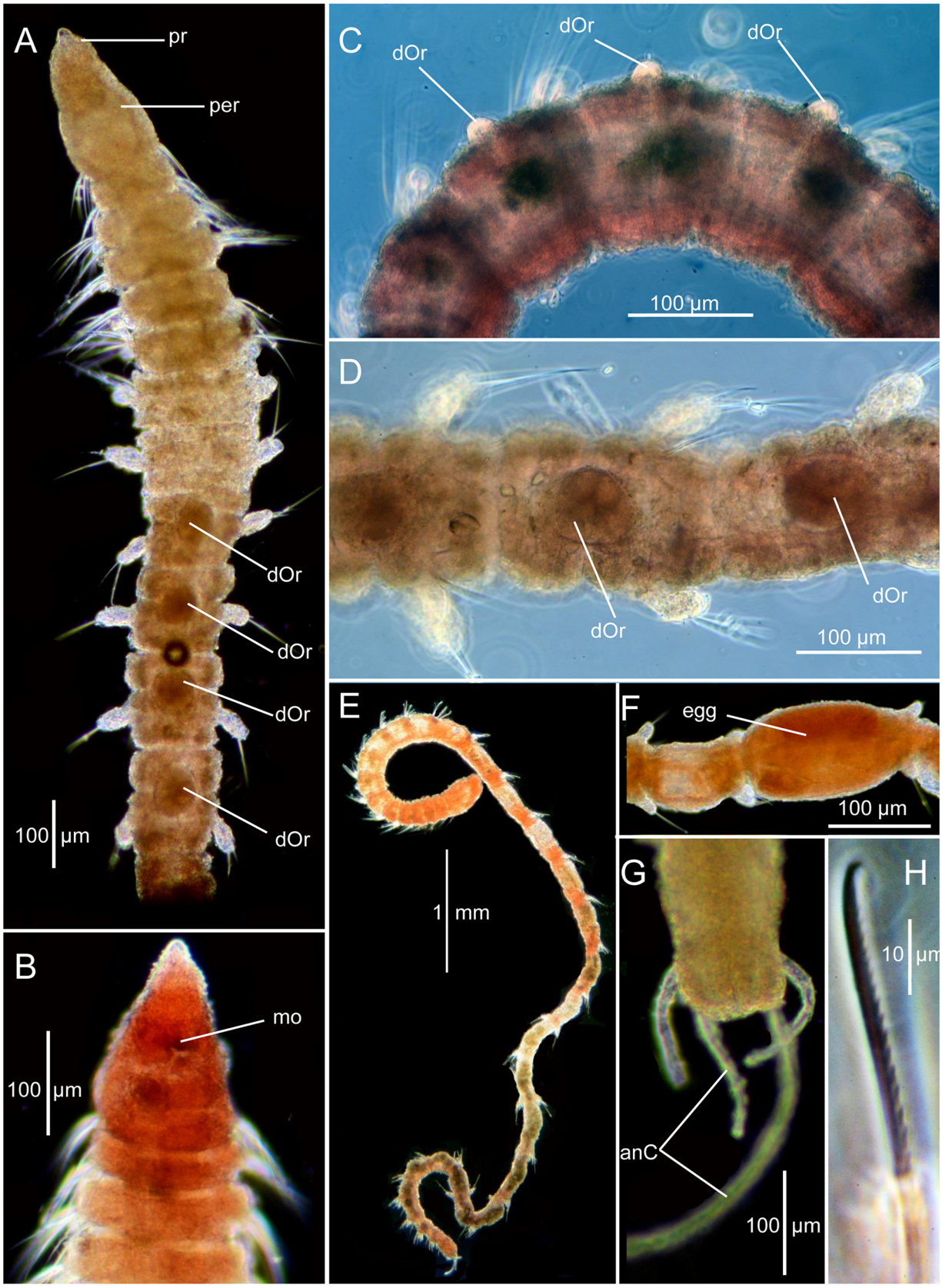

FIGURE 48. *Microrbinia linea* Hartman, 1965. (USNM 1622392): A, anterior end, dorsal view; B, anterior end, ventral view; C, anterior abdominal setiger with dorsal organs, lateral view; D, anterior abdominal setiger with dorsal organs, dorsal view; E, entire worm showing threadlike nature of body; F, abdominal ovigerous segment, dorsal view; G, posterior end with anal cirri; H, abdominal notopodial serrated spine. A–G stained with Shirlastain A.

Size classes of specimens from Sta. 4 were based on thoracic width: four size classes were present: 5–10 µm, 10–15 µm, 15–20 µm, 20–25 µm. The 10–15 µm size class was most abundant in November 1983, and May and July 1984, while the 15–20 µm size class was most abundant in May, September, and November 1985. No seasonal trends are apparent from these data. The presence of females with large eggs in each seasonal set of samples and the relatively uniform size class data suggested that reproduction and recruitment is year round (Blake 1993).

Distribution. U.S. Atlantic continental slope, New England to South Carolina; 600–3015 m; off mouth of the Amazon River, 770–1500 m.

Genus *Orbiniella* Day, 1954

Type-species: *Orbiniella minuta* Day, 1954, by monotypy.
Synonym: *Falklandiella* Hartman, 1967. *Fide* Buzhinskaja 1992: 76. **Type species**: *Falklandiella annulata* Hartman, 1967, by monotypy.

Diagnosis: (after Blake 2017) Body elongate, with separation between thorax and abdomen indistinct, anterior segments may be narrower than more posterior segments, but changing gradually over several segments, or no change in appearance between anterior and posterior segments; prostomium broad or elongate with paired nuchal organs usually present, these sometimes pigmented, eyespots present or absent; peristomium with 1–2 asetigerous rings. Noto- and neuropodia poorly developed, consisting of low tori from which setae emerge; with only simple post-setal lamellae, or these entirely absent; posterior parapodia not elevated and shifted dorsally as in genera of Orbiniinae. Capillary noto- and neurosetae always crenulated or weakly camerated with pointed bristles apparent at relatively low magnification (100x); prominent acicular spines present or absent in either noto- and neuropodia, or entirely absent; furcate setae absent. Branchiae absent.

Remarks. According to Blake (2017, 2020), there are 19 valid species of *Orbiniella*. Of these, ten species are reported from deep-water habitats exceeding 1000 m. In the present study, three new species of *Orbiniella* were identified in the ACSAR samples, all of which are from deep water, thus indicating that the majority of species in the genus (13 of 22) occur in deep water.

1. *Orbiniella acsara* **n. sp.**
2. *Orbiniella armata* **n. sp.**
3. *Orbiniella mimica* **n. sp.**

Orbiniella acsara new species

Figures 49–50
urn:lsid:zoobank.org:act:0FC5DEE6-9F49-44EF-838D-6ABB6690E779

Orbiniella sp. 1: Maciolek *et al*. 1987a: D-4; Maciolek *et al*. 1987b: D-3; Blake *et al*. 1987: C4; Hilbig 1994: 942.

Material examined (*79 specimens*). **Off New England, U.S. North Atlantic ACSAR program**, coll. G.W. Hampson, Chief Scientist. **Sta. 14**: Cruise N-1, Rep. 1, 09 Dec 1984, 39°40.90′N, 70°54.20′W, 2105 m, **holotype** (USNM 1622440) and 1 **paratype** (USNM 1622441); Cruise NA-2, Rep. 2, 05 May 1985, 39°40.93′N, 70°54.21′W, 2092 m, 1 **paratype** (USNM 1622442). **Sta. 2**: Cruise NA-1, Rep. 2, 08 Nov 1984, 40°57.20′N, 66°13.87′W, 2095 m, (2, USNM 1622443); Cruise NA-3, Rep. 2, 03 Jul 1985, 40°57.22′N, 66°13.73′W, 2100 m, 2 **paratypes** (USNM 1622444); Cruise NA-4, Rep. 1, 23 Nov 1985, 40°57.30′N, 66°13.75′W, 2114 m, 1, **paratype** (USNM 1622445); Cruise NA-6, Rep. 3, 25 Jul 1986, 40°57.23′N, 66°13.82′W, 2103 m, (1, USNM 1622446). **Sta. 3**: Cruise NA-6, Rep. 2, 08 Nov 1984, 41°01.03′N, 66°20.03′W, 1370 m, (1, USNM 1622447). **Sta. 5**: Cruise NA4, Rep. 2, 25 Nov 1985, 40°05.09′N, 67°29.84′W, 2071 m (2, USNM 1622448); Rep. 3, 25 Nov 1985, 40°05.07′N, 67°29.81′W, 2071 m (3, USNM 1622449); Cruise NA5, Rep. 1, 29 Apr 1986, 40°05.06′N, 67°29.94′W, 2052 m (1, USNM 1622450); Rep. 2, 29 Apr 1986, 40°05.07′N, 67°29.87′W, 2072 m (2, USNM 1622451); Rep. 3, 30 Apr 1986, 40°05.01′N, 67°29.90′W, 2085 m (1, USNM 1622452); Cruise NA-6, Rep. 1, 26 Jul 1986, 40°05.08′N, 67°29.79′W, 2063 m, 2 **paratypes** (USNM 1622453); Rep. 2, 26 Jul 1986, 40°05.03′N, 67°29.95′W, 2078 m (1, USNM 1622454). **Sta.**

6: Cruise NA-1, Rep. 3, 06 Nov 1984, 40°05.14′N, 67°29.35′W, 2112 m, 1 **paratype** (USNM 1622455); Cruise NA-2, Rep. 1, 29 Apr 1985, 40°05.03′N, 67°29.13′W, 2108 m, 1 **paratype** (USNM 1622456); Rep. 2, 29 Apr 1985, 40°05.06′N, 67°29.13′W, 2107 m (1, USNM 1622457); Cruise NA-5, Rep. 3, 01 May 1986, 40°05.10′N, 67°29.13′W, 2109 m, **paratype** (USNM 1622458); Cruise NA-6, Rep. 1, 26 Jul 1986, 40°05.07′N, 67°29.07′W, 2110 m, (1, USNM 1622459). **Sta**. **8**: Cruise NA-5, Rep. 3, 29 Apr 1986, 40°10.14′N, 67°37.45′W, 2130 m, 1 **paratype** (USNM 1622460). **Sta. 9**: Cruise NA-1, Rep. 3, 12 Nov 1984, 39°50.53′N, 70°01.68′W, 1225 m (1, USNM 1622461). **Sta. 10**: Cruise NA-6, Rep. 1, 28 Jul 1986, 39°48.06′N, 70°05.26′W, 1226 m (1, USNM 1622462); Cruise NA-6, Rep. 3, 28 Jul 1986, 39°48.09′N, 70°05.25′W, 1228 m (1, USNM 1622463). **Sta. 15**: Cruise NA-2, Rep. 1, 05 May 1985, 39°40.08′N, 70°54.26′W, 2150 m, 1 **paratype** (USNM 1622464); Cruise NA-5, Rep. 2, 05 May 1986, 39°39.95′N, 70°54.19′W, 2164 m (1, USNM 1622465); Cruise NA-6, Rep. 1, 28 Jul 1986, 39°40.05′N, 70°28′W, 2153 m (2, USNM 1622466).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR** program, coll. Rosemarie Petrecca, Chief Scientist. **Sta. 1**: Cruise Mid-2, Rep. 1, 03 Aug 1984, 38°36.12′N, 72°53.06′W, 2209 m (1, USNM 1622467). **Sta. 2**: Cruise Mid-3, Rep. 3, 02 Dec 1984, 38°35.68′N, 72°53.69′W, 2015 m (2, USNM 1622468); Cruise Mid-4, Rep. 1, 17 May 1985, 38°35.66′N, 72°53.81′W, 2010 m (1, USNM 1622469); Rep. 2, 17 May 1985, 38°35.66′N, 72°53.80′W, 2011 m (1, USNM 1622470); Cruise Mid-5, Rep. 3, 05 Aug 1985, 38°35.69′N, 72°53.78′W, 2005 m (1, USNM 1622471). **Sta. 3**: Cruise Mid-1, Rep. 3, 04 May 1984, 38°36.86′N, 72°51.29′W, 2060 m (2, USNM 1622472); Cruise Mid-4, Rep. 3, 16 May 1985, 38°36.75′N, 72°51.60′W, 2052 m (1, USNM 1622473); Cruise Mid-5, Rep. 3, 05 Aug 1985, 38°36.82′N, 72°51.54′W, 2050 m (1, USNM 1622474); Cruise Mid-6, Rep. 1, 12 Nov 1985, 38°36.73′N, 72°51.62′W, 2064 m (2, USNM 1622475). Sta. 5: Cruise Mid-1, Rep. 3, 08 May 1984, 38°50.46′N, 72°33.14′W, 2080 m (1, USNM 1622476); Cruise Mid-2, Rep. 3, 01 Aug 1984, 38°50.52′N, 72°32.96′W, 2074 m (1, USNM 1622477). **Sta. 6**: Cruise Mid-1, Rep. 1, 03 May 1984, 39°05.61′N, 72°02.98′W, 2090 m (1, USNM 1622478); Cruise Mid-3, Rep. 1, 28 Nov 1984, 39°05.58′N, 72°02.81′W, 2090 m (1, USNM 1622479); Rep. 2, 28 Nov 1984, 39°05.57′N, 72°02.83′W, 2090 m (2, USNM 1622480); Rep. 3, 28 Nov 1984, 39°05.58′N, 72°02.81′W, 2085 m (1, USNM 1622481); Cruise Mid-4, Rep. 1, 15 May 1985, 39°05.61′N, 72°03.26′W, 2090 m (1, USNM 1622482); Rep. 2, 15 May 1985, 39°05.66′N, 72°03.25′W, 2045 m (1, USNM 1622483); Cruise Mid-6, Rep. 1, 10 Nov 1985, 39°05.67′N, 72°03.36′W, 2089 m (3, USNM 1622484). **Sta. 7**: Cruise Mid-1, Rep. 2, 06 May 1984, 38°27.30′N, 73°03.43′W, 2100 m (1, USNM 1622485); Cruise Mid-2, Rep. 2, 03 Aug 1984, 38°27.32′N, 73°03.38′W, 2104 m (1, USNM 1622486); Cruise Mid-3, Rep. 3, 02 Dec 1984, 38°27.25′N, 73°03.44′W, 2110 m (1, USNM 1622487); Cruise Mid-5, Rep. 3, 07 Aug 1985, 38°27.31′N, 73°03.54′W, 2088 m (1, USNM 1622488). **Sta. 8**: Cruise Mid-1, Rep. 1, 06 May 1984, 38°27.36′N, 73°05.09′W, 2150 m (1, USNM 1622489); Rep. 2, 06 May 1984, 38°27.36′N, 73°04.88′W, 2150 m (1, USNM 1622490). **Sta. 9**: Cruise Mid-1, Rep. 3, 06 May 1984, 38°17.23′N, 73°14.60′W, 2108 m (1, USNM 1622491); Cruise Mid-5, Rep. 3, 09 Aug 1985, 38°17.19′N, 73°14.63′W, 2100 m (1, USNM 1622492); Cruise Mid-6, Rep. 3, 17 Nov 1985, 38°17.23′N, 73°14.65′W, 2104 m (1, USNM 1622493). **Sta. 10**: Cruise Mid-4, Rep. 2, 19 May 1985, 37°51.75′N, 73°19.97′W, 2095 m (1, USNM 1622494); Cruise Mid-5, Rep. 1, 09 Aug 1985, 37°51.76′N, 73°20.04′W, 2095 m (2, USNM 1622495); Rep. 3, 09 Aug 1985, 37°51.75′N, 73°20.054′W, 2095 m (1, USNM 1622496). **Sta. 12**: Cruise Mid-1, Rep. 1, 07 May 1984, 38°29.34′N, 72°42.23′W, 2501 m (1, USNM 1622497); Rep. 3, 08 May 1984, 38°29.33′N, 72°42.24′W, 2500 m (1, USNM 1622498); Cruise Mid-5, Rep. 1, 07 Aug 1985, 38°29.23′N, 72°42.22′W, 2495 m (1, USNM 1622499). **Sta. 13**: Cruise Mid-3, Rep. 1, 30 Nov 1984, 37°53.32′N, 73°45.10′W, 1615 m (1, USNM 1622500); Cruise Mid-5, Rep. 1, 09 Aug 1985, 37°53.26′N, 73°45.21′W, 1607 m (3, USNM 1622501). **Sta. 14**: Cruise Mid-1, Rep. 3, 02 Apr 1984, 37°53.86′N, 73°44.68′W, 1503 m (1, USNM 1622502).—**Southeastern USA, U.S. South Atlantic ACSAR program,** coll. J.A. Blake, Chief Scientist. **Off Cape Lookout, North Carolina**, **Sta. 4**: Cruise SA-5, Rep. 1, 24 Sep 1985, 34°11.27′N, 75°38.63′W, 2032 m (1, USNM 1622503); Cruise SA-6, Rep. 2, 24 Nov 1985, 34°11.21′N, 75°38.61′W, 2049 m (1, USNM 1622504). **Sta. 5**: Cruise SA-3, Rep. 3, 12 Jul 1984, 34°05.60′N, 75°19.10′W, 3019 m (1, USNM 1622505). **Off Cape Fear, North Carolina**, **Sta. 11**: Cruise SA-4, Rep. 1, 22 May 1985, 33°04.86′N, 76°25.13′W, 800 m (1, USNM 1622506). **Sta. 12**: Cruise SA-4, Rep. 3, 22 May 1985, 33°00.20′N, 76°07.25′W, 2000 m (1, USNM 1622507); Cruise SA-5, Rep. 1, 22 Sep 1985, 33°00.36′N, 76°07.27′W, 2004 m (1, USNM 1622508). **Off Charleston, South Carolina**, **Sta. 14**: Cruise SA-6, Rep. 3, 18 Nov 1985, 32°23.70′N, 77°01.06′W, 799 m (1, USNM 1622509). **Sta. 16**: Cruise SA-5, Rep. 1, 14 Sep 1985, 31°35.19′N, 75°10.39′W, 3009 m (1, USNM 1622510).

Description. A long, narrow, threadlike species (Fig. 50A); holotype with 38 setigers, 4.78 mm long and 0.17 mm wide; paratype (USNM 1622444) with 43 setigers, 4.4 mm long, 0.19 mm wide. Body cylindrical in cross

section throughout, with longitudinal grooves and ridges not apparent. Distinction between thoracic region and abdominal segments vague, mostly due to change in proportional size of anterior and middle segments with anterior 6–8 setigers short, about three times wider than long; middle segments longer, about 1.5 times longer than wide; segments again shorter in far posterior segments. Intersegmental areas narrow not enlarged (Fig. 49A–B). Color distinctive, body light tan with dark particles concentrated into fecal pellets in gut providing characteristic dark internal patches along body in most specimens (Figs. 49B, 50A–C). Close inspection of these pellets indicate multiple smaller particles comprising larger patches enclosed in membranes.

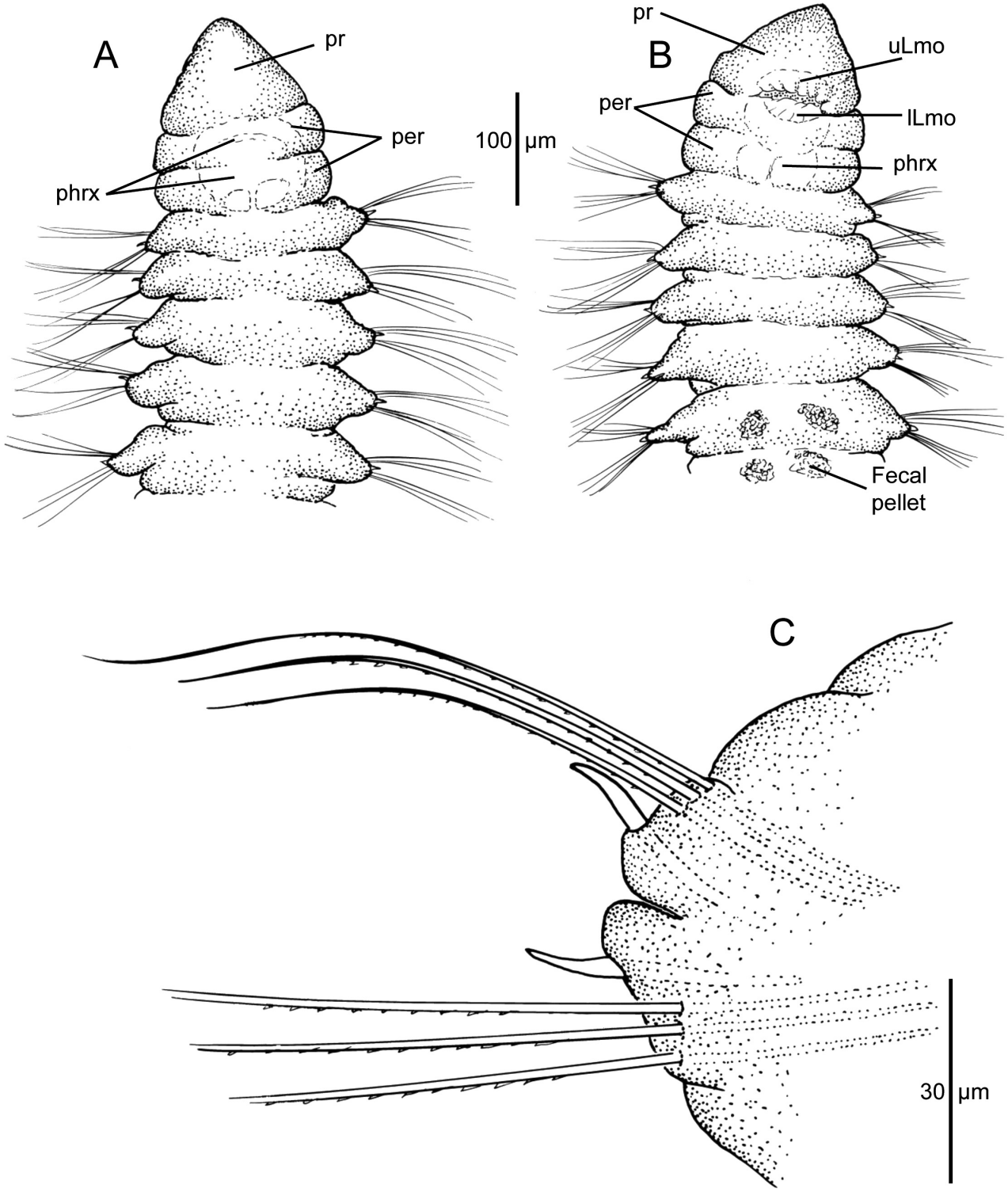

FIGURE 49. *Orbiniella acsara* **n. sp.** A, anterior end, dorsal view; B, anterior end, ventral view; C, setiger 5, anterior view. A–B (USNM 1622468); C (USNM 1622502).

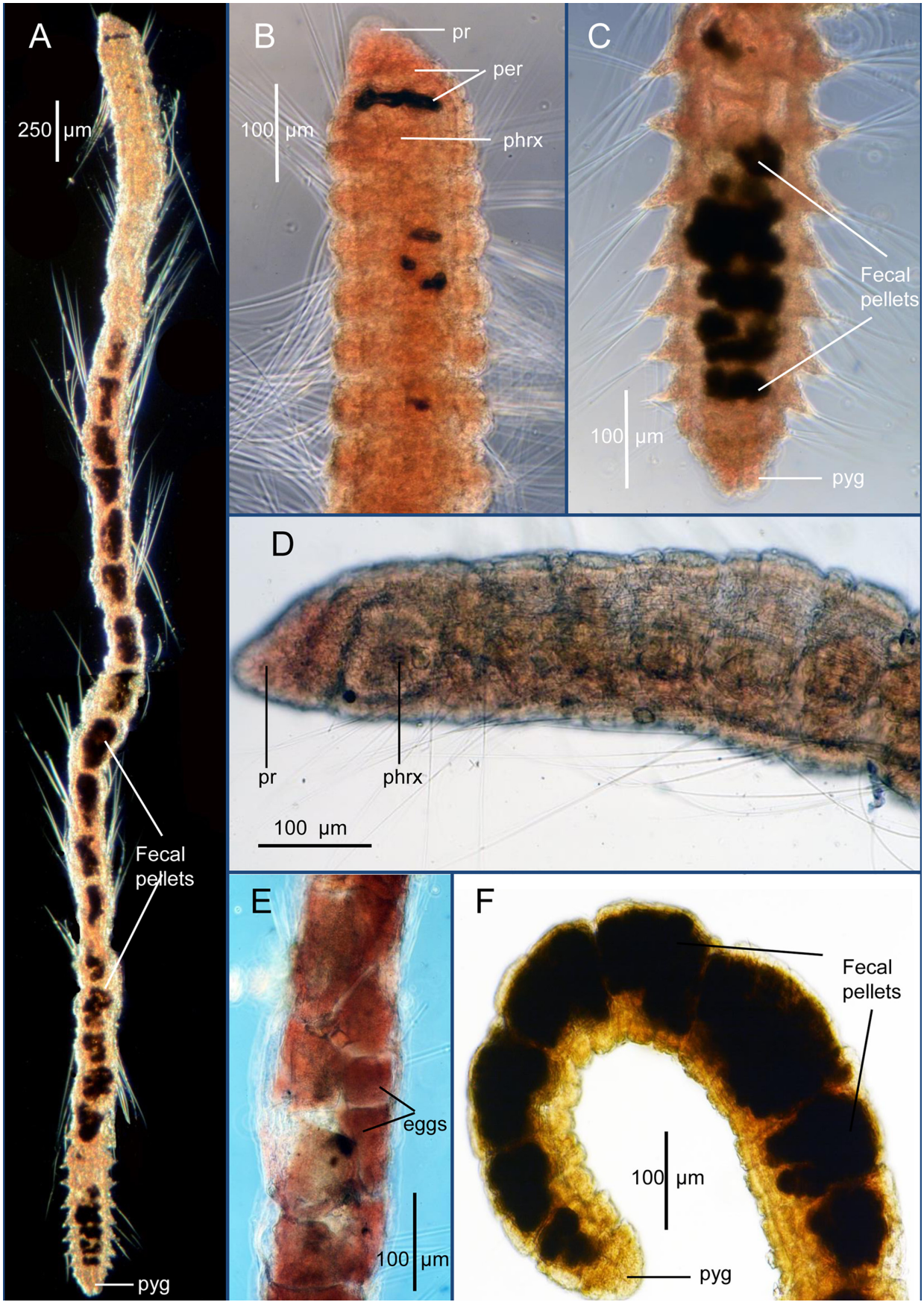

FIGURE 50. *Orbiniella acsara* **n. sp.** A, entire worm, dorsal view; B, anterior end, dorsal view; C, posterior end, dorsal view; D, anterior end, left lateral view; E, abdominal segments with eggs; F, posterior end, lateral view. A–C, holotype (USNM 1622440); D, F, paratype (USNM 1622444); E, (USNM 1622502). All stained with Shirlastain A.

Pre-setiger region about as long as first 2½ setigers (Fig. 49A–B). Prostomium triangular, tapering to narrow rounded tip (Figs. 49A–B, 50A–B, D); eyespots absent; nuchal organs not observed. Peristomium with two narrow rings, weakly separated from one another (Fig. 49A–B); ventrally forming anterior and posterior lips of mouth. Mouth a narrow slit with upper lip formed of about six short lobes; lower lip with lobes indistinct (Fig. 49B). Internal outline of pharynx visible dorsally (Figs. 49A, 50B), ventrally (49B) and laterally (Fig. 50D); no specimens observed with everted proboscis.

Parapodia lateral along entire body, not shifted dorsally (Fig. 49C); noto- and neuropodia close together, reduced to short rounded tori from which setae emerge, best seen in lateral view; in dorsal and ventral views, parapodia only projecting laterally in a few anterior setigers and newly formed posterior setigers (Fig. 50A–C); postsetal lobes absent.

Noto- and neurosetae including long serrated capillaries on all segments, with 3–5 capillaries in notopodia and 2–4 capillaries in neuropodia. Long capillaries prominent along entire body (Fig. 50A). Noto- and neuropodia also with 1–2 short curved acicular spines, directed towards one another, vis-à-vis (Fig. 49C).

Pygidium simple, rounded, bi-lobed, surrounding anal opening; anal cirri absent (Fig. 50A, C, F).

Remarks. Among the ten deep-water species of *Orbiniella* compared by Blake (2020), *O. acsara* **n. sp**. with smooth acicular spines and no postsetal lobes is most similar to *O. aciculata* Blake, 1985 from the Galápagos Rift hydrothermal vents and *O. eugeneruffi* Blake, 2020 from off Brunei in the South China Sea. *Orbiniella acsara* **n. sp**. differs from these species in having both peristomial rings large, of an equivalent size, and incomplete instead of one or both rings being narrow and complete. In addition, *O. acsara* **n. sp**. has no anal cirri on the pygidium instead of two or four anal cirri.

Orbiniella acsara **n. sp**. is also unusual in having a long, narrow, threadlike body with long capillary noto- and neurosetae. Most species of the genus have shorter, more compact bodies where the individual segments are often separated by thickened intersegmental areas producing a biannulate appearance. With *O. acsara* **n. sp**., the intersegmental areas are irregular and not formed into well-defined rings between the parapodia. In addition, the dark fecal pellets that occur in the intestine of nearly all specimens assist with recognition.

Biology. Eggs were observed in a few specimens. An ovigerous specimen (USNM 1622502) was packed with eggs along most of the body, with smaller eggs in anterior segments and larger ones in mid-body segments (Fig. 50E). The largest eggs in this specimen were 83 x 107 µm and 83 x 116 µm; this would equate to an average width of ca. 95–100 µm; each visible egg was observed to have a smooth cytoplasm and a distinct germinal vesicle.

The groups of dark fecal pellets in the intestine of most specimens were observed to consist of silt particles confined by a thin membrane consistent with fecal pellet formation. *Orbiniella acsara* **n. sp**. is primarily a lower slope species (1500–3000 m) and as such occurs in sediments having a high silt + clay content (Blake *et al*. 1987; Blake & Grassle 1994; Maciolek *et al*. 1987a–b). Owing to its small size and threadlike body, it is likely that the species resides in the upper 1–2 cm where it has access to and feeds at the sediment-water interface where newly deposited fine-grained flocculent sediments occur.

Etymology. The name *acsara* is derived from the acronym, ACSAR, for the Atlantic Continental Slope and Rise program (1983–1987); the new species was collected from all three survey regions.

Distribution. U.S. Atlantic continental slope: off New England, 1225–2164 m; off Delaware and New Jersey, 1503–2500 m; off North and South Carolina, 799–3019 m.

Orbiniella armata new species

Figures 51–52

urn:lsid:zoobank.org:act:967A793B-364C-4DD7-BE43-085BEEA6AD7E

Orbiniella sp. 2: Blake *et al*. 1987: C-4; Hilbig 1994: 942 (in part).

Material examined. (*5 specimens*) **Southeastern USA, U.S. South Atlantic ACSAR program,** coll. J.A. Blake, Chief Scientist. **Off Charleston, South Carolina, Sta. 16**: Cruise SA-6, Rep. 2, Cruise SA-6, Rep. 2, 20 Nov 1985, 31°35.10′N, 75°10.34′W, 3009 m, **holotype** (USNM 1622553) and 1 **paratype** (USNM 1622554); Cruise SA-5, Rep. 2, 16 Sep 1985, 31°35.14′N, 75°10.28′W, 3000 m, 1 **paratype** (USNM 1622555); Rep. 3, 16 Sep 1985, 31°35.14′N, 75°10.28′W, 3011 m, 1 juvenile (USNM 1622556).—**Off Cape Fear, North Carolina**, **Sta. 13**: Cruise SA-6, Rep 3, 21 Nov 1985, 32°55.25′N, 75°50.08′W, 3006 m, 1 **paratype** (USNM 1622557).

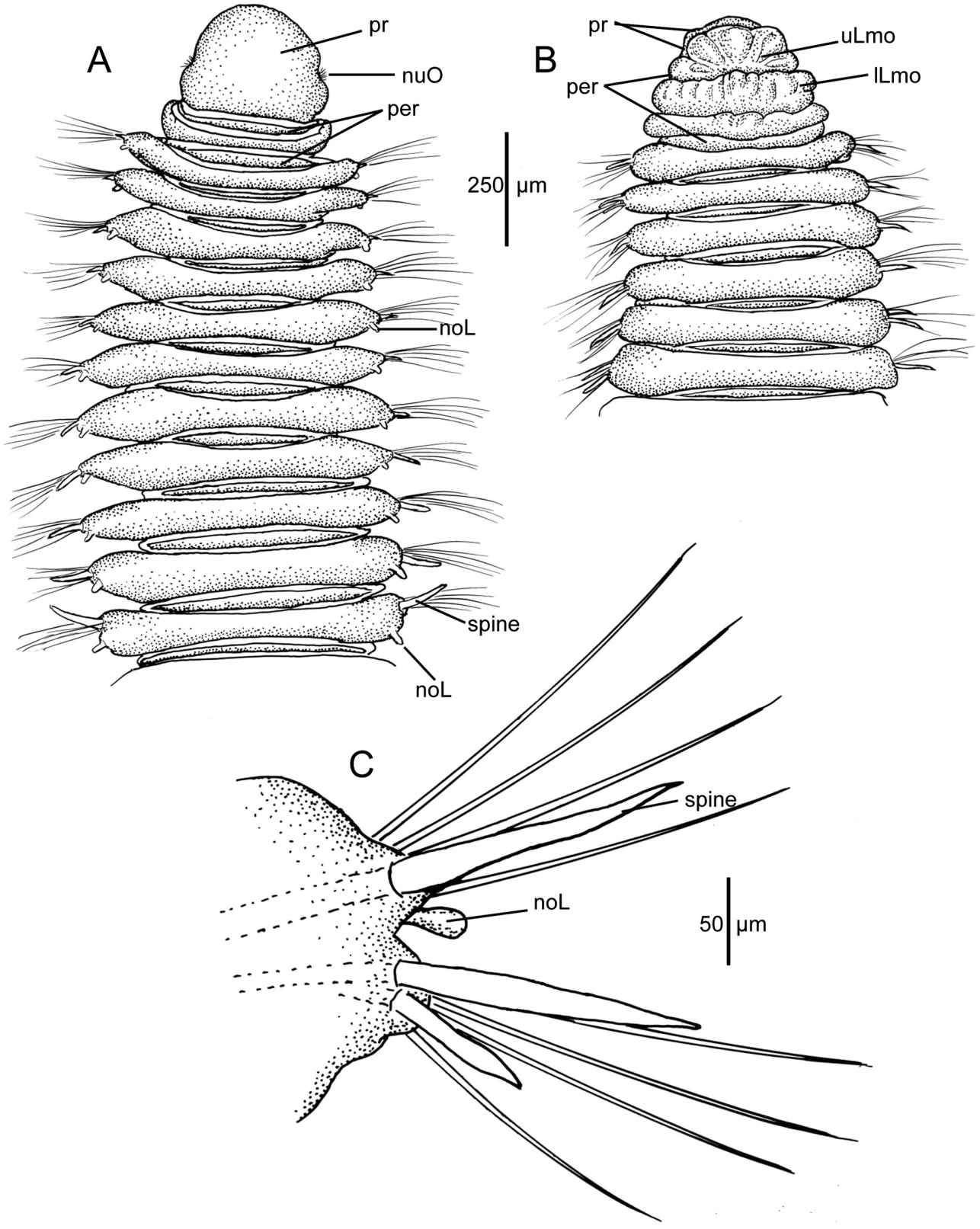

FIGURE 51. *Orbiniella armata* **n. sp.** A, anterior end, dorsal view; B, anterior end, ventral view; C, middle body parapodium, anterior view. A, holotype (USNM 1622553); B–C, paratype (USNM 1622554). A–B stained with Shirlastain A.

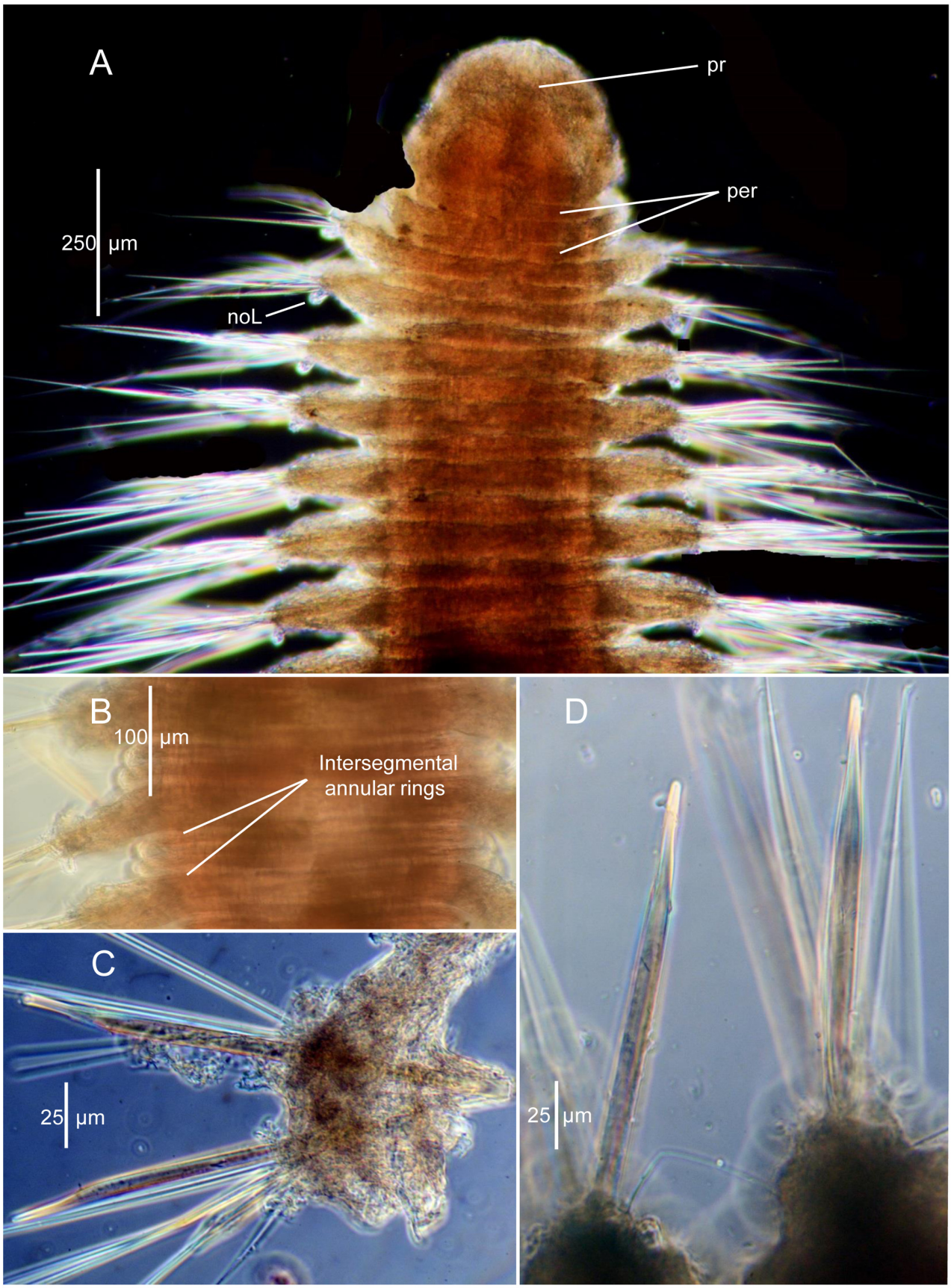

FIGURE 52. *Orbiniella armata* **n. sp**. A, anterior end, dorsal view; B, middle body segment, dorsal view, showing intersegmental rings; C, middle body parapodium, anterior view; D, two middle body segments, dorsal view with spines and capillaries. A–B, holotype (USNM 1622553); C–D, paratype (USNM 1622554).

Description. A small species, largest specimen an incomplete paratype (USNM 1622554) with 47 setigers, 5.45 mm long and 0.51 mm long; holotype (USNM 1622553) complete but with posterior end damaged, with 33 setigers, 4.0 mm long, 0.5 mm wide. Body elongate, more or less uniform in width throughout; body segments similar, lacking a separate thorax and abdomen. Individual segments short, about six times wider than long; lacking dorsal and ventral longitudinal grooves or ridges (Figs. 51A–B, 52A). Individual segments with a single intersegmental ring in anterior setigers (Figs. 51A–B, 52A), increasing to two or three narrow rings in middle and posterior setigers (Fig. 52B), producing tri- and quadriannulate segments. Color in alcohol: light tan to opaque white.

Pre-setiger region narrower than following segments, about as long as first 4–5 setigers (Figs 51A–B, 52A). Prostomium wider than long, broadly rounded on anterior margin (Figs 51A, 52A); dorsal surface relatively smooth; eyespots absent; nuchal organs ciliated depressions on lateral margins. Peristomium with three rings (Figs. 51A–B, 52A); dorsally with first ring narrow, second ring largest, and third ring narrow (Fig. 51A); ventrally with first ring expanded, surrounding mouth with five large lobes forming upper lip of mouth and numerous lobes along lower lip of mouth (Fig. 51B); middle and posterior rings narrower, relatively smooth (Fig. 51B). Proboscis not everted on any specimens.

Setiger 1 and following segments with relatively simple noto- and neuropodia formed of short tori from which spines and capillaries emerge (Figs, 51C, 52C). Single short, digitate postsetal lobe present in notopodia (Fig. 51A, C); absent in neuropodia.

Noto- and neuropodia typically with a single exceptionally large acicular spine and 4–8 long, serrated capillaries (Figs. 51C, 52C); spines may increase up to two or three per noto- or neuropodium in some middle and posterior setigers but inconsistent between specimens; individual spines unusually long, thick, tapering apically to a blunt tip (Fig. 52D). Capillaries not camerated, each with minute, sharply pointed barbs along length.

Pygidium damaged, narrow, cirri not observed on types. One juvenile with three thin cirri.

Remarks. *Orbiniella armata* **n. sp**. from lower slope and abyssal depths off the Southeastern USA is most similar morphologically to *O. abyssalis* Blake, 2020 from the abyssal plain of the north equatorial Pacific Ocean in having similarly shaped large elongate noto- and neuropodial spines along the body. The main difference between the two species, however, is that the peristomium of *O. armata* **n. sp**. is formed of three separate rings, whereas that of *O. abyssalis* consists of only a single smooth ring.

Etymology. The epithet is from *armatura*, Latin for a weapon or an item used to defend. In this instance the armature are the unusually large projecting spines present in the noto- and neuropodia of this species.

Distribution. Off South Carolina, lower continental slope or abyssal depths, 3000–3011 m.

Orbiniella mimica new species

Figures 53–54

urn:lsid:zoobank.org:act:AF091D23-7398-420E-B018-9D25E04A516F

Orbiniella sp. 2: Maciolek *et al*. 1987a: D-4; Hilbig 1994: 942 (in part).

Material examined. (*34 specimens*) **Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR** program, coll. Rosemarie Petrecca, Chief Scientist. **Sta. 11**: Cruise Mid-4, Rep. 1, 17 May 1985, 38°40.10′N, 72°56.43′W, 1519 m, **holotype** (USNM 1622511) and 3 **paratypes** (USNM 1622512); Cruise Mid-1, Rep. 1, 07 May 1984, 38°40.22′N, 72°56.27′W, 1520 m, 2 **paratypes** (USNM 1622513); Rep. 3, 07 May 1984, 38°40.22′N, 72°56.27′W, 1520 m, 1 **paratype** (USNM 1622514); Cruise Mid-2, Rep. 1, 04 Aug 1984, 38°40.20′N, 72°56.30′W, 1514 m (1, USNM 1622516); Cruise Mid-3, Rep. 1, 04 Dec 1984, 38°40.13′N, 72°56.27′W, 1540 m (3, USNM 1622517); Rep. 2, 04 Dec 1984, 38°40.14′N, 72°56.31′W, 1520 m (2, USNM 1622518); Cruise Mid-5, Rep. 1, 06 Aug 1985, 38°40.12′N, 72°56.45′W, 1505 m, 1 **paratype** (USNM 1622519); Rep. 2, 06 Aug 1985, 38°40.12′N, 72°56.47′W, 1502 m (4, USNM 1622520); Rep. 3, 06 Aug 1985, 38°40.14′N, 72°56.46′W, 1505 m, 2 **paratypes** (USNM 1622521). **Sta. 2**: Cruise Mid-3, Rep. 3, 02 Dec 1984, 38°35.68′N, 72°53.69′W, 2015 m (1, USNM 1622522). **Sta. 9**: Cruise Mid-5, Rep. 2, 06 Aug 1984, 37°17.21′N, 73°14.69′W, 2100 m (1, USNM 1622523). **Sta. 13**: Cruise Mid-1, Rep. 1, 02 April 1984, 37°53.33′N, 73°45.09′W, 1613 m (2, USNM 1622524); Rep. 2, 02 Apr 1984, 37°53.38′N, 73°45.10′W, 1613 m, 1 **paratype** (USNM 1622525); Cruise Mid-2, Rep. 1, 07 Aug 1984, 37°53.33′N, 73°45.01′W, 1614 m (1, USNM 1622526); Rep. 2, 07 Aug 1984, 37°53.28′N, 73°45.26′W, 1619 m (1, USNM 1622527); Rep. 3, 08 Aug 1984, 37°53.22′N, 73°45.17′W, 1619 m, 1 **paratype** (USNM 1622528); Cruise Mid-3, Rep. 1, 30 Nov 1984,

37°53.32′N, 73°45.10′W, 1615 m, 1 **paratype** (USNM 1622529); Rep. 2, 30 Nov 1984, 37°53.35′N, 73°45.00′W, 1615 m, 3 **paratypes** (USNM 1622530); Cruise Mid-4, Rep. 2, 19 May 1985, 37°53.29′N, 73°45.30′W, 1607 m (1, USNM 1622531); Cruise Mid-5, Rep. 1, 09 Aug 1985, 37°53.26′N, 73°45.21′W, 1607 m (1, USNM 1622532); Rep. 2, 09 Aug 1985, 37°53.27′N, 73°45.28′W, 1605 m (1, USNM 1622533); Rep. 3, 10 Aug 1985, 37°53.30′N, 73°45.27′W, 1608 m (1, USNM 1622534); Cruise Mid-6, Rep. 2, 16 Nov 1985, 37°53.27′N, 73°45.30′W, 1611 m, 1 **paratype** (USNM 1622535). **Sta. 14**: Cruise Mid-1, Rep. 3, 02 Apr 1984, 37°53.86′N, 73°44.68′W, 1503 m, 1 **paratype** (USNM 1622536); Cruise Mid-6, Rep. 1, 15 Nov 1985, 37°53.69′N, 73°44.69′W, 1515 m, 1 **paratype** (USNM 1622537).

Description. A small species, holotype (USNM 1622511) complete, with 36 setigers, 5.6 mm long and 0.8 mm wide; paratype (USNM 1622513) with 30 setigers, 5.76 mm long and 1 mm wide, another paratype (USNM 1622519) with 34 setigers, 5.45 mm long and 0.9 mm wide; and a larger paratype (USNM 1622525) with 38 setigers, 7.3 mm long and 0.9 mm wide. Body with similar segments throughout, lacking separate thorax and abdomen. Body dorsoventrally flattened with narrow mid-dorsal groove along most of body and narrow, mid-ventral ridge formed of bulges where segmental rings meet mid-ventrally. Segmentation including a prominent ring extending from each parapodium across dorsal and ventral surfaces; each segmental ring separated from next segment by one and then two intersegmental rings along most of body, producing a tri-annulate appearance (Figs. 53A, 54C); anterior and posterior-most segments with only a single intersegmental ring (Figs. 53A–C, 54A). Each parapodium and segmental ring with numerous glands (Fig. 53A) that stain with Methyl Green (Fig. 54D); these glands not apparent in intersegmental rings. Parapodia all lateral (Fig. 53D), not shifted dorsally in posterior segments. Prostomium and parapodia of some anterior setigers with a band of short cilia extending across dorsal surface; these cilia not readily apparent except at 1000x magnification in light microscope, appearing as cells or groups of short cilia. Color in alcohol light tan to opaque white; a few scattered dark pigment spots apparent dorsally over peristomium and setiger 1 on a few specimens; a few anterior notopodia dusky brown on some specimens.

Pre-setiger region narrower than setiger 1 and following segments (Figs. 53A–C, 54A), longer than wide, about as long as first 3–4 setigers. Prostomium wider than long, broadly rounded on anterior margin (Figs. 53A–B, 54A); dorsal surface covered with numerous papillae (Fig. 53A), ventrally with vestibule leading to mouth opening on peristomium (Fig. 53B); eyespots absent; nuchal organs lateral ciliated patches on posterior margin (Fig. 53A). Peristomium formed of two separate rings entirely crossing dorsal (Figs. 53A, 54A) and ventral surfaces (Fig. 53B); anterior ring with anterior border sculptured with short rounded lobes on dorsum (Fig. 53A); posterior ring relatively smooth on anterior border. Ventrally, anterior peristomial ring forming posterior lip of mouth with 5–6 short medial lobes (Fig. 53B); a narrow medial groove continuing to anterior border of second peristomial ring, with 2–3 mounds on anterior edge (Fig. 53B). Mouth opening on peristomium enclosed by two lateral folds. Proboscis not fully everted on any specimens; one specimen (USNM 1622525) with partially everted rounded lobe.

Setiger 1 and those following with relatively simple noto- and neuropodia formed of short tori from which spines and capillaries emerge. A single short, digitate postsetal lobe present in notopodia; absent in neuropodia (Fig. 53D).

Noto- and neuropodia typically with a single smooth, pointed acicular spine and 6–12 long, serrated capillaries (Fig. 53D–F); spines may increase up to two or three per noto- or neuropodium in some middle and posterior setigers but inconsistent between specimens. Capillaries not camerated, each with minute, sharply pointed barbs along length (Fig. 53F).

Pygidium narrow, terminating in four lobes around anal opening, each lobe with long, thin anal cirrus; dorsal pair shorter than ventral pair (Figs. 53C, 54B). Thin anal cirri often lost, broken off from the basal lobes, best observed entirely intact in smaller specimens.

Remarks. Among deep-water species *of Orbiniella* tabulated by Blake (2020) and having postsetal lamellae limited to the notopodia, *O. mimica* **n. sp**. is most similar to *O. petersenae* Parapar *et al*., 2015 from the northeast Atlantic in having triannulate segmentation along most of the body. *Orbiniella mimica* **n. sp**. differs, however, in having a papillated dorsal surface on the prostomium instead of a smooth surface, in having instead of lacking a mid-dorsal groove along the body, and having four long, thin pygidial cirri instead of short, thickened rounded lobes. SEMs of the pygidial lobes of *O. petersenae* in Parapar *et al*. (2015: Fig. 6A, D, F) do not show any indication that longer lobes had broken off. In addition, there are differences in the oral and other aspects of peristomial morphology. The transverse rows of minute ciliated cells observed on the dorsum of the prostomium and a few anterior setigers of some specimens of *O. mimica* **n. sp**. were not evident on other SEMs published for *O. petersenae* (Parapar *et al*. 2015).

Etymology. The epithet is from *mimicus*, Latin for an imitator, in reference to the fact that during the ACSAR programs *O. mimica* **n. sp.** and *O. armata* **n. sp.** were collectively identified as *Orbiniella* sp. 2 because differences were not recognized at the time. In addition, both species are also similar to *O. petersenae* recently described from the northeastern Atlantic. The differences between the two North American species, including the large noto- and neuropodial spines of *O. armata* **n. sp**. were not recognized until the more careful morphological comparisons in the present study.

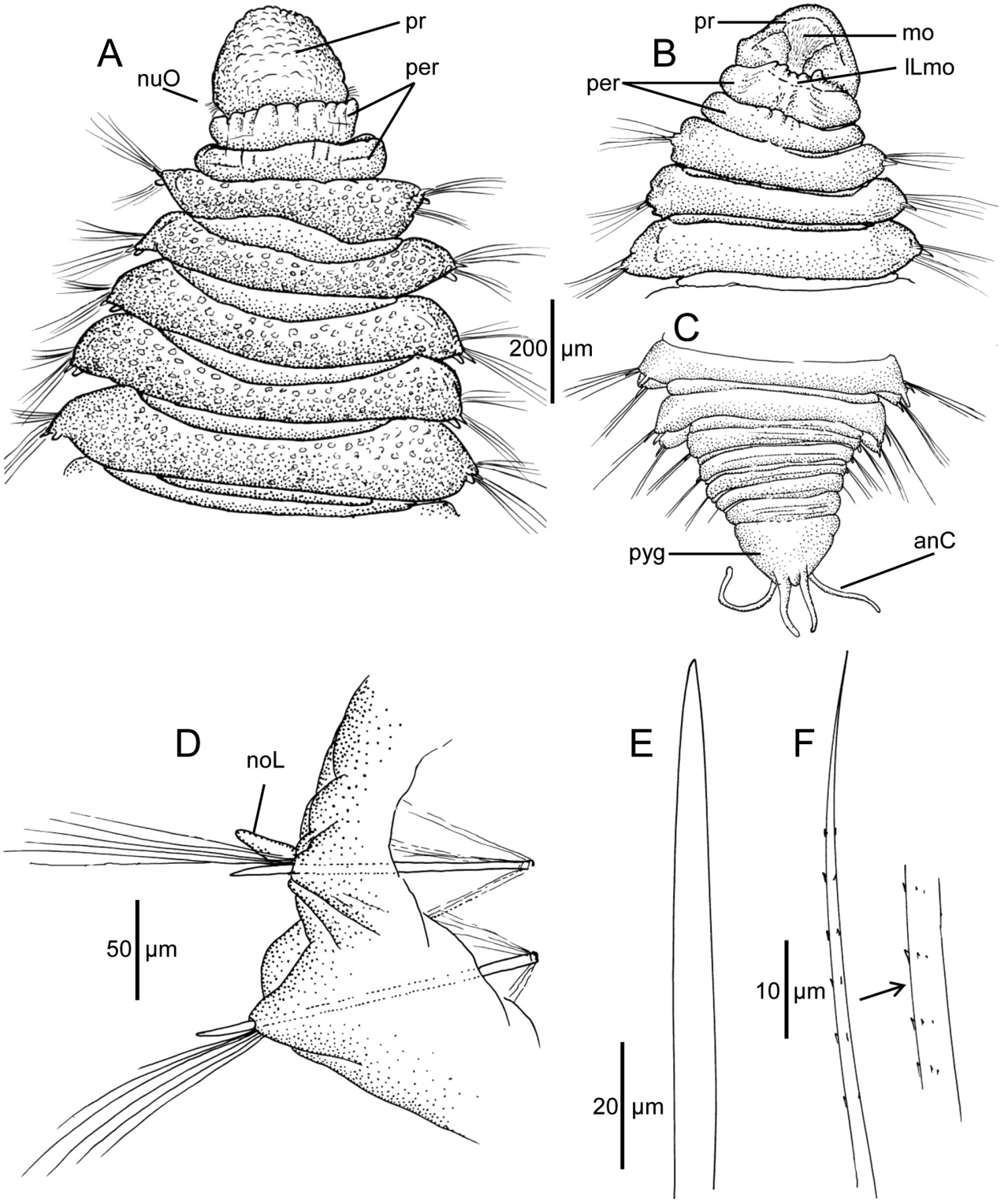

FIGURE 53. *Orbiniella mimica* **n. sp**. A, anterior end, dorsal view; B, anterior end ventral view; C, posterior end, dorsal view; D, parapodium from mid-body, posterior view; E, notopodial acicular spine; F, capillary seta with detail (inset not to scale). Paratypes: A, D–F (USNM 1622530); B–C (USNM 1622526).

Biology. Lower slope sediments at the Mid-Atlantic stations off New Jersey and Delaware where *Orbiniella mimica* **n. sp.** was most prevalent consisted of 96+ percent silt-plus-clay with only minimal amounts of sand-sized particles (Maciolek *et al*. 1987a).

Distribution. Continental slope off the U.S. Mid-Atlantic region, 1502–2144 m; most common in the 1500–1620 m depth range.

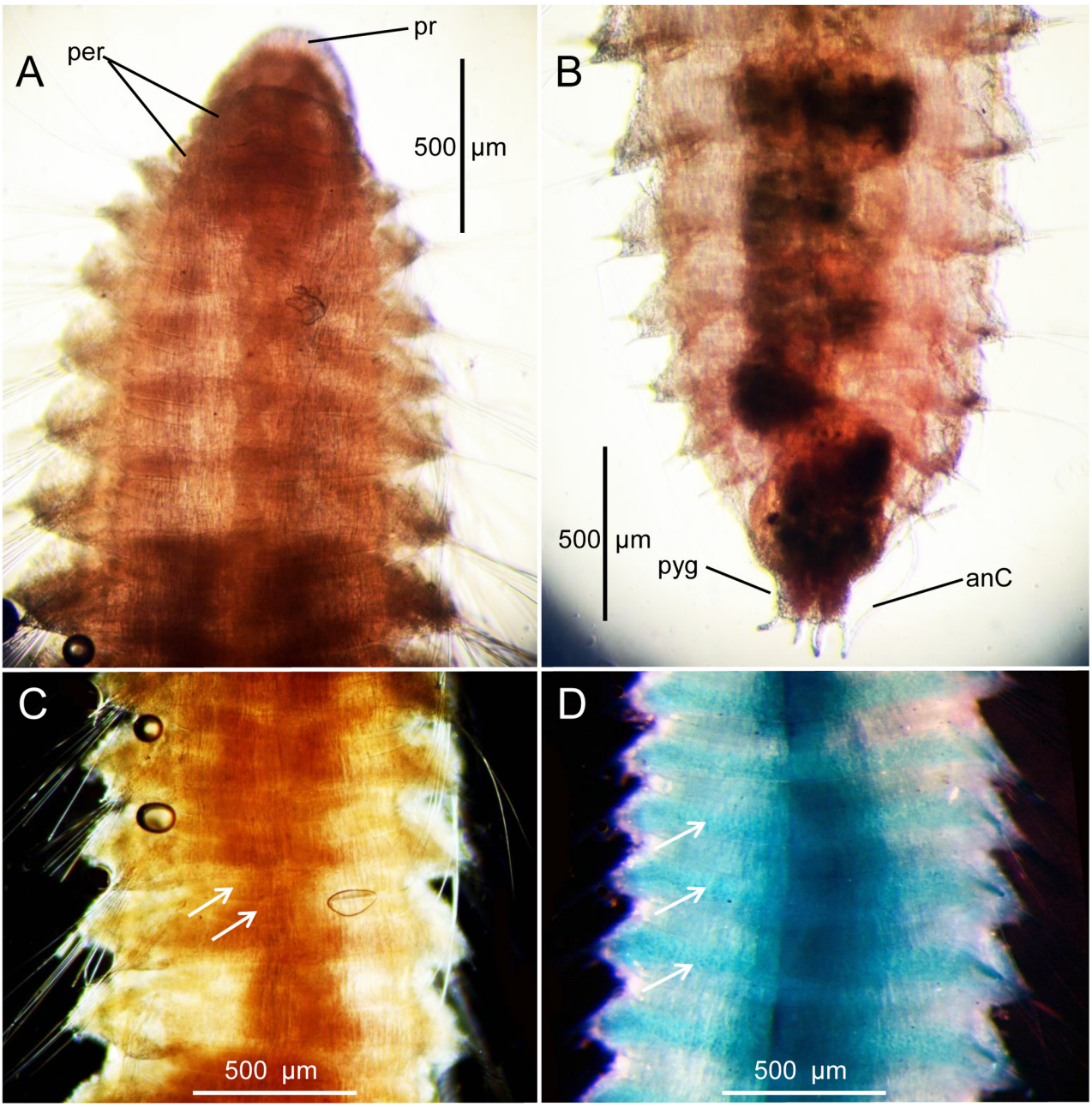

FIGURE 54. *Orbiniella mimica* **n. sp**. A, anterior end, dorsal view; B, posterior setigers and pygidium, dorsal view; C, mid-body setigers with interramal segmental rings (arrows); D, posterior setigers, dorsal view with stained glandular bands (arrows). A–C, holotype (USNM 1622511); D, paratype (USNM 1622525). A–C, stained with Shirlastain A; D, stained with Methyl Green.

Subfamily Questinae Hartman, 1966b. New status

Diagnosis. Same as genus *Questa* (below).

Remarks. It is now generally agreed that *Questa* belongs in the Orbiniidae rather than as a stand-alone family (Read & Fauchald 2020b). Based on molecular data by Bleidorn (2005), Bleidorn *et al.* (2009), and Rousset *et al*. (2007), two species of *Questa* formed a separate clade within the Orbiniidae. While the serrated and/or camerated

capillaries and furcate setae are similar to those found in other species of Orbiniidae, *Questa* species have unique setal and reproductive characteristics that differ from other orbiniids. The reproductive characteristics of *Questa* have been shown to exhibit similarity to oligochaetes in being sexually dimorphic with males having distinct cup-like dorsal folds believed to serve as male copulatory organs and females with seminal receptacles and similar gland-like epidermal areas similar to a clitellum (Giere & Riser 1981; Giere *et al*. 2008). However, the bidentate hooks or crotchets found in all species of *Questa* are similar to those of some deep-sea species of Paraonidae, genus *Levinseni*a. At present *Questa* species are not assigned to either of the two orbiniid subfamilies. Based on unique morphology and supported by molecular data, I propose that Hartman′s family Questidae be revalidated as a subfamily within the Orbiniidae.

Genus *Questa* Hartman, 1966b

Type species: *Questa caudicirrata* Hartman, 1966b, by monotypy.

Diagnosis. (Emended) Body elongate, threadlike, up to 10 mm long with 45–65 setigerous segments; body segments cylindrical in cross section; setigerous segments with 2–3 intersegmental annulations in anterior setigers, up to 7–8 in middle segments, decreasing posteriorly. Prostomium conical, tapering to narrow rounded tip; nuchal organs paired slits on posterior lateral margins. Peristomium typically with 2–3 asetigerous rings, with dorsal surfaces smooth, entire; ventrally forming anterior and posterior lips of mouth. Thoracic and abdominal regions only vaguely identified by shorter, wider segments anteriorly and longer, narrower segments posteriorly. Paired branchiae present dorsally in posterior segments or entirely absent. All parapodia biramous, composed of low mounds bearing noto- and neurosetae; setae serrated or weakly camerated capillaries and bidentate hooks with geniculate shafts in both rami; furcate setae present or absent in notopodia. Pygidium with 0, 2, or 4 anal cirri. In mature males segments 13–14 (15) with elevated cup-like or slit-like dorsal fold. Mature females of almost all species with more-or- less papillated glandular epidermis in anterior segments. Extension and shape of papillation on females species-specific, but also depending on stage of maturity. Egg region (mostly segments 12–13) of mature females slightly swollen due to formation of 2–3 large eggs.

Remarks. In addition to the external morphology highlighted in the Diagnosis, species of *Questa* have been discovered to have reproductive morphology that bears some similarity to that of oligochaetes. Both sexes have gonads limited to a few anterior segments that exhibit external genitalia (Giere & Riser 1981). Females have a glandular epidermis on a few anterior segments that resembles the clitellum of oligochaetes (Bleidorn & Helm 2019). The males have sperm sacs in segments 10–12 that connect to gonopores opening externally into an inflated dorsal fold on setiger 13 that is an unusual cup-like structure.

Reproductive behavior has not been observed, but Giere & Riser (1981), working with *Questa trifurcata*, hypothesized that males attach their cup-like dorsal fold to the spermathecal segments of females. The worms would then separate after the spermathecae are filled. Afterwards, the female would secrete a cocoon containing fertilized eggs. A cocoon of *Q. trifurcata* found and cultured by Giere & Riser (1981) contained a single embryo that hatched with seven setigers after a month. The juvenile was identified as *Q. trifurcata* due to the setae, which in addition to the capillaries and characteristic hooks included a furcate seta.

Ten species of *Questa* are known globally; a single species, *Q. trifurcata,* occurs along the eastern U.S. from Maine to New Jersey (Hobson 1970; Giere & Riser 1981; Giere & Erséus 1998). This species was collected on Georges Bank during the benthic monitoring program performed for MMS in the 1980s. The specimens recorded here constitute a range extension of the species from nearshore intertidal and subtidal depths to the outer continental shelf.

Questa trifurcata (Hobson, 1970)

Figures 55–56

Novaquesta trifurcata Hobson 1970: 191–194, Fig. 1; Giere & Riser 1981: 95–103, Figs. 1–5; Taylor & Gathof 1984: 3-4 to 3-5, Fig. 3-4; Jamieson & Webb 1984: 30–31.

Questa trifurcata: Giere & Erséus 1998: 345–360, Figs. 1G, 2G–H, 3H.

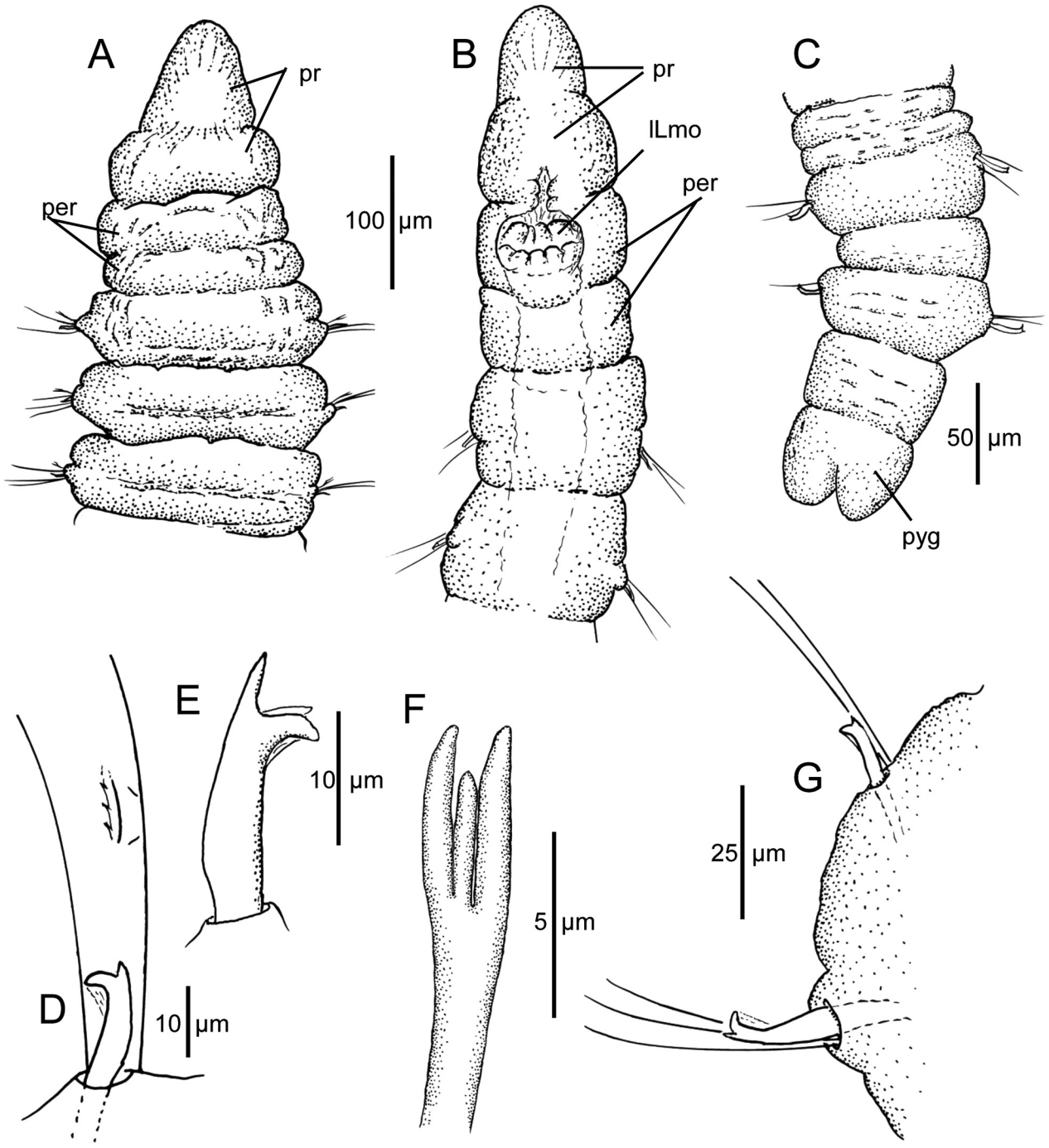

FIGURE 55. *Questa trifurcata* (Hobson, 1971). A, anterior end, dorsal view; B, anterior end, ventral view; C, posterior end, dorsal view; D, neuropodial hooked seta with capillaries (inset not to scale); E, notopodial furcate seta; G, middle body parapodium with hooks and capillaries. A, C, D–G (USNM 1622548); B (USNM 1622540).

Material examined. (*31 specimens*) **Northeastern USA, off New England, Georges Bank, Benthic Infauna Monitoring Program (1981–1984),** coll. G.W. Hampson, Chief Scientist. **Sta. 2**: Cruise M-1, Rep. 2, Jul 1981, 40°59.0′N, 66°55.8′W, 70 m (2, USNM 1622538); Cruise M-11, Rep. 5, 03 Feb 1984, 40°59.0′N, 66°55.8′W, 79 m (4, USNM 1622539); Rep. 6, 03 Feb. 1984, 40°59.0′N, 66°55.8′W, 79 m (2, USNM 1622540). **Sta. 13**: Cruise M-2, Rep. 6, 9 Nov. 1981, 40°29.5′N, 70°12.6′W, 60 m (1, USNM 1622541). **Sta. 5-3**: Cruise M-4, Rep. 4, 14 May 1982, 40°39.8′N, 67°46.1′W, 84 m (1, USNM 1622542). **Sta. 5-**5: Cruise M-1, Rep. 1, Jul 1981, 40°39.3′N, 67°46.2′W, 70 m (1 (USNM 1622543). **Sta. 5-6**: Cruise M-4, Rep. 3, 14 May 1982, 40°39.5′N, 67°45.4′W, 110 m (1, USNM 1622544. **Sta. 5-11**: Cruise M-2, Rep. 1, 19 Nov 1981, 40°39.2′N, 67°46.6′W, 80 m (1, USNM 1622545).

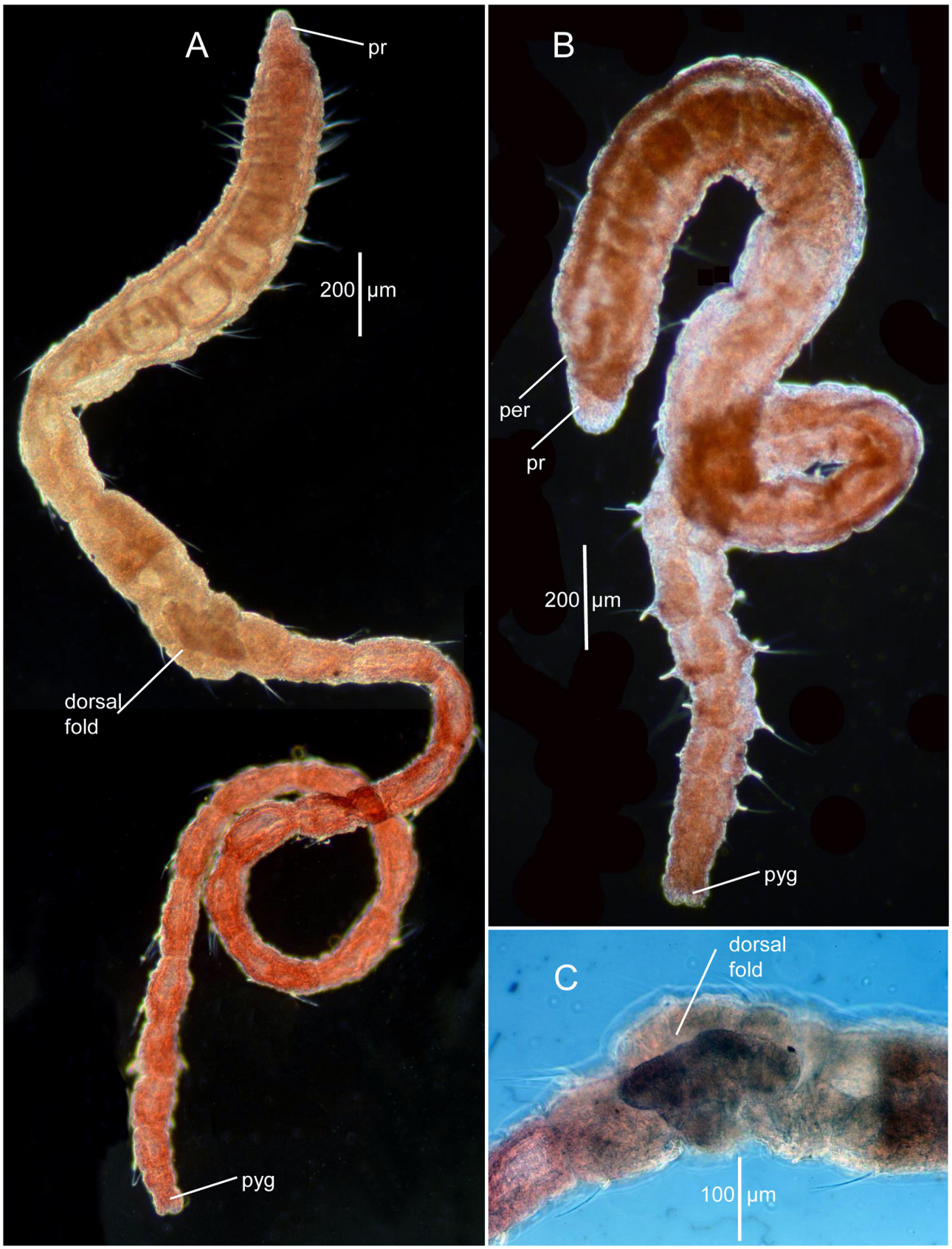

FIGURE 56. *Questa trifurcata* (Hobson, 1971). (USNM 1622549): A. entire worm, dorsolateral view; B, smaller specimen, dorsolateral view; C, dorsal fold of mid-body segments of male. A–C All stained with Shirlastain A.

Sta. 5-12: Cruise M-2, Rep. 1, 20 Nov 1981, 40°39.0′N, 67°46.1′W, 79 m (1, USNM 1622546). **Sta. 5-14**: Cruise M-2, Rep. 2, 19 Nov 1981, 40°39.6′N, 67°44.4′W, 82 m (1, USNM 1622547). **Sta. 5-16**: Cruise M-2, Rep. 2, 18 Nov 1981, 40°40.6′N, 67°46.1′W, 79 m (6, USNM 1622548). **Sta. 5-18**: Cruise M-1, Rep. 1, Jul 1981, 40°39.6′N, 67°47.6′W, 80 m (5 USNM 1622549); Cruise M-2, Rep. 1, 18 Nov. 1981, 40°39.6′N, 67°46.3′W, 80 m (2, USNM 1622550). **Sta. 5-22**: Cruise M-2, Rep. 3, 20 Nov 1981, 40°39.5′N, 67°43.3′W, 80 m (1, USNM 1622551). **Sta. 5-28**: Cruise M-1, Rep. 2, Jul 1981, 40°39.5′N, 67°41.9′W, 80 m (2, USNM 1622553); Cruise M-2, 20 Nov 1981, 40°39.5′N, 67°43.3′W, 80 m (1, USNM 1622552).

Description. A small, threadlike species, originally reported up to 4–6 mm long, and 0.3–0.4 mm wide and about 30 setigers (Hobson 1970). Giere & Riser (1981) recorded living specimens 9 mm long, 0.25 mm wide and 26–33 setigers. Present materials from Georges Bank up to 4.5 mm long, 0.2 mm wide, with 31 setigers. Body generally cylindrical in cross section throughout, widest in first 10–12 setigers, then narrowing posteriorly (Fig. 56A–B); no dorsal or ventral grooves or ridges along body. Anterior segments with 1–2 narrow intersegmental rings increasing to 5–6 in middle segments, decreasing posteriorly. Males with prominent pair of flaps forming a dorsal fold at about setigers 13–14 (Fig. 56A, C); females with ovaries and eggs in setigers 12–13. Color in alcohol opaque white; pink in life (Giere & Riser 1981).

Pre-setiger region about as long as first 3–4 setigers. Prostomium weakly divided into a narrow conical anterior part, tapering to rounded apex and wider posterior part (Fig. 55A–B), with narrow, slit-like nuchal organs on posterior lateral margins. Peristomium with two narrow rings, relatively smooth dorsally (Fig. 55A); ventrally with mouth located on anterior ring and posterior margin of prostomium (Fig. 55B). Mouth with two rows of short lobes on posterior margin forming posterior lips; anterior part of mouth extending onto prostomium as narrow slit with a pair of lateral lobes (Fig. 55B).

Parapodia reduced to low mounds from which setae emerge, or setae emerging directly from body wall; no postsetal lobes or lamellae; branchiae entirely absent. Setae of each ramus including single bidentate hook arranged vis-à-vis with opposite and 2–3 serrated capillaries from setiger 1 (Fig. 55G); sometimes up to four capillaries present. Capillaries narrow, with short pointed barbs along one edge (Fig. 55D inset); bidentate hooded hooks with geniculate shape, with main fang at right angle to shaft surmounted by pointed apical tooth; closely adhering hood or sheath extending from tip of main fang to shaft (Fig. 55D–E). One or two furcate setae present in notopodia of first 5–8 setigers; furcate setae with two subequal thick tynes and a single medial prong producing a tridentate appearance (Fig. 55F).

Pygidium with two thick lobes surrounding anal opening; anal cirri absent (Figs. 55C, 56A–B).

Remarks. Among ten known species of *Questa*, only four are reported to have furcate setae in the notopodia. Of these, *Q. retrospermatica* Giere *et al*., 2008 from Hawaii is the only species to have furcate setae with two long lateral tynes and two short medial tynes. *Questa trifurcata*, *Q. riseri* Giere & Erséus, 1998 from the Bermuda Islands, and *Q. media* Westheide, 1981 from the Galápagos Islands each have furcate setae with two long tynes and a single shorter medial prong producing a trifurcate or trident appearance. *Questa trifurcata* differs from both *Q. riseri* and *Q. media* in having no branchiae and no anal cirri instead of paired branchiae in posterior setigers and four anal cirri.

A detailed description of the internal anatomy of *Q. trifurcata* was provided by Giere & Riser (1981). This report largely focused on the unusual reproductive morphology summarized in the Genus Remarks (above). Most recent studies of *Questa* systematics have compared the internal morphology among species where available.

Reports of an additional tooth on the bidentate hooks (Giere & Erséus 1998) appear to represent a thin extension of hood around main fang to upper surface (Fig. 55E).

Distribution. East coast of North America, Maine to New Jersey, intertidal and shallow subtidal to outer continental shelf depths on Georges Bank (60–110 m); Gulf of Mexico, off Florida, 37 m.

Discussion

This study deals with species of Orbiniidae that occur offshore along the U.S. Atlantic coast. The largest collections are from continental shelf habitats (~50–200 m) and continental slope and rise (deep-sea) habitats (255–3000 m) and represent the most extensive coverage of offshore orbiniids from the Western North Atlantic. Some intertidal and shallow-water collections that serve to add new species and expand descriptions and records of previously reported species are also included.

In the present study, 24 species of Orbiniidae including 12 new to science are reported. Another six shallow-water species reported in the literature are not included in the present study; some of these appear to be rare or possibly misidentified (see following list and comments).

Annotated list of species recorded from the U.S. Atlantic coast not included in the present study.

In addition to the 24 species reported in the present study from waters off the U.S. Atlantic coast, at least six other orbiniid species have been recorded or are known to be present along the U.S. Atlantic coast but are not included in this study.

***Leitoscoloplos foliosus* (Hartman, 1951).** This species was originally described from the Texas coast in the Gulf of Mexico by Hartman (1951). Day (1973) subsequently recorded two juveniles from off North Carolina; his identification has not been confirmed with adults. Mackie (1987) redescribed the holotype and determined that an unusually long abdominal notopodial lobe was distinctive for the species. The lobe had been erroneously attributed to the neuropodium by Hartman (1951, 1957). There are no other reports or descriptions of *L. foliosus* from the U.S. Atlantic coast or elsewhere.

***Scoloplos capensis* (Day, 1961).** Originally described from South Africa, *S. capensis* was later recorded by Day (1973) from off Beaufort, North Carolina, and by Taylor (1984) from the Gulf of Mexico. These identifications have not been confirmed.

***Leodamas rubrus* (Webster, 1879**). Originally described from Virginia by Webster (1879), the species was subsequently reported from the vicinity of Beaufort, North Carolina, by Andrews (1891), Hartman (1945), and Day (1973). Hoagland (1919) reported the species from Key West, Florida. Hartman (1951, 1957) redescribed the species in detail from specimens collected along the west coast of Florida (Gulf of Mexico). Taylor (1984) later recorded the species more widely in the Gulf of Mexico from off Florida to Texas. This species thus appears to be limited to the southeastern and Gulf coasts of the United States in shallow water.

***Naineris quadricuspida* (Fabricius, 1780).** This species has been reported widely in the North Atlantic (Hartmann-Schröder 1996). Pettibone (1963) provided an illustrated description of the species based on specimens from eastern Canada to Massachusetts. The species is typically found in intertidal or shallow depths where it inhabits algal holdfasts or other cryptic habitats. I have collected *N. quadricuspida* in Maine and Massachusetts in rocky intertidal habitats. One specimen available from Manomet, Massachusetts, is a juvenile.

***Orbinia americana* Day, 1973**. This species was originally described from a single 38-setiger specimen with 21 thoracic setigers from off Beaufort, North Carolina. As noted in the comments for *O. swani*, Day (1973) noted the similarity of *O. americana* to *O. swani* but that his specimen had fewer thoracic neuropodial postsetal lobes and fewer subpodial lobes. It is probable that Day's specimen is a juvenile of *O. swani* because the characters of smaller specimens of *O. swani* reported in the present study overlap those of *O. americana* reported by Day. The species was reported from Florida to Texas in the Gulf of Mexico by Taylor (1984). However, the flail setae mentioned by Day (1973) were not noted by Taylor and it is not certain if he was dealing with the same species.

***Orbinia riseri* (Pettibone, 1957).** This species was originally described as *Scoloplos riseri* based on a single incomplete specimen collected intertidally from the vicinity of Woods Hole, Massachusetts. Day (1973) reported and redescribed the species from off Beaufort, North Carolina in 120–160 m and transferred it from *Scoloplos* to *Orbinia*. The species was subsequently reported and described from shallow subtidal depths off Florida in the Gulf of Mexico by Taylor (1984). Given the rarity of this species and the widely reported locations and range of depths recorded (intertidal to 160 m) it is likely that more than one species is present and the various records deserve further study.

Deep-water species of Orbiniidae (~500 m and greater).

To date, including new species described in the present study, there are approximately 237 known species of Orbiniidae, of which about 58 (24%) occur in depths ~500 m or greater. Out of 24 species treated in this study, 12 consistently occurred in depths greater than 500 m; of these, eight occurred in depths of 2000 m or greater, and three ranged into the continental rise at 3000 m depths. Seven of the 12 new species are reported from deep water.

Among orbiniids, the majority of species in the genera *Berkeleyia* (5 of 6), *Califia* (4 of 5), *Methanoaricia* (1 of 1), *Microrbinia* (1 of 1), and *Orbiniella* (13 of 22) are reported from deep-water habitats. About half the species of *Leitoscoloplos* (16 of 33) are from deep water, whereas the remaining genera in the following list are mostly from

nearshore and shelf habitats. Species of *Orbinia*, *Naineris*, and *Questa*, while well represented in nearshore habitats, are entirely absent or rare in deep-sea collections analyzed to date.

The following list of 58 deep-water Orbiniidae has been compiled from recent publications (Blake 2000, 2017, 2020, this study). Of these, only 14 species have been recorded from depths greater than 3000 m (*).

Subfamily Orbiniidae Hartman, 1957

**Berkeleyia abyssala* Blake, 2017. Antarctic seas, 3111–4176 m.

**Berkeleyia hadala* Blake, 2017. Off western South America, abyssal and hadal depths, 2681–6143 m.

Berkeleyia lelievre Blake, 2020. Eastern Pacific, hydrothermal vents, Juan de Fuca Ridge, 2196 m.

**Berkeleyia profunda* Hartman, 1971. Indian Ocean, Mozambique Basin, 5069 m.

Berkeleyia weddellia Blake, 2017. Weddell Sea, 2164 m.

Califia calida Hartman, 1957. Eastern Pacific, off Oregon to Mexico, 946–2730 m; Western Pacific off Japan, 180–740 m; South China Sea, off Brunei, 1127–1487 m.

**Califia chilensis* Hartman, 1967. Eastern Pacific, off Chile, 3651–3655 m.

Califia mexicana Fauchald, 1972. Eastern Pacific, off western Mexico, 2030–2560 m.

Califia schmitti (Pettibone, 1957). Western North Atlantic, off New England to South Carolina, 544–2180 m.

**Leitoscoloplos abranchiatus* (Hartman, 1967). Southern Ocean, 1400–5338 m.

**Leitoscoloplos cliffordi* Blake, 2020. Eastern Pacific, California continental slope, 2600–3136 m.

**Leitoscoloplos drakei* (Hartman, 1967). Southern Ocean, Drake Passage, 3312–3532; Weddell Sea, 1622–4575 m; South African Basin, 4551 m.

**Leitoscoloplos eltaninae* Blake, 2017. South Atlantic Ocean, 3742–3806 m.

**Leitoscoloplos gordaensis* Blake, 2020. Eastern Pacific, Gorda Ridge, Escanaba Trough, hydrothermal vents, 3271 m.

Leitoscoloplos kerguelensis (McIntosh, 1885). Southern Ocean, widespread in subantarctic and Antarctic seas, low water to 1400 m.

Leitoscoloplos lunulus Blake, 2020. Eastern Pacific, California continental slope, 1020–1760.

Leitoscoloplos mexicanus (Fauchald, 1972): Eastern Pacific, Gulf of California, 1378–1421 m.

Leitoscoloplos obovatus Mackie, 1987: Western North Atlantic, off New England, 80–550; off the Carolinas, 640–800 m.

Leitoscoloplos olei Neal & Paterson in Neal *et al*., 2020. Southern Atlantic, North Falklands Basin, 426–464 m.

Leitoscoloplos pachybranchiatus Blake & Hilbig, 1990. Eastern Pacific, Juan de Fuca Ridge, Endeavor Segment, 2216 m.

Leitoscoloplos pustulus **n. sp.** Western North Atlantic, off Cape Hatteras, North Carolina, 579–640 m.

**Leitoscoloplos rankini* Blake, 2017. Southern Ocean: Drake Passage and Weddell Sea, 1622–3959 m.

Leitoscoloplos sahlingi Blake, 2020. Eastern Pacific, Cascadia Subduction Zone, off Oregon, 786 m.

**Leitoscoloplos simplex* Blake, 2017. Abyssal Pacific Ocean, 4843 m.

Leitoscoloplos williamsi Blake, 2020. Eastern Pacific, California continental slope, 1760 m.

Leodamas bathyalis Blake, 2020. South China Sea, off Brunei, Island of Borneo, 1260–1557 m.

Leodamas cirratus (Ehlers, 1897). Off Patagonia, Falkland Islands, Antarctic Peninsula, 593–598 m.

Leodamas cuneatus **n. sp.** Western North Atlantic, New England to off Delaware, 255–2060 m.

**Leodamas hyphalos* Blake, 2017. Southern Ocean, Drake Passage, 2888–4008 m.

Leodamas latum (Chamberlin, 1919). Off Panama, 588 m; off Burma (Myanmar), 457 m.

Leodamas marginatus (Ehlers, 1897). Southern Ocean, intertidal to 1674 m.

Leodamas mazatlanensis (Fauchald, 1972). Eastern Pacific, off Western Mexico, 2487–2560 m

Leodamas mucronatus **n. sp.** Western North Atlantic, off Charleston, South Carolina, 600–605 m.

Leodamas thalassae (Amoureux, 1982). Northeastern Atlantic, off France, 850–1400 m.

Methanoaricia dendrobranchiata Blake, 2000. Gulf of Mexico, off Louisiana, methane seeps, 650 m.

Naineris uncinata Hartman, 1957. Eastern Pacific, upper slope depths, including gas hydrate and seep sediments, 620–795 m.

Phylo norvegicus (M. Sars in G.O. Sars, 1872): Northeastern Atlantic, Arctic; Western North Atlantic, off New England to the Carolinas, 583–2150 m.

**Phylo nudus* (Moore, 1911). Eastern Pacific, California to Costa Rica, 760–3503 m.

**Scoloplos bathytatus* Blake, 2017. Southern Ocean, Drake Passage to South Georgia, 2800–3463 m.

Scoloplos californiensis Blake, 2020. Eastern Pacific, off California, 1730–1880 m.
Scoloplos ehlersi Blake, 1985. Southwest Pacific, Galápagos Rift hydrothermal vents, 2730 m.
Scoloplos intermedius (Hartman, 1965): Western North Atlantic, New England to North Carolina, 1210–2109 m.
Scoloplos papillatus **n. sp.** Off Cape Hatteras, North Carolina, 620–812 m.
Scoloplos sparsaciculus Blake, 2020. South China Sea, off Brunei, 1219–1955 m.

Subfamily Microrbiniinae Blake, 2000
Microrbinia linea (Hartman, 1965): Western North Atlantic, New England to South Carolina; 600–3015 m.
Orbiniella abyssalis Blake, 2020. Equatorial Pacific, Clarion-Clipperton Fracture Zone, 4844–4880 m.
Orbiniella aciculata Blake, 1985. Southwest Pacific, Galápagos Rift, sediments near vents, 2730 m.
Orbiniella acsara **n. sp.** Western North Atlantic, off New England, 1225–2164 m; off Delaware and New Jersey, 1503–2500 m; off North and South Carolina, 799–3019 m.
Orbiniella andeepia Narayanaswamy & Blake, 2005. Southern Ocean, Drake Passage, Weddell Sea, 2257–5338 m.
Orbiniella armata **n. sp.** Western North Atlantic, off South Carolina, 3000–3011 m.
Orbiniella eugeneruffi Blake, 2020. South China Sea, off Brunei, 1199–1260 m.
Orbiniella grasslei Blake, 2020. East Pacific Rise, hydrothermal vents, 1618–2616 m.
Orbiniella hobsonae Blake & Hilbig, 1990. Eastern Pacific, Juan de Fuca Ridge, hydrothermal vents, 2216 m.
Orbiniella longilobata Blake, 2020. South China Sea, off Brunei, 1199–2004 m.
Orbiniella mimica **n. sp.** Western North Atlantic, off U.S. Mid-Atlantic region, 1502–2144 m.
Orbiniella petersenae Parapar *et al*., 2015. Northeast Atlantic, 1490–1915 m.
Orbiniella rugosa Blake, 2020. South China Sea, off Brunei, 1199–2194 m.
Orbiniella tumida Blake, 2020. Eastern Pacific, off California continental slope, 2739–3221 m; abyssal plain, 4119 m.

Remarks on the Genus *Schroederella* Laubier, 1962

The collection of large numbers of juveniles of numerous species of polychaetes including several orbiniid species was made possible by the use of 300-µm-mesh sieves in the processing of samples collected in the sampling programs that were the source of much of the material used in the present study. Numerous juveniles of *Leitoscoloplos acutus*, *L. fragilis*, and *Scoloplos pettiboneae* **n. sp**. were initially thought to belong to the meiofaunal genus *Schroederella* described by Laubier (1962). However, a study of specimens of different sizes and maturity clearly demonstrated that they were juveniles of other taxa.

During the course of these investigations, the genus *Schroederella* Laubier, 1962 was found to be pre-occupied by *Schroederella* Enderlein, 1921, in the Insecta, Diptera, family Helomyzidae. A new name, *Gesaschroederella* **nomen nov.**, is therefore proposed to replace the polychaete junior homonym. See Diagnosis below.

To date, only three species of *Gesaschroederella* **nomen nov.** have been described (as *Schroederella*). All are from interstitial habitats of intertidal sands: (1) *G. pauliani* (Laubier, 1962), from Walvis Bay, South Africa; (2) *G. berkeleyi* (Laubier, 1971), from a beach at Centerville, Barnstable County, Massachusetts, USA; and (3) *G. laubieri* (Badalamenti & Castella, 1991) from the Italian coast of Sicily and the Island of Elba, Mediterranean Sea.

Schroederella berkeleyi, although originally collected from an easily accessible habitat near local marine research laboratories, has not been reported in the 50 years since it was described. After observations on numerous small specimens and comparison with the original description and holotype, it is evident that the species is in fact a juvenile of *Leitoscoloplos acutus*, and therefore a synonym (see description and comments for *L. acutus*). The other two species described as *Schroederella* from southern Africa and the Mediterranean Sea and should also be investigated as probable juveniles of other orbiniids, such as local species of *Scoloplos*.

Genus *Gesaschroederella* nomen nov.

Schroederella Laubier, 1962, junior **homonym** of *Schroederella* Enderlein, 1921. **Type-species**: *Schroederella paulini* Laubier, 1962.

Diagnosis. (Emended) Prostomium elongate, pointed; eyespots present or absent; peristomium with two rings, variously developed; body regions separated into thorax and abdomen; branchiae present from abdominal segments; all parapodia with camerated capillaries; acicular spines or uncini present in thoracic neuropodia; pygidium with dorsal anus and 2–4 anal cirri.

Etymology. *Gesaschroederella* is formed by adding the first name to the surname of Dr. Gesa Hartmann-Schröder, for whom the late Dr. Lucien Laubier originally named the genus.

Remarks. As reported in this study, juveniles of several species of *Leitoscoloplos* and *Scoloplos* have been found with characteristics of *Schroederella* as defined by Laubier (1962, 1971), here renamed *Gesaschroederella* **nomen nov**. The use of fine-mesh sieves permits the collection of juvenile orbiniids that were previously not available from surveys of benthic invertebrates. Both *G. paulini* and *G. laubieri* should be compared with local species of *Scoloplos* from South Africa and the Mediterranean Sea to explore the possibility that they are also juveniles of larger orbiniids.

Apart from being small and meiofaunal in habitat, there is nothing morphologically in the above definition except the presence of two peristomial rings that separates the two remaining species of *Gesaschroederella* from species of *Scoloplos*.

Acknowledgements

The majority of materials on which this study is based were collected as part of three major offshore monitoring and reconnaissance programs. Collection of samples from the Georges Bank Benthic Infauna Monitoring Program and Atlantic slope (ACSAR) material was made under contract Nos.14-12-0001-29192 and 14-12-0001-30064 from the Department of the Interior, Minerals Management Service (MMS), to Battelle Ocean Sciences (1983–1987). Field teams were led by the late Mr. George Hampson (WHOI; Georges Bank and U.S. North Atlantic surveys), Ms. Rosemarie Petrecca (then of WHOI; U.S. Mid-Atlantic surveys), and the author (then of Battelle Ocean Sciences; U.S. South Atlantic surveys). The samples from Massachusetts Bay were collected as part of the long-term benthic monitoring for MWRA in response to the siting and operation of an offshore ocean outfall. The author was manager of this project for several years and oversaw the collection and processing of benthic samples while with SAIC and ENSR. Mr. Kenneth Keay, manager of benthic monitoring at MWRA, is thanked for many years of support.

Other materials were from local projects throughout the northeastern United States intended to monitor impacts of PCB contamination (New Bedford Harbor for the US EPA and USACE), surveys of planned undersea pipeline routes including Long Island Sound and Eastchester Bay for Iroquois Gas and the Atlantic Ocean off New Jersey and Long Island for the Port Liberty LNG Project, and surveys at several dredged material disposal sites in Long Island Sound for the USACE. The author was manager of the marine ecology components of these projects for ENSR and AECOM. Various other samples were personally collected by the author, colleagues, or students at sites from Maine to Connecticut. Local surveys in Long Island Sound, New Bedford Harbor, and Massachusetts Bay were managed by Dr. Pamela L. Neubert and Ms. Isabelle P. Williams, both long-time colleagues of the author. Supplemental materials examined from the Gulf of Mexico were collected as part of surveys around two oil platforms off Louisiana managed by the author for Total E&P USA.

Curation of the materials used in this study and assignment of catalog numbers was by Ms. Katherine Ahlfeld (USNM) and Ms. Jennifer Trimble (MCZ). Owing to the numerous samples provided to these collection managers, their timely efforts are deeply appreciated. Over the years, many lab technicians at Battelle, ENSR, and AECOM carefully processed the benthic samples from these various projects that yielded the polychaete material. Senior polychaete taxonomists, including Dr. Brigitte (Hilbig) Ebbe, Dr. Nancy J. Maciolek, and the late Mr. R. Eugene Ruff worked closely with the author on most of these projects and provided many of the provisional identifications. The manuscript was thoroughly reviewed and carefully edited by Dr. Nancy J. Maciolek and whose effort is greatly appreciated. Drs. Brigitte Ebbe and Harlan K. Dean reviewed the manuscript and provided comments that greatly improved the manuscript.

References

Andrews, E.A. (1891) Report upon the Annelida Polychaeta of Beaufort, North Carolina. *Proceedings of the United States National Museum*, 14 (852), 277–302, pls. 12–18.
https://doi.org/10.5479/si.00963801.14-852.277

Amoureux, L. (1982) Annélides Polychètes recueillies sur la pente continentale de la Bretagne a l′Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre espèces nouvelles pour la science. II. Inventaire taxonomique annoté

de toutes les polycheès sédentaires. *Cahiers de Biologie Marine*, 23, 179–214.
https://doi.org/10.21411/CBM.A.5E35F37E
Audouin, J.V. & Milne-Edwards, H. (1833) Classification des Annélides et descriptions de celles qui habitent les côtes de la France. *Annales des Sciences Naturelles Paris*, Series 1, 29, 388–412.
https://doi.org/10.5962/bhl.part.8010
Augener, H. (1934) Polychaeten aus den Zoologischen Museen von Leiden und Amsterdam. – IV. (Schluss).*Zoologische Mededeelingen, Leiden,* 17 (8), 67–160.
Badalamenti, F. & Castelli, A. (1991) *Schroederella lauberi*, a new species of the subfamily Protoariicinae (Polychaeta, Orbiniidae), with some notes of the genus *Schroederella* Laubier, 1962, *Bollettino di Zoologia Italiana*, 58, 95–98.
https://doi.org/10.1080/11250009109355735
Berkeley, E. & Berkeley, C. (1952) Polychaeta Sedentaria. *Canadian Pacific Fauna*, 9b (2), 1–139, figs. 1–292.
Blainville, H. de. (1828) *Dictionnaire des Sciences naturelles*, 57, 368–501. [https://biodiversitylibrary.org/page/25316890]
Blake, J.A. (1980) The larval development of Polychaeta from the Northern California coast. IV. *Leitoscoloplos pugettensis* and *Scoloplos acmeceps* (Family Orbiniidae). *Ophelia*, 19, 1–18.
https://doi.org/10.1080/00785326.1980.10425502
Blake, J.A. (1985) Polychaeta from the vicinity of deep-sea geothermal vents in the Eastern Pacific I: Euphrosinidae, Phyllodocidae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae, Orbiniidae, and Maldanidae. *Bulletin of the Biological Society of Washington*, 6, 67–101. [https://www.researchgate.net/publication/279962731]
Blake, J.A. (1993) Life history analysis of five dominant infaunal polychaete species from the continental slope off North Carolina. *Journal of the Marine Biological Association of the United Kingdom*, 73, 123–141.
https://doi.org/10.1017/S0025315400032689
Blake, J.A. (1994) Vertical distribution of benthic invertebrates from the continental slope off Cape Lookout, North Carolina. *Deep-Sea Research II*, 41, 919–927.
https://doi.org/10.1016/0967-0645(94)90054-X
Blake, J.A. (1996) Chapter 1. Family Orbiniidae Hartman, 1942. *In*: Blake, J.A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. Annelida. Part 3. Polychaeta: Orbiniidae to Cossuridae*. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 1–26.
Blake, J.A. (2000) A new genus and species of polychaete worm (Family Orbiniidae) from methane seeps in the Gulf of Mexico, with a review of the systematics and phylogenetic interrelationships of the genera of Orbiniidae. *Cahiers de Biologie Marine*, 41, 435–449.
https://doi.org.10.21411/CBM.A.84F1D61E
Blake, J.A. (2017) Polychaeta Orbiniidae from Antarctica, the Southern Ocean, the abyssal Pacific Ocean, and off South America. *Zootaxa*, 4218 (1), 1–145.
https://doi.org/10.11646/zootaxa.4218.1.1
Blake, J.A. (2020) New species and records of deep-water Orbiniidae (Annelida, Polychaeta) from the Eastern Pacific continental slope, abyssal Pacific Ocean, and the South China Sea. *Zootaxa*, 4730 (1), 1–61.
https://doi.org/10.11646/zootaxa.4730.1.1
Blake, J.A., Arnofsky, P.A., Lewis, D., Maciolek, N.J., McGrath, D., Mitchell, D. & Williams, I.P. (2001) *New Bedford Harbor Long-Term Monitoring Survey III: Summary Report Submitted to U.S. Army Corps of Engineers, New England District, Concord, Massachusetts under Contract No. DACW33-96-D-0004, Delivery Order No. 037*. 28 pp., 9 Appendices.
https://doi.org/10.13140/RG.2.2.20275.04646
Blake, J.A. & Grassle, J.F. (1994) Benthic community structure in the U.S. South Atlantic off the Carolinas: Spatial heterogeneity in a current dominated system. *Deep-Sea Research II*, 41, 835–874.
https://doi.org/10.1016/0967-0645(94)90051-5
Blake, J.A., Hecker, B., Grassle, J.F., Brown, B., Wade, M., Boehm, P., Baptiste, E., Hilbig, B., Maciolek, N., Petrecca, R., Ruff, R.E., Starczak, V. & L.E. Watling, L.E. (1987) *Study of Biological Processes on the U.S. South Atlantic Slope and Rise. Phase 2. Prepared for the U.S. Department of the Interior, Minerals Management Service, Washington, D.C. OCS Study MMS 86-0096: Vol. 2. Final Report*. National Technical Information Service (NTIS) No. PB 87-214342 and PB 87-214359. ii + 414 pp., 13 Appendices. Available from: https://espis.boem.gov/final%20reports/4698.pdf (accessed 20 January 2021)
Blake, J.A. & Hilbig, B. (1990) Polychaeta from the vicinity of deep-sea hydrothermal vents in the eastern Pacific II: New species and records from the Juan de Fuca and Explorer Ridge Systems. *Pacific Science*, 44, 219–253. [http://hdl.handle.net/10125/1280]
Blake, J.A. & Hilbig, B. (1994) Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. *Deep-Sea Research II*, 41, 875–899.
https://doi.org/10.1016/0967-0645(94)90052-3
Blake J.A., Williams I.P., Gallagher E.D., Hecker B., Rhoads, D.C. & Arnofsky P.L. (1998) *Massachusetts Bay outfall monitoring program: Benthic biology and sedimentology baseline monitoring for 1997 and retrospective analysis of the 1992–1997 database. Report ENQUAD*, 98-16. Massachusetts Water Resources Authority, Boston, Massachusetts, 221 pp. + Appendices. [http://www.mwra.state.ma.us/harbor/enquad/pdf/1998-16.pdf]
Bleidorn, C. (2005) Phylogenetic relationships and evolution of Orbiniidae (Annelida, Polychaeta) based on molecular data.

Zoological Journal of the Linnean Society, 144, 59–73.
https://doi.org/10.1111/j.1096-3642.2005.00160.x
Bleidorn, C. & Helm, C. (2019) 7.1.4 Orbiniidae Hartman, 1942. *In*: Purschke, G., Böggemann, M. & Westheide, W. (Eds.), *Handbook of Zoology. Annelida. Vol. 1. Annelida Basal groups and Pleistoannelida, Sedentaria I*. DeGruyter, Berlin, pp. 251–269.
Bleidorn, C., Hill, N., Erséus, C. & Tiedemann, R. (2009) On the role of character loss in orbiniid phylogeny (Annelida) Molecules vs. morphology. *Molecular Phylogenetics and Evolution*, 52, 57–69.
https://doi.org/10.1016/j.ympev.2009.03.022
Bleidorn, C., Kruse, I., Albrecht, S. & Bartolomaeus, T. (2006) Mitochondrial sequence data expose the putative cosmopolitan polychaete *Scoloplos armiger* (Annelida, Orbiniidae) as a species complex. *BMC Evolutionary Biology*, 6 (47), 1–13 pp.
https://doi.org/10.1186/1471-2148-6-47
Brown, B. (1982) Spatial and temporal distribution of a deposit-feeding polychaete on a heterogeneous tidal flat. *Journal of Experimental Marine Biology and Ecology*, 65, 213–227.
https://doi.org/10.1016/0022-0981(82)90054-5
Buzhinskaja, G.N. (1992) *Orbiniella plumisetosa* sp. n. First find of a polychaete of the subfamily Protoariciinae in the northwestern Pacific and characteristics of the genus *Orbiniella* (Polychaeta: Orbiniidae). *In*: Buzhinskaja, G.N. (Ed.), *Polychaeta and their Ecological Significance*. *Explorations of the Fauna of the Seas. 43 (51)*. Zoological Institute, Russian Academy of Sciences, St. Petersburg, pp. 76–81, figs. 1–3. [in Russian, English translation April 1995 by A.V. Verashchaka, P.P. Shirshov Institute of Oceanology, Moscow]
Chamberlin, R.V. (1919a) New polychaetous annelids from Laguna Beach. *Journal of Entomology and Zoology, Pomona College*, 11, 1–23. [http://biodiversitylibrary.org/page/12263520]
Chamberlin, R.V. (1919b) The Annelida Polychaeta (*Albatross* Expeditions). *Memoirs of the Museum of Comparative Zoology at Harvard College*, 48, 1–514. [http://www.biodiversitylibrary.org/ia/memoirsofmuseumo4801harv]
Claparède, R.-É. (1868) Les annélides chétopodes du Golfe de Naples. *Mémoires de la Société de physique et d'histoire naturelle de Genève*, 19 (Pt.2), 313–584, 16 pls. [http://biodiversitylibrary.org/page/48090491]
Curtis, M.A. (1969) Synonymy of the polychaete *Scoloplos acutus* with *S. armiger*. *Journal of the Fisheries Research Board of Canada*, 26 (12), 3279–3282.
https://doi.org/10.1139/f69-317
Day, J.H. (1954) The Polychaete of Tristan da Cunha 1937–1938. *Results of the Norwegian Expedition to Tristan da Cunha 1937–1937, Oslo*, No. 29, 1–35.
Day, J.H. (1961) The polychaete fauna of South Africa. Part 6 sedentary species dredged off Cape coasts with a few new records from the shore. *Journal of the Linnean Society of London,* 44 (299), 463–560.
https://doi.org/10.1111/j.1096-3642.1961.tb01623.x
Day, J.H. (1973) New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Technical Report, National Marine Fisheries Circular*, 375, 1–140. [https://repository.library.noaa.gov/view/noaa/3030]
https://doi.org/10.5962/bhl.title.62852
Day, J.H. (1977) A review of the Australian and New Zealand Orbiniidae (Annelida: Polychaeta). *In*: Reish, D.J. & Fauchald, K. (Eds.), *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman.* Allan Hancock Foundation, University of Southern California, Los Angeles, pp. 217–246.
Dean, H.K. & Blake, J.A. (2015) The Orbiniidae (Annelida: Polychaeta) of Pacific Costa Rica. *Zootaxa*, 3956 (2), 183–198.
https://doi.org/10.11646/zootaxa.3956.2.2
Ehlers, E. (1874) Annulata nova vel minus cognita in Expeditione Porcupine capta. *Annals &. Magazine of Natural History, London*, Series 4, 13, 292–298.
https://doi.org/10.1080/00222937408680863
Ehlers, E. (1897) Polychaeta. *In*: *Hamburger Magalhaenischen Sammelreise*. Friedrichsen & Co., Hamburg, pp. 1–148, 9 pls. [https://www.biodiversitylibrary.org/page/46140179]
Ehlers, E. (1900) Magellanische Anneliden gesammelt während der schwedischen Expedition nach den Magellansländern. *Nachrichten von der Gesellschaft der Wissenschaften zu Göttingen, Mathematisch-Physikalische Klasse*, 1900, 206–223. [http://www.digizeitschriften.de/dms/resolveppn/?PID=GDZPPN002498812]
Ehlers, E. (1901) Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. *Festschrift zur Feier des Hundertfünfzigjährigen Bestehens der königlichen Gesellschaft der Wissenschaften zu Göttingen*, 1901, 1–232, 25 pls. [http://www.annelida.net/docs/Ehlers1901_PolychaetenMagellanischenChilenischenStrandes.pdf]
Eibye-Jacobsen, D. (2002) The Orbiniidae (Annelida: Polychaeta) of the BIOSHELF Project, Andaman Sea, Thailand. *Phuket Marine Biological Center, Special Publication*, 24, 77–99.
Enderlein, G. (1921) Dipterologische Studien XVII. *Zoologisches Anzeiger*, 52, 219–232. [https://www.biodiversitylibrary.org/page/9735076]
Eisig, H. (1914) Zur Systematik, Anatomie und Morphologie der Ariciiden nebst Beiträgen zur generallen Systematik. *Mitteilungen aus der Zoologischen Station Neapel*, 21, 153–600, pls. 10–27, 23 figs. [https://biodiversitylibrary.org/page/47117120]
Fabricius, O. (1780) *Fauna Groenlandica. Impensis Ioannis Gottlob Rothe, Hafniae et Lipsiae*, *xvi* + 452 pp., 12 figs.
https://doi.org/10.5962/bhl.title.61754

Fauchald, K. (1972) Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology*, 7, 1–575, 69 pls. [http://hdl.handle.net/10088/6207]

Fauchald, K.; Granados-Barba, A. & Solís-Weiss, V. (2009) Polychaeta (Annelida) of the Gulf of Mexico. *In*: Felder, D.L. & Camp, D.K. (Eds.), *Gulf of Mexico. Origin, Waters, and Biota. Vol. 1. Biodiversity.* Texas A&M University Press, College Station, Texas, pp. 751–788.

Fauvel, P. (1927) Polychètes sédentaires. *Faune de France*, 16, 1–494, 152 figs. [http://faunedefrance.org/bibliotheque/docs/P.FAUVEL(FdeFr16)Polychetes-sendentaires.pdf]

Giangrande, A. & Petraroli, A. (1991) Reproduction, larval development and post-larval growth of *Naineris laevigatus* (Polychaeta, Orbiniidae) in the Mediterranean Sea. *Marine Biology*, 111, 129–137. [https://link.springer.com/article/10.1007/BF01986354]
https://doi.org/10.1007/BF01986354

Giere, O, Ebbe, B. & Erséus, C. (2008) *Questa* (Annelida, Polychaeta, Orbiniidae) from Pacific regions—new species and reassessment of the genus *Periquesta*. *Organisms, Diversity & Evolution*, 7, 304–319.
https://doi.org/10.1016/j.ode.2007.04.001

Giere, O. & Erséus, C. (1998) A systematic account of the Questidae (Annelida, Polychaeta), with description of new taxa. *Zoologica Scripta*, 27, 345–360.
https://doi.org/10.1111/j.1463-6409.1998.tb00466.x

Giere, O.W. & Riser, N.W. (1981) Questidae—Polychaetes with oligochaetoid morphology and development. *Zoologica Scripta*, 10, 95–103.
https://doi.org/10.1111/j.1463-6409.1981.tb00488.x

Hansen, G.A. (1882) Recherches sur les annélides recueillies par M. le professeur Édouard van Benedon pendant son voyage au Brésil et à la Plata. *Mémoires Couronnes et Mémoires des Savants Etrangers publiés par L'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 44 (3), 1–29. [https://www.biodiversitylibrary.org/page/5943290]

Hartman, O. (1942) A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin of the Bingham Oceanographic Collections*, 8, 1–98.

Hartman, O. (1944) New England Annelida. Part 2. Including the unpublished plates by Verrill with reconstructed captions. *Bulletin of the American Museum of Natural His*tory, 82 (7), 327–344, pls. 45–60. [http://hdl.handle.net/2246/1052]

Hartman, O. (1945) The marine annelids of North Carolina. *Bulletin of the Duke University Marine Laboratory*, 2, 1–51, 10 pls.

Hartman, O. (1948) The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Arkiv fur Zoologi*, 42A (1), 1–137, 18 pls.

Hartman, O. (1951) The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science*, 2 (1), 7–124, 27 pls. [https://repositories.lib.utexas.edu/handle/2152/22162]

Hartman, O. (1953) Non-pelagic Polychaeta of the Swedish Antarctic Expedition 1901–1903. *Zoological Results of the Swedish Antarctic Expedition 1901–1903*, 4 (11), 1–83, 21 figs., 1 chart.

Hartman, O. (1956) Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology. *Bulletin of the American Museum of Natural History*, 109 (2), 243–310. [http://hdl.handle.net/2246/1145]

Hartman, O. (1957) Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pacific Expeditions*, 15 (3), 211–393, pls. 20–44, 1 chart. [https://biodiversitylibrary.org/page/4160176]

Hartman, O. (1959) Catalogue of the polychaetous annelids of the world. *Allan Hancock Foundation Publications, Occasional Paper*, 23, 1–628.

Hartman, O. (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Occasional Paper*, 28, 1–378. Available from: https://digitallibrary.usc.edu/cdm/ref/collection/p15799coll82/id/20299 (accessed 4 July 2019)

Hartman, O. (1966a) Polychaeta Myzostomidae and Sedentaria of Antarctica. *In*: *Antarctic Research Series. Vol. 7*. American Geophysical Union, Washington, D.C., pp. 1–158, 46 pls, 5 charts.
https://doi.org/10.1029/AR007

Hartman, O. (1966b) Quantitative survey of the benthos of San Pedro Basin, southern California. Part II. Final results and conclusions. *Allan Hancock Pacific Expeditions*, 19, 187–455. [https://www.biodiversitylibrary.org/page/27911715]

Hartman, O. (1967) Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology*, 2, 1–387, 51 pls.

Hartman, O. (1971) Abyssal polychaetous annelids from the Mozambique Basin off Southeast Africa, with a compendium of abyssal polychaetous annelids from world-wide areas. *Journal of the Fisheries Research Board, Canada*, 28, 1407–1428.
https://doi.org/10.1139/f71-219

Hartman, O. & Fauchald, K. (1971) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas Part II. *Allan Hancock Monographs in Marine Biology*, 6, 1–327. [https://repository.si.edu/handle/10088/3458?show=full]

Hartmann-Schröder, G. (1965) Die Polychaeten des Sublitorals. *In*: Hartmann-Schröder, G. und Hartmann, G., (Eds.), Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen des Hamburgischen Zoologischen Museums und Instituts, Supplement*, 62, 59–305, 300 figs.

Hartmann-Schröder, G. (1971) Annelida, Borstenwürmer, Polychaeta. *In*: *Die Tierwelt Deutschlands*. *Vol. 58. 1st Edition*. Gus-

tav Fischer Verlag, Jena, pp. 1–594.
Hartmann-Schröder, G. (1974) Polychaeten von Expeditionen der "Anton Dohrn" in Nordsee und Skagerrak. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven*, 14, 169–274.
Hartmann-Schröder, G. (1996) Annelida, Borstenwürmer, Polychaeta. *In*: *Die Tierwelt Deutschlands*. *Vol. 58. 2nd Edition*. Gustav Fischer Verlag, Jena, pp. 1–648.
Hartmann-Schröder, G. & Rosenfeldt, P. (1990) Die Polychaeten der "*Walther Herwig*"—Reise 68/1 nach Elephant Island (Antarktis) 1985 Teil 1: Aphroditidae bis Cirratulidae. *Mitteilungen des Hamburgischen Zoologischen Museums und Instituts, Supplement*, 87, 89–122.
Hernández-Alcántara, P. & Solís-Weiss, V. (2014) Anatomical and morphometric analysis of a new species of Leitoscoloplos (Annelida: Orbiniidae) with numerous stomach papillae, from the Gulf of California, Eastern Pacific. *Contributions to Zoology*, 83 (2), 133–150. [http://www.ctoz.nl/vol83/nr02/a04]
https://doi.org/10.1163/18759866-08302004
Hilbig, B. (1994) Faunistic and zoogeographical characterization of the benthic infauna on the Carolina continental slope. *Deep-Sea Research II*, 41, 929–950.
https://doi.org/10.1016/0967-0645(94)90055-8
Hobson, K.D. (1970) *Novaquesta trifurcata*, a new genus and species of the family Questidae (Annelida, Polychaeta) from Cape Cod Bay, Massachusetts. *Proceedings of the Biological Society of Washington*, 83, 191–194. [https://www.biodiversitylibrary.org/page/34572815]
Hobson, K.D. & Banse, K. (1981) Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences*, 209, 1–144, 29 figs.
Hoagland, R.A. (1919) *Polychaetous annelids from Porto Rico, the Florida Keys, and Bermuda. Bulletin of the American Museum of Natural History, 41, 571–591, 4 pls. [*http://hdl.handle.net/2246/1161]
Horn, E.C. & Bookhout, C.G. (1950) *The early development of Haploscoloplos bustoris (Eisig)*. *Journal of the Elisha Mitchell Scientific Society, 66 (1), 1–9, 4 pls. [*https://dc.lib.unc.edu/cdm/singleitem/collection/jncas/id/2038/rec/1]
Jamieson, B.G.M. & Webb, R.I. (1984) The morphology, spermatozoal ultrastructure and phylogenetic affinities of a new species of questid (Polychaeta: Annelida). *In*: Hutchings, P.A. (Ed.), *Proceedings of the First International Polychaete Conference, Linnean Society of New South Wales, Sydney*, 1984, pp. 21–34.
Kinberg, J. (1866) Annulata nova. *Öfversight af Kungliga Vetenskaps—Adakemiens Förhandlingar, Stockholm*, 22, 239–258. [https://biodiversitylibrary.org/page/32339515]
Kruse, I. & Reise K. (2003) Reproductive isolation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae) indicates sibling species in the North Sea. *Marine Biology*, 143, 511–517.
https://doi.org/10.1007/s00227-003-1112-x
Kruse, I., Reusch, T.B.H. & Schneider, M.V. (2003) Sibling species or poecilogony in the polychaete *Scoloplos armiger? Marine Biology*, 142, 937–947.
https://doi.org/10.1007/s00227-002-1007-2
Kruse I., Strasser M. & Thiermann F. (2004) The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae). *Journal of Sea Research*, 51:53–62.
https://doi.org/10.1016/j.seares.2003.05.004
Laubier, L. (1962) *Schroederella pauliani* gen. nov., sp.nov., un nouvel Orbiniidé (polychètes sédentaires) de fauna interstitielle d'Afrique. *Annals of the Transvaal Museum*, 24, 231–238. [https://hdl.handle.net/10520/AJA00411752_326]
Laubier, L. (1971) *Schroederella berkeleyi* sp. n., un nouvel Orbiniidé (Polychète Sédentaire) de la faune interstitielle littorale de Massachusetts (USA). *Journal of the Fisheries Research Board of Canada*, 289 (10), 1483–1486.
https://doi.org/10.1139/f71-227
Maciolek-Blake, N, Grassle, J.F. & Neff, J.M. (Eds.) (1985) *Georges Bank Benthic Infauna Monitoring Program. Final Report for third Year of Sampling. U.S. Department of the Interior, Minerals Management Service. Performed under Contract No. 14-12-0001-29192. Vol. 2 & 3*. Battelle New England Marine Research Laboratory, Duxbury, Massachusetts, 333 pp. & Appendices A–K. [report: https://espis.boem.gov/final%20reports/4633.pdf, appendices: https://espis.boem.gov/final%20reports/4634.pdf]
Maciolek, N., Grassle, J.F., Hecker, B., Boehm, P.D., Brown, B., Dade, B., Steinhauer, W.G., Baptiste, E. Ruff, R.E. & Petrecca, R. (1987a) *Study of biological processes on the U.S. Mid-Atlantic slope and rise. Final report prepared for the U.S. Department of the Interior, Minerals Management Service, under contract no. 14-12-0001-30064. Vol. 1. Executive Summary & Vol. 2. Final Report*. 44 pp. & 310 pp. + appendices. Available from: https://espis.boem.gov/final%20reports/4722.pdf (accessed 20 January 2021)
Maciolek, N., Grassle, J.F., Hecker, B., Brown, B., Blake, J.A., Boehm, P.D. Petrecca, R. Duffy, S., Baptiste, E. & Ruff, R.E. (1987b) *Study of biological processes on the U.S. North Atlantic slope and rise. Final report prepared for the Department of the Interior, Minerals Management Service, under contract no. 14-12-0001-30064. Vol. 1. Executive Summary & Vol. 2. Final Report*. 41 pp. & 362 pp. + appendices. Available from: https://espis.boem.gov/final%20reports/4724.pdf (accessed 20 January 2021)
Mackie, A.S.Y. (1987) A review of the species currently assigned to the genus *Leitoscoloplos* Day, 1977 (Polychaeta: Orbiniidae), with descriptions of species newly referred to *Scoloplos* Blainville, 1828. *Sarsia*, 72, 1–28, 24 figs.
https://doi.org/10.1080/00364827.1987.10419701

McIntosh, W.C. (1885) Report on the Annelida Polychaeta collected by H.M.S. *Challenger* during the years 1873–76. *Challenger Reports*, 12, 1–554, pls. 1–55 + 1a–39a. [https://www.biodiversitylibrary.org/page/50688432]
McIntosh, W.C. (1910) s.n. *In*: *A Monograph of the British Annelids. Vol. II. Part II. Polychaeta: Syllidae to Ariciidae*. Ray Society, London, pp. 235–524, pls. XLIII–LXXXVII. [https://www.biodiversitylibrary.org/page/38533042]
Monro, C.C.A. (1930) Polychaete worms. *Discovery Reports*, 2, 1–222, 91 figs. [https://www.biodiversitylibrary.org/page/15904802]
Monro, C.C.A (1933a) On a collection of Polychaeta from Dry Tortugas, Florida. *Annals & Magazine of Natural History*, Series 10, 12, 244–269.
https://doi.org/10.1080/00222933308655413
Monro, C.C.A. (1933b) The polychaete Sedentaria collected by Dr. C. Crossland at Colon, in the Panama region, and the Galapagos Islands during the expedition of the S.Y. ST. GEORGE. *Proceedings of the Zoological Society of London*, 1933, 1039–1092.
https://doi.org/10.1111/j.1096-3642.1933.tb01640.x
Moore, J.P. (1911) The polychaetous annelids dredged by the U.S.S. "Albatross" off the coast of southern California in 1904. III. Euphrosynidae to Goniadidae. *Proceedings of the Philadelphia Academy of Natural Sciences*, 63, 234–318, pls. 15–21. [https://biodiversitylibrary.org/page/26283655]
Müller, O.F. (1776) *Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium.* typis Hallageriis, Havniae, xxxii + 282 pp.
https://doi.org/10.5962/bhl.title.13268
Narayanaswamy, B.E. & Blake, J.A. (2005) A new species of *Orbiniella* (Polychaeta: Orbiniidae) from deep basins of Antarctica. *Journal of the Marine Biological Association of the United Kingdom*, 85, 843–846.
https://doi.org/10.1017/S0025315405011793
Neal, L. Patterson, G.L., Blockley, D., Scott, B., Sherlock, E., Huque, C. & Glover, A.G. (2020) Biodiversity data and new species descriptions of polychaetes from offshore waters of the Falkland Islands, an area undergoing hydrocarbon exploration. *Zookeys*, 938, 1–86.
https://doi.org/10.3897/zookeys.938.49349
Okuda, S. (1937) Some ariciid worms from Japan. *Annotationes Zoologicae Japanenses*, 16, 99–105, 6 figs.
Okuda, S. (1946) Studies on the development of the Annelida Polychaeta. I. *Journal of the Faculty of Science Hokkaido Imperial University*, 9, 115–219, 17 pls. [http://hdl.handle.net/2115/27055]
Parapar, J., Moreira, J. & Helgason, G.V. (2015) First record of genus *Orbiniella* Day, 1954 (Polychaeta: Orbiniidae) in North Atlantic Ocean with the description of a new species. *Zootaxa*, 4006 (2), 330–346.
https://doi.org/10.11646/zootaxa.4006.2.5
Pettibone, M.H. (1957) North American genera of the family Orbiniidae. *Journal of the Washington Academy of Science*, 47, 159–167, 4 figs. [https://biodiversitylibrary.org/page/39753528]
Pettibone, M.H. (1963) Marine polychaete worms of the New England region. *Bulletin of the United States National Museum*, 227, 1–346. [https://biodiversitylibrary.org/page/39753528]
https://doi.org/10.5479/si.03629236.227.1
Proctor, W. (1933) Annelida. *In*: *Biological Survey of the Mount Region. Part 5*. Wistar Institute of Anatomy and Physiology, Philadelphia, Pennsylvania, pp. 132–155, figs. 31–37. [https://www.biodiversitylibrary.org/page/5972293]
Ramey, P.A., Fiege, D. & Leander, D.S. (2006) A new species of *Polygordius* (Polychaeta: Polygordiidae): from the inner continental shelf and in bays and harbours of the north-eastern United States. *Journal of the Marine Biological Association of the United Kingdom*, 86 (5), 1025–1034.
https://doi.org/10.1017/S0025315406014007
Rathke, H. (1843) Beiträge zur Fauna Norwegens. *Verhandlungen Kaiserlichen Leopoldinisch-Carolinischen Akademie Naturforscher, Breslau*, 20, 1–264. [https://www.biodiversitylibrary.org/page/51510790]
https://doi.org/10.5962/bhl.title.120119
Read, G. & Fauchald, K. (Ed.) (2020a) *World Polychaeta database*. Orbiniidae Hartman, 1942. Accessed through: World Register of Marine Species. Available from: http://www.marinespecies.org/aphia.php?p=taxdetails&id=902 (accessed 12 July 2020)
Read, G. & Fauchald, K. (Ed.) (2020b) *World Polychaeta database*. *Questa* Hartman, 1966. Accessed through: World Register of Marine Species. Available from: https://www.marinespecies.org/aphia.php?p=taxdetails&id=129517 (accessed 13 Nov 2020)
Rhoads, D.C. & Hecker, B. (1994) Processes of the continental slope off North Carolina with special reference to the Cape Hatteras region. *Deep-Sea Research II*, 41, 965–980.
https://doi.org/10.1016/0967-0645(94)90057-4
Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007) A molecular phylogeny of annelids. *Cladistics*, 23, 41–63.
https://doi.org/10.1111/j.1096-0031.2006.00128.x
Rozbaczylo, N. (1985) Los Anélidos Poliquetos de Chile. Indice Sinonímico y distribución geográfica de especies. *Facultad de Ciencias Biologicas Pontificia Universidad Católica de Chile, Monografías Biológicas*, No. 3, 1–284.
Quatrefages, A. De. (1866) *Histoire naturelle des Annélides marines et d'eau douce. Annélides et Gephyriens. Vol. 2*. Librarie

Encylopédique de Rôret, Paris, 336 pp. [https://www.biodiversitylibrary.org/page/5211923]
https://doi.org/10.5962/bhl.title.122818
Sars, G.O. (1872) Diagnoser af nye Annelider fra Christianiaforden, efter Professor M. Sar′s efterladte Manuskripter. *Forhandlinger i Videnskabs-Selskabet i Christiania,* 1871, 406–417. [https://www.biodiversitylibrary.org/page/44067539]
Sars, G.O. (1873) *On some remarkable forms of animal life from the great deeps off the Norwegian coast. I. Partly from posthumous manuscripts of the late Professor Dr. Michael Sars*. Brugger & Christie, Christiana, 88 pp., 6 pls. [http://books.google.com/books?id=FV9IAAAAYAAJ]
https://doi.org/10.5962/bhl.title.11274
Savigny, J.C. (1820) Système des Annélides, principalement de celles des côtes de l′Égypte et de la Syrie, offrant les caractères tant distinctifs que naturèles des orders, families et genres, avec la description de espèces. Description de l′Égypte. *Historie naturelle, Paris*, 1 (3), 1–128. [https://www.biodiversitylibrary.org/page/49077062]
https://doi.org/10.5962/bhl.title.66284
Støp-Bowitz, C. (1948) Polychaeta from the Michael Sars North Atlantic deep-sea expecition 1910. *Reports of the Scientific Results Michael Sars North Atlantic Deep-Sea Expedition 1910*, 5 (No. 8), 1–91. [http://www.annelida.net/docs/scans.html]
Sumner, F.B, Osburn, R.C. & Cole, L.J. (1913) Annulata, In, A Biological Survey of the Woods Hole and vicinity. *Bulletin of the U.S. Bureau of Fisheries*, 31 (2), 615–636. [https://www.biodiversitylibrary.org/page/11193354]
Sun, Y, Sui, J. & Li, X. (2018) A new species of *Leodamas* Kinberg, 1866 (Polychaeta: Orbiniidae) from the Yellow Sea and East China Sea. *Acta Oceanologica Sinica*, 37 (10), 130–135.
https://doi.org/10.1007/s13131-018-1313-2
Taylor, J.L. (1984) Family Orbiniidae Hartman, 1942. *In*: Uebelacker, J.M. & Johnson, P.G. (*Eds*.), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Vol. 1*. Barry A. Vittor & Associates, Mobile, Alabama, pp. 1-1–1-38,
Taylor, J.L. & Gathof, J.M. (1984) Family Questidae Hartman, 1966. *In*: Uebelacker, J.M. & Johnson, P.G. (*Eds*.), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico. Vol. 1*. Barry A. Vittor & Associates. Mobile, Alabama, pp. 3-1–3-7,
Treadwell, A.L. (1941) New species of polychaetous annelids from the vicinity of Galveston, Texas. *American Museum Novitates*, 1139, 1–3. [http://hdl.handle.net/2246/4786]
Trott, T.J. (2004) Cobscook Bay Inventory: A Historical Checklist of Marine Invertebrates Spanning 162 Years. *Northeastern Naturalist*, 11 (Special Issue 2), 261–324. [https://www.researchgate.net/publication/232692065]
https://doi.org/10.1656/1092-6194(2004)11[261:CBIAHC]2.0.CO;2
Verrill, A.E. (1873) Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Report of the U.S. Fish Commission, for 1871–1872, 1873, pp. 295–778, 39 pls. [*https://biodiversitylibrary.org/page/12087501]
Verrill, A.E. (1874) Explorations of Casco Bay by the U.S. Fish Commission in 1873. *Proceedings of the American Association for the Advancement of Science*, 22, 340–395, 6 pls. [https://books.google.com/books/about/Explorations_of_Casco_Bay_by_the_U_S_Fis.html?id=cI4uAAAAYAAJ&utm_source=gb-gplus-shareExplorations]
Verrill, A.E. (1881) New England Annelida Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Transactions of the Connecticut Academy of Science*, 4 (2), 285–324, pls. 3–12. [https://www.biodiversitylibrary.org/page/27743258]
Webster, H.E. (1879) The Annelida Chaetopoda of the Virginian coast. *Transactions of the Albany Institute,* 9, 202–269, pls. I–XI. [https://biodiversitylibrary.org/page/43082522]
https://doi.org/10.5962/bhl.title.11296
Webster, H.E. & Benedict, J.E. (1884) The Annelida Chaetopoda from Provincetown and Wellfleet, Massachusetts. *Report of the U.S. Fish Commission for 1881, 1884*, pp. 699–747, pls. 1–8. [https://books.google.com/books/about/The_Annelida_Chaetopoda_from_Provincetow.html?id=_XpIAAAAMAAJ]
Webster, H.E. & Benedict, J.E. (1887) The Annelida Chaetopoda from Eastport, Maine. *Reports of the U.S. Fish Commission for 188*, 707–755. [https://books.google.com/books/about/The_Annelida_Chaetopoda_From_Eastport_Ma.html?id=4C0tAAAAYAAJ]
Westheide, W. (1981) Interstitielle Fauna von Galapagos. XXVI. Questidae, Cirratulidae, Acrocirridae, Ctenodrilidae (Polychaeta). *Mikrofauna des Meeresbodens*, 82, 1–24.
Zhadan, A.E. (1998) Taxonomy of the genus *Scoloplos* (Orbiniidae) in the White, Barents and North Seas. *Zoologicheski Zhurnal*, 77 (2), 177–190. [in Russian]