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INTERSPECIFIC VARIATION IN GENITAL SPINE,
SPERM, AND LARVAL MORPHOLOGY IN
SIX SIBLING SPECIES OF *CAPITELLA*

Kevin J. Eckelbarger and Judith P. Grassle

Abstract.—Interspecific variation was examined in six species of *Capitella* (sp. I, Ia, II, III, IIIa and ORLEANS) from the Woods Hole region with respect to genital spine, sperm and larval morphology. The stability of spine number in the eighth and ninth thoracic setigers was examined and found to reach a maximum value at an early age in setiger 9. Spine number showed greater variability in setiger 8 although the number in the oldest animals studied appeared to reach a maximum value. Genital spine number and morphology should be included in future descriptions of *Capitella* species.

Significant differences in mature sperm morphology are evident in five *Capitella* species including variation in the length of the acrosome, nucleus and middlepiece; these differences may be correlated with previously reported morphological differences in the egg envelopes of these species.

The larvae of five *Capitella* species differ strikingly with regard to size, larval mode (length of time in the plankton), and features of their external cilia. Large differences were seen in the length of cilia and the density of prototrochal and telotrochal ciliary bands and the shape of the neurotroch. Distinct bands of pygidial cilia are reported for the first time in four of the five species studied. Differences with respect to the presence and distribution of sensory cilia may reflect behavioral differences between the larvae in their responses to environmental cues.

Capitella capitata (Fabricius), formerly regarded as a cosmopolitan opportunistic polychaete species, is now recognized as a complex of genetically distinct sibling species that have great morphological similarity but which differ in many aspects of their biology (Grassle and Grassle 1976, Grassle 1980). Because of this morphological similarity, ecologists and systematists face considerable difficulty when attempting to use superficial features of the adult to separate members of this important complex. Many workers have minimized or ignored the problem of *Capitella* sibling species by continuing to refer to specimens as *C. capitata* without qualification (Warren 1976a, Pearson and Rosenberg 1978, Rhoads et al. 1978, Ewing and Dauer 1981, Boesch 1982, Tsutsumi and Kukuchi 1983). Others have recognized the problem but have been forced to cite *Capitella* spp. when sorting field specimens (Hannan 1981; Zajac and Whitlatch 1982a, b; Fournier and Levings 1982). Those doing laboratory studies on specimens of known origin (Tenore 1981, Bhup and Marsden 1982)

have applied the numerical system assigned to the *Capitella* species that were found to be sympatric at the Woods Hole sewer outfall (Grassle and Grassle 1976).

Clark (1977) noted that since the concept of a species depends upon reproductive isolation, variations in reproductive habitat or reproductive physiology are likely to be potent factors in speciation, particularly since polychaetes are so reproductively diverse. He also remarked that when dealing with sibling groups, one must generate new systematic characters not previously regarded as diagnostic. Other authors have observed that information generated from reproductive and life history studies can be particularly useful in delineating members of sibling complexes since the adults show such morphological similarity (Blake 1969, Reish 1977, Clark 1977, Christie 1982, Wilson 1983, Akesson 1984, Guerin and Kerambrun 1984).

Some members of the *Capitella* sibling species complex not only show differences in chromosome number (Grassle, Gelfman and Mills, this

volume) but also great genetic differences based on electrophoretic mobilities of allozymes at selected enzyme loci. They also show striking differences in life history features including reproductive mode, breeding season, egg size, and dispersal capability of the larvae. Studies by the authors have also revealed consistent ultrastructural differences in the eggs and ovarian follicle cells of four sibling species of *Capitella* (Eckelbarger and Grassle 1983). The purpose of the present paper is to present new information on interspecific differences between six species of *Capitella* from the Woods Hole region with regard to the external morphology of adult male genital spines, sperm, and larvae.

Materials and Methods

Animals used in this study belong to six genetically distinct *Capitella* species that occur in the vicinity of Woods Hole, Massachusetts. Formal taxonomic descriptions of these species will be presented separately in a forthcoming paper. The material from *Capitella* spp. I, II, IIIa and ORLEANS was obtained from laboratory strains. *Capitella jonesi* (*Capitella* sp. III, Grassle and Grassle 1976) and *Capitella* sp. Ia individuals were collected in the field and maintained in the laboratory. Worms were kept in filtered, standing sea water at 10° or 15°C and were provided azoic mud as food and substrate. Food and water were changed at bi-weekly intervals.

Although six species of *Capitella* will be discussed in this paper, it was not possible to use all six species in the separate studies of genital spine, sperm, and larval morphology. For instance, *Capitella* sp. III is omitted from our results of genital spine and sperm morphology because we were unable to obtain an adequate number of individuals from the field during the study period. *Capitella* sp. IIIa is omitted from the comparisons of larval morphology because it undergoes direct development and therefore lacks a free-swimming larval stage.

For studies of genital spine morphology, animals were relaxed in 8% MgCl₂ in sea water, placed dorsal side up on a microscope slide and examined with a Zeiss WL compound research microscope using phase, bright field, and Nomarski differential interference-contrast optics. Photographs were taken with Kodachrome 64, processed, and finally projected with an enlarger

onto drawing paper upon which outlines were made with ink. All photographs and drawings were made at the same magnification.

For SEM of larvae, specimens were fixed, dehydrated, critical point dried and mounted on aluminum stubs following the procedures of Eckelbarger and Chia (1976). Specimens were sputter-coated with gold-palladium and examined and photographed with a Novascan 30 scanning electron microscope using an accelerating voltage of 15 kV.

Tissue fixation and preparation for TEM of larvae and mature sperm was carried out using procedures outlined in Eckelbarger (1979). Longitudinal sections of mature sperm were obtained by serial sectioning paired genital ducts located between the seventh and eighth thoracic setigers in mature males. Thin sections of embedded larvae and sperm sacs were cut on a Porter-Blum MT-2B ultramicrotome with a diamond knife, stained with aqueous saturated uranyl acetate followed by lead citrate, and examined with a Zeiss EM-9S2 transmission electron microscope.

Results

Genital spines.—The notopodial hooded hooks in the eighth and ninth setigers are replaced by large, middorsal, specialized genital spines in male *Capitella* as the animals mature (Figs. 1–4). These spines have a light yellow or light green appearance in living material, are slightly falcate distally and are somewhat flattened when viewed with SEM (Figs. 1, 2). The genital spines of from five to 13 males each were examined from *Capitella* spp. I, Ia, II, IIIa and ORLEANS to determine the extent of interspecific variation. Figure 5 shows three representative spines from both the eighth and ninth setigers of each species to show morphological variation observed in the specimens. Although there appear to be consistent differences between species, the general morphology of the genital spines is quite similar. However, there are notable differences, such as the reduction in distal curvature and the stouter nature of the ninth setiger spines in *Capitella* sp. I (Fig. 5a). The genital spines of both setiger 8 and 9 in *Capitella* sp. II also show more extreme distal curvature than those of the other species (Fig. 5c). Table 1 shows the range, mean and standard deviation of genital spine number in the five *Capitella* species. In all five species, spine

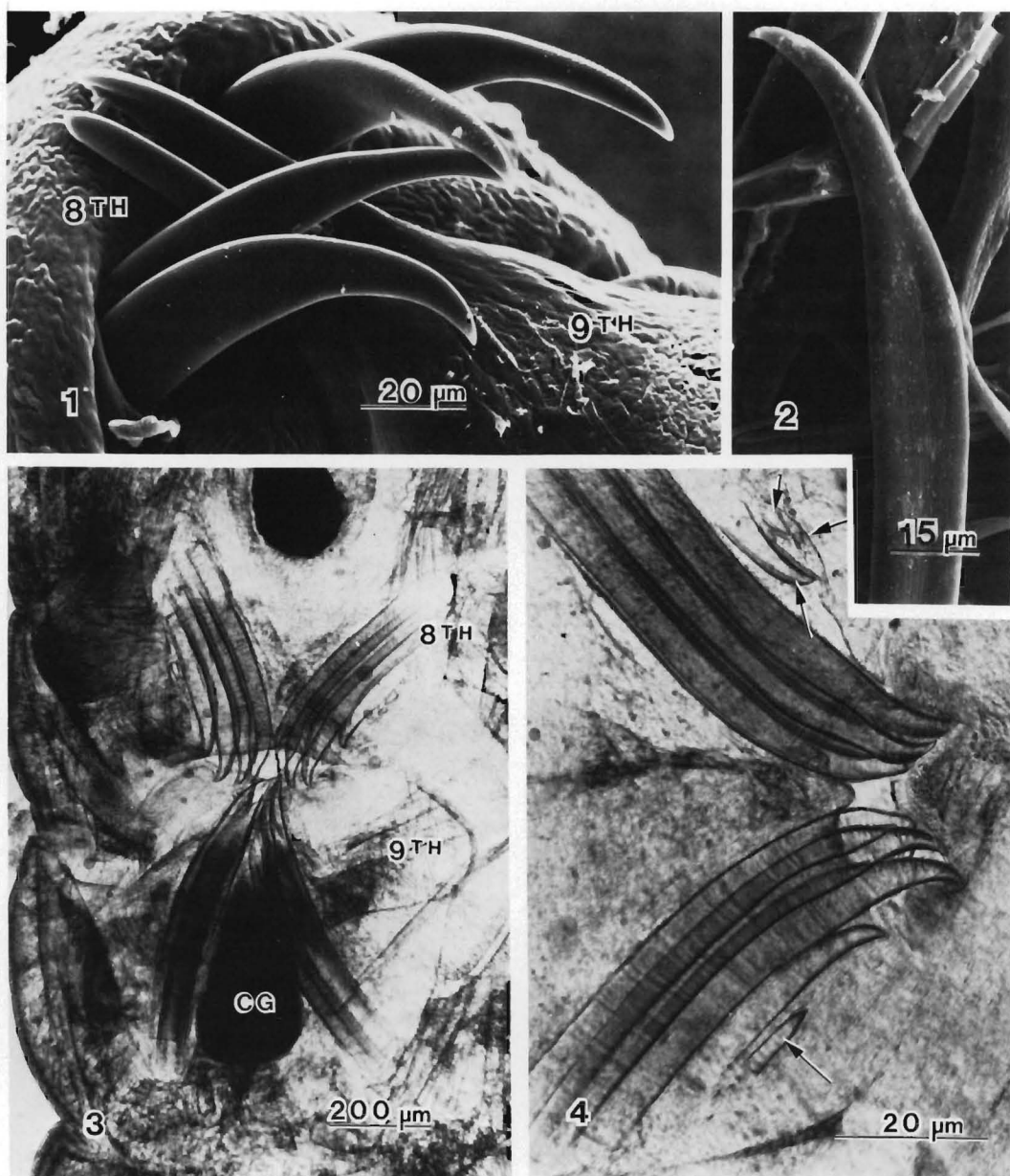


Fig. 1. Scanning electron micrograph showing dorsal-lateral view of genital spines of *Capitella* sp. IIIa in setigers 8 and 9.

Fig. 2. SEM view of isolated genital spine from *Capitella* sp. I showing flattened appearance of spine.

Fig. 3. Dorsal view of eighth and ninth setigers of live *Capitella* sp. I showing genital spines. CG, copulatory gland.

Fig. 4. Genital spines from the eighth setiger of *Capitella* sp. I showing replacement spines forming within setal sacs (arrows).

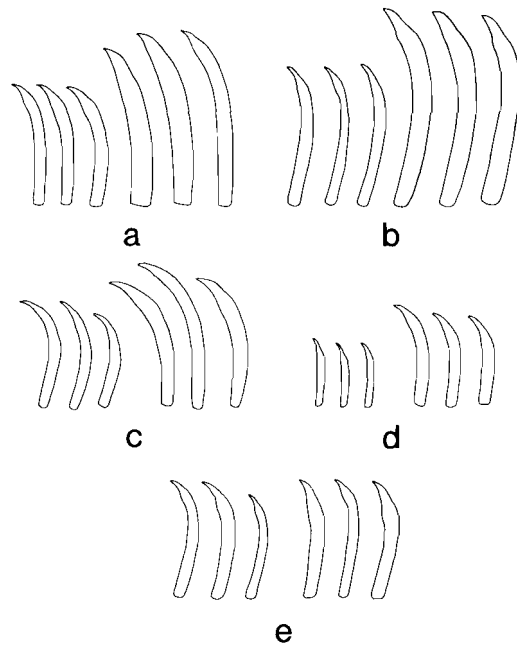


Fig. 5. Representative genital spines drawn from 5 sibling species of *Capitella* showing interspecific differences in spine morphology. Within each set, 3 spines are shown on the left (eighth setiger) and 3 on the right (ninth setiger). a, *C. sp. I*; b, *C. sp. Ia*; c, *C. sp. II*; d, *C. sp. IIIa*; e, *C. sp. ORLEANS*.

number in setiger 9 is less than in setiger 8 with all species having approximately four genital spines in this segment except *sp. IIIa* which averaged two. The number of spines in setiger 8 showed a greater range than in setiger 9 and averaged six in all species except *Capitella sp. ORLEANS*.

To determine the extent of intraspecific variation in spine number and morphology in at least one *Capitella* species, 8–14 live males of *Capitella sp. I* from four laboratory cultures were ex-

amined. The worms differed in age, geographic origin and degree of inbreeding. These included 39 and 38 generation males from an isofemale line originating from Falmouth, Massachusetts which were 61 and 128 days old, respectively; fifth generation males from New Bedford Harbor, Massachusetts; and third generation males from Marseille, France. Four genital spines from both the eighth and ninth setigers are shown in Fig. 6. The spines were selected from different individuals to demonstrate the representative morphological variation observed in the individuals sampled. The figure shows considerable variation in spine morphology from both setigers but particularly the formation of proximal constrictions and annulations in the inbred specimens from the Falmouth locality. In addition, spines from the ninth setiger from the Marseille population tend to be thicker and more robust than those illustrated from the other populations. Table 2 shows the number of spines observed in the eighth and ninth setigers from these four groups. While the number of spines in the ninth setiger was approximately four in each of the groups, spine number showed wider variation in setiger 8, with the total number being greatest in the older, highly inbred line from Falmouth where all individuals had 10.

Males from laboratory and field collections sometimes appear to have damaged or missing genital spines. Males also appear to lose spines as they age (Grassle, unpublished) although replacement appears possible in younger males since about 95% of the specimens observed in the present study had small, rudimentary spines in setal sacs at the base of the fully developed spines (Fig. 4). The rudimentary spines were in many phases of development and in most individuals, were fewer in number than the fully developed spines. It is interesting to note that the

Table 1.—Male genital spine number in five species of *Capitella*.

Species	Origin of lab population	n	Age in days (15°C)	No. spines in 8th setiger		No. spines in 9th setiger	
				Mean (\pm SD)	Range	Mean (\pm SD)	Range
I	Kirley Park, CA	9	81	6.44 \pm 0.88	6–8	3.77 \pm 0.44	3–4
Ia	Boston Harbor	5	unknown*	6.00 \pm 0.00	6	4.20 \pm 0.45	4–5
II	Falmouth, MA	13	unknown*	6.38 \pm 0.96	5–8	3.92 \pm 0.27	3–4
IIIa	Falmouth, MA	6	unknown*	6.00 \pm 0.00	6	2.16 \pm 0.41	2–3
ORLEANS	Orleans, MA	7	123	7.43 \pm 0.79	6–8	4.00 \pm 0.41	4

* Field specimens.

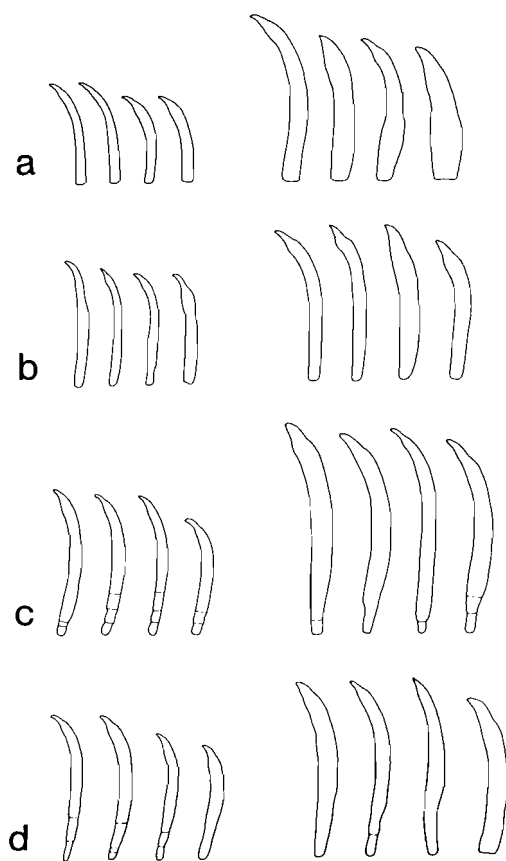


Fig. 6. Representative genital spines drawn from individuals from 4 cultures of *Capitella* sp. I having differences of age, geographic origin and degree of inbreeding. Within each set, 4 spines are shown on the left (eighth setiger) and 4 on the right (ninth setiger). a, 3rd generation, Marseille, France, 81 days old; b, 5th generation, New Bedford Harbor, MA, 88 days old; c, 38th generation, Falmouth, MA, 128 days old; d, 39th generation, Falmouth, MA, 61 days old. c and d are from the same isofemale line and differ by one generation of inbreeding and in age.

oldest males examined in this study (123 days—see Table 2) still had replacement spines in reserve setal sacs even though the animals appear to have reached a plateau in the number of spines in setiger 8 (10 spines).

Sperm morphology.—All *Capitella* species (I, Ia, II, IIIa, ORLEANS) from this study possess paired sac-like genital ducts suspended in the lateral coelom between the seventh and eighth thoracic setigers. Descriptions of sperm were made from serial sections of these sacs since they

nearly always contain numerous mature sperm in the adult animal. The morphology and function of these sacs and a detailed description of spermatogenesis and mature sperm ultrastructure will be presented in a forthcoming paper (Eckelbarger and Grassle, in press).

The mature sperm of all the species examined show some morphological similarity including a conical acrosome, an elongated, tapering nucleus and a middlepiece composed of a cytoplasmic sleeve or collar which extends posteriorly along the proximal portion of the flagellum. Profiles of mitochondria and substantial deposits of glycogen-like granules were also observed within the cytoplasm of the middlepiece. Table 3 lists the comparative dimensions of various sperm organelles measured from each of the five *Capitella* species. Comparisons of combined acrosome and nuclear length (total head length) and comparisons of acrosome and nuclear length alone, indicate a statistically significant difference ($P = <0.001$) between all species except between species II and ORLEANS when applying Student's T-test. There is an apparent difference in the proportional relationship between various regions of the mature sperm in the five species with regard to acrosome, nuclear and middlepiece length (Fig. 7). Intraspecific variation in sperm dimensions is very small.

Larval morphology.—The general morphology of the *Capitella* species larvae is similar in that all are barrel-shaped and have a prototroch, neurotroch and telotroch, and pygidial cilia which are usually arranged in distinct bands (Figs. 8–22). In addition to differences in larval size, there are a number of distinct interspecific differences in the morphology of larval structures.

Although all the *Capitella* species larvae have complete prototrochal and telotrochal ciliary bands, there is wide variation in the length and density of the cilia. For instance, the prototrochal and telotrochal cilia in sp. III are weakly developed compared to the other species studied (Fig. 17). The length and shape of the neurotroch also shows consistent interspecific variation ranging from a tapering band along the ventral midline as in *Capitella* spp. I and ORLEANS (Figs. 8, 20) to a dense elliptical patch which partially surrounds the larval mouth, covering nearly the entire ventral surface in sp. Ia (Fig. 11).

With the exception of sp. III larvae, all *Capitella* larvae examined have clearly defined bands

Table 2.—Genital spine number of male *Capitella* sp. I in relation to geographic origin, age and degree of inbreeding.

Origin of lab population*	n	Age in days (15°C)	No. spines in 8th setiger		No. spines in 9th setiger	
			Mean (\pm SD)	Range	Mean (\pm SD)	Range
1. Falmouth, MA	14	61	7.71 \pm 0.83	6–8	4.00 \pm 0.13	4–5
2. Falmouth, MA	10	128	10.00 \pm 0.00	10	4.35 \pm 0.53	4–5
3. New Bedford Harbor, MA	8	88	6.50 \pm 0.93	6–8	3.90 \pm 0.35	3–4
4. Marseille, France	13	81	6.47 \pm 1.71	4–10	4.00 \pm 0.41	2–6

* 1. Sibling mated, 39 generations (highly inbred)—isofemale line. 2. Sibling mated, 38 generations (highly inbred)—isofemale line. 3. Sibling mated, 5 generations (slightly inbred)—isofemale line. 4. Sibling mated, 3 generations (distant inbred)—isofemale line.

of cilia over the surface of the pygidium radiating from the anus. Some minor interspecific variation was observed in the pattern of the bands but in all cases, the dorsal surface of the pygidium was free of cilia. In *Capitella* sp. II, the bands are more clearly defined than in the other species since they are narrower and the cilia are shorter (Fig. 16). In *Capitella* sp. III, there are no bands although a small, single patch of cilia is located on the ventral border of the pygidium (Figs. 17, 19).

No apical tufts were observed on the prostomium of any of the five species although scattered solitary cilia or ciliary tufts of presumed sensory function were common (Figs. 9, 12, 15, 18, 21). The ciliary tufts occur not only over the prostomial cuticle but on other surfaces of the larvae in patterns which appear characteristic of the species.

The larvae of all five *Capitella* species are covered by randomly distributed mucous glands which appear in the SEM as stalked structures emerging from cuticular pits. The stalked structures often have swollen tips and represent mucous secretions which were being released from

the underlying cell when fixed (Figs. 23, 24). This material is often present in long rope-like strands which adhere to the surface of the larval cuticle (Figs. 12, 23). Table 4 summarizes some of the general external morphological differences observed in the *Capitella* species larvae.

Discussion

Polychaetes are important members of the marine and estuarine benthic community but they often present difficult taxonomic problems for ecologists, environmental biologists and systematists (Clark 1969, 1977; Fauchald 1977). The occurrence of sibling species in which members of natural populations are morphologically similar or identical yet reproductively isolated are particularly troublesome and yet appear to be rather common when detailed biological studies are conducted (see Mayr 1963, for discussion). Sibling species in polychaetes have been revealed in a variety of ways including the analysis of morphological data (Clark 1952, Ramos 1976); reproductive biology (Akeson 1972, 1977; Gibson 1978; Day and Blake 1979; Clark 1979; Smith 1958; Christie 1982; Wilson 1983); physiological

Table 3.—Dimensions (μ m) of mature sperm from five sibling species of *Capitella*.*

	I	Ia	II	IIIa	Orleans
Sperm head					
Nucleus (length)	3.10 \pm 0.22	5.20 \pm 0.14	4.95 \pm 0.15	6.10 \pm 0.24	4.62 \pm 0.27
Nucleus (width)	0.84 \pm 0.03	0.79 \pm 0.03	0.82 \pm 0.03	0.79 \pm 0.03	0.83 \pm 0.03
Acrosome (length)	1.38 \pm 0.06	1.16 \pm 0.06	0.94 \pm 0.05	1.35 \pm 0.04	1.15 \pm 0.04
Acrosome (width)	0.64 \pm 0.04	0.56 \pm 0.02	0.56 \pm 0.02	0.54 \pm 0.03	0.58 \pm 0.03
Middlepiece (length)	2.60 \pm 0.25	2.93 \pm 0.45	2.73 \pm 0.15	3.61 \pm 0.21	3.60 \pm 0.19

* n = 30 sperm/species.

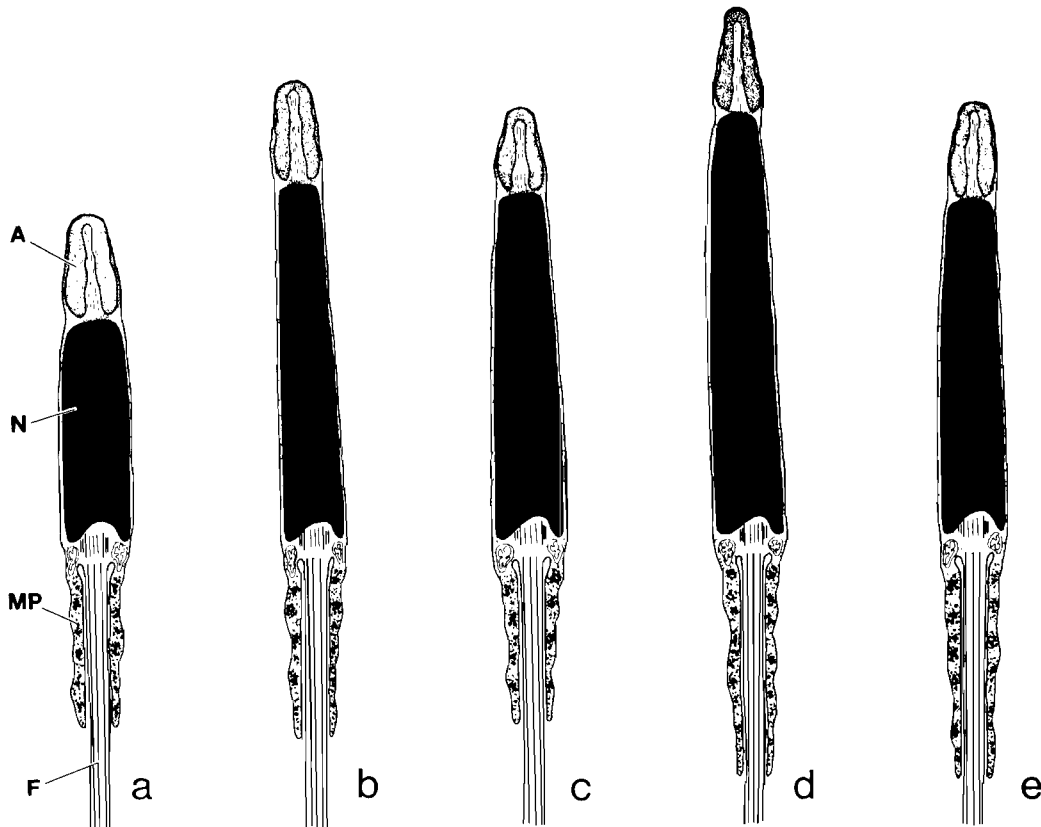


Fig. 7. Drawings of mature sperm from 5 sibling species of *Capitella*. A, acrosome; F, flagellum; N, nucleus; MP, middlepiece. a, *C. sp. I*; b, *C. sp. Ia*; c, *C. sp. II*; d, *C. sp. IIIa*; e, *C. sp. ORLEANS*.

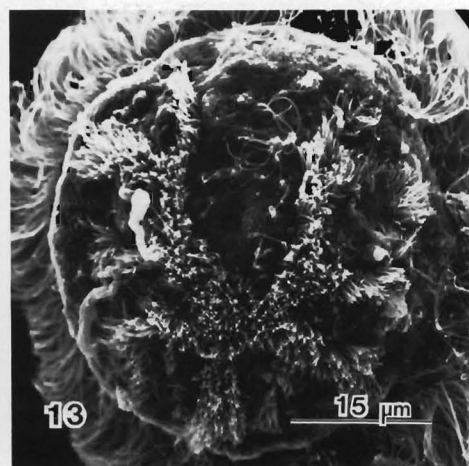
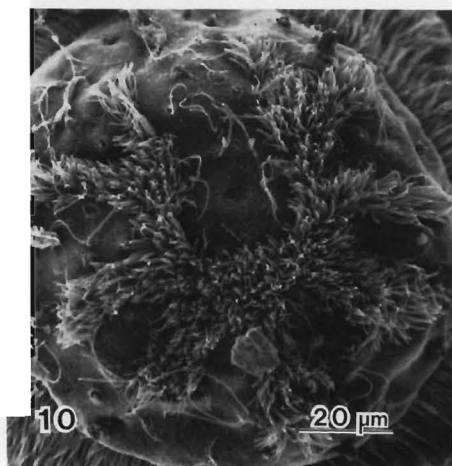
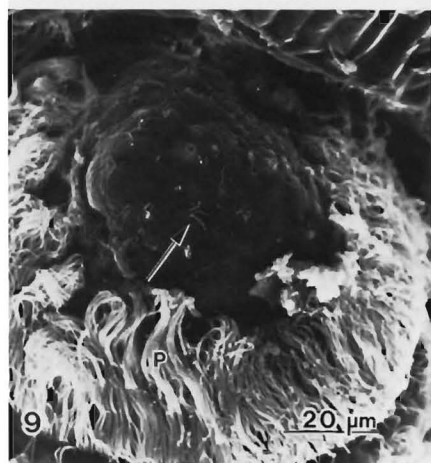
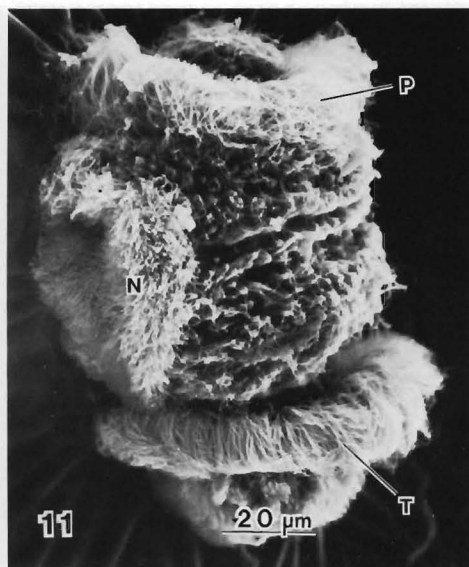
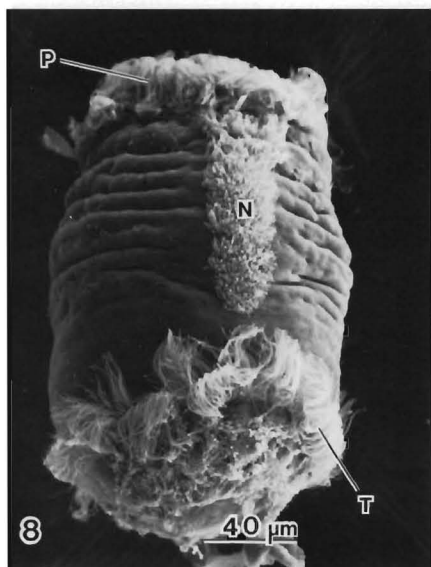
responses (Mangum 1963, Curtis 1978), electrophoretic patterns of selected enzymes (see Rice and Simon 1980, for review), or a combination of these approaches (Grassle and Grassle 1976). The study of reproductive processes in polychaetes is a particularly valuable means of sorting out differences between suspected sibling species complexes (Schroeder and Hermans 1975, Clark 1977), especially with regard to features of larval development (Hannerz 1956, Blake 1969, Levin 1984) and sperm morphology (Franzen 1956; 1970; Olive 1983; Sawada 1984).

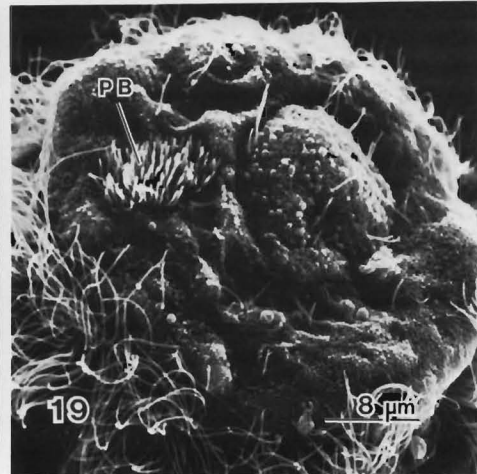
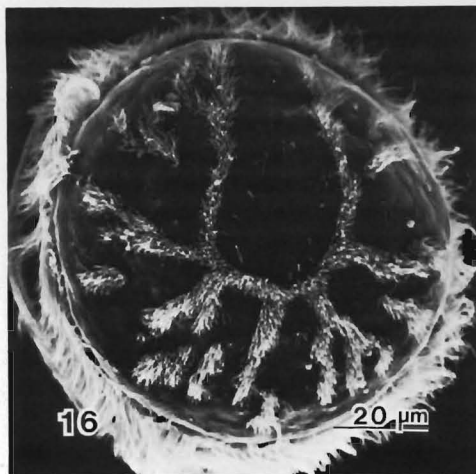
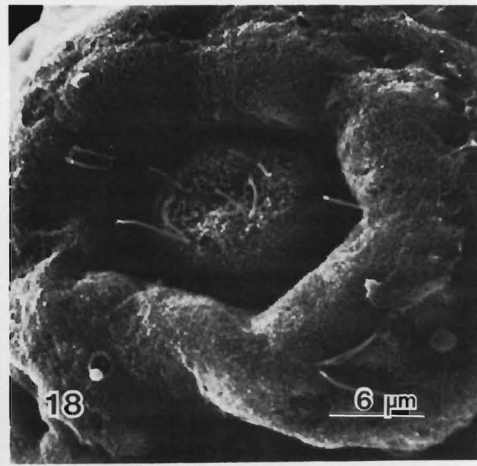
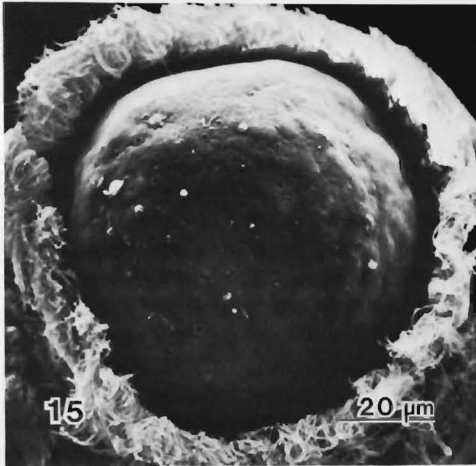
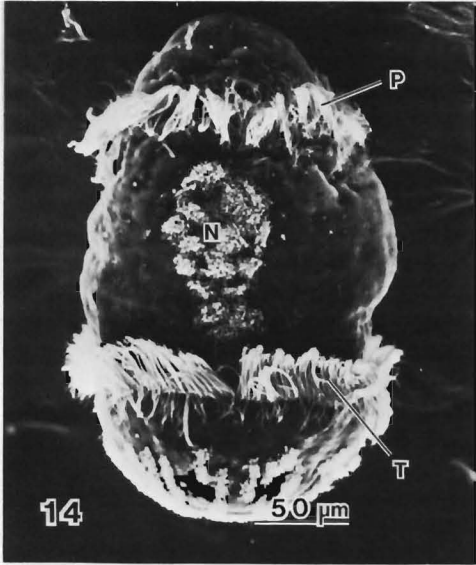
The presence of genital spines in *Capitella* is a very useful feature when one wishes to sex a

specimen at an early age, particularly since sexual dimorphism in polychaetes is uncommon (Schroeder and Hermans 1975). Our studies have indicated, however, that spermatogenesis precedes genital spine formation since young males with barely discernible spines already have genital ducts filled with mature sperm (Eckelbarger and Grassle, in press).

Genital spines have occasionally been illustrated in the literature beginning with Eisig (1887) who drew a dorsal view of the eighth and ninth setigers of *Capitella capitata* showing the general position of the spines. Gravier (1911) characterized the spines of *Capitella perarmata* while

Figs. 8–13. Newly emerged *Capitella sp. I* (Figs. 8–10) and *sp. Ia* (Figs. 11–13) larvae as viewed by SEM. P, prototroch; N, neurotroch; T, telotroch. Fig. 8, Ventral view; Fig. 9, Apical view; note sensory tuft (arrow); Fig. 10, Pygidial ciliary bands; Fig. 11, Ventrolateral view; Fig. 12, Apical view; arrow indicates mucus secretion emerging from gland neck; Fig. 13, Pygidial ciliary bands.





Hartman (1947) described and illustrated the genital spines of *Capitella ovincola* without placing any special systematic value on them. Although their presence is usually noted, the value of genital spines as a systematic character has not been carefully explored. This is perhaps due to the fact that the spines are only found in sexually mature males while field collections are usually dominated by juveniles of unknown sex. Warren (1976b) reported wide variation in spine number which appeared unrelated to size or age in *Capitella capitata capitata* although she did not indicate how age could be determined from field specimens.

Based on our studies of genital spine distribution and morphology in the five *Capitella* sibling species discussed in this paper, we conclude that spine size and morphology show some subtle interspecific differences. These differences in morphology are not dramatic, however, and taken together with the demonstrable intraspecific variation in *Capitella* sp. I males, would indicate that they are of little systematic value. The biggest intraspecific differences were observed between highly inbred males (irrespective of their age) and animals inbred for just a few generations. This degree of inbreeding is not likely to occur in any field situation.

Although genital spine morphology is not viewed as a practical systematic character, it probably should be included in species descriptions. Also, our findings suggest that maximum spine number, particularly in the ninth setiger does show stability (see Tables 1 and 2) and might be useful in formal descriptions of *Capitella* species. In *Capitella* sp. I, for example, individuals appear to reach a maximum spine number (4) in setiger 9 as young adults and maintain that number with age. Spine number in setiger 8 appears to increase with age although it is difficult at present to separate age effects from inbreeding effects. The oldest *Capitella* sp. I males examined reached an almost invariant number of genital spines, particularly in the eighth setiger (see Ta-

ble 2), but due to high mortality rates in the field, it is unlikely animals would attain this age.

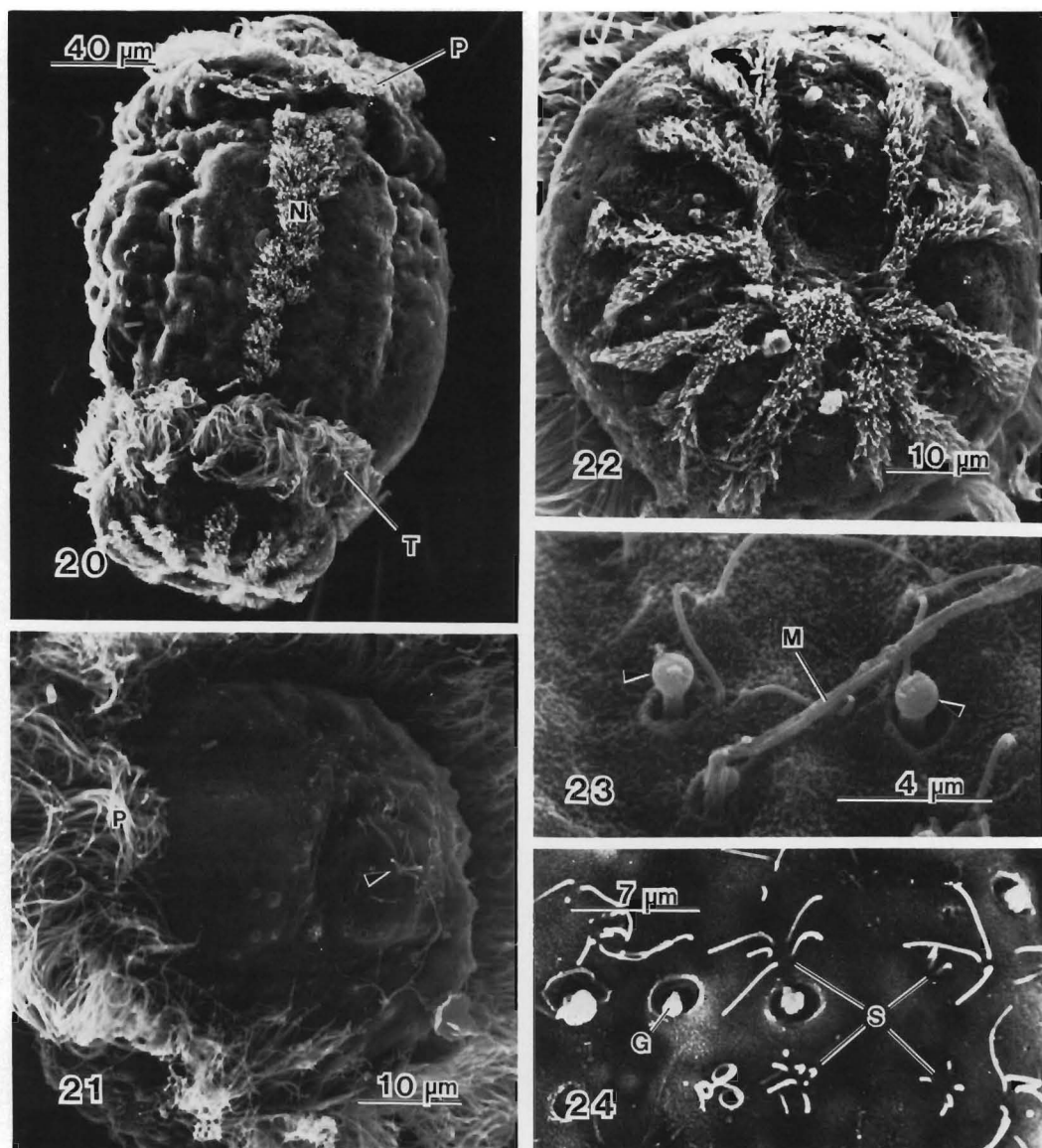
In this study, we also counted the number of small immature spines developing in setal sacs next to the fully developed spines in most individuals. The immature spines are not generally mentioned in the literature although Warren (1976a) noted them in her description of *Capitella giardi*. These spines are presumably replacement spines since it is evident that adult spines are sometimes damaged or lost. The number of such spines, however, appears to vary rather widely between specimens and in any event might be difficult to see in preserved material and therefore not of great taxonomic value.

The use of sperm morphology in animal systematics dates back to Gustaf Retzius (1904, 1910) who demonstrated distinct interspecies differences in sperm. In vertebrates, for example, sperm morphology is used for taxonomic purposes in mammals (Hughes 1965) and Beatty (1975) suggested that sperm characteristics be added to formal descriptions of inbred strains of laboratory mice. Sperm morphology has added greatly to the systematic understanding of some invertebrate groups (e.g. the Gnathostomulida, Graebner and Adam 1983) and has been used in polychaetes to separate closely related species, for example in the nereidids (Hauenschild 1951, see also Clark 1977), the serpulids (Franzen 1956, Potswald 1967), the spionids (Söderström 1920, Franzen 1956, Guerin 1975), the polynoids (Daly 1972) and the sigalionids (Christie 1982).

While sperm morphology is useful in distinguishing closely related polychaete species, it is particularly valuable in separating sibling species (Rice and Simon 1980, Olive 1983, Christie 1982). Since sperm morphology is influenced both by phylogeny and fertilization biology (Franzen 1956, 1970), it is necessary to have a thorough understanding of at least one of these factors when analyzing the causes of variation (Afzelius 1979). In the case of the *Capitella* species, there is a relatively close phylogenetic relationship be-

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Figs. 14–19. Newly emerged *Capitella* sp. II (Figs. 14–16) and sp. III (Figs. 17–19) larvae as viewed by SEM. P, prototroch; N, neurotroch; T, telotroch. Fig. 14, Ventral view; Fig. 15, Apical view; Fig. 16, Pygidial ciliary bands; Fig. 17, Ventral view; Fig. 18, Apical view, note scattered cilia; Fig. 19, Pygidial view showing scattered cilia and single ventral-lateral pygidial band (PB).



Figs. 20–24. Newly emerged *Capitella* sp. ORLEANS (Figs. 20–22) and *C. sp. I* (Figs. 23–24) larvae as viewed by SEM. P, prototroch; N, neurotroch; T, telotroch. Fig. 20, Ventral view; Fig. 21, Apical view, note ciliary tuft (arrow); Fig. 22, Pygidial ciliary bands; Fig. 23, Mucus glands with emerging secretions (arrows) and extended mucus strand (M); Fig. 24, Sensory tufts over apical surface of larva (S) and surrounding mucous gland pores (G).

tween the species and based on our observations, there are no detectable differences in the mechanism of sperm transfer. The observed interspecific variation in sperm morphology suggests differences in the fertilization process.

Although many capitellids are reported to have primitive sperm, modified sperm occur in *Cap-*

itella (Schroeder and Hermans 1975, Franzen 1956, George 1984). Franzen attributes this to the occurrence of spermatophores (reported by Eisig 1887), and maternal brood care. However, we have not observed spermatophore production in any of these *Capitella* species. Olive (1983) reports that there is evidence of sperm storage

Table 4.—Comparative larval morphology of *Capitella* sibling species.

<i>Capitella</i> species	Length (μ)*	Larval mode	Prototroch/telotroch	Neurotroch	Body cilia	Pygidial bands
I	210	Lecithotrophic	Well developed	Narrow band	No	Yes
Ia	110	Planktotrophic	Well developed	Large elliptical patch	Yes	Yes
II	200	Lecithotrophic	Well developed	Broad tapering band	No	Yes
III	72	Planktotrophic	Poorly developed	Small elliptical patch	Yes	No
ORLEANS	260	Lecithotrophic	Well developed	Narrow band	No	Yes

* After fixation for SEM.

prior to fertilization although no references are given. However, recent studies by the authors confirm the existence of sperm storage structures in the male as originally reported by Eisig (1887). The modification of *Capitella* sperm from that of the primitive plan may be due to the storage of sperm prior to release from the male. However, since the storage organs appear very similar in all species examined, interspecific differences in sperm morphology may be related to previously reported variation in egg envelope morphology among the *Capitella* species (Eckelbarger and Grassle 1983). A number of authors have reported a correlation between sperm morphology and specializations of the egg envelope in polychaetes and other invertebrates (see Eckelbarger 1984, for discussion).

A number of studies on larval development of *Capitella* have been published (Claparède and Metschnikoff 1869, Eisig 1887, Leschke 1903, Thorson 1946, Rasmussen 1956, Boletzky and Dohle 1967, Reish 1974) that show varying degrees of developmental similarity. However, since the more recent demonstration of the existence of sibling species in *Capitella* (Grassle and Grassle 1976, Grassle 1980), it is evident that earlier descriptions of development probably refer to several distinct species. Also, reports of wide geographic variation in morphology, reproductive mode and larval developmental pattern (see Tsutsumi and Kukuchi 1984) in *Capitella* are probably due to the presence of sibling species.

The present study indicates some common features in the larval morphology of five sibling species of *Capitella* but more importantly, clear distinctions between them. Besides larval size, there are a variety of features involving larval cilia including the length and density of larval ciliary bands, the shape of the neurotroch, the presence or absence of pygidial ciliary bands, and the presence and distribution of sensory cilia.

One interesting finding of the present study is the first demonstration of pygidial ciliary bands in *Capitella* larvae. Although earlier authors clearly recognized cilia on the pygidium (i.e. Eisig 1887, Rasmussen 1956, Boletzky and Dohle 1967), their banded arrangement was not reported. Our observations of living larvae indicate that this banding pattern is not apparent even when superior optics are available. The SEM is uniquely adapted to revealing this larval feature, demonstrating its usefulness when applied to some systematic problems. Determination of the function of these ciliary bands is also of some interest. In living larvae, the cilia in these bands beat away from the anus in synchronous waves, suggesting some function with regard to fecal pellet expulsion.

Larvae of the *Capitella* species described in this study would provide interesting models for an investigation into the functional role of cilia during pelagic larval life. There are striking differences in the size, number and distribution of swimming and feeding cilia between the five *Capitella* species examined, particularly between the two planktotrophic (widely dispersing) species, Ia and III. *Capitella* sp. Ia appears well-equipped for life in the plankton while sp. III does not.

The differences in the distribution of sensory cilia over the surfaces of the larvae of the *Capitella* species suggest that they may show behavioral differences in response to environmental cues. The larvae also possess well-developed nuchal organs which will be described in a separate publication. These organs are known to be highly developed in the Capitellidae (Mill 1978) and Bhup and Marsden (1982) reported their development in *Capitella* sp. I. Relatively small scale differences in distribution between the *Capitella* sibling species in the field are reported (Grassle 1980, and unpublished). Differences in sensory

structures may be related to the behavior of *Capitella* spp. larvae near the sediment when they are close to metamorphosis. Cuomo (1984) has shown that *Capitella* sp. I larvae are capable of responding to a narrow concentration range of dissolved H₂S in the water.

An apical tuft was not observed in any of the *Capitella* larvae described in this study. This is unexpected since Boletzky and Dohle (1967) and Reish (1974) indicate small apical cilia in their drawings of *Capitella* larvae while Rasmussen (1956) describes and figures an apical tuft up to 140 μ m in length. Wilson (1933) and Bookhout (1957) also figured a prominent apical tuft in their studies of development in *Notomastus* and *Dasybranchus*, respectively. Although the SEM revealed the presence of scattered cilia over the surface of some *Capitella* species (most notably spp. Ia and III), these are difficult to resolve in the light microscope and do not qualify as true apical cilia as the term is generally applied to polychaete larvae.

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