Postnaupliar Development of a Looking-glass Copepod, *Pleuromamma xiphias* (Giesbrecht, 1889), with Analyses of Distributions of Sex and Asymmetry

FRANK D. FERRARI

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Postnaupliar Development of a Looking-glass Copepod, *Pleuromamma xiphias* (Giesbrecht, 1889), with Analyses of Distributions of Sex and Asymmetry

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ABSTRACT

Ferrari, Frank D. Postnaupliar Development of a Looking-glass Copepod, *Pleuromamma xiphias* (Giesbrecht, 1889), with Analyses of Sex and Asymmetry. *Smithsonian Contributions to Zoology,* number 420, 55 pages, 23 figures, 9 tables, 1985.—The calanoid copepod *Pleuromamma xiphias* was studied from samples collected in the eastern North Atlantic Ocean from the upper 1200 m at 17°50′N, 25°30′W over a six-day period. Only stages II to VI were found among 9546 copepodids in various aliquots from 28 samples. Ontogenetic changes in the external skeletal morphology result in increasing complexity in the number of body tagmata, appendages, appendage segments, and armature. Changes in the last three are more pronounced in swimming and reproductive appendages than in feeding appendages. A modified, scythe-like terminal spine on the first swimming leg exopod of CII is the only specialized skeletal structure not present in adults; a simple, attenuate spine is present in all later stages. The degree of sexual dimorphism is greatest in CVI, expressed primarily as changes in male morphology, and includes asymmetry of the swimming legs.

Ontogenetic changes in vertical distribution include compact but progressively deeper distributions during the day, with upward and downward dispersion at night. Both sexes of CV exhibit a bimodal distribution. In CVI this bimodality is asymmetrical, with more females at the shallow, primary mode and more males at the deeper, secondary mode.

Pleuromamma xiphias exhibits statistically significant reductions in proportion of males and left females between CV and CVI. These reductions are assumed to be biologically significant. If sex is genetically controlled, balancing selection should act to favor males during a period of ontogeny when sexual dimorphism is not expressed phenotypically, unless CVI males are selected against after their reproductive potential is realized. A balanced dimorphism is hypothesized for the distribution of asymmetry in females; selection for right females during ontogeny is balanced by preference for left CVI females by CVI males during mating.

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Contents

Postnaupliar Development of a Looking-glass Copepod, *Pleuromamma xiphias* (Giesbrecht, 1889), with Analyses of Distributions of Sex and Asymmetry

Frank D. Ferrari

Introduction

Marine copepods of the metridiniid genus *Pleuromamma* are known for marked diel changes in vertical distribution exhibited by most species (Moore, 1949; Moore and O'Berry, 1957; Roe, 1972). These calanoids are easily recognized in pelagic samples by a small dark organ on one side of the body. Their name, *Pleuromamma,* is derived from the Greek words "side" and "teat," an apparent reference to this dark organ. The name was proposed by Giesbrecht (see Giesbrecht and Schmeil, 1898) for all species of Claus's (1863) genus *Pleuromma* (from "side" and "eye"), which was preoccupied.

The function of the dark organ is unknown, although it is not a simple structure (Blades-Eckelbarger, pers. comm.). It has been described as a luminous organ by Dahl (1893), but its luminescence has not been observed by Parrish (pers. comm.).

Variations in the position of the dark organ have been noted by a number of authors. Steuer (1932) first presented an exhaustive treatment of its position on adults and noted its correlation with the position of other asymmetrical characters on males. Ferrari (1984) surveyed a more extensive number of asymmetrical characters on males and females of most species. He noted that positions of these characters on an animal did not change with respect to one another. He called this constant, positional relationship of phenotypic characters "unique concordance," avoiding the term "linkage," because the latter is generally applied to genes on a chromosome. On basically bilaterally symmetrical animals, this suite of asymmetrical phenotypic characters can occupy one of only two possible positions. The resulting two groups of animals appear as mirror-images. Ferrari proposed a common name for these calanoids, "looking-glass copepods."

In this paper the terms left and right describe the position of the dark organ on a particular animal. Unique concordance then determines the position of all other asymmetrical structures.

Very little is known of the vertical distribution

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or asymmetry of *Pleuromamma* juveniles. Copepodid ontogeny has not been described for any species of the genus. *Pleuromamma xiphias* (Giesbrecht, 1889) was chosen for this study for two reasons. With respect to asymmetry females commonly, but males only infrequently, exhibit dimorphic asymmetry. This condition may simplify subsequent analysis of the process maintaining dimorphism. In addition, copepodid stages are easily recognized. In pelagic samples from the North Atlantic Ocean, they are separated from congeners by larger size, crested forehead, and sloping head region. Morphologically similar copepodids of *P. abdominalis* show overlap in size with the preceding copepodid stage of *P. xiphias;* however, their heads are highly vaulted and their foreheads lack a crest.

The purpose of this study is to describe copepodid ontogeny of *P. xiphias,* discuss distribution of sex and asymmetry among individuals, and suggest several hypotheses to explain these distributions. In developing the suggestions, pertinent information about the biology of other calanoid copepods is introduced as applicable.

Methods

Data on collection of samples are provided in Table 1. Twenty-eight samples of pelagic animals were collected by the United Kingdom's Institute of Oceanographic Sciences (IOS) from 12 to 18 November 1969 at *Discovery* sta 7089. At time of collection, *Discovery*'s position varied around the geographic coordinates 17°50′N and 25°30′W. Samples were taken with an RMT 1, a rectangular midwater trawl with an acoustically controlled opening-closing net system. The mouth opening of this trawl varies with towing speed (Roe et al., 1980). An average speed of 2 knots and mouth opening of 0.74 m^2 were assumed for this study. Mesh size of the net was 320 μm. Elapsed time and distance traveled varied for each sample but averaged about 2 hrs and 7 km, respectively.

Vertical depth strata of approximately 100 m increments from 1000 to 100 m were sampled once each during day and night. Day-night samples also were collected from 1200 to 1000 m. Above 100 m, strata included 10–0, 25–10, 50–25, and 100–50 m. Estimates of distance traveled were used to determine amounts of water filtered for each tow.

Vertical distributions of heat and salt in the upper 1200 m were measured on four different occasions during the biological sampling: 12 Nov, 2011–2112; 13 Nov, 1910–1951; 15 Nov, 1959–2044; and 17 Nov, 1951–2053. These parameters were recorded continuously, their analog traces digitized, and values at 21 standard depths computed and plotted (Figure 1).

Initial aliquots of from 1/8 to 1/64 of each sample (Table 1) were taken, and two lots of calanoid copepods (CVI and CV–CI) were sorted at IOS. The ontogeny of free-swimming copepods generally includes five postnaupliar copepodid stages (CI–CV) prior to a terminal adult (CVI) instar. Four of these stages (CII–CV) of *P. xiphias,* plus the adult, were identified in *Discovery* sta 7089 samples. All CII–CVI copepodids of *P. xiphias* were identified and counted from these initial aliquots. Data were included in initial analyses of vertical distribution and distribution of dimorphisms (Tables 2, 3).

From 10 to 15 specimens of each stage (CII–CVI) were removed and cleared in lactic acid for morphological study. After initial observations, each was stained by adding a solution of Chlorazol Black E dissolved in 70% ethanol/30% water.

Postzygotic ontogeny of copepods can be considered to be a temporally sequential appearance of a discrete series of growth stages terminating in a sexually reproducing animal. Changes from one stage to the next follow molts during which an animal's morphology changes. Generally, these changes are manifested by increasing complexity of structure and function. This sequence cannot be observed in a quasi-synoptic set of preserved samples. However, it is presumed to be reflected here by the presence of animals whose morphological similarity suggest this sequential development.

Descriptions of the external skeleton are pre-

sented in this paper as an aid in further identification of the copepodids. These descriptions do not represent an exhaustive morphological treatment of the animals.

Although no attempt was made to quantify variation in the size of segments or armature elements, intraspecific variation in the numbers of elements was qualified. All armature elements were counted on left and right members of each appendage from at least five specimens. If variation in element numbers was observed, the largest number found was assumed present in each case, and careful counts of each appendage were repeated. Variation was noted only after the second set of counts.

One kind of intraspecific variation will not be treated in this paper: a single CVI female lacking a black organ was recovered from sample #27. The morphology of this animal will be reported later.

Under the thin external skeleton of most CII and CIII specimens, presumptive cuticular tissue of the succeeding ontogenetic stage could be seen. Presence of this presumptive tissue complicates the resolution of segment boundaries and setal numbers, but the formation of presumptive cuticle does permit easy confirmation of morphological correlation between two stages of development. The problem of presumptive tissue formation does not occur often in CIV or CV; however, enough such specimens were found to confirm the morphological correlation for each sex from CIV to CVI.

The following morphological abbreviations are used in the descriptive text and figure legends:

Body segments	
Pr	prosome
Cph	cephalosome
Pg	pediger
Ur	urosome
CR	caudal ramus

Appendages	
AI	first antenna
AII	second antenna
Mn	mandible
MxI	first maxilla
MxII	second maxilla
Mxp	maxilliped
P	swimming legs

Appendage elements	
Bspd	basipodal segment
Re	expodal segment
Ri	endopodal segment
Li	inner lobe
Le	outer lobe

Appendage armature	
Se	external spine or seta
Si	internal spine or seta
St	terminal spine or seta

For appendages with repeated elements or elements with repeated armature, abbreviations may be combined as in the following examples:

MxlLil: first inner lobe of first maxilla.
P1Ri2: second endopodal segment of first swimming leg.
P4Re3Sel: first external spine on third exopodal segment of fourth swimming leg.

Statistical tests of hypotheses for changes in proportions of males relative to females, and left females relative to right females, between various stages were performed on data from the initial aliquots. Male vs. female and left vs. right are each assumed exclusive and exhaustive phenotypic categories for specimens of *P. xiphias*. For such studies the binomial is a useful distribution. From a population with the parameters mean "np," variance "npq," "p" can be estimated from a sample as a proportion $\bar{X} = X/n$, where X is the number of animals with a particular attribute from a sample of size n. The statistic

$$(\bar{X} - p)/[p(1 - p)/n]^{1/2}$$

has an approximately normal distribution with zero mean and unit variance.

A test for equality of proportions between two samples of unequal size from the same population utilizes the following statistic (from Dixon and Massey 1969):

$$(\bar{X}_1 - \bar{X}_2)/[\hat{p}(1 - \hat{p})(1/n_1 + 1/n_2)]^{1/2} < z_{1-\alpha},$$

where

$$\hat{p} = (n_1\bar{X}_1 + n_2\bar{X}_2)/n_1 + n_2$$

and $\hat{p}$ is an estimate of the population proportion of animals having the particular attribute being considered.

Previous analyses (Ferrari, 1984) and preliminary observations of proportions from initial aliquots suggested that ontogenetic reductions of 5%–10% for left females and 10%–30% for males may occur during late-stage

ontogeny of *P. xiphias*. These two reductions were explored by statistical tests of proportions outlined above. A power analysis was used to detect the probability that a test for equality of proportions of left females or males will lead to a rejection. In the absence of a specific alternate hypothesis to equality of proportions, an "effect size" (Cohen, 1977) was defined as the degree to which the phenomenon responsible for a particular reduction is acting during ontogeny. In this study the corresponding effect size is presumed similar to that difference in proportions observed between two ontogenetic stages.

Power, then, is a function of sample size, effect size, and alpha level (the probability of rejecting the hypothesis of equality when it is true). Alpha levels of 10% were chosen for tests of equality because this study of the distributions of sex and asymmetry is exploratory. Greater consideration was given to accepting a true alternate hypothesis of reduction in proportions. Concern for rejecting a true null hypothesis of equality of proportions was given less consideration.

To determine the power of a test for equality of proportions, an effect-size index "h" (Cohen, 1977) for the difference between two proportions is calculated as (arcsin in radians):

$$h = 2 \arcsin (\bar{X}_1^{1/2}) - 2 \arcsin (\bar{X}_2^{1/2}).$$

Power is also dependent on size of the samples used to calculate "h." These sample sizes are presumed equal; if unequal the quantity

$$n' = 2(n_1)(n_2)/n_1 + n_2$$

is substituted for the sample sizes.

The initial test for equality of proportions of left females between CV and CVI was rejected. Power of the test was about 50%. Subsequently larger sample sizes were sought to increase power. Approximate sample sizes for various powers can be obtained by computing a coefficient "delta-square" (Sokal and Rohlf, 1969:609) (arcsin in degrees):

$$\text{delta-square} = [\arcsin (\bar{X}_1)^{1/2} - \arcsin (\bar{X}_2)^{1/2}]^2.$$

Comparisons of the coefficient with tabulated values from Sokal and Rohlf suggest samples of 1057 or 1465 animals would provide powers of 80% or 90% at alpha 10% for an effect size similar to that initially observed.

Because it was impossible to return to sta 7089 and resample CIV–CVI animals, the unsorted subsamples were utilized for this purpose. Unsorted subsamples fall into two groups (Table 4): those whose projected remaining number of females is at least 100 for at least one of the last three stages (IV, V, or VI)—#29, 28, 27, 26, 25, 24, 23, 22, 17, 16, 13, and 11; those that project no more than 50 females for the most abundant stage—all others. The latter group was eliminated from further consideration. Equal aliquots of qualifying, unsorted subsamples were chosen, such that the anticipated total number of animals counted would be about 1500. From length of tow data (Table 1), roughly equal volumes of water filtered were assumed for each qualifying sample.

For several reasons, animals that had been removed with the sorted initial aliquots of all trawl samples could not be replaced (e.g., each trawl sample had been sampled without replacement). However, because the original aliquot size had not been chosen relative to the number of *P. xiphias* found or anticipated in the sample, and because the number of animals removed was relatively small (amounting to no more than about 1/8 of the total in the sample), qualifying unsorted subsamples were considered to represent samples from similar volumes of water.

The total projected number of CV and CVI females for the 12 qualifying samples is 9108. The only subsampling device available for this study was a Folsom plankton splitter, which takes

$$1/2^n$$

aliquots of a sample. Except for #26, 1/4 aliquots (25%) of the unsorted subsamples selected above were taken to obtain the requisite 1500 animals with certainty.

All animals in unsorted subsample #26 were counted to provide basic information on accuracy of projection for counts from a small

aliquot (1/64). The proportion of animals in a 1/4 aliquot was projected back from the total. Counts of CIV–CVI animals from 1/4 of the unsorted subsamples from #29, 28, 27, 25, 24, 23, 22, 17, 16, 13, and 11 and all of unsorted subsample #26 (Table 6) were then combined with initial counts for a second analysis of vertical distribution of the later stages (Table 7).

Present samples place restrictions on the following interpretations.

1. Morphological Development of External Skeleton: Mesh size of the nets was coarse; no nauplii or CI specimens were collected. Evaluation of structural diversity and homologies are restricted to CII–CVI.

2. Vertical Distribution: For purposes of interpreting vertical distributions, this set of trawl samples is considered a quasi-synoptic collection of copepodids whose individual behavioral differences result in a vertical group structure. Interpretations are based on numbers collected for a fixed volume of water filtered. However, in addition to absence of CI, other early stages (CII, CIII, and CIV) may have been underestimated. Avoidance by larger animals, particularly CVI, adds another question to efficiency of capture and further complicates comparisons between stages. Long distances and times of tows obscure subtle changes in animal behavior that may alter the vertical parameters of the population. Variations in the time that animals spend in a particular stage are unknown. Circumstantial evidence based on presumptive cuticle formation suggests that CII and CIII are much shorter than CIV–CVI.

3. Distribution of Dimorphisms: For analyses of dimorphisms, specimens were treated as if they were collected from a population in the simplest statistical sense "a group or aggregate of things about which some information is required" (Snedecor and Cochran, 1967) (e.g., *P. xiphias* copepodids present at sta 7089 during collection by *Discovery*). Statisticians may apply more rigor to their definition of a population, "a set of individuals having some common observable characteristic" (Dixon and Massey, 1969). Biological definitions of a population often emphasize one or more observable characteristics in common among animals, shared attributes; however, biological definitions vary. The shared attribute may be an immediate property of the animal (e.g., gene, chromosome, molecule, seta, function of a maxilliped, or swimming behavior pattern), a relationship shared directly, exclusively, and exhaustively with others (e.g., animals potentially capable of interbreeding), or a relationship shared indirectly, exclusively, and exhaustively (e.g., descent from a common ancestor). Although the simple definition of population is utilized, variations within this group of animals are noted and discussed.

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Results

Morphology

CII

Length range, 1.12–1.26 mm; Pr/Ur, 2.7. Pr 5 segments (Figure 2A); laterally dorsal Pr margin not highly vaulted, tapering from rostral area. Ur 2 segments. Dark organ a simple light

round area, lacking pigment, appearing as cluster of irregular polygons on the exoskeleton.

CR 4 apical, 1 dorsal, 1 lateral setae (Figure 2C).

Al 17 distinct segments; cuticle at base of distal seta on A11 and proximal seta on A12 produced into a point; segments armed as in Figure 2B.

A11 (Figure 3A) basal segment with several incomplete and offset articulation lines; 1 proximomedial seta, 2 distomedial setae. Re 8 segments, articulation line incomplete between 2–3; Re1–7 each with 1 distomedial seta; Re8 with 1 distomedial and 3 apical. Ri 3 segments; Ri1 2 medial setae at midlength; Ri2 5 apical setae and several apical hairs; Ri3 6 apical setae and several apical hairs.

Mn (Figure 3B) Bspd1 a gnathobase with hairs at base of teeth; Bspd2 4 medial setae. Re 5 segments, each with 1 distomedial seta, Re5 also with apical seta. Ri 2 segments; Ri1 4 setae on distomedial corner separate from the remainder of the segment by an indistinct line, small spines on posterior face, hairs distolaterally, Ri2 7 apical setae and distolateral hairs.

Mx1 (Figure 3C) Li1 3 posterior spines, 7 medial spines, 3 anterior spines and proximal hairs. Li2 3 setae. Li3 4 setae. Le 6 setae. Bspd2 slightly produced distomedially with 3 setae. Re 1 segment with 8 setae. Ri 1 segment with 3 midmedial and 8 apical setae.

Mx11 (Figure 3D) with 6 Li + Ri. Li1 4 apical spines, 1 seta on proximal margin, and spinules on posterior surface. Li2–4 each with 3 apical spines and spinules on posterior surface. Li5 larger with 4 apical spines and spinules on posterior surface. Li6 2 apical spines. Ri 1 segment with 6 spines.

Mxp (Figure 3E) 5 segments. Mxp1 with groups of 1,2,3,3 medial setae, spinules at base of distal group, a few smaller medial hairs. Mxp2 medially with 4 small setae followed by 1,1,2 large setae, distal pair on a lobe separated from the remainder of segment by an indistinct line, row of spinules along segment. Mxp3–4 1 distomedial seta each, latter with medial hairs. Mxp5 2 medial, 1 lateral, 1 terminal setae.

P1 (Figure 3F) Bspd1 1 medial seta; Bspd2 1 lateral seta and 1 larger distomedial seta recurved over tubercule of Ri. Re 2 segments; Re1 with medial hairs, 1 Se as a stout spine open at tip with smaller hair protruding from opening; Re2 with 3 Se similar to Re1, 4 Si, St inwardly curved distally, with outer margin attenuate proximally. Ri 1 segment with spinulose anterior tubercule, 1 Se, 4 Si, 2 apical setae.

P2 (Figure 3G) Bspd1 1 distomedial seta; Bspd2 medial hairs. Re 2 segments; Re1 3–4 small proximal spines on anterior face, 1 short Se with lateral hyaline flanges; Re2 with a large distal pore, 2 Se, 4 Si; St simple with lateral flange. Ri 1 segment, 2 slightly recurved points medially and anteriorly, 2 Se, 3 Si, 2 apical seta.

P3 (Figure 3H); Bspd1–2 unarmed. Re 1 segment with 1 anteriodistal pore, 3 Se, 3 Si, 1 St. Ri 1 segment 3 Si, 1 Se, 2 apical seta.

P4 1 segment armed with 5 elements as in Figure 3J.

C111

Length range, 1.48–1.70 mm; Pr/Ur, 2.9. Pr 5 segments (Figure 4A); laterally dorsal Pr margin not highly vaulted, tapering from rostral area. Ur 2 segments. Dark organ with pigment and lens-like cover.

CR 4 apical, 1 dorsal, 1 lateral setae (Figure 5A).

AI 25 distinct segments; cuticle at base of 2 distal setae sets on A11 and setae set on A13 attenuate; lengths of these cuticular elongations vary; segments armed as in Figure 6A.

A11 (Figure 5C) 2 basal segments; Bspd1 1 seta on distomedial knob; Bspd2 2 distomedial setae. Re 8 segments, articulation line incomplete between 2–3; Re1–7 each with 1 distomedial seta; Re8 with 1 distomedial and 3 apical setae. Ri 3 segments; Ri1 2 midmedial setae; Ri2 6 apical setae and several apical hairs; Ri3 7 apical setae and several apical hairs.

Mn (Figure 6B) Bspd1 a gnathobase with hairs at base of teeth and near Bspd2 insertion; Bspd2 4 medial setae. Re 5 segments, each with 1 dis-

tomedial seta, Re5 also with apical seta. Ri 2 segments; Ri1 4 setae on distomedial corner separate from the remainder of the segment by an indistinct line; small spines on posterior face, distolateral hairs; Ri2 7 apical setae and distolateral hairs.

Mx1 (Figure 6C) Li1 3 posterior spines, 8 medial spines, 1 distal spur, 3 anterior spines, and proximal hairs. Li2 4 setae. Li3 4 setae. Le 9 setae. Bspd2 slightly produced distomedially with 4 setae. Re 1 segment with 9 setae. Ri 1 segment with 3 midmedial, 3 distomedial, 5 apical setae, subterminal hairs.

Mx11 (Figure 6D) with 6 Li + Ri. Li1 4 apical spines, 1 seta on proximal margin, and spinules on posterior surface. Li2–4 each with 3 apical spines and spinules on posterior surface. Li5 larger with 4 apical spines and spinules on posterior surface. Li6 3 apical spines. Ri 4 segments with 1,1,1,4 spines.

Mxp (Figure 5D) 6 linearly arranged segments. Mxp1 with groups of 1,2,4,4 medial setae, spinules at base of distal group, a few smaller medial hairs. Mxp2 4 small setae followed by 1,1,1,2 larger setae, distal pair on a lobe separated from the remainder of segment by an indistinct line, row of spinules along segment. Mxp3–5 1 distomedial seta each; Mxp3,5 with medial hairs. Mxp6 2 medial setae, and 1 lateral, 1 terminal setae on an apical bump.

P1 (Figure 5E) Bspd1 1 medial seta; Bspd2 posterior spine-like bump below Re, 1 lateral seta and 1 larger distomedial seta recurved over tubercule of Ri. Re 2 segments; Re1 1 Se as a stout spine open at tip with smaller hair protruding from opening, medial hairs, 1 Si; Re2 with 3 Se similar to Re1, 4 Si, St simple. Ri 2 segments; Ri1 1 Si, anterodistal spinulose tubercule; Ri2 1 Se, 4 Si, 2 apical setae.

P2 (Figure 5F) Bspd1 1 distomedial seta; Bspd2 unarmed. Re 2 segments; Re1 with row of small proximal spines on anterior face, 1 Si, medial hairs, 1 short Se with lateral hyaline flanges; Re2 with a large distal pore, lateral margin hairs, 3 Se, 5 Si; St simple with lateral flange. Ri 1 segment with 3 slightly recurved points, 1 medial, 1 axial and 1 anterior, 2 sets lateral margin hairs, 2 Se, 4 Si, 2 apical setae.

P3 (Figure 6E) Bspd1 1 distomedial seta; Bspd2 unarmed. Re 2 segments; Re1 1 Se, medial hairs; Re2 with 2 anteriodistal pores, 2 Se, 4 Si, St simple. Ri 1 segment 4 Si, 2 Se, 2 apical seta, 2 sets lateral margin hairs.

P4 (Figure 6F); Bspd1 unarmed, Bspd2 with distomedial seta. Re 1 segment with 1 anteriodistal pore, 3 Se, 3 Si, 1 St. Ri 1 segment 3 Si, 1 Se, 2 apical seta, medial and lateral rows of hairs.

P5 1 segment with at most 3 apical elements, but with numerous combinations (see Figure 4B).

C1V Female

Length range, 2.12–2.50 mm (left 2.12–2.50; right 2.10–2.43); Pr/Ur, 2.5. Pr 5 segments (Figure 7A); laterally forehead slightly produced as a small crest, dorsal Pr margin not highly vaulted, tapering from rostral area. Ur 3 segments; Ur3 ventrally with 2 small distal pores. Dark organ with brown cover.

CR with ventral distal pore, 4 apical, 1 dorsal, 1 lateral setae (Figure 7B).

A1 25 distinct segments; articulation lines between 8–9 and 9–10 incomplete; A11 with small knob on posterior margin; cuticle at base of distal setae set on A11 and setae set on A12,4,5,6 attenuate, latter 3 diminutive, lengths of these cuticular elongations vary; pores on anterodorsal margins of A11,3,5,6,7; segments armed as in Figure 7C; ventral patches of hairs on A11–10.

A11 (Figure 10A) 2 basal segments; Bspd1 1 seta on distomedial knob; Bspd2 2 distomedial setae. Re 8 segments, articulation line incomplete between 2–3, 5–6, and 6-7; Re1–7 each with 1 distomedial seta; Re8 with 1 distomedial and 3 apical. Ri 3 segments but with incomplete articulation line in Ri3; Ri1 2 midmedial setae; Ri2 7 apical setae and several apical hairs; Ri3 7 apical setae and several apical hairs.

Mn (Figure 8A) Bspd1 a gnathobase with hairs at base of teeth and proximally; Bspd2 4 medial setae. Re 5 segments, each with 1 distomedial seta, Re5 also with apical seta. Ri 2 segments;

Ri1 4 setae on distomedial corner separate from remainder of segment by an indistinct line; small spines on posterior face, hairs distolaterally; Ri2 8 apical setae and distolateral hairs.

MxI (Figure 8B) Li1 4 posterior, 9 medial, 3 anterior spines and proximal hairs. Li2 5 setae. Li3 4 setae. Le 9 setae. Bspd2 4 setae. Re 1 segment with 9 setae, marginal hairs. Ri 1 segment with 4 midmedial and 9 apical setae, marginal and apical hairs.

MxII (Figure 8C) with 6 Li + Ri; patch of spinules on outer margin. Li1 4 apical spines, 3 setae on proximal margin, and spinules on posterior surface. Li2–4 each with 3 apical spines and spinules on posterior surface. Li5 larger with 4 apical spines and spinules on posterior surface. Li6 with apical spur, 3 apical spines. Ri 4 segments with 1,1,1,4 spines.

Mxp (Figure 10B) 7 segments. Mxp1 with groups of 1,2,4,4 medial setae; spinules at base of groups; a few smaller medial hairs. Mxp2 4 small setae followed by 1,1,1,2 large setae, distal pair on a lobe separated from the remainder of segment by an indistinct line, row of spinules along segment. Mxp3–4 2 distomedial setae each. Mxp5–6 1 distomedial seta. Mxp7 2 medial, 1 lateral, 1 apical setae.

P1 (Figure 9A) Bspd1 1 medial seta; Bspd2 posterior spine-like bump below Re, 1 lateral seta and 1 larger distomedial seta recurved over tubercule of Ri, hairs at base of this seta. Re 2 segments; Re1 1 Se as a stout spine open at tip with smaller hair protruding from opening, 1 Si, medial hairs; Re2 with 3 Se similar to Re1, 4 Si, St simple, 2 sets lateral margin hairs. Ri 2 segments; Ri1 1 Si, anterodistal spinulose tubercule; Ri2 1 Se, 4 Si, 2 apical setae.

P2 (Figure 9B) Bspd1 1 distomedial seta; Bspd2 with lateral spinules. Re 2 segments; Re1 with small proximal spines, 1 Si, 1 short Se with lateral hyaline flanges; Re2 with a large distal pore, lateral margin hairs, 3 Se, 5 Si; St simple with lateral flange. Ri 1 segment, 3 slightly recurved points, 1 medial, 1 axial, and 1 anterior, 2 sets lateral margin hairs, 2 Se, 5 Si, 2 apical setae.

P3 (Figure 9C) Bspd1 1 distomedial seta; Bspd2 unarmed. Re 2 segments; Re1 1 Se, 1 Si, medial hairs; Re2 with 2 anteriodistal pores, 3 Se, 5 Si, St simple. Ri 1 segment 5 Si, 2 Se, 2 apical seta, 2 sets lateral margin hairs.

P4 (Figure 9D) Bspd1 1 distomedial seta; Bspd2 1 lateral seta. Re 2 segments; Re1 1 Se, medial hairs; Re2 with 2 anteriodistal pores, 3 Se, 5 Si, St simple. Ri 1 segment 4 Si, 2 Se, 2 apical setae, 2 sets lateral margin hairs.

P5 2 segments; 1st a bspd united to a coupler; 2nd with medial indentation, 2 Se, 1 Si, 1 apical seta, medial hairs as shown in Figure 10C.

CIV Male

Length range, 2.33–2.58 mm. Morphologically similar to female except P5 3 segmented; 1st a bspd united to a coupler; 2nd 1 Se; 3rd 2 Se, 2 Si, 2 apical setae, with variations as shown in Figure 10E.

CV Female

Length range, 3.11–3.52 mm (left 3.13–3.52; right 3.11–3.43); Pr/Ur, 2.5. Pr 5 segments (Figure 11A;) laterally forehead produced as a pointed crest with 3 adjacent pores (Figure 13A), dorsal Pr margin not highly vaulted, tapering from rostral area. Ur 4 segments; Ur2–4 with dorsal pair of pores; Ur4 2 ventrodistal pores, distolateral edges produced into small knobs. Dark organ with brown cover.

CR with 4 ventral, 3 dorsal pores, 4 apical, 1 dorsal, 1 lateral setae (Figure 11B,C).

A1 25 distinct segments; articulation lines between 8–9 and 9–10 incomplete; AI1 with small knob on posterior margin; cuticle at base of distal setae set on AI1 and setae set on AI2,4,5,6 attenuate, latter 3 diminutive, lengths of these cuticular elongations vary; pores on anterodorsal margins of AI1–12; segments armed as in Figure 13B; ventral patches of hairs on AI1–7.

AI1 (Figure 12A) 2 basal segments; Bspd1 1 seta on distomedial knob; Bspd2 2 distomedial setae. Re 8 segments, articulation line incomplete between 2–3 and 5–6; Re1–7 each with 1 distomedial seta; Re8 with 1 distomedial and 3 apical.

Ri 3 segments but with incomplete articulation lines on Ri3; Ri1 2 midmedial setae; Ri2 8 apical setae and several apical hairs; Ri3 7 setae.

Mn (Figure 12B) Bspd1 a gnathobase with hairs at base of teeth and proximally; Bspd2 4 medial setae. Re 5 segments, each with 1 distomedial seta, Re5 also with apical seta. Ri 2 segments; Ri1 with indistinct incomplete articulation line toward middle of segment, 4 setae on distomedial corner separate from remainder of segment by indistinct line; small spines on posterior face, hairs distolaterally; Ri2 9 apical setae and distolateral hairs.

Mx1 (Figure 12C) Li1 4 posterior, 9 medial, 3 anterior spines and proximal hairs. Li2 5 setae. Li3 4 setae. Le 9 setae. Bspd2 5 setae. Re with 1 seta at base, 1 segment with 10 setae, marginal hairs. Ri 1 segment with 5 midmedial and 10 apical setae, marginal and apical hairs.

Mx11 (Figure 12D) with 6 Li + Ri; patch of spinules on outer margin. Li1 4 apical spines, 4 setae on proximal margin, and spinules on posterior surface. Li2–4 each with 3 apical spines and spinules on posterior surface, Li5 larger with 4 apical spines and spinules on posterior surface. Li6 4 apical spines. Ri 4 numerous indistinct lines and 7 spines.

Mxp (Figure 12E) 7 segments. Mxp1 with groups of 1,2,4,4 medial setae, 1 Se, spinules at base of groups. Mxp2 4 small setae followed by 1,1,1,2 large setae, distal pair on a lobe separated from the remainder of segment by an distinct but incomplete line, row of spinules along segment. Mxp3–4 3 distomedial setae each. Mxp5–6 2 distomedial setae. Mxp7 1 medial, 1 lateral, 1 apical setae.

P1 (Figure 11D) Bspd1 1 medial seta, lateral hairs; Bspd2 posterior spine-like bump below Re, 1 lateral seta and 1 larger distomedial seta recurved over tubercule of Ri, hairs at base of this seta. Re 3 segments; Re1 1 Se as a stout spine open at tip with smaller hair protruding from opening, spinules at base of Se, 1 Si; Re2 1 Se, 1 Si lateral margin hairs; Re3 2 sets lateral margin hairs, 2 Se, 4 Si, St distolaterally curved with inner margin hairs. Ri 3 segments; Ri1 1 Si, anterodistal spinulose tubercule, lateral margin hairs; Ri2 2 Si, lateral margin hairs; Ri3 1 Se, 2 Si, 2 apical setae.

P2 (Figure 11E) Bspd1 1 distomedial seta, 1 pore; Bspd2 with lateral spinules. Re 3 segments; Re1 with small proximal spines, inner margin hairs, 1 Si, 1 Se with lateral hyaline flanges; Re2 1 Se, 1 Si, 2 distolateral pores, medial and lateral margin hairs; Re3 3 pores, 2 sets lateral margin hairs, 3 Se, 5 Si; St simple with lateral flange. Ri 3 segments; Ri1 3 well-developed recurved points, 1 medial, 1 axial, and 1 anterior, 2 pores, lateral margin hairs; Ri2 2 Si, 1 pore, lateral margin hairs; Ri3 2 Se, 4 Si, 2 apical setae, 1 set lateral margin hairs.

P3 (Figure 11F) Bspd1 1 distomedial seta, 2 pores, lateral spinules; Bspd2 unarmed. Re 3 segments; Re1 1 Se, 1 Si, medial hairs, 2 pores; Re2 1 Se, 1 Si, medial and lateral margin hairs, 3 pores; Re3 3 Se, 5 Si, St simple, 7 pores. Ri 3 segments; Ri1 1 Si, lateral margin hairs; Ri2 2 Si, lateral margin hairs; Ri3 4 Si, 2 Se, 2 apical setae, lateral margin hairs.

P4 (Figure 11G) Bspd1 1 distomedial seta; Bspd2 1 lateral seta. Re 3 segments; Re1 1 Se, 1 Si, medial hairs, 3 pores; Re2 1 Se, 1 Si, medial and lateral margin hairs, 2 pores; Re3 3 Se, 5 Si, St simple, 6 pores. Ri 3 segments; Ri1 1 Si, lateral margin hairs; Ri2 2 Si, lateral margin hairs, 1 pore; Re3 3 Si, 2 Se, 2 apical setae, lateral margin hairs.

P5 (Figure 13C) 4 segments; 1st a bspd united to a coupler; 2nd 1 Se, 1 pore; 3rd 1 Se, medial hairs; 4th 1 Si, 2 apical setae, medial hairs.

CV Male

Length range, 3.43–4.04 mm. Morphologically similar to female except P5 (Figure 13D) 4 segmented and asymmetrical; 1st a bspd united to a coupler; 2nd 1 Se, 1 pore; 3rd 1 Se, 1 pore; 4th elongate, 2 Se, 3 Si, 2 apical setae, 4 pores distally. Right 4th segment longer than left on males with dark organ on left side; this asymmetrical structure maintains unique concordance with dark organ.

CV1 Female

Length range, 4.56–5.13 mm (left 4.70–5.13; right 4.56–5.08); Pr/Ur, 2.5. Pr 5 segments (Figure 14A); laterally forehead produced as a pointed crest with 3 adjacent pores; tiny hairs below frontal organ (see CV); dorsal Pr margin not highly vaulted, tapering from rostral area. Ur 3 segments; Ur1 (genital segment) with darkened ventral protuberance toward center; internally a chamber with tubule exiting dorsally and passing toward anterior end of segment to turn left in females with right dark organ, or vice versa; this tubule and dark organ are the only asymmetrical structures found on females and they maintain unique concordance; Ur3 ventrally with lateral hairs, distolateral edges produced into small knobs with pores. Dark organ with brown cover.

CR dorsal row of hairs and 2 pores, ventrally 1 large pore near insertion of lateral seta; 4 distal pores, 4 apical, 1 dorsal, 1 lateral setae (Figure 14D,E).

A1 24 distinct segments (7–8 of CV fused); articulation lines between 7–8 and 8–9 incomplete; A11 with small knob on posterior margin; cuticle at base of distal setae set on A11 and setae set on A12,4,5,6 attenuate, latter 3 diminutive, lengths of these cuticular elongations vary; A11 1 pore lateral, 3 pores on anterodorsal margin, 1 pore each on A12–6, 2 on A17, 1 each on A18–11; segments armed as in Figure 16A; complex ventral sets of hairs on A11–9.

A11 (Figure 17A) 2 basal segments; Bspd1 1 seta on distomedial knob; Bspd2 2 distomedial setae. Re 8 segments, articulation line incomplete between 2–3; Re1–7 each with 1 distomedial seta; Re8 with 1 distomedial and 3 apical. Ri 3 segments, with incomplete articulation lines on Ri3; Ri1 2 midmedial setae; Ri2 9 apical setae and several apical hairs; Ri3 7 apical setae.

Mn (Figure 17D,E) Bspd1 a gnathobase with hairs at base of teeth and proximally; Bspd2 4 medial setae. Re 5 segments, each with 1 distomedial seta, Re5 also with apical seta. Ri 2 segments; Ri1 4 setae on distomedial corner, large spines on posterior face, small distomedial spines, distolateral hairs; Ri2 10 apical setae, and distolateral hairs.

Mx1 (Figure 17B) Li1 4 posterior, 9 medial, 3 anterior spines and proximal hairs. Li2 5 spines. Li3 4 setae. Le 9 setae. Bspd2 5 setae, 1 pore. Re with 1 seta at base, 1 segment with 11 setae, marginal hairs. Ri 1 segment with 6 midmedial and 11 apical setae, marginal and apical hairs.

Mx11 (Figure 17C) with 6 Li + Ri; set of spinules on outer margin. Li1 4 apical spines, 5 setae on proximal margin, and spinules on posterior surface. Li2–4 each with 3 apical spines and spinules on posterior surface. Li5 larger with 4 apical spines, spinules on posterior surface, 2 pores. Li6 4 apical spines. Ri 7 spines on 7 medial lobes.

Mxp (Figure 16B) 7 segments. Mxp1 with groups of 1,2,4,4 medial setae, 1 Se, spinules at base of distal group, a few smaller medial hairs. Mxp2 4 small setae followed by 1,1,1,2 large setae, distal pair on a separate lobe; row of spinules along segment. Mxp3–4 4 distomedial setae each, spinules on Mxp3. Mxp5–6 3 distomedial seta. Mxp7 2 medial, 1 lateral, 1 apical setae.

P1 (Figure 15A) Bspd1 1 medial seta, 1 pore; Bspd2 posterior spine-like bump below Re, 1 lateral seta and 1 larger distomedial seta recurved over tubercule of Ri, hairs at base of this seta, 1 pore. Re 3 segments; Re1 1 Se as a stout spine open at tip with smaller hair protruding from opening with spinules at base of Se, 1 Si, medial hairs; Re2 1 Se, 1 Si, medial and lateral margin hairs; Re3 2 sets lateral margin hairs, 2 Se, 4 Si, St distolaterally curved with inner margin hairs. Ri 3 segments; Ri1 1 Si, anterodistal spinulose tubercule, lateral margin hairs; Ri2 2 Si, lateral margin hairs; Ri3 1 Se, 2 Si, 2 apical setae, lateral margin hairs.

P2 (Figure 15B) Bspd1 1 distomedial seta, 6 pores; Bspd2 lateral spinules, 1 pore. Re 3 segments; Re1 with small proximal spines, 1 Si, 1 Se with lateral hyaline flanges, medial hairs, 1 pore; Re2 1 Se, 1 Si, 2 distolateral pores, medial and lateral margin hairs; Re3 8 pores, 1 set lateral margin hairs, 3 Se, 5 Si; St simple. Ri 3 segments;

Ri1 3 well-developed recurved points, 1 medial, 1 axial and 1 anterior, 2 pores, lateral margin hairs; Ri2 2 Si, 1 pore, lateral margin hairs; Ri3 2 Se, 4 Si, 2 apical setae, hairs on anterior face, 1 set lateral margin hairs.

P3 (Figure 15C) Bspd1 1 distomedial seta, 2 pores, lateral spinules; Bspd2 unarmed. Re 3 segments; Re1 1 Se on digitform process, 1 Si, medial hairs, 5 pores; Re2 1 Se, 1 Si, medial and lateral margin hairs, 2 pores; Re3 3 Se, 5 Si, St simple, 6 pores. Ri 3 segments; Ri1 1 Si, lateral margin hairs, 1 pore; Ri2 2 Si, lateral margin hairs, 1 pore; Ri3 4 Si, 2 Se, 2 apical setae, 1 set lateral margin hairs, distal hairs, 2 pores.

P4 (Figure 15D) Bspd1 1 distomedial seta, lateral spinules, 1 pore; Bspd2 1 lateral seta, 2 pores. Re 3 segments; Re1 1 Se on digitiform process, 1 Si, medial hairs, 1 pore; Re2 1 Se, 1 Si, medial and lateral margin hairs, 2 pores; Re3 3 Se, 5 Si, St simple, 9 pores, 1 set lateral margin hairs. Ri 3 segments; Ri1 1 Si, lateral margin hairs, 3 pores; Ri2 2 Si, lateral margin hairs, 1 pore; Ri3 3 Si, 2 Se, 2 apical setae, lateral margin hairs, 2 pores.

P5 (Figure 16C,D) 4 segments; 1st a bspd united to coupler; 2nd 1 Se, 1 pore; 3rd 1 Se, medial and lateral hairs; 4th 3 subapical setae, medial hairs, 2 small anterodistal spines, 1 pore.

CV1 Male

Length range, 4.64–5.59 mm; Pr/Ur, 2.5. A bizarre, asymmetrical creature. A11, Mn, Mx1, MxI1, Mxp identical to CV1 female. Remaining morphology very complex. Notes and simple illustrations follow with apologies. All structures are discussed as they appear on an animal with dark organ on left. The unique concordance of all asymmetrical structures is maintained when position of black organ is reversed (see Ferrari, 1984). Segments of swimming legs of preserved animals do not lie in the same plane. In order to accurately represent the morphology, endopodal and exopodal segments were often dissected. Segments so separated are represented as distinct figures in the illustrations.

Pr 5 segments (Figure 18A); laterally forehead produced as a pointed crest with 3 adjacent pores, tiny hairs below frontal organ; dorsal Pr margin not highly vaulted, tapering from rostral area. Ur 5 segments (Figure 18B,C); all urosome segments asymmetrical, various knobs, bumps, pores, protuberences, hairs or setae impart the asymmetry to simple cylindrical segments; Ur1 genital opening asymmetrical, on left. Dark organ with brown cover.

CR (Figure 19B) asymmetrical in structure and lateral spine.

A1 left (Figure 19A) 22 distinct segments; A17–10 of CV partially fused with indistinct articulation lines; A11 with ear-shaped lobe on posterior margin; cuticular points on A11 absent, on A12–6 diminutive; pores on anterodorsal margins of A11–9 (A11–12 of CV).

A1 right (Figure 19C) 16 distinct segments; segments more modified in shape including geniculation; pores on proximal segments in groups of 3; armature more modified, especially asthetes.

P1 (Figure 20) all segments and much armature modified or asymmetrical, particularly Ri and Bspd2 medial margin. Bspd2 margin with indentation on left appendage apparently to receive the knob on medial margin of right P1.

P2 (Figure 21) all segments and much armature modified and asymmetrical, particularly Re1 with small proximal spines on left replaced by hairs on right Re1; right Se modified; Re3 3 Se modified, lateral margin curves posteriorly; Ri1 3 recurved points large on left, reduced and altered on right; Ri3 right more elongate.

P3 (Figure 22) all segments and much armature modified and asymmetrical, particularly left Re1 Se and Re3 lateral margin, Se, Si; right Re2 Si.

P4 (Figure 23) all segments and much armature modified and asymmetrical, particularly Bspd2 left and right medial margin, Re2 Se; Ri all 3 segments and armature, especially apical setae.

P5 (Figure 18E,F) modified as spermatophore holder (left) and female grasper (right).

Vertical Distribution

Profiles of heat and salt (Figure 1) in the upper 1200 m conform to known distributions of these parameters at the eastern edge of the North African Basin (Worthington, 1976). Temperatures reflect isothermal conditions in the upper 25 m, where salt content is homogenous. A thermocline and salinity maximum are present between 25 and 110 m. Temperatures and salinities decrease slowly below 120 m. Temperature and salinity profiles were taken above the influence of the warmer, more saline, Mediterranean Intermediate Water.

The isothermal, isohaline Equatorial Surface Water (temperatures greater than 19°C, salinities less than 36.4‰) is formed south of the subtropical basin in the adjacent equatorial Guinean Basin (Worthington, 1976). Salinity Maximum Water (temperatures greater than 19°C, salinities greater than 36.4‰) is formed locally; its characteristics can vary widely in response to short term changes in the strength of the trade winds. Above and below the Salinity Maximum Water are traces of Western North Atlantic Water and 18° Water formed in the adjacent western subtropical basin.

Data for the analysis of vertical distribution are provided in Table 3 for CII and CIII, and Table 7 for CIV, CV, and CVI. These data indicate a day-night disparity in numbers of *P. xiphias* collected per unit of water sampled. This disparity is greatest for CV animals with daytime capture of both sexes representing about 25% of the total for each sex of CV. Percentages increase slightly for CII–CIV. Day-night captures approach equality for CVI females and CVI males. Roe (1972) noted a similar diel difference in samples collected near the Canary Islands, north of Cape Verde.

Variations in percent differences for different stages suggest a diel change in behavior pattern of CV–CII individuals also may explain the data. During the night CV–CII animals alter their daytime behavior, making them more susceptible to capture at night. Behavioral changes of individuals also may be reflected in the more compact daytime distribution of the group. These variations should not affect the following discussion of relative changes in distribution, unless variations in behavior within a stage occur. If true, animals found at a particular depth may be more easily captured than those animals at adjacent depths.

Most CII animals are found between 100 and 300 m during the day. CIII animals are found slightly deeper, 100–400 m. At night the distributions of both stages change as some animals disperse upward. This is particularly noticeable for CIII.

CIV females and males are found between 200 and 400 m during the day. At night, individuals of both sexes move upwards, some to within 10 m of the surface, although a few animals of both sexes occur as deep as 800 m at night.

The daytime upper limit for CV animals of both sexes is 200 m. Relative to CIV, CV animals are more dispersed and occur continuously to 700m with specimens collected to 1000 m. At night the animals form a bimodal distribution. The upward dispersion of both sexes to within 10 m of the surface forms a primary mode between 50 and 200 m and a secondary mode is apparent between 400 and 700 m.

The distribution for CVI animals of both sexes during the day is more compact than that of CV. Most CVI males are found between 400 and 600 m. CVI females occur to 300 m with a few individuals collected below 600 m. At night CVI males form a bimodal distribution with modes at 100–200 m, and 500–700 m; however, most animals are found in the lower range. At night most CVI females occur between 50 and 200 m. Scattered individuals are found to 700 m with a secondary mode formed between 400 and 700 m.

Distribution of Dimorphisms

A total of 1764 copepodids of *P. xiphias* were found in the initial aliquots (Table 2). Their

categorization by asymmetry and sex (if determined; f = female, m = male) is as follows:

	VIf	VIm	Vf	Vm	IVf	IVm	III	II
left	92	125	135	346	58	160	135	105
right	181	0	212	1	91	1	68	54

Three points are evident from these data.

1. A reduction in proportion of males between CIV and CVI is indicated by the sequence (CIV=.519, CV=.500, CVI=.314). A statistical test for equality of proportions between CV and CVI suggests that proportions are not equal. A power analysis (below) suggests the probability is 99% that the proportion of CVI males is less than CV and has been correctly detected.

TEST: Null—proportion of CVI males equal to CV males.
Alternate—proportion of CVI males less than CV males.

	VI	V
males	125	347
stage total	398	694
proportion of males	.314	.500

$$(\bar{X}_1 - \bar{X}_2)/\{[(n_1\bar{X}_1 + n_2\bar{X}_2)/n_1+n_2] - [(n_1\bar{X}_1 + n_2\bar{X}_2)/n_1+n_2]^2 \times (1/n_1 + 1/n_2)\}^{1/2} < z_{1-\alpha}.$$

$$(.500 - .314)/\{[694(.500) + 398(.314)/694+398] - [694(.500) + 398(.314)/694+398]^2 \times (1/694 + 1/398)\}^{1/2} < z_{0.90} = 1.26.$$

This calculated value is 6.63. If the proportions are equal, the probability of observing a value equal to or greater than 6.63 due to chance alone is much less than 0.1%.

Reject at 10% that proportions are equal.

POWER: $h = 2 \arcsin(\bar{X}_1^{1/2}) - 2 \arcsin(\bar{X}_2^{1/2})$.
$h = 2 \arcsin(.500^{1/2}) - 2 \arcsin(.314^{1/2})$.
$h = 1.57 - 1.12 = 0.38$.
$n' = 2(398)(694)/398+694 = 506$.

With alpha of 10% and adjusted sample size of 506, power is 99% for the above test.

2. Right males are rare in CIV–CVI.

3. A reduction in proportion of left females is indicated by the sequence CIV=.389, CV=.389, CVI=.337. A statistical test for equality of proportions between CV and CVI suggests that proportions are not equal. A power analysis suggests a probability of 51.6% that a proportion of left CVI females is less than left CV females and can be detected.

TEST: Null—proportion of left CVI females equal to CV.
Alternate—proportion of left CVI females less than CV.

		VI	V
	left females	92	135
	female total	273	347
proportion	left females	.337	.389

$$(.389 - 337)/\{[347(.389) + 273(.337)/347+273] - [347(.389) + 273(.337)/347+273]^2 \times (1/347 + 1/273)\}^{1/2} < z_{0.90} = 1.26.$$

The calculated value is 1.34. If the proportions are equal, the probability of observing a value equal to or greater than 1.34 due to chance alone is about 9.13%.

Reject at 10% that proportions are equal.

POWER: $h = 2 \arcsin(.389^{1/2}) - 2 \arcsin(.337^{1/2})$.
$h = 1.35 - 1.24 = 0.11$.
$n' = 2(273)(347)/273+347 = 305$.

With alpha of 10% and sample size of 305, power is 51.6% for the above test.

To improve power for the test of proportions of left females between CV and CVI, a larger sample of animals was obtained by counting the number of animals in 1/4 aliquots from 12 unsorted subsamples as outlined in the "Methods" section.

All animals from unsorted subsample #26 (representing 63/64 of the sample) were counted to provide basic information on accuracy of projection for counts from a small aliquot (1/64). These data were used to project back to numbers of animals expected in 1/4 of 63/64 for #26 only (see Table 6). Table 5 indicates the number of females expected in the unsorted subsample of #26 (CVI=567, CV=2142, CIV=378) compared to the numbers actually found (CVI=566, CV=1409, CIV=121). Similar numbers for males are as follows: expected (CVI=63, CV=2142, CIV=189); observed (CVI=16, CV=1941, CIV=176). These numbers suggest rather wide fluctuations from expected values within a sample for animals of similar shape. All observed values were less than expected values. Variability did not depend on initial number counted; the best estimate is for 9 CVI females, the worst for 34 CV females.

Data from the unsorted subsample of #26 were used to test for equality of proportions between CV and CVI left females in one large sample. In

this case the downward trend in proportions from CV (.391) to CVI (.373), although possibly biologically significant, is not statistically significant.

TEST: Null—proportion of left CVI females equal to CV.
Alternate—proportion of left CVI females less than CV.

	VI	V
left females	211	551
female total	566	1409
proportion left females	.373	.391

The calculated value is 0.75. The probability of observing a value equal to or greater than 0.74 is about 23%.

Accept at 10% that proportions are equal.

The power of this test, if it had been needed, could not be calculated. With the small percentage difference present, the effects-size index of about 0.04 is not tabulated (Cohen, 1977).

A total of 4613 CIV–CVI specimens of *P. xiphias* were found in ¼ aliquots of 12 unsorted subsamples (Table 6). Their categorization by sex and asymmetry is as follows:

	VIf	VIm	Vf	Vm	IVf	IVm
left	269	200	495	1298	192	642
right	511	0	716	2	288	0

The reduction in proportion of males (CIV=.573, CV=.518, CVI=.204) is more pronounced for this larger sample size than for the initial aliquots; statistical significance is assumed. Right males remain rare. A reduction in left females between CV and CVI is indicated (CIV=.400, CV=.409, CVI=.345). A statistical test for equality of proportions between CV and CVI, with about 87% power, suggests that proportions are not equal.

TEST: Null—proportion of left CVI females equal to CV.
Alternate—proportion of left CVI females less than CV.

	VI	V
left females	269	495
female total	780	1211
proportion left females	.345	.409

The calculated value is 2.86. If the proportions are equal, the probability of observing a value equal to or greater than 2.86 due to chance alone is about 0.2%.

Reject at 10% that proportions are equal.

POWER: $h = 2 \arcsin(.409') - 2 \arcsin(.345')$.
$h = 1.39 - 1.26 = 0.13$.
$n' = 2(1211)(780)/1211+780 = 949$.

With alpha of 10% and sample size of 949, power is at least 86.7%.

Discussion

Although the descriptions of external skeletal morphology are not definitive, several points should be emphasized. No females with attached spermatophores were found. External skeletal morphology of the ontogenetic stages proceeds generally by increasing complexity through the addition of entire appendages (only swimming and reproductive appendages), appendage segments, and armature elements. Feeding appendages gain segments and armature but are much more similar than swimming appendages to homologous appendages of CVI animals. A modified terminal spine on the first swimming leg exopod of CII is the only specialized structure not present in CVI. This element is absent in CIII and later stages.

The second maxilla of calanoids is generally considered to have no more than five inner lobes plus an endopod (see review by Vaupel Klein, 1982). This appendage of *P. xiphias* CII bears six inner lobes. These six are present in all later stages, although in CVI the last lobe may be obscured by lobe 5 and the developed endopod.

Caution should be exercised in suggesting homologies of the first antenna. The 25 free segments present in CIII are not the same 25 present in CIV or CV. The ultimate segment of the latter two stages is subdivided into 3 segments in CIII. The 25 segments in CIV and CV may be obtained by division of the first two segments in CIII. The 24 segments of CVI female may be obtained by fusion of segments 7–8 of CV female. The 22 segments on the left (non-geniculate) AI of CVI male may be obtained by fusion of segments 7–10 of CV male. However, the corresponding 16 segments on the right (geniculate) AI of CVI male cannot be easily obtained from CV male, although fusion of distal segments seems to occur. The homologies of this appendage may be ultimately discerned by comparative adult male morphology of related species.

The degree of sexual dimorphism expressed in CVI is primarily a result of changes in CV males, particularly the development of secondary sex characters (as is true for most calanoids). Thus CVI males differ much more from CV males than CVI females differ from CV females. In *P. xiphias,* CVI males are larger than CVI females, a situation usually reversed in calanoids. Sexual dimorphism is not manifested by reductions of male head appendages; rather dimorphism is increased by the asymmetry of the male swimming legs. Whether these appendages function only as simple swimming appendages in these animals is open to question. The unique concordance of these asymmetrical appendages with known primary and secondary asymmetrical sex characters (Ferrari, 1984) suggests they may be used during copulation. Implications for reduced swimming ability, for these unusually asymmetrical animals, are discussed later.

Ontogenetic changes in behavior of *P. xiphias* result in compact but progressively deeper distributions during the day for CII–CIV (Table 3), and both upward and downward dispersion at night. Both sexes of CV animals continue the daytime trend, but a major behavioral change relative to CIV occurs with the formation of a bimodal nighttime distribution, similar in both sexes (Table 7). A behavioral change from CV to CVI results in a change in distribution of both CVI sexes. Each sex exhibits a more compact distribution during the day, whereas at night more CVI females are found at depths coincidental with the shallower, primary mode of CV animals. At the same time, more CVI males are found at depths coincidental with the deeper, secondary mode of CV. A similar bimodal distribution for CVI *P. xiphias* may be inferred from Roe's (1972) figure 8.

Daytime distributions of all stages of *P. xiphias* are found below high-temperature, low-salinity, surface waters and the salinity maximum. Neither of these features seem to confine the vertical distribution of *P. xiphias* at night. CVI animals are not found in the immediate surface waters; it is difficult to determine if they are avoiding the conditions of the Equatorial Surface Waters.

Several aspects of the copepodid distribution of *P. xiphias,* including dispersion of earlier stages at night and development of bimodal distribution for both CV sexes, asymmetrically echoed in CVI, suggest a changing behavioral repertory. Individuals belonging to the same stage but found at different points in the water column may not be exhibiting simple dispersion about a mean behavioral pattern for that stage. These individuals may undergo a continuous time-related change in the ontogeny of swimming behavior within a stage, which results in intrastage variability in behavior among individuals. Changes in behavior and distribution between stages may be continuous, not abrupt as the episodic morphological changes that form the traditional basis for grouping the animals. For example, recently molted CV animals may behave more like CIV animals than CV animals immediately prior to their molt to CVI. Further, the behavior of some individuals may differ from night to night. A CV animal may migrate down to the deep mode during one night and up to the shallow mode during the following night. All individuals may move, yet each may not always undertake the maximum migration that can be derived from the abstract distribution tables presented herein.

Pleuromamma xiphias exhibits dimorphisms of sex and asymmetry. Late-stage copepodids show statistically significant changes in these dimorphisms (specifically, reductions in males and left females between CV and CVI). This statistical significance is assumed to reflect an underlying, but as yet undetermined, biological significance or causality. A further point about statistical analyses should be noted. Large sample sizes were needed and obtained for these analyses. Implicit in this method is the assumption that patterns observed within a group of animals under consideration are caused by group-wide processes. Exceptions to this assumption will be mentioned later, particularly within the context of assortative mating.

Table 8 shows variation in proportions of

males and left females within and among samples. Total numbers of animals were not corrected for volume of water filtered or aliquot size examined. Smaller sample sizes predominate and may obscure trends within the group. An attempt to resolve any pattern was made in Table 9, where all values from Table 8 based on sample sizes less than 10 animals have been deleted.

The reduction in proportion of males, particularly between CV and CVI, is maintained within samples (Table 9): (1) throughout the day, when the distribution is compact, and (2) above 300 m at night, where the presence of most CVI females enhances the trend in reduction of males. As already noted, most CVI males are found at 500–700 m. At those depths their presence is responsible for increased proportions of males, which locally reverse the overall trend in reduction of proportion of males.

There are noticeable differences in degree of reduction of male proportions among various samples (compare #27 or #26 to #23, or #24 to #13). The vertical displacement of CVI females and males may explain this variation at night, but not during the day. Distributions are compact during the day, and there is less likelihood of such gross behavioral sorting.

The general pattern in reduction of left females is also apparent in Table 9; however, variation among samples is pronounced. For example, the proportion of left CV females in #25 is lower than that for CVI females in any sample. Disparate trends can be seen in comparing #24 to #13, or #27 to #23.

Comparisons within samples support the general trend in reduction of left females. In large samples (e.g., #26, as noted previously) the reduction is not statistically significant; in others (#27) this reduction is quite pronounced. Further questions about whether the reductions of CVI males and left females occur uniformly among the animals represented in these samples, with variation due to behavioral sorting, or whether vertical variation in selection exists will require more specialized study.

Four simple causes of these reductions will be considered: (1) sampling artifact suggests a slight, indirect biological impact on the animals relative to timing or mechanical behavior of the trawl; (2) the direct biological impact of phenotypic switching avoids selective mortality in the population; (3) selective mortality can act alone if it occurs after the reproductive potential of an animal is fulfilled; (4) if selective mortality occurs before individual reproductive potential is fulfilled, some kind of balancing selection will be needed, unless the phenomena of these reductions are temporally transient.

Spatial or temporal segregation of animals, or their differential capture, may be manifest as a disparity in the number found in trawl samples. Males of *P. xiphias* are not known to be temporally more restricted than females. Although some studies of Atlantic Ocean stations (Farran, 1926; Leavitt, 1938; Wheeler, 1970) have reported a few specimens of *P. xiphias* below depths sampled here, most other studies or summaries (Dahl, 1894; Steuer, 1932; Grice and Hulsemann, 1965; Park, 1970; Roe, 1972; Deevey and Brooks, 1977), many using closing or opening-closing nets with flowmeters, indicate that the species is confined to the upper 1000 m. No study has suggested that the animals are distributed below 1200 m. CVI males may be more restricted temporally than CVI females. Reductions in proportions of males could represent a temporally local shortage of CVI males, perhaps due to delayed maturation, during a period when mating is minimal. At present there are no data that support or deny this explanation.

CVI animals may have different abilities to detect an oncoming trawl and swim out of its path. The following order of efficiency in detection would explain reduced proportions of males and left females: CVI males, left CVI females, right CVI females. Although plausible, this hypothesis is not supported by comparative morphology. Unlike the situation in CVI females, swimming legs of CVI males are not flattened swimming "oars" associated with efficient locomotion of calanoids; rather they are unusually gnarled, asymmetrical appendages. Their unique

concordance with other asymmetrical secondary sex characters and the relative size reduction in the fifth legs suggest that these appendages may function during mating behavior, perhaps for clasping the female, as well as for swimming. Like the fifth legs of *Euchaeta norvegica* CVI males (Ferrari, 1978), these modified legs may even hinder efficient swimming, thus making males more susceptible to selection by predation or capture by trawls.

Left and right CVI females exhibit only two gross morphological differences: position of the dark organ and the tubule anterior to the seminal receptacle. Although changes in behavior need not have a morphological basis, in this case morphology provides no a priori reason to assume left females are more efficient in avoiding trawl capture. Finally, a smaller sample size of CV and CVI *P. xiphias* collected with an Isaacs Kidd midwater trawl (mouth opening 3 m^2) during a survey of Deepwater Dumpsite 106 showed a similar reduction in the proportion of males and left females (Ferrari, 1984, and unpublished data). If detection and avoidance is causal for *P. xiphias,* these reductions should not be so noticeable with this larger trawl.

Lack of information about the control of sex and asymmetry in *P. xiphias* hampers understanding of a natural occurrence of the observed reductions. Generally, sex in crustaceans is considered to be genetically controlled (for a review see Ginsburger-Vogel and Charniaux-Cotton, 1982), although in the few studies of calanoid copepods, the evidence is inferential and equivocal. For example, when Goswami and Goswami (1973) suggested males of *Acartia* were heterogamic, XO, they assumed the only presumed morphologically differing pair of chromosomes were the sex chromosomes.

Non-genetic control of sex has been suggested for some crustaceans. This may result from internal or external factors modifying the expression of the genetic mechanism itself or directing developmental expression of the phenotype. No studies of calanoid copepods have suggested such factors can modify the expression of a genetic mechanism. However, both Paffenhöfer (1970) and Heinle (1970), studying laboratory-cultured calanoids, have inferred that external factors may direct the developmental expression of the phenotype. Paffenhöfer suggested that different phytoplankton food species cause changes in sex ratios of *Calanus helgolandicus* (now *C. pacificus*). He qualified this statement because he observed experimental mortality in rearing nauplii through copepodids. If gametic, zygotic, or embryonic selection are not factors in this case, Paffenhöfer's proportions of males seem low enough to suggest a non-genetic mechanism for this species. Paffenhöfer did not study the morphology of his animals. Ontogenetic selection in calanids is more difficult to follow in field collections, because phenotypic expression of sexual dimorphism is not manifest until late CV (Tande and Hopkins, 1981).

Heinle (1970) suggested that genotypic males of *Acartia tonsa* can become phenotypic females under both laboratory and field conditions. Heinle "exploited" his cultures of *A. tonsa* by periodically removing 50% of the water in which they were maintained. The animals removed were preserved and counted. He sexed only CVI animals, although sex in *A. tonsa* can be determined at CIV. Heinle reported that proportions of females increased to .80 in the "exploited" sample. He suggested that as proportions of males decreased to zero, females produced "sterile" eggs and the culture failed. Heinle inferred that as natural population densities became too low, genotypic males become phenotypic females, and this switching led to the reduced proportions of males. He did not report on the morphology of individual animals.

Heinle's CVI male proportions of .20 do not seem alarming when compared to CVI *P. xiphias;* however, many of his conclusions are based on the assumption that females and males exhibited no behavioral differences as the "exploited" water was removed. Thus numbers of animals counted in "exploited" water samples were presumed similar to, rather than an inverse of, those in the remaining water.

Seasonal changes in proportions of males have been studied for the calanoid copepods *Euchaeta norvegica*, by Hopkins (1982) and *Calanus finmarchicus*, by Tande and Hopkins (1981) and suggest phenotypic switching for these calanoids. During most of the year, *E. norvegica* also exhibits a noticeable reduction in proportion of CVI males relative to CV and CIV. An exceptional period occurs just prior to peak spermatophore placement. During this period, proportions of CVI males attain a maximum, while CV males reach a minimum (both about .310). Hopkins mentioned individual variation in presence or absence of simple fifth legs in CIV females. Because CV and CVI females do not possess a fifth pair of legs, he suggested this variation could indicate phenotypic switching from females to males.

Tande and Hopkins (1981) found that sexual dimorphism in primary sex characters of *Calanus finmarchicus* is observable in late CV animals. Seasonal changes in proportions of CV males follow closely those of CVI males, although graphs of these proportions suggest differences when males are common.

Experimental studies have indicated sex is determined much earlier in the ontogeny of a marine harpacticoid copepod. Takeda (1950), in early studies of effects of the externally administered chemicals potassium chlorate and potassium chloride on sexual development of *Tigriopus japonicus*, found that adult sexual condition was determined by CI. Egami's experiments (1951) supported this finding, although his results, like Takeda's, should be interpreted with a degree of caution. Both workers seemed to have exerted intense artificial sibling selection on experimental cultures by discarding all animals in an experiment if one animal died before reaching maturity.

Pleuromamma xiphias exhibited variability in armature size of the 1-segmented fifth leg of CIII (at this stage animals cannot be sexed) and in the armature size, shape, and relative length of segment 3 in fifth legs of CIV males. There was no variability in the number of fifth leg segments or elements in CIV males or similar variability in CIV females. For these reasons, no CIV animals were categorized as intersexes. Similar variability was not noted in fifth legs of CV females or males. Further, the reduction in males of *P. xiphias* takes place primarily between CV and CVI. This reduction is not responsible for scarcity of right males, because these animals are rare even in CIV. These data do not support a hypothesis of phenotypic switching of CV males (overwhelmingly left) to CVI females, with the concomitant reduction in proportion of males.

If the reduction in proportion of males in *P. xiphias* is caused by a factor acting to alter individual phenotypic expression of sex between CV and CVI by switching genotypic CV males to phenotypic CVI females, that factor must also alter the individual phenotypic expression of asymmetry. CIV–CVI males remain overwhelmingly left, while the proportion of right females increases from CIV to CVI. If altered males are the source of the increase in females, their asymmetry must shift from left to right.

Following Heinle's model, a second hypothesis involving phenotypic switching, of females to males, would not require change in asymmetry. The reduction in proportion of left females could be caused by switching of left females to left males. This hypothesis suggests that the reduction in proportion of males actually is more severe than observed in these samples, because the switch of females to males has provided at least partial compensation. As noted above, however, there is no evidence in external skeletal morphology of CIV or CV that phenotypic switching of sexes occurs in *P. xiphias*.

If sex in *P. xiphias* is genetically controlled, and biologically significant numbers of males are lost during ontogeny of CIV–CVI, males must be selected for gametically, zygotically, embryonically, or in naupliar or early copepodid stages, unless selection does not affect reproduction. *Pleuromamma xiphias* CVI males, unlike calanids and euchaetids, possess mouthparts morphologically similar to CVI females. Adult males probably continue to feed, so their life expectancy may not differ from females, in contrast to calanids and euchaetids (Campbell, 1934; Ferrari, 1978).

If selection against males occurs after their potential copulatory period is complete, that is, against completely spent males, males would not have to be selectively compensated earlier in their life history.

Similar problems prevail for the interpretation of statistically significant, and presumed biologically significant, distribution of asymmetry. Causal factors controlling asymmetry are not known. Differential selection after attainment of reproductive potential could affect the reduction in left CVI females. This possibility would obviate the need for a balancing selection, but it is not easily explained biologically. It seems unlikely that an environmental factor acts to modify the phenotypic expression of asymmetry from CV to CVI. Two different methods of expression would be altered, as asymmetry in co-occurring males is not similarly affected during the same stages. Although no right CVI males were found in this study, only 325 CVI males were observed. Elsewhere right CVI males have been reported by Steuer (1932) and Ferrari (1984) at frequencies similar to those found here for CV and CIV males (0.0012–0.0018).

Steuer (1932) attempted to show that changes in asymmetry proportions of left and right adults of *P. indica* (a species in which the dimorphism is frequently expressed in both sexes) could be correlated with latitude of capture (and presumably heat content of the water). However, apart from a large and unusual collection from the Gulf of Aden (about 2000 animals with only 8 right females and 5 right males), the number of animals per locality was very small, and the analysis appeared strained. Steuer's unusual finding from the Gulf of Aden may be explained by geographical changes in selection pressure in a balanced dimorphic system.

Historical data about the distribution of asymmetry in *P. xiphias* are limited, confined to CVI, and not broken down by locality (Steuer, 1932; Ferrari, 1984). The results indicate few right males and proportions of left CVI females (about .333) similar to *Discovery* sta 7089 in 1969. These results, especially Steuer's collections before 1932, suggest that female dimorphism of asymmetry in *P. xiphias* is not temporally transient.

Dimorphisms expressed in only one sex are well-known among insects (Ford, 1975). For the butterflies *Colias* and *Argynnis*, similar sex-limited dimorphisms in females have been investigated genetically and ecologically. Remington (1954) provides a clear summary for *Colias*, and Watt (1973) suggests that sexual selection balances pupal advantages of the genotype for white females of these sulfur butterflies. In this genus of small arthropods, sexual dimorphism is expressed directly at each individual cell, not through hormonal distribution by the blood. Like most Lepidoptera, sulfur butterfly males are homogamic. In many of the 50-odd *Colias* species, female wings are colored yellow, orange, etc., depending on the species. White females also are found in many populations. In several cases white is the most numerous morph, and in a few the colored morph is rare or unknown.

In species of *Colias* studied, white females express the dominant of two alleles (color is recessive) located on an autosomal pair of chromosomes. Phenotypic distinctions between homozygote and heterozygote have not been discovered. Expression of this autosomal "alba" system is suppressed in males, although like females, males carry one of three "alba" genotypes (AA, Aa, aa). Viability of "alba" females differs in different species, and within a species proportions may vary in different environments. Part of this variation is due to linked lethal or semilethal modifying genes. This "alba" system is presumed to be ubiquitous in the genus, as it is inherited in many interspecific crosses.

Although the autosomal "alba" system is suppressed in males, which are almost always the non-white color of the females, rare white males have been found. In one genetic system responsible for color in these males, the white allele is recessive; it is not sex-limited. This same system also produces rare white females that can be differentiated from the "alba" system white female phenotype.

Knowledge about the biology of *P. xiphias* is disappointingly incomplete, particularly in regard to origin and maintenance of asymmetry.

The sex-limited autosomal system of sulfur butterflies has many obvious parallels for the distribution of adult phenotypes of *Pleuromamma*. A simple binary alternative of asymmetry in a basically bilaterally symmetrical animal will mask any multiple interacting systems, because phenocopies from differing systems cannot be separated. In addition, in simple sex-limited autosomal or sex-linked systems, which explain changes in proportions of asymmetry as a balanced genetic dimorphism, reduction in males between CV and CVI may be a product of their selection as males, or as left animals. If the latter case is true, selection for males also may occur with selection of left females. Despite parallels to an epistatic, sex-limited, autosomal system, a second hypothesis involving a single-locus, sex-linked system, and sexual selection is outlined for *P. xiphias*.

According to this hypothesis both asymmetry and sex in *P. xiphias* are determined and controlled genetically. Males are homogamic ZZ. Male asymmetry is controlled by a left allele at a single locus on both Z chromosomes. Occurrence of the right male phenotype (4/2775 = 0.0015 among CIV–CVI males) reflects a recurrent rate of mutation of the Z-left allele to the alternate Z-right dominant. The Z-right allele of a right male may be his mutation or inherited from his mutant mother. These rare males develop normally into adults.

Females are heterogamic, ZW. A single locus on the W chromosome and two alleles (right or left) control asymmetry for a female. The condition of an Z-left allele will not be a factor, as there is no variation in homozygous and heterozygous phenotypes. Right allele on the W chromosome is dominant to left.

Mutant Z-right alleles are removed from the population by female sexual selection acting against the right male phenotype. By definition, a female passes her Z chromosome to her son. Her daughters receive their Z chromosome from their fathers. Any Z-right allele may remain in the population for at most two generations. By the second generation it will be found in a male and then eliminated.

Dimorphism in females of *P. xiphias* is a balanced genetic system. Left females are selected against during ontogeny. The balance is restored by sexual selection at CVI, as left males prefer to copulate with left females.

This hypothesis relies on sexual selection to remove all Z-right alleles from males and to favor Z-left alleles in females. There is no direct evidence for sexual selection in calanoid copepods. Circumstantial evidence that males prefer like-sided females in *Pleuromamma* is provided by Ferrari (1984). He listed nine possible categories of *Pleuromamma* species based on frequency of expression of asymmetry between sexes. *Pleuromamma indica* is the only species in which asymmetry is frequently expressed in both sexes. *Pleuromamma abdominalis* joins *P. xiphias* in a second category, with asymmetry frequently expressed in females but with left predominant in males. In all other species, overwhelming numbers of both males and females are right. Left individuals are infrequent but have been found in both sexes for most of these latter species. There are no extant species of *Pleuromamma* in which overwhelming numbers of males are left while females are right, or vice versa.

It is a useful exercise to consider ways to falsify this hypothesis. The discovery of assortative mating by *P. xiphias* would obviate the need for sexual selection by males. However, assortative mating would be extremely difficult to detect in field collections for the following reasons.

1. Mating may occur in a very restricted range of the habitat of CVI animals; Hayward (1981) has suggested that *P. piseki* males with well-developed spermatophores in the bursa (and presumably ready to copulate) are found at shallower depths than those males without a well-developed spermatophore. Table 9 suggests two depth zones (510–400 m during the day and 200–110 m at night) in which assortative mating could be relevant; in these zones relatively large numbers of CVI males co-occur with higher proportions of CVI left females.

2. Characters of males and females in condition immediately prior to copulation, now unknown, would need to be determined, as have

been outlined by Tande and Hopkins (1981) for *Calanus finmarchicus* and by Watras (1983) for species of *Diaptomus*.

3. The actual assortment need only be slight (and thus difficult to detect) to balance a reduction of left females of about 5% between CV and CVI (this reduction assumes no further gametic, zygotic, naupliar, or early copepodid selection).

Studies of mating behavior to determine the existence of sexual selection would encounter the same difficulty of detecting slight changes in selection. The hypothesis can be most easily falsified by culturing the offspring of controlled matings. The results of the following pairings are necessary consequences but are not sufficient to establish the genetic model; negative results will falsify the following hypothesis.

1. Left male with right female should produce one-half left sons and one-half right daughters.

2. Left male with left female should produce one-half left sons and one-half left daughters.

3. Virtually no right males should be found, because these result solely from the recurrent mutation rate of the Z-left allele of a male or passed on to him from his mother. The dominant Z-right allele is lost immediately after its phenotypic expression in a male, because right males are rejected as unsuitable mates by either left or right females. If this ecological/genetical model is correct, there could be more intense selection at CVI to restore a theoretical 15% reduction in left females.

Regardless of which process is found to control the distribution of asymmetry in *P. xiphias,* one conclusion seems clear. Interpretations of the phylogeny of any calanoid group, if it involves patterns of distribution of asymmetry, will depend on knowledge of the process maintaining the asymmetry. Several authors have commented on the value of patterns of asymmetrical secondary sex characters in interpreting the phylogeny of calanoids (e.g., Steuer, 1932, and Ferrari, 1984, for *Pleuromamma;* Andronov, 1973, and Fleminger, 1983, for calanoids in general). For these authors, a caveat is apropos. Evolving patterns cannot be categorized without an understanding of underlying processes.

NOTE.—Clarke (1980, 1982) recovered *P. xiphias* from stomachs of Hawaiian mesopelagic fishes; a majority (598 of 644) examined were CVI animals. If statistically significant reductions in proportions of males and left females occur between CV and CVI, effects of this predation on these changes should be considered in further studies.

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TABLE 1.—For each sample (#) are listed the collecting date in 1969 (day/month), time code (Tc, day or night), local time period (T, astronomical time, hours and minutes), depth range (D, in m), initial aliquot examined (A), length of tow (L, in km), and volume of water filtered (V, in m^3).

#	Date	Tc	T	D	A	L	V
3	12/11	n	0204–0404	300–210	1/16	6.66	4928
4	12/11	d	0933–1135	890–800	1/8	7.38	5461
5	12/11	d	1456–1655	790–700	1/8	6.46	4780
8	13/11	n	0424–0626	1010–900	1/8	6.16	4558
9	13/11	d	1012–1212	700–610	1/8	7.22	5343
11	13/11	n	2158–2358	400–300	1/8	9.15	6771
12	14/11	n	0324–0524	900–800	1/8	8.33	6164
13	14/11	d	0914–1114	600–515	1/8	6.47	4788
14	14/11	d	1359–1559	1020–910	1/8	6.30	4662
15	14/11	n	2010–2204	785–700	1/8	7.66	5668
16	14/11	n	0003–0203	700–610	1/8	8.23	6090
17	15/11	n	0332–0532	600–505	1/8	7.81	5779
19	15/11	d	1321–1521	194–112	1/16	8.55	6327
20	15/11	d	1618–1818	100–55	1/32	6.54	4840
22	16/11	n	0154–0355	500–410	1/8	7.86	5816
23	16/11	n	0451–0650	200–110	1/16	6.06	4484
24	16/11	d	0959–1159	500–410	1/8	5.81	4299
25	16/11	d	1404–1604	290–210	1/16	8.51	6297
26	16/11	n	2105–2305	100–49	1/64	7.15	5291
27	17/11	n	0143–0343	60–25	1/32	8.59	6357
28	17/11	n	0415–0610	25–10	1/64	5.99	4433
29	17/11	d	0950–1151	400–305	1/8	6.90	5106
30	17/11	d	1322–1522	50–20	1/32	7.63	5646
31	17/11	d	1620–1759	20–12	1/32	6.57	4862
32	17/11	n	2220–0333	1200–1000	1/8	17.71	13105
33	18/11	n	0445–0650	10–0	1/64	7.86	5816
34	18/11	d	1029–1520	1200–1000	1/8	17.84	13202
35	18/11	d	1420–1620	10–0	1/8	8.03	5942

TABLE 2.—Number of left and right *P. xiphias* specimens (left/right) for each stage and sex (if determined) from initial aliquots of each sample (#). Day samples by depth (D, in m) in upper block; night samples by depth in lower block. (T = total; f = female; m = male.)

#	D	VIf	VIm	Vf	Vm	IVf	IVm	III	II
					DAY				
35	10–0	–	–	–	–	–	–	–	–
31	20–12	–	–	–	–	–	–	–	–
30	50–20	–	–	–	–	–	–	–	–
20	100–55	–	–	–	–	–	–	–	–
19	194–112	–	–	–	–	0/1	–	5/5	35/18
25	290–210	0/2	–	8/24	25/1	17/29	67/0	32/16	3/3
29	400–305	10/17	–	18/24	86/0	11/12	24/0	14/5	1/1
24	500–410	17/32	16/0	9/9	17/0	1/0	1/0	–	–
13	600–515	34/71	41/0	6/7	10/0	–	–	–	–
9	700–610	0/2	6/0	1/3	9/0	–	–	–	–
5	790–700	1/1	1/0	1/2	–	–	–	–	–
4	890–800	–	–	0/1	–	–	–	–	–
14	1020–910	1/3	–	3/3	1/0	–	–	–	–
34	1200–1000	–	–	–	–	–	–	–	–
					NIGHT				
33	10–0	–	–	–	–	–	2/0	2/0	–
28	25–10	0/1	–	1/2	11/0	5/5	6/0	0/1	–
27	60–25	11/28	1/0	13/18	42/0	5/8	9/0	5/4	4/2
26	100–49	3/6	1/0	12/22	34/0	3/3	3/0	4/1	0/3
23	200–110	13/16	7/0	11/11	19/0	5/11	19/0	6/6	3/0
3	300–210	–	2/0	–	–	1/1	5/0	10/8	56/24
11	400–300	–	–	8/14	13/0	10/21	13/0	57/22	3/3
22	500–410	1/2	4/0	11/14	19/0	–	1/0	–	–
17	600–505	1/0	11/0	23/41	39/0	–	5/1	–	–
16	700–610	–	29/0	4/13	12/0	–	3/0	–	–
15	785–700	–	6/0	0/2	3/0	–	1/0	–	–
12	900–800	–	–	6/1	3/0	–	–	–	–
8	1010–900	–	–	0/1	–	–	–	–	–
32	1200–1000	–	–	–	3/0	–	1/0	–	–
T		92/181	125/0	135/212	346/1	58/91	160/1	135/68	105/54

TABLE 3.—Number of *P. xiphias* collected per 1000 m^3 of water filtered for each stage and sex (if determined) from initial aliquot examined (A) of each sample (#). Day samples by depth (D, in m) in upper block; night samples by depth in lower block. (Td = total for day, 1200–0 m; Tn = total for night, 1200–0 m; T = total for day and night, 1200–0 m.)

#	D	A	VIf	VIm	Vf	Vm	IVf	IVm	III	II
					DAY					
35	10–0	1/8	–	–	–	–	–	–	–	–
31	20–12	1/32	–	–	–	–	–	–	–	–
30	50–20	1/32	–	–	–	–	–	–	–	–
20	100–55	1/32	–	–	–	–	–	–	–	–
19	194–112	1/16	–	–	–	–	3	–	26	134
25	290–210	1/16	5	–	81	66	116	170	122	15
29	400–305	1/8	43	–	66	135	37	38	30	3
24	500–410	1/8	92	30	34	31	1	1	–	–
13	600–515	1/8	176	69	22	16	–	–	–	–
9	700–610	1/8	3	10	5	14	–	–	–	–
5	790–700	1/8	4	1	5	–	–	–	–	–
4	890–800	1/8	–	–	1	–	–	–	–	–
14	1020–910	1/8	7	–	11	1	–	–	–	–
34	1200–1000	1/8	–	–	–	–	–	–	–	–
					NIGHT					
33	10–0	1/64	–	–	–	–	–	22	22	–
28	25–10	1/64	15	–	43	160	145	87	15	–
27	60–25	1/32	196	5	157	212	65	46	46	30
26	100–49	1/64	110	12	411	411	73	37	61	35
23	200–110	1/16	104	26	78	68	57	68	43	11
3	300–210	1/16	–	7	–	–	7	16	58	260
11	400–300	1/8	–	–	26	15	37	15	93	7
22	500–410	1/8	4	5	35	26	–	1	–	–
17	600–505	1/8	1	15	89	54	–	8	–	–
16	700–610	1/8	–	38	22	16	–	4	–	–
15	785–700	1/8	–	8	3	4	–	1	–	–
12	900–800	1/8	–	–	10	4	–	–	–	–
8	1010–900	1/8	–	–	1	–	–	–	–	–
32	1200–1000	1/8	–	–	–	1	–	1	–	–
Td			330	110	225	263	157	209	178	152
Tn			430	116	875	971	384	306	338	343
T			760	226	1100	1234	541	515	516	495

TABLE 4.—From the initial aliquot examined (A) of each sample (#) the number of *P. xiphias* females of copepodid stages IV, V, and VI counted (c) is projected (pr) for the remaining unsorted subsample (pr = (c × 1/A) − c). Those samples whose unsorted subsample was selected for further study are noted (*).

#	A	CVI		CV		CIV	
		c	pr	c	pr	c	pr
35	1/8	0	0	0	0	0	0
34	1/8	0	0	0	0	0	0
33	1/64	0	0	0	0	0	0
32	1/8	0	0	0	0	0	0
31	1/32	0	0	0	0	0	0
30	1/32	0	0	0	0	0	0
*29	1/8	27	189	42	294	23	161
*28	1/64	1	63	3	189	10	630
*27	1/32	39	1209	31	961	13	403
*26	1/64	9	567	34	2142	6	378
*25	1/16	2	30	32	480	46	690
*24	1/8	49	343	18	126	1	7
*23	1/16	29	435	22	330	16	240
*22	1/8	3	21	25	175	0	0
20	1/32	0	0	0	0	0	0
19	1/16	0	0	0	0	0	0
*17	1/8	1	7	64	448	0	0
*16	1/8	0	0	17	119	0	0
15	1/8	0	0	2	14	0	0
14	1/8	4	28	6	42	0	0
*13	1/8	105	735	13	91	0	0
12	1/8	0	0	7	49	0	0
*11	1/8	0	0	22	154	31	217
9	1/8	2	14	4	28	0	0
8	1/8	0	0	1	7	0	0
5	1/8	2	14	3	21	0	0
4	1/8	0	0	1	7	0	0
3	1/16	0	0	0	0	2	30

TABLE 5.—From initial aliquots examined (A) of samples chosen for further study (#), the number of females counted (c) from CIV, CV, and CVI is projected for the remaining unsorted subsample (pr) and for one-quarter of the remaining unsorted subsample (¼). These are compared with the actual number found (Ac). #26 is an exception, because the entire unsorted subsample was counted.

#	A	CVI				CV				CIV			
		c	pr	¼	Ac	c	pr	¼	Ac	c	pr	¼	Ac
29	1/8	27	189	47	31	42	294	74	122	23	161	40	30
28	1/64	1	63	16	5	3	189	47	89	10	630	158	57
27	1/8	39	1209	302	252	31	961	240	148	13	403	101	85
26	1/64	9	567	n/a	566	34	2142	n/a	1409	6	378	n/a	121
25	1/16	2	30	8	0	32	480	120	113	46	690	173	137
24	1/8	49	343	86	72	18	126	32	30	1	7	2	1
23	1/16	29	435	109	82	22	330	83	77	16	240	60	63
22	1/8	3	21	5	13	25	175	44	81	0	0	0	1
17	1/8	1	7	2	8	64	448	112	101	0	0	0	2
16	1/8	0	0	0	6	17	119	30	21	0	0	0	1
13	1/8	105	735	184	166	13	91	23	38	0	0	0	0
11	1/8	0	0	0	3	22	154	39	39	31	217	54	73

TABLE 6.—Number of left and right *P. xiphias* specimens (left/right) for each stage and sex from ¼ of the remaining unsorted subsample (S). Exception: ¼ of the remaining unsorted subsample for #26 was projected back from the count for the entire unsorted subsample (bottom line). (T = total; f = female; m = male.)

#	S	CVI		CV		CIV	
		f	m	f	m	f	m
29	7/32	12/19	1/0	67/55	164/0	12/18	52/0
28	63/256	3/2	0/0	42/47	57/0	24/33	71/0
27	7/32	63/189	7/0	53/95	242/0	35/50	102/0
*26	63/256	53/89	4/0	138/214	485/1	12/18	44/0
25	15/64	0/0	2/0	28/85	97/0	51/86	253/0
24	7/32	25/47	28/0	11/19	25/0	1/0	2/0
23	15/64	34/48	25/0	31/46	65/1	26/37	47/0
22	7/32	3/10	8/0	44/37	38/0	1/0	8/0
17	7/32	6/2	25/0	41/60	66/0	2/0	7/0
16	7/32	0/6	40/0	8/13	30/0	0/1	2/0
13	7/32	70/96	59/0	17/21	14/0	0/0	5/0
11	7/32	0/3	1/0	15/24	15/0	28/45	49/0
T		269/511	200/0	495/716	1298/2	192/288	642/0
*26	63/64	211/355	16/0	551/858	1939/2	49/72	176/0

TABLE 7.—Number of *P. xiphias* collected per 1000 m^3 of water filtered for both sexes of CIV to CVI from initial aliquots examined (A) of each sample plus ¼ aliquots of samples 29, 28, 27, 25, 24, 23, 22, 17, 16, 13, 11, and all of sample 26. Day samples by depth (D, in m) in upper block; night samples by depth in lower block. (Td = total for day, 1200–0 m; Tn = total for night, 1200–0 m; f = female; m = male.)

#	D	A	VIf	VIm	Vf	Vm	IVf	IVm
				DAY				
35	10–0	1/8	–	–	–	–	–	–
31	20–12	1/32	–	–	–	–	–	–
30	50–20	1/32	–	–	–	–	–	–
20	100–55	1/32	–	–	–	–	–	–
19	194–112	1/16	–	–	–	–	3	–
25	290–210	19/64	1	1	78	66	99	172
29	400–305	11/32	34	1	93	142	30	43
24	500–410	11/32	82	30	32	28	1	3
13	600–515	11/32	165	61	31	15	–	3
9	700–610	1/8	3	10	5	14	–	–
5	790–700	1/8	3	1	5	–	–	–
4	890–800	1/8	–	–	1	–	–	–
14	1020–910	1/8	7	–	11	1	–	–
34	1200–1000	1/8	–	–	–	–	–	–
				NIGHT				
33	10–0	1/64	–	–	–	–	–	22
28	25–10	67/256	5	–	80	58	58	66
27	60–25	11/32	132	4	81	130	45	50
26	100–49	entire	107	3	266	368	23	34
23	200–110	19/64	84	24	74	64	60	50
3	300–210	1/16	–	7	–	–	5	16
11	400–300	11/32	1	1	26	12	45	41
22	500–410	11/32	6	4	39	21	1	3
17	600–505	11/32	4	18	82	53	1	7
16	700–610	11/32	3	32	18	20	1	3
15	785–700	1/8	–	8	3	4	–	1
12	900–800	1/8	–	–	10	4	–	–
8	1010–900	1/8	–	–	1	–	–	–
32	1200–1000	1/8	–	–	–	1	–	–
Td			295	104	256	266	133	221
Tn			342	101	680	735	239	293

TABLE 8.—Proportion of males (r1, left block) and left females (r2, right block) for CIV, CV, and CVI from each sample (#) by depth (D, in m) for all animals sorted. (T1 = females plus males; T2 = total females; f = female.)

#	D	CVI		CV		CIV		CVIf		CVf		CIVf	
		r1	T1	r1	T1	r1	T1	r2	T2	r2	T2	r2	T2
						DAY							
35	10–0												
31	20–12												
30	50–20												
20	100–55												
19	194–112					.000	1					.000	1
25	290–210	.500	4	.459	268	.636	503	.000	2	.248	145	.372	183
29	400–305	.017	59	.604	414	.589	129	.379	58	.518	164	.434	53
24	500–410	.267	165	.467	90	.600	5	.347	121	.417	48	1.000	2
13	600–515	.270	371	.320	75	1.000	5	.295	237	.451	51		
9	700–610	.750	8	.692	13			.000	2	.250	4		
5	790–700	.333	3	.000	3			.500	2	.333	3		
4	890–800			.000	1					.000	1		
14	1020–910	.000	4	.143	7			.250	4	.500	6		
34	1200–1000												
						NIGHT							
33	10–0					1.000	2						
28	25–10	.000	6	.425	160	.535	144	.500	6	.467	92	.433	67
27	60–25	.027	299	.613	463	.531	209	.254	291	.369	179	.408	98
26	100–49	.029	592	.578	3418	.585	306	.372	575	.390	1443	.409	127
23	200–110	.224	143	.462	184	.455	145	.423	111	.424	99	.392	79
3	300–210	1.000	2			.714	7					.500	2
11	400–300	.250	4	.315	89	.373	166	.000	3	.377	61	.365	104
22	500–410	.429	28	.350	163	.900	10	.250	16	.519	106	.000	1
17	600–505	.800	45	.389	270	.867	15	.788	9	.388	165	1.000	2
16	700–610	.920	75	.525	80	.833	6	.000	6	.316	38	.000	1
15	785–700	1.000	6	.600	5	1.000	1			.000	2		
12	900–800			.300	10					.857	7		
8	1010–900			.000	1					.000	1		
32	1200–1000			1.000	3	1.000	1						

TABLE 9.—Proportion of males (r1, left block) and left females (r2, right block) for ClV, CV, and CV1 from samples (#) in Table 8 in which T1's and T2's are greater than 9. (D = depth in m; T1 = females plus males; T2 = total females; f = female.)

#	D	CV1		CV		ClV		CV1f		CVf		ClVf	
		r1	T1	r1	T1	r1	T1	r2	T2	r2	T2	r2	T2
						DAY							
35	10–0												
31	20–12												
30	50–20												
20	100–55												
19	194–112												
25	290–210			.459	268	.636	503			.248	145		
29	400–305	.017	59	.604	414	.589	129	.379	58	.518	164	.372	183
24	500–410	.267	165	.467	90			.347	121	.417	48	.434	53
13	600–515	.270	371	.320	75			.295	237	.451	51		
9	700–610			.692	13								
5	790–700												
4	890–800												
14	1020–910												
34	1200–1000												
						NIGHT							
33	10–0												
28	25–10			.425	160	.535	144			.467	92	.433	67
27	60–25	.027	299	.613	463	.531	209	.254	291	.369	179	.408	98
26	100–49	.029	592	.578	3418	.585	306	.372	575	.390	1443	.409	127
23	200–110	.224	143	.462	184	.455	145	.423	111	.424	99	.392	79
3	300–210												
11	400–300			.315	89	.373	166			.377	61	.365	104
22	500–410	.429	28	.350	163	.900	10	.250	16	.519	106		
17	600–505	.800	45	.389	270	.867	15			.388	165		
16	700–610	.920	75	.525	80					.316	38		
15	785–700												
12	900–800			.300	10								
8	1010–900												
32	1200–1000												

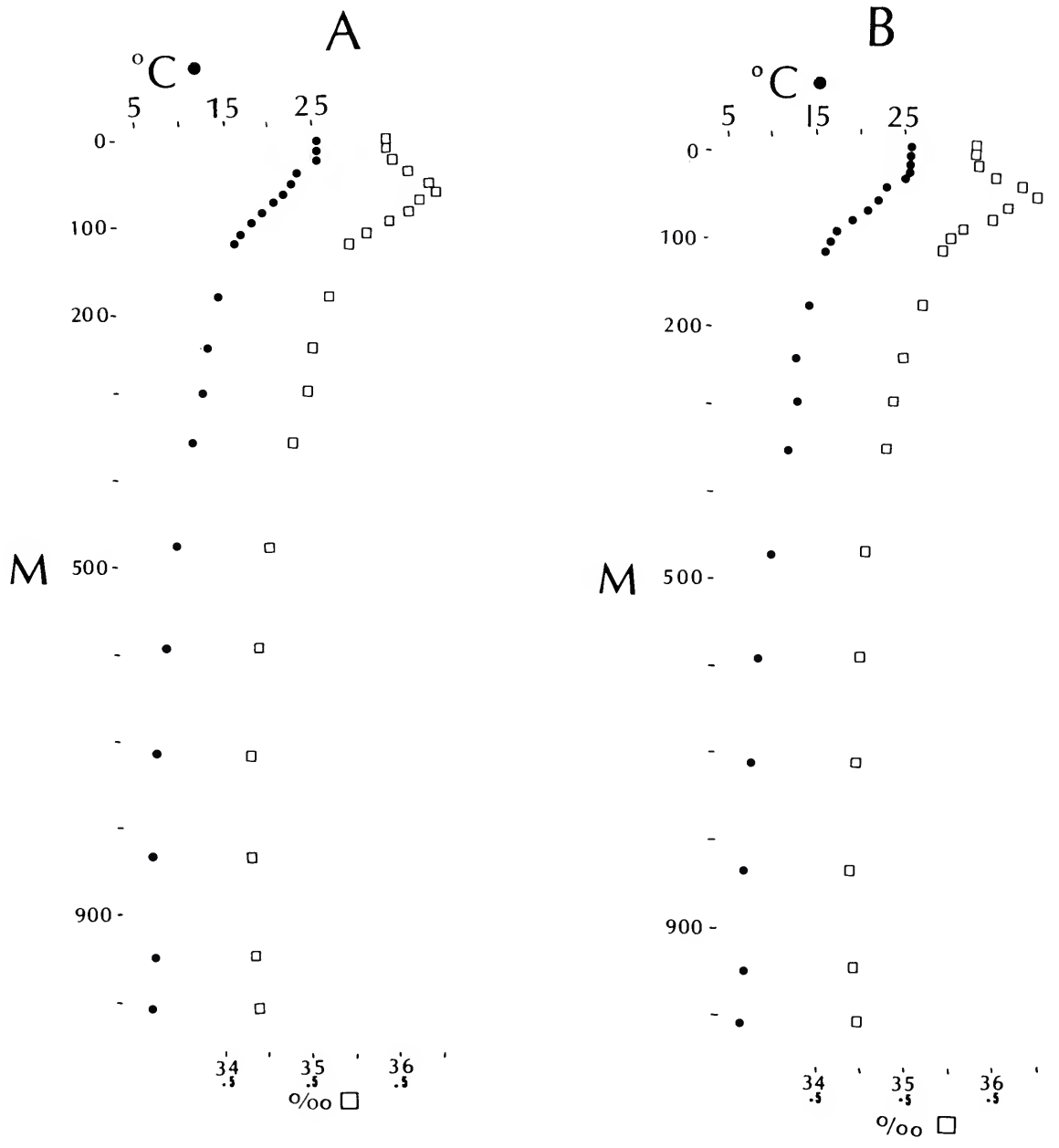
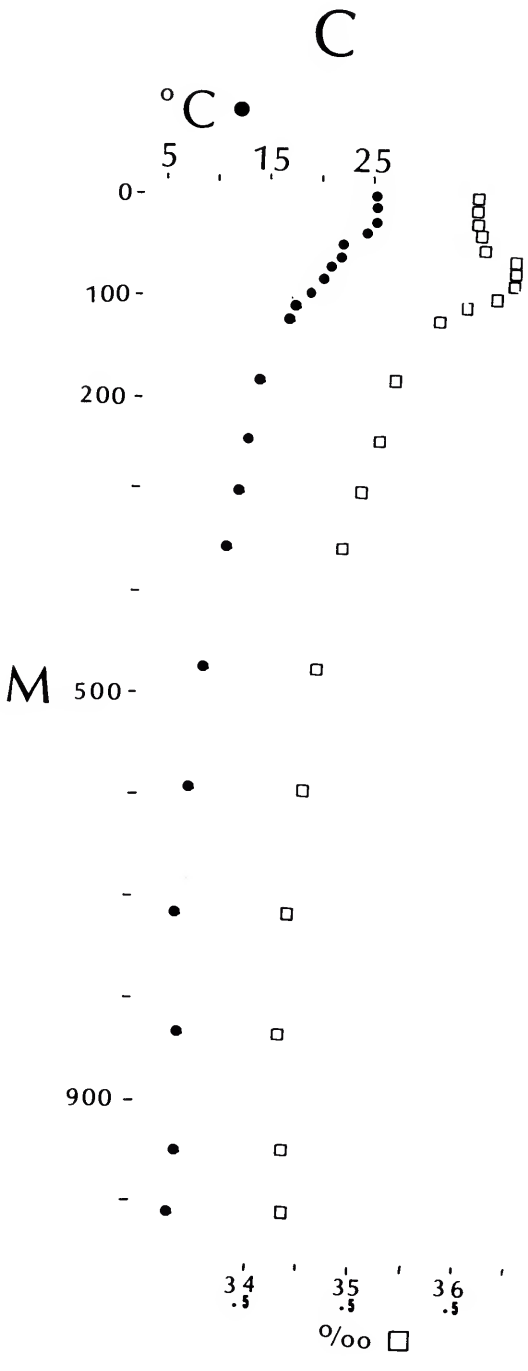


FIGURE 1.—Distribution of heat (°C top scale) and salt (‰ bottom scale) by depth (M) in sampling area: A, at 2011–2112 on 12 Nov 1969; B, at 1910–1951 on 13 Nov 1969; C, at 1959–2044 on 15 Nov 1959; D, at 1951–2053 on 17 Nov 1969.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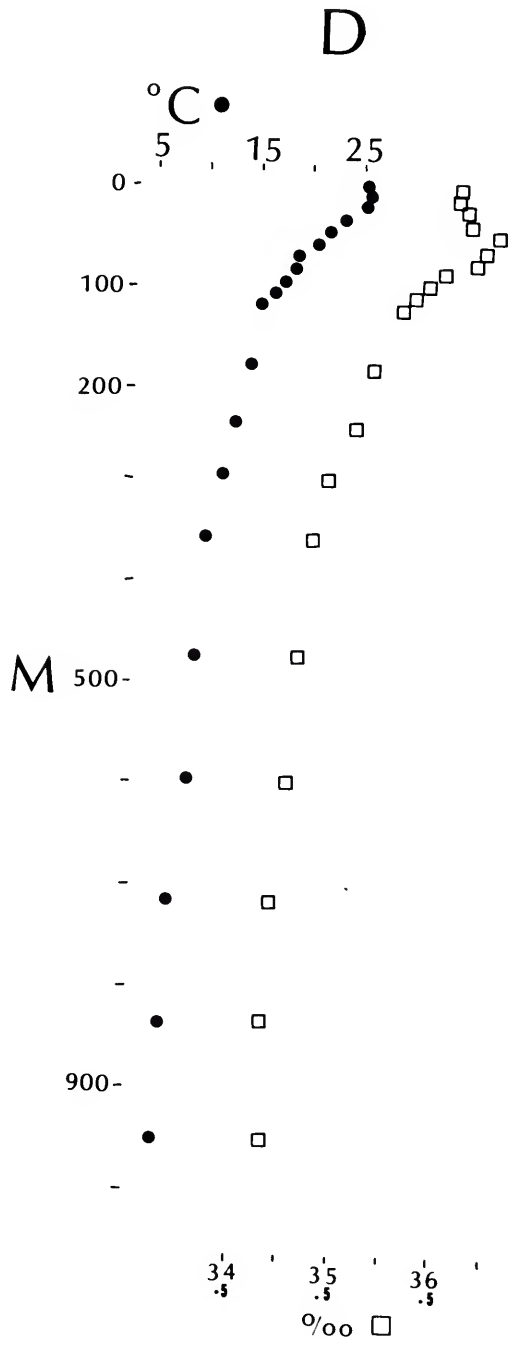
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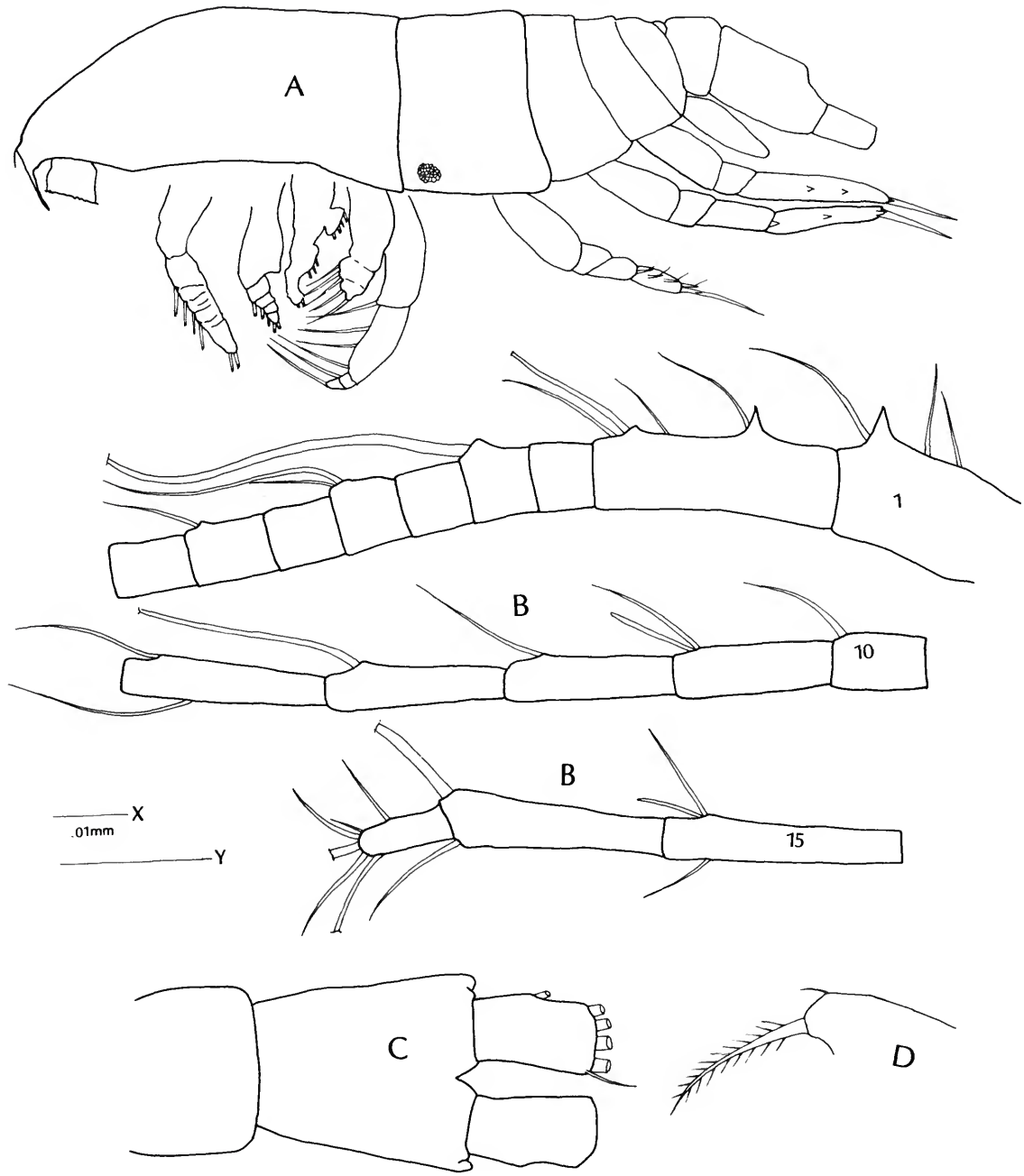

FIGURE 2.—Copepodid II: A, habitus, lateral; B, AI (proximal segment of series numbered); C, Ur, ventral; D, rostrum (A on scale X; B–D on scale Y).

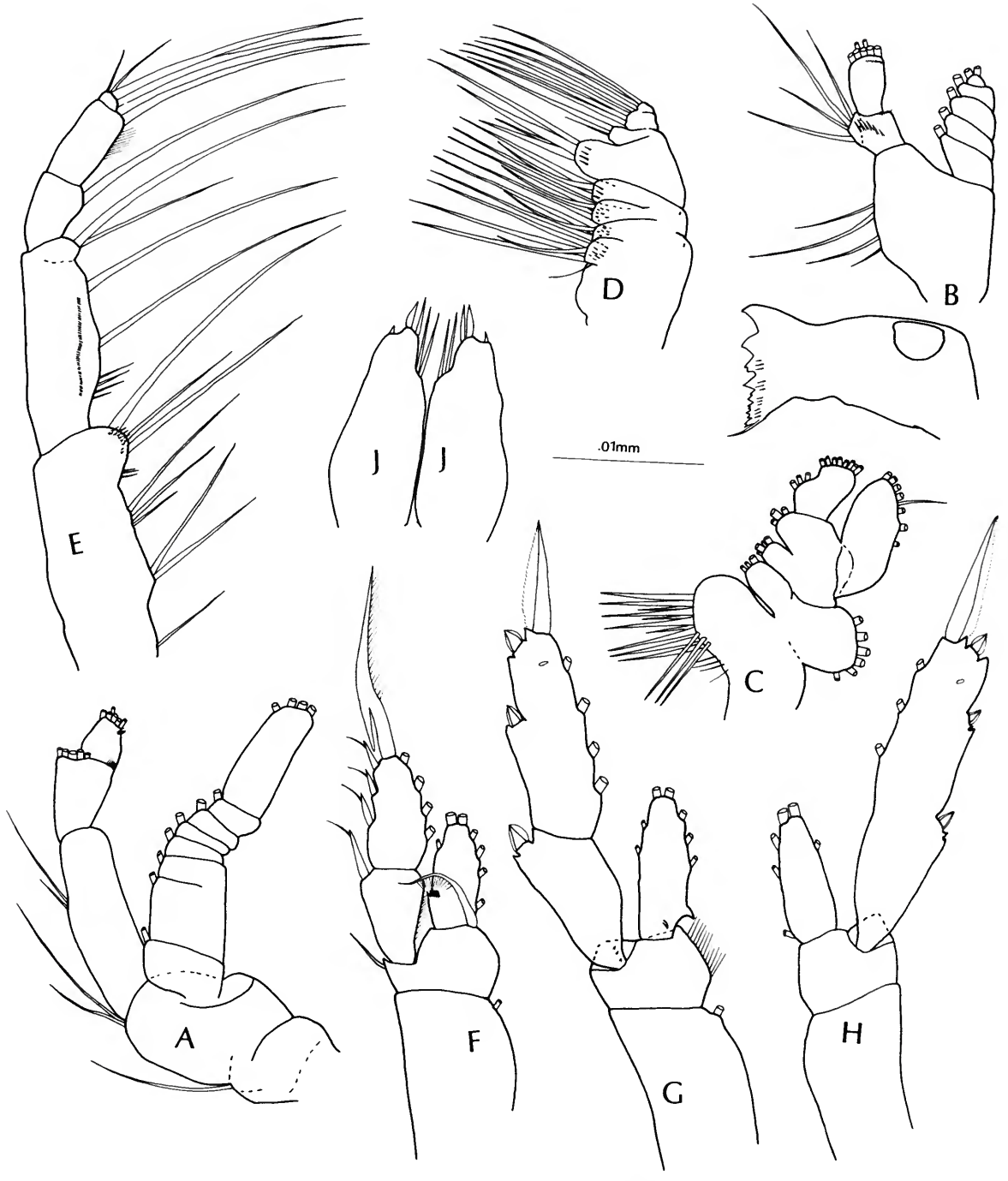

FIGURE 3.—Copepodid II: A, AII; B, Mn; C, MxI; D, MxII; E, Mxp; F, P1; G, P2; H, P3; J, P4.

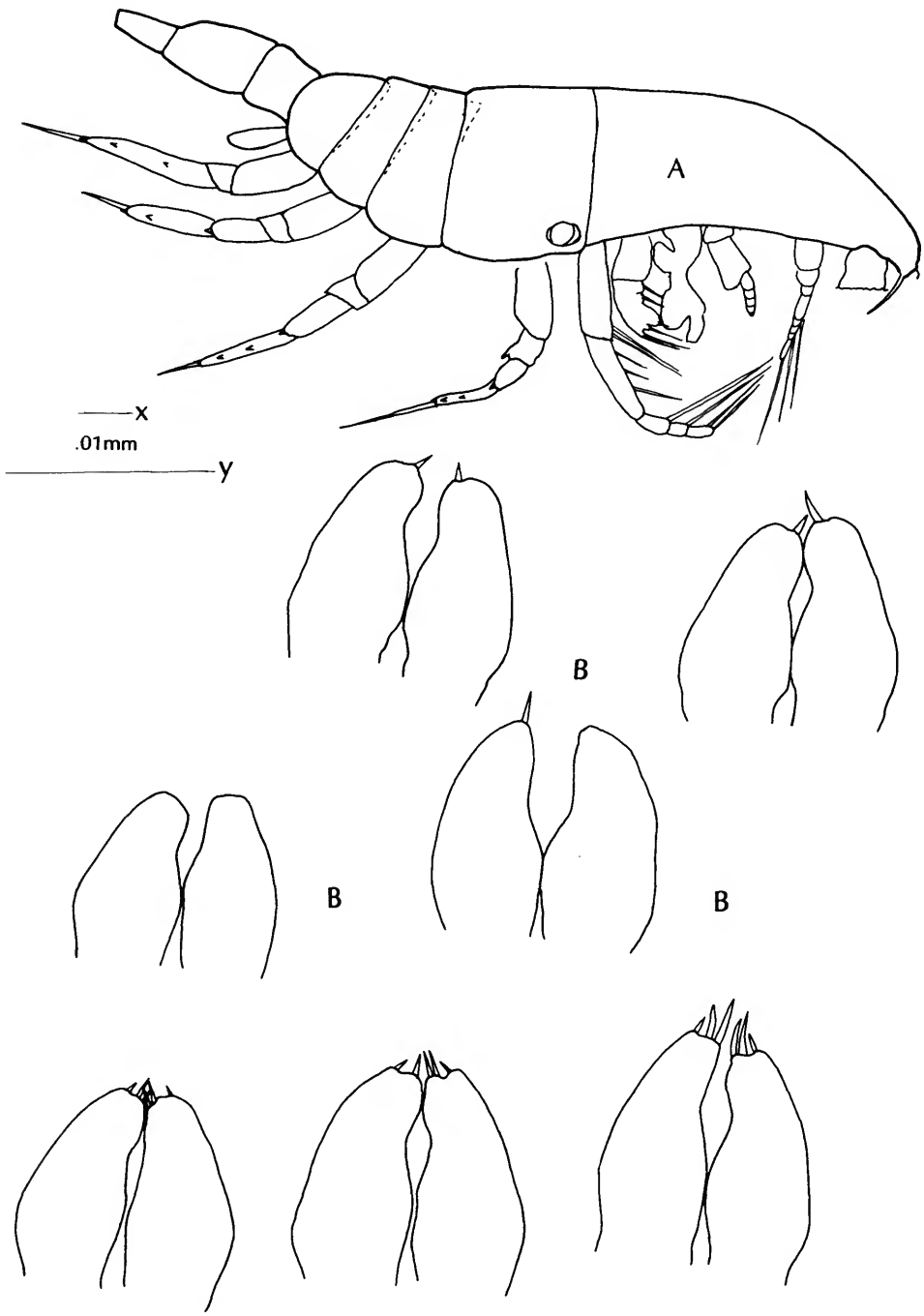

FIGURE 4.—Copepodid III: A, habitus, lateral; B, intraspecific variation in P5 from 7 specimens (A on scale X; B on scale Y).

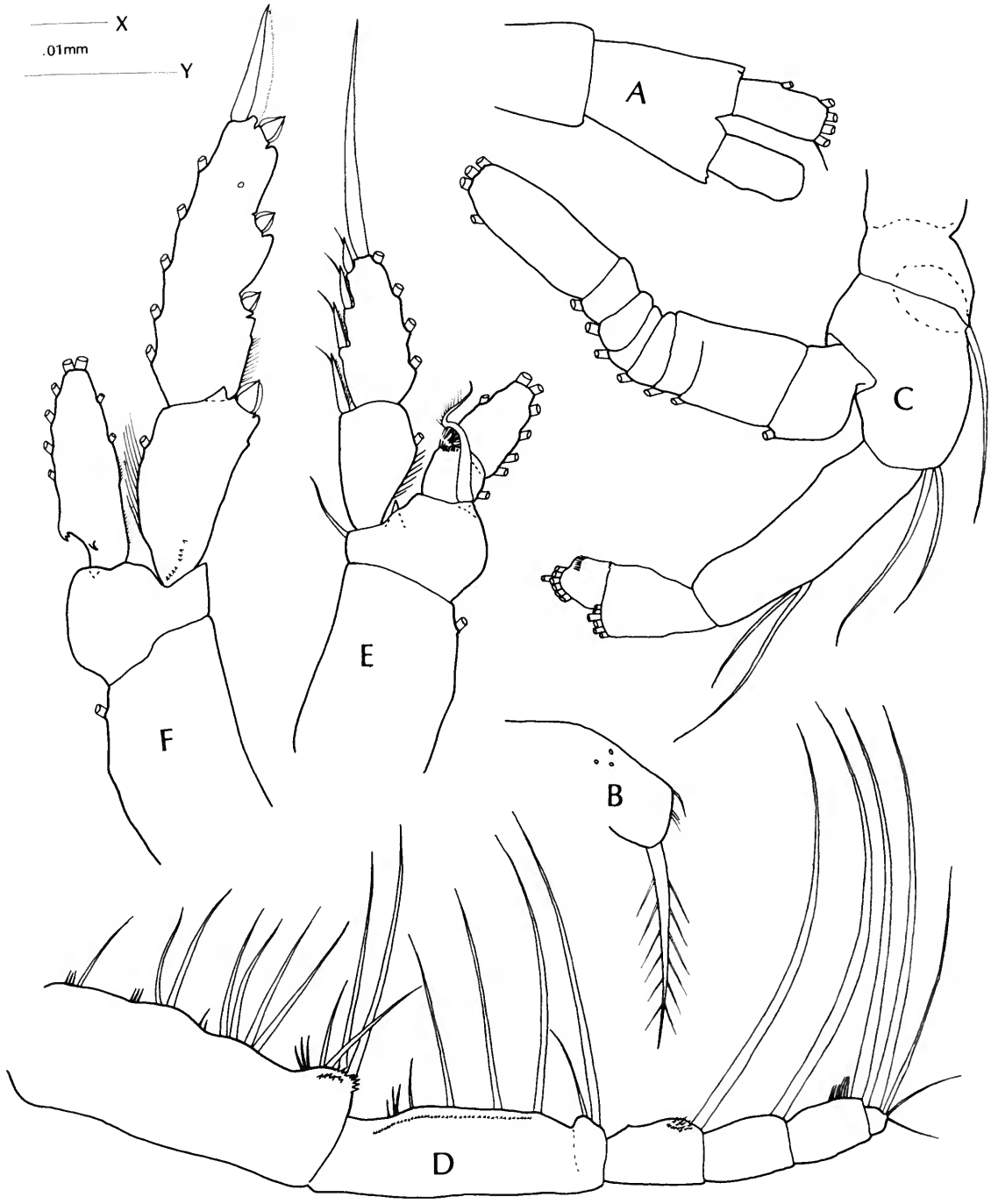

FIGURE 5.—Copepodid III: A, Ur, ventral; B, rostrum; C, AII; D, Mxp; E, P1; F, P2 (A on scale X; B–F on scale Y).

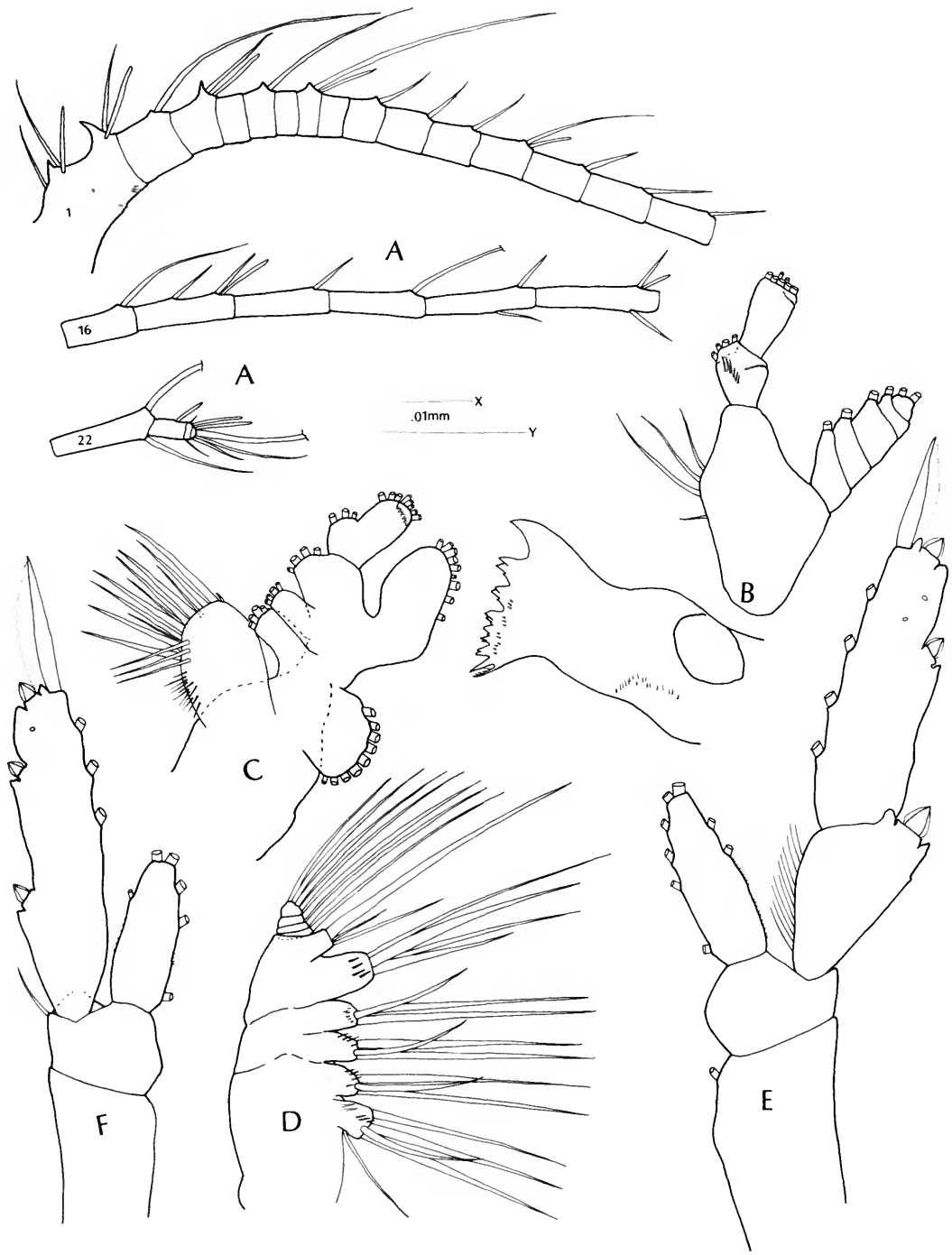

FIGURE 6.—Copepodid III: A, A1 (proximal segment of series numbered); B, Mn; C, MxI; D, MxII; E, P3; F, P4 (A on scale X; B–F on scale Y).

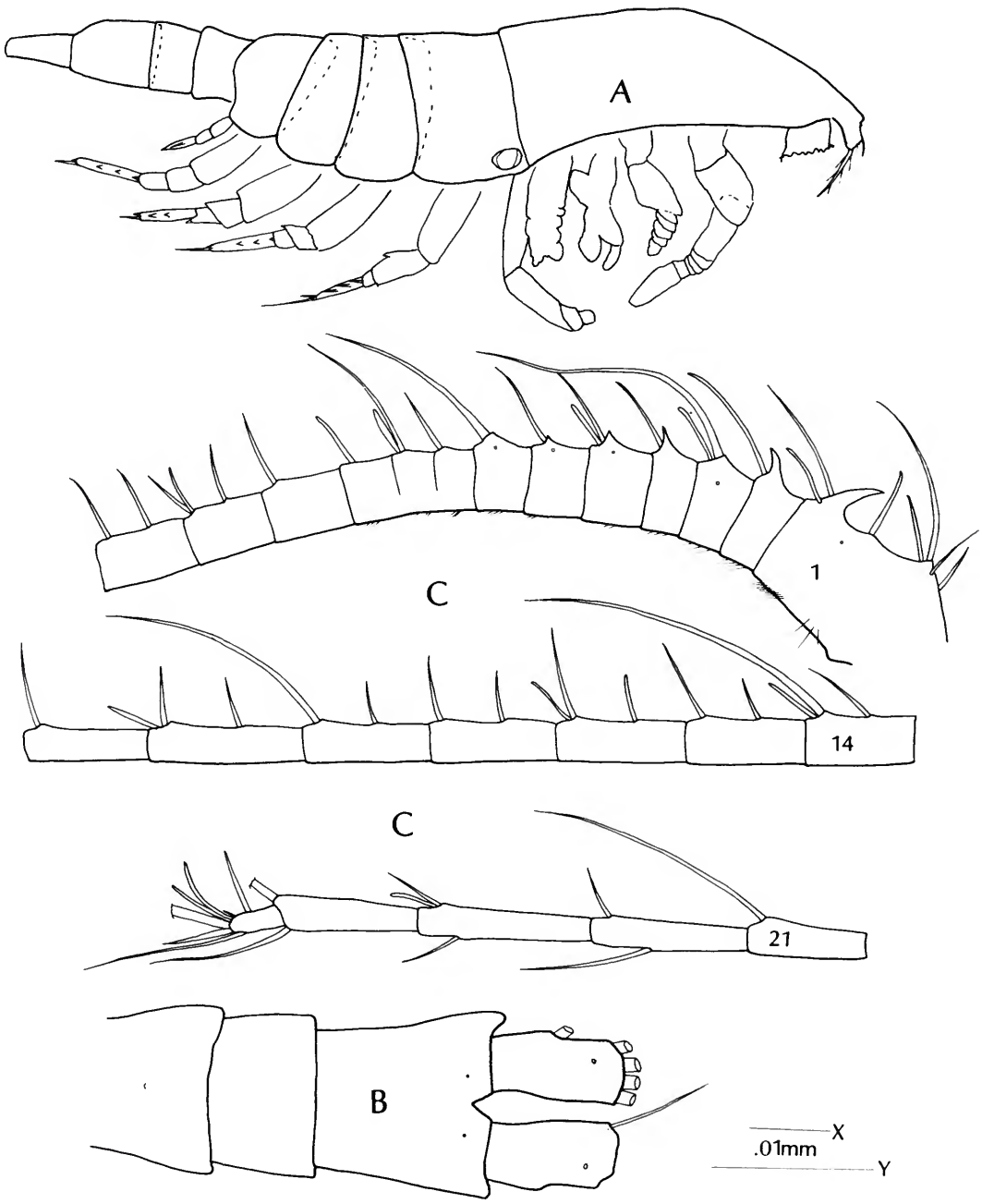

FIGURE 7.—Copepodid IV female: A, habitus, dorsal; B, Ur; C, A1 (proximal segment of series numbered) (A on scale X; B, C on scale Y).

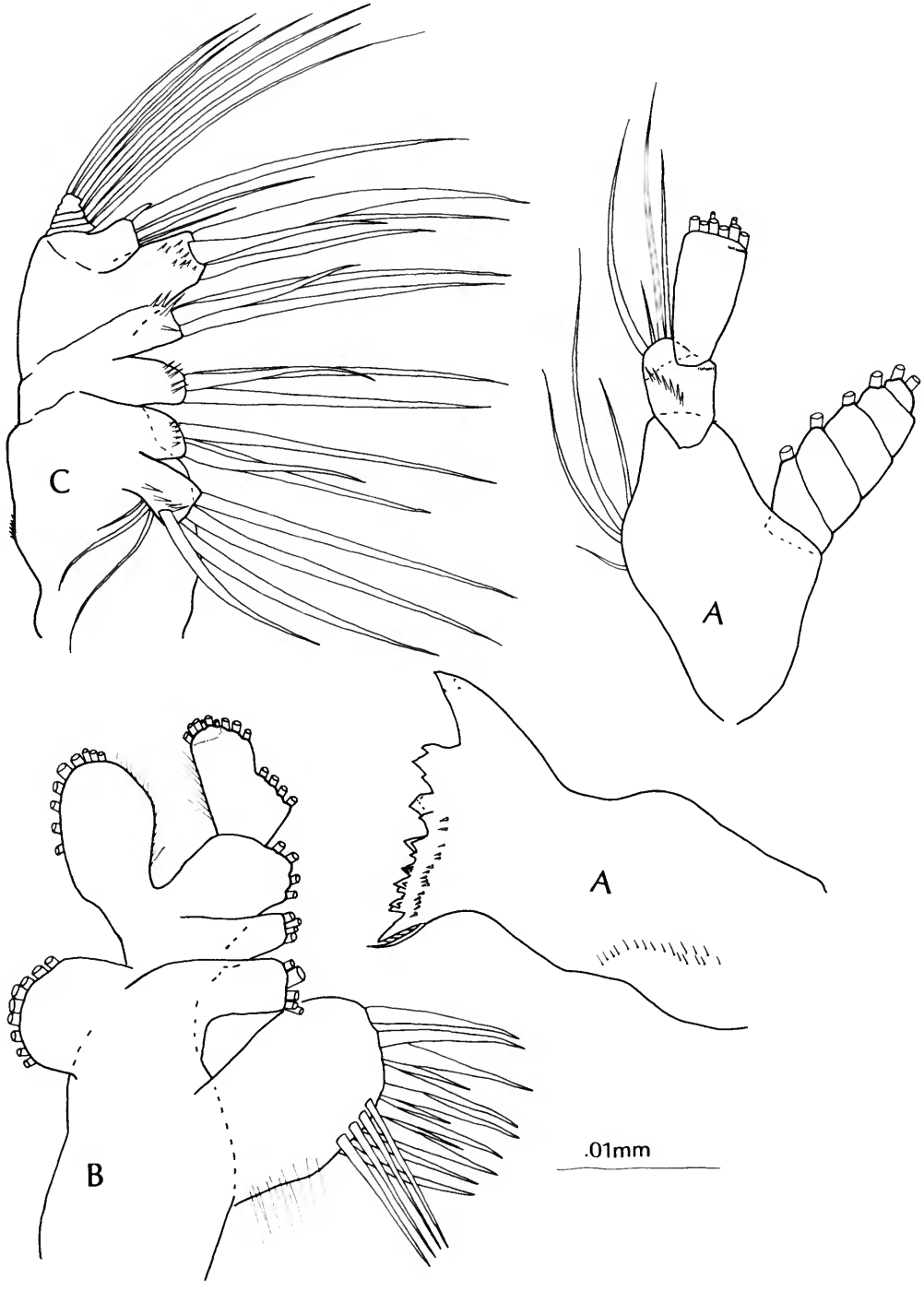

FIGURE 8.—Copepodid IV female: A, Mn; B, MxI; C, MxII.

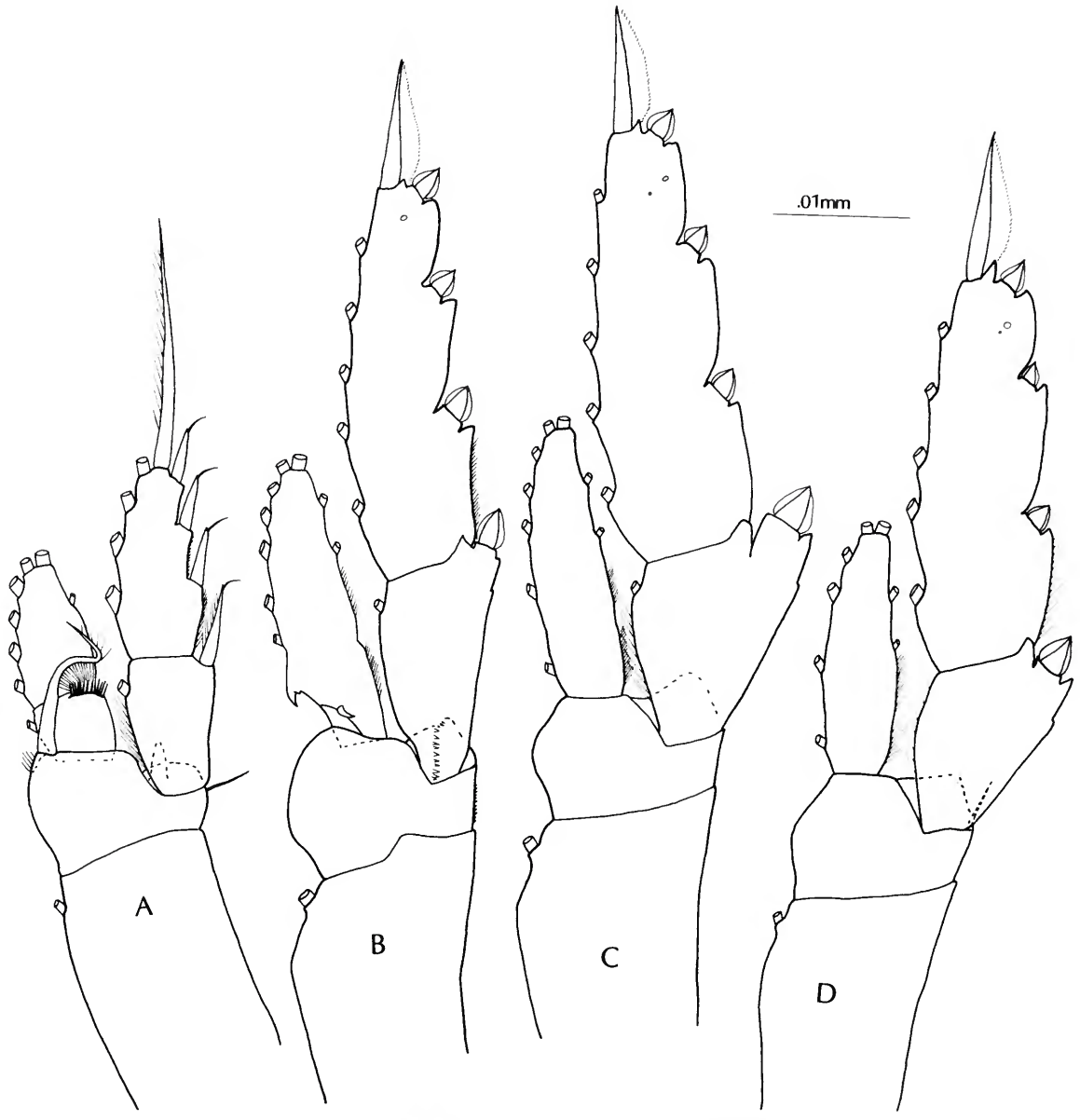

FIGURE 9.—Copepodid IV female: A, P1; B, P2; C, P3; D, P4.

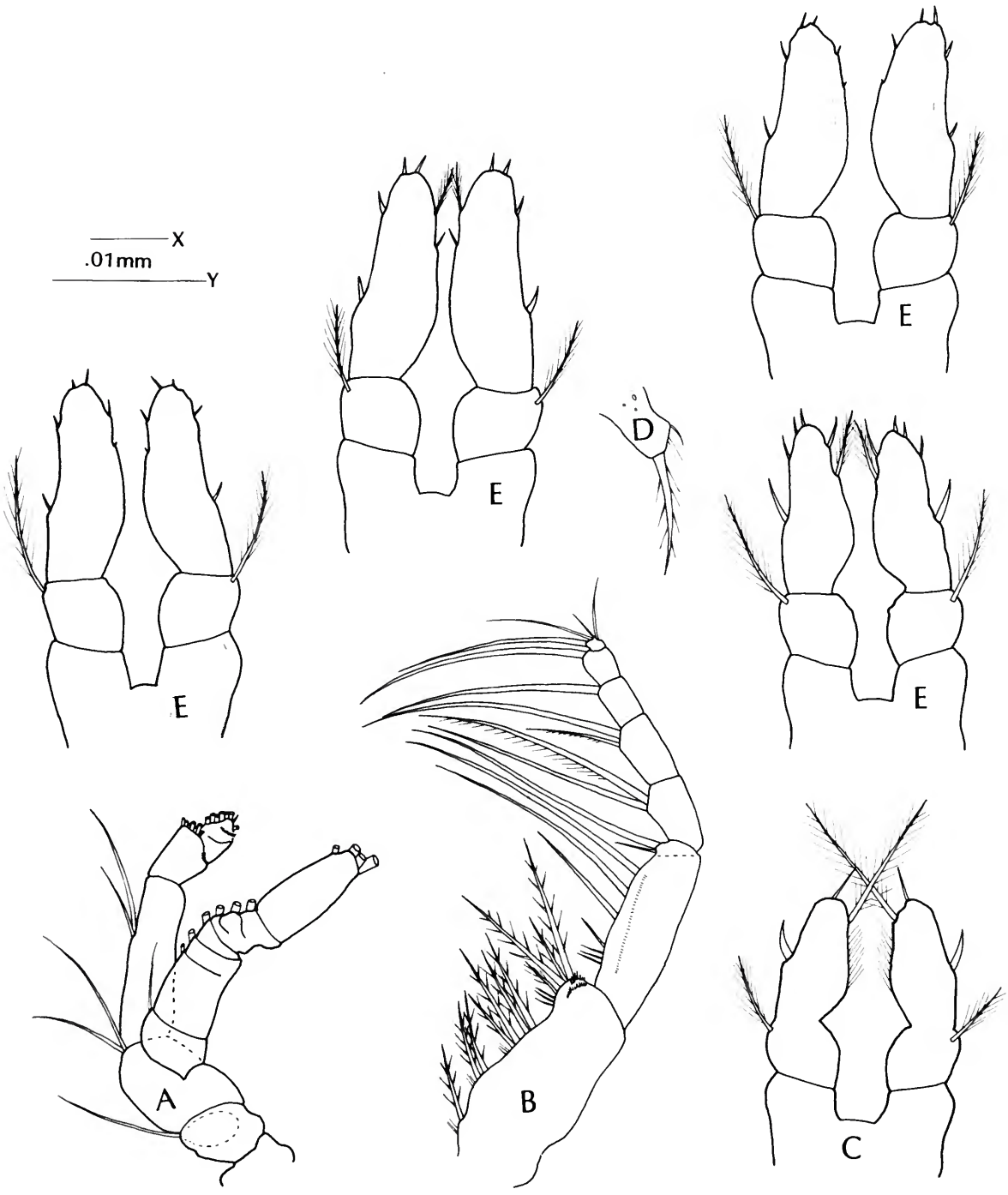

FIGURE 10.—Copepodid IV female: A, AII; B, Mxp; C, P5; D, rostrum. Male: E, intraspecific variation in P5 from 4 specimens. (A, B on scale X; C–E on scale Y.)

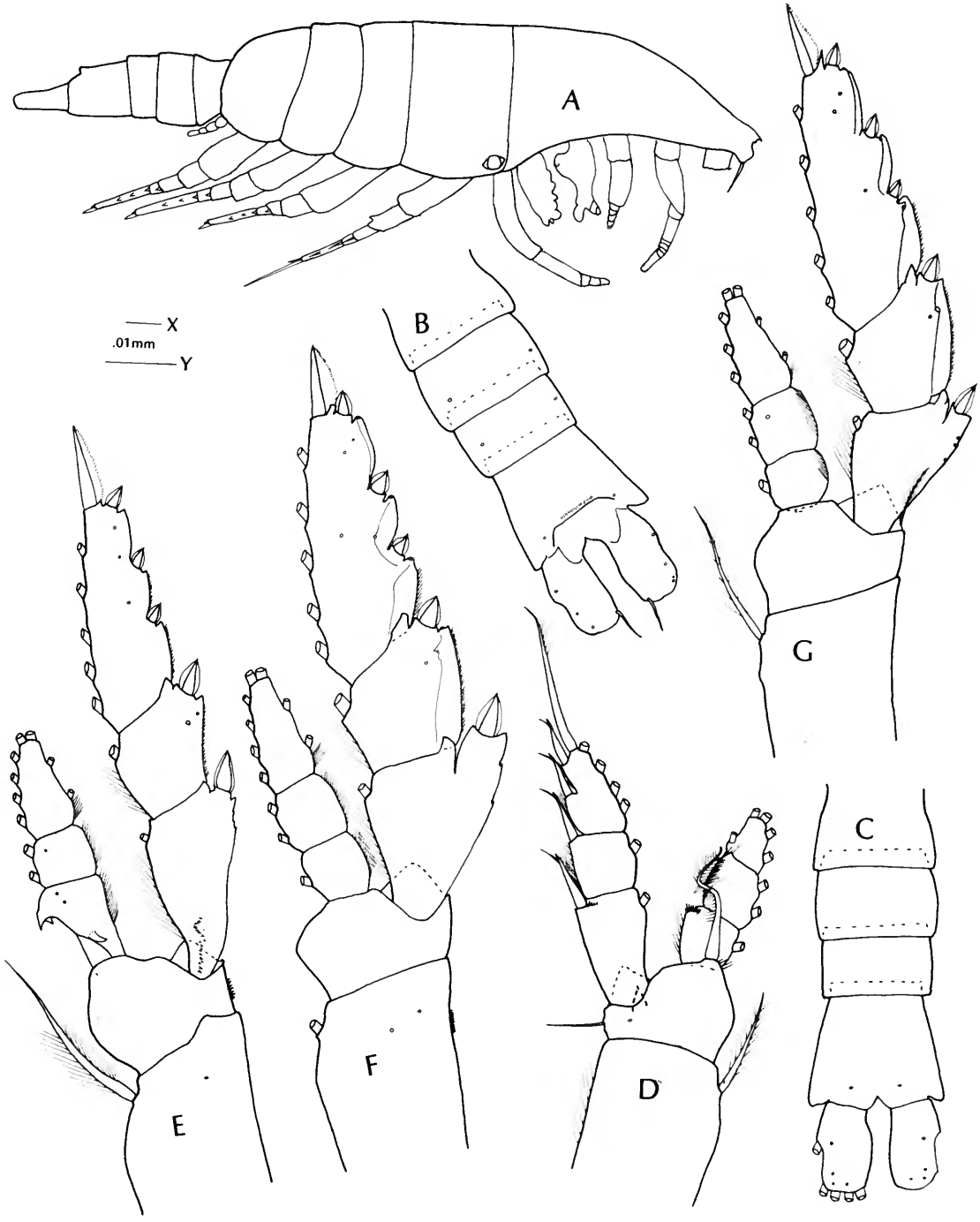

FIGURE 11.—Copepodid V female: A, habitus, lateral; B, Ur, dorsal; C, Ur, ventral; D, P1; E, P2; F, P3; G, P4 (A on scale X; B–G on scale Y).

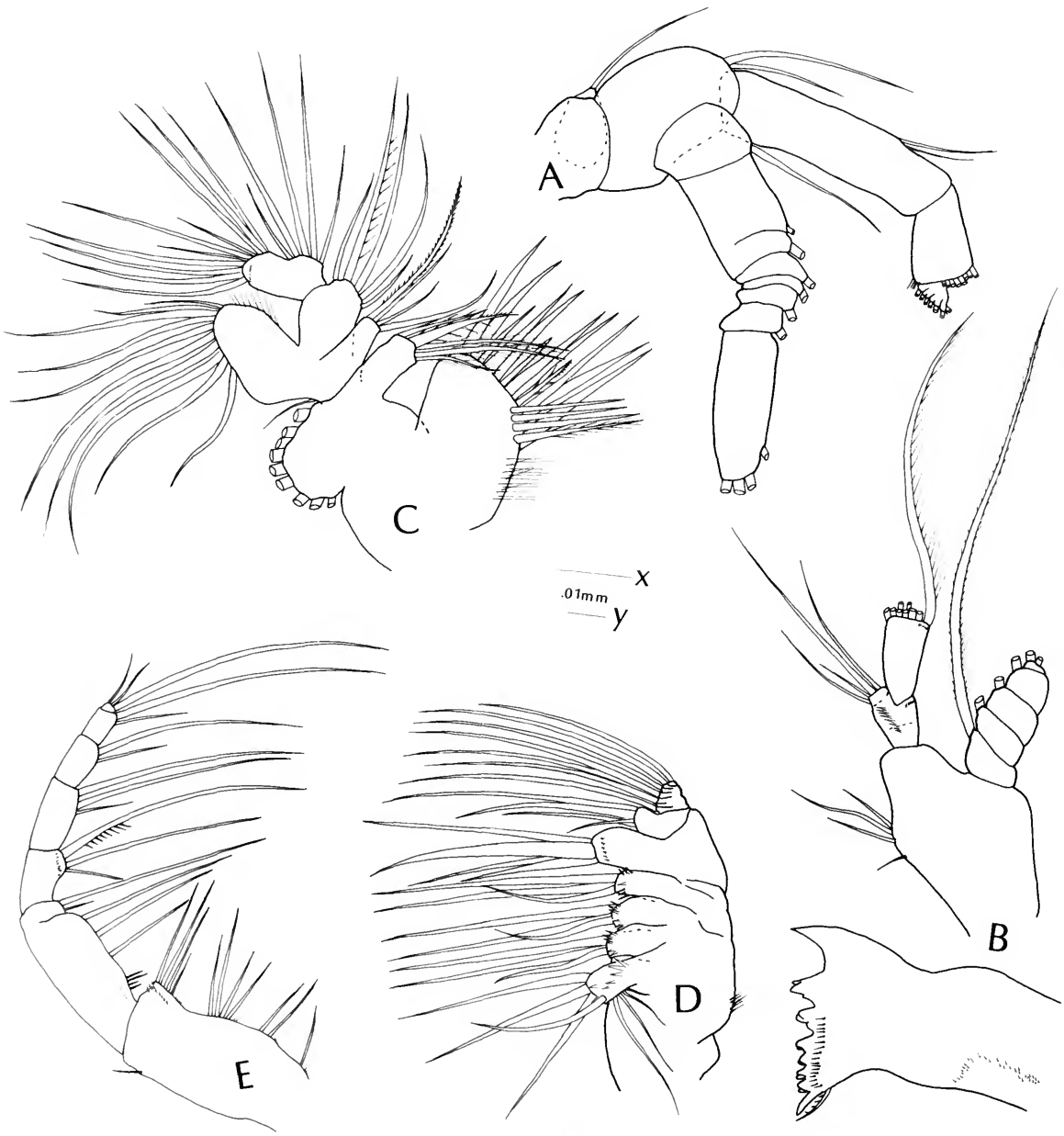

FIGURE 12.—Copepodid V female: A, AII; B, Mn; C, MxI; D, MxII; E, Mxp (A–D on scale X; E on scale Y).

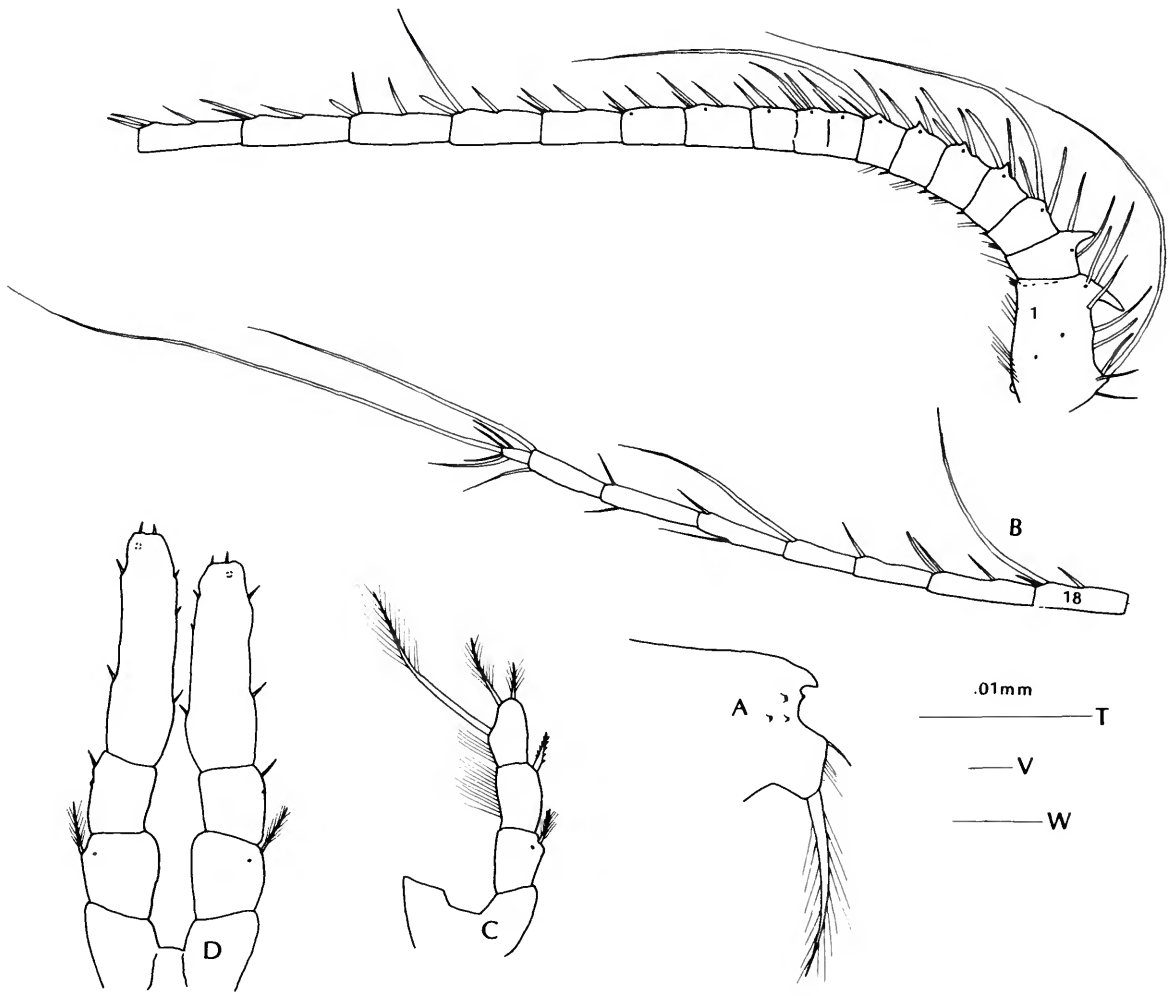

FIGURE 13.—Copepodid V female: A, rostrum; B, AI (proximal segment of series numbered); C, P5. Male: D, P5. (A on scale T; B on scale V; C, D on scale W.)

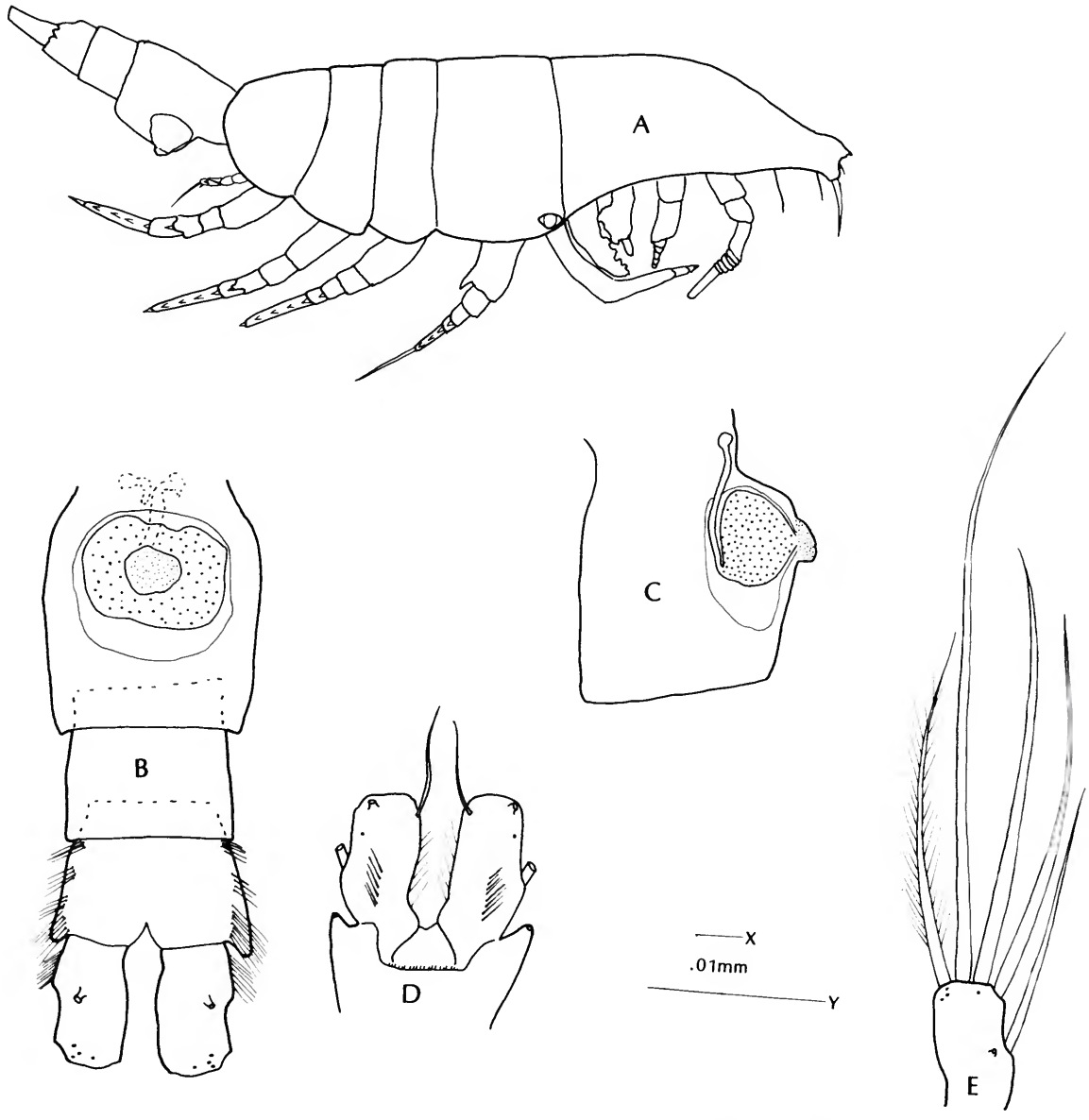

FIGURE 14.—Copepodid VI female: A, habitus, lateral; B, Ur, ventral; C, genital segment, lateral; D, CR, dorsal; E, CR, ventral (A on scale X; B–E on scale Y).

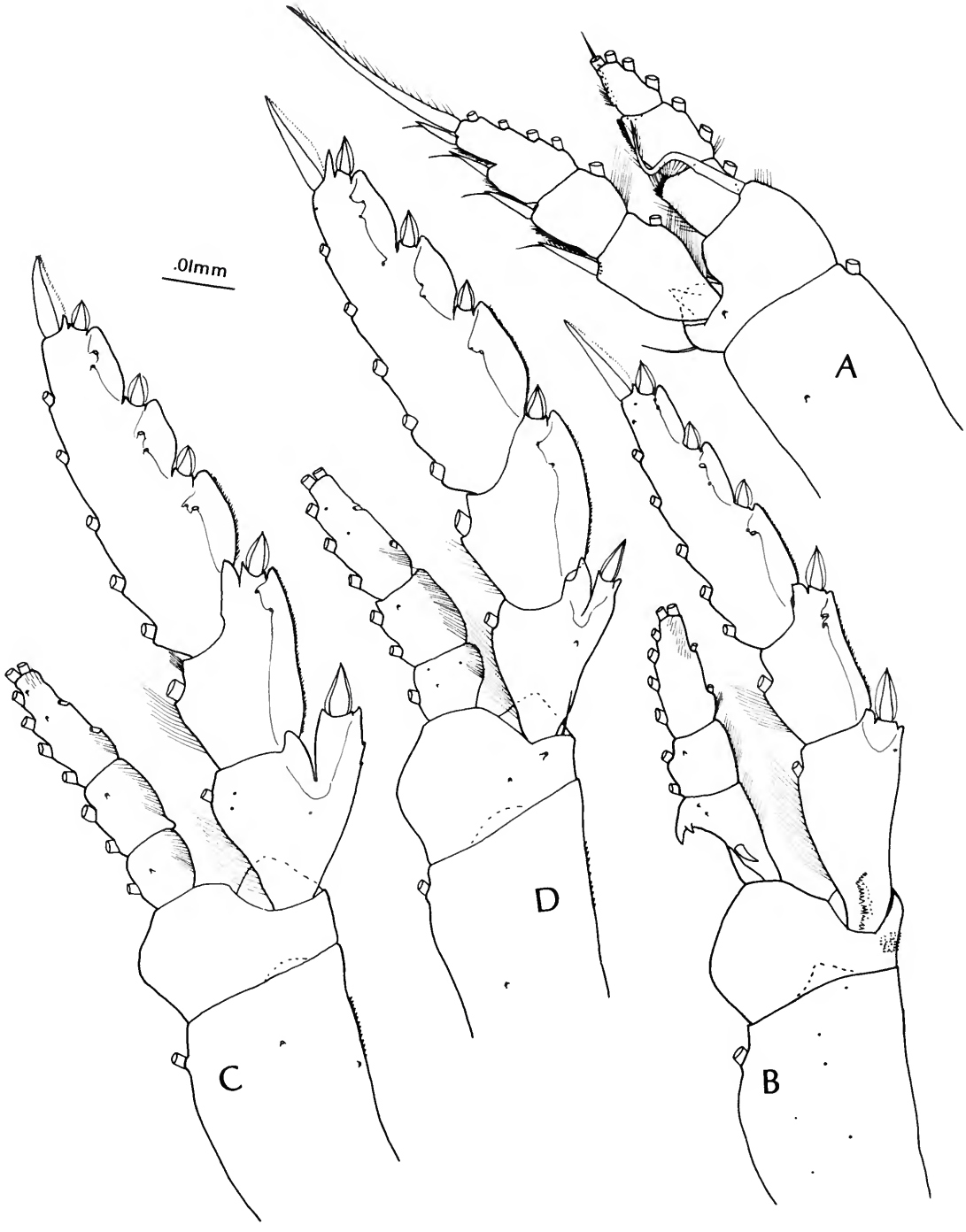

FIGURE 15.—Copepodid VI female: A, P1; B, P2; C, P3; D, P4.

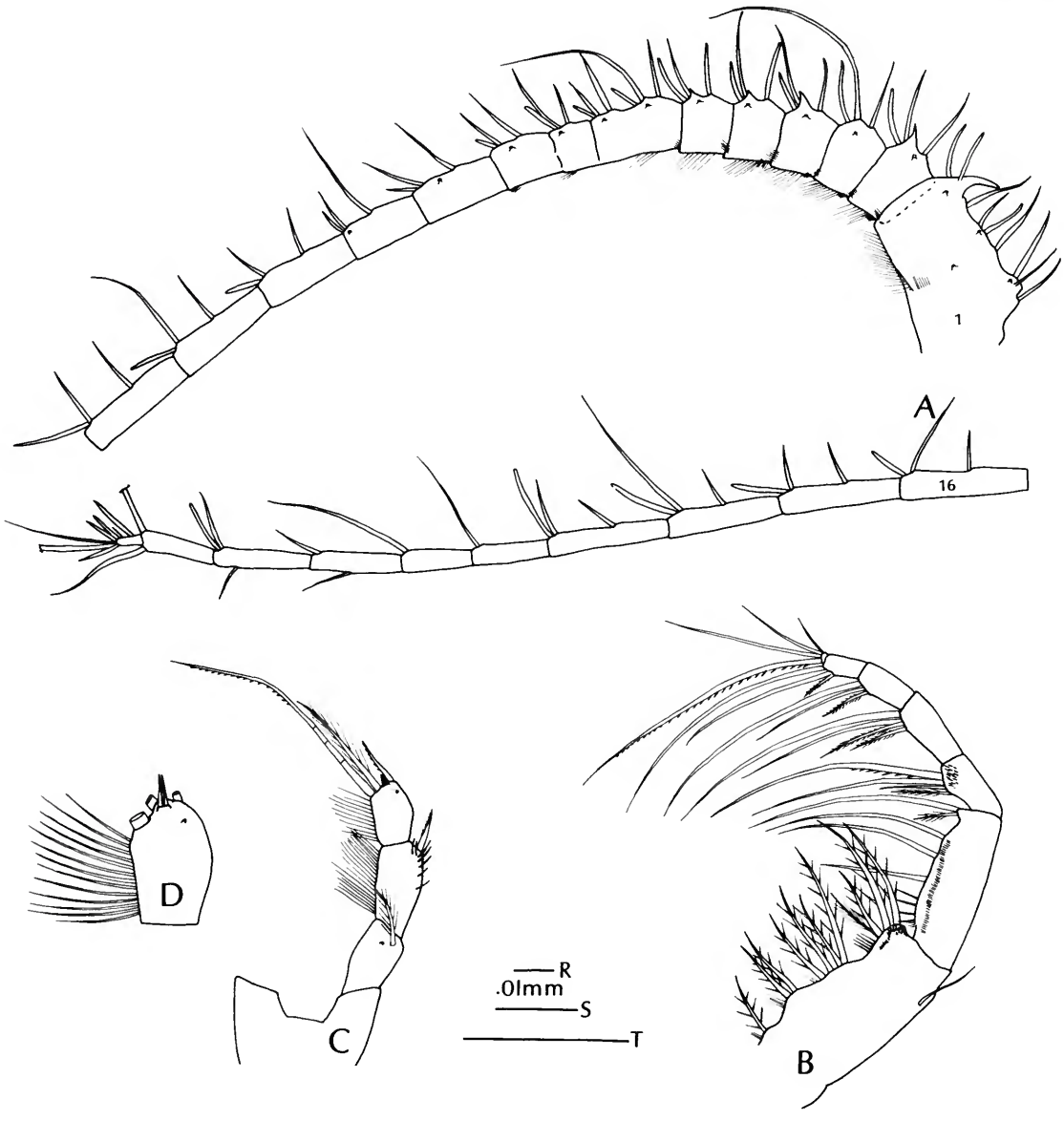

FIGURE 16.—Copepodid VI female: A, AI (proximal segment of series numbered); B, Mxp; C, P5; D, P5, terminal segment (A, B on scale R; C on scale S; D on scale T).

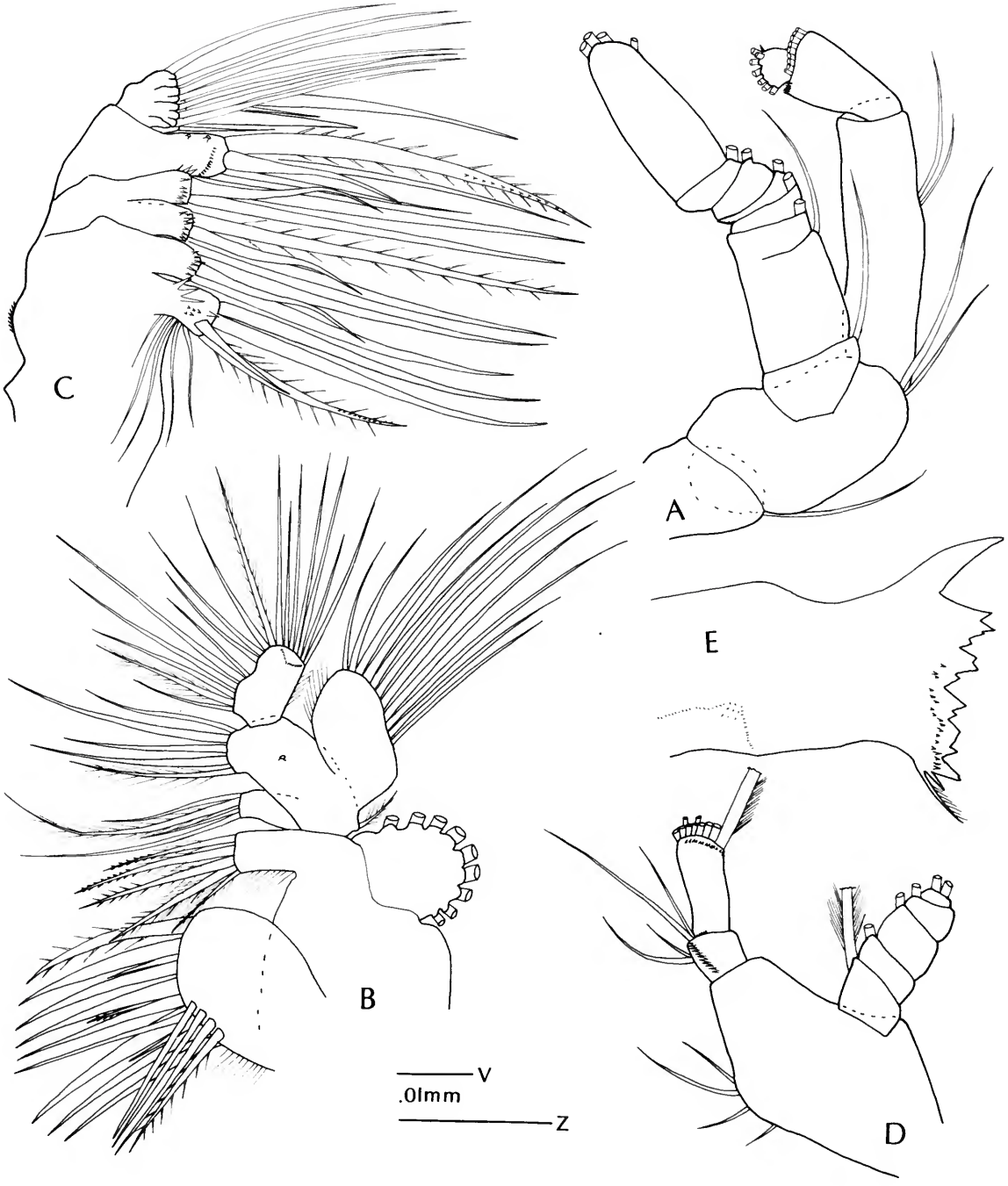

FIGURE 17.—Copepodid VI female: A, AII; B, MxI; C, MxII; D, Mn (Bspd2, Re, Ri); E, Mn (gnathobase) (A–C on scale V; D, E on scale Z).

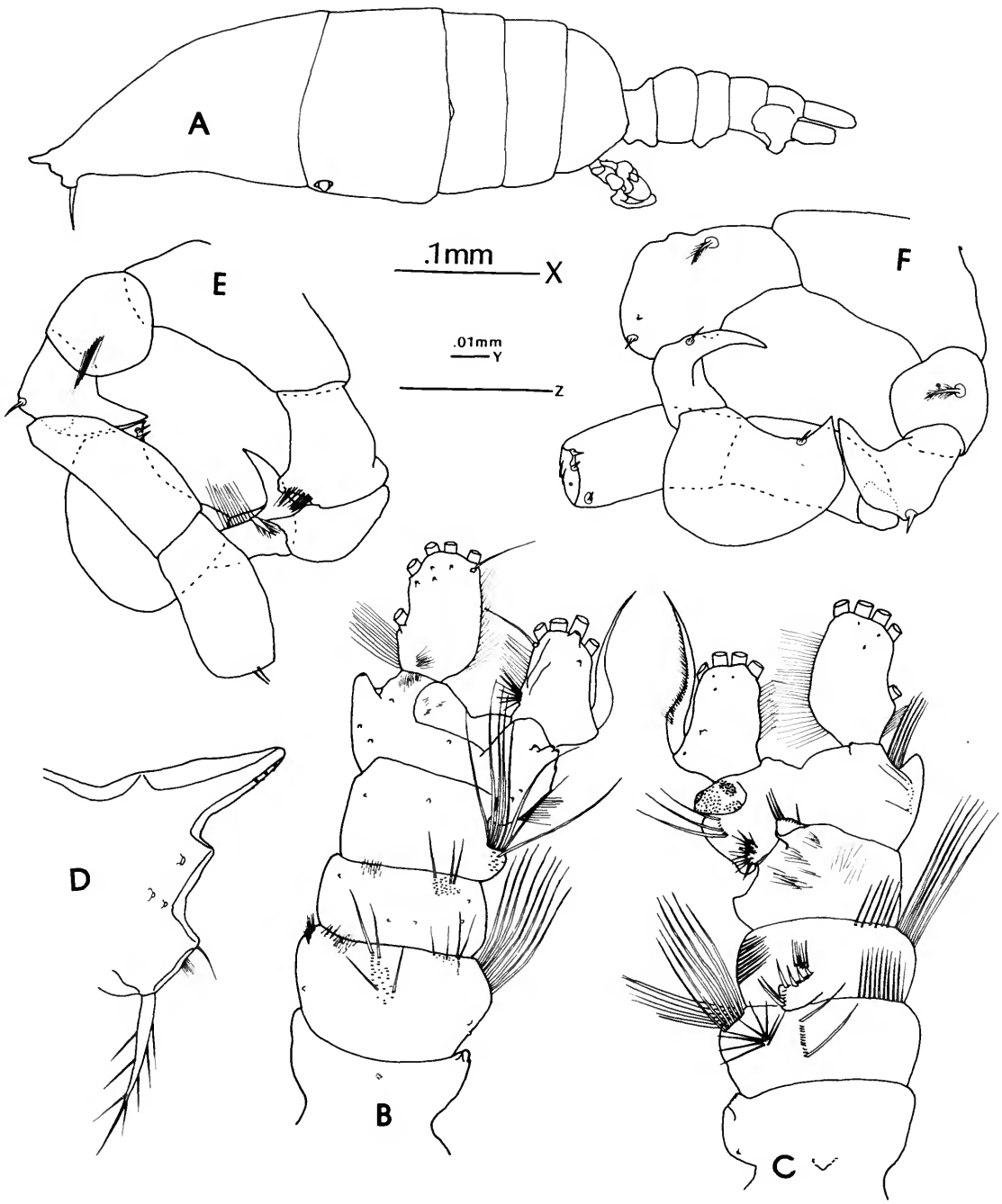

FIGURE 18.—Copepodid VI male: A, habitus, lateral; B, Ur, dorsal; C, Ur, ventral; D, rostrum; E, P5, anterior; F, P5, posterior (A on scale X; B, C on scale Y; D–F on scale Z).

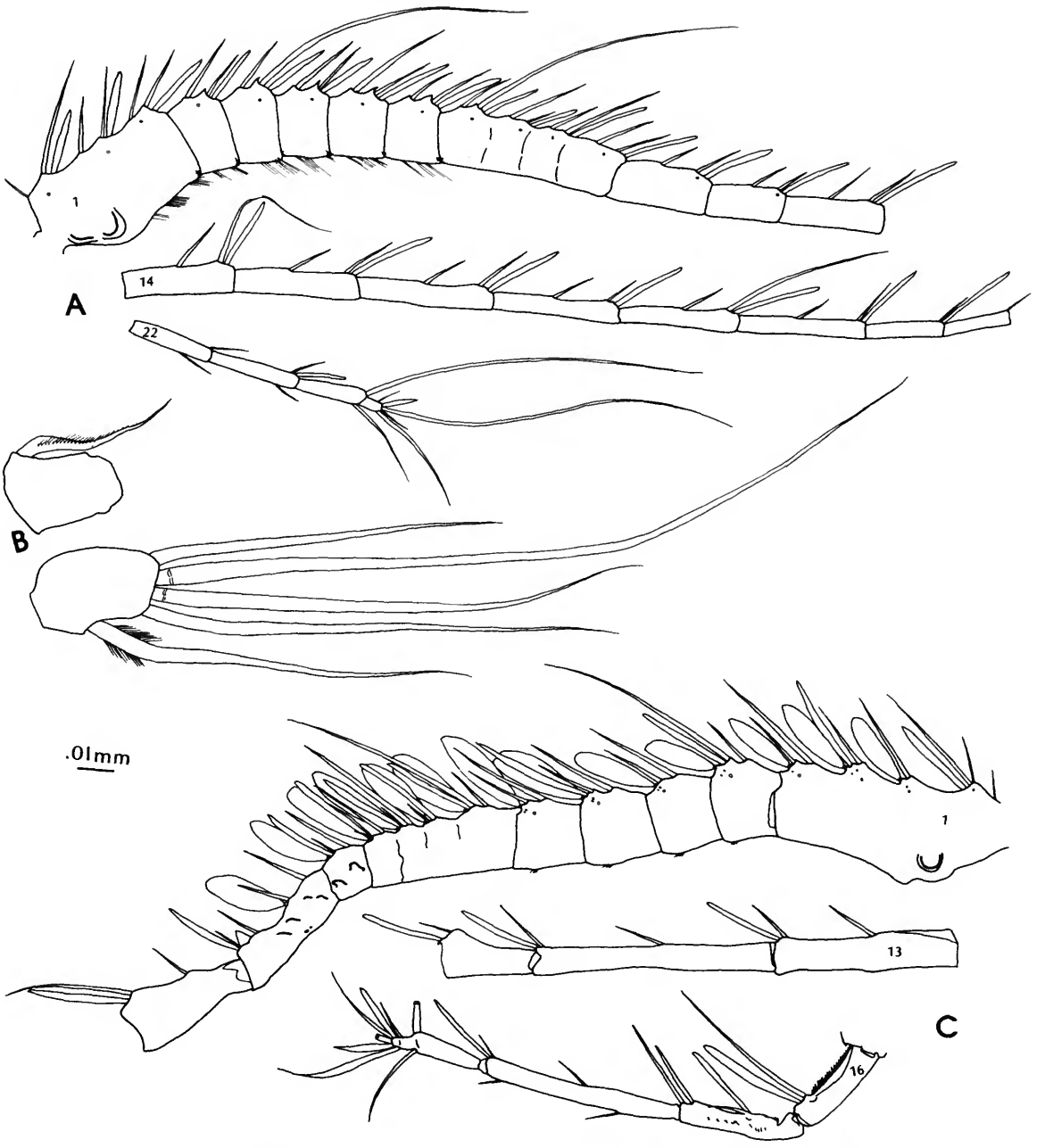

FIGURE 19.—Copepodid VI male: A, left AI (proximal segment of series numbered); B, CR, ventral; C, right AI (proximal segment of series numbered).

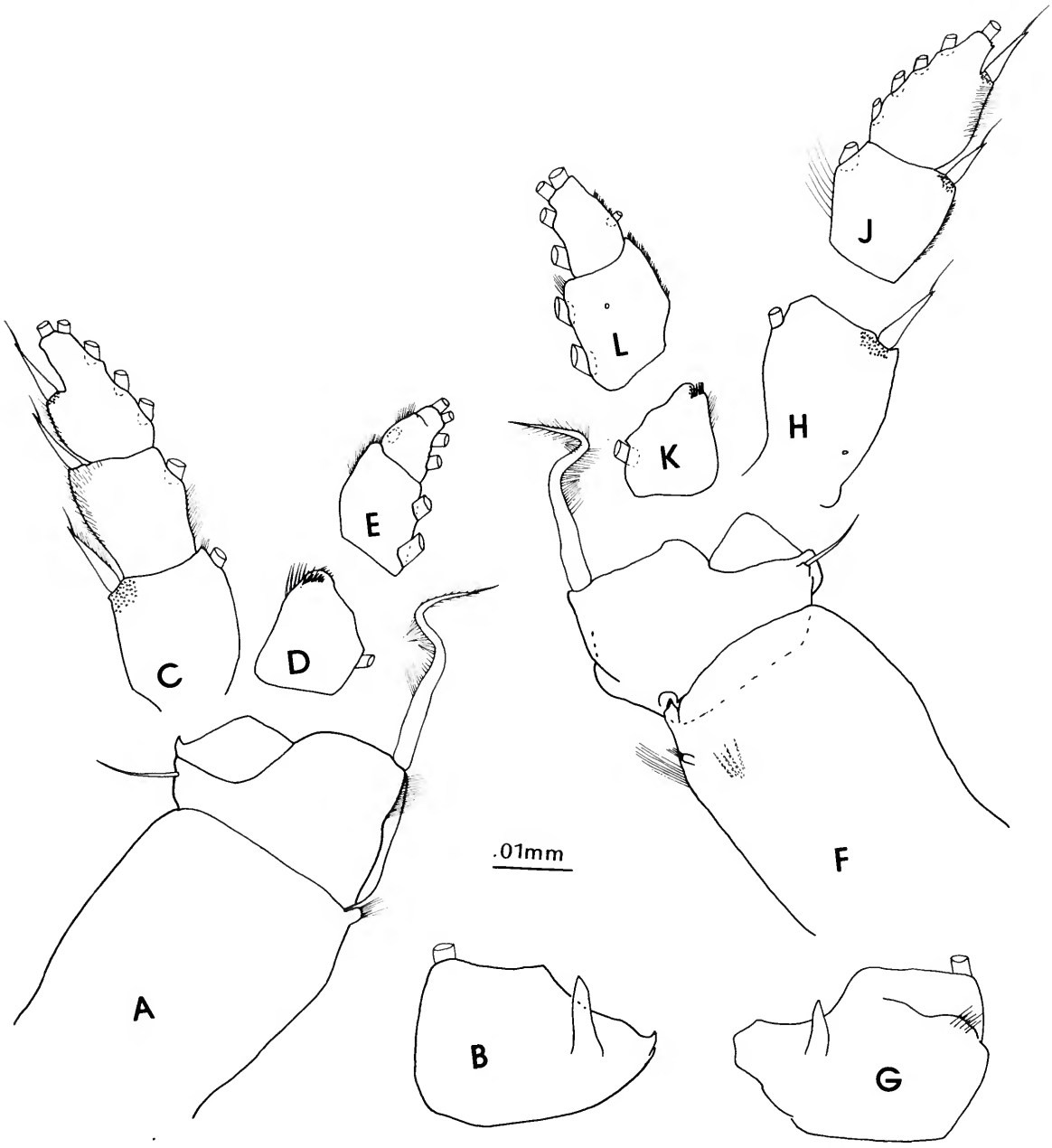

FIGURE 20.—Copepodid VI male P1 (all views anterior except as noted): A, left Bspd1–2; B, left Bspd2, posterior; C, left Re1–3; D, left Ri1; E, left Ri2–3; F, right Bspd1–2; G, right Bspd2 posterior; H, right Re1; J, right Re2–3; K, right Ri1; L, right Ri 2–3.

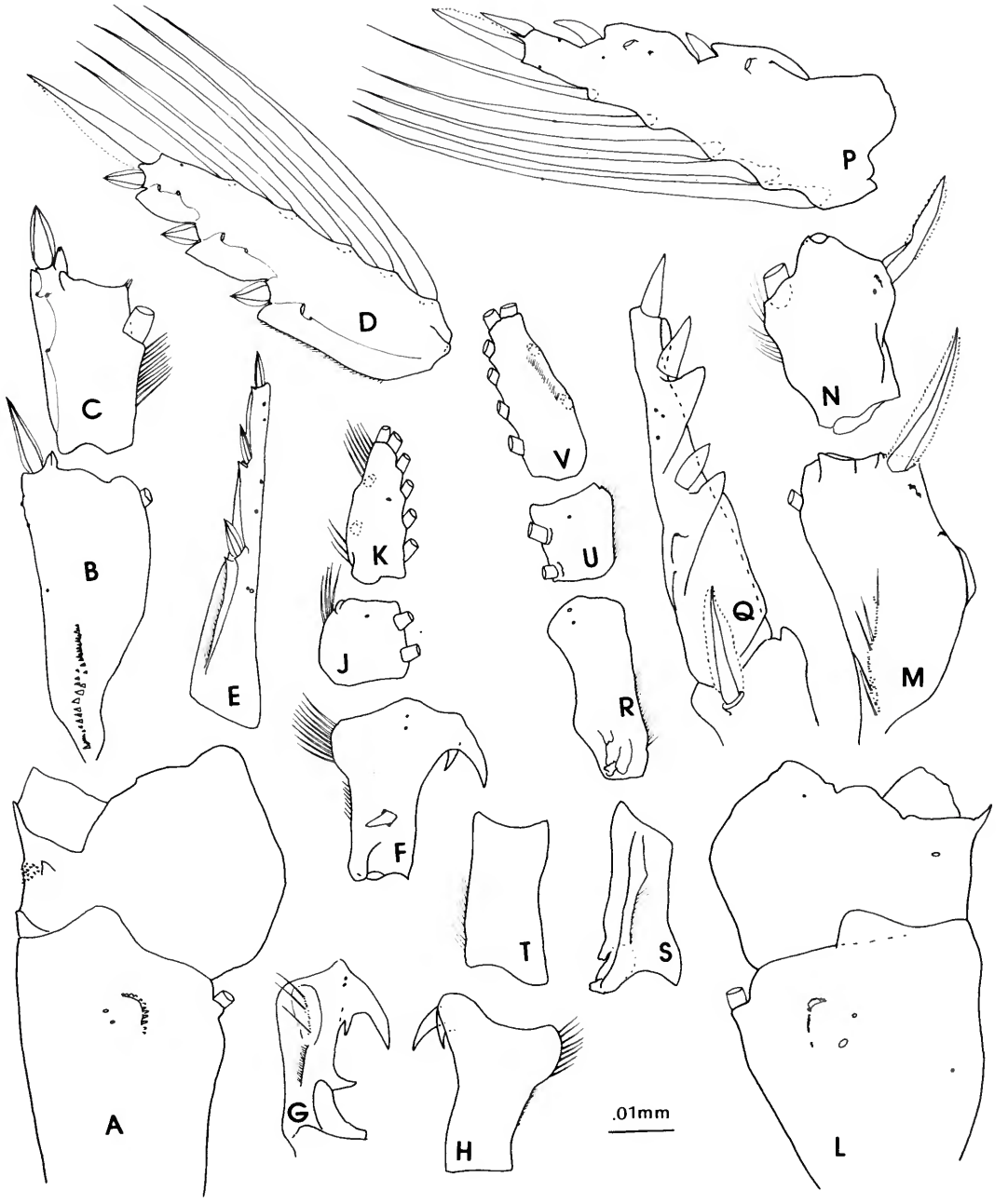

FIGURE 21.—Copepodid VI male P2 (all views anterior except as noted): A, left Bspd1–2; B, left Re1; C, left Re2; D, left Re3; E, left Re3, lateral; F, left Ri1; G, left Ri1, lateral; H, left Ri1, posterior; J, left Ri2; K, left Ri3; L, right Bspd1–2; M, right Re1; N, right Re2; P, right Re3; Q, right Re3, lateral; R, right Ri1; S, right Ri1, lateral; T, right Ri1, posterior; U, right Ri2; V, right Ri3.

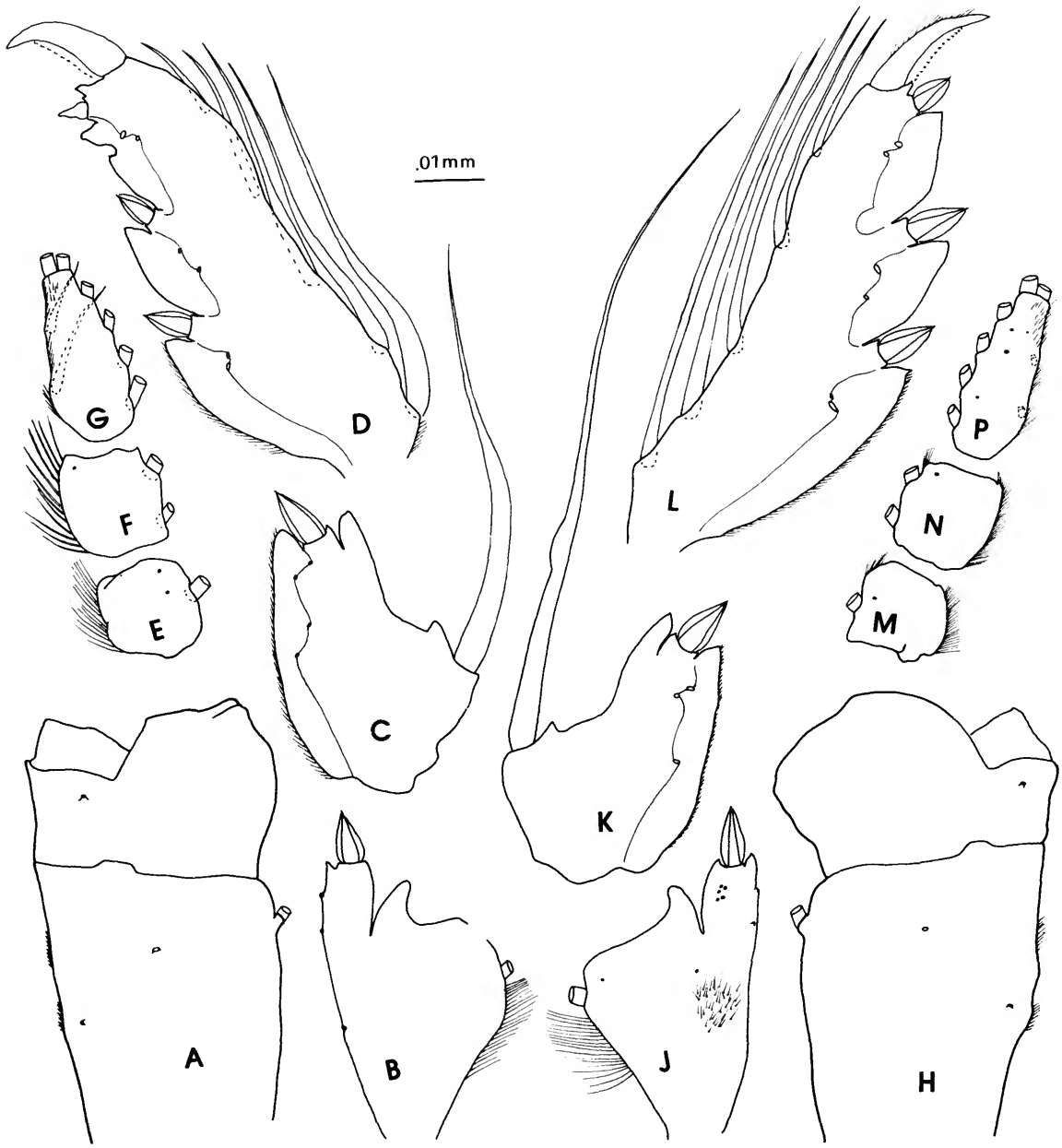

FIGURE 22.—Copepodid VI male P3: A, left Bspd1–2; B, left Re1; C, left Re2; D, left Re3; E, left Ri1; F, left Ri2; G, left Ri3; H, right Bspd1–2; J, right Re1; K, right Re2; L, right Re3; M, right Ri1; N, right Ri2; P, right Ri3.

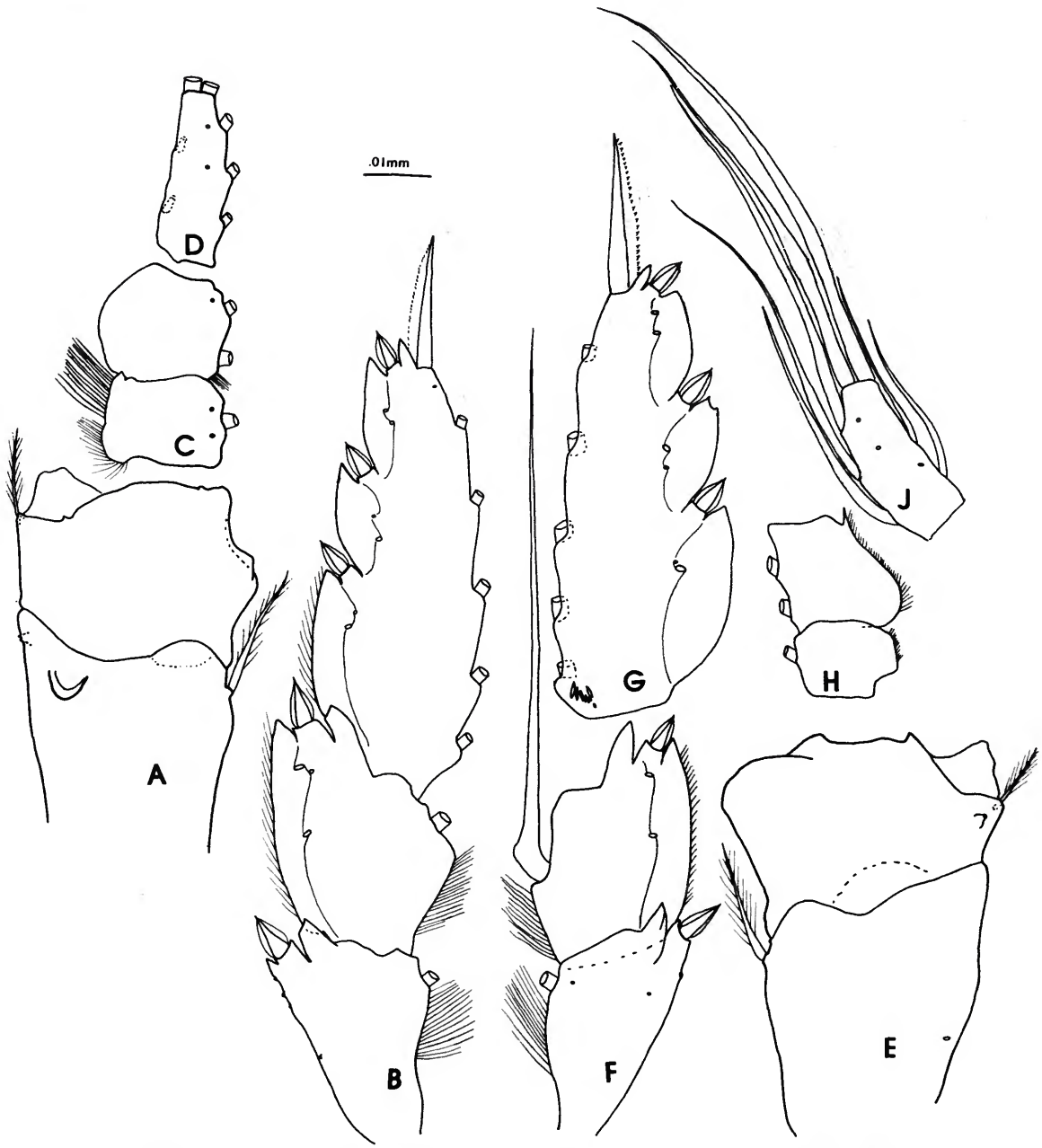

FIGURE 23.—Copepodid VI, male P4: A, left Bspd1–2; B, left Re; C, left Ri1–2; D, left Ri3; E, right Bspd1–2; F, right Re1–2; G, right Re3; H, right Ri1–2; J, right Ri3.

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