Description of the life-history stages of *Amphiascus undosus* Lang (Copepoda, Harpacticoida)

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The six naupliar and six copepodite stages of the harpacticoid copepod *Amphiascus undosus* Lang are described in detail. Thoracic leg segmentation and armature are presented in tabular form for the copepodite stages. The species becomes sexually dimorphic at the fourth copepodite stage. Average egg-to-adult development time is approximately 31.5 days at 22° ± 1°C. Up to four successive pairs of egg sacs from a single female are produced in the laboratory, yielding a maximum of 76 progeny. Some discrepancies exist between the original description of the California type specimens and the present British Columbia material, particularly in the adult male maxillule, maxilliped, and first, fifth, and sixth legs, and the caudal setae of the adult female. A brief comparison is made with the developmental similarities and differences of six other diosaccid harpacticoid copepods.

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On trouvera ici la description détaillée des six stades nauplies et des six stades copépodites du copépode harpacticoïde *Amphiascus undosus* Lang. La segmentation et l'armature des pattes thoraciques chez les copépodites sont présentées sous forme de tableau. L'espèce acquiert son dimorphisme sexuel au quatrième stade copépodite. La durée moyenne du développement de l'oeuf à l'adulte est d'environ 31,5 jours à 22 ± 1°C. Une seule femelle peut produire jusqu'à quatre paires successives d'ovisacs en laboratoire, donnant lieu à une progéniture de 76 rejetons au maximum. Il existe des différences entre la description originale des spécimens types de Californie et le matériel de Colombie-Britannique utilisé ici, particulièrement en ce qui a trait aux maxillules, aux maxillipèdes, aux pattes 1, 5 et 6 du mâle adulte et aux soies caudales de la femelle adulte. Les ressemblances et différences entre le développement de cette espèce et celui de six espèces de copépodes harpacticoïdes diosaccidés sont exposées brièvement.

[Traduit par la rédaction]

Introduction

Amphiascus undosus is a sediment-dwelling benthic harpacticoid copepod belonging to the family Diosaccidae. The species was described by Lang (1965) from collections from Tomales Bay, California. It was distinguished from other members of the genus, and from the *Amphiascus pacificus* group, because of the unique shape of the adult female proximal inner terminal seta on the caudal ramus, the fifth leg, and the antennule. Specimens resembling *Amphiascus undosus* were collected at Roberts Bank near Vancouver, British Columbia, and formed the parental stock for this study. This paper is the first description of all of the life-history stages of the species.

Knatz (1986) reports that *A. undosus* was the most abundant of 38 harpacticoid species in the Los Angeles – Long Beach Harbor area in southern California during a 1-year period. Although harpacticoids are generally classified as *r*-strategists (with respect to their life-history attributes) (Gee and Warwick 1984) on the *r–K* continuum (Pianka 1970), *A. undosus* remained reproductively active throughout all seasons, showing peak densities of 160 individuals/10 cm^2 during September and 30 individuals/10 cm^2 in February. Knatz (1986) surmised that *A. undosus* may have achieved perennial predominance over the other recorded harpacticoids by capitalizing on a nonlimited food supply in the experimental area.

Preliminary studies (McMillan 1988)[1] also suggest that *A. undosus* is tolerant to varying environmental conditions. The species withstood laboratory salinities between 6.0 and 59.7 ppt and temperatures between 1 and 37°C, indicating the ability to survive in intertidal and shallow subtidal regions.

Materials and methods

Specimens of *Amphiascus undosus* were obtained from intertidal sediments (particle size 50–1000 μm) at Roberts Bank (48°59'N, 123°05'W) near Vancouver, British Columbia. In the laboratory, they were maintained at 35 ppt salinity and pH 8.0 in 1000-mL Pyrex Erlenmeyer flasks and the salt solution (SOW) from an artificial seawater medium (AQUIL; Morel *et al.* 1979). The salt solution was passed through a cation-exchange resin (Chelex-100, 100-200 mesh, Bio-Rad Laboratories) to reduce the concentration of metal contaminants from the reagent grade salts. (Chelex-100 was obtained in the Na^+ form and was converted to the ionic form and pH of the solution to be purified to avoid any alkalinity changes that might occur in the medium.) Temperature was maintained at 22 ± 1°C on a 16 h light : 8 h dark cycle.

Each of the stock cultures was fed with nonaxenic *Dunaliella tertiolecta*, washed fragments of *Ulva* sp., boiled barley cubes, and an unidentified blue–green alga. One millilitre of a dense suspension of *Dunaliella* was added for every 150 mL of SOW every 3 days, in a manner similar to that described by Battaglia (1970) and Bergmans (1979, 1984). *Ulva* sp. was first washed in tap water for 20 min to reduce the number of epiphytes, then cut into 2-cm squares (cf. Battaglia 1970). Two squares were used for every 150 mL of SOW and were replaced every 1–2 months. Barley grains were boiled whole in glass-distilled water for 20 min, the chaff was removed, and the protein-rich aleurone layer, pericarp, and endosperm were dissected, providing fragments of about 1 mm^3 (cf. wheat grains used by Battaglia 1970 and Brand 1985). Every 4 weeks the equivalent of one-half of one barley grain was added for every 150 mL of SOW. Blue–green algae occurred in the original collection and required no maintenance.

Organisms used for the life-history study were isolated in 3 mL of SOW in 5-mL slide wells (Nunclon™) and maintained under stock culture conditions. Water in the wells was changed every 24 h, at which

[1]G. J. McMillan. 1988. The life history stages of *Amphiascus undosus* Lang (Copepoda, Harpacticoida), with a brief investigation of salinity and temperature tolerance and food preference B.Sc. thesis, University of British Columbia, Vancouver.

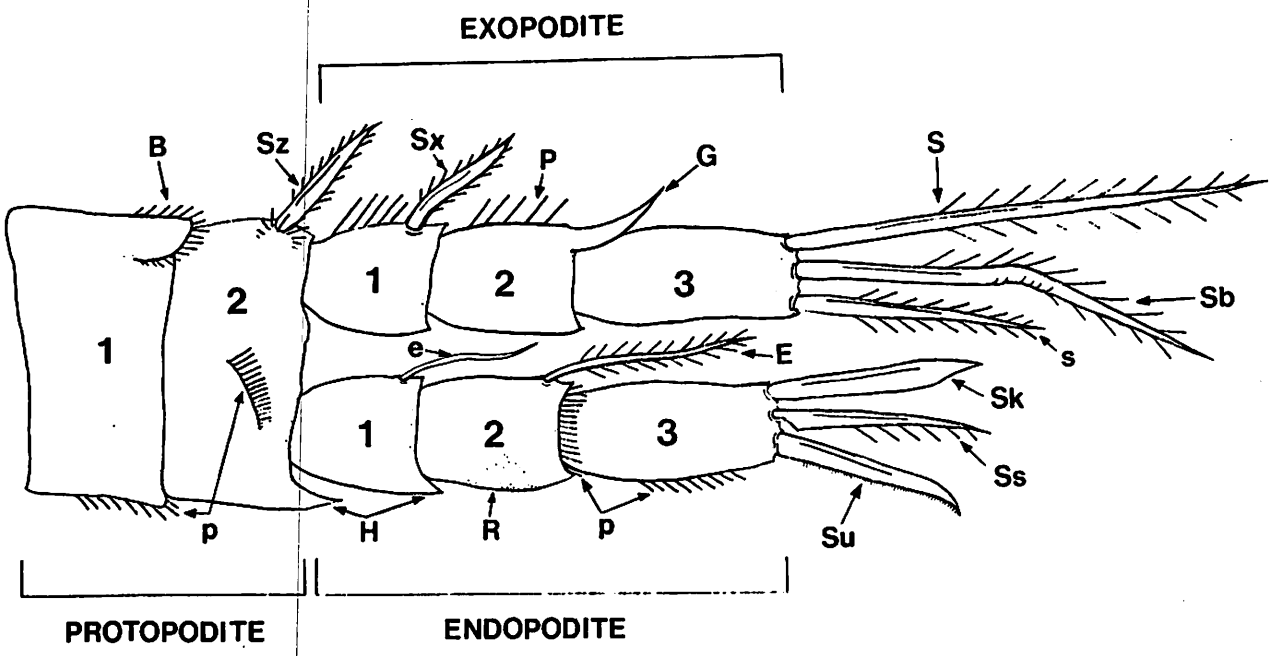


FIG. 1. Hypothetical thoracic leg showing various armature elements. B, plumose papilla; E, plumose setule; *e*, naked setule; G, spine-like extension of segment; H, ceratoid projection; P, large plumosities; *p*, small plumosities; R, sclerotized area; S, large plumose seta; *s*, small plumose seta; Sb, bent plumose seta; Sk, knife-shaped plumose seta; Ss, sabre-like seta; Su, unguiform seta with bristled inner edge; Sx, spiniform plumose seta; Sz, spiniform plumose seta with bristled base.

TABLE 1. Armature of the hypothetical thoracic leg (I) shown in Fig. 1

	Protopodite		Exopodite			Endopodite		
Margin	1	2	1	2	3	1	2	3
Outer	B	Sz	P, Sx	P, G	S, Sb	*e*	E, P	Ss, Sk
Inner	*p*	*p*, H			*s*	H	R, *p*	*p*, Su

NOTE: For all tables, when more than one element is indicated, they will be presented in the order in which they occur proximally to distally along the appendage. "Inner" or "outer" margin implies the entire medial or lateral half of the segment. If a structure extends into the opposite side of a segment, it will be included on both margins. A dash indicates that the segment is absent, and a space denotes an unornamented surface.

time exuvia were removed and new food was added. The food was the same mixture used for the stock cultures except that *Ulva* was not used. (Naupliar stages attach to the *Ulva*, making observations difficult.)

Specimens used for illustrations and dissections were killed by being placed in distilled water for 3 min (which prevented antennule retraction). Nauplii were used unstained and copepodites were stained in SOW-based Lignin Pink for 4 min. Glycerine, a 2.5 cm diameter spacer, and a 2.5-cm^2 cover slip were used to mount whole specimens. However, it was necessary to carefully penetrate the specimens with a Minuten-Nadeln to prevent the glycerine from changing the body dimensions. Mounts of appendages were made with glycerine and a 1-cm^2 cover slip. Drawings were made with the assistance of a camera lucida (Wild) and a phase-contrast compound microscope (Wild M20). A minimum of five specimens at each life-history stage were dissected to determine variability. Body dimensions of all developmental stages were obtained with an ocular micrometer, using living specimens (n = 10). Measurements were made along the greatest dimension: across the lateral surface of the nauplii and from the posterior edge of the rostrum to the posterior edge of the caudal rami of the copepodites.

The armature and segmentation of the copepodite thoracic legs are presented in tabular form. Figure 1 and Table 1 provide an explanation of the various armature elements. The tabular method of description was chosen because it provides a more comprehensive representation than either verbal or numerical expression. Where appropriate, a verbal description is also given. Appendages and processes other than the thoracic legs are illustrated and described.

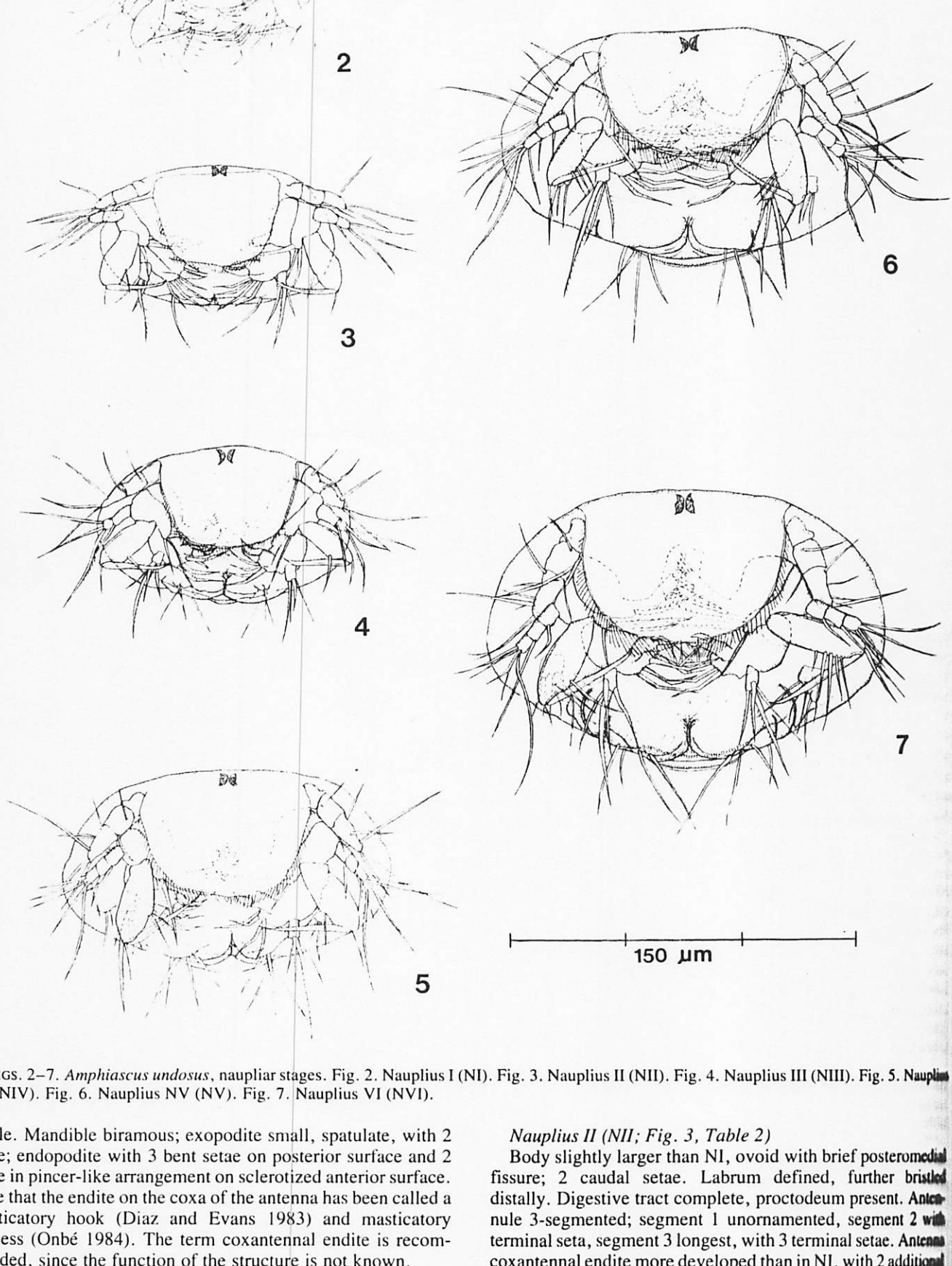
Description of *Amphiascus undosus*

Naupliar stages (Figs. 2–7)

Body wider than long, dorsoventrally compressed; unpigmented except for two red, crescent-shaped ocelli on anterodorsal surface. Naupliar stages thigmotactic, with crablike sideways crawl. Mean developmental time (nauplius I to copepodite I) 11.5 days at 22° ± 1°C.

Nauplius I (NI; Fig. 2, Table 2)

Body obovoid, width approximately twice the length, without apparent body segmentation; 2 caudal setae. Labrum semicircular, incompletely formed; posterior crest with 2 notches and small bristles. Digestive tract incomplete, stomadeum present but proctodeum absent. Antennule 1-segmented, with 3 naked styliform terminal setae. Antenna biramous, sclerotized, coxa with single rudimentary sublabral endite (coxantennal endite) bearing 4 terminal spinules. Basis with small endite bearing 2 naked terminal setae. Exopodite 1-segmented, armed with 3 terminal setae. Endopodite 2-segmented, subchelate, basal segment with subterminal setule and medial



FIGS. 2–7. *Amphiascus undosus*, naupliar stages. Fig. 2. Nauplius I (NI). Fig. 3. Nauplius II (NII). Fig. 4. Nauplius III (NIII). Fig. 5. Nauplius IV (NIV). Fig. 6. Nauplius NV (NV). Fig. 7. Nauplius VI (NVI).

setule. Mandible biramous; exopodite small, spatulate, with 2 setae; endopodite with 3 bent setae on posterior surface and 2 setae in pincer-like arrangement on sclerotized anterior surface. Note that the endite on the coxa of the antenna has been called a masticatory hook (Diaz and Evans 1983) and masticatory process (Onbé 1984). The term coxantennal endite is recommended, since the function of the structure is not known.

Nauplius II (NII; Fig. 3, Table 2)

Body slightly larger than NI, ovoid with brief posteromedial fissure; 2 caudal setae. Labrum defined, further bristled distally. Digestive tract complete, proctodeum present. Antennule 3-segmented; segment 1 unornamented, segment 2 with terminal seta, segment 3 longest, with 3 terminal setae. Antenna coxantennal endite more developed than in NI, with 2 additional

TABLE 2. Development time and greatest body measurement (width or length) for the life-history stages of *Amphiascus undosus* Lang, 1965

	Development time (h)	Width (μm)	Length (μm)
Egg (embryo)	53±12	55.9±6.1	
Nauplius I	36±11	86.6±4.0	
Nauplius II	49±12	104.3±4.9	
Nauplius III	61±12	123.7±5.1	
Nauplius IV	60±15	145.2±5.2	
Nauplius V	37±10	158.1±3.9	
Nauplius VI	48±14	169.5±4.4	
Copepodite I	68±20		223.3±7.8
Copepodite II	84±21		263.5±9.1
Copepodite III	61±15		352.0±8.7
Copepodite IV	65±21		442.0±21.8
Copepodite V	60±14		544.3±26.1
Copepodite VI	528±120*		
Male			582.2±21.9
Female			676.9±35.2

NOTE: Data are given as mean ± 1 standard deviation (n = 10). Time for development to the egg (embryo) is from ovulation to hatching at 22 ± 1°C; in all other stages it is from initiation of moulting from the previous stage to initiation of moulting to the subsequent stage.
*Moult of copepodite V to death.

small subterminal spinules; exopodite and endopodite 2-segmented. Exopodite segment 1 with single seta, segment 2 with 3 terminal setae; endopodite armature unchanged from NI; basal endite with 3rd seta, innermost seta longest. Mandible exopodite with cluster of 3 setae, longest seta plumose, others naked; endopodite with 4th bent seta in row on posterior surface.

Nauplius III (NIII; Fig. 4, Table 2)

Posteromedial body fissure deepened, flanked by conical protrusions; 6 caudal setae present. Oral furrow marked, stomadeum enlarged. Antennule with second seta on segment 2. Antenna coxantennal endite larger with 3rd subterminal spinule. Exopodite and endopodite as in NII; basal endite medial seta longer, uncinate distal region extends under labrum to oral furrow. Mandible exopodite with 4th seta in terminal cluster; endopodite as in NII except for bristled anterior surface of pincer-like setae.

Nauplius IV (NIV; Fig. 5, Table 2)

Body more arcuate, bulges caudally, length to width ratio greater than in NIII. Eight caudal setae present, caudal protrusions present in previous stages of more concentric, laminar nature. Antennule segment 3 with 2 subterminal setae. Antenna coxantennal endite with subterminal plumose seta. Exopodite indistinctly 3-segmented, segments 1 and 2 each with terminal seta, segment 3 with terminal cluster of 5 setae, medial seta plumose; endopodite segment 1 with second subterminal seta, segment 2 elongated; basal endite setation as in NIII although middle seta elongate, distally uncinate. Mandible exopodite and endopodite with only minor changes from NIII. Maxillule first visible posterolaterally to mandible; nodular, with 2 distal naked setae.

Nauplius V (NV; Fig. 6, Table 2)

Body length to width ratio greater than in NIV. Eight caudal setae as in NIV; second broadly rounded projection at penultimate posterior surface along with small groove lateral to central fissure. Labrum as in NIV although posterior bristles slightly longer. Antennule segment 3 with 3rd subterminal and 4th terminal setae. Antenna coxantennal endite with 4th spinule in subterminal row; closely situated in oral furrow; endopodite segment 1 with 3rd fine setule on medial surface. Mandible exopodite as in NIV although 3 largest setae now plumose. Maxillule Anlagen, consisting of 2 protuberances, armed with i long and 2 short setae.

Nauplius VI (NVI; Fig. 7, Table 2)

Body arcuate, proportionately longer than NV. Caudal region with 2 grooves bilaterally, denoting future segmentation; caudal protrusions very prominent, with central fissure extending anteriorly to proctodeum. Eight caudal setae present, slightly longer than in NV. Labral bristles longer than in NV. Antennule segment 3 with 4th subterminal seta. Antenna coxantennal endite enlarged, angled anteromedially, almost completely convergent upon stomadeum. Exopodite and basal endite as in NV; endopodite segment 1 with 4th and 5th subterminal setules on medial surface. Mandible elements and armature similar to condition in NV. Maxillule of trilobed subtriangular shape, with 4 naked setae. Maxilla and maxilliped absent.

Copepodite stages (Figs. 8–88, Tables 3–8)

Copepodite stages translucent, light greyish colour, with prominent rostrum and red eyespot comprising three ocelli. body shape distinct from that of the nauplius; more elongate, ovoid in cross section, tapering slightly towards posterior end. Body distinctly segmented, with identifiable prosome and urosome. Prosome consists of cephalon and thoracic-leg-bearing segments. Urosome comprises structures distal to point of articulation with prosome; may include genital complex, P_5, P_6, anal segment, and caudal rami. Maxillae, maxillipeds, and thoracic legs present. Copepodites negatively phototactic, exhibiting surfacing behaviour in darkness; forage either in available water column or on substratum.

Copepodite I (CI; Figs. 8–13, Tables 2, 3)

Prosome includes 3 thoracic-leg-bearing segments; urosome 2-segmented. Caudal rami with 2 terminal setae (usually fused anteriorly), innermost seta longest, outermost with short plumosities; 3 subterminal spiniform setae. Antennule (A_1) (Fig. 10) 5-segmented, segments 1 and 2 largest, distal section of 3 smaller segments. Setation formula of successive segments (proximal to distal): 1/5 + aesthetasc/1/3/5. Antenna (A_2) (not illustrated) similar to adult configuration. Segmentation and armature of thoracic legs I and II (P_1 and P_2) as shown in Figs. 11 and 12 and Table 3. P_3 (Fig. 13) rudimentary, single lunate plate with 1 distal naked seta, 1 lateral naked seta.

Copepodite I (CI; Figs. 8–13, Tables 2, 3)

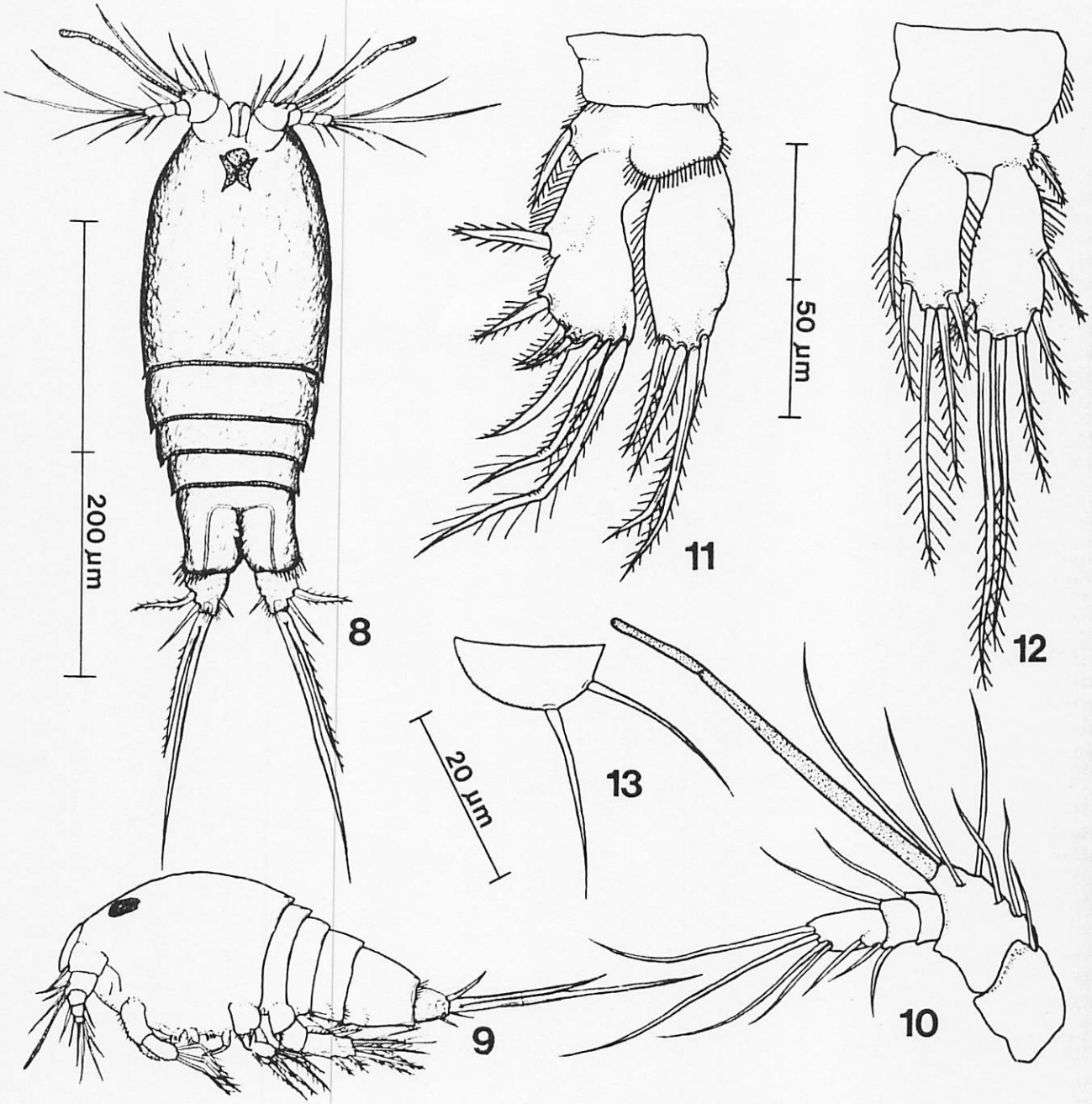
Prosome includes 3 thoracic-leg-bearing segments; urosome 2-segmented; body more fusiform than that of CI. Two caudal setae exserted separately from caudal rami. A_1 (Fig. 16) 6-segmented, segments 1 and 2 largest, distal section of 4 smaller segments. Setation of successive segments: 1/5 + aesthetasc/1/1/3/6. P_1–P_3 armature and segmentation as in Figs. 17–19 and Table 4. P_4 (Fig. 20) Anlagen, a single lunate structure with long terminal seta and lateral naked seta.

Copepodite III (CIII; Figs. 21–28, Tables 2, 5)

Prosome of 4 segments, urosome 3-segmented; untapered, extends approximately 70% the length of prosome. A_1 (Fig. 23) 6-segmented, segment 2 longer than in CII. Setation of successive segments: 1/7 + aesthetasc/1/2/2/6. P_1–P_4 armature and segmentation as in Figs. 24–27 and Table 5. P_5 (Fig. 28) Anlagen, semicircular plate with 2 slender naked setae, lateral seta longer.

Copepodite IV (CIV; Figs. 29–39, Tables 2, 6)

Prosome of 4 segments, urosome 4-segmented, longer than prosome. Sexes distinguishable by structure and setation of P_5

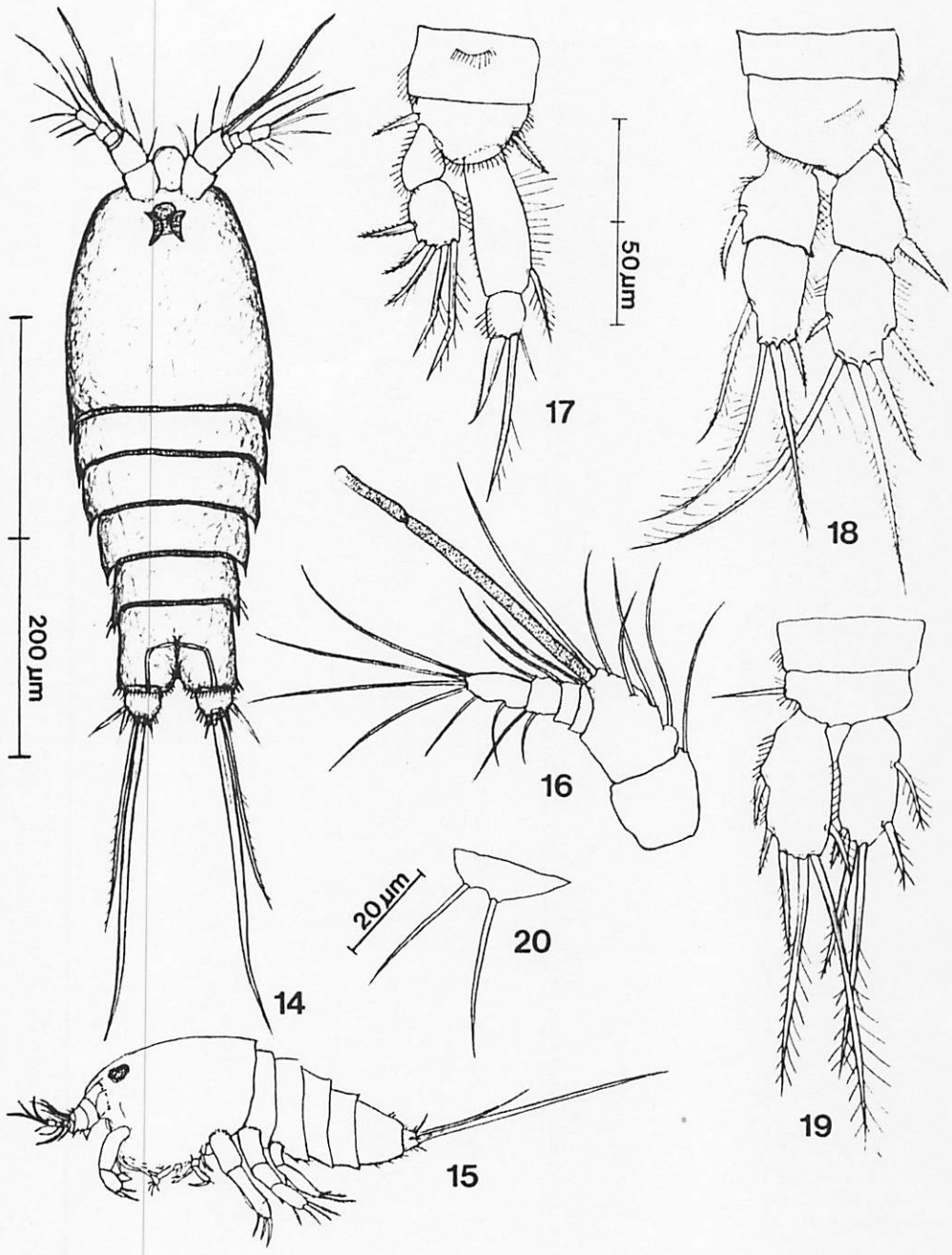


FIGS. 8–13. *Amphiascus undosus*, copepodite I (CI). Fig. 8. Dorsal. Fig. 9. Lateral. Fig. 10. A_1. Fig. 11. P_1, Fig. 12. P_2. Fig. 13. P_3. Scale bars: Figs. 8 and 9, 200 µm; Figs. 10–12, 50 µm; Fig. 13, 20 µm.

and P_6. Female genital region not developed. A_1 (male and female) (Fig. 31) 7-segmented, 3 basal segments larger than 4 distal segments. Setation of successive segments: 1/5/8 + aesthetasc/1/3/2/6. P_1–P_4 armature and segmentation as in Figs. 32–35 and Table 6. P_5 (male) (Fig. 36) bilobed, with sclerotized keel extending from base of lateral naked seta to medial surface. Inner expansion shorter than outer expansion, with prominent medial papilla and 2 apical plumose setae. Outer expansion parabolically rounded, twice the width of inner expansion; outer margin with 3 plumose setae, subapical seta longest; inner surface with plumosities, short plumose seta, long terminal plumose seta. P_5 (female) (Fig. 37) bilobed, hyaline keel and outer expansion structurally similar to those of male P_5. Inner expansion convexly rounded, small frill of hairs on lateral surface, 2 apical plumose setae; medial surface with 1 short and 1 long plumose seta. Outer expansion lateral surface with 3 plumose setae, 1 terminal plumose seta; inner margin with plumosities and 1 subterminal plumose seta. P_6 (male) (Fig. 38) wedge-shaped, tapered medially, with 2 slender falcate setae on lateral surface. P_6 (female) (Fig. 39) similar to male structure although 2 setae shorter.

Copepodite V (CV; Figs. 40–53, Tables 2, 7)

Prosome of 4 segments, urosome 5-segmented, body slightly wider and deeper than CIV. Sexes distinguishable by morphology of A_1, P_1, P_2, P_5, and P_6. A_1 (male) (Fig. 42) 8-segmented,



FIGS. 14–20. *Amphiascus undosus*, copepodite II (CII). Fig. 14. Dorsal. Fig. 15. Lateral. Fig. 16. A_1. Fig. 17. P_1. Fig. 18. P_2. Fig. 19. P_3. Fig. 20. P_4. Scale bars: Fig. 14, 200 µm; Figs. 16–19, 50 µm; Fig. 29, 20 µm.

segments 4 and 5 more swollen than in female A_1 (Fig. 43). Setation of successive segments: male, 1/6/5/6 + aesthetasc/2/2/3/6; female, 1/6/6/3 + aesthetasc/2/1/3/7. P_1–P_4 (male and female) armature and segmentation as in Figs. 44–49 and Table 7. P_5 (male) (Fig. 50) bilobed, inner and outer expansions subequal in dimensions; sclerotized keel as in CIV; anterolateral papilla with slender terminal seta. Lateral aspect of outer expansion with strong plumose seta, posteriorly directed plumose seta and subterminal falcate plumose seta; inner surface with long bristles, 1 subterminal seta and long apical plumose seta. Inner expansion medial surface with tuft of bristles and 1 terminal plumose seta; outer edge with short bristles and short

TABLE 3. Armature of copepodite I (CI) thoracic legs I and II (P_1 and P_2) (see Fig. 1 and Table 1 for explanation)

		Protopodite			
Leg	Margin	1	2	Exopodite 1	Endopodite 1
I	Outer	*p*	*p*, Sx, P	P, Sx, *p*, Sx, 2*s*	P, 2*s*
	Inner	*p*	P	2Sb, Sk	R, 2S
II	Outer	P	Sz	P, Sx, *p*, Sx, *s*	P, 2*s*
	Inner		H	*s*, 2S	E, *s*, S

TABLE 4. Armature of copepodite II (CII) thoracic legs I–III (P_1–P_3) (see Fig. 1 and Table 1 for explanation)

		Protopodite		Exopodite		Endopodite	
Leg	Margin	1	2	1	2	1	2
I	Outer	*p*, *p*	Sx, *p*	P	*P*, Sx, 2*s*	*p*	P, Su
	Inner	*p*	*p*, Sz, *p*		P, 2Sb	P, *s*	*e*, Sb
II	Outer	*p*	*p*, *p*, Sx	P, Sx, *p*	P, 2Sx	P, *p*	P, *s*
	Inner		*p*	*P*	*p*, *s*, 2S	P, *s*, *p*	3S
III	Outer	*p*	*p*, *e*, *p*	*p*, Sx, *p*, Sx, *s*	—	P, *s*, S	—
	Inner			*s*, 2S	—	E, *s*, S	—

TABLE 5. Armature of copepodite III (CIII) thoracic legs I–IV (P_1–P_4) (see Fig. 1 and Table 1 for explanation)

		Protopodite		Exopodite		Endopodite	
Leg	Margin	1	2	1	2	1	2
I	Outer	P	*p*, Sx, *p*	P, Sx, P	P, Sx, 2*s*	*p*	P, Su
	Inner	*p*	*p*, Sz, *p*	*p*	P, 2Sb	P, *s*	*e*, Sb
II	Outer	*p*	*p*, Sx, *p*	P, Sx, *p*	P, 2Sx, *s*	P	P, *s*, S
	Inner		*p*, H, P	*p*, E, *p*	*p*, 2*E*, 2S	P, E, H	2E, S
III	Outer	*p*, *p*	*p*, Sx	P, Sx, *p*	P, Sx, *s*	*p*	*p*, *s*, S
	Inner	*p*	*p*, H, P	H, *p*	*p*, E, 2S	*p*, *s*, *p*	3E, S
IV	Outer		*p*, *e*, *p*	P, 2Sx, *s*	—	P, 2S	—
	Inner	P	H	*s*, 2S	—	E, 2S	—

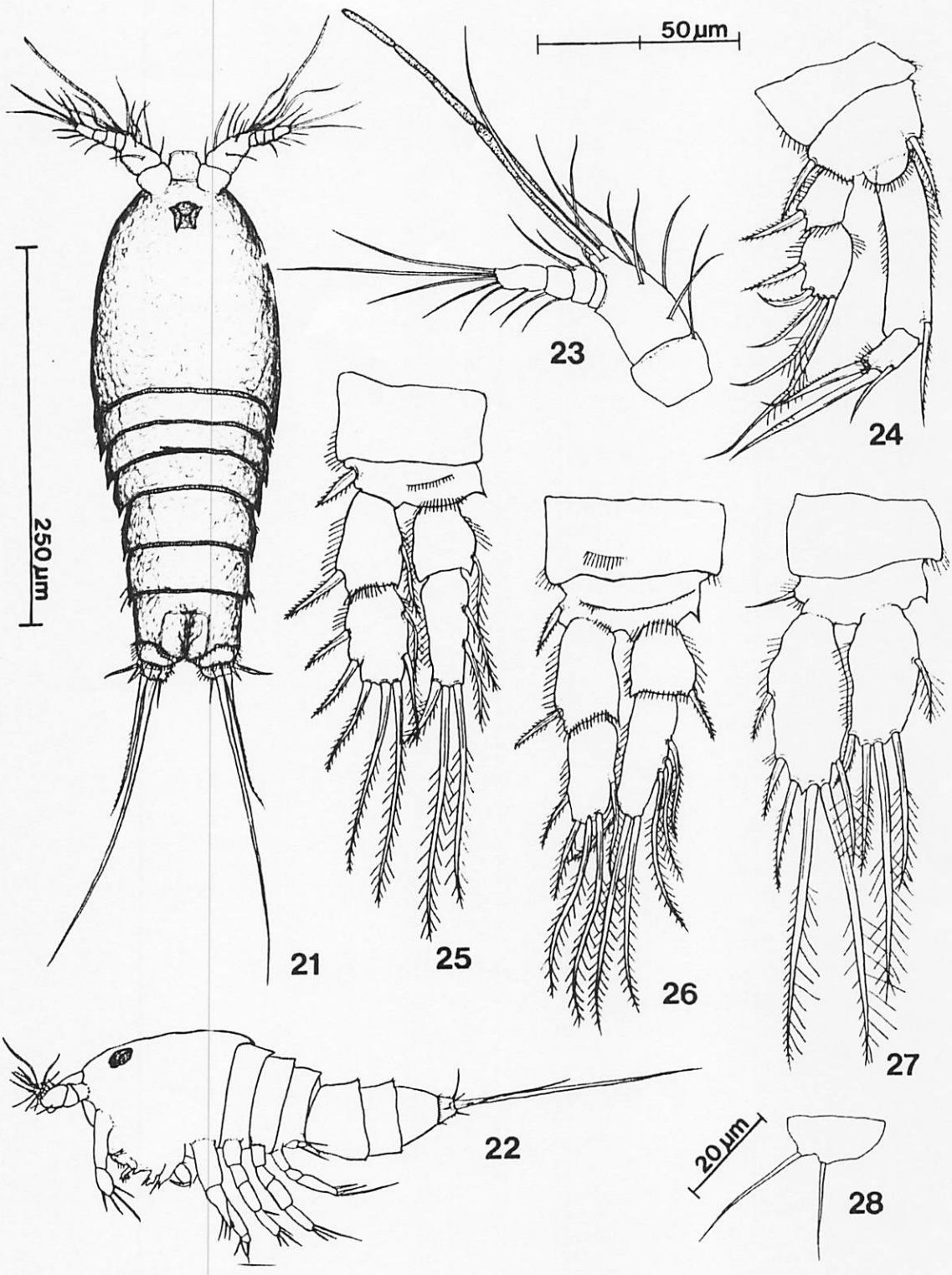
subterminal plumose seta. P_5 (female) (Fig. 51) bilobed, sclerotized ridge extends from anteromedial margin to base of lateral papilla; papilla with naked seta. Outer expansion circa twice the length of inner, with 4 plumose setae laterally; medial surface with region of short bristles, 1 plumose seta and long styliform plumose seta at apex. Inner expansion medial edge with 3 plumose setae; lateral surface with small row of hairs, 1 short plumose seta and 1 long apical plumose seta. P_6 (male) (Fig. 52) wedge-shaped plate with 2 long naked setae laterally, 1 shorter plumose seta medially. P_6 (female) (Fig. 53) as in male leg although with 2 very short naked setae laterally, longer plumose seta medially.

Copepodite VI (CVI, adult; Figs. 54–88, Tables 2, 8)

Prosome of 4 segments, urosome 6-segmented. Body tapered distally; proximal urosome segment reduced longitudinally, second urosome segment in female often wider than first. Ovisacs small, obovoid; initial 3 broods typically containing 8–11 eggs per sac, fourth brood, if present, with 4 or 5 eggs per sac.

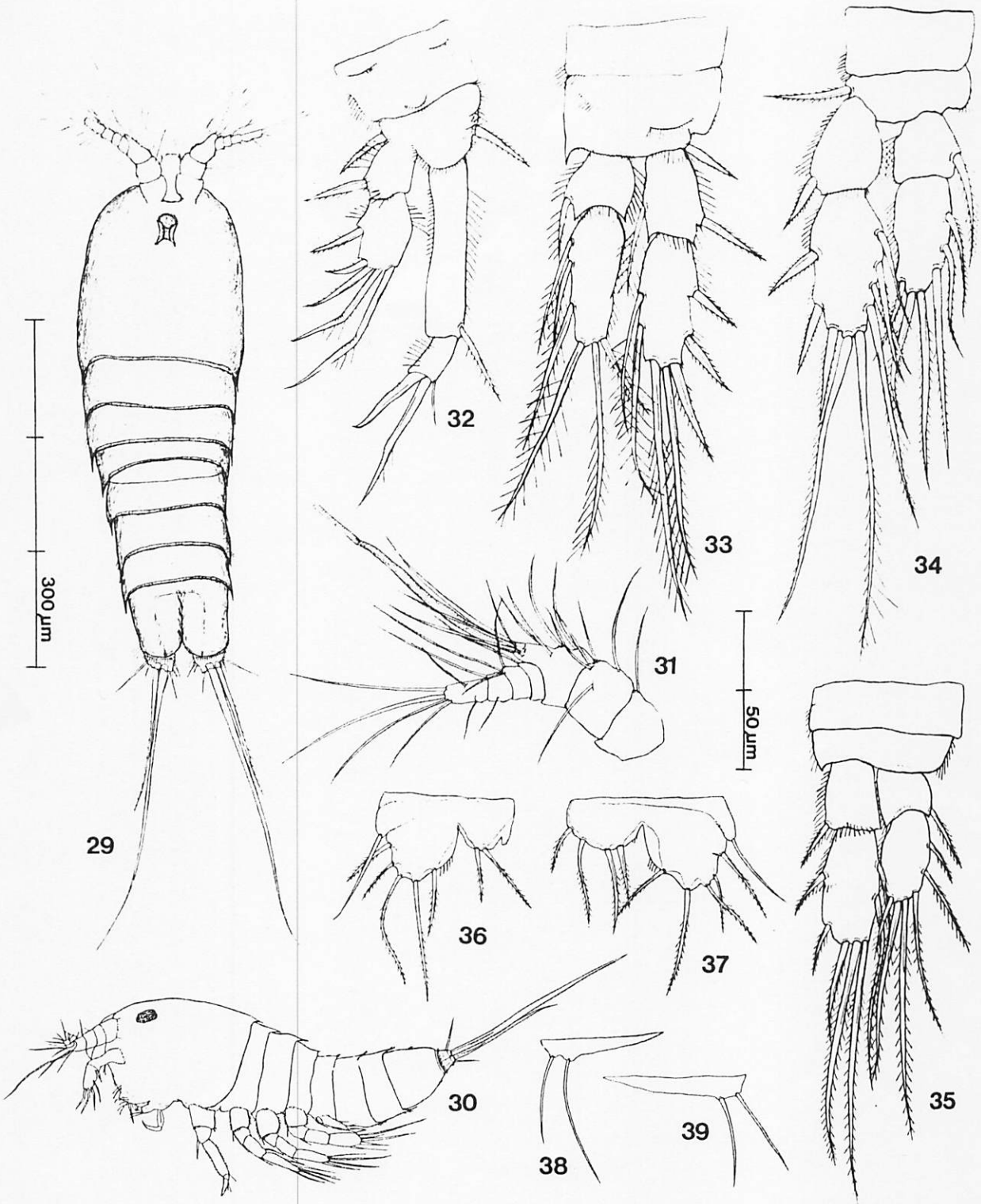
Note that except where otherwise indicated, the descriptions of the cephalic appendages pertain to the male of the species.

Rostrum (Fig. 58) triangular, tapered anteriorly to rounded tip with subterminal hair on lateral margins; sclerotized central keel merges with 2 similar ridges to form cristate patch. Labrum (Fig. 59) hoof-shaped in situ, broadening towards site of attachment; anterior surface with row of long delicate hairs, penultimate surface with shorter fine bristles bordered laterally by stronger bristles. Antepenultimate surface with brief row of strong bristles astride longitudinal midline; reticulations on inner surface. A_1 (Figs. 60, 61) 10-segmented, haplocer; segments 2 and 4 largest, segment 5 narrow, segment 8 indistinct; distal region of segments 5–10 forming clasping apparatus. Setation of successive segments: 1/8/4/6 + aesthetasc/0/1/0/0/2/5. A_1 (female) (Fig. 62) 8-segmented, nonhaplocer; segments 1 and 4 largest, distal 4 segments smaller. Setation of successive segments: 1/8/6/4 + aesthetasc/2/2/4/7. A_2 (Fig. 63) endopodite 3-segmented, coxa smallest, unornamented; segment 2 with bristles on lateral surface, 1 lateral plumose seta at midpoint; terminal segment with 2 naked setae on outer surface; terminus with plumosities, 3 naked setae, 3 bent plumose setae, 1 styliform plumose seta, naked seta, and 4 spinules. Exopodite with 3-segmented allobasis; segment 1 longest, bearing 1 small plumose seta, segment 2 very narrow, unornamented; terminal segment 0.6 times length of segment 1, with 1 basal plumose seta, 2 apical plumose setae and plumosities laterally. Mandible (Fig. 64), anterior surface of precoxa irregularly serrated. Coxa, basis 1-segmented, armed with 3 apical plumose setae; coxal surface with 2 frills of delicate hairs. Exopodite 2-segmented, segment 1 with naked seta, segment 2 with 1 plumose seta and 1 naked seta. Endopodite twice the length of exopodite, with 2 proximal plumose setae and 5 naked terminal setae. Maxillule (Fig. 65), precoxal arthrite with 2 naked setae extending from ridge on surface, 8 juxtaposed plumose spiniform setae at apex. Basis with subterminal naked seta, 2 apical setae; largest seta plumose. Exopodite 1-segmented, with 4 terminal bare setae, inner edge with row of small plumosities. Endopodite 1-segmented, broader, one-half the length of exopodite, with 2 terminal plumose setae. Maxilla (Fig. 66), syncoxa with 3 endites; middle endite with line of sclerotization at midline, bilaterally flanked by pair of plumose setae; inner endite with 1 naked seta; outer endite with 4 very small plumose setae. Basis ending in strong claw, with 1 plumose seta, cluster of 5 uncinate



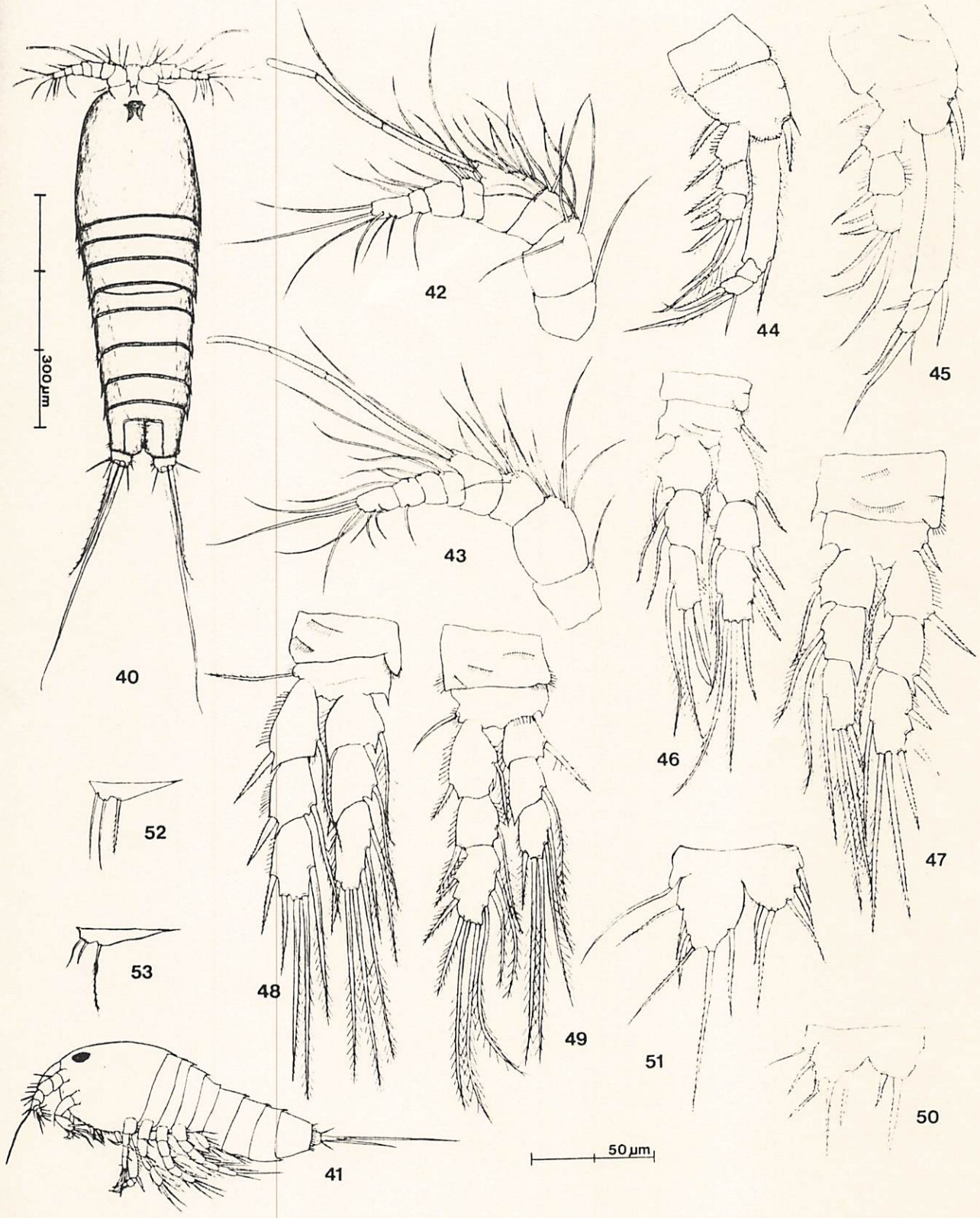
FIGS. 21–28. *Amphiascus undosus*, copepodite III (CIII). Fig. 21. Dorsal. Fig. 22. Lateral. Fig. 23. A_1. Fig. 24. P_1. Fig. 25. P_2. Fig. 26. P_3. Fig. 27. P_4. Fig. 28. P_5. Scale bars: Fig. 21, 250 µm; Figs. 23–27, 50 µm; Fig. 28, 20 µm.

setae near apex. Maxilliped (Fig. 67) subchelate, 3-segmented. Coxa small, narrow, unornamented. Basis with 2 fans of hairs; distal process on inner edge, with 1 subapical and 2 terminal plumose setae. Endopodite segment 1 longest, with inner longitudinal row of hairs from proximal surface to midpoint near exsertion of oblique naked seta; ridge on midsurface with long procession of hairs, naked terminal seta. Second endopodite segment with apron-like shroud at base, with 1 naked spinule; terminus with strong claw and 2 smaller setules on medial edge. P_1–P_4 (male and female) armature and segmentation as in Figs. 68–73 and Table 8. Male P_2 shows evidence of fusion of 2 distal endopodite segments (Figs. 70, 74–77). P_5 (Fig. 78) basioendopodite with lateral papilla bearing terminal naked seta; inner edge with row of plumosities and 1 strong



FIGS. 29–39. *Amphiascus undosus*, copepodite IV (CIV). Fig. 29. Dorsal. Fig. 30. Lateral. Fig. 31. A_1. Fig. 32. P_1. Fig. 33. P_2. Fig. 34. P_3. Fig. 35. P_4. Fig. 36. P_5, male. Fig. 37. P_5, female. Fig. 38. P_6, male. Fig. 39. P_6, female. Scale bars: Fig. 29, 300 µm; Figs. 31–39, 50 µm.

terminal plumose seta; outer aspect with plumosities and short subterminal plumose seta. Exopodite inner edge with small group of plumosities, 1 subterminal and 1 strong terminal plumose seta; outer edge with 2 naked setules, 2 plumose setae and 1 oblique naked seta. Leg distinguishable from CV P_5 by increased number of plumosities and distinct segmentation of exopodite. P_5 (female) (Fig. 79) basioendopodite with papilla bearing naked seta on outer edge; inner surface with 3 subterminal and 2 terminal plumose setae. Exopodite ovoid, outer surface with row of plumosities, 3 subterminal plumose setae, 2 terminal plumose setae; inner edge with plumosities and subterminal plumose seta. Leg distinguishable from CV female P_5 by more distinct segmentation of exopodite. P_6 (Figs. 80, 81) rectangular, medially rounded shape (appearing fluke-shaped in situ), inner edge unornamented, outer margin with 1 plumose seta, 2 longer naked setae laterally. Legs may overlap but do not



FIGS. 40–53. *Amphiascus undosus*, copepodite V (CV). Fig. 40. Dorsal. Fig. 41. Lateral. Fig. 42. A_1, male. Fig. 43. A_1, female. Fig. 44. P_1, male. Fig. 45. P_1, female. Fig. 46. P_2, male. Fig. 47. P_2, female. Fig. 48. P_3, male and female. Fig. 49. P_4, male and female. Fig. 50. P_5, male. Fig. 51. P_5, female. Fig. 52. P_6, male. Fig. 53. P_6, female. Scale bars: Fig. 40, 300 µm; Figs. 42–53, 50 µm.

unite; transverse dimension variable. P_6 (female) (Fig. 82) proportionately smaller than male P_6, situated nearer genital field. Armature comprises 1 long inner plumose seta, 2 short falcate naked setae laterally. Plumose seta longest, outer setae proportionately shorter than that of CV female P_6. Caudal rami (male and female) (Figs. 83–85), caudal setae with circumferential fringe of spinules at anterior margin. Male rami (Fig. 83) each with mesial naked seta, medial row of denticulations; outer edge with 1 long naked seta, 1 plumose seta; caudal setae with no undulations. Female rami with armature as in male; caudal

TABLE 6. Armature of copepodite IV (CIV) thoracic legs I–IV (P_1–P_4) (see Fig. 1 and Table 1 for explanation)

		Protopodite		Exopodite		Endopodite	
Leg*	Margin	1	2	1	2	1	2
I	Outer	*p*, *p*, *p*	Sx, *p*	P, Sx, P	P, Sx, 2*s*	*p*	P, Su
	Inner	*p*, *p*	P, Sz, *p*		P, 2Sb	P, *s*	*e*, Sb
II	Outer	*p*	*p*, P, Sx, *p*	P, Sx, *p*	P, Sx, Sz, *s*	P, *p*	p, *s*, S
	Inner	*p*	*p*, H, *p*	E, *p*	E, 3S	P, *s*, H, *p*	2E, 2S
III	Outer	*p*	*p*, Sx	P, Sx, *p*	*p*, 2Sx, *s*, S	P	*p*, *s*, S
	Inner		*p*	P, *p*	3E, 2S	*s*	2E, 2*s*
IV	Outer	*p*	*p*, H	P, Sx, P	*p*, Sx, *p*, Sx, *s*	*p*	*p*, E, S
	Inner		*p*	*p*	2E, 2S	E	2E, 2S

*Male and female.

TABLE 7. Armature of copepodite V (CV) thoracic legs I–IV (P_1–P_4) (see Fig. 1 and Table 1 for explanation)

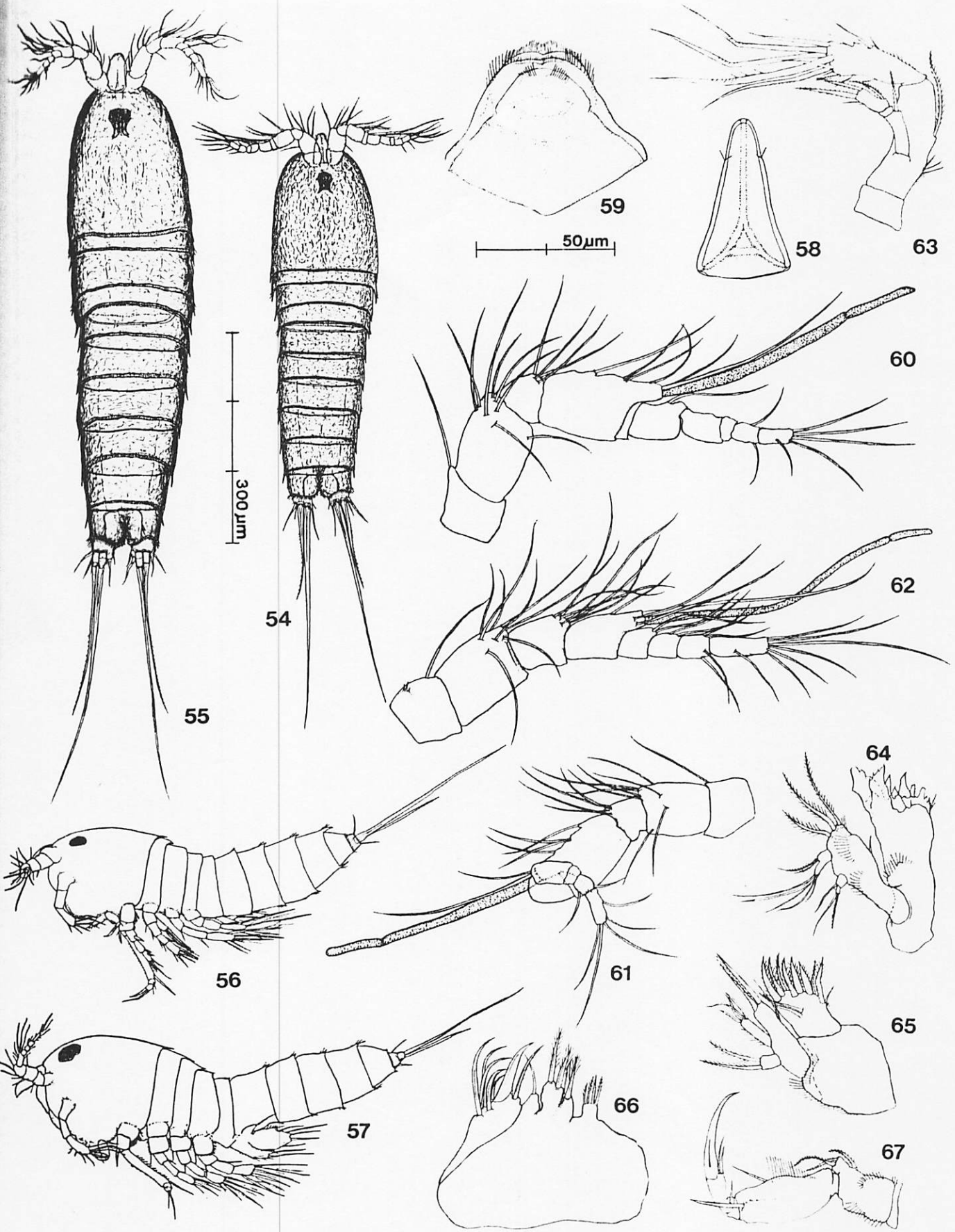
		Protopodite		Exopodite			Endopodite		
Leg	Margin	1	2	1	2	3	1	2	3
I									
Male	Outer	P, *p*	*p*, Sx, P	P, Sx, *p*	*p*, Sx	*p*, Sx, 2*s*	*p*	P	P, Su
	Inner	P, *p*	P, *e*, Sz, *p*		P	2Sb	P, *s*		*e*, Sb
Female	Outer	*p*, P	Sx, P	P, Sx	P, Sx	Sx, 2*s*	*p*	P	P, Su
	Inner	P, P	P, Sz, *P*		P	2Sb	P, *s*		*e*, Sb
II									
Male	Outer	*p*, B	Sx, *p*	P, Sx	P, Sx, G	*p*, 2Sx, *s*	*p*	P, G	P, 2Ss
	Inner		2*p*, H	E	*p*, E	*s*, 2S	P, *s*, H, p	*p*, 2S	2S
Female	Outer	*p*, P, B	Sx	P, Sx	P, Sx, G	P, 2Sx, *s*	*p*	*p*, G	*p*, *s*, S
	Inner	3*p*, H	H	*p*, E, H	*p*, E	3S	*p*, *s*, H	*p*, 2S	*p*, 2S
III*	Outer	*p*, *p*	*p*, E	P, Sx, G	P, Sx, G	P, Sx, *s*, S	P, G	P, G	P, *s*, S
	Inner	B	H	*s*, *p*	*s*	2S	S, *p*, H	S, H	S, *s*, 2S
IV*	Outer	3*p*	Sz	P, Sx	P, Sx	P, 2Sx, *s*, S	*p*	*p*, G	*p*, *s*, S
	Inner	2*p*	H, P	*p*, *e*, H	P, E	E, *s*, 2S	*s*, H	S	3S

*Male and female.

TABLE 8. Armature of copepodite VI (CVI, adult) thoracic legs I–IV (P_1–P_4) (see Fig. 1 and Table 1 for explanation)

		Protopodite		Exopodite			Endopodite		
Leg	Margin	1	2	1	2	3	1	2	3
I									
Male	Outer	*p*, P, B	Sx, *p*	P, Sx	P, Sx	*p*, Sx, S, Sb		P	P, Su
	Inner	*p*, *p*	*e*, Sz, *p*		P	*p*, 2Sb	P, *s*		*e*, Sb
Female	Outer	*p*	*p*, Sx	P, Sx	P, Sx	P, Sx, *s*, Sb	*p*	P	P, Su
	Inner		*p*, Sz, *p*		*p*	P, 2Sb	P, *s*		*e*, Sb
II									
Male	Outer		*p*, *p*, Sx	P, Sx, G	P, Sx, G	2Sx, S	P, G	P, R, 2Ss	—
	Inner		*p*, *p*	*p*, E, *p*	P, E	*p*, 3S	P, E, H	E, *s*, R, S, *s*	—
Female	Outer	*p*, *p*, P	Sx	P, Sx, G, *p*	P, Sx, G	*p*, 2Sx, *s*	*p*, *p*	P, H	P, *s*, S
	Inner	*p*	H	E, *p*	E	3S	P, E, H, *p*	*s*, S, H	2S
III*	Outer		E, *p*, *p*	P, Sx, *p*	P, Sx, G	P, 2Sx, *s*	P	P, G	*p*, E, S
	Inner	*p*	*p*, *p*, H	*p*	E	*p*, 3S	*p*, S, *p*	S, *p*,	4S
IV*	Outer	P	*s*	P, Sx	P, Sx	*p*, 2Sx, *s*, S	*p*	*p*	*p*, 2S
	Inner		H	E, H, *p*	P, S	4S	S, H	S, H	3S

*Male and female.



FIGS. 54–67. *Amphiascus undosus*, copepodite VI (CVI, adult). Fig. 54. Male, dorsal. Fig. 55. Female, dorsal. Fig. 56. Male, lateral. Fig. 57. Female, lateral. Fig. 58. Rostrum, dorsal. Fig. 59. Labrum, ventral. Fig. 60. A_1, male. Fig. 61. A_1, male, contracted. Fig. 62. A_1, female. Fig. 63. A_2. Fig. 64. Mandible. Fig. 65. Maxillule. Fig. 66. Maxilla. Fig. 67. Maxilliped. Scale bars: Figs. 54–55, 300 µm; Figs. 59–67, 50 µm.

setae with very slight undulations (Fig. 84) or of biplatform appearance (Fig. 85), probably due to regeneration of damaged setae.

Abdomen (male, ventral) (Fig. 86), second urosome segment bearing sixth pair of legs and 2 ventral apertures for origin of spermatophore. Third and fourth segments each with single row of spinules on caudal aspect. Fifth segment with bilateral frills of delicate hairs on antepenultimate surface.

Genital field (female, ventral) (Fig. 87), double somite of urosome segments 2 and 3 incompletely subdivided by sclerotized margin. Copulatory pore heart-shaped, with sclerotized perimeter; orifice leading to paired cornuate tubules each terminating in ovoid sac situated deep and lateral to opening. Two paired frills of hairs lateral to genital orifice, 2 pairs of sensillae at proximal border of sclerotized strip. Sixth legs situated anterolaterally to copulatory pore, near intersegmental junction.

Anal operculum (male, ventral) (Fig. 88) vaulted anteriorly, leading to bulbous internal antechamber of hindgut lined by long fine bristles. Distal external surface with continuous row of small fine hairs.

Discussion of morphology

The specimens described in this paper were identified as *Amphiascus undosus* on the basis of their overall similarity to Lang's description (1965), particularly in the setation and segmentation of the female A_1 and A_2 and the male P_5 and P_6. However, they differ from Lang's description in the adult male maxillule, maxilliped, P_1, P_5, and P_6, and the proximal inner caudal seta of the adult female.

The precoxal arthrite of the adult male maxillule is armed with 8 spiniform terminal setae. Lang (1965) shows 4 of these setae to be bifid in the female maxillule.

The second segment of the adult male maxilliped differs from that of the female, as given by Lang, in having a distinct papilla bearing 3 plumose setae rather than a ridge armed with 2 setae. However, this difference may be a result of sexual dimorphism as seen in the maxilliped of some *Tisbe* spp. (Bergmans 1979).

The P_1 of the male, as described by Lang (1965), has a small seta at the terminus of the second endopodite segment. This armature element was not found in the male British Columbia specimens or in the Lang's syntype material (one male was dissected, four were superficially examined).

The male P_5 exopodite, as described by Lang (1965), is armed with 5 setae and 4 bristles. The British Columbia specimens have, in addition to this armature, 2 short slender setules, with distinct implantation sites, on the proximal outer surface of the exopodite. Lang's syntype material did not have these armature elements.

The male P_6 as illustrated by Lang (1965) is fluke-shaped, with its armature elements directed obliquely. This differs from both the British Columbia specimens and Lang's syntypes examined in the present study. However, Lang shows the male P_6 in situ from a ventral viewpoint. This gives a distorted view of the P_6 due to its curvature. When the P_6 is partially isolated and flattened, the medially rounded rectangular form and more posteriorly directed armature elements become apparent (see Figs. 80 and 81). As a result, the armature and shape of the male P_6 of both Lang's syntype material and the British Columbia material agree, with the exception that the sixth legs of the British Columbia specimens do not join, but may overlap.

The pronounced undulations found by Lang (1965) on the proximal inner surface of the large caudal setae of the adult female were only slight or absent in the British Columbia specimens (Figs. 84, 85). Distinct undulations did exist, however, in the 2 females from Lang's syntype material. This is important because the name (*undosus*) refers to these undulations.

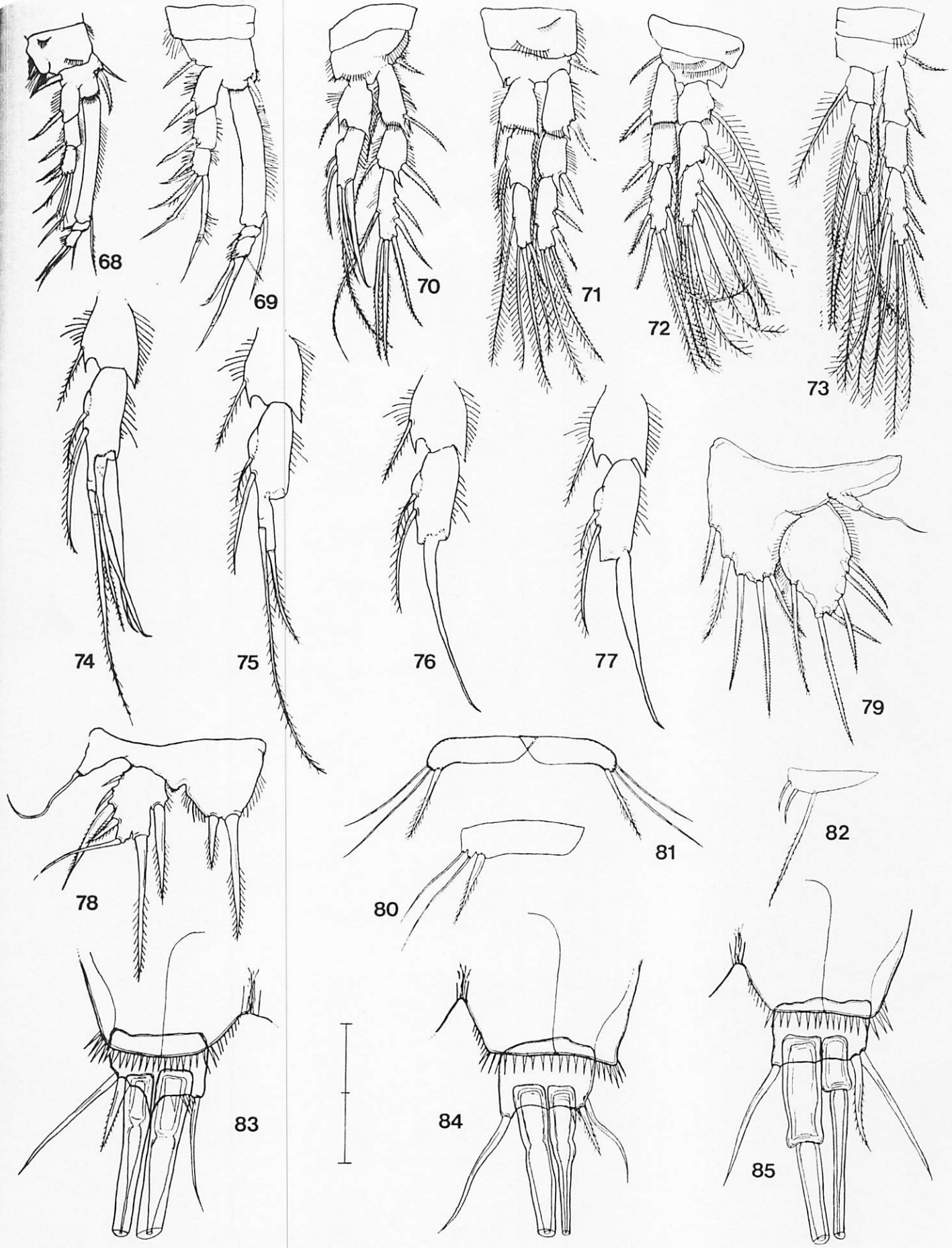
This is also of significance because of the similarities that now arise between the British Columbia *A. undosus* material and *Amphiascus parvus* (Sars 1911). Sars' (1911) drawings, and those of the redescription of *A. parvus* by Yeatman (1970), show great similarity to the British Columbia *A. undosus* in the female A_1, A_2, P_1–P_4, and P_5; neither author offers illustrations of the male P_6. Differences in the P_5 could, however, depend on Sars' and Yeatman's viewing procedures, although these are not specified. Yeatman (1970) distinguishes *A. parvus* from *A. undosus* on the basis of the female proximal inner caudal seta being straight instead of sinuous. Therefore, only three inconclusive features remain that separate the two species. First, Lang (1948) reports the length of the *A. parvus* adult female as 0.46 mm and Yeatman (1970) indicates it to be about 0.45–0.55 mm. These values indeed differ from the 676.9 ± 35.2 μm length of the British Columbia adult female *A. undosus*, as well as from Lang's (1965) value of approximately 0.75 mm. However, size in copepods is not considered a reliable basis on which to identify a species as it can be strongly influenced by environmental factors (Miller *et al.* 1977), as well as by the methods of preservation and observation (Gurney 1931). Second, the male A_1 in *A. parvus* is 8-segmented, according to Yeatman (1970) (although the structure is not illustrated), whereas in the present description of *A. undosus*, 10 segments are reported. Moreover, Lang (1965) does not indicate segment number in his description of the male A_1, nor is a drawing given. Third, the arrangement of the male P_2 terminal setae of *A. parvus*, as drawn by Lang (1948), differs slightly from the present description of the male P_2 of *A. undosus*. However, this is not diagnostic because of the lack of detail in Lang's (1948) drawing of the male P_2, and Yeatman (1970) does not provide an illustration.

Because of the discrepancies between Lang's (1965) description of *A. undosus* and the British Columbia specimens, in addition to the similarities between the British Columbia specimens and *A. parvus*, a more thorough description of *A. parvus* is needed, particularly of the adult male.

The developmental stages of *Amphiascus undosus* exhibit several similarities to and differences from six other diosaccid harpacticoids (*Amphiascus minutus*, *Robertgurneya* sp., *Robertsonia propinquua*, *Amphiascoides debilis*, *Schizopera knabeni*, and *Paramphiascella fulvofasciata*), as summarized in Rosenfield and Coull (1974).

The nauplii of *A. undusus* exhibit "standard" diosaccid gross form and developmental changes during ontogeny. Body form

FIGS. 68–85. *Amphiascus undosus*, copepodite VI (CVI, adult). Fig. 68. P_1, male. Fig. 69. P_1, female. Fig. 70. P_2, male. Fig. 71. P_2, female. Fig. 72. P_3, male and female. Fig. 73. P_4, male and female. Fig. 74. Detail of 2 distal segments of P_2 male endopodite. Fig. 75. P_2 endopodite, male, terminal inner armature isolated. Fig. 76. P_2 endopodite, male, terminal middle armature isolated. Fig. 77. P_2 endopodite, male, terminal outer armature isolated. Fig. 78. P_5, male. Fig. 79. P_5, female. Fig. 80. P_6, male, isolated. Fig. 81. P_6, male, in situ. Fig. 82. P_6, female. Fig. 83. Caudal ramus, male. Figs. 84 and 85. Caudal ramus, female. Scale bar: Figs. 68–73 and 79, 100 μm; Figs. 74–78 and 80–82, 50 μm; Figs. 83–85, 30 μm.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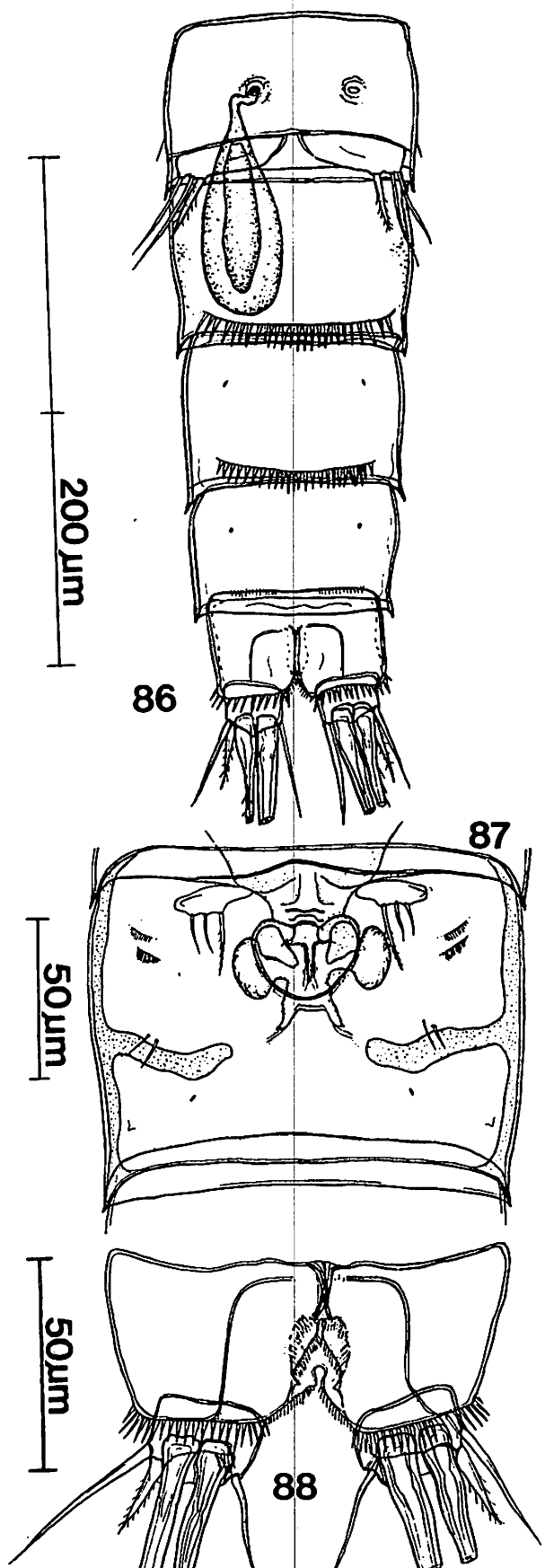

FIGS. 86–88. *Amphiascus undosus*, copepodite VI (CVI, adult). Fig. 86. Abdomen, male, ventral. Fig. 87. Genital field, female, ventral. Fig. 88. Anal operculum, male, ventral.

is ovoid at first, becoming more arcuate with development. Naupliar appendage structure and location strongly parallel those of *Paramphiascella fulvofasciata* (Rosenfield and Coull 1974). The coxantennal endite of the six diosaccids does not conventionally appear until the NII stage; in *A. undosus*, an Anlagen structure is apparent in the NI stage. However, *A. undosus* is similar to these species in adding a posterior spine in the coxantennal endite at the NIII stage. The naupliar *A. undosus* maxillule also differs in development from that of the other six diosaccids by bearing only 2 setae, adding 1 seta per stage until the NVI. The other diosaccids show 3 setae on the NIV maxillule, ending with 5 setae in the NVI. The maxilla of *A. undosus* is absent in the NVI, whereas in *P. fulvofasciata* a naked lobe representing the promaxilla is apparent (Rosenfield and Coull 1974). As with the others, the maxilliped remains absent until the CI stage. At the NVI stage there is internal evidence of the developing copepodite urosome segmentation (see Fig. 7). This is also apparent in the NVI of *P. fulvofasciata*.

The copepodite stages of *A. undosus* show further developmental similarities with those of *P. fulvofasciata* (Rosenfield and Coull 1974). These two species display a profound metamorphosis to the CI stage, with this stage showing typical harpacticoid form, comprising 5 body segments. The A_1 of both species is 5-segmented in the CI, lags at 6 segments in the CII and CIII stages, then continues progressive segmentation with each stage until dimorphism occurs in the adult (i.e., 8 segments in the female and 10 segments in the male of both species). As in *Amphiascus minutus* (Lang 1965), *P. fulvofasciata*, and *A. undosus*, a trend of sexual dimorphism exists in the adult A_1, P_1, P_2, and P_5. In the latter two species, sexual divergence of the A_1 begins at the CV stage where proportionate segmental size and shape between the male and female is visible. The P_1 basis of the *A. undosus* adult male shows an additional inner spine not present in the adult female. A similar modification of the adult male P_1 basis of *P. fulvofasciata* manifests as a blunt knob in the same region of the structure (Rosenfield and Coull 1974). The P_1 endopodite of *A. undosus* first becomes 3-segmented in both sexes of the CV stage, whereas in *P. fulvofasciata* it remains 2-segmented until the adult stage. The male P_2 endopodite of both species begins modification at the CV stage; ultimately, segments 2 and 3 become fused in the adult male. Dimorphism of the P_5 in these species is first apparent at the CIV stage. The female genital double somite (urosome segments 2 and 3) is visible only at the adult stage in both *A. undosus* and *P. fulvofasciata*.

Acknowledgements

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