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New species and records of *Caulleriella* (Annelida, Cirratulidae) from shelf and slope depths of the Western North Atlantic Ocean

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Abstract

Six species of *Caulleriella* (Cirratulidae), four new to science, are reported from continental shelf and slope depths of the western North Atlantic. The majority of new material was collected as part of deep-water reconnaissance and monitoring surveys along the 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 species include: *Caulleriella filiformia* **n. sp**., *C. nobska* **n. sp**., *C. pintada* **n. sp**., and *C. rodmani* **n. sp**. In addition, new records and comments are provided for *C. venefica* Doner & Blake, 2016 a widespread shelf species and *C*. sp., a potential new species represented by a few specimens from rocky nearshore New England habitats. The latter may be related to the enigmatic *C. fragilis* (Leidy, 1855). A review of known deep-water species of *Caulleriella* is provided.

Key words: Annelida, benthos, new species, New England, Delaware, New Jersey, North Carolina, South Carolina

Introduction

Cirratulid polychaetes are typically the dominant species of nearshore benthic communities along continental margins and also in some deep-sea locations. Cirratulids are classified and organized into bitentaculate and multitentaculate genera. While the multitentaculates are common in intertidal and nearshore shelf habitats, they are rare in deep water. In contrast, the bitentaculates are widespread in all habitats including the deep sea (Blake & Magalhães 2019). Recent studies have reported new species of Cirratulidae, mostly bitentaculates, from the Caribbean Sea, South America, the Southern Ocean and Antarctica, the Pacific Ocean, and Southeast Asia (Blake 1996, 2006, 2015, 2016, 2018, 2019; Blake & Dean 2019; Doner & Blake 2006; Elías & Rivero 2009, 2011; Magalhães & Brock 2013). Several of these studies are from offshore deep-water surveys.

In the present study bitentaculate cirratulids of the genus *Caulleriella* Chamberlin, 1919 are reported from reconnaissance and monitoring surveys along the U.S. Atlantic coast from New England to the Carolinas. Four new species of *Caulleriella* are described; three are from deep-sea continental slope habitats off the U.S Atlantic coast and one is from nearshore benthos in New England. In addition, new records and morphological details are recorded for *C. venefica* Doner & Blake, 2006 from nearshore and shelf habitats.

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), during the 1980s. These studies were intended to evaluate the potential impact of oil and gas exploration and development on Georges

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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).

Additional samples from the northeastern United States from Massachusetts to New Jersey accumulated from various local collections or 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 Museum of Comparative Zoology (MCZ), Harvard University.

The MMS samples were collected using 300-µm-mesh sieves. These fine-mesh sieves resulted in the retention of fragile threadlike specimens from deep-water that otherwise would have been lost or damaged.

Morphological observations. Specimens were examined using a Wild M-5 stereomicroscope and a Zeiss RA research microscope equipped with phase contrast optics. Photomicrographs were taken with a Nikon D7100 camera mounted on both the stereo- and compound microscopes. For observation, specimens were first stained with an aqueous solution of Shirlastain A to highlight difficult-to-see surficial morphology. Some specimens were stained with a saturated solution of Methyl Green (MG) in 70% ethyl alcohol (ETOH) in order to identify staining patterns of subdermal glands evident on some species. Line drawings were first sketched in pencil using a drawing tube or *camera lucida* on the Zeiss RA and later transferred to Dura-Lar® matte film and inked.

Additional specimens were prepared for scanning electron microscopy (SEM) by dehydration in an ascending ETOH series of 70–95% for 10 min each, followed by three changes of 100% ETOH for 15 min each. Specimens were critically point dried with a Samdri 795 Critical Point Dryer, mounted on aluminum stubs, coated with gold using an EMS-550 Sputter coater, and viewed with a Hitachi S-2460N SEM or FEI Quanta 250 SEM at Hofstra University in Dr. Jason Williams' laboratory.

Abbreviations used on figures: anC, anal cirrus; br, branchiae; dCr, dorsal crest; dT, dorsal tentacle; eso, esophagus; int, intestine; mo, mouth; neP, neuropodia; noP, notopodia; nuO, nuchal organ; per, peristomium; phrx, pharynx; pr, prostomium; prob, proboscis; pyg, pygidium; Set, setiger; vGr, ventral groove.

Results

Family Cirratulidae Ryckholt, 1851

Diagnosis. Body elongate with numerous short segments; not divided into distinct regions but anterior and/or posterior segments sometimes expanded and crowded. Prostomium narrow and conical or broad and wedge shaped, without appendages; eyespots present or absent; paired dorsolateral nuchal organs present. Peristomium achaetous, smooth or with two or more distinct annuli. Grooved dorsal tentacles arise as a single pair or as multiple groups of filaments on posterior margin of peristomium or on one or more anterior setigerous segments. Branchiae long, filamentous, usually occurring over numerous segments. Parapodia biramous with rudimentary podial lobes. Setae simple, including capillaries, acicular spines or bidentate hooks. Pygidium a simple lobe sometimes with sub-anal disk, or terminal cirri. Pharynx ventral, unarmed. Sexual and asexual reproduction may occur.

Genus Caulleriella Chamberlin, 1919

Type species: *Cirratulus viridis* Langerhans, 1881. Original designation by Chamberlin 1919.

Diagnosis. (after Blake & Magalhães 2019). Prostomium elongate, conical to pointed; peristomium elongated to short, dorsal tentacles usually beginning anterior to setiger 1. Middle body segments not beaded; parapodia often with noto- and neuropodia widely separated laterally. Modified setae including capillaries and bidentate, crotchet-like hooks, not arranged into modified cinctures. In some species, unidentate hooks may occur in some regions of the body in addition to bidentate hooks. Pygidium either a simple conical lobe or with one or two anal cirri.

Remarks. To date, approximately 45 species of *Caulleriella* are known (Read & Fauchald 2020; Blake & Magalhães 2019). The current definition of the genus essentially dates from Blake (1996), who, among other things, determined that in addition to having bidentate hooks, most species of *Caulleriella* differ from other bitentaculate

cirratulids in having the noto- and neuropodia widely separated from one another along the body; this generalization, however, does not hold up in species that have long, narrow threadlike bodies.

Bidentate hooks. Three types of bidentate hooks have been reported for species of *Caulleriella*. (1) One type is a typical bidentate crotchet, found in most species, where the apical tooth appears to emerge directly from the end of shaft with no hood or flange along the shaft. This type of hook is characteristic of most species. (2) A second type of hook has a hood or flange on the convex side of the shaft that extends apically forming the apical tooth. This type of seta was first described for *C. alata* by Southern (1914). Although not stated, Southern's name for the species appears to be derived from *alatus*, Latin for winged and refers directly to the transparent hood on the convex side of the shaft that merges with the apical tooth. These 'alate' hooks have been reported in nine species of *Caulleriella* (see list in Discussion section) and likely occur in others where details of the bidentate teeth are not well described. (3) A third type of hook has a transparent hood that extends from the main fang to the concave side of the shaft, similar to hoods found in some spionids and paraonids. This type of hook is only known from *C. bathytata* Blake, 2019 an abyssal species from the Pacific Ocean.

The nature of the 'alate' hooks is not well understood. There is some evidence that the so-called hood or flange on the convex side of the shaft is actually an artifact of the shaft having a groove on the lateral or convex side and that a change in thickness along the shaft produces a lighter or more transparent area that is the 'hood' observed in light microscopy. Likewise, details of 'alate' hooks suggest that the apical tooth may actually be a projecting ridge or an extension of the shaft that only appears as a tooth when observed in lateral view. *Caulleriella kacya*e Blake, 2018 from the Weddell Sea, Antarctica has a broad accessory sheath on the convex side of the shaft that terminates on the tip of the shaft as a ridge above the main fang; in some views this sheath appears to be divided producing a tridentate appearance (Blake 2018). The 'alate' bidentate hooks of *C. pacifica* E. Berkeley, 1929 were illustrated with SEM by Magalhães & Bailey-Brock (2015). The convex side of the curved shaft has a distinct channel or groove that could appear as the hood in light microscopy at certain angles. In addition, the apical tooth is short and appears to be a low ridge. In contrast the SEMs of the bidentate hooks of *C. venefica* Doner & Blake, 2006 (see Figure 8 in *C. venefica* section below) show no evidence of a groove along the shaft and the apical tooth is narrow and pointed. These observations suggest that an in-depth investigation of these hooks may yield additional characters useful in species delimitation.

Parapodia. Most species of *Caulleriella* have the noto- and neuropodia widely separated along the body (Blake 1996; Blake & Magalhães 2019); in some species such *C. quadrata* Blake & Dean, 2019, the podia are so widely separated they appear at four corners of the body when viewed in cross section (Blake & Dean 2019). This generalization, however, is not as obvious in deep-water species where the bodies are long and thin; however, even in these taxa, the podial lobes are distinctly separated from one another rather than being close as in species of *Tharyx*.

Bathymetry. Recent studies have added numerous new species of *Caulleriella* and expanded descriptions of others (Blake 2018, 2019; Blake & Dean 2019). However, only five of the 45 previously known species of *Caulleriella*, four from around Antarctica and one from the abyssal Pacific, are known from depths of 500 m or greater (Blake 2018, 2019): *C. antarctica* (Hartman, 1978) (1120 m), *C. bathytata* Blake, 2019 (4877 m), *C. eltaninae* Blake, 2018 (870 m), *C. fimbriata* Blake, 2018, (1884 m), and *C. kacyae* Blake, 2018 (1035 m). Three additional deep-water and one shallow water species of *Caulleriella* are newly described in the present study bringing the number of known species for the genus to 49 of which only eight occur in deep water. Additional records and descriptive comments for *Caulleriella venefica*, a widespread nearshore and continental shelf species along the U.S. Atlantic coast, are also provided. In addition several specimens of an additional small species of *Caulleriella*, are reported from rocky habitats in Cape Cod Bay. These specimens are not named but may be conspecific with or related to *C. fragilis* (Leidy, 1855), which has not been described since the original report. The following species are treated in this study.

1. *Caulleriella filiformia* **n. sp**.
2. *Caulleriella nobska* **n. sp.**
3. *Caulleriella pintada* **n. sp**.
4. *Caulleriella rodmani* **n. sp.**
5. *Caulleriella venefica* Doner & Blake, 2006
6. *Caulleriella* sp.

***Caulleriella filiformia* new species**
Figures 1–2
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Caulleriella sp. B: Maciolek *et al.* 1987a: D-2 (in part); 1987b: D-2 (in part); Hilbig 1994: 940 (in part)
Caulleriella sp. 3: Blake *et al.* 1987: C-2 (in part); Hilbig 1994: 940 (in part).

Material examined. (*48 specimens*) **Southeastern USA, off Charleston, South Carolina, U.S. South ACSAR Program,** coll. J.A. Blake, Chief Scientist. **Sta. 15**: Cruise SA-5, Rep. 2, 18 Sep 1985, 32°11.99′N, 76°42.23′W, 1991 m, **holotype** (USNM 1642576); Rep. 1, 18 Sep 1985, 32°12.00′N, 76°42.23′W, 1988 m, 2 **paratypes** (USNM 1642575); Rep. 3, 18 Sep 1985, 32°11.97′N, 76°42.24′W, 1991 m, 1 **paratype (**USNM 1642577); Cruise SA-4, Rep. 1, 16 May 1985, 32°12.02′N, 76°42.18′W, 1993 m, 1 **paratype (**USNM 1642572); Rep. 2, 16 May 1985, 32°12.05′N, 76°42.18′W, 1991 m, 4 **paratypes (**USNM 1642573); Rep. 3, 16 May, 1985, 32°10.74′N, 76°42.93′W, 2003 m, 2 **paratypes** (USNM 1642574).—**Off New England, U.S. North Atlantic ACSAR Program,** coll. G.W. Hampson, Chief Scientist. **Sta. 5**: Cruise NA3, Rep. 1, 04 Jul 1985, 40°05.11′N, 67°29.84′W, 2058 m, (3, USNM 1642578); Cruise NA4, Rep 2, 25 Nov 1986, 40°05.09′N, 67°29.84′W, 2071 m (2, USNM 1642579); Rep. 3, 25 Nov 1985, 40°05.07′N, 67°29.81′W, 2071 m (1, USNM 1642580); Cruise NA5, Rep. 1, 29 Apr 1986, 40°05.06′N, 67°29.94′W, 2052 m (2, USNM 1642581); Rep. 3, 29 Apr 1986, 40°05′.01′N, 67°29.90′W, 2085 m (2, USNM 1642582); Cruise NA6, Rep. 1, 26 Jul 1986, 40°05.07′N, 67°29.08′W, 2063 m (1, USNM 1642583); Rep. 3, 26 Jul 1986, 40°05.09′N, 67°29.67′W, 2055 m (1, USNM 1642584). **Sta. 6**: Cruise NA2, Rep. 1, 29 Apr 1985, 40°05.04′N, 67°29.99′N, 2108 m (1, USNM 1642585); Rep. 2, 29 Apr 1985, 40°05.03′N, 67°29.13′N, 2108 m (1, USNM 1642586); Rep. 3, 29 Apr 1985, 40°05.06′N, 67°29.13′N, 2107 m (1, USNM 1642587); Cruise NA5, Rep. 2, 30 Apr 1986, 40°05.11′N, 67°29.21′N, 2110 m (2, USNM 1642588); Rep. 3, 01 May 1986, 40°05.10′N, 67°29.13′W, 2109 m (1, USNM 1642589). **Sta. 8**: Cruise NA2, Rep. 1, 28 Apr 1985, 40°10.24′N, 67°37.16′W, 2185 m (1, USNM 1642590); Cruise NA4, Rep. 3, 25 Nov 1985, 40°10.25′N, 67°37.41′N, 2182 m (4, USNM 1642591); Cruise NA6, Rep. 2, 27 Jul 1986, 40°10.23′N, 67°37.25′N, 2193 m (2, USNM 1642592); Rep. 3, 27 Jul 1986, 40°10.21′N, 67°37.28′N, 2188 (3, USNM 1642593). **Sta. 14**: Cruise NA2, Rep. 1, 05 May 1985, 39°40.91′N, 70°54.17′W, 2095 m (4, USNM 1642594); Rep. 2, 5 May 1985, 39°40.93′N, 70°54.21′W, 2092 m (1, USNM 1642595). **Sta. 15**: Cruise NA2, Sta. 15, Rep. 2, 5 May 1985, 39°40.07′N, 70°54.27′W, 2145 m (1, USNM 1642596); Rep. 3, 6 May 1985, 39°40.10′N, 70°54.31′W, 2140 m. (1, USNM 1642597).—**Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR, Program,** coll. R. Petrecca, Chief Scientist. Mid-6, **Sta. 2**: Rep. 3, 13 Nov 1985, 38°35′.83′N, 72°53.91′W, 1994 (3, USNM 1642598).—**Off New Jersey, U.S. EPA DWD-106 Site Survey**, R. Petrecca, Chief Scientist: **Sta. G**, Rep. 3, 18 Nov 1985, 38°55.60′N, 72°02.62′W, 2509 m (1, MCZ 161720).

Description. A long, thin, threadlike species (Figs. 1A–C, 2A, C–E); holotype complete, 9.1 mm long, 0.16 mm across anterior segments and 0.12 mm across far posterior segments, for 58 setigers; one complete paratype (USNM 1642576), 8 mm long for 60 setigers. Body generally cylindrical throughout, with no evidence of dorsal or ventral grooves. All segments moniliform to some extent (Fig. 2A, C–F); 5–8 anteriormost setigers relatively short, constituting thoracic region (Figs. 1A–B, 2A–B), about 1.5–2.0 times as wide as long, then segments becoming longer, about 1.5 times as long as wide (Fig. 1A, 2A, C–E); posterior segments becoming shorter, rounded, about as long as wide, weakly moniliform (Figs. 1C, 2F), continuing to pygidium bearing two narrow anal cirri (Figs. 1A, 2F–G). Individual segments along most of body transparent, with intestinal track and coelom clearly apparent (Fig. 2A–F); heart body evident in anteriormost segments of some specimens; epidermis of anterior and middle body segments lumpy, but not producing transverse annulations. Color in alcohol opaque white, with no pigment apparent on body.

Pre-setiger region narrow, about 2.3 times as long as wide, about as long as first four setigers (Figs. 1A–B, 2A–B). Prostomium triangular, tapering to narrow rounded apex (Fig. 1A–B); eyespots absent; nuchal organs not observed. Peristomium elongate, narrow, with weak lateral grooves in anterior one-third, not producing annular rings (Figs. 1A, 2A); holotype with grooves producing lateral pockets (Fig. 1B). Dorsal tentacles widely spaced, arising from near posterior border of peristomium (Fig. 1A–B); first pair of branchiae arising immediately posterior to dorsal tentacles on peristomium; second pair of branchiae arising on posterior border of setiger 1, dorsal to notosetae (Fig. 1A–B). Subsequent segments with branchiae in similar position; branchiae long, thin, present along most of body to near posterior end.

Parapodia reduced; anterior segments with weakly developed podial lobes from which setae arise. Noto- and neuropodial setal fascicles distinctly separated from one another anteriorly, becoming widely separated from one

another in middle and posterior setigers. Noto- and neurosetae of anteriormost setigers with 5–8 long capillaries per fascicle; notoacicular bidentate hooks first present from setigers 7–10 (setiger 8 in holotype); neuroacicular hooks similar in distribution (beginning setiger 7 in holotype). Hooks mostly replacing capillaries, 1–3 per fascicle at first, increasing to 4–5 in middle and posterior segments, reduced to 1–3 in far posterior segments. Hooks with a thick, slightly curved shaft tapering to thick main fang surmounted by a thin apical tooth as an extension of an 'alate' flange on convex side of shaft (Figs. 1D–E, 2H–I); neuropodial hooks shorter and thicker (Fig. 1D) than notopodial hooks (Fig. 1E). Hooks of far posterior segments becoming longer, less curved, prominently visible on segments anterior to pygidium.

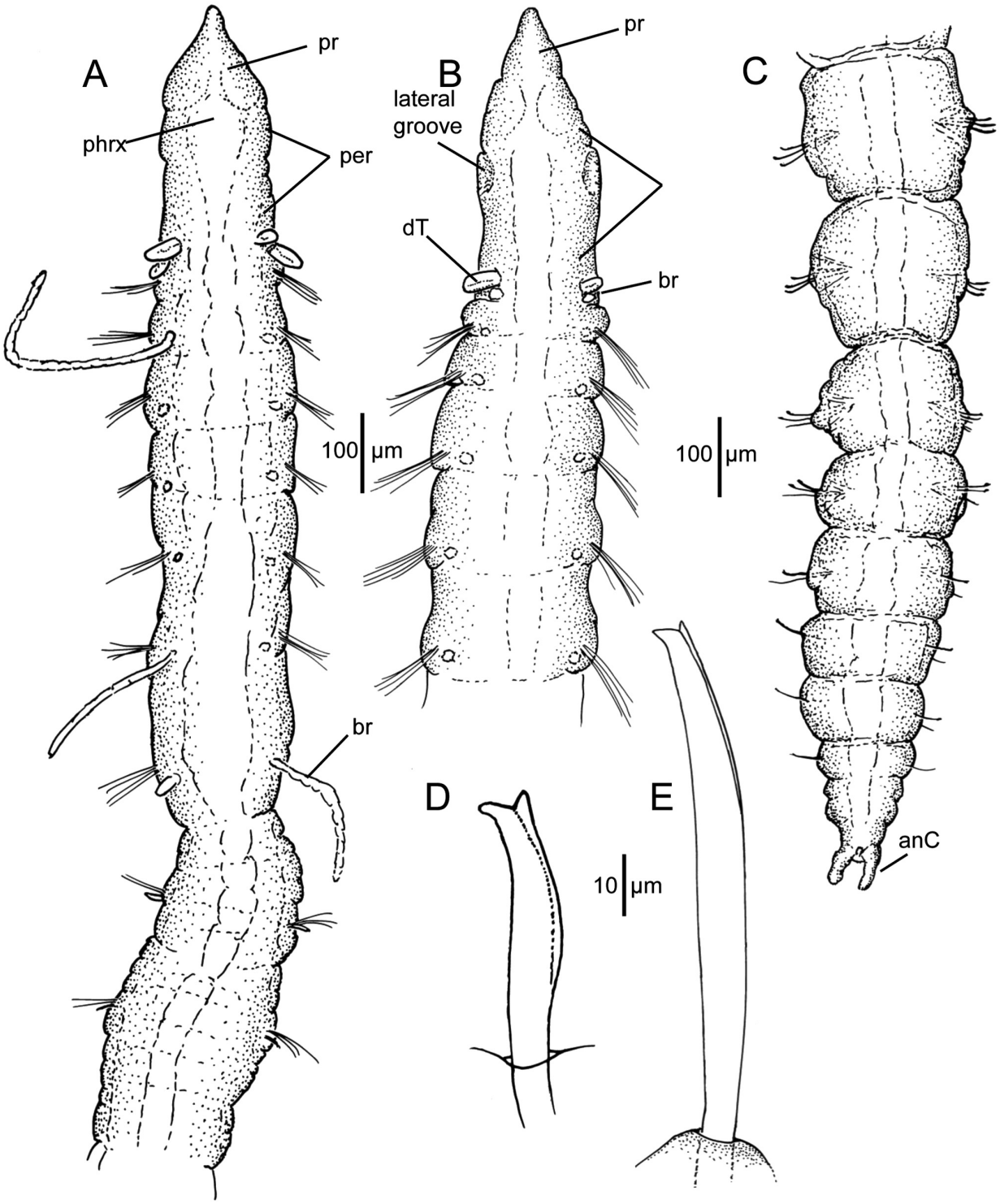

FIGURE 1. ***Caulleriella filiformia*** **n. sp**. Paratype (USNM 1642572); A, anterior end, dorsal view: Holotype (USNM 1642576): B, anterior end, dorsal view; C, posterior end, dorsal view; D, neuropodial hook; E, notopodial hook.

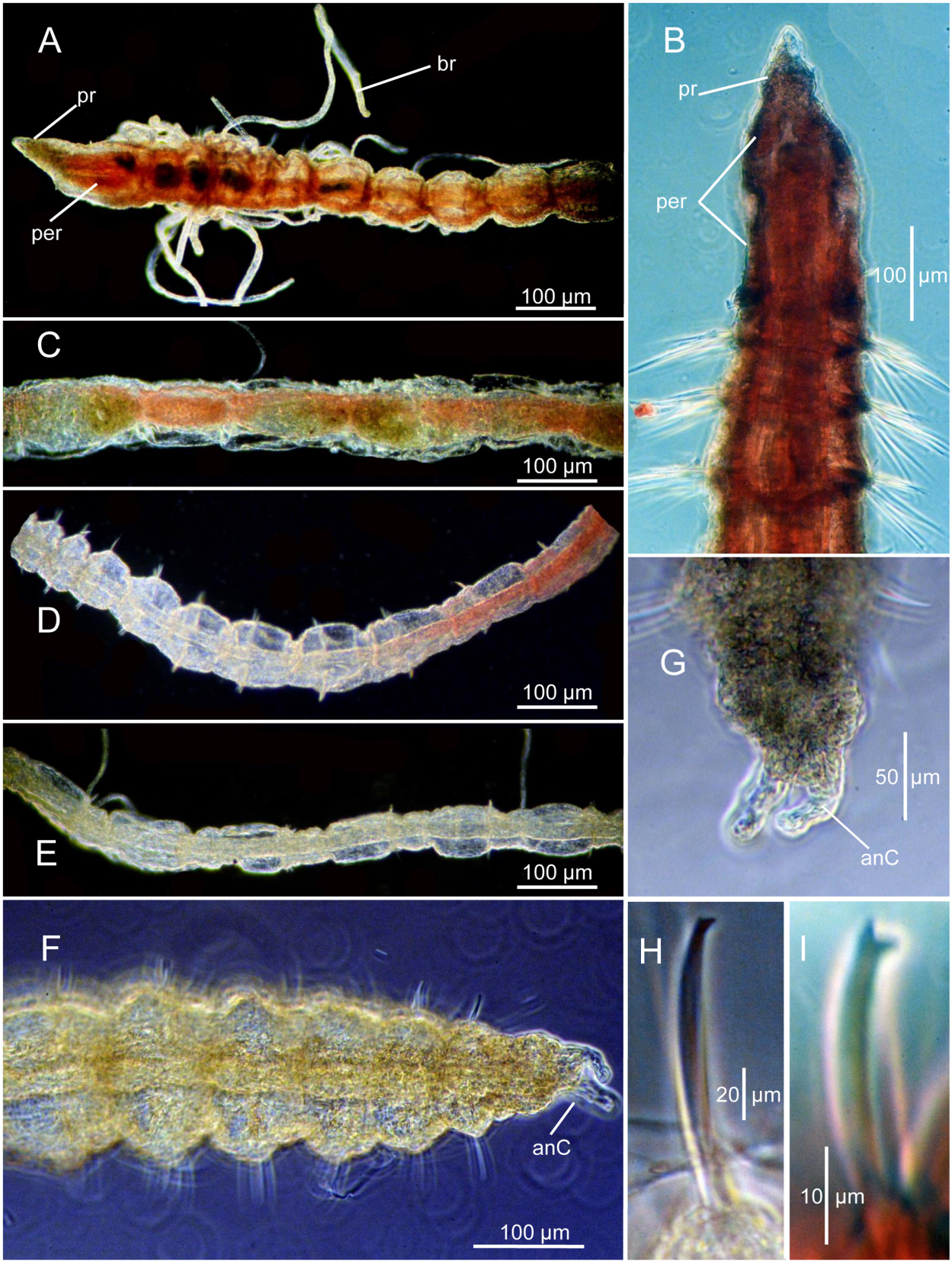

FIGURE 2. ***Caulleriella filiformia* n. sp**. A, Anterior end, left lateral view; B, Anterior end, dorsal view; C, mid-body setigers, dorsal view; D, transition from mid-body to posterior setigers, dorsal view; E, posterior setigers, dorsal view; F, far posterior setigers with pygidium; G, pygidium dorsal, view; H, notopodial hook; I, neuropodial hook. A, G, I (Sta. 15, SA-4, Rep 2, USNM 1642573); B–E, H (USNM 1642577); F, holotype (USNM 1642576). Stained with Shirlastain A.

Pygidium with two short anal cirri (Figs. 1C, 2F–G); one or both sometimes missing, but scars or stubs usually present.

Variability. The most obvious variability among the material is with the beaded or moniliform segments. In some specimens all segments are at least weakly moniliform with anterior segments short and rounded, middle segments elongated and posterior segments again short and rounded. In other specimens the anterior most segments while distinctly separated from one another are weakly crowded, but transition to moniliform segments along most of the body. In other specimens the middle body segments and some posterior segments appear to be stretched or pulled out, thus obscuring the moniliform shape. Finally, the middle segments of other specimens have an intestinal fold that when filled with particles, elevates the dorsum of individual segments thus exaggerating the moniliform appearance.

Methyl Green staining. No pattern.

Remarks. *Caulleriella filiformia* **n. sp**. is distinctive among species of *Caulleriella* in having a long, thin threadlike body with most specimens having moniliform or bead-like segments along nearly the entire length; segments are short and beadlike in anterior and posterior segments, longer in middle segments and stretched, but still weakly moniliform in shape.

Caulleriella filiformia **n. sp**. is closely related to *C. rodmani* **n. sp**. (see below) with which it may occur. In *C. filiformia* **n. sp**. the first pair of branchiae arise lateral to the dorsal tentacles on the posterior margin of the peristomium; the second pair and subsequent branchiae occur on setiger 1 dorsal to the notosetae. In contrast, the first pair of branchiae of *C. rodmani* **n. sp**. arise dorsal to the notosetae on setiger 1. Rounded or moniliform segments typically occur along the entire of body of *C. filiformia* **n. sp**., while only the first 3–5 thoracic segments of *C. rodmani* **n. sp**. are rounded. Two short anal cirri occur on the pygidial segment of *C. filiformia* **n. sp**., whereas the pygidium of *C. rodmani* **n. sp.** is rounded and lacks anal cirri. One or two of the anal cirri may be damaged or broken, but scars or stubs are usually apparent when stained with Shirlastain A. The bidentate hooks of *C. filiformia* **n. sp**. have an 'alate' flange on the convex side that forms the apical tooth, whereas in *C. rodmani* **n. sp.**, there is no flange and the apical tooth emerges directly from the shaft.

Biology and Habitat. One paratype (USNM 1642573) has a few large eggs in posterior parapodia that measure up to 350 μm in the longest dimension; the large size suggesting direct development. Sediments associated with Sta. 15, the type locality off Charleston, SC, were sampled on only two surveys (Blake *et al*. 1987). Samples were collected in water depths of 1944–2003 m: SA-4 (May 1985) and SA-5 (Sep 1985). The sediments consisted of 64.1% sand and 35.9% silt + clay on SA-4 and 62.3% sand and 37.7 % silt + clay on SA-5 (Blake *et al.* 1987). Thus, the sediments were about 2/3 sand and 1/3 silt + clay. The fauna was dominated by *Microrbinia linea* Hartman, 1965 a common threadlike orbiniid polychaete that was often the most abundant invertebrate in benthic samples in 2000–3000 m depths throughout U.S. South Atlantic study area (Blake *et al.* 1987; Blake 2021). *Caulleriella filiformia* **n. sp**. ranked sixth out of the 20 most abundant taxa, but comprised only 2.8 % of the total fauna (Blake & Grassle 1994). Sites off New England where *C. filiformia* **n. sp**. was collected were in depths of 2055–2193 m.

Etymology. The epithet *filiformia* is an adjective derived from the Latin, *filum*, a thread, in reference to the thin, threadlike body of this species.

Distribution. U.S. Atlantic continental slope, off New England to the Carolinas, 1944–2185 m.

Caulleriella nobska new species

Figure 3

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Material examined. (*71 specimens*) **Northeastern USA, off Nobska Point, Woods Hole, Massachusetts**, coll. Oct 1975, N.J. Maciolek, 41°30.86′N, 70°39.36′W. ca. 5–10 m, **holotype** (MCZ 161683), 70 **paratypes** (MCZ 161684).

Description. A moderately sized species, with long narrow body widest in middle segments; holotype complete, with 88 setigers, 21.5 mm long, 0.3 mm wide across anterior setigers, 0.44 mm wide across middle setigers, narrowing again in posterior setigers. Body rounded dorsally, flattened ventrally with shallow mid-ventral groove extending from peristomium to posterior segments (Fig. 3A). Color in alcohol opaque white to light tan; most specimens with light brown cast in middle segments; some specimens with dark brown spots or short bands in variable patterns along body, but not consistent.

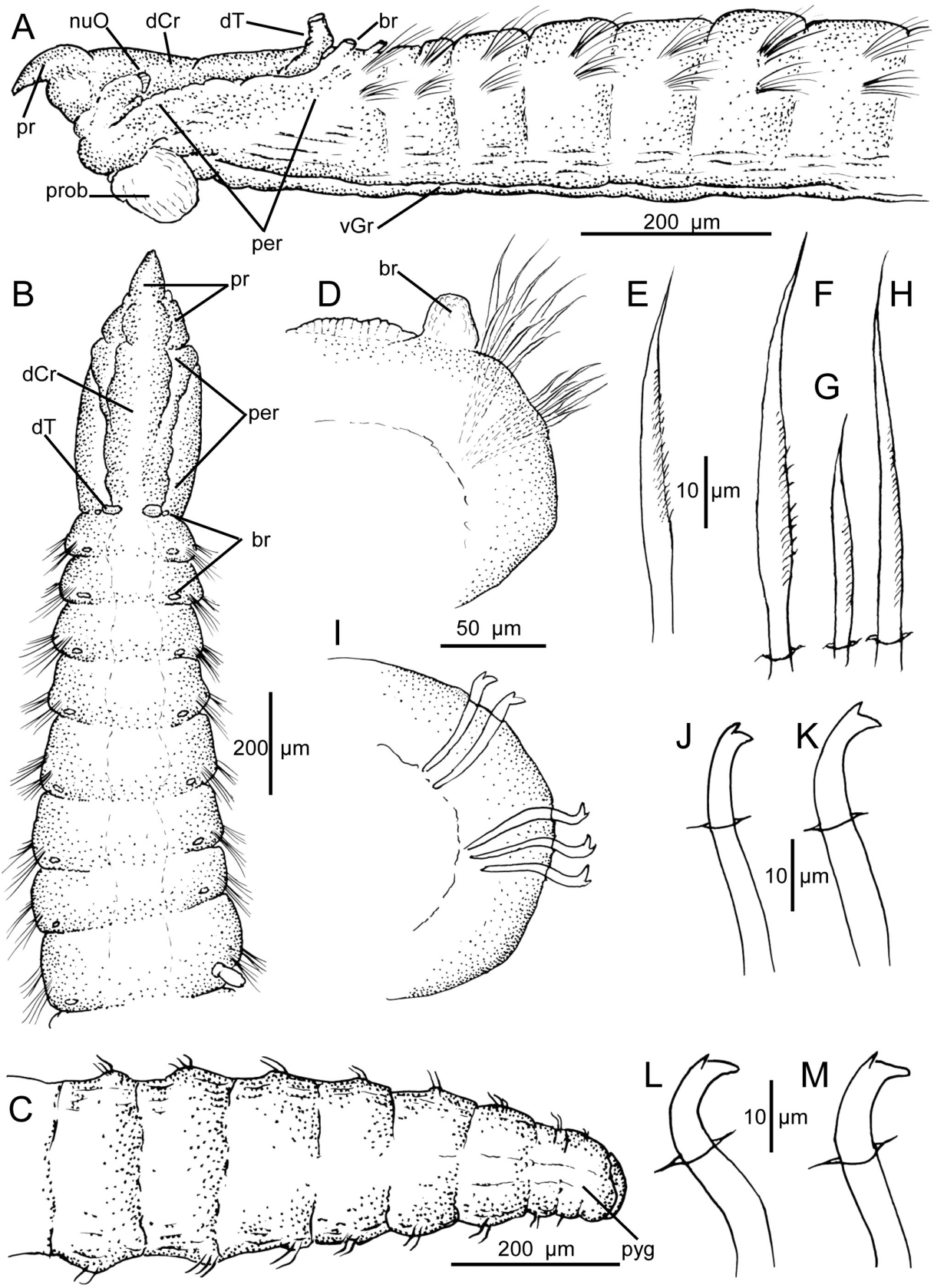

FIGURE 3. ***Caulleriella nobska*** **n. sp**. A, anterior end, left lateral view; B, anterior end, dorsal view; C, posterior end, dorsal view; D, setiger 4, anterior view; E, anterior notopodial capillary seta; F–H, anterior neuropodial capillaries; I, middle body setiger, anterior view; J–K, notopodial bidentate hooks; L–M, neuropodial hooks. A–C, holotype (MCZ 161683); D–M, paratypes (MCZ 161684).

Pre-setiger region long, narrow, as long as first 3½ setigers (Fig. 3A–B). Prostomium triangular in dorsal view, tapering to pointed tip (Fig. 3B), relatively narrow in lateral ventral view (Fig. 3A); nuchal organs semicircular grooves on lateral posterior margin; eyespots absent. Peristomium long, narrow, not divided but with well-developed broad dorsal crest (Fig. 3A–B); dorsal tentacles arise from posterior margin (Fig. 3A–B); first branchiae lateral to dorsal tentacles (Fig. 3A–B); second pair of branchiae dorsal to notosetae on setiger 1 and in same location on subsequent setigers (Fig. 3B).

Parapodia reduced, with no distinct podia or postsetal lobes apparent; setae arising directly from body wall. Noto- and neuropodia not widely separated as in related species. Notosetae of first 10–12 setigers all capillaries; hooks first present from setigers 11–13 (13 in holotype). Neurosetae of first 9–10 setigers all capillaries; hooks first present from setigers 10–11 (11 in holotype). Capillaries of both noto- and neuropodia numbering about 8–10 in larger specimens, arranged in two rows with capillaries of first row shorter and thicker than capillaries of second row; notosetae longer than neurosetae (Fig. 3D). Capillaries with broad blades and distinct fimbriated edge with individual fibrils often separated producing the appearance of a serrated edge (Fig. 3E–H). Hooks accompanied by 1–2 capillaries for 1–3 segments, then capillaries entirely absent along body in both noto- and neuropodia (Fig. 3I). Hooks numbering one per noto- or neuropodium through first third of body, then increasing to two and three hooks in middle and posterior setigers. Hooks in noto- and neuropodial fascicles directed toward one another, vis-à-vis (Fig. 3I). Individual hooks with recurved shaft tapering to distinct bidentate apex; main fang directed at about 45° to shaft with short pointed apical tooth; hood and sheath absent. Hooks of neuropodia appearing slightly thicker and more sigmoidally curved (Fig. 3L–M) than those of notopodia (Fig. 3J–K).

Pygidium with two simple lobes; anal cirri absent (Fig 3C).

Methyl Green staining. No pattern.

Remarks. Unlike most shallow-water species of *Caulleriella*, *C. nobska* **n. sp**. has a long narrow body lacking a distinct separation of the thorax and abdomen. The peristomium is unusually long and bears a prominent dorsal crest. In addition, the noto- and neuropodia are only moderately separated from one another. However, the nature of the recurved bidentate hooks is similar to other species where a hood or sheath is lacking.

Caulleriella nobska **n. sp**. is most similar to *C. venefica*, another species from the northeastern United States that is widespread on the continental shelf. Both species have a pointed prostomium, an elongate, smooth peristomium with a dorsal crest, and bidentate hooks lacking a crest or sheath. *Caulleriella nobska* **n. sp**. differs from *C. venefica* in having a shorter prostomium, up to three hooks in posterior neuropodia instead of two, and no anal cirri on the pygidium instead of two cirri. In addition, the bidentate hooks of *C. venefica* as illustrated by Doner & Blake (2006) and as observed in this study, have the main fang at a more acute angle than the 45° angle observed in *C. nobska* **n. sp**. and *C. venefica* may have a single thin capillary seta accompanying the hooks in middle and posterior setigers instead of capillaries being entirely absent in posterior setigers of *C. nobska* **n. sp**.

Etymology. The epithet is from the collecting locality off Nobska Point, a promontory in Woods Hole, Massachusetts and the location of a historic lighthouse.

Distribution. Massachusetts, shallow subtidal.

Caulleriella pintada new species

Figures 4–5

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Caulleriella sp. 3: Blake *et al.* 1987: C-2 (in part); Blake & Grassle, 1994: 854–855; Hilbig 1994: 940 (in part).

Material examined. (*83 specimens*). **Southeastern USA, off Charleston, South Carolina,** U.S. South ACSAR Program, J.A. Blake, collector: **Sta**. **14A**: Cruise SA-5, R/V *Gyre*, Rep. 1, 20 Sep 1985, 32°32.25′N, 77°15.24′W, 600 m **holotype** (USNM 1642599), 40 **paratypes** (USNM 1642600); Rep. 2, 20 Sep 1985, 32°32.26′N, 77°15.29′W, 605 m, 21 **paratypes** (USNM 1642601); Rep. 3, 20 Sep 1985, 32°32.22′N, 77°15.31′W, 605 m, 20 **paratypes** (USNM 1642602).

Description. A moderately large, elongate, threadlike species with body generally narrow throughout (Figs. 4A–B; 5A, C); some groups of anterior setigers variably inflated, but overall consistently narrow throughout, narrowest in far posterior setigers. Holotype complete, 11.2 mm long, 0.4 mm wide across anteriormost segments, about 0.2 mm wide in mid-body and posterior segments, with 67 setigerous segments. Anterior and middle setigers relatively

short, about twice as wide as long (Fig. 4B); posterior setigers about as wide as long, weakly moniliform (Fig. 5F); some specimens with eggs in middle segments (Fig. 5G). Venter with shallow groove in anterior and middle segments, sometimes outlined with dark pigment (Fig. 4A); dorsal surface rounded throughout. Color in alcohol opaque white to light tan; larger specimens with dark brown to black pigment in variable patterns, sometimes outlining parapodia or ventral groove; pigment intense on some specimens including holotype (Figs. 4A, D, 5A), lighter on others; smallest specimens generally not exhibiting pigment.

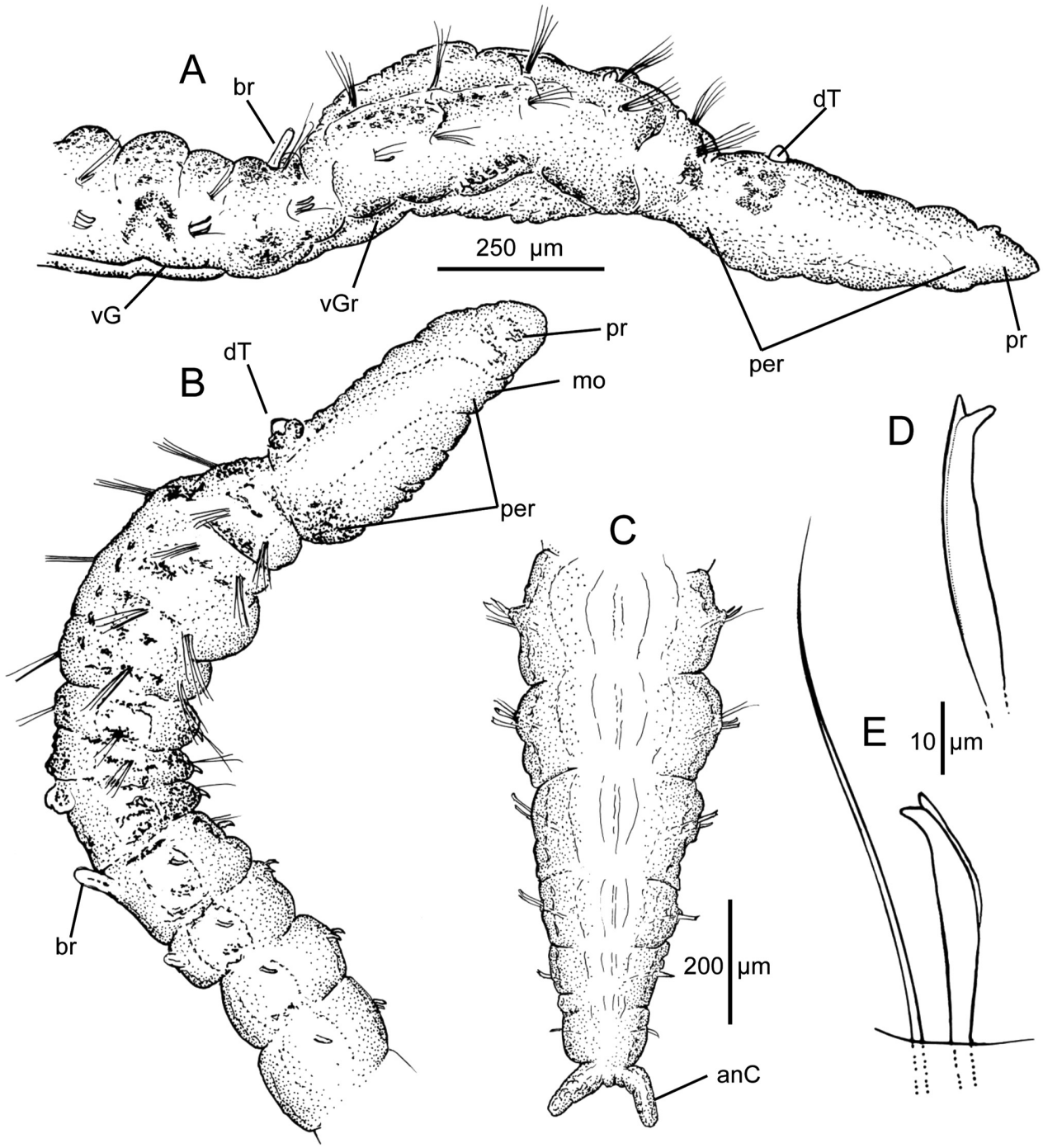

FIGURE 4. ***Caulleriella pintada*** **n. sp**. A, Anterior end, right lateral view; B, anterior end, dorsolateral view; C, posterior end, dorsal view; D, notopodial hook; E, neuropodial hook and capillary. A, C, holotype (USNM 1642599); B, D–E, paratype (USNM 1642600).

Pre-setiger region elongate, cylindrical, up to as long as first five setigers in holotype and largest paratypes (Figs. 4A–B, 5A, C); some specimens with peristomium medially inflated (Fig. 5C–D). Prostomium conical, tapering to bluntly rounded apex (Figs. 4A–B, 5A, C–D); eyespots absent; nuchal organs low mounds at posterior-lateral

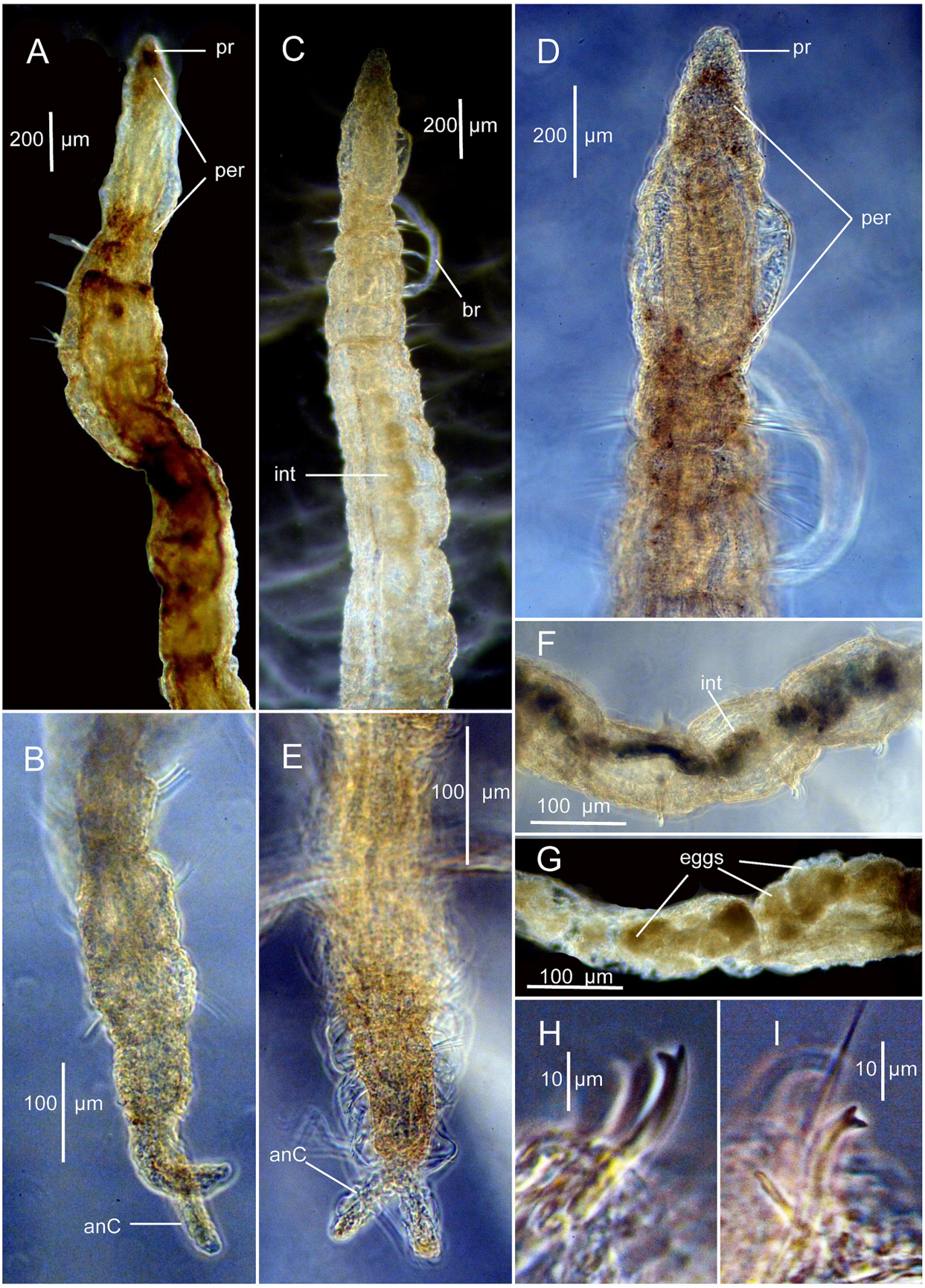

FIGURE 5. ***Caulleriella pintada*** **n. sp**. A, anterior end dorsolateral view; B, posterior end, lateral view; C–D, anterior end dorsal view; E, posterior end dorsal view; F, posterior segments, dorsal view; G, middle body segments with eggs; H, neuropodial hooks; I, notopodial hook and capillary. A–B, holotype (USNM 1642599); C–I, paratypes (USNM 1642600).

margins prostomium. Peristomium indistinctly separated from prostomium, with no visible annular rings, entire surface smooth, or wrinkled in larger specimens (Figs. 4A–B, 5A, C–D); paired dorsal tentacles arising from near posterior margin (Fig. 4A–B). First branchiae arising dorsal to notosetae on setiger 1; subsequent branchiae in similar position. Most branchiae missing or limited to scars, when retained branchiae long and thin.

Parapodia reduced, weakly developed podia present only in anterior-most setigers, thereafter no podial lobes or lamellae observed, with setae arising directly from body wall. Notosetae of anteriormost setigers with 4–5 capillaries; notoacicular bidentate hooks first present from setiger 8 in holotype; with one hook at first, increasing to two hooks through mid-body segments, usually accompanied by 1–2 thin capillaries; posterior setigers with 2–3 hooks and 1–2 thin capillaries. Neuropodia with 4–5 long capillaries on setigers 1–4, replaced by bidentate hooks from setiger 5; one hook at first increasing to 2–3 hooks through mid-body segments; with 3–5 hooks in posterior setigers; neuropodial hooks accompanied 1–2 thin capillaries. Hooks in noto- and neuropodial fascicles directed toward one another, vis-à-vis. Individual hooks with relatively thick shaft, weakly curved, tapering to blunt-tipped main fang directed at about 45° with shaft (Figs. 4D–E, 5H–I); apical tooth smaller, point conforming to curve of shaft, directed forward and appearing to be an extension of an 'alate' flange or hood on the convex side of shaft (Fig. 4D–E). Neuropodial hooks heavier and shorter (Figs. 4E, 5H) than notopodial hooks (Figs. 4D, 5I).

Pygidium a simple lobe bearing two ventral anal cirri (Figs. 4C, 5B, E).

Methyl Green staining. No pattern.

Remarks. Specimens identified as *Caulleriella* sp. 3 during the ACSAR program actually include two different species: (1) *C. pintada* **n. sp.**, which appears to be restricted to sandy sediments at 600 m off South Carolina, and (2) *C. filiformia* **n. sp.**, which occurred in fine-grained sediments along the 2000 m isobath off North and South Carolina and off New England.

Caulleriella pintada **n. sp**. is unusual among species of *Caulleriella* in the nature of the elongate narrow peristomium that consists of a single ring that is distinctly wrinkled and pigmented in larger specimens. The body has brown to black pigment in variable patterns along the body; this pigment is intense on the holotype and most paratypes. This species, like *C. filiformia* **n. sp.**, has bidentate setae with an apical tooth that is an extension of an 'alate' hood or flange on the convex side of the shaft, but differs in having the elongate pre-setiger region, branchiae from the posterior margin of the peristomium instead of setiger 1, and distinct pigmentation.

Biology and Habitat. Cruise SA-5, was the only ACSAR survey on which samples were collected at Sta. 14A. The results presented by Blake *et al*. (1987) and Blake & Grassle (1994) indicate that *Caulleriella pintada* **n. sp**. (as *Caulleriella* sp. 3) was the most abundant invertebrate species encountered at the site with 14% of the total number of individuals. The sediment consisted of 94–95% sand with low water content. The coarse grain size of the sediments at Sta. 14A appears to be important for this species because it was not encountered at other 600 m stations off Cape Lookout and Cape Hatteras where the sediments have a high silt + clay content. Several paratypes were mature females with eggs about 100–110 μm in diameter (Fig. 5G).

Etymology. The epithet *pintada*, is from the Spanish *pintado*, for painted or mottled, referring to the irregular pigmentation patterns found on the larger specimens of this species.

Distribution. Off Charleston, South Carolina, 600–605 m.

Caulleriella rodmani new species

Figures 6–7

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Caulleriella sp. 1: Blake *et al*. 1987: C-2; Maciolek *et al*.1987a: D-2; Hilbig 1994: 194.

Material Examined. (*70 specimens*) **Off New Jersey and Delaware, U.S. Mid-Atlantic ACSAR** program, coll. Rosemarie Petrecca, Chief Scientist. **Sta. 5**: Cruise Mid-4, Rep. 2, 16 May 1985, 38°50.48′N, 72°33.19′W, 2080 m, **holotype** (USNM 1642603); Rep. 1, 16 May 1985, 38°50.46′N, 72°33.23′W, 2080 m, 2 **paratypes** (USNM 1642604); Cruise Mid-1, Rep. 3, May 1984, 38°36.88′N, 72°51.34′W, 2055 m, **paratype** (USNM 1642605); Cruise Mid-3, Rep. 1, 5 Dec 1984, 38°50.42′N, 72°, 33.04′W, 2085 m, (1, USNM 1642606); Cruise Mid-5, Rep. 1, 3 Aug 1985, 38°50.44′N, 72°33.18′W, 2077, 2 **paratypes** (USNM 1642607). **Sta. 1**: Cruise Mid-2, Rep. 3, 03 Aug 1984, 38°35.99′N, 72°52.87′W, 2194 m (1, USNM 1642608); Cruise Mid-4, Rep. 3, 17 May 1985, 38°35.88′N, 72°53.13′W, 2195 m, **paratype** (USNM 1642609). **Sta. 2**: Cruise Mid-2, Rep. 1, 03 Aug 1984, 38°35.77′N, 72°53.58′W, 2019 m

(1, USNM 1642610); Cruise Mid-3, Rep. 3, 02 Dec 1984, 38°35.68′N, 72°53.69′W, 2015 m (3, USNM 1642611). **Sta. 4**: Cruise Mid-3, Rep. 3, 05 Dec 1983, 38°44.40′N, 72°41.08′W, 2105 m, 2 **paratypes** (USNM 1642612); Cruise Mid-4, Rep. 2, 16 May 1985, 38°44.45′N, 72°41.26′W, 2091 m, 2 **paratypes** (USNM 1642613); Cruise Mid-5, Rep. 1, 3 Aug 1985, 38°44.43′N, 72°41.24′W, 2095 m, **paratype** (USNM 1642614); Cruise Mid-6, Rep. 3, 11 Nov. 1985, 38°44.40′N, 72°41.26′W, 2105 m (1, USNM 1642615). **Sta. 6**: Cruise Mid-3, Rep. 3, 28 Nov 1984, 39°05.65′N, 72°03.08′W, 2085 m, 2 **paratypes** (USNM 1642616). **Sta. 7**: Cruise Mid-1, Rep. 3, 06 May 1984, 38°27.30′N, 73°03.43′W. 2100 m, (1, USNM 1642617); Cruise Mid-5, Rep. 2, 07 Aug 1985, 38°27.32′N, 73°03.54′W, 2095 m, **paratype** (USNM 1642618); Rep. 3, 07 Aug 1985, 38°27.31′N, 73°03.54′W, 2088 m, (2, USNM 1642619); Cruise Mid-6, Rep. 1, 14 Nov 1985, 38°27.29′N, 73°03.58′W, 2096 m, **paratype** (USNM 1642620). **Sta. 8**: Cruise Mid-1, Rep. 1, 06 May 1984, 38°27.36′N, 73°05.09′W, 2148 m, **paratype** (USNM 1642621); Rep. 3, 06 May 1984, 38°27.36′N, 73°04.81′W, 2150 m, **paratype** (USNM 1642622); Cruise Mid-2, Rep. 1, 05 Aug 1984, 38°27.21′N, 73°04.79′W, 2159 m (1, USNM 1642623); Cruise Mid-3, Rep. 3, 01 Dec 1984, 38°27.15′N, 73°04.79′W, 2155 m, 2 **paratypes** (USNM 1642624). **Sta. 9**: Cruise Mid-3, Rep. 1, 30 Nov. 1984, 38°17.20′N, 73°14.38′W, 2110 m (1, USNM 1642625); Cruise Mid-4, Rep. 2, 18 May 1985, 38°17.20′N, 73°14.65′W, 2105 m, **paratype** (USNM 1642626). Cruise Mid-5, Rep. 1, 08 Aug 1984, 38°17.24′N, 73°14.63′W, 2100 m, 2 **paratypes** (USNM 1642627); Cruise Mid-6, Rep. 1, 16 Nov 1985, 38°17.24′N, 73°14.92′, 2108 m, (1, USNM 1642628). **Sta. 10**: Cruise Mid-4, Rep. 2, 19 May 1985, 37°51.75′N, 73°19.97′W, 2095 m, **paratype** (USNM 1642629). **Sta. 11**, Cruise Mid-5, Rep. 3, 06 Aug 1985, 38°40.14′N, 72°56.46′W, 1502 m, (1, USNM 1642630). **Sta. 12**: Cruise Mid-1, Rep. 1, 8 May 1984, 38°29.34′N, 72°42.23′W, 2501 m, **paratype** (USNM 1642631); Rep. 2, 8 May 1984, 38°29.33′N, 72°42.19′W, 2500 m, **paratype** (USNM 1642632); Cruise Mid-6, Rep. 3, 14 Nov. 1985, 38°29.22′N, 72°42.33′W, 2499 m, **paratype** (USNM 1642633).—**Off New Jersey, U.S. EPA DWD-106 Site Survey**, **Sta. G**, Rep. 3, 18 Nov 1985, 38°55.60′N, 72°02.62′W, 2509 m (2, MCZ 161720).—**Off New England, U.S. North Atlantic ACSAR program**, coll. G.W. Hampson, Chief Scientist. **Sta. 3**: Cruise NA-2, Rep. 1, 25 Apr 1985, 41°01.38′N, 66°20.18′w, 1340 m, 3 **paratypes** USNM 1642634). **Sta. 5**: Cruise NA-3, Rep. 2, 04 Jul 1985, 40°05.08′N, 67°29.85′W, 2060 m, (1, USNM 1642635); Cruise NA-4, Rep. 1, 25 Nov 1985, 40°05.06′N, 67°29.86′W, 2074 m (1, USNM 1642636); Rep. 3, 25 Nov 1985, 40°05.07′N, 67°29.81′W, 2071 m (1, USNM 1642637); Cruise NA-5, Rep. 1, 29 Apr 1986, 40°05.06′N, 67°29.94′W, 2052 m, **paratype** (USNM 1642638); **Sta. 6**: Cruise NA-1, Rep. 1, 05 Nov 1984, 40°05.09′N, 67°29.23′W, 2117 m, **paratype** (USNM 1642639); Cruise NA-2, Rep. 1, 29 Apr 1985, 40°05.04′N, 67.°29.99′W, 2108 m, **paratype** (USNM 1642640); Rep. 2, 25 Apr 1985, 40°05.03′N, 67°29.13′W, 2108 m (1, USNM 1642641); Rep. 3, 25 Apr 1985, 40°05.06′N, 67°29.13′W, 2107 m, **paratype** (USNM 1642642). **Sta. 8**: Cruise NA-1, Rep. 1, 10 Nov 1984, 40°10.37′N, 67°37.43′W, 2175 m, **paratype** (USNM 1642643); Cruise NA-4, Rep. 1, 25 Nov 1985, 40°10.21′N, 67°37.24′W, 2184 m (1, USNM 1642644); Cruise NA-5, Rep. 2, 25 Nov. 1985, 40°10.25′N, 67°37.33′W, 2179 m (1, USNM 1642645). **Sta. 9**: Cruise NA-2, Rep. 1, 03 May 1985, 39°50.43′N, 70°01.58′W, 1235 m (1, USNM 1642646); Rep. 3, 03 May 1985, 39°50.42′N, 70°01.64′W, 1225 m (1, USNM 1642647). **Sta. 10**: Cruise NA-1, Rep. 2, 13 Nov 1984, 39°48.10′N, 70°05.29′W, 1234 m, **paratype** (USNM 1642648); Cruise NA-2, Rep. 3, 03 May 1985, 39°48.12′N, 70°05.24′W, 1210 m (2, USNM 1642649); Cruise NA-6, Rep. 3, 28 Jul 1986, 39°48.09′N, 70°05.29′W, 1228 m, 2 **paratypes** (USNM 1642650). **Sta. 13**: Cruise NA-6, Rep. 3, 30 Jul 1986, 39°48.25′N, 70°54.28′W, 1273 m, 2 **paratypes** (USNM 1642651). **Sta. 14**: Cruise NA-2, Rep. 2, 05 May 1985, 39°40.93′N, 70°54.21′W, 2092 m (2, USNM 1642652). **Sta. 15**: Cruise NA-2, Rep. 2, 05 May 1985, 39°40.07′N, 70°54.27′W, 2145 m, 2 **paratypes** (USNM 1642653); Cruise NA-5, Rep. 3, 06 May 1986, 39°40.10′N, 70°54.31′W, 2140 m, **paratype** (USNM 1642654).—**Southeastern USA, U.S. South Atlantic ACSAR program,** Off Cape Fear, North Carolina, coll. J.A. Blake, Chief Scientist. **Sta. 12**: Cruise SA-5, Rep. 1, 22 Sept 1985, 33°99.36′N, 76°97.27′W, 2004 m, **paratype** (USNM 1642655).

Description. A small, threadlike species; most specimens between 2.5 and 7 mm long. Holotype complete, 5.15 mm long, 0.07 mm across peristomium, 0.05 across far posterior setigers, with 24 setigers; large paratype a male, (USNM 1642634) complete in two parts, 7.27 mm long, 0.12 mm wide across peristomium, with 31 setigers. First 3–5 segments short, narrow, oval in shape, up to 1.5 times long as wide (Figs. 6A, C, 7A–E); following segments becoming elongated, moniliform, up to three to five times as long as wide (Figs. 6A, C–D, 7A–B); last 2–3 segments narrowing, bearing rounded pygidial lobe (Figs. 6B, 7F). Body generally cylindrical in cross section, no evidence of dorsal or ventral grooves. Color in alcohol; opaque white, with no pigment on body; most specimens with few to many elongate dark fecal masses (pellets) in middle setigers (Fig. 7A–B).

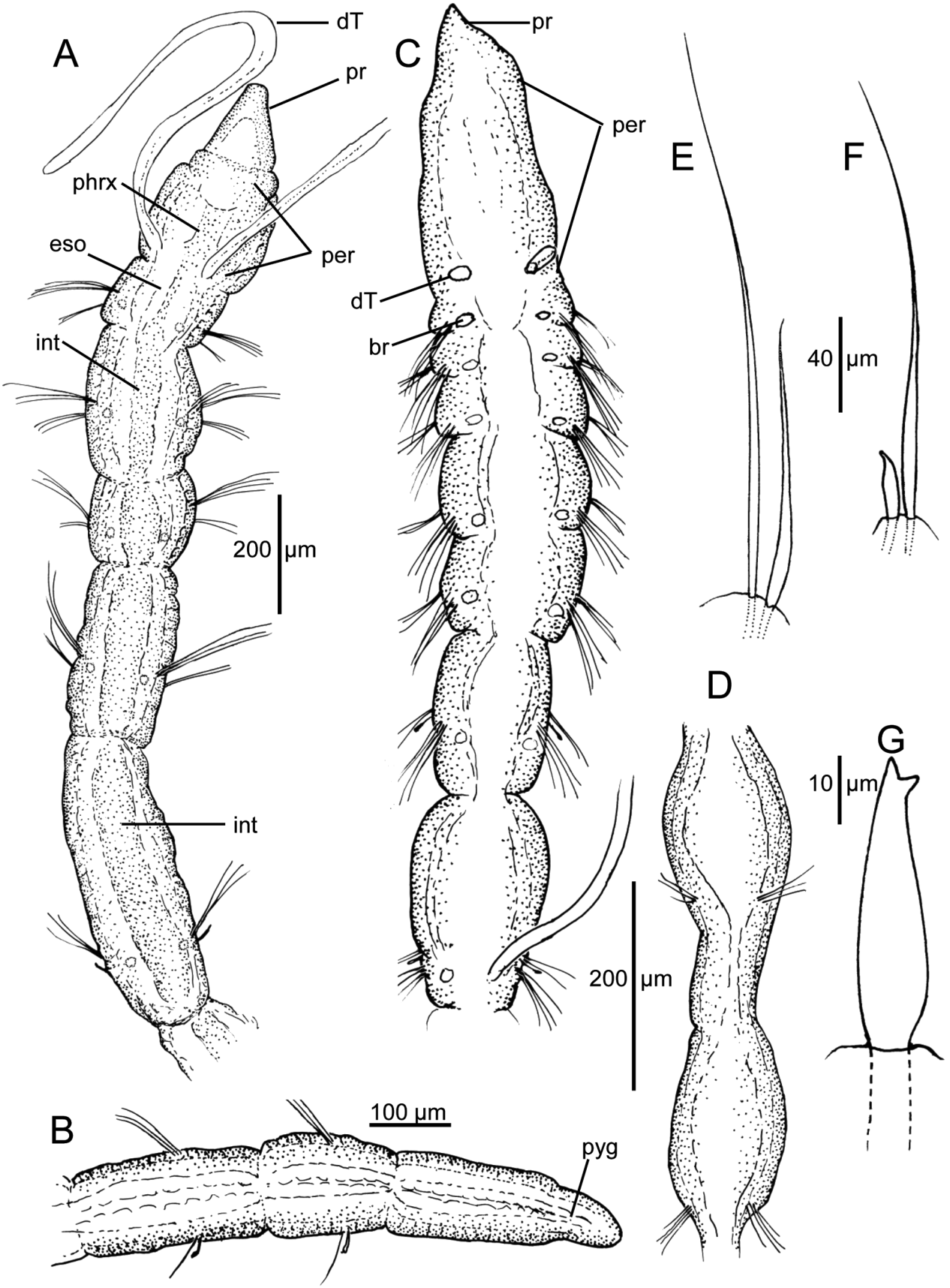

FIGURE 6. ***Caulleriella rodmani*** **n. sp**. A, anterior end, dorsal view; B, posterior end, dorsal view; C. anterior end dorsal view; D, mid-body setigers; E, notopodial capillaries, anterior setigers; F, neuropodial hook and capillary, from anterior setiger 12; G, neuropodial bidentate hook. A–B, holotype (USNM 1642603); C–G, paratype (USNM 1642634).

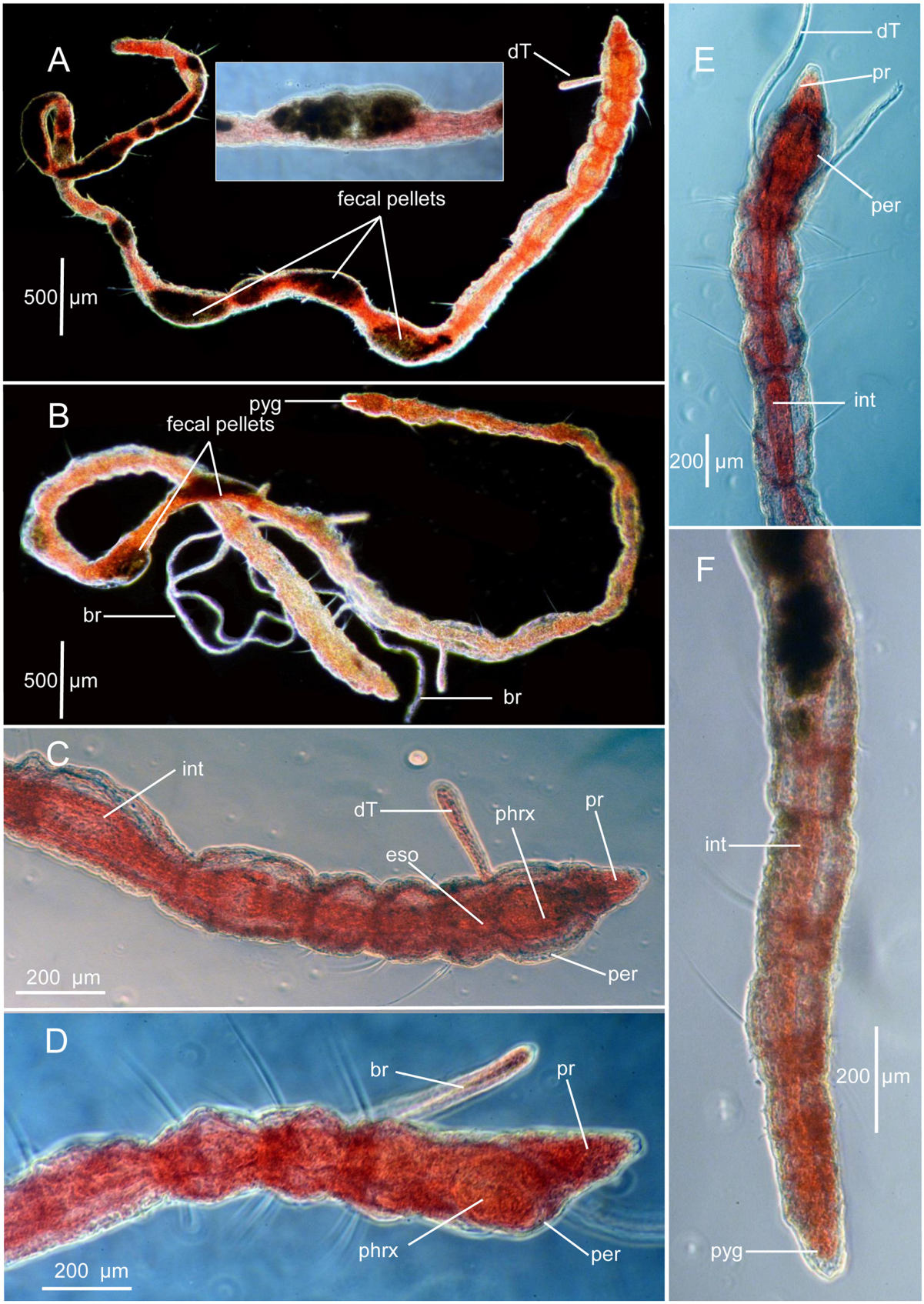

FIGURE 7. ***Caulleriella rodmani*** **n. sp**. A, entire worm, lateral view (inset of segment with fecal pellet not to scale); B, entire worm, dorsolateral view; C, anterior end, right lateral view; D, anterior end, right lateral view; E, anterior end, dorsal view; F, posterior end, dorsal view. A, C, (paratype, USNM 1642648); B, (paratype, USNM 1642633); D–F, holotype (USNM 1542603).

Pre-setiger region narrow, tapering anteriorly, up to twice as long as wide. Prostomium, triangular, weakly set off from peristomium, conical tapering to narrow, apex (Figs. 6A, C, 7C–E); eyespots absent; nuchal organs narrow slits on posterior lateral margins of prostomium, difficult to observe with light microscope. Peristomium smooth, with no apparent annular rings (Fig. 6A, C). Dorsal tentacles arise from posterior margin of peristomium (Figs. 6A–B, 7A, C, E). First pair of branchiae on setiger 1 dorsal to notosetae (Fig. 6C); subsequent branchiae in same location; branchiae or stubs only rarely observed on small specimens. Dorsal tentacles and branchiae when present long, thin, weakly expanded apically.

Parapodia reduced with setae appearing to arise directly from body wall. Noto- and neuropodia distinctly separated from one another, separation not as wide in anterior segments. Capillaries present throughout; anterior notosetae numbering 3–4 per fascicle, longer than neurosetae, which number 2 or 3 per fascicle. Neuropodial bidentate hooks first present from setiger 3–6; hooks numbering one per fascicle at first, increasing to no more than two hooks over last 10–12 setigers, accompanied by 1–2 capillaries throughout. Notopodial bidentate hooks first present from far posterior setiger 21, with one hook at first, second hook present or absent in posterior-most segments; smallest specimens lacking notopodial hooks. Individual hooks with thickened, weakly curved shaft, tapering to bidentate tip with main fang and apical tooth each about same length (Fig. 6G); hood or sheath absent.

Far posterior segments narrowing to a rounded, bulbous pygidium (Figs. 6B, 7F); anal cirri absent.

Methyl Green staining. No pattern.

Remarks. The majority of 70 specimens identified as *C. rodmani* **n. sp**. from the U.S. Atlantic continental slope are small and rarely exceeded more than one specimen per 0.09 m^2 box core sample. The specimens are so thin that after being emptied from the sample vials into a clean Stender dish with alcohol, they can often only be located visually after a careful search; if specimens cannot be located, the entire dish needs to be searched using the stereomicroscope; the labels and cotton plugs may also need to be rinsed and examined.

The long, thin, fragile body of this species indicates it is meiofaunal in habitat and that most specimens were likely not retained on the 0.3-mm-mesh-sieves used in the ACSAR program. The largest paratype was the only specimen determined to be sexually mature; it is a male with numerous sperm packets in the coelom.

Caulleriella rodmani **n. sp**. is closely related to *C. filiformia* **n. sp**., another threadlike species with which it may occur. In *C. rodmani* **n. sp**. the first pair of branchiae arise on setiger 1, dorsal to the notosetae, whereas in *C. filiformia* **n. sp**. the first branchiae are lateral to the dorsal tentacles on the posterior margin of the peristomium, with the second pair on setiger 1 dorsal to the notosetae. Rounded or moniliform segments typically occur along the entire of body of *C. filiformia* **n. sp**., while only the first 3–5 thoracic segments of *C. rodmani* **n. sp**. are rounded. Two short anal cirri occur on the pygidial segment of *C. filiformia* **n. sp**., whereas the pygidium of *C. rodmani* **n. sp.** is rounded and lacks anal cirri. In addition, the bidentate hooks of the two species are different. In *C. filiformia* **n. sp**. the apical tooth is an extension of an 'alate' hood or flange on the convex side of the shaft, whereas in *C. rodmani* **n. sp**., the apical tooth directly emerges from the end of the shaft and is not associated with a hood or flange. The dark elongate fecal pellets found in the intestine on most specimens assist in recognition.

Etymology. This species is named for Dr. James E. Rodman, retired Program Director, Division of Environmental Biology, National Science Foundation. Dr. Rodman initiated the PEET (Partnerships for Enhancement and Expertise in Taxonomy) Program and provided funding to this author for the study of polychaetes and training of students.

Distribution. U.S. Atlantic continental Slope from off New England to North Carolina, 1210–2509 m.

Caulleriella venefica Doner & Blake, 2006

Figure 8

Caulleriella B: Maciolek-Blake *et al*. 1985: B-5.
Caulleriella venefica Doner & Blake 2006: 66–67, Figs. 1, 5B, E; Blake & Magalhães 2019: 382–383, Fig. 7.3.1.5.17B.

Material examined. (*406 specimens*) **Northeastern USA. New York, Atlantic Ocean, off Jones Beach, Long Island**, coll. I. P. Williams: **Sta. 02-1**, 27 Aug 2005, 40°32.8921′N, 73°26.7373′W, 53.6 m (50, MCZ 161685); **Sta. 04-1**, 27 Aug 2005, 40°32.2574′N, 73°26.2046′W, 61.4 m (11, MCZ 161686); **Sta. 11-1**, 27 Aug 2005, 40°33.1763′N, 73°25.2151′W, 67.1 m (12, MCZ 161687); **Sta. 13-1**, 26 Aug 2005, 40°32.0373′N, 73°24.8685′W, 65.0 m (10, MCZ 161688); **Sta. 14-1**, 27 Aug 2005, 40°32.8649′N, 73°24.6780′W, 57.9 m (27, MCZ 161689); **Sta. 18-1**, 27 Aug 2005, 40°34.4606′N, 73°20.5860′W, 62.1 m (10, MCZ 161690); **Sta. 20-1**, 26 Aug 2005, 40°32.5438′N,

73°23.8709′W, 55.7 m (12, MCZ 161691); **Sta. 28-1**, 26 Aug 2005, 40°33.7790′N, 73°19.4410′W, 62.9 m (16, MCZ 161692); **Sta. 29-1**, 26 Aug 2005, 40°32.5810′N, 73°22.4412′W, 63.0 m (12, MCZ 161693); **Sta. 32-1**, 27 Aug 2005, 40°34.0382′N, 73°22.0921′W, 60.0 m (23, MCZ 161694); **Sta. 35-1**, 26 Aug 2005, 40°32.9924′N, 73°21.5735′W, 62.9 m (10, MCZ 161695); **Sta. 37-1**, 26 Aug 2005, 40°33.9938′N, 73°21.0607′W, 57.9 m (7, MCZ 161696); **Sta. 61-1**, 27 Aug 2005, 40°33.3697′N, 73°23.7731′W, 60.0 m (15, MCZ 161697).—**Connecticut, Millstone, Power Plant Effluent**, coll. Battelle field team, Jun 1979, 41°18.48′N, 72°9.96′W, 15–20 m in sand: sample 1701 (1, MCZ 161698); 1702 (7, MCZ 161699); 1705 (3, MCZ 161700); 1707 (1, MCZ 161701), 1708 (8, MCZ 1617012); 1709 (3, MCZ 161703).—**Off Massachusetts, Georges Bank**, **MMS Benthic Infauna Monitoring Program**, coll. G.W. Hampson, Chief Scientist: **Sta. 2**: Cruise M1, Rep 4, Jul 1981, 40°59.0′N, 66°55.8′W, 79 m (5, USNM 1642656); Cruise M2, Rep. 6, 14 Nov 1981, 40°59.2′N, 66°55.9′W, 70 m (1, USNM 1642657); Cruise M4, Rep. 1, 12 May 1982, 40°59.1′N, 66°55.9′W, 66 m (1, USNM 1642658); Rep. 2 (7, USNM 1642659); Rep. 3 (3, USNM 1642660); Cruise M6, Rep. 1, 22 Nov 1982, 40°59.2′N, 66°55.9′W, 71 m (6, USNM 1642661); Rep. 2, (5, 1642662); Cruise M7, Rep. 1, 07 Feb 1983, 40°59.2′N, 66°55.9′W, 71 m (1, USNM 1642663); Rep. 3, (5, USNM 1642664); Rep. 4 (5, USNM 1642665); Rep. 5 (2, USNM 1642666); Rep. 6 (2, USNM 1642667); Cruise M8, Rep. 1, 13 May 1983, 40°59.3′N, 66°55.9′W, 73 m (1, USNM 1642668); Rep. 3 (1, USNM 1642669); Cruise M9, Rep. 1, 14 Jul 1983, 40°59.2′N, 66°55.8′W, 79 m (2, USNM 1642670); Rep. 2 (6, USNM 1642671); Rep. 3 (1, USNM 1642672); Rep. 4 (3, USNM 1642673); Cruise M10, Rep. 1, 15 Nov 1983, 40°59.2′N, 66°55.8′W, 79 m (2, USNM 1642674); Rep. 5 (4, USNM 1642675). **Sta. 5-1**: Cruise M1, Rep. 2, Jul 1981, 40°39.4′N, 67°46.4′W, 81 m (4, USNM 1642676); Rep. 3 (3, USNM 1642677); Rep. 5 (2, USNM 1642678); Cruise M2, Rep. 4, 19 Nov 1981, 40°39.5′N, 67°45.7′W, 81 m (3, USNM 1642679); Cruise M3, Rep. 4, 15 Feb. 1982, 40°39.6′N, 67°45.9′W, 81 m (6, USNM 1642680); Cruise M4, Rep. 2, 14 May 1982, 40°39.5′N, 67°45.8′W, 80 m (4, USNM 1642681); Rep. 3 (12, USNM 1642682); Rep. 4 (3, USNM 1642683); Rep. 6 (5, USNM 1642684); Cruise M5, Rep. 3, 26 Jul 1982, 40°39.5′N, 67°45.9′W, 75 m (3, USNM 1642685); Cruise M7, Rep. 2, 10 Feb 1983, 40°39.5′N, 67°45.9′W, 81 m (6, USNM 1642686); Cruise M8, Rep. 1, 17 May 1983, 40°39.5′N, 67°45.9′W, 81 m (3, USNM 1642687); Rep. 2 (4, USNM 1642688); Rep. 4 (5, USNM 1642689); Rep. 5 (5, USNM 1642690); Rep. 6 (3, USNM 1642691); Cruise M9, Rep. 4, 16 Jul 1983, 40°39.5′N, 67°46.2′W, 84 m (7, USNM 1642692); Rep. 5 (4, USNM 1642693); Rep. 6 (5, USNM 1642694); Cruise M10, Rep. 1, 16 Nov 1983, 40°39.5′N, 67°46.2′W, 84 m (11, USNM 1642695); Rep. 5 (1, USNM 1642696); Rep. 6 (2, USNM 1642697). **Sta. 9**: Cruise M10, Rep. 1, 19 Nov 1983, 40°26.7′N, 68°09.8′W, 144 m (1, USNM 1642698). **Sta. 15**: Cruise M1, Rep. 4, Jul 1981, 41°27.2′N, 68°00.7′W, 37 m (7, USNM 1642699); Rep. 5 (2, USNM 1642700); Rep. 6 (4, USNM 1642701); Cruise M2, Rep. 1, 15 Nov. 1981, 41°27.4′N, 68°00.5′W, 37 m (1, USNM 1642702); Rep. 2 (2, USNM 1642703); Rep. 3 (1, USNM 1642704). **Sta. 16**: Cruise M1, Rep. 2, Jul 1981, 40°34.2′N, 68°012.3′W, 142 m (1, USNM 1642705); **Sta. 17**: Cruise M8, Rep. 3, 16 May 1983, 40°35.0′N, 67°11.3′W, 141 m (1, USNM 1642706).—Specimens for SEM: Georges Bank **Sta. 5-28**: Cruise M10, Rep. 4, 13 Nov. 1983, 40°39.5′N, 67°41.7′W, 84 m (4, USNM 1642707).

Description. A moderately-sized species, 11–15 mm long, 0.4–0.5 mm wide for 95–105 setigers. Body long, thickened throughout with narrow, crowded segments. Body dorsoventrally flattened with narrow ventral groove; typically coiled in preservation. Longitudinal muscles apparent along medial dorsal surface. Color in alcohol light tan to brown; no obvious pigmentation except dark internal area in prostomium, possibly indistinct nuchal pigmentation.

Pre-setiger region as long as first eight setigers. Prostomium unusually long, narrow, tapering to pointed tip (Fig. 8A–E); eyes absent; nuchal organs elongate lateral slits on posterior lateral margin. Peristomium enlarged, an achaetous single ring with one or two lateral grooves not crossing dorsum; surmounted by prominent dorsal crest extending from posterior margin of prostomium to setiger 1. Dorsal tentacles arising from posterior margin of peristomium; first pair of branchiae located posterior and lateral to tentacles; second pair of branchiae dorsal to notosetae, continuing throughout. Dorsal tentacles thick with ciliated groove; branchiae long, thin.

Parapodia of anterior setigers reduced to low rounded lobes, becoming low vertical ridges on segments with hooks; noto- and neuropodia widely separated. Notosetae of anterior setigers 4–6 thickened capillaries; bidentate hooks first present from setiger 13–14, with capillaries reduced to a single threadlike seta or entirely absent; up to two hooks per notopodium. Neuropodia with a single bidentate hook from setiger 9–10, increasing to two hooks per fascicle in posterior segments with single threadlike capillary. Hooks of noto- and neuropodia directed toward each other vis-á-vis; hooks with shaft curved on concave side; main fang with apical tooth narrow, short, hood absent (Fig. 8G–H).

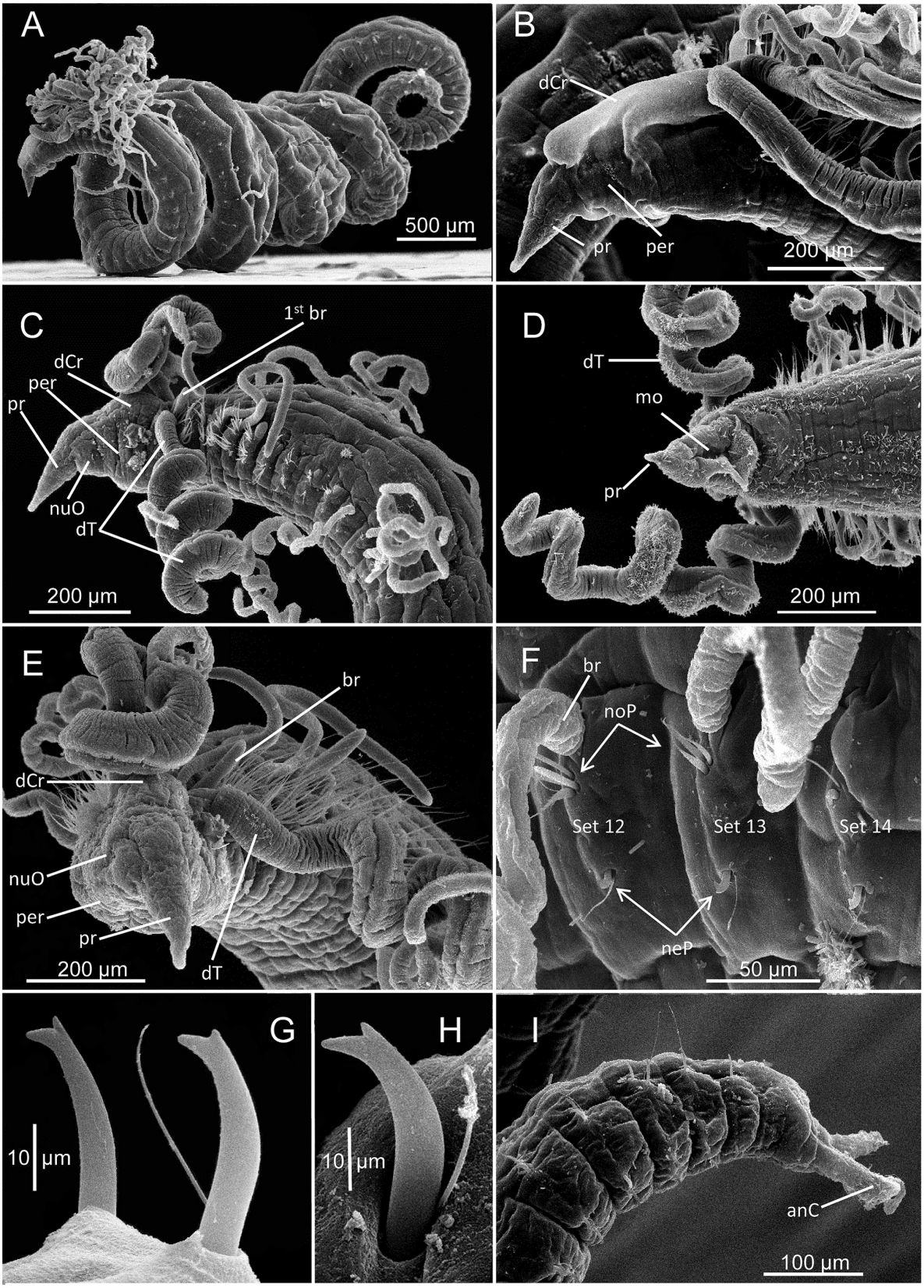

FIGURE 8. ***Caulleriella venefica*** **Doner & Blake, 2006**. A, Entire worm, coiled; B, anterior end, left lateral view; C, anterior end, left lateral view of another specimen; D, anterior end, ventral view; E, anterior end, frontal view; F, left lateral view of setigers 12–14, noto- and neuropodia with capillaries and hooks evident; G, two neuropodial hooks and one capillary; H, one neuropodial hook and one capillary; I, posterior end, left lateral view. SEMs from three specimens on stub from Georges Bank Sta. 5-28, Cruise M10, Rep. 4, coll. 13 Nov. 1983 (USNM 1642707).

Posterior end narrow, tapering; pygidium with two short anal cirri (Fig. 8A, I).

Methyl Green staining. Body stains uniformly; anterior half of prostomium not staining.

Remarks. *Caulleriella venefica*, an offshore shelf species, is most similar locally to *C. nobska* **n. sp**., a nearshore species. Both species share a pointed prostomium, an elongate peristomium with a dorsal crest, and bidentate hooks that lack a hood or sheath. However, the prostomium *of C. venefica* is longer, narrower, and more acutely pointed than that of *C. nobska* **n. sp**. *Caulleriella venefica* has maximally two instead of three hooks in posterior neuropodia and there are two anal cirri instead of none. In addition, the bidentate hooks of *C. venefica* have the main fang at a more acute angle than the 45° angle observed in *C. nobska* **n. sp**. *Caulleriella venefica* has a single thin capillary seta accompanying the hooks in middle and posterior setigers instead of these being entirely absent in *C. nobska* **n. sp**. The additional records recorded here suggest that the species is widespread throughout the northeastern United States in continental shelf depths having sandy sediments.

Biology and Habitat. On Georges Bank, *Caulleriella venefica* inhabits sediments having 98–99% sand, consisting of primarily very coarse to medium-sized sand particles (Maciolek *et al*. 1985). The long pointed prostomium and narrow elongate body suggest that the species is adapted to burrowing through these larger sediment particles. Other specimens examined as part of this study are also from sediments having high sand inventories.

Distribution. Northeastern US continental shelf, 35–145 m.

Caulleriella sp.

Material examined. **Massachusetts, Cape Cod Bay**, off Manomet Point, approximately 41°55.62′N, 70°32.28′W, among rocks and algal holdfasts, 6–8 m, coll. May 1990, 3 small specimens, one complete (JAB).

Description. The complete specimen from Manomet Point is a small, mature female, with 30 setigers, 1.9 mm long and 0.25 mm wide across anterior setigers. All segments are short, not beaded, and with widely separated noto- and neuropodia; a ventral groove is present along anterior and middle setigers. In alcohol, the color is opaque white; when stained with Shirlastain A, a prominent internal orange-colored heart body is obvious along the first one-third of the body.

The prostomium is short, tapering to a rounded apex; eyes are absent; nuchal organs were not observed. The peristomium appears to be a single ring, with a distinct dorsal crest. The dorsal tentacles arise from the posterior margin of the peristomium; the first branchiae arise from setiger 1 and continue for about half the length of the body. Notosetae include 2–4 thin capillaries on setigers 1–11, with 1–2 hooks replacing them from setiger 12; neurosetae include capillaries on setigers 1–2, replaced by hooks from setiger 3 with up to 5–6 per fascicle in middle body segments. Hooks bidentate, sigmoid, very small, difficult to study in light microscope possibly 'alate' with narrow flange on curved convex side. Pygidium a rounded lobe, with a least one short anal cirrus present. Eggs are present in setigers 12–18, at least two per segment, each large relative to the small size of the worm, ca. 85 μm in diameter.

Remarks. In May 1990, several small specimens of *Caulleriella* were collected as part of a monitoring program off Manomet Point, a promontory south of Plymouth, Massachusetts, on Cape Cod Bay. The samples were collected by divers who scraped algae and other encrusting materials from the surface of rocks from a depth of about 6–8 m. At least three different cirratulid polychaetes were identified: *Caulleriella* sp., *Cirratulus* sp., and *Dodecaceria* sp. The short description the *Caulleriella* specimens allows some comparison with Leidy's (1855) account of *C. fragilis* from a similar habitat.

History. *Caulleriella fragilis* was originally described by Leidy (1855) from under intertidal rocks at Point Judith, Rhode Island near the entrance to Narragansett Bay. The species was described as *Cirrhatulus* [sic] *fragilis* and was referred to the genus *Caulleriella* by Chamberlin (1919: 372) in a footnote. The species was also recognized as belonging to the genus *Caulleriella* by Hartman (1944) as part of her publication of Verrill's unpublished plates. Hartman (1959) also listed *Caulleriella fragilis* in her Catalogue. Despite being the oldest named cirratulid from the U.S. Atlantic coast, *C. fragilis* has rarely been reported and not described since the original report.

Records of *Caulleriella fragilis*. Leidy (1855: 147) described the species as follows: "*Body cylindrical, narrowed towards the extremities, reddish orange color, posteriorly greenish. Mouth inferior, circular; upper lip conical. Eyes two. Cirri numerous, orange colored; the first pair commencing at the second setigerous segment and the most robust. Setae in two rows, simple, in fasciculi of three to five. Podal hooks in two rows, five to eight in each fasciculus, sigmoid, bifid at the free extremity. Intestine cylindrical, constricted. Ovaries on each side of*

the intestine, extending four-fifths the length of the body. Worm three lines long, by one-fourth of line broad and composed of forty annulations. Found under stones, on the shores of Point Judith." Leidy (1855: plate XI, figs. 39–43) illustrates the worm as being long, narrow, and with segments being similar and almost moniliform along the body. The prostomium is large and pear-shaped bearing two large eyespots and followed by a single achaetous segment (peristomium); dorsal tentacles appear to arise on the second setiger, but the points of origin are not indicated. Leidy's (1855) Fig. 43 shows the pygidium as having two rounded lobes and shows a recurved hook with two apical teeth.

The only subsequent reports of the species are by Verrill (1873) from rocky habitats in Vineyard Sound and Webster (1879) from tidal flats of Great Egg Harbor, New Jersey. Verrill (1873: 397) found the species associated with ascidians on rocky and gravelly bottoms. "*The* Cirrinereis fragilis*, which is a small and delicate species, furnished with conspicuous eyes, and related to the large* Cirratulus*, occurs beneath the stones*." Hartman (1944), as part of her unpublished plates by Verrill, assigned Plate 19, fig. 3 to *Caulleriella fragilis*. This figure illustrates an entire worm in dorsal view and (3a), the same anterior end in ventral view. In this illustration in contrast to that of Leidy, the prostomium is short, conical and bears two small eyespots; this is followed by a peristomium that appears to consist of two rings, the first short and narrow, the second larger which overlaps setiger 1 mid-dorsally. The dorsal tentacles appear to arise from setiger 1 together with the first branchiae. The body segments are short, wider than long. The pygidium consists of a cup-like structure below the anal opening. Setae are not illustrated. This illustration differs from the description and figures of Leidy (1855) in several respects, the most important being differences in the pre-setiger morphology and placement of the dorsal tentacles (setiger 2 in Leidy; setiger 1 in Verrill); as well as different pygidial morphology (two lobes in Leidy and a single cup-like lobe in Verrill).

Webster (1879: 122) identified a specimen as *Cirrhinereis fragilis* and noted: "*Rare; a single injured specimen was found which probably belongs to this species*." No further information was presented.

As near as can be determined from the literature and personal communications, there have been no other reports of the species from along the U.S. Atlantic coast and no descriptive remarks since the original account 165 years ago by Leidy (1855). There are no existing specimens of *C. fragilis* from the original collections (M.E. Petersen, in correspondence). The lack of reports of *C. fragilis* are likely due to their cryptic habitat under rocks and nestled among algae and other encrusting organisms. As a result, the identity and status of *C. fragilis* based on differences between the original description and illustrations by Leidy (1855) and notes by Verrill (1873) and illustrations by Verrill published by Hartman (1944) represent a modern-day enigma.

Comparison of the Cape Cod Bay specimens with *Caulleriella fragilis*. The Cape Cod Bay specimens differ from Leidy's original depiction of *C. fragilis* in several respects. The new specimens have a relatively short, compact body with short crowded segments; the dorsal tentacles arise from the posterior margin of the peristomium; no eyespots are present; and the pygidium consists of a single lobe with at least one anal cirrus. In contrast, the body of *C. fragilis* as illustrated by Leidy (1855) is long and narrow with individual segments mostly as wide as long; the dorsal tentacles were said to arise from setiger 2; a pair of eyespots were present; and the pygidium consisted of two rounded lobes lacking anal cirri. The distinctive color pattern reported by Leidy (1855) was apparently from life, precluding any comparison with the new specimens. Both forms are reported as sexually mature females with eggs. Leidy (1855) was explicit in stating that the first and most robust tentacles began on setiger 2. Such a placement of tentacles has not been recorded in other species of *Caulleriella*. The absence of eyespots in the Cape Cod Bay specimens may be real or possibly due to fading of the pigments after 30 years in alcohol.

Nevertheless, based on experience of dealing with cirratulids for many years, it is my opinion that the Cape Cod Bay specimens represent a different species than *C. fragilis* as it was originally described and illustrated. The Cape Cod Bay specimens likely represent a species new to science. The placement of the dorsal tentacles, shape of the body, presence or absence of eyespots and pygidial morphology appear to be different between the two forms. The new specimens also differ from Verrill's illustration of *C. fragilis* in Hartman (1944). However, the three Cape Cod Bay specimens are fragile and were damaged with each effort to make observations. For this reason, no effort has been made to formally describe them in this paper. It should be possible, however, to collect additional specimens from rocky habitats along the western side of Cape Cod Bay and perhaps elsewhere in New England. The Cape Cod Bay specimens are therefore, being retained for further study with the expectation that additional materials will be obtained. Hopefully, taking a closer look at the smaller invertebrate fauna encrusting or under intertidal rocks will result in additional specimens of the Cape Bay species as well as determine the identity of *C. fragilis*.

TABLE 1. Taxonomic Characters of Eight Species of *Caulleriella* from deep-sea habitats, 500 m or greater.

Species	Prostomium	Number. peristomial rings	Nature of segment 1	Position of first pair of branchiae	Position of dorsal tentacles	Capillaries in posterior notopodia	Capillaries in posterior neuropodia
C. antarctica Hartman, 1978	Short, triangular	2	Setigerous complete	Lateral to dT on per	Post end of per	Present	Present or absent
C. bathytata Blake, 2019	Short, triangular	1, smooth, merging with setiger 1	Setigerous complete	Post to dT on posterior margin of per	Near post end of per	Present	Present
C. eltaninae Blake, 2018	Short, triangular, possible eyespots	3	Achaetous	Dorsal to notosetae, set 1	On achaetous segment	Present	Present
C. fimbriata Blake, 2018	Short, triangular	1, large, inflated	Setigerous, complete	Dorsal to notosetae, set 1	Near post end of per	Present	Present
C. kacyae Blake, 2018	Elongate, narrow	3	Setigerous, complete	Dorsal to notosetae, set 1	Post margin per	Present	Absent
C. filiformia Blake **n. sp.**	Short, triangular	1, with weak lateral grooves not crossing dorsum	Setigerous, complete	Post to dT on posterior margin of per	Near post end of per	Few, mostly replaced by hooks	Few, mostly replaced by hooks
C. pintada Blake **n. sp.**	Conical, tapering to rounded tip	1, long narrow, wrinkled in larger specimens	Setigerous, complete	Dorsal to notosetae, set 1	Near post margin of per	1–2 thin capillaries	1–2 thin capillaries
C. rodmani Blake **n. sp.**	Short, triangular	1, smooth, no lateral grooves	Setigerous, complete	Dorsal to notosetae, set 1	Near post. margin of per	Present	Present

.....continued on the next page

TABLE 1. (Conntinued)

Species	Hooks start set & maximum number	Nature of posterior hooks	Pygidium	Unique characters	Distribution & depth
C. antarctica Hartman, 1978	No: 8–9 (2) Ne: 6 (2–5)	Geniculate; noto hooks long, thin with short knobs; neuro hooks shorter, thicker bidentate, with apical tooth formed by sheath or hood on convex side of shaft	With 1 anal cirrus	Threadlike body; middle segs moniliform; notohooks straight, with blunt, tips neurohooks curved, bidentate; hooks with sheath on convex side of shaft extended to form apical tooth	Antarctica, shelf and slope depths to 1120 m. Blake 2018
C. bathytata Blake, 2019	No: 39 Ne: 31	Long, curved with main fang at 45° angle and short apical tooth; short transparent hood present ventral to main fang on concave side of shaft	With 1 ventral lobe	Threadlike body; middle segs elongate, not moniliform; bidentate hooks with hood on concave side between main fang and shaft	Abyssal Pacific Ocean, Clarion-Clipperton Fracture Zone, 4504–4877 m. Blake 2019.
C. eltaninae Blake, 2018	No: absent Ne: 19–21 (6–7)	Geniculate with teeth short, blunt tipped; without sheath	Short papillae around anus; 1 ventral cirrus	Body thickened, not threadlike; vGr along entire body; notohooks absent; neurohooks curved toward vGr	Antarctic Peninsula, Ross Sea, 201–870 m. Blake 2018
C. fimbriata Blake, 2018	No: 23 (3–4) Ne: 6 (2–3)	Elongate, curved, noto-hooks without apical tooth; neuro-hooks with both teeth, short, pointed	1 ventral cirrus	Threadlike body; pr with glandular band on post margin	Southern Ocean, 1884 m. Blake 2018
C. kacyae Blake, 2018	No: 105 (1–2) Ne: 18 (6)	Noto hooks long, thin blunt tipped; neuro hooks short, curved with large main fang and 2 apical teeth formed by sheath	5 papillae dorsal to anus & 2 lateral cirri	Body elongate, with all segs short, narrow; with vGr; notohooks blunt-tipped; neurohooks appearing tridentate	Antarctica, Weddell Sea, 1035 m. Blake 2018
C. filiformia Blake **n. sp.**	No: 7–10 (1–3) Ne: 7–10 (1–3)	Long, geniculate, with main fang surmounted by thin apical tooth formed as extension of sheath on convex side of shaft	With 2 short anal cirri	Threadlike with moniliform segments along most of body segs	Western North Atlantic, New England to North Carolina, 1900–2185 m. This study.
C. pintada Blake **n. sp.**	No: 8 (1–2) Ne: 5 (4–5)	Shaft thick, tapering; blunt, narrow main fang; short apical tooth formed as extension of sheath on convex side of shaft	With 2 elongate anal cirri	Threadlike, segs narrow, not moniliform, pigment along much of body, sometimes intense; vGr in ant and middle segs	Western North Atlantic; off South Carolina, 600–605 m. This study
C. rodmani Blake **n. sp.**	No: 21 (1–2) Ne: 3–6 (1–2)	Hooks with thickened shaft, tapering to bidentate tip with both teeth equivalent; no sheath or hood.	Conical, no cirri	Threadlike body; few th sets moniliform; middle body segs elongate; dark fecal pellets present in gut	Western North Atlantic, New England to North Carolina, 1220–2025 m. This study.

Abbreviations: ant, anterior; dT, dorsal tentacle; Ne, neuropodia; No, notopodia; per, peristomium; post, posterior; pr, prostomium; seg, segment(s); set, setiger(s); th, thoracic; vGr, ventral groove.

Discussion

Remarks on the known species of *Caulleriella*

Number of valid species. Read & Fauchald (2021) list 44 valid species of *Caulleriella*. In addition, Blake & Magalhães (2019) referred *Chaetozone armata* Hartman 1963 to *Caulleriella*. Four additional species described in the present paper bring the total known species of *Caulleriella* to 49. Of these, 33 species or 67% were described over the past 25 years. At the same time, another 11 species originally described as *Caulleriella* were referred to other genera as the definitions of *Caulleriella* and other bitentaculate genera were redefined (Blake 1991, 1996, 2017). The following is a list of the 49 valid species of *Caulleriella* with known geography and bathymetry. (*) = species reported with 'alate' hooks.

1. **Caulleriella acicula* Day, 1961.South Africa, subtidal.
2. **Caulleriella alata* (Southern, 1914) E. North Atlantic, low water.
3. *Caulleriella angusticrista* Blake & Dean, 2019. Caribbean Sea, Panama, shallow subtidal.
4. **Caulleriella antarctica* Hartman, 1978. Antarctica, deep water 400–1129 m. See Blake 2018.
5. *Caulleriella apicula* Blake, 1996. Southern California, 24 m.
6. *Caulleriella armata* (Hartman, 1963). Southern California, 27–180 m. *Fide* Blake & Magalhães 2019.
7. *Caulleriella bathytata* Blake, 2019. Pacific Ocean, abyssal, 4877 m.
8. *Caulleriella bioculata* (Keferstein, 1862) E. North Atlantic, widely reported.
9. *Caulleriella bremecae* Elías & Rivero, 2008. Argentina, intertidal.
10. *Caulleriella cabbsi* Pocklington & Coates, 2010. Bermuda, intertidal.
11. *Caulleriella capensis* (Monro, 1930). South Africa, subtidal.
12. **Caulleriella chilensis* Carrasco, 1977. Off Chile, 2–45 m. *Fide* Blake 2018.
13. *Caulleriella convexacapa* Blake & Dean, 2019. Caribbean Sea, Honduras, 10–20 m.
14. *Caulleriella cordiformia* Magalhães & Bailey-Brock, 2013. Hawaii, 102 m.
15. *Caulleriella cristata* Blake, 1996. Central California, intertidal.
16. *Caulleriella cucula* Dean & Blake, 2007. Pacific Costa Rica, 9–46 m.
17. *Caulleriella dulcensis* Dean & Blake, 2007. Pacific Costa Rica, intertidal.
18. *Caulleriella ecuadoriana* Blake, 2018. Off Ecuador, 8–20 m.
19. *Caulleriella eltaninae* Blake, 2018. Antarctica, 210–870 m.
20. **Caulleriella filiformia* **n. sp.** U.S. Atlantic continental slope, off New England to the Carolinas, 1944–2185 m.
21. *Caulleriella fimbriata* Blake, 2018. Southern Ocean, 1884 m.
22. *Caulleriella fragilis* (Leidy, 1855). U.S. Atlantic, New England, intertidal in rocks.
23. *Caulleriella fucata* Blake, 2018. Antarctic Peninsula, 11–12 m.
24. *Caulleriella galeanoi* Elías & Rivero, 2008. Argentina, intertidal.
25. *Caulleriella glabra* Gallardo, 1968. South Vietnam, intertidal.
26. *Caulleriella hamata* (Hartman, 1948).NE Pacific, Alaska to Washington, intertidal to shallow water.
27. **Caulleriella kacyae* Blake, 2018. Weddell Sea, 1035 m.
28. *Caulleriella lajolla* Blake, 1996. Southern California, in algal holdfasts.
29. *Caulleriella magnaoculata* Hartmann-Schröder, 1962. Peru, 9 m.
30. *Caulleriella mediterranea* Lezzi, 2017. Off Italy, 8 m.
31. *Caulleriella microbidentata* Blake & Dean, 2019. Caribbean Sea, Honduras, shallow subtidal.
32. *Caulleriella minuta* Dean & Blake, 2007. Pacific Costa Rica, intertidal.
33. *Caulleriella moralesensis* Dean & Blake, 2007. Pacific Costa Rica, intertidal.
34. *Caulleriella murilloi* Dean & Blake, 2007. Pacific Costa Rica, intertidal in mangroves.
35. *Caulleriella nobska* **n. sp.** U.S. Atlantic, Massachusetts, shallow subtidal.
36. **Caulleriella pacifica* E. Berkeley, 1929. Eastern North Pacific, shallow subtidal.
37. *Caulleriella parapicula* Blake & Dean, 2019. Caribbean Sea, Panama, seagrass, intertidal.
38. *Caulleriella parva* Gillandt, 1979. North Sea, Helgoland, shallow subtidal.
39. *Caulleriella parvinasa* Blake & Dean, 2019. Caribbean Sea, Honduras, intertidal in sand.
40. *Caulleriella petersenae* Díaz-Díaz -, Cardenas-Oliva & Linero-Arana, 2014. NE Venezuela, shallow subtidal.

41. **Caulleriella pintada* **n. sp.** Off Charleston, South Carolina, 600–605 m.
42. *Caulleriella quadrata* Blake & Dean, 2019. Caribbean Sea, Panama, 5 m in sand.
43. *Caulleriella rodmani* **n. sp.** U.S. Atlantic continental Slope from off New England to North Carolina, 1210–2501 m.
44. *Caulleriella suroestense* Blake, 2018. Chile, shallow subtidal.
45. **Caulleriella tricapillata* Hutchings & Rainer, 1979. Australia, New South Wales, intertidal.
46. *Caulleriella trispina* Elías & Rivero, 2011. Argentina, intertidal.
47. *Caulleriella typhlops* (Willey, 1905). Indian Ocean, Gulf of Manaar.
48. *Caulleriella venefica* Doner & Blake, 2006. U.S. Atlantic, New England, 35–145 m.
49. *Caulleriella viridis* (Langerhans, 1881). E. North Atlantic, Madeira.

Deep-water species of *Caulleriella*

Out of 49 known species of *Caulleriella*, only eight have been reported from depths of 500 m and greater, with *C. bathytata* from the abyssal Pacific Ocean in 4877 m being the deepest species of the genus yet recorded. The eight deep-water species are characterized in Table 1. All of these except *C. eltaninae* have long, threadlike bodies.

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