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Capitella teleta, a new species designation for the opportunistic and experimental *Capitella* sp. I, with a review of the literature for confirmed records

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Abstract

This paper provides a morphological description of *Capitella teleta* sp. nov., an opportunistic capitellid that is also commonly used as an experimental polychaete under the provisional designation *Capitella* sp. I. The species is widely distributed along the east and west coasts of North America and also reported from Japan and the Mediterranean. The species belongs to a group having distinct sexual dimorphism, yet with hermaphrodites occurring under certain conditions. Morphologically, *C. teleta* has a long, narrow body, with all thoracic segments similar except for sexual modifications on setigers 8–9; the prostomium/peristomium combined are long, narrow and about 2.5 times as long as setiger 1. Capillary setae are present in noto- and neuropodia of setigers 1–7; setigers 8–9 have hooded hooks in noto- and neuropodia of females; genital spines replace notopodial hooks in males. A methyl green staining pattern is limited to some thoracic setigers of females; males lack a distinct staining pattern. The cytochrome oxidase I (COI) sequence is presented. Relationships of *C. teleta* with the type-species, *C. capitata* and other known species including siblings identified in laboratory culture are discussed. The syntype of *Ancistria acuta* Verrill, 1874, the only known species of *Capitella* described from New England was examined and determined to be *incertae sedis*. *C. teleta* is a highly opportunistic species and appears to be the same as the *C. capitata* identified from southern California as the "polluted zone indicator" by D.J. Reish in the late 1950s. An appendix with over 200 published references to research conducted on *C. teleta* is included.

Key words: sibling species, morphology, taxonomy, reproduction, opportunistic species, Massachusetts, California, Japan

Introduction

Polychaetes of the genus *Capitella* are typically considered to be opportunistic in disturbed or otherwise stressed organically enriched sediments. Historically, a single species, *C. capitata* (Fabricius), believed to be cosmopolitan in distribution, was thought to be the only species of *Capitella* found in stressed habitats. This concept began to break down when detailed studies were conducted on cultures of *Capitella* taken from sediments contaminated by fuel oil during the West Falmouth, Massachusetts, oil spill in September 1969. Capitellids identified at the time as *C. capitata* were the most opportunistic invertebrate species found in recovering sediments (Sanders et al. 1980). *Capitella* was later collected from five populations in the vicinity of Woods Hole, Massachusetts, and two populations in Gloucester, Massachusetts, in an effort to further understand the population structure and life history. Subsequent allozyme electrophoresis and life history studies

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on these populations showed that no fewer than six sibling species were present in the samples. These sibling species were similar morphologically, but showed distinct differences in life history and reproduction; in terms of genetics, virtually no alleles were found in common at eight allozyme loci (Grassle & Grassle 1976; Grassle 1980). The sibling species were given provisional designations: *Capitella* sp. I, Ia, II, IIa, III, and IIIa. Three of these sibling species (I, II, and III) were identified from the site of the Wild Harbor oil spill; four (I, Ia, II, and III) from the Sippewissett Marsh, three (Ia, II, IIIa) from Gloucester, and all six from the vicinity of the Woods Hole Outfall (Grassle 1980). Subsequent investigations on sperm morphology, setal structure, larval morphology, and chromosomes further demonstrated distinct differences among these original six species (e.g., Eckelbarger & Grassle 1987a–b; Grassle et al. 1987). Subsequent to the discovery of the suite of *Capitella* sibling species identified from the Woods Hole region and Gloucester, other workers discovered additional sibling species (Pearson & Pearson 1991; Gamenick et al. 1998; Mendez 2002, 2006; Wu et al. 1991). To date, these authors have defined approximately 12–13 sibling species from the various studies over the past 30 years.

Capitella sp. I is one of the original sibling species identified by J.P. Grassle and has been maintained in culture for more than 30 years. Specimens from these cultures have been shared with numerous investigators who have conducted experiments on a wide variety of biological subjects. Because of the importance of this species and the numerous published papers that now bear the provisional *C.* sp. I designation, we here provide a formal taxonomic description and name for the species following the criteria of the International Code of Zoological Nomenclature. The incentive to prepare this description arose partially from the first author's effort to define *C. capitata sensu stricto* from the type-locality in West Greenland. This investigation showed that the type-species is very distinctive and likely restricted to Arctic and subarctic habitats. The redescription of *C. capitata* is published as a companion paper in this same issue and establishes a taxonomic baseline from which the numerous sibling species of *Capitella* can now be compared, described, and named (Blake 2009, this volume). In addition to providing observations on the adult morphology and a new name to replace the provisional species designation, we also present as an appendix, an annotated guide to more than 200 papers that have appeared in the literature as *C.* sp. I or that otherwise refer to this species.

Materials and methods

Collections of *Capitella* sp. I were assembled in the second author's laboratory from cultures maintained at Rutgers University. The specimens were derived in part from stocks originally collected from the Woods Hole region, which serves as the type locality for the new species. Specimens included sexually mature males and females, hermaphrodites, and juveniles. All were preserved in 4% formalin and transferred to 80% ethanol (ETOH). Observations were made with light microscopy using phase contrast optics and magnifications up to 1500×. Methyl green (MG) stain saturated in 80% ETOH was used to determine MG staining patterns. Several specimens and dissected parts were dehydrated in 100% ETOH, cleared with xylene, and mounted directly in Permount® on slides that were dried for 48 h on a warming table before examination. Photomicrographs were taken with a Nikon D80 SLR camera mounted on a Wild M-5 stereomicroscope and a Zeiss RA compound scope equipped with Phase Contrast optics. Images were taken at 10.2 megapixel resolution and subsequently edited in Photoshop® CS3 software.

Selected specimens were prepared for scanning electron microscopy (SEM) by dehydration in 100% ETOH followed by critical point drying. Specimens were mounted on stubs and sputter-coated with gold-palladium. SEM observations were carried out using a JEOL JSM-840 in the Electron Microscopy Laboratory, Marine Biological Laboratory (MBL), in Woods Hole, MA. The genome was sequenced (with 8× coverage) by the Joint Genome Institute (Department of Energy, Walnut Creek, CA, USA). The COI sequence (Protein ID: 228595) is available at: http://genome.jgi-psf.org/cgi-bin/dispGeneModel?db=Capca1&id=228595. The holotype and a selection of paratypes were deposited in the collections of the National Museum of Natural History, Washington, D.C (USNM); additional paratypes were deposited in the Los Angeles County Museum of Natural History, Los Angeles, California (LACM), and the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ).

Results

Family Capitellidae Grube, 1862
Genus *Capitella* Blainville, 1828

Type species. *Capitella capitata* (Fabricius, 1780) as *Lumbricus capitatus*. Redescribed by Blake 2009.
Type locality. West Greenland.

Diagnosis. Prostomium conical to bluntly rounded, sometimes dorsoventrally flattened, with dorsal groove present or absent, with nuchal organs as paired slits at border between prostomium and peristomium; eyes present or absent. Peristomium a single asetigerous ring. Thorax with nine segments, all setigerous with capillary setae in both rami of setigers 1–3, 1–4, 1–6, or 1–7, otherwise with capillaries and hooks in various combinations in both rami; setigers 8–9 with hooded hooks, mixed capillaries and hooks, or all capillaries, these arrangements sometimes growth dependent; prominent genital spines present in setigers 8–9 of males and hermaphrodites; females usually with enlarged lateral genital pores between setigers 7–8 or 8–9. Capillaries unilimbate, with narrow wings; hooded hooks with multiple rows of denticles above main fang. Abdominal segments with hooded hooks in both rami; capillaries absent. Branchiae absent. Pygidium without appendages.

Capitella teleta sp. nov.

Figures 1–3

Capitella capitata: Reish, 1974: 181–195, figs. 1–7; 1980: 36–53, figs. 9–16.—Probably Berkeley & Berkeley 1952: 100–101, figs. 206–208. Not Fabricius 1780.

Capitella sp. I: Grassle & Grassle 1976: 567–569 (first designation); Eckelbarger & Grassle 1987a: 62–76. See annotated bibliography for numerous additional records.

Material examined. Holotype, male removed from laboratory culture 08 Nov 2006, original stocks from Woods Hole, Massachusetts, see Appendix footnotes (USNM 1123180).—**Paratypes**, from same culture stock, 2 males, 2 females, 2 hermaphrodites (USNM 1123181); 9 females (USNM 1123182); 3 hermaphrodites (USNM 1123183); 2 males, 2 females (LACM-AHF-Poly 2218); 2 males, 2 females, (MCZ 81196). Additional paratypes from same culture stocks preserved 17 Dec 2007, 20 males (USNM 1123184); 18 females (USNM 1123185); 3 hermaphrodites (USNM 1123186).

Description. Body elongate, widest anteriorly, thoracic segments only slightly larger than abdominal segments (Fig. 1A−B), gradually narrowing posteriorly. Ventral groove present from setiger 5 in both males and females, extending to posterior end of body. Lateral groove present in posterior one-half of abdominal segments; groove more or less distinct probably depending on preservation. Males, females, and hermaphrodites similar in size; largest specimens from 08 Nov 2006 sample, largest male 24 mm long, 1 mm wide for 52 setigers (holotype); largest female 20 mm long, 0.6 mm wide for 52 setigers; largest hermaphrodite 22.5 mm long, 0.7 mm wide for 58 setigers. Long-term observations suggest that females and hermaphrodites typically larger than males (J.P. Grassle, unpublished data).

Color in life of young and/or healthy specimens: head semi-translucent, thorax white or cream with underlying pinkish color proportional to concentration of hemoglobin-containing cells; abdominal setigers translucent, light to bright red, with color proportional to concentration of red blood cells. Gut containing black or brown sediment, visible through body wall. Females or hermaphrodites in female phase with developing paired ovaries on ventral side of 10−12 anterior abdominal setigers, usually beginning with setiger 10 (see Eckelbarger et al. 1984); oocytes white to cream initially, then yellowish white at maximal diameter. In males or hermaphrodites in male phase, testes not visible macroscopically. No apparent difference in color between living males and females. Older worms become browner or blackish brown, presumably because hemoglobin converted into modified heme pigments. Pair of red eyespots visible in larvae, juveniles, and adults. Color in alcohol: light tan with minute brown speckles scattered over body surface.

Prostomium flattened dorsoventrally, as wide as long, demarcated from peristomium by weak lateral curved nuchal organs (Figs. 1A−C; 2A−B); prostomium and peristomium combined forming a head half as long as wide, with weak dorsal depression extending from posterior half of prostomium posteriorly over anterior half of peristomium (Fig. 2B). Prostomium and peristomium combined 2.5 × longer than setiger 1 and as long as setigers 1–2. First setiger 1.25 × wider than peristomium (Fig. 1C). Prostomium and peristomium with large subdermal glands visible dorsally; similar glands present on some anterior thoracic setigers. Pair of red prostomial eyes present laterally, anterior to nuchal groove; each eye with dark red, irregularly pigmented ocellus surrounded by clear lens (Fig. 1B, inset).

Setigers 1–7 similar, parapodia reduced to low mounds from which capillary setae arise in both noto- and neuropodia (Fig. 1A−B; 2A); capillaries 4–6 per row. Setigers 8–9 of females similar in size to those of 1–7, but with capillaries replaced with 5–6 hooded hooks (Fig. 1A). Large inflated genital organ present laterally, on setigers 7–8 of females; central peak and genital pore apparent (Fig. 1A). Males with setigers 8–9 highly modified, muscular, with capillary notosetae replaced by large genital spines (Figs. 1B; 2A–C; 3G); spines of setiger 8 directed posteriorly toward setiger 9, spines of setiger 9 directed anteriorly (Fig. 2C−D); prominent copulatory organ present between paired genital spines of setiger 9 (Fig. 3G−H); phase contrast observations of whole mounted specimen suggest lumen filled with numerous nuclei (Fig. 3G−I, arrows), histological observations by KJE confirm a secretory structure filled with numerous zymogen-like secretory granules; sperm not observed. Neurosetae of setigers 8–9 with 5–6 hooded hooks per fascicle. Males with internal oval-shaped organ, apparent externally between setigers 7–8 when stained with methyl green (Fig. 3B, D), this organ identified as genital duct (Eckelbarger & Grassle 1987b). Abdominal setigers with 5–6 hooded hooks in both noto- and neuropodia, reduced to 2–3 hooks in posterior setigers and one hook in far posterior setigers.

Genital spines of setiger 8 numbering 6–8; spines of setiger 9 larger and more robust than those of setiger 8; usually with four emergent spines. Individual spines variable in shape, with those of setiger 8 more sharply curved (Fig. 2C−D); spines of setiger 9 larger, less curved, sometimes flattened and with grooved apical end; sometimes pairs of spines fused, with shallow groove directed toward setiger 8 (Fig. 2D), replacement spines apparent upon dissection. Capillary setae unilimbate with narrow transparent wing. Hooded hooks with short but thick main fang and at least three pairs of apical teeth; hood inflated, shaft with distinct manubrium or enlargement (Fig. 2F−G).

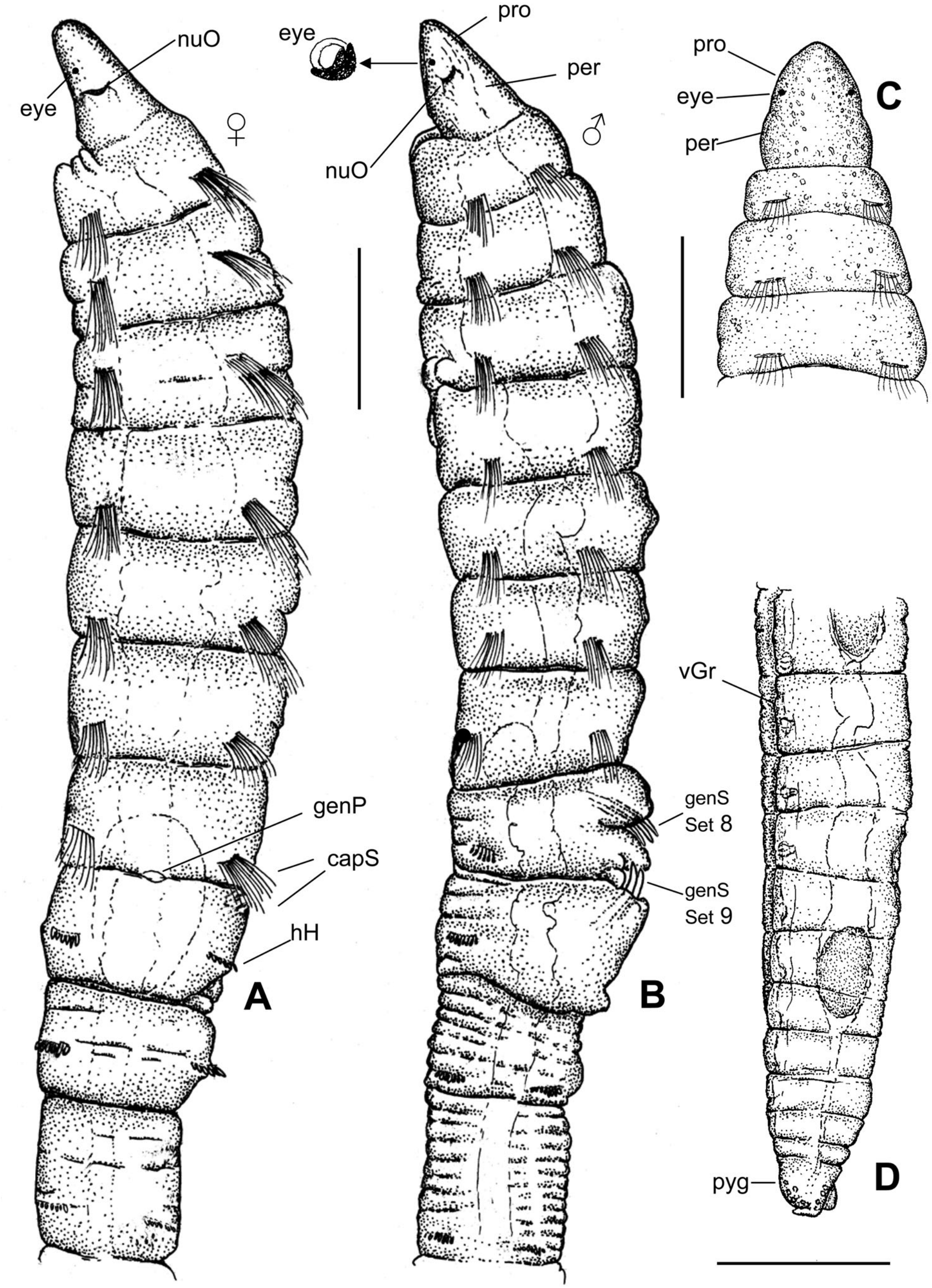

FIGURE 1. *Capitella teleta* sp.nov. A, anterior end of female, left lateral view; B, anterior end of male, left lateral view; C, anterior end, dorsal view; D, posterior end, left lateral view. Abbreviations: capS, capillary setae; genP, genital pore; genS, genital spines; hH, hooded hooks; nuO, nuchal organ; per, peristomium, pro, prostomium; pyg, pygidium; vGr, ventral groove. Scale bar: A–D, 500 µm.

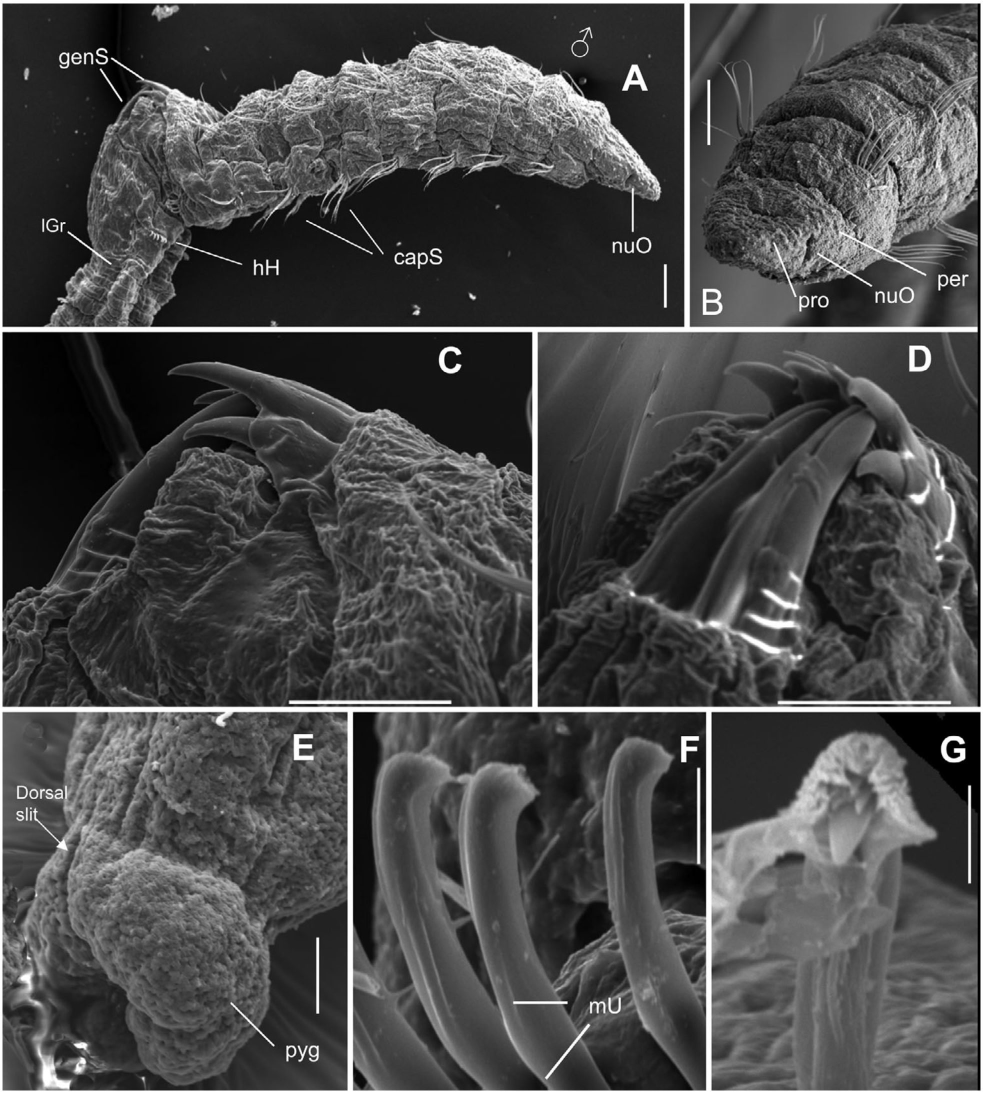

FIGURE 2. *Capitella teleta* sp. nov. A−G, scanning electron micrographs. A, anterior end of male specimen in right lateral view showing entire thoracic region; B, anterior end in dorsal-frontal view; C, detail of setigers 8–9 of male in right lateral view; D, same, in posterior view from setiger 9 (white lines are charged adhering ligaments); E, pygidium in right dorsolateral view; F, hooded hooks from abdominal neuropodium of male showing shape of shaft inside sheath and manubrium (swelling) on shaft; G, abdominal hooded hook in frontal view. Abbreviations: capS, capillary setae; hH, hooded hooks; lGr, lateral groove; mU, manubrium; nO, nuchal organ; per, peristomium; pro, prostomium; pyg, pygidium. Scale bars: A, 200 µm; B–E, 100 µm; F, 10 µm; G, 5 µm.

Pygidium with two rounded lobes and narrow dorsal slit-like notch (Figs. 1D, 2E, 3E−F); lipid drops apparent in lobes (Fig. 3F).

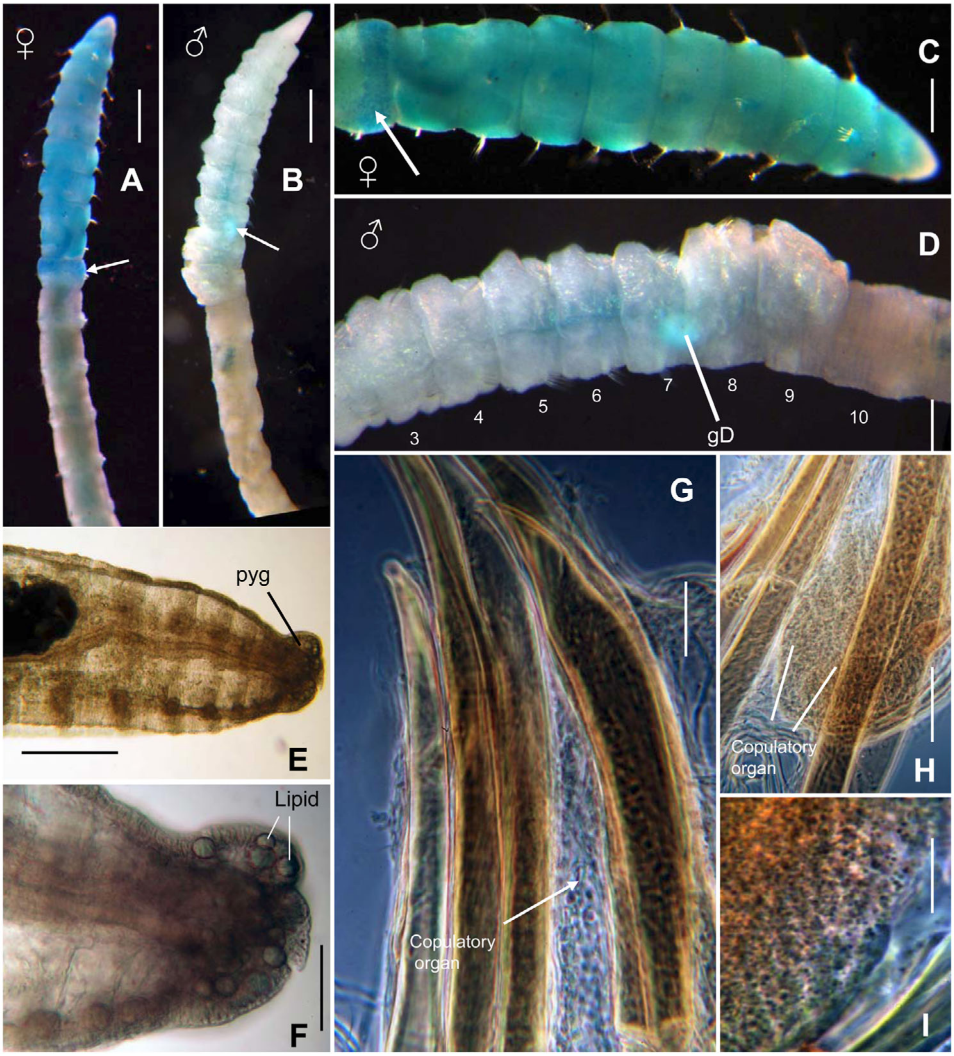

FIGURE 3. *Capitella teleta* sp. nov. A–I, photomicrographs. A, anterior end of female, dorsal view showing methyl green staining reaction; B, anterior end of male in right lateral view showing methyl green staining reaction; C, detail of female showing turquoise-colored band; D, detail of male showing segmentation and location of genital duct; E, posterior end, left lateral view; F, pygidium, left lateral view showing lipid droplets; G–H, genital spines from setiger 9 showing position of copulatory organ; I, detail of copulatory organ tissue showing zymogen-like granules. Abbreviations: gD, genital duct; pyg, pygidium. Scale bars: A–B, 500 µm; C–E, 300 µm; F, 100 µm; H, 200 µm; I, 100 µm.

Hermaphrodites. Hermaphrodites are defined by having genital spines in setigers 8 and 9 and some evidence of female reproduction in the abdominal setigers. They are protandric in that males with no evidence of female reproductive activity turn into hermaphrodites. It is not possible to say by macroscopic inspection whether a hermaphrodite is in the male phase, i.e., a functional male, except by mating such individuals with virgin females and determining whether the female's eggs become fertilized. The weight of evidence is that once having become hermaphroditic, they are simultaneous hermaphrodites for a period of time (J.P. Grassle, pers. obs.).

Methyl green staining pattern. Males initially retaining stain, but after differentiation (destaining), no staining pattern is apparent except for the internal organ in setiger 7 (Fig. 3B, D). Females retaining stain on thoracic setigers 6–9, with a distinct turquoise speckled band encircling the anterior half of setiger 9 on most specimens (Fig. 3A, C, arrow); abdominal segments not retaining stain after differentiation. Genital organs in setigers 7−8 of females staining a milky green color.

Cytochrome oxidase I (COI). The sequence of the entire predicted open reading frame and flanking 5 and 3' UTR (underlined) is:

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   1 TGGTTAACTTCCACTAATCATAAGGAGATTGGTACTCTATATTTTATTATAGGAATTTGAGGTGGACTTG 70
  71 TGGGGACAACTATGAGAGTCTTAATTCGTACAGAATTAGCTGTTCCAGGTTCTTTTTTAGGTGAGCAAGT 140
 141 TTATAACACTGTTGTTACTGCTCACGCGTTTTTGATAATTTTTTTTTTAGTGATGCCTGTGTTTATAGGA 210
 211 GGCTTTGGTAATTGGTTAATTCCGTTAATGTTATCTGCTCCTGATATGGCTTTTCCCCGTATAAATAATT 280
 281 TAAGGTTTTGGTTATTACCGCCTTCTCTTATTCTTCTTTTAGCTTCTTCTGCTGTTGAAGGAGTGACTGT 350
 351 TTATAATATGCGAACATCTTCTATAATTATGGAGCGGGTTACTTTATTAGTTTGGTCTCTTTCTATTACG 420
 421 GCTATGTTATTAATTGGGTCTCTTCCTGTGTTAGCTGCTGGGATTACTATATTATTAACTGATCGGGGTG 490
 491 GTGATCCTGTTCTGTATCAACACTTATTCTGGTTTTTTGGGCACCCTGAGGTGTATATTTTAATTCTTCC 560
 561 GGCTTTTGGTGTGATTTCTCACGTTGTGAGGCATTATTCACATAAAAAATCGACTTTTGGCCCTTTAGGA 630
 631 ATGATTTATGCTATAATGGCTATTGGGTTTTTAGACGTGGACACTCGAGCTTATTTTTCTTCTGCCACTA 700
 701 TAATTATTGCTGTTCCCACTGGTATTAAATTTGAGCCGGCTTTACTTTGGGCTTTAGGATTTATTGGTTT 770
 771 ATTTACTATGGGGGATGTTGCTCTTCATGACACCTATTATGTTGTAGCCCATTTTCATTATGTGTTGTCA 840
 841 ACTGGGGCTGTTTTTGGGCTTTTCTGTGGTTTTATTCACTGGTTTCCTTTATTTACAGGGGTAACTATTC 910
 911 ACCCTCGTTGGGCTAATGCGCATTTTTTTATAATGTTGATTGGTGTTAATTTAACTTTCTTCCCCCAACA 980
 981 TTTCCTTGGATTAGCAGGACTTCCTCGTCTAGGGGCTATTATGTCTTTCTTATCTTTAATGTTTTTCGTT 1050
1051 TTTATTGTTTGGGAAGCTCTTTCTGCTCAACGGCCTATGATTACTTCAGGGTATATGGCTACTTCTTTAG 1120
1121 AGTGAAAAAGGGTTCTTCCTAGAGCTTCTCATAACAGGGGTGAAAATCCTAAAATGATGGGTTATATTGA 1190
1191 AGGCTAAATTAATTTAGCTATGTGAGTTGTTATTAACCTAAGGGTTTAAATTAA 1244
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Etymology. The epithet *teleta* is from the Greek *telete*, defined as "initiation," and refers to *Capitella* sp. I, the initial or first sibling species of *Capitella* identified in laboratory culture.

Geographic distribution and habitat. *Capitella teleta* sp. nov. is widely distributed in North America, occurring in intertidal to shallow-water habitats along the northeastern U.S. coast with confirmed records from Boston Harbor to Long Island, in the eastern Pacific from Long Beach Harbor, California, north to the Elkhorn Slough, California (Grassle & Grassle 1976; Grassle 1980, 1984), and probably extending north to British Columbia. The species is also known from Japan (see papers by Tsutsumi in Appendix 1). Specimens from Europe were sent to the second author for identification in culture and by allozyme electrophoresis. *Capitella* sp. I was not found in samples from Oslo, Norway; Reykjavik, Iceland; Newcastle-upon-Tyne, England; Firth-of-Clyde, Scotland; Wadden Sea, Holland; or Helgoland and Sylt, Germany. The species was confirmed, however, from samples provided in 1984 by J.-P. Guérin from the Cortiou and Fos localities in the Port of Marseilles in the Mediterranean.

Examination of the syntype of *Capitella acuta* (Verrill, 1874). The only species of *Capitella* to have been described from New England waters was *C. acuta* (Verrill) as *Ancistria acuta* Verrill, 1874 from Casco Bay, Maine, from a depth of about 30–40 m. The original report included an illustration of an anterior end published in one account (Verrill 1874a: pl. VI, fig. 3, published May, 1874), and a brief description in a separate paper (Verrill 1874b: 386). A specimen believed to be the type of this species was subsequently examined and briefly described by Hartman (1942: 69–70) and is possibly the same as the *C. capitata* included among the unpublished illustrations of A.E. Verrill included in Hartman (1944: pl. 59, figs. 3, 3a−b). In order to compare *C. teleta* sp. nov. with these earlier accounts of *C. acuta*, the syntype (YPM 2712) was requested from the Yale Peabody Museum of Natural History and examined.

Verrill's (1874b: 386) description of *Ancistria acuta* was very brief and included the following:

> "Body elongated, terete, slender, but shorter than the preceding, thickest anteriorly, composed of numerous short, distinct segments, of which the anterior ones are biannulated. Head conical, acute. The seven anterior segments bear fascicles of several long, slender, acute, bent setae, both above and below. The succeeding segments bear fascicles of elongated uncini. Diameter of body, 0.5 mm to nearly 1 mm. Broad Sound, Casco Bay, fifteen to twenty fathoms."

This original account appears to describe a female with capillaries on setigers 1–7 and an elongate, conical prostomium. The figure depicts a worm with a conical head with an acute tip and no distinction between the prostomium and peristomium, nine anterior setigers, the first seven of which are biannulate and exhibit capillary setae, followed by setigers 8–9 which are multiannulate and have fascicles of small hooks, but no genital spines.

Hartman (1942: 69–70) provided the following comments on the single specimen of *Ancistria acuta* she found in the Peabody Museum collections:

> "The … single specimen [is] in two pieces. The prostomium is somewhat spatulate or broadly rounded anteriorly, about as long as broad. The first segment is achaetous. The next 6 segments have pointed setae dorsally and ventrally; the seventh has pointed setae and uncini, the eighth and ninth have uncini only. Between the eighth and ninth, on the dorsal side, are stout copulatory hooks. The abdominal segments are provided with uncini only. This [specimen] therefore is to be referred to *Capitella*. In so far as its characters are still determinable, it agrees with *C. capitata* (Fabricius) but the minute, imperfect condition of the specimen renders positive identity difficult. The prostomium is anteriorly more truncate than in typical *C. capitata*, but the surface epithelium has been dried out at some time so that this may not be significant."

Hartman's account differs so greatly from that of Verrill in the shape of the prostomium, setation of the thoracic region, and nature of setigers 8–9 that one can only conclude that different specimens were being described.

As part of her publication of the unpublished plates of Verrill intended for his "New England Annelida," Hartman (1944: plate 59, figs. 3, 3a−b) presented figures identified by her as *Capitella capitata*. Figure 3 is the dorsal view of a male with an elongated prostomium, distinct peristomium, setigers 1–6 with capillaries, setiger 7 with hooks and capillaries (but with noto- and neuropodial positions reversed), and genital spines and hooks on setigers 8–9. Figure 3a is an anterior dorsal view of a juvenile specimen with a short, rounded prostomium with a pair of eyes, setigers 1–4 with capillaries, and setigers 5–10 with hooks (Hartman thought this was a female). Figure 3b is a detailed illustration of the copulatory apparatus of a male showing genital spines on setigers 8–9 and a large copulatory organ on setiger 9. Figure 3b may be from the same specimen illustrated in fig. 3. The illustration of the male (fig. 3) agrees with the specimen described by Hartman (1942) except that the prostomium is elongate instead of truncate. Hartman (1942: 332) noted that Verrill was known to have made many of his illustrations from living material and it is possible that if fig. 3 is the same as the specimen that Hartman examined, then the truncated prostomium could have been an artifact of preservation.

The syntype (YPM 2712) from the Yale Peabody Museum of Natural History is the same specimen examined by Hartman (1942) and more or less agrees with her account except that it is now in three parts instead of two. The specimen is small: the three fragments together are 2.4 mm long and 0.37 m wide for ca. 20 setigerous segments including a narrow, asetigerous posterior end. The first fragment consists of the prostomium/and setigers 1–6; the second fragment includes setigers 7–10; the last fragment consists of 11–20 setigers and the narrow pygidial area. The prostomium is short, rounded anteriorly, 2.5 × as wide as long, and eyes are not apparent; the peristomium is separated from the prostomium by a groove, 3.3 × as wide as long and recessed into setiger 1. The first six setigers have only capillaries; setiger 6 is the widest segment on the body; setiger 7 has capillary notosetae and hooked neurosetae. Distinct genital spines are present on setiger 7; they are not visible on setiger 9. Setiger 10 and following have only hooded hooks.

The specimen is very small, <3.0 mm, and has only 20 setigers; although genital spines are present on setiger 8, the specimen is not a fully developed adult. The presence of neuropodial hooded hooks on setiger 7, a short rounded prostomium, and an elongate and narrow asetigerous posterior region suggest that it had not fully developed adult morphology. Because of this, it is not possible to refer the specimen to any described species of *Capitella* including *C. teleta*. Further, the 30–40 m depth range in Casco Bay, Maine, where the specimen is said to have been collected is deeper than expected for *C. teleta*, an intertidal or shallow subtidal species. With no characters to distinguish the species from its congeners, *C. acuta* should be considered *incertae sedis.*

Discussion

Capitella teleta and *C. capitata*

C*apitella teleta* sp. nov. is one of at least a dozen sibling species that have been confirmed in laboratory culture and, in most cases, genetically (Grassle & Grassle 1976; Eckelbarger & Grassle 1987a–b; Wu et al. 1991; Gamenick et al. 1998; Mendez 2002, 2006). As *Capitella* sp. I, the species has been the subject of extensive research on many aspects of its biology, physiology, genetics, and ecology; the published literature on this species represents the most extensive for any deposit-feeding polychaete. No attempt is made here to review this literature, but the sources of material and records of more than 200 publications that deal with the species are summarized in Appendix 1.

Blake (2009) considers *C. capitata* to be an Arctic-subarctic species and suggests that other records from boreal and temperate localities represent different species. When compared with *C. capitata* from Greenland (Blake 2009), *C. teleta* appears more slender, with an elongate, narrow body instead of one that is large, robust, and thickened along most of its length; except for setigers 8–9, the thoracic region of *C. teleta* is not as enlarged as in *C. capitata*. In *C. teleta* the prostomium/peristomium is longer than wide, flattened, with only a weak dorsal notch or none at all, and is merged with the first setiger, which is only 1.5 × wider than the posterior margin of the peristomium. In contrast, the prostomium/peristomium of *C. capitata* is shorter and much smaller than setiger 1, into which the peristomium is usually recessed. Setigers 1–7 of both species have capillary setae and setigers 8–9 have either noto- and neuropodial hooded hooks or the dorsal hooks are replaced by genital spines in males; however, unlike *C. capitata*, capillaries have not been observed in the neuropodia of setigers 8–9. The hooded hooks of *C. teleta* have three rows of apical teeth, whereas the hooks of *C. capitata* have at least four rows. Setigers 8–9 of *C. teleta* males are greatly enlarged proportionally compared with the first seven thoracic setigers and the genital spines are larger and more prominent than in *C. capitata,* where the first seven thoracic setigers are enlarged and setigers 8–9 are reduced and lack heavy musculature on specimens with genital spines. While males of *C. teleta* have heavy dorsal musculature surrounding the spines on setiger 9, females show no evidence of either genital spines or the heavy musculature of males. However, some hermaphroditic specimens that are present in the collections exhibit a mixture of male and female morphology. Males of *C. teleta* have no apparent methyl green staining reaction, whereas females retain stain on posterior thoracic segments and have a distinct turquoise-colored speckled band on setiger 9; this band is sometimes on the anterior margin of the segment, the posterior margin, or both.

In terms of reproduction and development, there are also distinct differences between *C. capitata* and *C. teleta*. In *C. capitata* the majority of specimens (>80%) have genital spines and the species appears to be hermaphroditic (Blake 2009). In contrast, *C. teleta* is primarily a sexually dimorphic species with protandric hermaphrodites being produced from feminized males when densities of females are low (Holbrook & Grassle 1984; Petraitis 1988). Blake (2009) reports *C. capitata* from Greenland collections as having large eggs ($\bar{x}$ diameter = 312 µm) and with 1125–1300 eggs being spawned into their tubes, whereas in *C. teleta* (as *C*. sp. I) the eggs are also large (260 × 180 µm), but with only 30–400 eggs spawned into individual tubes (Grassle & Grassle 1976). The greater number of eggs per spawning in *C. capitata* undoubtedly is related to its much larger size.

Capitella teleta **and European accounts of** ***C. capitata***

European descriptions of *C. capitata* date from Eisig (1887), who provided careful descriptions of *Capitella* from the Bay of Naples, Italy. *C. teleta* sp. nov. is more similar to this cosmopolitan concept of *C. capitata* reported from European waters than to the new description from Greenland provided by Blake (2009).

Eisig (1887) reported that *C. capitata* from Naples had capillaries only in setigers 1–6, followed by a transitional segment (setiger 7) with capillaries, hooks, or mixed fascicles. Warren (1976a) found that most British specimens had capillaries on setiger 7 and that rarely capillaries were also present in neuropodia of setigers 8–9. These differing accounts of the thoracic setal patterns from Naples and Britain suggest that more than one species is present, with *C. teleta* appearing to be intermediate by having capillaries in setigers 1–7 and none on setigers 8–9. The presence of cryptic or sibling species of *Capitella* in European waters is suggested by Pearson & Pearson (1991) from Scotland, Gamenick et al. (1998) from the North Sea and the Mediterranean, and Mendez (2002) from Spain. Additional morphological differences between *C. teleta* and Eisig's account of *C. capitata* may include the degree of development of the modified setigers 8–9 in males. Eisig (1887: plate 27, fig. 4) shows the profile of a male specimen in which setigers 8–9, despite bearing genital spines, are not enlarged relative to setigers 7 and 10. In contrast, setigers 8–9 of *C. teleta* are larger and more prominent than other thoracic and anterior abdominal setigers. The prostomial shape and proportions are similar between the two accounts, but the small red eyes present in *C. teleta* were not reported nor illustrated by Eisig (1887). Small prostomial eyes were reported for *C. capitata* from German waters by Hartmann-Schröder (1996), who illustrated a specimen in which setigers 8–9 were actually smaller than other thoracic setigers, again suggesting that multiple sibling species of *Capitella* are present in Europe.

Eisig (1887) reported that *C. capitata* from Naples had large eggs (>288 µm) similar to those of *C. teleta* (260 × 180 µm). However, the Naples species produced planktotrophic larvae that were planktic for seven days instead of the lecithotrophic larvae of *C. teleta* that only spend a few hours in the plankton (Grassle & Grassle 1976). In contrast to the large egg diameters reported for *Capitella* from Naples and Woods Hole, Massachusetts, Warren (1976b) reported egg diameters <100 µm and with upwards of 10,000 or more fertilized eggs being deposited in the tubes of females from Devon, England. The differences in egg diameters and numbers of fertilized eggs produced per female brood tube between the two European accounts of *C. capitata* coupled with the observations of sibling species by Pearson & Pearson (1991), Gamenick et al (1998), and Mendez (2002) from different parts of Europe suggest that there is as much cryptic speciation present in European populations of *Capitella* as has been identified in the northeastern United States by Grassle & Grassle (1976).

The sexually dimorphic nature of the European *C. capitata* in Eisig's and Warren's accounts agrees with that of *C. teleta*, although the latter species appears to produce hermaphrodites when female densities are reduced. Similar observations are not available for European populations.

These results suggest that the European literature refers to several closely related species. There is scanty but unequivocal evidence that *C. teleta* and *C.* sp. II, another of the Grassle North American sibling species complex, occur in the Port of Marseilles (J.P. Grassle, unpublished). Specimens were provided by J.-P. Guérin from the Cortiou and Fos localities in 1984. The Fos sample had pieces of four worms belonging to at least two species. One species was identified by allozyme electrophoresis as *Capitella* sp. I. The other Fos fragments belonged to a species with small eggs, ~90µm, and at least one of the individuals was probably a hermaphrodite. There were more individuals in the Cortiou sample and it was possible to culture some of the worms with lecithotrophic eggs. They were confirmed as *Capitella* sp. II. It is therefore probable that European sibling species of *Capitella* include both endemic species and some of the sibling species complex identified from North America in laboratory culture by the second author and others (Grassle & Grassle, 1976; Eckelbarger & Grassle 1987a). The taxonomy of European species of *Capitella* is thus highly complex.

Sibling species of *Capitella* from the northeastern United States

At least six sibling species of *Capitella* from the northeastern United States have been identified from specimens collected in the field and cultured in the laboratory (Grassle & Grassle 1976; Grassle 1980, 1984, Eckelbarger & Grassle 1987a–b). Morphological and life history characteristics of five of these species are compared with *C. capitata* from Greenland (as reported by Blake 2009) (Table 1). Another sibling species, *C*. "ORLEANS," is not included because of the lack of morphological information (but see summaries by Eckelbarger & Grassle 1987a; Blake 2000, 2009).

Capitella teleta sp. nov. is described here; *C. jonesi* was described by Hartman (1959), and *C. capitata* is redescribed by Blake (2009). *C. teleta* and *C. capitata* have already been compared earlier in this discussion (see above). There is little published information on the morphology of sibling species *Capitella* Ia, II, and IIIa.

Capitella jonesi was originally described as *Capitellides jonesi* by Hartman (1959) because both males and females had genital spines, which at the time was a differentiating character for the genus *Capitellides*. The genus *Capitellides* was subsequently referred to *Capitella* by Warren (1976a). *C. jonesi* differs significantly from all species of *Capitella* by having thoracic setigers with capillary noto- and neurosetae limited to setigers 1–3 instead of the typical distribution on setigers 1–6 or 1–7. In this respect, *C. jonesi* is neotenous—all species of *Capitella* pass through a developmental phase in which capillaries are limited to setigers 1–3. In other species capillaries eventually replace hooded hooks on subsequent thoracic setigers. Setiger 9 of *C. jonesi* is the longest thoracic segment instead of the shortest as in *C. capitata*, or of equivalent length as in *C. teleta*.

Because morphological descriptions of *C*. sp. Ia, II, and IIIa are not available, adults cannot be fully compared with *C. teleta*, *C. jonesi*, and *C. capitata*. There are however, sufficient differences in reproductive biology, larval morphology and development, chromosome counts, and genetics to readily distinguish the sibling species from the named species and from one another (Table 1). These differences have been discussed extensively by Grassle & Grassle (1976), Eckelbarger & Grassle (1987a–b), Grassle (1980, 1984), and Grassle et al. (1987).

TABLE 1. Morphology and life history traits in six species of *Capitella*.

Morphology/ Species	***C. teleta* (I)**	**Ia**	**II**	***C. jonesi* (III)**	**IIIa**	***C. capitata* (Greenland)**
Prostomium	Broadly triangular, with weak dorsal groove	Sharply conical	Long, triangular	Broadly triangular	Broadly triangular	Broad, wide, with deep dorsal groove
Peristomium	Wider than long, merged with prostomium	Partly fused to prostomium	Partly fused to prostomium	Partly fused to prostomium	Distinct, from prostomium, narrow, very wide	Wider than long, distinct from prostomium
Pygidium:						
Shape	Lobed	Plain	Lobed	Flared	Lobed	Simple lobe
Dorsal cleft	Narrow slit	Absent	Present	Present	Present	Absent
						5 (5–6)
Hooded hooks:	3 (3–5)	3 (0–5)	3 (0–3)	3 (3–4)	?	4 (~7)
No rows apical teeth	2 (4–6)	2 (3–4)	2 (4–5)	2 (4–5)		3 (~5)
(No. teeth per row)	1 (5)	1 (5)	1 (4)	1 (2–3)		2 (~4)
						1 (2–3)
No. ♂ genital spines:						
Setiger 8	6	6	6	?	6	6
Setiger 9	4	4	4	?	2	4
Body weight (mg)	3–12	10.1	12.0	1–4	1.7	?
Diploid No. chromosomes	20	20	26	14	26	?
Sex	♂, ♀, P♂/♀	♂, ♀, ? ♂/♀	♂, ♀, P ♂/♀	P ♂/♀	♂,♀	P ♂/♀
Ave. Egg diameter (µm)	260 × 180	75	230	50	250	312
No. eggs/brood	30–400	200–2000	30–400	200–1000	30–50	1100–1300
Sperm (µm) (Ave. ± 1 SD):						
Nuclear length	3.10 ± 0.22	5.20 ± 0.14	4.95 ± 0.15	?	6.10 ± 0.24	?
Acrosome length	1.38 ± 0.06	1.16 ± 0.06	0.94 ± 0.05		1.35 ± 0.04	
Middle piece	2.60 ± 0.25	2.93 ± 0.45	2.73 ± 0.15		3.61 ± 0.21	
Larval development mode	Lecithotrophic	Planktotrophic	Lecithotrophic	Planktotrophic	Direct	Lecithotrophic
Larval cilia:						
Prototroch & telotroch	Well devel.	Well devel.	Well devel.	Poorly devel.	?	Well devel.
Neurotroch	Narrow band	Large patch	Broad band	Small patch	?	?
Body cilia	Absent	Present	Absent	Present	?	Absent
Pygidial bands	Present	Present	Present	Absent	?	?
Time planktic	Several hours	Several days	6–24 hours	≤ 2 weeks	None	

Modified from Blake (2009). Data from Hartman (1959); Grassle & Grassle (1976); Grassle et al. (1987); Eckelbarger & Grassle (1987a–b); ♂/♀ = hermaphrodite, P = protandrous.

Capitella teleta, an opportunistic polychaete

Capitella teleta sp. nov., as *Capitella* sp. I, was identified as the prime opportunistic species in post-spill samples collected as part of the West Falmouth, Massachusetts, oil spill study (Grassle & Grassle 1974; Grassle & Grassle 1976; Sanders et al. 1980). Of the several sibling species of *Capitella* reported from the northeastern United States, *C. teleta* appears to be the most opportunistic. According to Grassle (1980), the species had the most rapid response to disturbed habitats, the highest rate of increase, largest maximum population size, and highest mortality. Grassle (1980) suggested that the species might be uniquely adapted to exploit organically enriched sediments.

The highly opportunistic nature of *C. teleta* might explain its wide distribution from the northeastern United States to southern and central California, Japan, and the Mediterranean. The records from California are of particular interest because specimens provided by D.J. Reish were identified as *Capitella* sp. I by J.P. Grassle after comparison of results from allozyme electrophoresis and cross-breeding experiments (see Appendix 1). These results are important because they demonstrate that at least some of the results of Reish's studies on marine pollution impacts involved this species (as *C. capitata sensu* Reish). Reish (1957, 1959, 1960, 1970) was one of the first biologists to demonstrate the relationship of *C. capitata* to waste discharges of biological origin in southern California waters. He classified benthic communities into different zones, with *C. capitata* regarded as the indicator of the polluted zone. Later, with support from the U.S. Environmental Protection Agency, Reish (1980a–b) established culture protocols for *C. capitata* and other polychaetes that have been widely applied to environmental toxicity or bioassay tests. The results from southern California are similar to those from the West Falmouth oil spill study where *C. teleta* (as *C. capitata*) was an initial successful colonizer of the heavily contaminated sediments (Sanders et al. 1980).

The wide distribution of *C. teleta* and its opportunistic nature in shallow-water organically enriched sediments suggests that the species is probably one that is transported in ballast water and that it may have been introduced into some areas where it has been reported, such as the Port of Marseilles on the Mediterranean. At this time, however, we cannot speculate as to the geographic origin of the species except that the concentration of six or more closely related sibling species identified from a small geographic area in the northeastern United States suggests a focal point.

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APPENDIX 1. Annotated Guide to Literature Pertaining to *Capitella* sp. I, now referred to the new species designation, *Capitella teleta* Blake, Grassle, & Eckelbarger.

[1] Kennneth R. Tenore initiated his *Capitella* sp. I culture with worms collected in the Woods Hole region, probably in 1970, which were identified by J. P. Grassle using allozyme electrophoresis and controlled breeding experiments. His cultures were always large and multi-generational, and after Tenore moved the cultures to the Skidaway Institute of Oceanography (SIO) in 1975, the species identity was rechecked by Grassle using worms sent from SIO in November 1978. The cultures were moved again to the University of Maryland's Chesapeake Biological Laboratory in 1985, where they were maintained for several years. Studies using *Capitella* sp. I from these cultures are identified with the superscript[1].

[2] Thomas L. Forbes and Valery E. Forbes established *Capitella* sp. cultures using worms collected from Setauket Harbor, Long Island, New York in 1984. J. P. Grassle confirmed the identity of worms from the Setauket Harbor culture as *Capitella* sp. I using allozyme electrophoresis and cross-breeding with known *Capitella* sp. I in June 1985. Tom Forbes maintained this culture at SUNY/ Stony Brook and then at Roskilde University, Denmark for several years. Valery Forbes has continued to maintain this culture to the present, and no *Capitella sp.* I from any other geographic sources have ever been added to the culture. Studies using *Capitella* sp. I from this source are marked with the superscript [2].

[3] Study of *Capitella* sibling species began as part of a wider study of the response of infaunal benthic communities to an oil spill in West Falmouth Harbor in 1969 (Sanders et al. 1980). High mortalities in the community were rapidly followed by huge population increases of opportunistic species, chiefly polychaetes, and most prominently worms referred to as *Capitella capitata*. Worms collected in 1969 and 1970 from several intertidal and subtidal sites in the Wild Harbor estuary, and the nearby Sippewissett Marsh, were frozen for subsequent allozyme electrophoresis, and some worms were kept in laboratory mass cultures. Early allozyme studies using two malate dehyrogenase loci were misinterpreted as evidence for intraspecific genetic variability in "*C. capitata*" (Grassle and Grassle 1974), but once other allozyme loci had been examined in concert with laboratory pair-mating experiments, this error was corrected (Grassle and Grassle 1976, 1977). It was apparent that at least six *Capitella* sibling species found in the Woods Hole region were profoundly genetically different, that they did not mate with each other, and that they had very different life history characteristics, most especially their reproductive modes and larval types. The cultures set up in J. F. Grassle's laboratory at WHOI in 1970 by Robert Andrews were subsequently transferred to J. P. Grassle at MBL in September 1972, where both inbred and outcrossed strains of *Capitella* sp. I were maintained until a laboratory malfunction killed many of the cultures in 2003. These worms were used to supply many of the researchers whose work is represented here (identified with the superscript [3]), and to check the identity of *Capitella* spp. collected in the field or sampled from other workers' ongoing laboratory cultures. Subsequent to 2003, *Capitella* sp. I inbred and outcrossed cultures were re-established in Grassle's lab using worms from S. D. Hill and W. G. Wallace. Their cultures were originally established using *Capitella* sp. I received from Grassle prior to 2003.

[4] Elaine C. Seaver established her *Capitella* sp. I culture at the University of Hawaii in 1999 using worms from the cultures of S. D. Hill (see footnote #6), which had in turn come from J. P. Grassle. It is likely that the origins of these cultures include worms from both the west and east coasts of the USA. Seaver and R. M. Savage prepared the biological material that was submitted to the Joint Genome Institute for sequencing of the *Capitella* sp. I genome. Savage obtained his *Capitella* sp. I material directly from J. P. Grassle. Studies using *Capitella* sp. I from these cultures are marked with the superscript [4].

[5] Hiroaki Tsutsumi sent worms from Tomoe Cove, Japan in 1989, 1991, and 1993 that were confirmed as *Capitella* sp. I by crossbreeding them with known *Capitella* sp. I in Grassle's cultures. Since 1992 he has maintained large cultures of Tomoe Cove *Capitella* sp. I for his subsequent research. In some studies, cultures were re-initiated with worms collected from several additional field sites in Japan, e.g., from Dokai Bay (Tsutsumi et al. 2002), Tomioka Bay (Wada et al. 2006), and Kusuura Bay (Kinoshita et al. 2008). Individual papers should be consulted for the origin of the *Capitella* sp. used in the studies marked with the superscript [5]. Tsutsumi (2005), using *Capitella* sp. collected from the Kotsuki River, Kyushu which were identified by crossing them with known Tomoe Cove *Capitella* sp. I, found no genetic difference between embryos that developed and metamorphosed within the parental brood tube and those that swam out of the tube as the expected lecithotrophic larvae.

[6] Susan D. Hill (Michigan State University, MSU) began her research on *Capitella* sp. I in collaboration with J. P. Grassle in the summer of 1985 at MBL. She soon established her own mass culture of worms at MSU using *Capitella* sp. I from J. P. Grassle sent in 1986 and 1988. Joint efforts were made initially to keep this culture as outcrossed as possible, and the strains used included those established with both west coast US worms (e.g. from Kirby Park, California), and strains originating from eastern Massachusetts sites. Subsequently, Hill's cultures were used to establish those of Elaine Seaver, University of Hawaii. Seaver and R. M. Savage prepared the *Capitella* sp. I material that was subsequently used to sequence the *Capitella* sp. I genome (JGI 2007), with Savage receiving his *Capitella* sp. I directly from J. P. Grassle's cultures.

[7] Donald J. Reish initiated his cultures with *Capitella* sp. collected from Los Angeles Harbor (LA). J. P. Grassle subsequently confirmed the identity of one culture as *Capitella* sp. I in a large sample of worms received on 7 December 1978. This was done using allozyme electrophoresis and cross-breeding between LA worms and inbred strains of *Capitella* sp. I originating in Woods Hole (WH). Several of these east-west lines were maintained in Grassle's lab until 2003, where they were intermittently used to produce non-inbred worms by outcrossing them with other strains. Soon after the LA worms were acquired in 1978, pair-matings were set up between male and female LA *Capitella* sp. I and their east coast counterparts (WH) in all possible combinations at 15° C. Irrespective of the identity of the male parents, LA females produced broods with significantly lower numbers of larvae than WH females, and their offspring reached maturity in significantly shorter times (Grassle, unpublished). These results suggested that there were some intraspecific genetic differences between the LA and WH *Capitella* sp. I, although this was not apparent in the allozyme electrophoresis.

[8] With the availability of the *Capitella* sp. I genome on the web http://genome.jgi-psf.org/Capca1/Capca1.home.html, studies are starting to appear based on those sequence data rather than on cultured material.

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