

Redescription of *Capitella capitata* (Fabricius) from West Greenland and designation of a neotype (Polychaeta, Capitellidae)

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Abstract

Capitella capitata (Fabricius, 1780), the type species of the genus, was originally described from the SW coast of Greenland; however, current definitions of the species are largely based on Eisig (1887), who described specimens from Naples on the Mediterranean coast. Eisig's excellent account of the morphology of a sexually dimorphic species has subsequently been applied to specimens collected from worldwide locations. *C. capitata* was considered cosmopolitan in its distribution until J.P. Grassle and others identified numerous sibling species in laboratory culture. A large collection of *Capitella* from locations along the W, SW, and SE coasts of Greenland was provided by the Zoological Museum, University of Copenhagen (ZMUC). The collections included about 680 specimens with distinctive prostomial, thoracic, and setal morphology that differs from the typical depiction of the species in most faunal accounts. A neotype was selected from an excellent collection of approximately 250 specimens from Mårmorilik on the Affarlikasså Fjord on the inner Uummannaq Fjord system, north of Disko Bay. All available collections from the ZMUC are believed to belong to the same species, which is here considered to be Arctic and subarctic in distribution. Additional material from the Alaskan Arctic supports this hypothesis. The Greenland species has a short, cup-shaped, wider-than-long prostomium joined to a narrow peristomial ring that is retracted slightly into setiger 1. In most specimens, the first four thoracic setigers gradually increase in size, with setiger 4 being the largest thoracic segment, and then decrease over the next five setigers, with setiger 9 being smaller than subsequent anterior abdominal segments. The thoracic region is thus markedly distinct visually from the abdominal region. Setigers 8–9 typically lack fascicles of notosetae, but 80% of the specimens examined have genital spines and most have copulatory organs that are secretory in nature: they contain numerous small secretion granules but no sperm. Many of these specimens have eggs and larvae within their tubes, suggesting functional hermaphroditism. The present redescription of *C. capitata* serves to establish a baseline against which the many known but undescribed species can be compared. Previous accounts of *C. capitata* based on the Eisig concept and largely from boreal and temperate localities should be reevaluated.

Key words: Type species, reproduction, larval development

Introduction

Capitella capitata was originally described as *Lumbricus capitatus* by Otto Fabricius (1780) from a location believed to be near the present community of Paamiut on the Frederikshåb peninsula on the SW coast of Greenland. According to the curators of the Zoological Museum, University of Copenhagen (ZMUC), the specimens originally described by Fabricius no longer exist, but numerous collections of *C. capitata* from along the W and SW coasts of Greenland reported by Wesenberg-Lund (1950) are available, as are additional collections including those used for

observations on the reproduction of *C. capitata* in the Disko Bay area (Curtis 1977). A representative collection of *Capitella* from this material was made available by Dr. Danny Eibye-Jacobsen and provided the basis for a redescription and reconsideration of the type species of *Capitella*. Additional comparative material from the Alaskan Arctic was provided by the National Museum of Natural History, Washington, DC (USNM).

A redescription of *C. capitata* is necessary because at the same time that numerous genetically distinct, yet morphologically similar, species of *Capitella* are known to exist (Grassle 1980), a separate body of literature reports *C. capitata* from worldwide locations. Biological studies on a local population of *Capitella* were initiated by Grassle & Grassle (1976), who demonstrated differences in chromosome karyotypes (Grassle et al. 1987) as well as gametogenesis, larval morphology, and development (Eckelbarger & Grassle 1987); however, these results were reported with only limited adult morphology. To date, approximately 12–13 biologically distinct sibling species have been identified in laboratory culture (Grassle & Grassle 1976; Eckelbarger & Grassle 1987; Blake 2000; Wu et al. 1991; Gamenick et al. 1998; Mendez 2002; Blake et al. 2009). *Capitella* sp. I, originally collected from sites in the vicinity of Woods Hole, Massachusetts, has been maintained in culture for over 30 years and is now widely used in experimental studies. This species is described and named in a separate paper in this volume (Blake et al. 2009).

In this paper, a description of the adult morphology of *C. capitata* from W Greenland is presented together with limited observations on reproduction, brooding, and larval development taken from preserved materials. A neotype is selected from a sample taken at Marmorilik, on the Affarlikasså Fjord, just north of Disko Bay or about one-third of the way up the coast of W Greenland (Fig. 1). *C. capitata* is compared with its closest relatives and related species groups are summarized. This study demonstrates that current definitions of *C. capitata* based on the work of Eisig (1887) from the Gulf of Naples and supported by Hartman (1947) and Warren (1976a) refer to other species that differ significantly from the Greenland specimens. By defining the type species, a baseline for a future revision of the *Capitella* species complex is established.

Materials and methods

Collections of *Capitella capitata* from numerous localities along the coast of Greenland (Fig. 1) were provided by the ZMUC. All samples are believed to belong to a single species. Observations were made with light microscopy using phase contrast optics and magnifications up to 1500×. Methyl green (MG) stain saturated in 80% ethanol (ETOH) was used to determine MG staining patterns. Several specimens and dissected parts were dehydrated in 100 % ETOH, cleared with Xylene, and mounted directly on slides with Permount®. These slides were dried for 48 hours on a warming table before use. 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 majority of the more than 670 specimens examined, including the neotype, have been returned to the ZMUC. A subset of specimens from the Marmorilik collection from which the neotype was selected have been provided to the following institutions: USNM, Los Angeles County Museum, Natural History, Los Angeles, California (LACM), and the Museum of Comparative Zoology,

Harvard University, Cambridge, Massachusetts (MCZ). Additional specimens will eventually be provided to other institutions. A few specimens, including those on SEM stubs, have been retained for additional study (JAB).

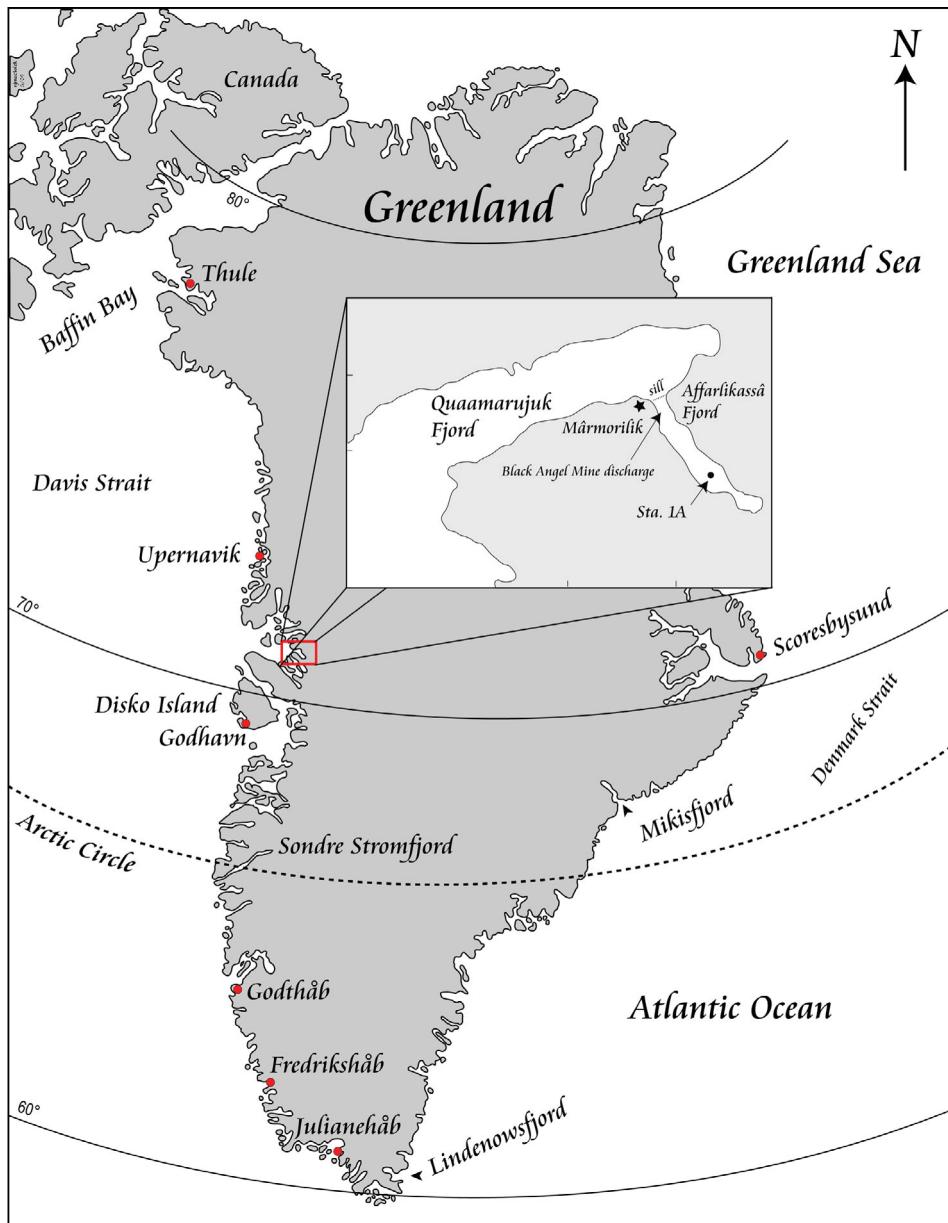


FIGURE 1. Map of Greenland with main collection sites indicated. Inset shows location of Mårmorilik on the Affarlikasså Fjord.

Results

Family Capitellidae Grube, 1862

Genus *Capitella* Blainville, 1828

Type species. *Capitella capitata* (Fabricius, 1780) as *Lumbricus capitatus*.

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 setigerous 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 capitata (Fabricius, 1780) Emended

Figures 2–5

Lumbricus capitatus Fabricius, 1780: 279.

Capitella capitata: Wesenberg-Lund 1950: 91–92; Pettibone 1954: 298–300, fig. 33 r–u; Curtis 1977: 332–33, fig.

6.—Not Eisig 1887: 849–857. pl. 27, figs 1–13; Fauvel 1927: 154–155, fig. 55 a–g; Warren 1976a: 195–209; 1991: 275–282.

Material examined. W Greenland, inshore.—Thule, Thule Harbor, 14 m, coll. 14–15 Aug 1936, Finn Salomonsen, det. Wesenberg-Lund (E. W-Lund), 3 specimens (ZMUC-POL-1961); Tiningnekelak, sandy sediments with brown algae, coll. 05 Jul 1902, Krause, det. E.W-Lund, 16 specimens (ZMUC-POL-1962); Bay N. of Upernivik, 30 m, coll. 10 Aug 1931, Fr. Johansen, det. E.W-Lund, 78 specimens (ZMUC-POL-1963); Upernivik, in the harbor of Skibshavn, 6 m, coll. 16 June 1936, Finn Salomonsen, det. E. W-Lund, 2 specimens (ZMUC-POL-1964); Uummannaq Fjord, probably near the settlement of Uummannaq, coll. 11 Aug 1888, S. Hansen, det. E. W-Lund, 1 specimen (ZMUC-POL-1965); Uummannaq Fjord system, Affarlikasså Fjord, Mårmorilik, coll. 31 Aug. 1976, 20–40 m, Grønlands Fiskeriundersøgelser, Sta. 1A, 71°6.5'N, 51°17'W, ~210 specimens + eggs and larvae in tubes (ZMUC-POL-1966), neotype ZMUC-POL-1967, 5 specimens (USNM 1123187), 5 specimens (LACM 2217), 4 specimens (MCZ 81197). Tasiussaq, Godhavn Harbor, 10 m in clay, coll. 04 Mar 1959, G. H. Petersen, Sta. 62, det. M.A. Curtis, 97 specimens (ZMUC-POL-1968); Lyngmarksbugt, near Godhavn, 69°15'N, 53°30'W, 30 m, clay and stones coll. 12 May 1959, G. H. Petersen, Sta. 134, det. M. A. Curtis: 4 specimens all with genital spines, one with eggs in body (ZMUC-POL-1969); Godhavn, Harbor, Sta. 391, 4 m, sand, 06 Apr 1960, G.H. Petersen, det. M.A. Curtis: 25 specimens (ZMUC-POL-1970); Lyngmarksbugt, Godhavn, Sta. 400, 36 m, clay, 06 Apr 1960, G.H. Petersen, det. M.A. Curtis, 25 specimens (ZMUC-POL-1971); Sta. 158, 8 m, mud, sand, and green algae, coll. 23 Jun 1959, G. H. Petersen, det. M.A. Curtis, 12 specimens (ZMUC-POL-1972); Godhavn, Harbor, Sta.. 269, 9 m sand, coll. 07 Oct 1959, G.H. Petersen, det. M.A. Curtis, 6 specimens (ZMUC-POL-1973); Godhavn coll. Olrik 1 vial (date not stated), 5 specimens (ZMUC-POL-1974); Disko Bay, settlement of Egedesminde, coll. 20 Oct 1890, Bergendal, det. E. W-Lund (1

specimen, ZMUC-POL-1975).—W Greenland, offshore, off Søndre Strømfjord, 41 m, 66°50'N 54°28'W, Danish Ingolf Expedition, Sta. 30, coll. 10 July 1895, det. E. W-Lund, 2 large specimens (ZMUC-POL-1976).—SW Greenland, Kvanefjord, near Frederikshåb, Sta. 25, 115, clay with stones and shell gravel, 61°59'N, 49°45'W, coll. 03 Jul 1912, "Rink," det. E. W-Lund, 2 specimens (ZMUC-POL-1977).—S Greenland: Julianehåb Harbor, Sta. Vac., coll. 24 Aug 1912, "Rink", det. E. W-Lund, 1 specimen (ZMUC-POL-1978); Ikek, Julianehåb, coll. 11 Oct 1929, Poul M. Hansen, det. E. W-Lund, 6 specimens (ZMUC-POL-1979).—SE Greenland, Lindenows Fjord. Coll. Bertelsen. Jul 1935, from several stations, 145 specimens (ZMUC-POL-1980).—E Greenland, Mikis Fjord. Sta. 25, coll. 17 Aug 1933, coll. Bertelsen, det. E.W-Lund, 13 specimens (ZMUC-POL-1981).—Alaskan Arctic, Point Barrow, Arctic Research Laboratory, coll. G.E. McGinitie, det. M.E. Pettibone: 4.3 mi offshore, 65 m, 06 Oct 1949, 2 specimens (USNM 23093); 7.5 mi offshore, ~66 m, 01 Sep 1949, 9 specimens (USNM 23094); 7.5 mi offshore, 66 m, 21 Aug 1948, 1 specimen (USNM 23095); offshore, 22 m, 06 Sep 1949, 7 specimens (USNM 23098); 5 mi offshore, 56 m, 30 Aug 1949, 1 specimen (USNM 23098).

Description. Wide range of sizes available, but in general Greenland collections of *C. capitata* include moderate to relatively large specimens 42–45 mm long, 1.5 mm across thorax, with 55–60 setigerous segments; few rare asexual specimens sometimes larger. Typical specimen from Mårmorilik (Fig. 2A) 37 mm long for 56 setigers, setigers 1–4 of thoracic region 1.5 mm long and 4 mm wide, with setiger 4 largest segment, approximately three times wider than peristomium, subsequent thoracic setigers narrowing over setigers 5–9; abdominal segments narrow in middle setigers, then narrowing further in far posterior setigers. Several larger specimens mostly from deep water also present; two with female characteristics collected off Søndre Strømfjord (Danish Ingolf Expedition 10 July 1895), largest specimen robust, complete, 50 mm long, 3 mm wide across thorax for 74 setigers. Six specimens from Ikek, Julianehåb, coll. 11 October 1929 include four specimens with genital spines and two lacking genital spines but with hooded hooks in notopodia of setigers 8–9; one complete specimen with genital spines, 37 mm long, 3 mm wide across thorax for 84 setigers. Color in alcohol tan, with thoracic setiger 9 sometimes lighter in color than setiger 8 (Figs. 2A; 3A); first two abdominal setigers sometimes more darkly pigmented than posterior thoracic setigers 8–9 (Fig. 2A); oval area surrounding lateral genital pore between setigers 7 and 8 (Fig. 4D) sometimes pigmented dark brown.

Prostomium broad, bluntly rounded on anterior margin, as wide as long, thick, flattened, with distinct middorsal depression merging with and continuing onto peristomial ring (Figs. 2A, 4A–B); nuchal organs simple grooves in notches where peristomial ring joins prostomium (Fig. 4B–C). Peristomium simple incomplete asetigerous ring wider than long, prominent dorsally and laterally, merging into oral opening ventrally, becoming roof of mouth; combined prostomium and peristomium forming short, dorsoventrally flattened "head" with shallow dorsal groove, recessed into larger setiger 1 (Figs. 2A, 4C); eyes absent.

Thoracic region with three distinct parts: (1) first four setigers relatively smooth, often inflated, gradually increasing in size, with setiger 4 largest, all four setigers with shallow intersegmental furrows, lacking lateral and ventral grooves (Figs. 2A; 4A–B); (2) setigers 5–7 with midventral and lateral grooves and deep intersegmental furrows (Figs. 3A; 4A–B); (3) setigers 8–9 modified with male, female, or male/female characteristics (Figs. 3C, 4D–E), setiger 9 usually shortest thoracic segment, sometimes one-half length of setiger 8 and as narrow as one-third length of first abdominal setiger (10). Lateral grooves continuing on 4–6 anterior abdominal setigers; ventral groove continuing to posterior end. Anterior abdominal segments with deep intersegmental furrows and 6–8 creases and folds of cuticle (Fig 4B, D); middle and posterior abdominal segments with numerous similar creases and folds, but these inconspicuous except adjacent to ventral groove.

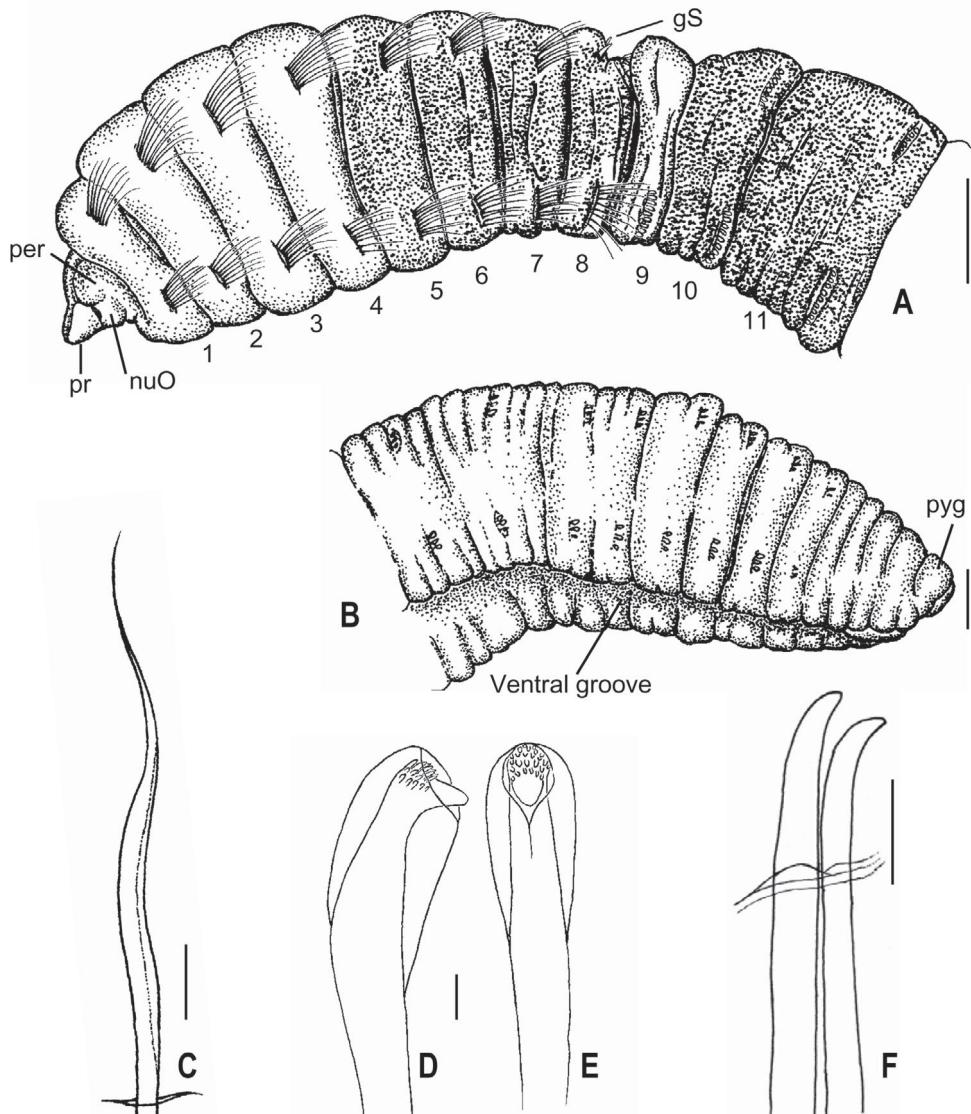


FIGURE 2. *Capitella capitata*. A–F, specimens from Mârmorilik, West Greenland (ZMUC). A, anterior end, lateral view; B, posterior end, lateral view; C, capillary neuroseta from thoracic region; D–E, neuropodial hooded hooks from anterior abdominal neuropodium; F, genital spines from setiger 8. Abbreviations: Gs, genital spines; per, peristomium; pr, prostomium; pyg, pygidium; nO, nuchal organ; vGr, ventral groove. Scale bars: A = 500 µm; B = 200 µm; C = 10 µm; D–E = 20 µm; F = 100 µm.

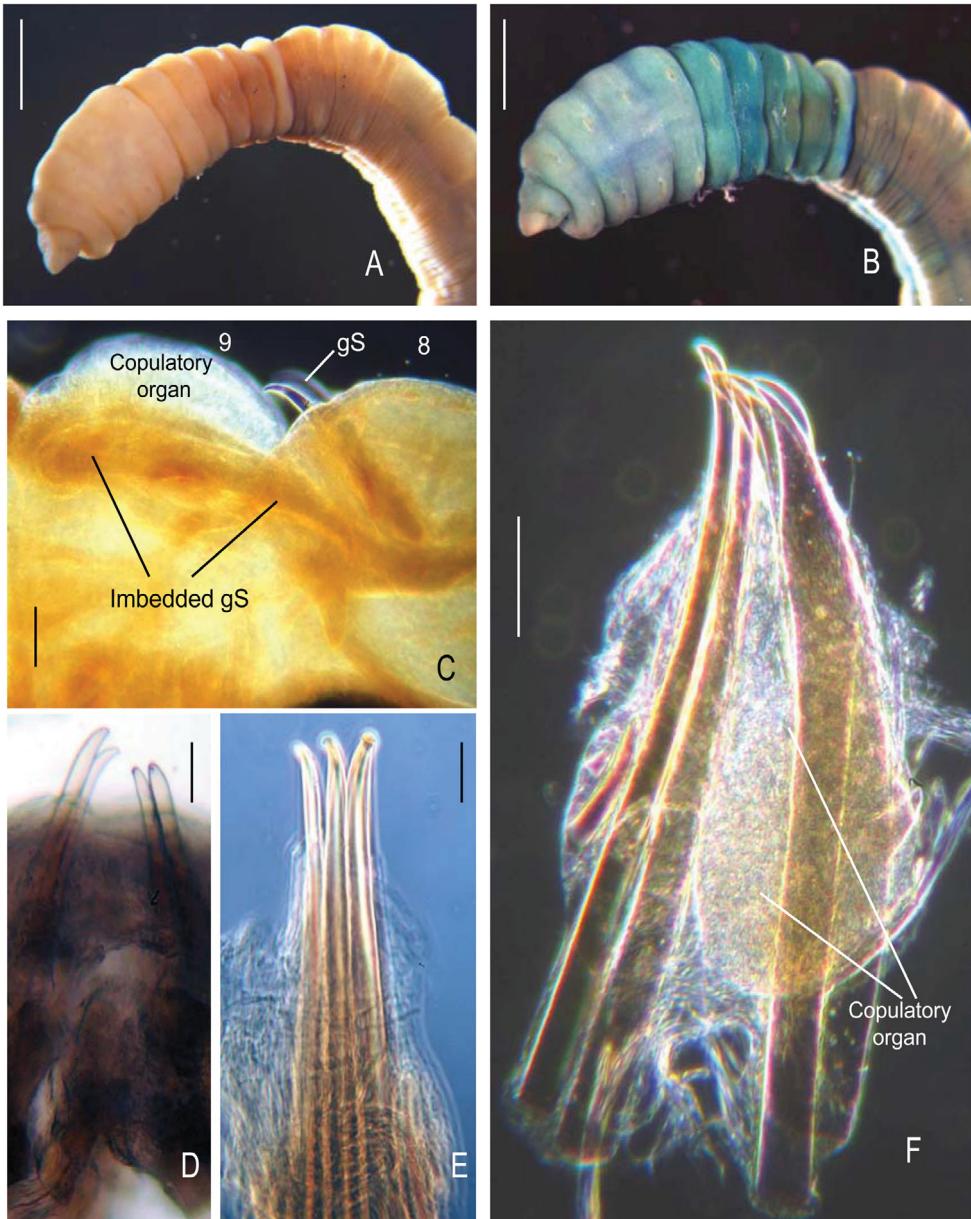


FIGURE 3. *Capitella capitata*. A–F, specimens from Marmorilik, West Greenland (ZMUC). Photomicrographs, A–B with reflected light; C, E–F with phase contrast optics. A, anterior end in lateral view; B, same specimen after methyl green stain applied; C, optical right lateral section of setigers 8–9 showing emergent genital spines of setiger 8, imbedded genital spines of setiger 9 and copulatory organ; D, genital spines of setiger 8 in posterior view in situ; E, entire fascicle of genital spines of setiger 8 dissected; F, entire fascicle of genital spines from setiger 9 dissected showing copulatory organ. Abbreviation: gS = genital spine. Scale bars: A–B = 500 µm; C–E = 100 µm; F = 50 µm.

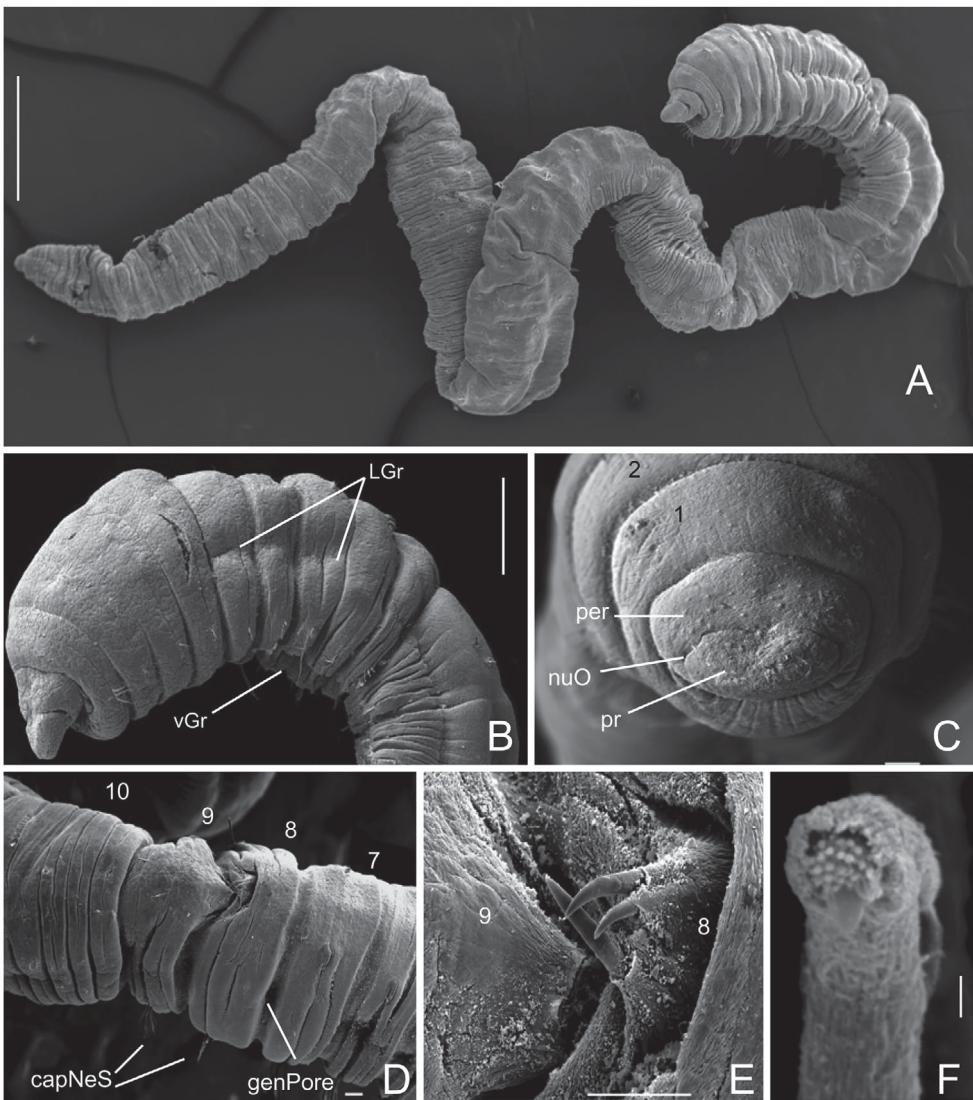


FIGURE 4. *Capitella capitata*. A–F, specimens from Mårmorilik, West Greenland (ZMUC), SEM micrographs. A, entire specimen, mostly in lateral view; B, anterior end of a second specimen in left lateral view; C, frontal view of a third specimen; D, right dorsolateral view of setigers 7–10 showing details of genital setigers 8–9; E, detail of same, showing emergent genital spines of setiger 8 overlying embedded genital spines of setiger 9; F, hooded hook from abdominal neuropodium. Abbreviations: capNeS, capillary neurosetae; genPore, genital pore; per, peristomium; pr, prostomium; nuO, nuchal organ; LGr, lateral groove; vGr, ventral groove. Scale bars: A = 1 mm; B = 500 µm; C–E = 100 µm; F = 1 µm.

Distribution of capillaries and hooded hooks on thoracic setigers (1–9) determined by size and age. Typically, specimens with 30–40 setigers with capillary noto- and neurosetae arranged in single

rows of 6–8 capillaries per fascicle on setiger 1, and 8–10 capillaries per fascicle on setigers 2–7; setigers 8–9 with noto- and neuropodial hooded hooks and dorsal genital spines; setal formula = %_c (1–7), GS/%_c (8), GS/%_h (9)¹. Larger specimens of about 45 setigers with mixed fascicles of hooks and capillaries in neuropodia of setiger 8, with capillaries having replaced some hooded hooks; largest specimens of 55 or more setigers with capillaries in neuropodia of setigers 1–9, having replaced all hooded hooks; these largest specimens with double rows of capillaries on setigers 4–5 and single fully developed row of capillaries plus partial second row on setiger 6, each fascicle with 18–20 capillaries; noto- and neuropodia of setigers 1–7 with capillaries; notopodial fascicles absent when genital spines present and neuropodia of setigers 8–9 with hooded hooks, these neuropodial hooks replaced by capillaries in largest specimens (%_c (1–7), GS/%_c (8–9); one anomalous specimen from Marmorilik with an extra curved spine among capillaries in right notopodium of setiger 7. Specimens lacking genital spines and having notopodial hooded hooks on setigers 8–9 rare, <10% of individuals examined. Individual capillary setae of thoracic region unilimbate, broad basally, becoming narrow apically (Fig. 2C).

Abdominal noto- and neuropodia of setigers 10–16 with up to 18–20 hooded hooks in a row, gradually decreasing to 8–10 hooks in middle abdominal segments, last few abdominal setigers with 2–3 hooks per fascicle; hooks small with details of dentition visible only using light microscopy with phase contrast illumination at 1500× or with SEM; main fang pointed, thick, relatively short, surmounted by numerous apical teeth arranged in at least five curved rows (Figs. 2D–E, 4F); hood transparent in light microscopy, with main fang protruding through frontal opening; SEM shows hood with fibrils continuous with those along setal shaft (Fig. 4F). Genital spines of setiger 8 visible externally, except in juveniles, usually consisting of four prominent spines and 1–3 developing replacements (Figs. 2F, 3D–F, 4E); these spines directed toward setiger 9; spines on setiger 9 larger, deeply imbedded, usually not visible externally, directed toward setiger 8 (Fig. 3C); smaller specimens sometimes with spines of setiger 9 visible externally, but juveniles typically with all spines imbedded, visible only upon dissection or when cleared and mounted. Spines of setiger 9 positioned in two groups of two each; between these two groups of spines a large sac-like structure present with narrow end directed toward intersegmental groove with setiger 8 (Fig. 3C, F). This saclike structure secretory in nature, containing numerous small secretory granules but no sperm; this organ may function during copulation of mating pairs, but exact role unknown, usually termed a “copulatory organ.” Spines of setiger 8 falcate, narrower than those of setiger 9, with tips sharply curved or bent (Figs. 2F, 3D–E, 4E). Spines of setiger 9 much larger than those of setiger 8, straighter, curved apically, but with blunt tips, not sharply curved (Fig. 3F). Most specimens having genital spines also with distinct lateral genital pore in intersegmental groove between setigers 7 and 8 (Fig. 4D). This species apparently hermaphroditic because some specimens with both genital spines and eggs in coelom, others with genital spines and eggs and embryos in adult tubes.

Last few segments narrow, asetigerous. Pygidium simple lobe, without anal cirri (Figs. 2B, 4A).

Methyl green (MG) staining pattern. Prostomium not staining, peristomium staining and recessed into darkly staining setiger 1; setigers 1–5 and sometimes 6 staining more prominently, setigers 7–9 staining darkly (Fig. 3B); abdominal segments not staining except for minute speckles caused by small glands or individual secretory cells scattered over entire integument; these small speckled cells uniformly distributed, sometimes concentrated around raised noto- and neuropodia; these cells seen only after staining with MG

1. The following notations are used for setal formulas throughout this paper: c = capillaries, h = hooded hooks, m = mixed capillaries and hooks, GS = genital spines, 0 = no setae present. Numbers in () indicate setiger number.

Variation. Some variation was noted in the specimens examined. Most variation related to body shape and form of the prostomium, probably due to preservation. For example, of 145 specimens from a sample collected from Lindenows Fjord on the SE coast of Greenland in July 1935 (ZMUC-Pol-1980), about 40% agreed well with the above description. The other 60%, however, did not appear to have been well preserved, or more likely were already under stress at the time of preservation. These specimens were very flaccid with thin, transparent cuticles and bodies that were stretched and distorted. The prostomium and peristomium of these specimens appeared expanded as did the entire thoracic region; sometimes the peristomium merged perfectly with setiger 1 instead of being recessed into it as in specimens that were well preserved.

In the Lindenows Fjord sample and others, specimens with genital spines were sometimes identified only after dissection of developing imbedded spines. The genital spines on these specimens and on specimens with newly emergent spines were very light in color or nearly transparent, in contrast to more mature specimens in which the spines were golden in color. Such specimens were considered to be in a developmental phase of sexual maturity.

The 20 specimens from Pt. Barrow, Alaska, determined by Pettibone (1954) agree in all respects with the Greenland collections. None, however, were of a size large enough to have anything other than hooded hooks in the neuropodia of setigers 8–9.

Neotype. A neotype was selected from the excellent materials from Mårmorilik, a site located at 71°6.5'N latitude on the Affarlikassá Fjord on the innermost part of the Uummannaq Fjord system north of Disko Bay (Fig. 1). The specimen (ZMUC-Pol-1967) is partially within a fragment of its tube, containing late-stage larvae.

Neotype specimen light tan in color, 40 mm long, 1.2 mm wide across thorax for 60 setigerous segments. Prostomium, peristomium, and overall aspect of thoracic region including ventral and lateral grooves as described above. Intersegmental groove between setigers 3–4 deeper than on some other specimens. Setal formula: v_c (1–7), gs_c (8), gs_h (9). Genital spines of setiger 8 protruding dorsally toward setiger 9; spines of setiger 9 imbedded except at tips, directed toward setiger 8; swollen mound over setiger 9 representing location of “copulatory organ” containing numerous small secretory granules, no sperm observed. Capillary setae typical, 15–16 per fascicle; hooks of setiger 9 and anterior abdominal setigers in single rows, numbering about 15–16 per fascicle in notopodia and up to 25 in neuropodia. Abdominal setigers longer than thoracic setigers, becoming twisted posteriorly. Last few segments narrow, asetigerous; terminal pygidium simple.

Justification for the neotype. A neotype is needed for *Capitella capitata*, the type species of the genus, because confusion over the identity of this species has precluded description and naming of the many sibling species identified over the past 30 years. A redescription will serve as a baseline from which the numerous sibling species of *Capitella* that have been identified in laboratory culture over the past 30 years can be formally described and contrasted with the type species. This baseline description will also serve to focus efforts to understand local populations from Europe, North America, and elsewhere that have been referred to *C. capitata*.

It is generally believed that the original material of *Lumbricus capitatus* of Otto Fabricius from W. Greenland no longer exists. Indeed, Fabricius states in the introduction to his “Fauna Groenlandica” that he left intact specimens behind after his stay in Greenland ended, relying on his notes to complete his “Fauna.” According to his introductory comments, Fabricius served as a missionary to the Frederikshåb colony in Greenland during a stay of six years beginning in 1768. During that time he studied the natural history of Greenland as an activity during his free time. It is not known how far afield he traveled around Greenland as part of his natural history studies or if any other persons collected material for him, but most of his notes on the habitats of marine organisms suggest that he collected along the shore in intertidal or shallow-water localities. It is likely that he

collected his specimens of *Capitella* from such habitats, probably from the vicinity of Frederikshåb, but this is not definitively stated in his “Fauna.”

Among the collections provided for study were two nearly complete specimens from Kvanefjord, which is on the southern border of the peninsula on which Frederikshåb is located. Both specimens agree very well with the description of the species as reported in this paper. The prostomium/peristomium, details of segmentation on the thoracic region, presence of dorsal and lateral grooves, and presence of capillaries in noto- and neuropodia of setigers 1–7 are as observed for most of the other Greenland material. Both specimens also have imbedded genital spines on setigers 8–9. Unfortunately, although these specimens are from collections made close to Frederikshåb, are in good condition, and definitely representative of the bulk of *Capitella* specimens examined as part of this study, they are from a depth of 115 m, which is two or three times deeper than other available subtidal collections. As deep-water specimens, they are not representative of the shallower habitat or geological horizon where Fabricius probably collected and should not be used as neotype material. In order to select a neotype from the collections at my disposal, therefore, it was necessary to look elsewhere in W Greenland.

The collections available for study were generally in excellent condition and, in my opinion, represent a single Arctic-subarctic species having a distinct combination of morphological characters that should readily distinguish *C. capitata* from congeners. The available collections from shallow-water habitats range from Thule in the far north (~77°N) to Julianehåb in the south (~62°N) and Lindenows Fjord on the SE tip of Greenland (~61°N) (Fig. 1). The majority of material comes from localities between 74° and 68°N or above the Arctic Circle. The most extensive collections are from the vicinity of Disko Bay and Godhavn, an area with extensive shallow-water habitats and the location of the Arctic Research Station of the University of Copenhagen. I have therefore decided to select a neotype from a large and well-preserved collection of *C. capitata* taken from Mårmorilik, a site located in the innermost part of the Uummannaq Fjord system north of Disko Bay at 71°N latitude. Mårmorilik is near the site of the Black Angel Mine, which was in operation from 1973 to 1990. During 17 years of mine operations a total of 500,000 tons per year of metal-rich particulate tailings were discharged into the local fjord system. The tailings consisted of pyrite, low grade zinc, and lead ore with traces of heavy metals (Loring & Asmund 1989; Asmund et al. 1991; Johansen et al. 1991; Josefson et al 2008). The capitellids available to me were taken as part of an environmental monitoring effort in 1976. The material included more than 250 specimens that were unusually well preserved; in addition to adults there were numerous adults in tubes containing eggs and larvae in all stages of development. The species is also well represented in collections from nearby locations in and around Godhavn, Disko Bay, Uummannaq Fjord, and further north at Upernivik, but many of these specimens were fragmented and not as well preserved, possibly having been roughly handled during separation from the sediment. Selection of a neotype from the rich Mårmorilik sample focuses the redescription on specimens from the vicinity of permanent research facilities and makes it likely that fresh material can be collected for further research on life history and genetics. It is less likely that similar studies can be made any time soon on deep-water material from Frederikshåb, a more remote area.

Basing a redescription of *C. capitata* on collections from approximately 1,000 km (600 mi) north of the area where Fabricius is believed to have worked and probably collected his material is not the ideal situation from a purist point of view. However, given the endless discussions about the identity of this species over the past 20–30 years, it seems preferable to move forward with a redescription based on good existing material rather than wait another 20 years before someone is able to mount a collecting expedition to Frederikshåb with no guarantee of success. I have discussed this solution to the *Capitella* type-species problem with several colleagues, all of whom provided enthusiastic

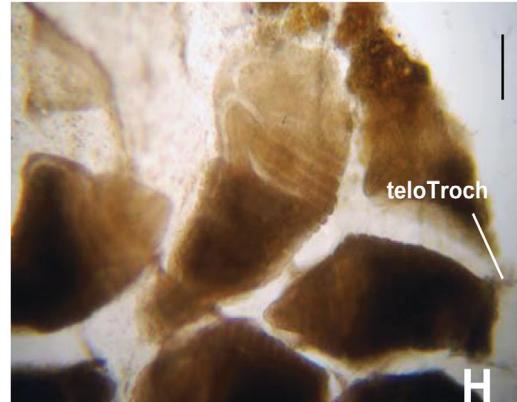
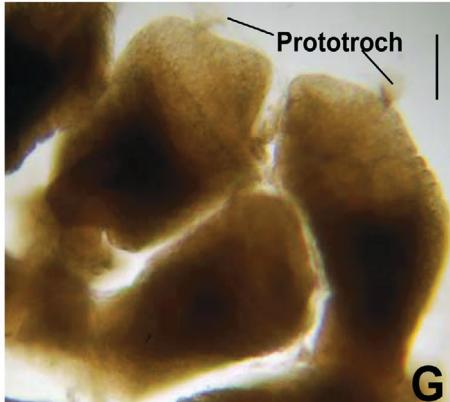
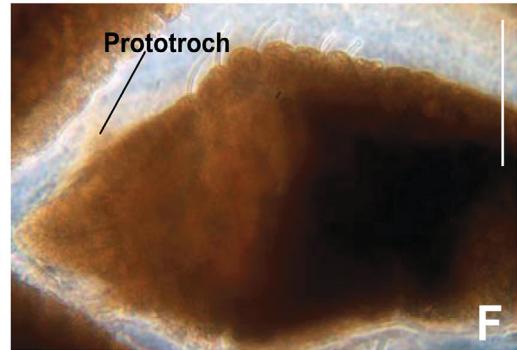
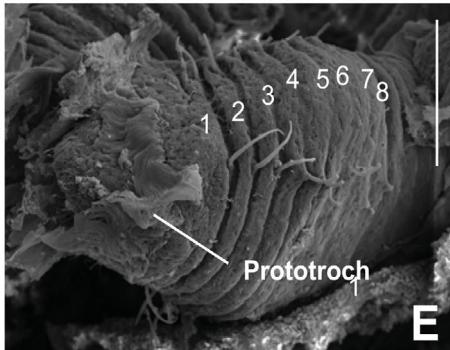
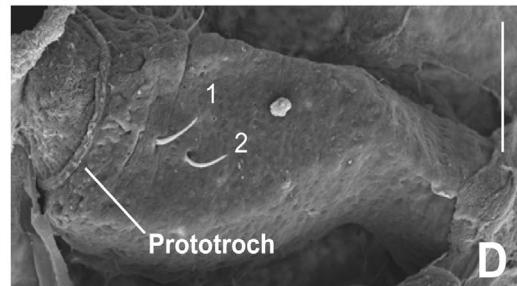
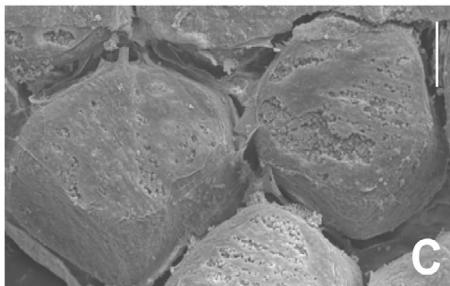
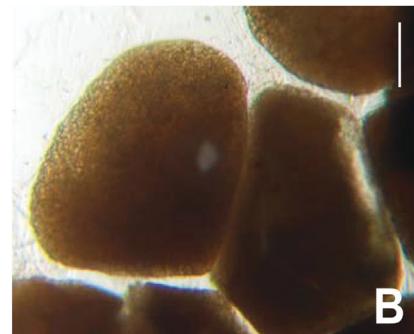
support for selection of a neotype. Four reviewers of this manuscript also provided strong support.

Reproduction and larval development. In the collections available from Greenland, specimens having genital spines, a character typically associated with males, far outnumbered specimens lacking such spines (Table 1) and were present in all months sampled from March to October. For example, in a collection of 145 specimens made in July 1935 from Lindenows Fjord, 115 or 79% had genital spines on setigers 8–9, 10 specimens or 7% had fascicles of notopodial hooded hooks instead of genital spines on setigers 8–9, and another 20 specimens or 14% had neither hooded hooks nor genital spines on setigers 8–9. The sample from Mârmorilik collected on 31 August 1976 on the central west coast of Greenland contained 250 specimens, of which 233 or 93.2% had genital spines on setigers 8–9, with the remaining 17 specimens lacking any evidence of such spines. All 20 specimens from Pt. Barrow, Alaska, had genital spines.

Of 115 specimens with genital spines from Lindenows Fjord, eight or 7% were found with eggs in the coelom; eggs were not found in specimens lacking genital spines. In the Mârmorilik collection, about 40 specimens with genital spines (17%) either had eggs in the coelom or the tubes contained eggs and larvae. Attainment of sexual maturity and subsequent production and spawning of mature eggs in *Capitella capitata* appears to coincide with development of genital spines. As noted in the description, the genital spines of setiger 9 are associated with a large “copulatory organ” that was found to contain numerous small secretory granules but no sperm. The presence of genital spines—together with eggs in the coelom and/or larvae in the tubes of the same specimen—strongly suggests that this species is hermaphroditic. Whether *C. capitata* is a cross- or self-fertilizing species cannot be determined from examination of preserved collections.

Several collections contained specimens with eggs in the coelom; others had tubes with larvae in different stages of development (Fig. 5A). The collection from Mârmorilik contained numerous specimens with tubes containing larvae and/or eggs in all stages of development. Eggs taken from tubes were large: two sets from Mârmorilik ranged from 240 to 309 μm ($\bar{x} = 283 \mu\text{m}$) and from 222.7 to 280 μm ($\bar{x} = 252 \mu\text{m}$), respectively; one set from Godhavn was larger, ranging from 366 to 427 μm ($\bar{x} = 412 \mu\text{m}$). The overall average egg diameter in these samples was 315 μm . There were at least 1125–1300 eggs per tube. Unfertilized eggs had a distinct germinal vesicle (Fig. 5B). Individual larvae removed from tubes ranged from embryonic pre-larval stages (Fig. 5C), to 2-setiger stages with a rudimentary prototroch (Fig. 5D), to 9-setiger stages having a prominent prototroch and telotroch (Fig. 5E–F). Segmentation and ciliation of the larvae were easily observed. Segmentation is demarcated by development of setae. The first setae to appear are capillaries on setigers 1–3; subsequent setigers have hooks. Presetal larvae removed from egg tubes were about 500 μm long, 180 μm wide at the level of the prototroch, and 130 μm wide at the posterior end. Larvae with 6–7 setigers were approximately 575 μm long, 180 μm wide across the prototroch, and 125 μm wide across the posterior end or telotroch. Ciliary bands were apparent in these larvae, including prototroch, telotroch, and possible apical cilia; a neurotroch was not observed. Pygidial cilia described by Eckelbarger & Grassle (1987) for several sibling species were not observed. Due to the large size of the eggs and larvae, *C. capitata* should have only a brief lecithotrophic stage in the plankton, if any. It is more likely that upon release from the tubes, the larvae or postlarvae have only a minimal dispersal capability and settle to the bottom immediately.

FIGURE 5. *Capitella capitata*. A–F, specimens from Mârmorilik, West Greenland (ZMUC). Photomicrographs: A (reflected light); B, F–H (phase contrast optics). SEM micrographs (C–E). A, tube of *C. capitata* specimen showing numerous late-stage larvae; B, unfertilized eggs from another tube; C, early embryos, with cilia from another tube; D, 2-setiger larva from tube; E, 9-setiger larva from tube; F, 7-setiger larva from tube; G–H, several late-stage larvae from tube. Scale bars: A = 1 mm; B–H = 100 μm .



Postlarvae were not available for study. Data from published sources on settling larvae of *Capitella* species indicate that the earliest postlarvae of *Capitella* have 11–13 setigers with little differentiation of the thorax and abdomen (Eisig 1887; Day 1936; George 1984). Capillary noto- and neurosetae are limited to setigers 1–3 or setal formula $\%_c$ (1–3); $\%_h$ (4–13). Several specimens from Godhavn collected 23 June 1959 and 07 October 1959 were small enough to document setal transformation across thoracic segments. The smallest specimen observed was from the October collection and had 23 setigers and 5–6 developing segments. This specimen measured 4.2×0.47 mm and had a setal formula of $\%_c$ (1–4); $\%_m$ (5–6); $\%_h$ (7); $\%_h$ (8–9). The April collections from Godhavn included specimens with 30 or more setigers. The smallest specimen, with 30 setigers, measured 6×0.7 mm and had a setal formula of $\%_c$ (1–5); $\%_m$ (6); $\%_h$ (7); $\%_h$ (8–9). A specimen with 30–31 setigers was 6×0.8 mm and had a setal formula of $\%_c$ (1–6); $\%_h$ (7); $\%_h$ (8–9). A specimen with 32 setigers was 7×1 mm and had a setal formula of $\%_c$ (1–6); $\%_m$ (7); $\%_h$ (8–9). A larger specimen with 32 setigers was 12×1.2 mm and had a setal formula of $\%_c$ (1–7); $\%_h^{GS}$ (8–9). These results suggest that setal transformation in the thoracic region, whereby capillaries replace hooks on setigers 4–7, takes place from the time of release from the tubes when juveniles would have about 12–13 setigerous segments to about the 30–32-setiger stages. Change appears to be rapid once the juveniles have at least 23 setigers; genital hooks appear as early as 32 setigers, but small precursor hooks might be found earlier if specimens are cleared. Further thoracic setal differentiation, with the replacement of neuropodial hooks by capillaries on setigers 8–9, was observed only in the largest specimens having 45 or more setigers. In the Mårmorilik collection, 7% of the individuals with genital spines had capillaries in the neuropodia of setigers 1–8 or 1–9.

Habitat, faunal associates, and distribution. *Capitella capitata sensu lato* has been reported from world-wide locations, but the species is here restricted to Arctic and subarctic localities until relevant collections can be examined. The species is most likely widely distributed in the Arctic. In Greenland, the materials examined were all from shallow subtidal habitats consisting of sand and mud, sometimes with stones and algae. The deepest records from Greenland are from ca. 41 m offshore Søndre Strømfjord and 115 m in Kvanefjord near Frederikshåb (Fig. 1). The Alaskan specimens from Point Barrow examined in this study were from 22–65 m on bottoms with rocks and gravel. Pettibone (1954) reported that 74 species of polychaetes occurred in this habitat.

There are no data from Greenland to suggest that *C. capitata* occurs in organically enriched sediments as has been suggested from worldwide reports (e.g., Reish 1980). However, the large collection from Mårmorilik is from an area known to be contaminated with metals from the Black Angel Mine tailings consisting mostly of zinc and lead (Fig. 1). Josefson et al. (2008) reported on long-term impacts of mining operations on the benthic fauna at Mårmorilik. The authors applied a before–after/control–impact (BACI) experiment employing the AZTI Marine Biotic Index (AMBI; Borja et al. 2000) in which the infauna is classified according to species sensitivity and opportunism with species in Group I being the most sensitive and those in Group V being the most opportunistic. *Capitella* sp. was the most opportunistic taxon (Group V) and dominated the heavily impacted sites even after cessation of mining operations. Other less opportunistic species included *Chaetozone setosa* Malmgren, 1865 (Group IV); *Spiochaetopterus typicus* Sars, 1853, and *Nereimyra punctata* (Müller, 1776) (Group III); *Lumbrineris* spp. and *Thyasira* spp. (Group II); and *Scoloplos armiger* (Müller, 1776), *Maldane arctica* Detinova, 1985, and *Nucula tenuis* (Montagu, 1808) (Group I, the most sensitive species).

Discussion

Taxonomy of *Capitella capitata*

Capitella capitata collections from W Greenland examined in this study are relatively robust with an enlarged thoracic region and narrow abdomen. The majority of specimens had genital spines and lacked notopodial fascicles of hooks or capillaries on setigers 8–9; many specimens had both male morphological characteristics and eggs and larvae in tubes suggesting functional hermaphroditism. Specimens lacking genital spines and exhibiting female characteristics were rare. Many small specimens superficially lacking genital spines were found, upon dissection, to have small imbedded spines, suggesting early development of hermaphroditism. These observations and other details reported here of the morphology of *C. capitata* from W Greenland differ markedly from the cosmopolitan concept of the species reported from worldwide locations.

The most widely accepted morphological concept of *C. capitata* is based on the work of Eisig (1887), whose collections were from the Gulf of Naples. Eisig's definition and detailed species description was supported by Hartman (1947) and expanded by Warren (1976a, 1991). Unfortunately, they and others do not appear to have considered that the species was originally described from Arctic and subarctic habitats in Greenland and that Eisig's species from the Mediterranean might actually be a different species. Indeed, nowhere in Warren (1976a, 1991) is there any note that the type locality of *C. capitata* is in Greenland. As revealed in the present study, there are many differences between Eisig's concept of *C. capitata*, based upon European collections, and the Arctic and subarctic specimens from the W and SW coasts of Greenland.

According to Eisig, *C. capitata* has only capillaries in setigers 1–6 followed by a transitional segment (setiger 7) that has various setal combinations (capillaries, hooks, or mixed). Warren (1976a) pointed out that most specimens from British waters have capillaries on setiger 7 and that rarely (2% of specimens) capillaries may also appear in the neuropodia of setigers 8–9. While these setal configurations are similar to those reported here for the Greenland collections, Warren (1976a) noted that sexual dimorphism in her version of *C. capitata* was common and hermaphrodites were rare. This is most definitely not the case with the Greenland material in which the majority of specimens (81.1%) exhibited genital spines and lacked notopodial fascicles on setigers 8–9 (Table 1). Numerous adult specimens were found with genital spines and eggs and/or larvae in their tubes. Other specimens with genital spines were dissected and found to have eggs in the coelom. These same specimens had a copulatory organ associated with the genital spines of setiger 9. Upon examination, numerous small granules that appeared to be nuclei were observed within the copulatory organ. Because these same features were observed in male specimens of *C. teleta* Blake, Grassle & Eckelbarger, 2009 (= *C. sp. I*), this information was relayed to Dr. Eckelbarger, who cut thin sections of the “copulatory organ” from imbedded specimens of *C. teleta*. He found that the organ was definitely secretory in nature, but suggested that the “nuclei” represented “zymogen-like secretion granules that fill the cells and spill out into the lumen upon secretion” (K. Eckelbarger, personal communication, 8 July 2008). There was no evidence of sperm. What role this “copulatory organ” serves during copulation and sperm transfer, if any, is not known.

Specimens with a “copulatory organ” also had eggs in the coelom; others had eggs and larvae in their tubes. When specimens lacking genital spines were found, they were usually found in the spring samples; most lacked notopodial fascicles of hooded hooks, suggesting that genital spines would eventually develop. However, imbedded thin and transparent spines were often found in these specimens upon dissection. Occasional large “females” that lacked genital spines but that had notopodial hooded hooks on setigers 8–9 were found, but these were rare (<10%, see Table 1).

TABLE 1. Summary of characteristics typically associated with male and female *Capitella* from specimens examined from Greenland.

Sample/Latitude-Longitude	Date of collection	Depth (m)	With GS/ set 8-9 (♂ chars)	Without GS/ set 8-9 (♀ chars)	Without GS/ without NoS set 8-9 (♀ chars)	Without GS/ without NoS	Ratio of GS: without GS	Ratio of specimens with ♂; ♀ chars
E. Greenland Mikis Fjord (ZMUC-POL-1981)	17 May 1933	15	3	10	0	3:10	3:10	115:10
SE. Greenland Lindenows Fjord (ZMUC-POL-1980)	July 1935	Not stated	115*	10	20	115:30	115:15	
S. Greenland Julianehåb, Havn (ZMUC-POL-1978)	24 Aug 1912	8-10, volcanic sand	0	1	0	0:1	0:1	
S. Greenland Julianehåb Ikek, (ZMUC-POL-1979)	11 Oct 1929	Not stated	4	2	0	4:2	4:2	
SW. Greenland, Kvanefjord, near Frederikshab (ZMUC-POL-1977)	03 Jul 1912	115	2	0	0	2:0	2:0	
W. Greenland, off Sandre Stromfjord, 66°50'N 54°28'W (ZMUC-POL-1976)	10 Jul 1895	41	0	2	0	0:2	0:2	
W. Greenland, Tiningnekkelak (ZMUC-POL-1962)	05 Jul 1902	Shallow, sand & brown algae	12	1	3	12:4	12:1	
W. Greenland Tasiusaq, Godhavn (ZMUC-POL-1968)	04 Mar 1959	10	68	15	14	68:29	68:15	
W. Greenland, Godhavn (ZMUC-POL-1974)	Unknown	Not stated	5	0	0	5:0	5:0	
W. Greenland, Lyngmarksbugt, Godhavn (ZMUC-POL-1969)	12 May 1959	30, clay & sand	4	0	0	4:0	4:0	
W. Greenland, Godhavn Harbor (ZMUC-POL-1970)	06 Apr 1960	4, sand	25*	0	0	25:0	25:0	

Sample/Latitude-Longitude	Date of collection	Depth (m)	With GS/ without NoS set 8-9 (♂ chars)		Without GS/ with NoS set 8-9 (♀ chars)		Ratio of GS: without NoS set 8-9	Ratio of specimens with ♂: ♀ chars
			With GS/ without NoS set 8-9 (♂ chars)	Without GS/ with NoS set 8-9 (♀ chars)	Without GS/ without NoS set 8-9	Without GS/ without NoS set 8-9		
W. Greenland, Lyngmarksbugt, Godhavn (ZMUC-POL-1971)	06 Apr 1960	36, clay	5*	0	0	0	5:0	5:0
W. Greenland, Godhavn (ZMUC-POL-1972)	23 Jun 1959	8, mud, sand, & green algae	12*	1	3	12:4	12:1	
W. Greenland, Godhavn (ZMUC-POL-1973)	07 Oct 1959	9, sand	5*	0	1	5:1	5:0	
W. Greenland, Uummannaq Fjord (ZMUC-POL-1965)	11 Aug 1888	Not stated	1	0	0	1:0	1:0	
W. Greenland Aftarlaksså Fjord, Mårmorilik (ZMUC-POL-1966-1967)	31 Aug 1976	20-30	233*	0	17	233:17	233:0	
Skitshavnne, Upernavik (ZMUC-POL-1964)	16 Jun 1936	6	0	2	0	0:2	0:2	
W Greenland, N. of Upernivik (ZMUC-POL-1963)	10 Aug 1931	30	52	12	14	52:26	52:12	
W. Greenland, Egedesminde (Disko Bay) (ZMUC-POL-1975)	20 Oct 1890	Not stated	1	0	0	1:0	1:0	
W. Greenland, Thule Havn (ZMUC-POL-1961)	14 Aug 1936	14	3	0	0	3:0	3:0	
TOTAL No. Specimens = 678	—	—	550 (81.1%)	56 (8.3%)	72 (10.6%)	550:128	550:56	

Abbreviations: GS = genital spines; NoS = notosetae; set = setiger(s); chars = characters.
*Some with eggs in tubes

In addition to the setal differences between Eisig's European concept of *C. capitata* and the collections from Greenland, there are obvious differences in the form of the prostomium/peristomium, differences among the nine thoracic setigers including sexual dimorphism, and the overall configuration of the thoracic region when compared to the abdominal segments. The anterior end of the body of *C. capitata* as depicted by Eisig (1887: plate 27, figs. 1–4) is of typical sexually dimorphic males and females with males having setigers 8–9 modified and enlarged dorsally, with genital spines and without notopodial hooded hooks; setigers 8–9 of the females are relatively unmodified, without genital spines, with notopodial hooded hooks, and with lateral intersegmental genital pores at the junction of setigers 7 and 8. The prostomium of these *Capitella* is flattened, about as long as wide, and joined to a relatively large asetigerous peristomial segment that is about 1.5 × as long as wide, which when joined with the prostomium forms a "head" that is conical in shape and about as long as wide in dorsal view. Eisig's figures depict a *Capitella* species having a consistently narrow thoracic region with individual segments that are no wider than subsequent abdominal setigers and barely twice the width of the peristomium. The anterior 3–4 thoracic setigers, however, are narrower than subsequent ones. *C. capitata* specimens from Greenland are entirely different.

Evidence of sexual dimorphism is rare in the Greenland material with most specimens having genital spines on setigers 8–9 and lacking notopodial fascicles and hooded hooks on the same segments. These specimens do not exhibit any conspicuous enlargement of setigers 8–9, and in fact these segments are usually smaller than preceding thoracic setigers and subsequent abdominal segments. The prostomium of the Greenland specimens is small, cup-shaped, wider than long and joined to a narrow peristomial ring that is smaller than setiger 1. In some specimens, the entire "head" appears to retract slightly into setiger 1. The thoracic region of the Greenland material varies in overall shape upon preservation, but on most specimens the first four thoracic setigers gradually increase in size, then decrease again over the remaining five setigers with setiger 9 being smaller than subsequent anterior abdominal segments; setiger 4 is the largest thoracic segment and is approximately three times the width of the peristomium. The thoracic region is thus very distinct visually from the abdominal region. The summation of these comparisons is that the typical definition and concept of *C. capitata* of Eisig (1887) and currently in use by European workers differs significantly from the true *C. capitata* from W Greenland, the type locality. These results suggest that the European literature probably refers to several closely related species that may or may not be related to the sibling species complex identified from North America (Grassle & Grassle, 1976; Eckelbarger & Grassle, 1987; Blake et al. 2009). Gamenick et al. (1998) and Mendez (2002) have already defined additional sibling species of *Capitella* in European waters.

The nearly universal occurrence of genital spines in specimens of a single species of *Capitella* is rare, but has been recorded for *C. giardi* (Mesnil, 1897) and *C. hermaphroditica* (Boletsky & Dohle, 1967) from Europe, *C. jonesi* (Hartman, 1959) and *C. caribaeorum* Warren & George, 1986 from Florida, and *C. capitata* by Pettibone (1954) from the Alaskan Arctic. The widespread occurrence of genital spines in both sexes of *Capitella*-like specimens was the basis for Mesnil (1897) establishing the genus *Capitellides*. Warren (1976a) referred *Capitellides* to *Capitella*, a decision which is supported in the present study because *C. capitata*, the type-species of *Capitella*, has the same characters that were defined for *Capitellides*.

Comparison of these species with *C. capitata* from Greenland demonstrates that each of the named species having genital spines in the majority of specimens is different. According to Warren (1976a), *C. giardi* has genital spines in setigers 8–9 of both sexes, but according to Warren & George (1986) there is no evidence that the species is hermaphroditic. Day (1936) also gave no indication that the species was hermaphroditic as part of his study on the larval development (as *Capitellides giardi* Mesnil). The thoracic setal arrangement for *C. giardi* differs from Greenland specimens of *C.*

capitata in that capillaries are present in noto- and neuropodia of setigers 1–6 with mixed fascicles in notopodia of setiger 7 and hooks in neuropodia of setiger 7. This pattern is similar to that of *C. caribaeorum*, but that species is definitely a hermaphrodite according to George (1984) and Warren & George (1986). In *C. capitata* from Greenland, all setae in setigers 1–7, and often in the neuropodia of setigers 8–9 as well, are capillaries. Warren (1976a) suggested that *C. capitata* described by Pettibone (1954) from Point Barrow, Alaska, should be referred to *C. giardi* because all specimens, including those with large yolk eggs, were reported to have genital spines. However, Pettibone's (1954) description agrees very well with that of *C. capitata* provided here and examination of her samples confirms that the Alaskan Arctic specimens are indeed *C. capitata*, suggesting that the type-species is widespread in the Arctic.

Capitella jonesi, originally described as *Capitellides jonesi* by Hartman (1959), is the same as *Capitella* sp. III from the J.P. Grassle cultures (Eckelbarger & Grassle, 1983; Blake, 2000). This species was originally referred to *Capitellides* because both males and females had genital spines. The species resembles *C. capitata* from Greenland in having an enlarged thoracic region, broadest at about setiger 5 and with setigers 8–9 being the narrowest. However, unlike *C. capitata*, setiger 9 is the longest thoracic segment instead of the shortest. *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 and should not be mistaken among other species of *Capitella*. *C. jonesi* is in effect neotenous as an adult because all species of *Capitella* pass through a developmental phase where capillaries are limited to setigers 1–3; with post-larval development, capillaries eventually replace hooded hooks on subsequent thoracic setigers in other species of *Capitella*. Grassle & Grassle (1976) identified *C. jonesi* (as *C. sp. III*) as being a protandrous hermaphrodite.

Capitella hermafroditica was originally collected from squid egg masses from the French Mediterranean (Banyuls-Sur-Mer) by Boletsky & Dohle (1967). The authors determined that the species was hermaphroditic, but not all specimens had genital spines (Warren, 1976a). *Capitella hermafroditica* differs from other species of the genus in having thoracic capillary setae limited to setigers 1–4, a situation similar to that of *C. jonesi*, in which the capillaries are limited to setigers 1–3.

In her review of *Capitella* species and records, Warren (1976a) recorded only *C. perarmata* (Gravier, 1911) from Antarctic waters as a species that consistently had capillaries in notopodia of setigers 1–7 and neuropodia of setigers 8–9. *C. capitata* from Greenland is here recorded as having that configuration in the largest specimens. No specimens of *Capitella* from the Southern Ocean were available for comparison with Greenland specimens of *C. capitata*.

Larvae of Capitellidae

Despite the numerous genera and species of Capitellidae known and available from the vicinity of marine laboratories, there are relatively few studies, apart from those on species or varieties of *Capitella*, that have been devoted to reproduction and larval development. Indeed, fewer than 20 species have been studied and for many of these the data presented are often incomplete. Further, many records of *C. capitata* are now known to refer to other species, the identity of which will be difficult to determine. Table 2 provides information on 14 such species that may be compared with the observations on *C. capitata* from Greenland presented in this paper.

TABLE 2. Reproductive and larval characteristics of capitellid polychaetes.

Species	Egg diameter (μm)	No. eggs per brood	Prototroch & telotroch	Neurotroch	Time in plankton	Developmental mode	Dominant sexual phase	Locality	Reference
<i>Capitella capitata</i> (Fabricius, 1780)	Ave. = 315 ¹	1125–1300	Well developed	Not observed	? Prob. <1 day	Lecithotrophic	Hermaphroditic	West Greenland	This paper
<i>Capitella capitata</i> sensu Eisig, 1887	>288	?	Well developed	Present	7 days	Planktotrophic	Dimorphic	Bay of Naples, Mediterranean	Eisig 1887, 1899
<i>Capitella capitata</i> sensu Reish, 1974 ²	250	150–250	Well developed	Present	Brief	Lecithotrophic	Dimorphic	Southern California	Reish 1974, 1980
<i>Capitella giardi</i> (Mesnil, 1897)	334 × 230	?, in tube	Poorly developed	Present	None	Direct	Dimorphic	England, U.K.	Day 1936
<i>Capitella hermafroditica</i> Boletzky & Dohle, 1967	?	?	Well developed	Short	>2 wks	Planktotrophic	Hermaphroditic	France, Mediterranean	Boletzky & Dohle 1967
<i>Capitella caribaeorum</i> Warren & George, 1986	300	24–50	Well developed	Present	<1 day	Lecithotrophic to direct	Hermaphroditic	Florida	George 1984; Warren & George 1986
<i>Capitella</i> sp. ¹	260 × 180	30–400	Well developed	Narrow band	Few hrs	Lecithotrophic	Dimorphic	Woods Hole, MA	Grassle & Grassle 1976; Eckelbarger & Grassle 1983, 1987
<i>Capitella</i> sp. Ia	75	200–2000	Well developed	Large patch	Several days	Planktotrophic	Dimorphic	Woods Hole, MA	Grassle & Grassle 1976; Eckelbarger & Grassle 1987
<i>Capitella</i> sp II	190–230	30–400	Well developed	Broad band	6–24 hrs	Lecithotrophic	Dimorphic	Woods Hole, MA	Grassle & Grassle 1976; Eckelbarger & Grassle 1983, 1987
<i>Capitella jonesi</i>	50	200–1000	Poorly developed	Small patch	≤ 2 wks	Planktotrophic	Hermaphroditic	Woods Hole, MA	Grassle & Grassle 1976; Eckelbarger & Grassle 1983, 1987

Species	Egg diameter (µm)	No. eggs per brood	Prototroch & telotroch	Neurotroch	Time in plankton	Developmental mode	Dominant sexual phase	Locality	References
<i>Capitella</i> sp. IIIa	250	30–50	?	?	None	Direct	Dimorphic	Woods Hole, MA	Grassle & Grassle 1976; Eckelbarger & Grassle 1983, 1987
ORLEANS	?	?	Well developed	Narrow band	?	Lecithotrophic	Dimorphic	Woods Hole, MA	Grassle & Grassle 1976; Eckelbarger & Grassle 1987
<i>Notomastus latircenus</i> Sars, 1851	150	?	Well developed	Present	~6 days	Planktotrophic	Dimorphic	Plymouth, U.K.	Wilson 1933
<i>Dasybranchus candicus</i> (Grube, 1846)	90–95	Many in jelly mass attached to tube	Well developed	Present	7 days	Planktotrophic	Dimorphic	Bimini, Bahamas	Bookhout 1957

¹Average of three different sets of eggs removed from tubes (two sets from Marmorlik; one set from Godhavn).

²*Capitella capitata* sensu Reish and *Capitella* sp. 1 *sensu* J.P. Grassle are the same species (see Blake et al. 2009, newly described as *C. teleta*).

The most widely cited reports of larval development of *C. capitata* are those of Eisig (1887, 1899) from the Bay of Naples and Reish (1974, 1980) from southern California, yet different patterns of development are apparent in those reports. Eisig's larvae were planktotrophic for seven days; Reish's larvae were lecithotrophic with less than a day in the plankton or no planktic stage at all, with the larvae forming tubes inside branches of the parent tube (Reish 1980). These observations suggest some plasticity in development in Reish's cultures. Eisig's (1899) study was remarkable in that he documented the entire cell lineage of his version of *C. capitata* from the earliest cleavage stages to nectochaete larvae.

Warren (1976b) studied a population she identified as *C. capitata* in Devon (UK) for an entire year (January 1973 to February 1974) and assessed size distribution, reproductive condition, and spawning. Females with ripe oocytes were nearly always present and most males contained ripe sperm. Females with fertilized eggs or larvae in their tubes were found in most samples taken during the study, suggesting that reproduction was continuous in the population. Warren noted that some larvae were large and lacked ciliary rings, suggesting some direct development in that population. These observations, like those of Reish, suggest plasticity in development or more likely demonstrate the existence of sibling species. Further evidence for the existence of sibling species of *Capitella* in the UK was shown by Pearson & Pearson (1991), who demonstrated that one of two potential sibling species of *Capitella* in Scotland produced eggs that averaged 231 µm in diameter and deposited more than 1,000 eggs per tube.

Considerable variability has been found in the reproduction and larval development of the six sibling species of *Capitella* studied by J.P. Grassle (Table 2; Blake 2000: table 4.1). Egg diameters range from 50 µm (*C. jonesi*) to 250 µm (*C. IIIa*). The range of egg diameters is clearly correlated to the type of development: species with the smallest eggs have planktotrophic larvae, whereas those with the largest eggs are either lecithotrophic or exhibit direct development. The larvae of planktotrophic species may remain pelagic for two or more weeks, while the lecithotrophic species are pelagic for only a matter of hours (Grassle & Grassle 1976). An excellent account of development in *C. giardi* (Mesnil) was published by Day (1936). This species produces large ovoid eggs that vary from 290 µm to 370 µm in diameter. Development is direct with a non-pelagic larval stage that gradually transforms into a juvenile. Ciliary bands are lost at the time of metamorphosis. George (1984) described development of a hermaphroditic species of *Capitella* from a mangrove swamp in Florida. This species, later named *C. caribaeorum* by Warren & George (1986), is completely hermaphroditic, with all specimens developing genital spines. George (1984) suggested that self-fertilization takes place. Large yolk eggs are laid in tubes in a mucous sleeve around the body of the adult with the entire development completed in the tube. These larvae have ciliary bands, yet the ability to swim appears to be limited.

The brief observations on reproduction and larval development of *C. capitata* presented here from W Greenland are not readily comparable with published accounts of *Capitella* development. One major difference is with the size of the eggs and numbers of eggs and larvae produced and deposited in tubes. The egg diameters of *C. capitata* removed from tubes of adults from Greenland were large, averaging ca. 312 µm in diameter. Curtis (1977), as part of a study of polychaete populations from the Disko Bay area of W Greenland, recorded egg diameters of up to 300 µm during spring, when he believed spawning took place. Although estimates of the number of eggs and larvae in tubes of adults recorded in this study are approximate, the numbers definitely exceeded 1,100 in five different observations, with one tube containing at least 1,300 larvae. The presence of so many eggs and larvae in tubes of adults is unusual for a species that produces large yolk eggs. The only similar record is that of Pearson & Pearson (1991) in Scotland (see above). Large numbers of eggs and larvae per tube have been recorded for two of the Grassle sibling species, *C. sp. Ia* and *C.*

jonesi, but these species produce small eggs with diameters of <100 µm diameter (Table 1).

The larvae described here for W Greenland specimens are large and are retained in the adult tubes up to and including having at least 9-setigerous segments and a well-developed prototroch and telotroch. Given that setae are well developed while the larvae are still within the tubes, it is unlikely that they would disperse very far upon release. Whether or not the late-stage larvae have a brief planktic phase cannot be determined, although the prototroch and telotroch appear to be sufficiently developed to provide limited locomotion in the water column.

A review of available literature reveals that little information has been developed for capitellid larvae concerning the size and number of setigers at metamorphosis, the differentiation of the thoracic region from abdominal segments, and the timing of setal transition along the thorax of juveniles. There does, however, appear to be a fundamental difference in segmentation between species of the genus *Capitella* and species of *Notomastus* and *Dasybranchus* at the time of metamorphosis. Metamorphosing metatrochophore larvae and early settling nectochaete larvae suggest that the earliest juveniles of *Capitella* species are larger and have many more segments than the two species of *Notomastus* and *Dasybranchus* studied thus far (Wilson 1933; Bookhout 1957). For example, a juvenile of *Capitella* reported by Eisig (1887) had 11 setigers and measured 1.5 mm long. There was little differentiation of the thorax and abdomen at this stage. A late metatrochophore or settling stage of *C. caribaeorum* reported by George (1984) as *C. n. sp.* had 13 setigerous segments and measured 500–600 µm. Day (1936) described late-stage metatrochophore larvae of *C. giardi* as 780 µm long and having 16 setigerous segments. For each of these examples, the earliest juveniles exhibited little or no evidence of distinct thoracic and abdominal regions. All of these juveniles had capillary noto- and neurosetae on setigers 1–3 and hooded hooks on subsequent parapodia. The only study to document setal replacement along the thoracic region in a species of *Capitella* is by George (1984) for *C. caribaeorum* (as *Capitella n. sp.*). He found that the thoracic region begins to enlarge between the 13- and 19-setiger stages, but that setal transformation with capillaries replacing hooks on setigers 4–5 took place between the 20- and 26-setiger stages. By the 27–33-setiger stages, capillaries replaced hooks in the neuropodia of setiger 5 and notopodia of setiger 6. At the same time, genital spines developed on setigers 8–9. After the 34-setiger stage, capillaries replaced hooks in neuropodia of setiger 6 and notopodia of setiger 7. The pattern of thoracic development reported by George (1984) for *C. caribaeorum* is very similar to that found in this study for *C. capitata* from Greenland and may be a consistent pattern in species of *Capitella* having large yolk eggs. There are no similar data for *Capitella* species having small eggs. In contrast to early juveniles that have 11–16 setigers at metamorphosis, Wilson (1933) reported juveniles of *Notomastus latericeus* Sars, 1851 to be 535 µm long with seven setigers and Bookhout (1957) reported juveniles of *Dasybranchus caducus* (Grube, 1846) with seven setigers to be ca. 340 µm long. Species of *Capitella* thus have more setigerous segments developed at the time of metamorphosis and are of a larger size than species of *Notomastus* and *Dasybranchus* studied to date. Bookhout (1957) developed detailed data on the replacement of hooks by capillaries along the thorax and his results for *D. cauducus* with 13 thoracic setigers as an adult differs from observations on *Capitella* with nine thoracic setigers as adults summarized in this paper. In *D. cauducus*, capillaries replace hooks between the 36- and 70-setiger stages; whereas in *C. caribaeorum* studied by George (1984) and for *C. capitata* in this study; setal transitions are mostly complete by 34–36 setigers. These results are based on very few species, but suggest that observations on post-larval morphology may be important in understanding phylogenetic relationships among the capitellid genera.

Conclusion

In my opinion, the account of adult morphology and limited observations on reproduction and larval development presented here suggest that *C. capitata* is adapted for life in Arctic and subarctic habitats. I suggest that a restudy of collections from Arctic locations will reveal that the true *C. capitata* will be circum-Arctic in distribution and that low-latitude records of the species by Eisig (1887), Hartman (1947), Warren (1976a, 1991), and others such as Fauvel (1927), Berkeley & Berkeley (1952), Hartmann-Schröder (1971, 1996), and Ewing (1984) will prove to be other species, possibly new to science or with names previously referred to synonymy with *C. capitata*. It is likely that sibling species of *Capitella* revealed in laboratory culture by J.P. Grassle and others (Wu et al. 1991; Gamenick et al. 1998; Mendez 2002, 2006) are either local in distribution or widely distributed. The systematics of this genus is obviously complex and careful study is required in order to define additional species and to determine their distributions.

In order to fully understand the systematics of the genus *Capitella* it will be important to develop comparative data on genetics, population biology, reproduction, and larval development. However, I firmly believe that adult morphology is crucial in defining species of *Capitella*. The adults of *C. capitata* from W Greenland and the Alaskan Arctic are entirely different in both gross appearance and many morphological details from those of *C. teleta* (formerly *Capitella* sp. I) described in Blake et al. (2009) and previously described for other species. Careful attention to details of the prostomium/peristomium, shape, size, and form of the thoracic segments, details of the genital spines, numbers of capillaries and hooks per setal fascicle, sexual phases, presence/absence of dorsal and lateral grooves, and methyl green staining patterns can all be used together with overall size and segment counts to define individual species.

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