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THE CALANOID COPEPOD *EUCHAETA ANTARCTICA* FROM SOUTHERN OCEAN ATLANTIC SECTOR MIDWATER TRAWLS, WITH OBSERVATIONS ON SPERMATOPHORE DIMORPHISM

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ABSTRACT

Stage V amd VI copepodids of the predatory calanoid copepod *Euchaeta antarctica* were counted from Southern Ocean Atlantic Sector trawl samples collected during 9 months over a 5-year period. The proportion of CVI males to all CVI animals reached a maximum in June; the proportion of CVI males to total males reached a maximum in July. Two morphologically distinct kinds of spermatophores were attached to 2 different areas on the genital segment of females, and were correlated with 2 kinds of spermatophores held in leg 5 and contained within the bursa of different males. Possible adaptive significance of spermatophore dimorphism and placement for Euchaetidae is discussed and further studies are outlined.

From 1962 to 1972, the National Science Foundation's United States Antarctic Research Program (USARP) supported surveys of Southern Ocean marine organisms. Collections included over 1,000 3-m Isaacs-Kidd midwater trawl samples of the pelagic midwater fauna. In the Atlantic Sector, samples were taken during most months of the year. Samples were collected initially by the research staff of the University of Southern California and later by scientists from the Smithsonian Oceanographic Sorting Center, Woods Hole Oceanographic Institution, and Texas A&M University working aboard the USNS *Eltanin.* Midwater samples, as well as numerous other pelagic and benthic samples, were deposited with the Smithsonian Oceanographic Sorting Center where aliquots were sorted, curated, and specimens subsequently made available for study. These sorted and unsorted aliquots form an extensive source of information, much only partly utilized, about deep-water pelagic animals of the Southern Ocean.

Among the more interesting and ubiquitous of these animals is a large predatory copepod, *Euchaeta antarctica* Giesbrecht, 1902. This species has been reported throughout most Southern Ocean areas south of the Antarctic Convergence (Giesbrecht, 1902; Wolfenden, 1908, 1911; Farran, 1929; Vervoort, 1951, 1957, 1965; Yamanaka, 1976; Park, 1978). Records north of the Antarctic Convergence by Yamanaka (1976) and Park (1978) off Argentina, and Vervoort (1957) in the Indian Ocean generally are from greater depths. Recently specimens have been collected from as shallow as 10 m off Isla Madre de Dios in the Chilean fjord system (Marin and Antezana, 1985).

The vertical distribution limits of *E. antarctica* have yet to be studied systematically through 1 year, although Hopkins (1985a) collected it to 1,000 m (his deepest samples) in March and April; Yamanaka (1976) reported specimens to 4,000 m in July, August, October, and December. Its presence in plankton samples taken under ice has been noted in the Ross Sea by Farran (1929) at Cape Evans, Ross Island, and by Bradford (1981) at McMurdo Sound. Littlepage (1964) studied seasonal changes in lipid content of adults from McMurdo Sound. Reports of biological interactions include an outline of its trophic position in the pelagic community during March and April (Hopkins, 1985b) (it fed on pelagic copepods, e.g., *Oncaea* and *Metridia,* and was eaten by a fish, *Electrona antarctica*), and its predation by a benthic brittle star, *Astrotoma agassizii* (Dearborn *et al.,* 1986).

In this paper copepodid stages V and VI (=CV and CVI) of *E. antarctica* are reported from *Eltanin* midwater trawl samples taken during 9 months over a 5-year period (1962–1966). Simple sample statistics, such as the proportion of male CV or CVI copepodids, are calculated. Incidences of spermatophore dimorphism and placement in this species are noted. Finally these findings are discussed as they relate to the reproductive biology of the species.

Materials and Methods

Thirty-five 3-m Isaacs-Kidd midwater trawl samples were selected from over 1,000 available for study among USARP collections (Table 1). Initial attempts were made to limit samples examined to Atlantic Sector stations so that the results would be compatible with several contemporary research projects on Southern Ocean zooplankton (Ward, in press; Victor Marin, personal communication). Samples in and west of Drake Passage to 129°W were included if these increased the number of animals examined for a particular month or provided data for another month (June).

Generally, primary emphasis during midwater surveys was on capture of fishes, squids, and shrimps rather than large copepods. Mesh size for trawl samples was not available from standard text references for the program (e.g., Savage and Geiger, 1965); cod end mesh sizes of 0.366 mm or 0.569 mm were referred to by Park (1978). Although shipboard methods of choosing sampling depths were not indicated, it is doubtful that sampling depths were selected with regard to the distribution of *E. antarctica* because very little was known about the vertical distribution of this animal at the time. Sampling depths were determined simply by measuring wire angle and amount of wire out, which introduced errors for deep tows.

Although the euchaetid fauna from Southern Ocean midwater trawls is diverse (Park, 1978), in this study *E. antarctica* most commonly co-occurred with 3 other species, the smaller *E. biloba* and *E. rasa,* and the larger *E. barbata* (which was not distinguished from *E. farrani*). CVI copepodid females of *E. antarctica* were identified by a ventral lappetlike projection from the anteroventral margin of the genital prominence, and CVI males by an elongate external spine on leg 2 exopod 2 and a lobe on the right leg 5 endopod. The latter character has been described also for males of *E. austrina* from the Pacific Sector by Giesbrecht (1902). Other members of the "*antarctica*" group (defined by Fontaine, in press) either are restricted to shelf waters (*E. erebi* and *E. tycodesma*), are much smaller than *E. antarctica* (*E. austrina*), or have a rostrum pointed anteroventrally (*E. similis*). *Euchaeta similis* was the only other member of the group encountered in this study; co-occurring CVI males and females were found at station 998. CV *E. antarctica* were distinguished by a combination of: (1) general characters for calanoids and euchaetids—male leg 5 and female genital segment simple, segmentation of swimming legs identical to CVI (particularly 3-segmented exopod on legs 3 and 4); (2) characters restricted to the "*antarctica*" group—prosome corners with tiny points (usually absent on adults), 9 setae on the exite of maxilla 1 (most co-occurring congeners with 5 setae); and (3) characters particular to *E. antarctica*—ventrally pointed rostrum and an elongate external spine on leg 2 exopod 2. CV males have a rudimentary leg 5 with simple, 1-segmented exopod and endopod, which is absent in females.

Park (1978) gave a taxonomic description for CVI females and males of *E. antarctica.* His paper provided a definition of terms and a description of both sexes. Descriptions provided below pertain to the female genital segment and male leg 5, features pertinent to this study.

The physical condition of the specimens exhibited a range of variation; some were opaque with well-developed, reddish brown internal musculature, while in others musculature and digestive tract were variously reduced in size or absent. In some specimens the reproductive tract was absent and only the exoskeleton was intact. These differences may be related to precapture physiological conditions of the animals (Wheeler, 1967; Miller *et al.,* 1984) or postcapture fixation and preservation (Griffiths *et al.,* 1976). All animals were counted regardless of physical condition. Attached spermatophores varied in physical condition from complete (with flask, neck, stalk, attachment plate, and occasionally fertilization tube) to attachment plate only; all were counted.

Specimens were cleared in 85% lactic acid for at least 16 h and studied using the wooden slide procedure of Humes and Gooding (1964). A drawing tube was used to prepare the illustrations. Terminology for attached spermatophores follows Ferrari (1978). Spermatophores initially were differentiated by their attachment sites on the female genital segment: (1) correct spermatophores attached to the ventral face of the prominence and over the genital opening, or (2) alternate spermatophores attached near two small bumps anterior to the genital prominence. When measurements of these attached spermatophores (including spermatophore flasks) suggested there were 2 morphologically different types of spermatophores, each restricted to one attachment site, the same 2 names were assigned to the spermatophore types (correct and alternate). When measurements of spermatophores

Table 1. Samples of *Euchaeta antarctica* studied. Cr = cruise; St = station; D/mo/yr = day, month, and year; Alq = aliquot; T = time in minutes; C = standardization factor, inverse of aliquot divided by time in hours; *N*/hr = number of CV and CVI stages of *E. antarctica* encountered per towing hour.

Cr	St	D/mo/yr	Depth	Latitude	Longitude	Alq	T	C	*N*/hr
21	278	2 Jan 66	470–670	57°00′S	85°05′W	1/8	60	8.0	16
21	279	3 Jan 66	700–850	57°02′S	85°06′W	1/8	60	8.0	48
6	449	15 Jan 63	1,610	60°12′S	59°00′W	1/16	123	7.8	23
22	1510	26 Jan 66	661–942	58°56′S	54°05′W	1/8	64	7.5	217
22	1516	29 Jan 66	1,398–2,039	55°56′S	51°46′W	1/8	64	7.5	97
22	1518	30 Jan 66	1,193–1,252	54°28′S	51°52′W	1/8	60	8.0	712
12	998	14 Mar 64	732–1,373	61°51′S	55°56′W	1/8	165	2.9	118
12	1014	19 Mar 64	560–630	65°08′S	47°45′W	1/8	120	4.0	196
22	1580	5 Mar 66	2,134–3,221	56°28′S	24°15′W	1/8	122	3.9	39
22	1584	8 Mar 66	1,131–1,548	56°23′S	35°05′W	1/8	60	8.0	288
22	1587	12 Mar 66	1,792–1,956	55°34′S	50°03′W	1/8	61	7.9	277
22	1590	13 Mar 66	675–708	55°15′S	53°30′W	1/8	60	8.0	96
12	1057	4 Apr 64	1,162–1,290	59°28′S	31°20′W	11/32	120	1.5	359
23	1607	2 Apr 66	1,150–1,311	54°56′S	75°46′W	1/8	61	7.9	0
23	1608	3 Apr 66	1,682–1,784	57°56′S	77°04′W	1/8	120	4.0	0
13	1121	29 May 64	834–849	64°14′S	89°55′W	1/8	60	8.0	1,888
13	1132	7 Jun 64	1,381–1,812	60°17′S	92°02′W	1/8	125	3.8	91
13	1133	7 Jun 64	560–791	66°04′S	92°38′W	1/8	120	4.0	132
13	1141	10 Jun 64	2,416–2,435	66°15′S	102°37′W	1/8	120	4.0	64
13	1167	28 Jun 64	1,047	55°28′S	129°45′W	1/8	75	6.4	6
13	1170	30 Jun 64	988–1,080	55°01′S	129°56′W	1/8	91	5.3	122
4	109	18 Jul 62	915	56°09′S	60°54′W	1/4	120	2.0	204
4	137	7 Aug 62	1,556	61°11′S	63°45′W	?	240	na	na
4	141	10 Aug 62	915	59°56′S	65°15′W	1	120	0.5	266
9	683	25 Aug 63	1,867	55°13′S	38°20′W	1/32	120	16.0	656
9	687	26 Aug 63	2,214	55°24′S	37°57′W	1/32	120	16.0	192
9	692	27 Aug 63	1,034	56°29′S	37°03′W	1/32	120	16.0	816
5	235	2 Oct 62	1,830	59°06′S	67°59′W	5/16	60	3.2	131
5	247	5 Oct 62	1,830	59°29′S	68°01′W	1/4	120	2.0	30
5	248	5 Oct 62	1,373	59°56′S	69°00′W	1/4	130	1.8	52
5	259	17 Oct 62	2,615	62°00′S	68°01′W	1	120	0.5	87
6	355	5 Dec 62	2,363–3,025	55°43′S	58°53′W	1/2	127	0.9	7
6	359	6 Dec 62	708–842	56°19′S	58°10′W	5/16	120	1.6	219
6	375	20 Dec 62	712–933	53°00′S	55°50′W	1/16	120	8.0	24
6	396	29 Dec 62	714–895	58°56′S	56°00′W	1/16	120	8.0	320

from male bursae correlated with the 2 groups of attached spermatophore flasks, the same 2 names were retained for bursa spermatophores.

Measurements of the spermatophores in lactic acid were made using an ocular micrometer or drawing tube. Flask length of alternate spermatophores (Fig. 2C, F) was taken from the distal end of the spermatophore flask to the junction of neck and spermatophore flask (as distinguished by the broader shoulders of this spermatophore flask). Measurements of correct spermatophores were more difficult because the spermatophore flask narrows gradually and indistinguishably to a neck. Flask length of correct spermatophores was measured from the distal end of the spermatophore flask to a point where this gradual narrowing ceased (Fig. 2B, E). The width of the spermatophore flask and thickness of its wall were measured at about midlength of the flask. The cylindrical tube connecting an alternate spermatophore flask to attachment plate (analogous to the neck and stalk reported by Ferrari, 1978) was measured as a single unit, the stalk/neck.

For scanning electron microscopy, specimens stored in sorting solution (0.5% propylene phenoxetol, 4.5% propylene glycol, and 95% distilled water) were transferred to 70% ethanol for about 8 h, then dehydrated through 2 concentrations of ethanol solutions (3 times through 95% and 4 times through 100%; each step for at least 1 h). Specimens remained in the final dehydration step for about 8 h and then were critical-point dried prior to attachment to aluminum stubs, carbon evaporation, and sputter-

coating with gold-palladium. Specimens were examined under a scanning electron microscope (Hitachi S-570).

Results

On CVI females of *E. antarctica* a conspicuous ventral genital prominence was located on the genital segment (Figs. 1A, B; 4A, B), with a subtriangular lappetlike process on the anteroventral surface of the prominence. This process distinguished CVI females of *E. antarctica* from all congeners. Immediately posterior to the lappetlike process was a very small boss with 2 transverse slits. A pair of conical genital flanges lies posterolateral to these slits. The posterior region of the genital prominence was produced on each side into a large, subtriangular flap, longer and much broader than the genital flange. The ventromedial area (Fig. 4C–F) was composed of a platelike structure, representing the genital operculum (or genital valve); its anterior section appears as multicreased cuticle. A conspicuous, central linguiform process (Fig. 4E) was flanked by 2 oblique bars toward the middle of the operculum. Posterior to the plate was a large opening, probably the genital cavity described by Geptner (1968). Egg sacs originated from the area of the operculum anterior to the genital flaps (Fig. 5A, B). The genital cavity houses the openings of the seminal receptacle (Geptner, 1968).

Directly anterior to the genital prominence was a pair of rounded bumps or anteroventral genital processes (Figs. 1A, B; 5C) ("conspicuous pair of folds" of Park, 1978, p. 221), with transverse rows of slits (Fig. 5C, D) at their bases; the slits extended sagittally on the genital prominence along the medial surface. In addition, a pair of transverse rows of small rounded pits (Fig. 5E, F) occurred on the anteromedial surface of the genital prominence.

Spermatophores were attached to the genital segment of female *E. antarctica* in any of 3 specific locations: directly on the ventral face of the genital prominence, a correct spermatophore (Fig. 2B), or in 2 anterior locations at the base of the genital prominence marked by the 2 anteroventral genital processes (Figs. 1B; 2A, C); spermatophores so attached are called here right or left alternate spermatophores. On 2 females alternate spermatophores were placed between the 2 bumps (called here median alternate spermatophores). Correct spermatophores of *E. antarctica* were placed in the genital cavity which is located posterior to the genital flanges (Fig. 6A–C). The attachment plate of an alternate spermatophore usually covered either left or right bumps (e.g., Fig. 6D, E). Occasionally spermatophore attachment plates were found lateral to the bumps, especially if more than one alternate spermatophore was placed on that side.

The CVI male leg 5 is asymmetrical (Fig. 1C–F). Its right exopodal segment 1 bore a slight protrusion with a setule at about midlength along the lateral margin; a shorter exopodal segment 2 terminated in a round tip. The right endopod (Fig. 1D) had an outer rounded process (Fig. 7A, B) with a corrugated area at about midlength and terminated in a sharp point. The corrugations were similar to those found on adhesion pads of some species of parasitic copepods (Cressey, 1967). The left leg 5 was long and slender; its exopod was 3-segmented with the basal segment longest. A complex segment 2 (Fig. 1E, F) bore a distolateral row of minute spinules, a lamella with relatively large denticles along the inner margin and smaller serrations along the distal part of the lateral margin, a medial lobelike process ("digitiform process" of Park, 1978, 223), and a haired, acuminate, setiform process. Exopodal segment 3, extending beyond the distal limit of the dentate lamella, was equipped along its inner margin with long setules and a subterminal cluster of long bristlelike setae. The left endopod was represented by a small lamellate structure situated near the base of the first exopodal segment.

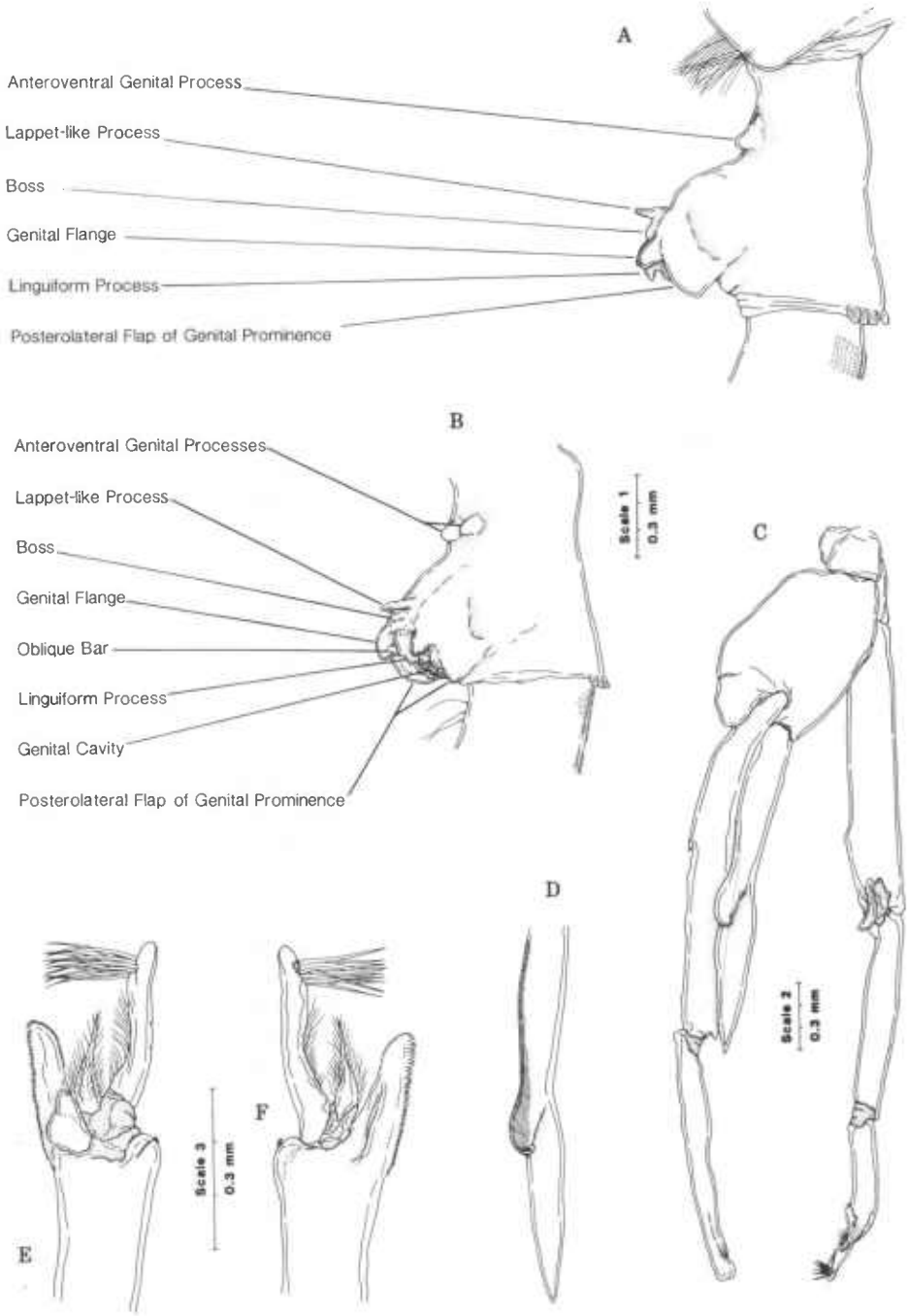

Fig. 1. *Euchaeta antarctica.* Female: A, genital segment, left lateral; B, genital segment, left ventrolateral. Male: C, leg 5, anterior; D, distal end of right endopod, anterior; E, tip of left exopod 2 and exopod 3, medial; F, tip of left exopod 2 and exopod 3, lateral. A, B, D drawn at scale 1; C at scale 2; and E, F at scale 3.

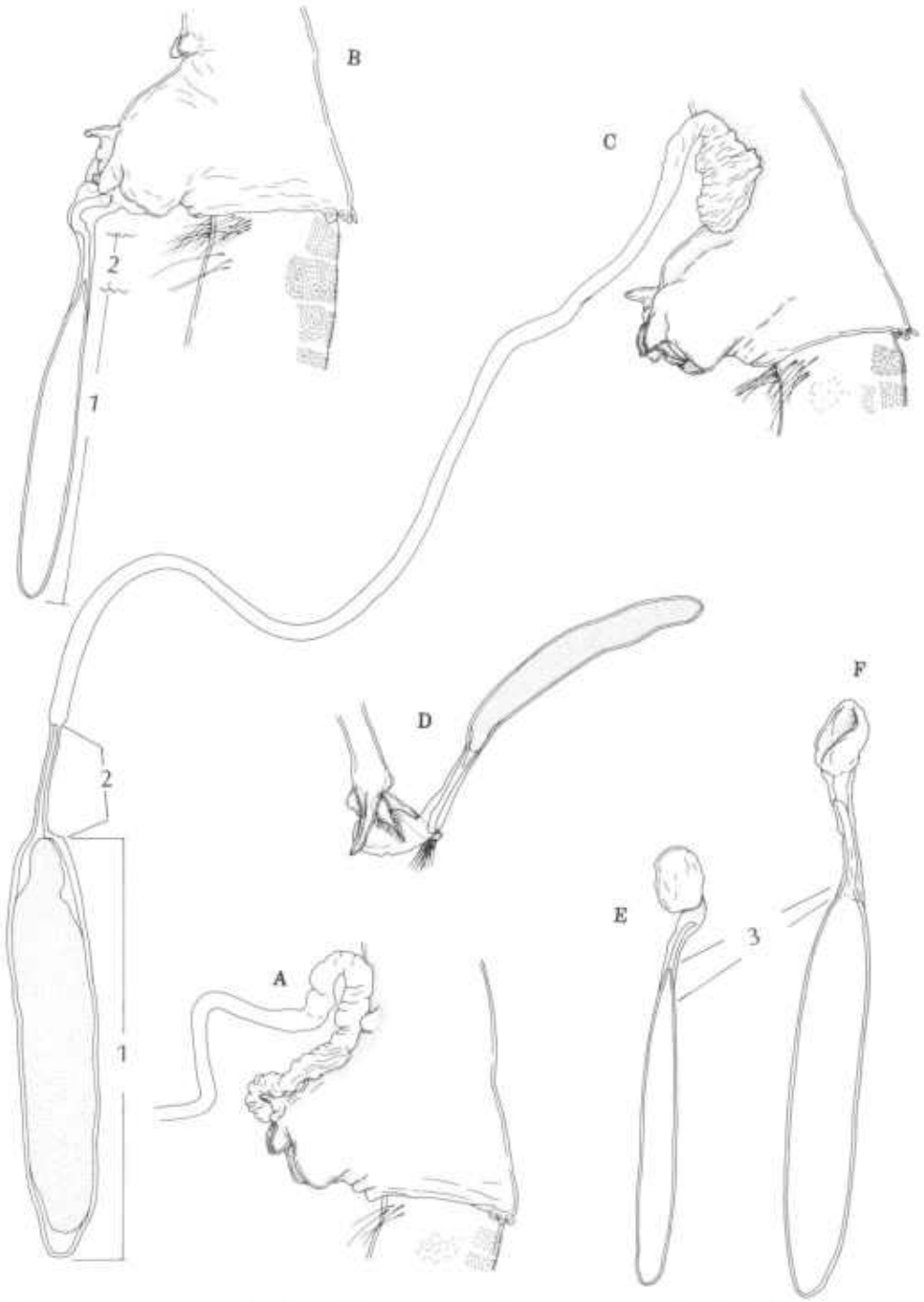

Fig. 2. *Euchaeta antarctica*. Female: A, genital segment with fertilization tube, left lateral; B, genital segment with correct spermatophore; C, genital segment with left alternate spermatophore. Male: D, distal end of left exopod with correct spermatophore, lateral; E, correct spermatophore from bursa; F, alternate spermatophore from bursa. (1 = flask and 2 = neck of alternate and correct attached spermatophores; 3 = flask/neck junction of alternate and correct bursa spermatophores). A–F drawn at scale 1 (refer to Fig. 1).

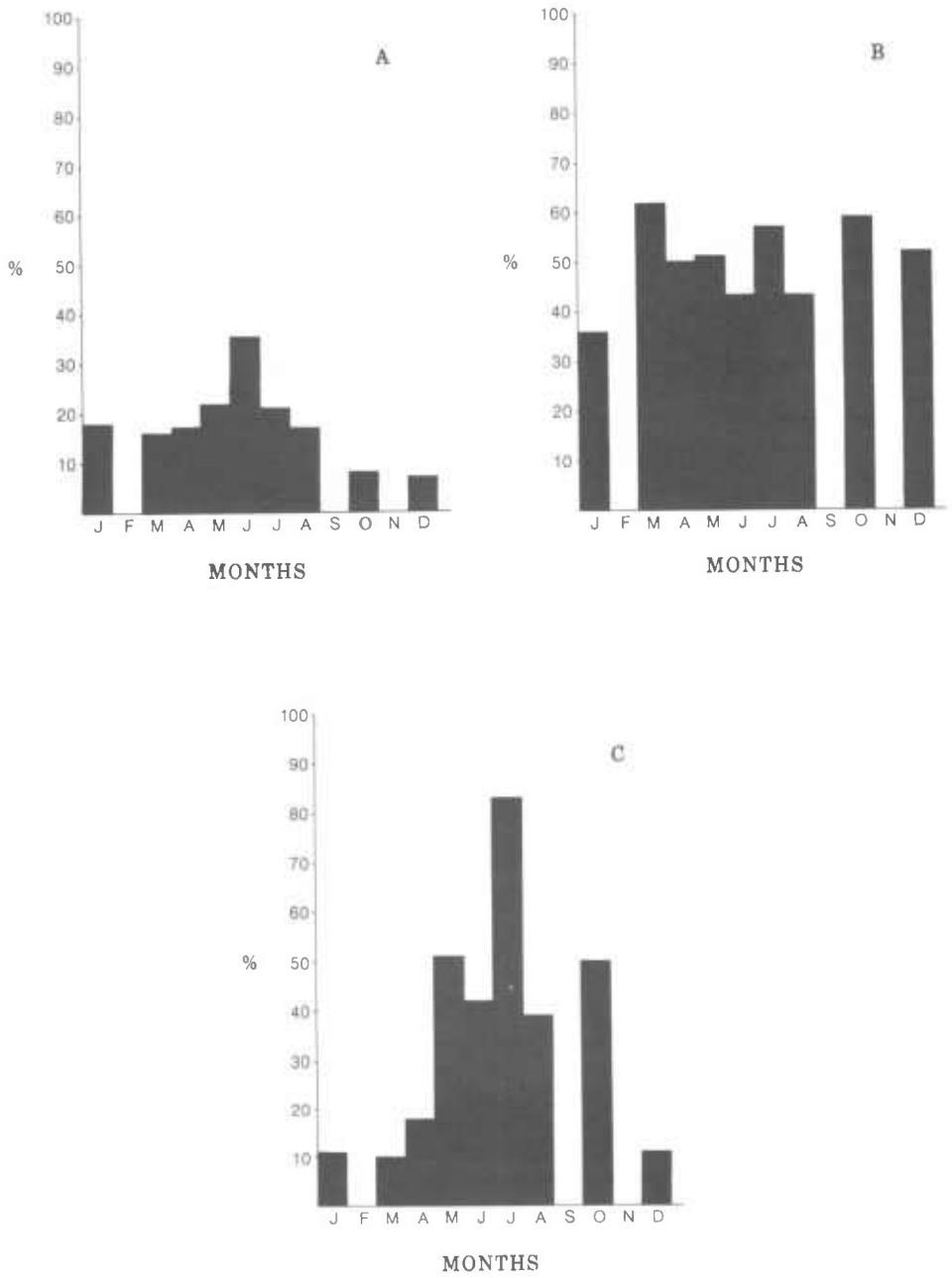

Fig. 3. *Euchaeta antarctica*. A, monthly percentage CVI males per all stage VI; B, monthly percentage CV males per all stage V; C, monthly percentage CVI males per CV plus CVI males.

Males held the terminal part of a spermatophore between exopodal segment 3 and the dentate lamella of the left leg 5 (Figs. 2D, 7C–E). The haired, setiform process remained on the same side as the lamella. The distal end of the digitiform process touched the terminal part of the spermatophore.

Males and females of both CVI and CV animals were found in samples from every month examined; CVI females with attached spermatophores were found in all months except June (Table 2). Counts of 4 classes of animals—CV males and females, and CVI males and females—were corrected for aliquot size and time of tow to give a rough numerical estimate of late-stage *E. antarctica* captured per hour towed. These data (Table 1) ranged from 0 (in April) to 1,888 specimens per hour (in late May) and indicated that the species may be encountered commonly during most months throughout the upper 1,500 m, and occasionally to below 2,500 m.

Adult males, as a percentage of total number of CVI animals, reached a maximum value in June (35%), from minima in October and December of less than 10% (Table 3, Fig. 3A). CV males, as a percentage of all CV animals, remain above 50% for most months and did not exhibit a distinctive trend (Table 3, Fig. 3B). An indication of changing proportions of CV and CVI animals was provided by the number of CVI males as a percentage of CV plus CVI males (Table 3, Fig. 3C). This percentage reached a maximum (83%) in July from a minimum in December and January (11%). Numbers of spermatophores per female with spermatophores (Table 3) appeared uniform through most of the year, with an exception in June.

Of 1,122 CVI females, 23% (263) had at least 1 attached spermatophore. For the year, the mean number of spermatophores per female was 0.31, with 1.3 spermatophores per female with at least 1 attached spermatophore. One hundred and ninety-two females (Table 4) had a single attached spermatophore; these represent 17% of all CVI females and 73% of those with at least 1 spermatophore. On these 192 females there were about 10% (19) correct spermatophores, about 49% (94) right alternate spermatophores, 40% (77) left alternate, and 2 median alternate. In total, females with alternate spermatophores comprised about 90% of the females with 1 spermatophore.

The 59 females with 2 attached spermatophores represented 22% of the females with at least 1 spermatophore. Of this group, none had double correct or correct-left, and only 2 had correct-right placements (Table 4). Forty-four females exhibited left-right placements; these comprised almost 75% of the females with double spermatophore attachments. Nine females had 3 attached spermatophores, representing 3% of females with at least 1 spermatophore. Only 2 females had 4 and a single female had 7. Most of these multiple spermatophores were alternate. There was no case in which spermatophores were either all left or all right (Table 4).

Of the 263 females with at least 1 attached spermatophore, 93% (244) had at least 1 alternate spermatophore; only 9% (23 females) carried a spermatophore in the correct area. These 2 percentages do not total 100% because 4 females with correct spermatophores also had alternate spermatophores, and 2 exhibited a median placement. There were 326 alternate spermatophores in the specimens examined. Forty-six per cent (149) were found in the right-alternate area and 54% (177) in the left-alternate. Finally, 263 females with 352 spermatophores co-occurred with 230 CVI males; there were 1.53 attached spermatophores per CVI male.

Fertilization tubes (Fig. 2A) were associated only with alternate spermatophores. All tubes connected the attachment plate of alternate spermatophores with the female genital opening. Of 326 spermatophores attached to an alternate area, 15% (50 spermatophores) had an associated fertilization tube. Twenty per cent (50) of 244 females with at least one alternate spermatophore had a fertilization tube. These tubes followed a path coinciding with the transverse rows of slits and small

rounded pits on the anteromedial surface of the genital prominence (Fig. 5C–F). These simply may provide a rugose area, on an otherwise smooth surface, for adhesion of the fertilization tube during initial stages of its formation.

The majority of egg sacs of *E. antarctica* were broken. Breakage may have occurred during capture in the net, or sorting and handling of samples. Remnants of attached egg sacs were counted; 64 females had egg sacs. These represented about 6% of CVI females.

Two groups of spermatophores were initially differentiated by 2 different attachment sites (correct and alternate) on the genital segment of females of *E. antarctica* (Fig. 2B, C). In addition to attachment site, these 2 groups of spermatophores differed in length and width of the spermatophore flask, shape of the neck area, thickness of the spermatophore wall, and length of the stalk/neck, the cylindrical tube connecting spermatophore neck with attachment plate (Table 5).

Correct spermatophores were attached to the genital field, the ventral face of the genital prominence, and had gradually tapering necks (Fig. 2B). Flasks of correct spermatophores averaged 1.09 mm long (range 1.00–1.17 mm) by 0.14 mm wide (range 0.12–0.17 mm), based on 9 attached spermatophores (Table 5). The flask wall thickness was approximately 0.005 mm; the stalk/neck was relatively short, about 0.19 mm. Alternate spermatophores were placed over or lateral to the anteroventral genital processes; the junction of the neck and flask were easily distinguished (Fig. 2B). Alternate spermatophore flasks averaged 1.36 mm long (range 1.14–1.70 mm) by 0.24 mm wide (range 0.22–0.27 mm), based on 25 attached spermatophores. Flask wall thicknesses averaged 0.009 mm, while spermatophore stalk/necks were 4.33 mm. Mean length and width of alternate spermatophore flasks were considerably greater than those of correct spermatophores (about 25% and 70%, respectively); wall thickness was almost twice that of correct spermatophores, while stalk/neck length of the former was more than 20 times longer than the latter.

The bursa of 230 CVI males was examined in this study. In male euchaetids, sperm and spermatophore material pass from a seminal vesicle into the bursa (also called spermatophore sac) of the linearly arranged reproductive tract (Hopkins, 1978). Here the spermatophore assumes its final shape prior to extrusion. Bursa spermatophores were dissected from 80 males collected during 6 different

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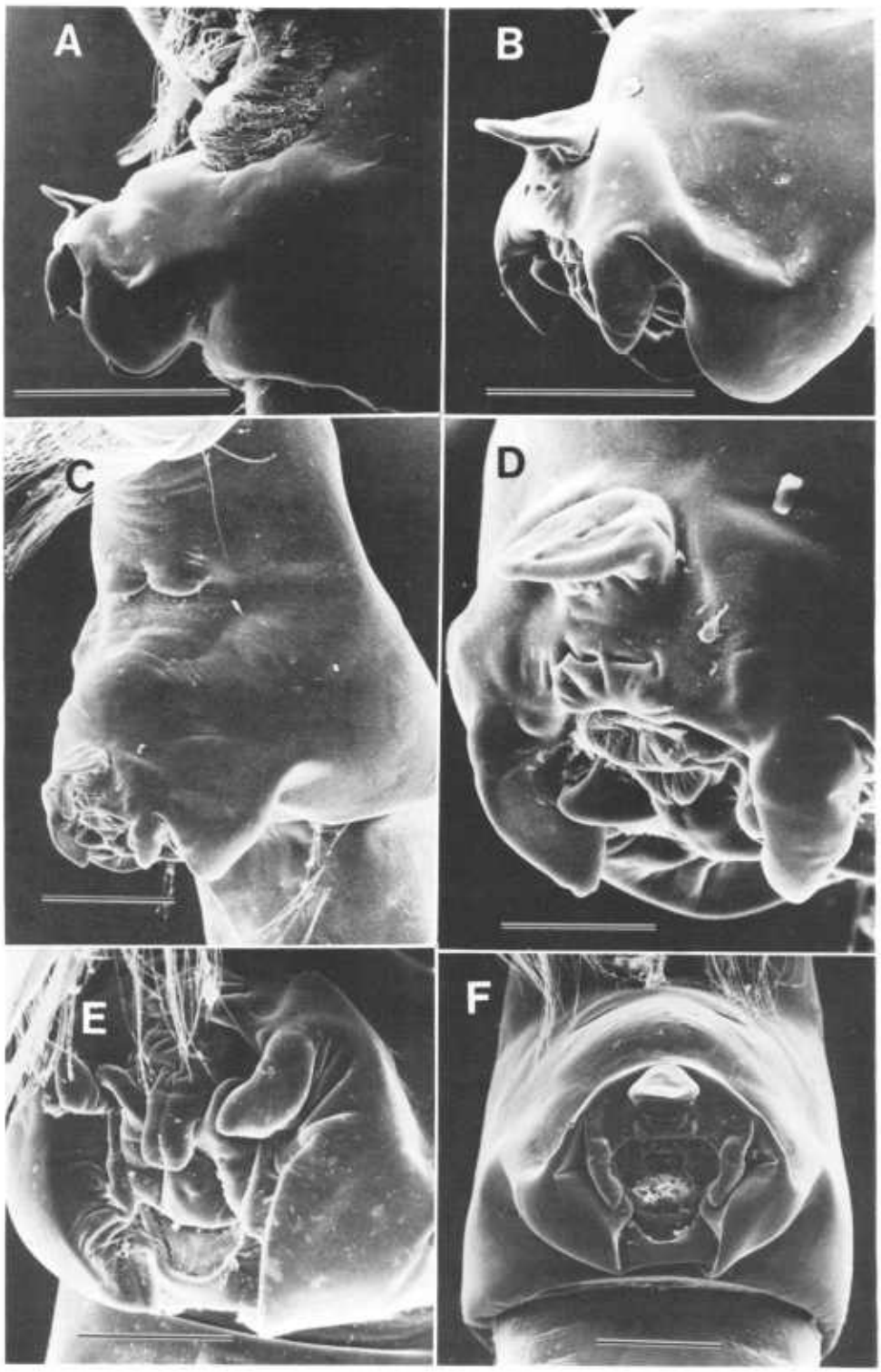
Fig. 4. *Euchaeta antarctica.* Female: A, genital segment with left alternate attachment plate of spermatophore, lateral; B, genital prominence, ventrolateral; C, genital segment, ventrolateral; D, genital field, ventrolateral and slightly anterior; E, genital prominence, ventrolateral; F, genital prominence with open genital valve, ventral. Scale: 400 μm in A; 200 μm in B, F; 250 μm in C; 75 μm in D; 136 μm in E.

Fig. 5. *Euchaeta antarctica.* Female: A, genital segment with torn egg sac, ventrolateral; B, genital prominence with torn egg sac, ventrolateral; C, anteroventral genital processes, ventrolateral; D, sagittal row of transverse slits on genital segment, ventrolateral; E, transverse row of small rounded pits on genital prominence, ventrolateral; F, same, face-on view. Scale: 400 μm in A; 200 μm in B; 75 μm in C; 20 μm in D; 23.1 μm in E; 17.6 μm in F.

Fig. 6. *Euchaeta antarctica.* Female: A, urosome with correct spermatophore, ventrolateral; B, genital prominence with correct spermatophore and its extensive attachment plate, ventrolateral; C, genital prominence with correct spermatophore and curved spermatophore stalk, ventrolateral; D, genital segment with left alternate attachment plate of spermatophore, ventrolateral; E, attachment plate of left alternate spermatophore, ventrolateral. Scale: 0.50 mm in A; 120 μm in B; 100 μm in C, E; 200 μm in D.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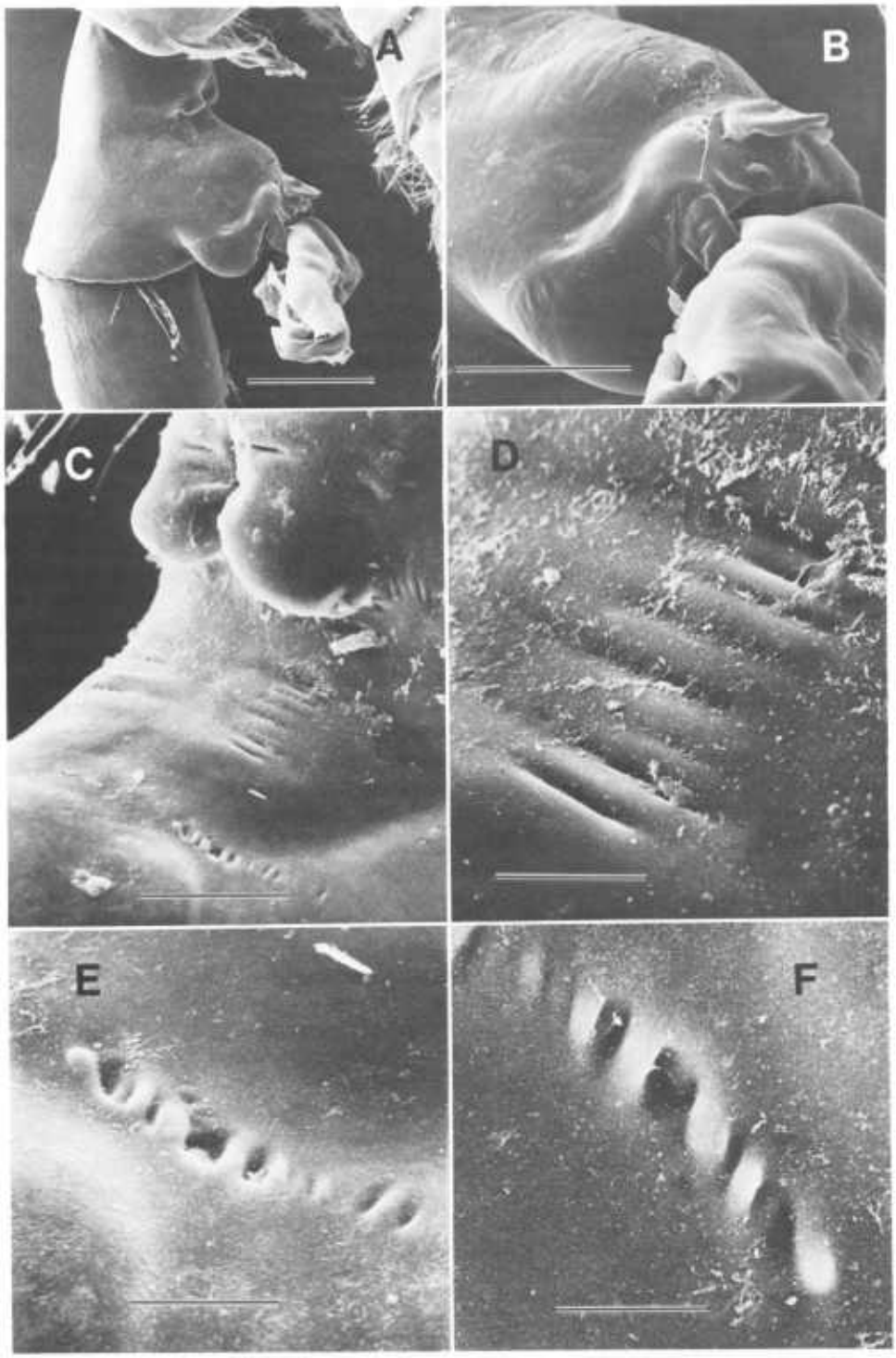
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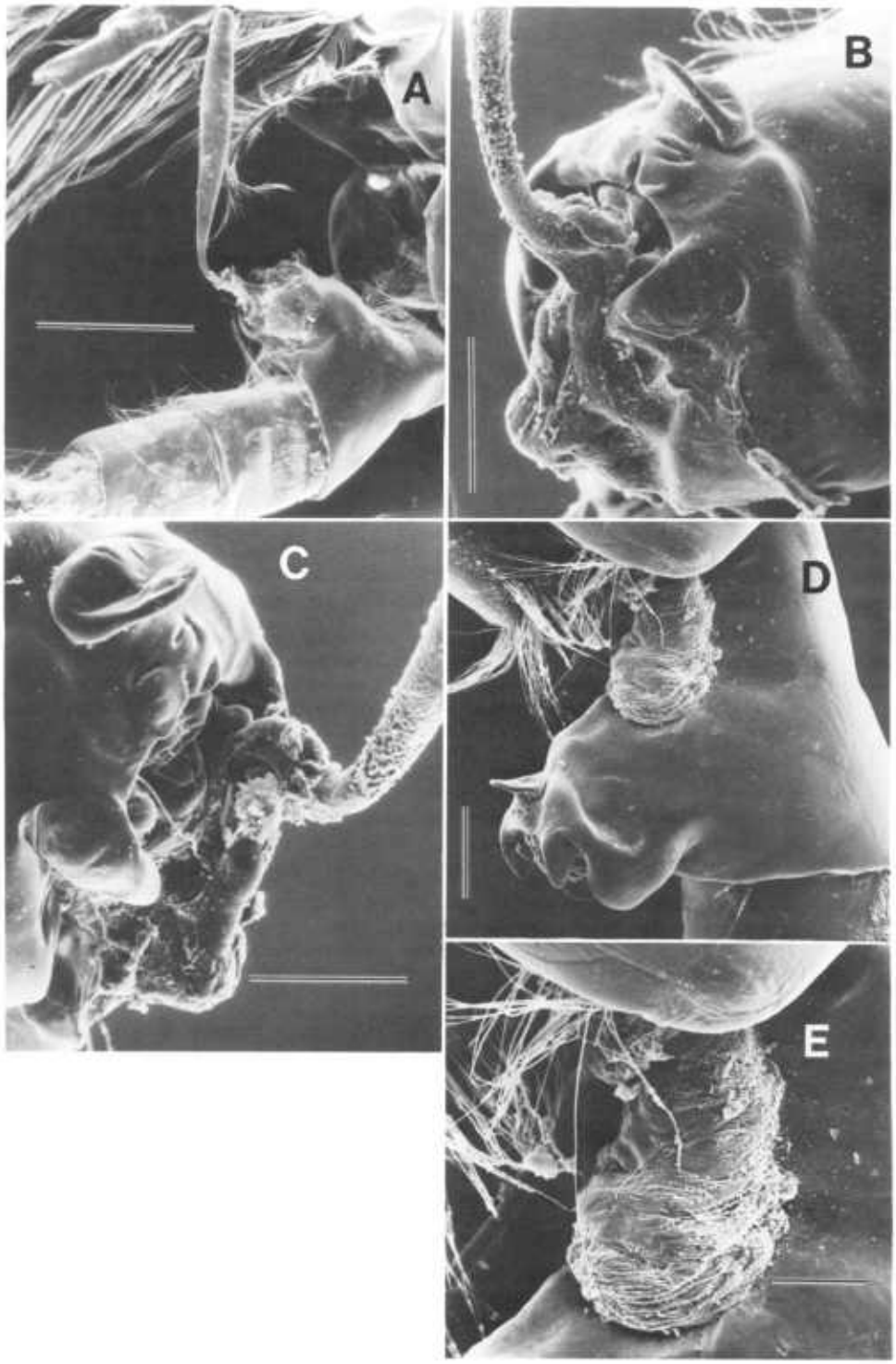
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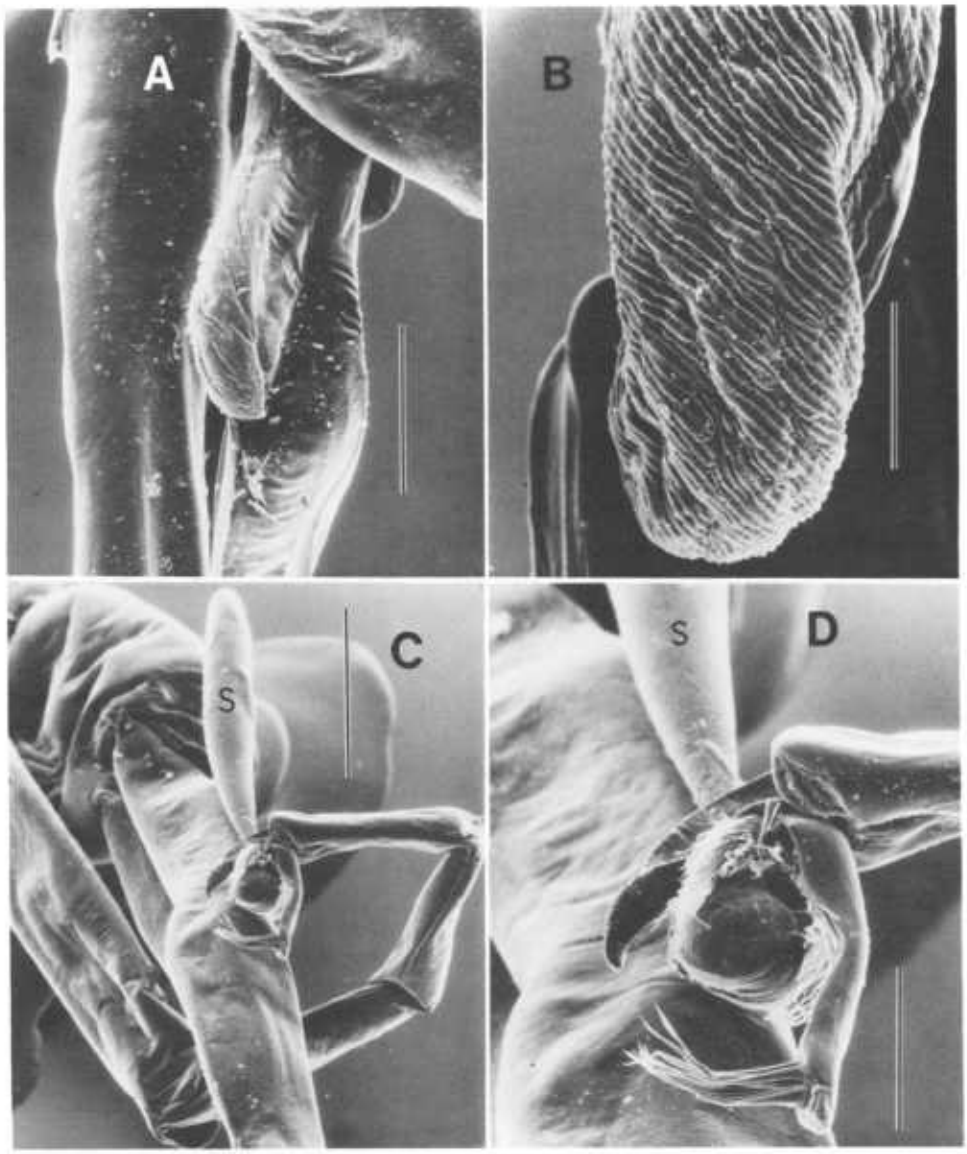

Fig. 7. *Euchaeta antarctica*. Male: A, rounded process on right leg 5 endopod, anterior; B, same, lateral; C, leg 5 left exopod holding correct spermatophore, lateral; D, same, magnified view (s = spermatophore). Scale: 150 μm in A; 38 μm in B; 0.33 mm in C; 120 μm in D.

months and were described assuming that there was no further development or modification within the bursa. These spermatophores were placed in 2 groups according to shape of the neck/flask junction (Fig. 2E, F). Lengths, widths, and thicknesses of these 2 groups corresponded to similar dimensions of correct or alternate spermatophores on female genital segments (Table 5). Besides neck shape, spermatophore width best characterized the 2 groups of bursa spermatophores; ranges of widths for correct and alternate bursa spermatophores seldom

Table 2. *Euchaeta antarctica*. Number of copepodid stage VI females (=Cvif), with spermatophores (=Ws), males (=Cvim), copepodid stage V females (=Cvf), males (=Cvm), and number of spermatophores (=S) from each sample studied; not corrected for aliquot size or duration of tow. Other headings as in Table 1.

Cr	St	D/mo/yr	Cvif	Cvim	Cvf	Cvm	S	Ws
6	449	15 Jan 63	3	0	0	0	1	1
21	278	2 Jan 66	0	0	1	1	0	0
21	279	3 Jan 66	6	0	0	0	5	4
22	1510	26 Jan 66	11	5	6	7	5	4
22	1516	29 Jan 66	0	0	8	5	0	0
22	1518	30 Jan 66	2	0	59	28	0	0
12	998	14 Mar 64	23	5	6	7	5	5
12	1014	19 Mar 64	1	0	20	28	0	0
22	1580	5 Mar 66	7	1	1	1	5	3
22	1584	8 Mar 66	11	3	1	21	4	4
22	1587	12 Mar 66	2	0	16	17	2	1
22	1590	13 Mar 66	3	0	4	5	0	0
12	1057	4 Apr 64	81	16	72	71	7	7
23	1607	2 Apr 66	0	0	0	0	0	0
23	1608	3 Apr 66	0	0	0	0	0	0
13	1121	29 May 64	131	37	33	35	48	35
13	1132	7 Jun 64	4	2	10	8	0	0
13	1133	7 Jun 64	13	1	12	7	0	0
13	1141	10 Jun 64	2	2	6	6	0	0
13	1167	28 Jun 64	0	1	0	0	0	0
13	1170	30 Jun 64	11	10	1	1	0	0
4	109	18 Jul 62	75	20	3	4	46	36
4	137	7 Aug 62	188	22	5	7	42	33
4	141	10 Aug 62	175	53	174	129	65	47
9	683	25 Aug 63	31	5	3	2	18	14
9	687	26 Aug 63	8	4	0	0	6	4
9	692	27 Aug 63	41	7	1	2	22	16
5	235	2 Oct 62	38	2	0	1	10	7
5	247	5 Oct 62	13	1	0	1	4	3
5	248	5 Oct 62	28	1	0	0	4	3
5	259	17 Oct 62	128	15	13	17	27	18
6	355	5 Dec 62	0	0	6	2	0	0
6	359	6 Dec 62	51	2	40	44	0	0
6	375	20 Dec 62	3	0	0	0	0	0
6	396	29 Dec 62	32	4	0	4	26	18

overlapped and often exhibited a distinct gap (May 1964, July 1962, October 1962).

Bursa spermatophore dimensions exhibited variations among months and between the years 1962 and 1964, as did male total length (Table 5). During July, August, and October of 1962 correct spermatophores were progressively smaller, as were male body lengths, while the smallest alternate spermatophores were found in August. Monthly occurrences of alternate spermatophores reached a minimum in August (4 alternate, 27 correct). Thirty-five additional spermatophores (10 alternate, 25 correct) were observed from undissected August males, suggesting occurrence of alternate spermatophores was lower in August (21%—14 alternate, 52 correct) than July (47%—8 alternate, 9 correct) or October (78%—10 alternate, 4 correct).

Eight males carried spermatophores in their left leg 5. Of these 8 spermato-

Table 3. *Euchaeta antarctica*. Monthly number of copepodid stage VI females (=Cvif), with spermatophores (=Ws), males (=Cvim), copepodid stage V females (=Cvf), males (=Cvm), number of spermatophores (=S), all stage VI animals (=Tcvi), all stage V animals (=Tcv), stage V plus VI males (=Tm), per cent CVI males of all stage VI animals (=% Mvi), per cent CV males of all stage V animals (=% Mv), per cent stage VI males of all males (=% Cvim), spermatophores per stage VI females (=S/Cvif), spermatophores per stage VI females with at least 1 attached spermatophore (=S/Ws); not corrected for aliquot size or duration of tow.

Month	Cvif	Cvim	Tcvi	% Mvi	Cvf	Cvm	Tcv	% Mv	Tm	% Cvim	S	Ws	S/Ws	S/Cvif
Jan	22	5	27	19	74	41	115	36	46	11	11	9	1.22	0.50
Mar	47	9	56	16	48	79	127	62	88	10	16	13	1.23	0.34
Apr	81	16	97	17	72	71	143	50	87	18	7	7	1.00	0.09
May	131	37	168	22	33	35	68	51	72	51	48	35	1.37	0.37
Jun	30	16	46	35	29	22	51	43	38	42	0	0	0	0.00
Jul	75	20	95	21	3	4	7	57	24	83	46	36	1.28	0.61
Aug	443	91	534	17	183	140	323	43	231	39	153	114	1.34	0.35
Oct	207	19	226	8	13	19	32	59	39	50	45	31	1.45	0.22
Dec	86	6	92	7	46	50	96	52	56	11	26	18	1.44	0.30

phores, 1 was torn and could not be measured. Neck shape and measurements of 6 spermatophores (Table 5) corresponded to correct spermatophores and suggested a probable placement over the genital opening. The seventh spermatophore, 1.47 by 0.26 mm with a 0.009-mm thick wall and with a well-defined neck, fell within the range for alternate spermatophores, and most likely would have been placed around one of the bumps anterior to the genital prominence. Bursa spermatophores were measured from 5 specimens with correct leg 5 spermatophores; all fell within the range of measurements for correct spermatophores. Including the specimen holding an alternate spermatophore, 3 specimens, whose fifth legs were used for illustrations, also had correct bursa spermatophores.

Observations of spermatophore dimorphism were extended by re-examining 18 of 26 males of *E. norvegica* holding spermatophores taken in July 1976 in the western North Atlantic Ocean (reported in Ferrari, 1978). Spermatophore width and wall thickness were determined as for *E. antarctica*. From co-occurring females with single and multiple placements, collected on *Albatross IV* cruise 2, stations 17A, 45C, 75A, 75B, 78A, 78B, and 78C, lengths of correct and alternate spermatophores were measured from the distal end of the flask to the remnant of their terminal, spherical part of the neck. Correct and alternate spermatophores varied in length and neck shape but showed no variation in width or wall thickness. Smaller spermatophores were always correct spermatophores and began to narrow toward their neck at the midpoint of the flask. Their mean length was 1.11 mm (Table 6). Larger spermatophores began to narrow toward their neck at the three-quarters point of the flask. They were usually alternate spermatophores with mean length 1.33 mm, although 3 similarly shaped spermatophores of lengths 1.25, 1.26, and 1.26 mm were correctly placed.

Eighteen co-occurring males held 1 spermatophore in leg 5; 15 spermatophores were considered small (mean length 1.06 mm) and 3 large (1.26, 1.28, and 1.37 mm) (Table 6). Of these males, 17 had a bursa spermatophore; 14 were considered small (mean length 1.06 mm) and 3 large (1.30, 1.31, and 1.78 mm). Two of these latter occurred in males holding large spermatophores (1.26 and 1.28 mm), but the largest bursa spermatophore (1.78 mm) occurred in a male with a smaller leg 5 spermatophore (1.20 mm).

Discussion

Hopkins' (1982) work on the breeding biology of *E. norvegica* remains the most complete study for a species of Euchaetidae. Compared with our data, he examined larger numbers of animals per sample (500 adult females with correspondingly encountered adult males and at least 200 CV and CIV animals) over more closely spaced time intervals (10 day periods between samples, over 1 year) from the same coastal area (Loch Etive, a fjord in Scotland) of a semi-isolated group of animals. Hopkins determined the proportion of CVI males which showed yearly primary (March) and secondary (July) maxima, the proportions of CV and CIV males which showed distinctive minima at the CVI primary maximum and downward shifts at the secondary maximum, and the proportions of females with attached spermatophores and egg sacs. Although Hopkins noted a close correlation between proportion of CVI males and CVI females with attached spermatophores, he chose a measure of the latter (proportion of attached spermatophores per unit female stock) to assess mating intensity.

Data for *E. antarctica* exhibited a maximum proportion of CVI males relative to total CVI animals in late austral fall or early winter (June), but this maximum (35%) did not approach those reported by Bradford (1981) for this species at

Table 4. *Euchaeta antarctica.* Distribution of attached spermatophores on females with at least 1 attached spermatophore. *N* = number of spermatophores, C = correct, L = left alternate, R = right alternate, M = median alternate, T = total.

N					T
1	C	L	R	M	
	19	77	94	2	192
2	LL	LR	RR	CR	
	5	44	8	2	59
3	LLR	LRR	CCR	CLR	
	3	4	1	1	9
4	LLRR	—	—	—	
	2	—	—	—	2
7	LLLRRRR	—	—	—	
	1	—	—	—	1

McMurdo Sound in June (58%) or August (47%). In the present study CV males comprised at least 50% of all CV animals in most months, but a yearly pattern was not apparent. The proportion of CVI males to CV plus CVI males reached a maximum in July. Patterns of spermatophore density per CVI female were variable, reaching maxima in January and July, and a minimum in June. However, the number of CVI females was low in those months. Numbers of spermatophores per female with spermatophores were similarly difficult to interpret.

Mating intensity for *E. antarctica* appeared highest in late austral fall or early winter, in contrast to *E. norvegica* in Loch Etive. This pattern for *E. antarctica* correlated with increasing lipid content to an August maximum and release of eggs, mid-July to mid-September, as reported by Littlepage (1964), and to the association of this predator with *Calanoides acutus* in the stomachs of *Astrotoma agassizii* (cf. Dearborn *et al.,* 1986) in austral fall. Various proportions of CVI and CV males were used to infer mating intensity; inferences based on a measure of spermatophore density may be misleading because of the presence of 2 spermatophore types in this species (see below).

Summary data for the year as mean number of spermatophores per female (0.31) and percentage of single placements (73%) among CVI females with at least 1 spermatophore were comparable to Bradford's (1981) data for *E. antarctica* in McMurdo Sound in June and August. Percentage of single placements also was comparable to the summary data of Hopkins and Machin (1977) for *E. norvegica* (about 70%), and Ferrari (1978) for *E. norvegica* in late July. Yearly summary data for alternate single placements are quite different in the 2 species: 90% for *E. antarctica* in this study, 30% for *E. norvegica* (Hopkins and Machin, 1977).

Although spermatophores have evolved among numerous animal groups (Mann, 1984), most instances of multiple spermatophores and spermatophore polymorphism have been reported for insects. Multiple spermatophores found inside the reproductive tract of one female insect often were known, or assumed, to result from multiple copulations, presumably from different males (e.g., Dreicktrah and Brindley, 1967; Khalifa, 1949). Spermatophore polymorphism, expressed as a diminution in size, from the same male cricket or lepidopteran was associated with reduced time intervals between copulation (Sakaluk, 1985; Sims, 1979). In addition, Gabbutt (1954) reported that 1 male cricket, *Nemobius sylvestris,* can set 2 spermatophores during 2 different stages of a copulatory encounter with 1 female. Both male and female behave differently during the stages, and sper-

Table 5. Monthly spermatophore measurements of *Euchaeta antarctica* from males with a spermatophore in the bursa (=M–BUR), males with a spermatophore in the bursa and leg 5 (=M–BUR + P5), females with a spermatophore attached to genital segment (=F–GEN); male body length (=Blg), number of specimens examined (=*N*), mean spermatophore length, width, and thickness (=Lg, Wd, Th) with range in parentheses below mean.

			Correct				Alternate			
Type	Blg	*N*	Lg	Wd	Th	*N*	Lg	Wd	Th	*N*
F–GEN										
Aug 62	—	0	1.09	0.14	0.005	9	1.36	0.24	0.009	25
	—		(1.00–1.17)	(0.12–0.17)	—		(1.14–1.70)	(0.22–0.27)	—	
M–BUR										
Jan 66	7.16	5	1.20	0.14	0.009	1	1.42	0.24	0.0134	2
	(6.97–7.27)		—	—	—		(1.40–1.44)	(0.23–0.24)	—	
Apr 64	7.74	9	1.26	0.17	0.009	6	1.60	0.24	0.021	3
	(7.09–8.31)		(1.12–1.34)	(0.14–0.20)	(0.008–0.010)		(1.45–1.81)	(0.20–0.27)	(0.018–0.025)	
May 64	7.91	6	1.16	0.14	0.008	2	1.54	0.28	0.14	4
	(7.73–8.08)		—	(0.13–0.14)	(0.007–0.008)		(1.36–1.89)	(0.24–0.37)	(0.013–0.016)	
Jul 62	7.12	20	1.29	0.16	0.008	9	1.35	0.22	0.010	8
	(6.77–7.48)		(1.19–1.35)	(0.13–0.17)	(0.006–0.009)		(1.26–1.43)	(0.20–0.24)	(0.008–0.013)	
Aug 62	6.99	32	1.13	0.12	0.007	27	1.18	0.18	0.012	4
	(6.62–7.36)		(0.95–1.36)	(0.09–0.14)	(0.006–0.010)		(1.14–1.24)	(0.14–0.20)	(0.010–0.017)	
Oct 62	6.95	15	1.03	0.11	0.006	10	1.77	0.25	0.015	4
	(6.66–7.26)		(0.90–1.22)	(0.10–0.13)	(0.004–0.010)		(1.37–2.09)	(0.23–0.27)	(0.009–0.026)	
M–BUR + P5										
Aug 62 P5	6.85	5	1.13	0.13	0.006	6	1.47	0.26	0.009	1
	(6.61–7.07)		(1.04–1.15)	(0.12–0.14)	(0.005–0.009)		—	—	—	
Aug 62 BUR	—	0	1.17	0.14	0.007	5	—	—	—	0
	—		(1.12–1.26)	(0.13–0.15)	(0.006–0.009)		—	—	—	

Table 6. Spermatophore measurements of *Euchaeta norvegica* from males with a spermatophore in the bursa and leg 5 (=M–BUR + P5), females with a spermatophore attached to its genital segment (=F–GEN); number of specimens examined (=*N*), mean spermatophore length (=Lg) with range in parentheses below mean.

	Correct		Alternate	
	Lg	*N*	Lg	*N*
F–GEN				
Jul 75	1.11 (0.92–1.25)	15	1.33 (1.24–1.43)	22
M–BUR + P5				
Jul 75 P5	1.06 (0.97–1.20)	15	1.30 (1.26–1.37)	3
Jul 75 BUR	1.06 (0.96–1.21)	14	1.46 (1.30–1.78)	3

matophores so set are dimorphic in size. Later, Mays (1971) showed that the first, smaller spermatophore contained no sperm and was removed by the female. The second, larger spermatophore contained sperm, presumably used to fertilize the eggs.

Multiple spermatophore attachments around the female genital opening have been reported for several calanoids (Fleminger, 1967; Hammer, 1978; Jacoby and Youngbluth, 1983). The related phenomena of dimorphism of spermatophore size and placement, and multiple spermatophore placements previously have been reported only for species of Euchaetidae. Zvereva (1976) described female genital segment morphology of *E. antarctica, E. birostrata, E. elongata,* and *E. weberi,* and attempted to relate differing morphology, particularly the degree of genital segment asymmetry, to spermatophore placement patterns. She noted various sites of spermatophore placements, alternate spermatophores, and fertilization tubes of *E. antarctica,* but did not discuss frequencies of the phenomena. Her figures appeared to depict 2 spermatophore sizes for *E. elongata* and *E. weberi.*

Hopkins and Machin (1977) studied *E. norvegica* collected over a year's period from Loch Etive, Scotland. They found up to 6 spermatophores per female, but 71.6% had only 1 spermatophore and 19.8% had 2. Spermatophores placed over the genital opening (direct placements) were most common (about 80%) followed by nondirect placement sites over a small bump anterior to the genital prominence, and less commonly on the right lateral side of the genital prominence. They presumed that spermatophores, after attachment, developed an extension tube of nonspermatozoan flask contents. Direct placement spermatophores had shorter extension tubes than nondirect placement. Very few nondirect placements had connection to a female genital opening.

From these data Hopkins and Machin (1977) suggested that the first spermatophore is attached by a male to the direct position; this represents precise and efficient behavior. They considered additional, nondirect placements by other males functionally unimportant, provided a majority of females already had been fertilized. Misplacements could not provide sperm to females because fertilization tubes were absent. Thus, according to these authors, sperm of nondirect placements were not "viable for fertilization" (p. 125). Based on the preponderance of a single spermatophore per female, they suggested 1 correctly placed spermatophore provides enough sperm to fertilize all eggs. They detected no rules for where spermatophores would be placed after the first, usually direct, placement. Differ-

ences in length of extension tubes were explained because during direct placements, part of this material disappears into the female seminal receptacle.

Ferrari (1978) studied specimens of *E. norvegica* collected in late July 1975 over continental slope waters to 1,000 m in the western North Atlantic. He found only two areas of spermatophore attachment: correct, over the genital opening (direct of Hopkins and Machin, 1977), and alternate, over the ridge anterior to the genital prominence (type B, nondirect placement of Hopkins and Machin). Ferrari found a large proportion of alternate placements, 55% among females with at least 1 spermatophore. Females with only 1 spermatophore comprised 73% of all females with at least 1 spermatophore; 64% of these spermatophores were alternately placed. In females with 2 spermatophores, only 37% of the spermatophores were placed correctly. Empty spermatophores comprised 3% of correct placements and 15% of alternates; most others were full except for a few alternates which were partly empty. Ferrari noted size dimorphism of spermatophore stalks (extension tube of Hopkins and Machin, 1977) and incorrectly attributed the spermatophore core substance as sperm.

Ferrari surmised that lower percentages of correct spermatophores resulted from a shorter time interval between placement, emptying, and removal by the female. He used varying proportions of alternate spermatophores which were full, partly empty, empty, or with fertilization tubes to infer that varying time intervals occurred between placement, fertilization tube formation, and emptying. He concluded that all alternate spermatophores potentially could form fertilization tubes, and thus their sperm could be used to fertilize eggs.

Hopkins (1978), working with Loch Etive specimens, noted that spermatophores attached at different areas of the female genital segment of *E. norvegica* exhibited a size dimorphism in flask and extension tubes. Directly placed spermatophores were smaller than nondirectly placed ones. This size dimorphism was not apparent among spermatophores held in the male leg 5 or contained within the bursa; their size correlated with directly placed spermatophores. During spermatophore development, Hopkins identified alpha particles formed in the core which produced the elongate extension tube by solidification after spermatophore attachment. He also suggested that a nonsperm-derived outer, distal, foamy substance acted to force out viable sperm which were found proximally, but outside, the spermatophore center core.

From his data Hopkins suggested spermatophore size dimorphism was a product of flask extension during spermatophore extrusion, in effect, a mechanical change. He hypothesized that a male punctures the neck of an extruded spermatophore prior to attachment, triggering extension tube formation. Any excess of this extension tube material could flow into the female seminal receptacles where it might take on a nutritive function. In nondirect spermatophores there was no need for this function, since these sperm were not needed for fertilization. Presence or absence of fertilization tubes was simply a product of final back pressure in the spermatophore core.

Bradford (1981) studied *E. antarctica, E. erebi,* and *E. similis* from continental shelf waters off Antarctica. She found over 70% of the females had only one spermatophore, but direct placement percentages were low (3.4–38.1%). She noted different size spermatophores among the various species, and attributed some of this variation in *E. erebi* to attachment by males of *E. antarctica.*

In the following discussion, questions of spermatophore dimorphism and multiple placements were approached by assuming that males cannot afford to waste sperm or spermatophores (Ferrari, 1978). Other authors (Zvereva, 1976; Hopkins and Machin, 1977; Uchima, 1985) have assumed that multiple or alternate sper-

matophores were not needed or utilized by females to fertilize eggs. In *E. antarctica* and *E. norvegica* a correlation is evident between 2 different spermatophore attachment sites on the female genital segment and 2 morphologically different kinds of spermatophores. Males showed evidence of 2 morphologically different types of spermatophores in the bursa and leg 5; these types corresponded to the 2 different attached spermatophores. Thus, morphologically different attached spermatophores were not a product of mechanical distortion during extrusion but had differentiated prior to extrusion, suggesting that these males can produce different spermatophore types. Finally the discovery of 1 male each of *E. antarctica* and *E. norvegica* with 1 kind of spermatophore in the bursa and another in a leg 5 suggested that the same male may produce both kinds.

These findings suggest that morphologically different spermatophores may function in different ways. Correct spermatophores may empty almost immediately after placement, quickly provide sperm to fertilize clutches of eggs, and may be easily removed from the female. These spermatophores may have relatively smaller quantities of the alpha granules that form the longer stalk of alternate spermatophores. Alternatively, however, very little of this material may be present in the smaller, correct spermatophores—only enough to provide a short connecting tube to compensate for imprecise spermatophore placement around the ventral face of the genital prominence.

Alternate spermatophores appeared structurally and, based on different placement sites, functionally different. All had longer stalks and many had fertilization tubes; their attachment plates seemed more resistant to detachment.

Alternate spermatophores may be adapted for adhesion to the female genital segment for longer periods of time, perhaps to provide sperm to fertilize clutches of eggs later, well after attachment. Their longer attachment time may overemphasize their representation in net-collected animals, especially later in the mating period when the proportion of alternate spermatophores increased (Ward and Robins, in press). If both correct and alternate spermatophores are present in a population, care should be taken when using incidences of spermatophore density to detect mating intensity.

Further studies should determine if both correct and alternate spermatophores may be attached by the same male during one prolonged copulation. Multiple placements during copulation have been reported for species of *Pseudodiaptomus* (Jacoby and Youngbluth, 1983). A further suggestion (Thomas E. Bowman, personal communication) should be explored: the more securely attached alternate spermatophores with long stalks may provide a mechanical barrier to amplexus, hindering later advances of competing males. Questions about purposeful placement of alternate spermatophores also remain unanswered. The suggestion of Ferrari (1978) that alternate spermatophores resulted from mechanical errors during copulatory behavior of males seems dubious in light of observations of Zvereva (1976) and Bradford (1981). If alternate spermatophores are useful spermatophores with viable sperm, their placement may be purposeful. The greater degree of spermatophore dimorphism expressed in *E. antarctica* relative to *E. norvegica* has helped establish the presence of alternate spermatophores. Further studies of greater degrees of variation in alternate placement sites, e.g., dorsally on the genital segment of *E. weberi* (Zvereva, 1976) or dorsolaterally on *E. erebi* and *E. similis* (Bradford, 1981), may establish purposeful behavior for alternate spermatophore attachments.

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Krazysztofowicz (1980, Folia Biologica Kraków 28: 79–82) described two types of spermatophores in *Tetrodontophora bielanensis,* a collembolan.