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PSEUDOCHIRELLA SQUALIDA GRICE & HULSEMANN, 1967, FROM CONTINENTAL SLOPE WATERS OFF DELAWARE (COPEPODA:CALANOIDA)

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Abstract.—The original description of copepodid stage VI female *Pseudochirella squalida* is augmented. Initial descriptions of stage VI male, stage V female, and stage V male are presented. Sexually dirmorphic characters in both stages are present in a variety of body segments, appendages, and their armature. Some of their presumed functions are discussed. Bilateral asymmetry is exhibited only in stage VI and is manifested in primary or secondary sexual characters.

Introduction

The establishment of *Pseudochirella squalida* by Grice & Hulsemann (1967) was based on a single copepodid stage VI female specimen collected in the Indian Ocean on 28 June 1964 at ANTON BRUUN station 351B (29°45′S, 64°58′E) between 350 and 1,710 m. Deevey & Brooks (1977) reported 2 females in the Sargasso Sea collected at Station "S" (32°10′N, 64°30′W) on July 1969 and February 1970 between 500 and 1,000 m. To date examination of calanoid copepods from midwater trawl samples of 2 cruises (July 1975, ALBATROSS IV, and February 1976, OREGON II) in the area of Deepwater Dumpsite 106 in continental slope waters off Delaware has shown *P. squalida* to be the most abundant species of the genus. In this paper I augment the description of the external morphology of copepodid stage VI female (hereafter VI ♀), describe copepodid stage VI male (VI ♂), copepodid stage V female (V ♀), and copepodid stage V male (V♂) and discuss sexual dimorphism and bilateral asymmetry among the various stages.

Materials and Methods

Specimens were examined from midwater trawl samples collected during cruises to Deepwater Dumpsite 106, an area encompassed by 70°31′–75°00′W and 36°00′–39°10′N. A more complete description of the gear and station positions is given by Krueger *et al.* (1977). Table 1 gives collection data for the samples containing *P. squalida.*

All specimens of *P. squalida* were removed from every sample and measured. They were prepared for examination by clearing in lactic acid and staining with chlorazol black E. In the following presentation VI ♀ is described and illustrated completely. VI ♂, V ♀, and V ♂ are compared to this description and only those structures differing significantly from VI ♀ are illustrated. For clarity, illustrations of spines, setae and their ornamentation are not complete. Generally for similar articles or elements in a series only one is illustrated completely. In a few cases individual variation occurs in the number of setae comprising large clusters, e.g. RiA2, RiMd or RiMx1. These instances are not reported as it is impossible to determine whether the setae were lost during preparation, not observed due to imperfect staining, or actually represent individual variation. Illustrations were made with the aid of camera lucida or drawing tube. Anatomical terminology and abbreviations follow Ferrari and Bowman (in press) except for the mouthparts where terminology and abbreviations of Giesbrecht (1892) are used.

Results

Pseudochirella squalida Grice & Hulsemann 1967

Pseudochirella squalida Grice & Hulsemann 1967:24, figs. 65–70.

Material.—71 VI ♀, 10 VI ♂, 18 V ♀, 61 V ♂ from 27 midwater trawl samples listed in Table 1.

Description.—VI ♀: Length range 5.5–6.8 mm. Cph/Pg1 articulation (Fig. 1e) free laterally, fused dorsally. Pg4/Pg5 fused. Ur1 (genital segment) (Figs. 1a, b; 4d, e) with row of hairs across dorsal surface. Left side of Ur1 produced midlaterally into slight bulge, accentuated by peripheral integumental ridges; posterolaterally a small bump; series of integumental ridges across ventrolateral face; small patch of anterolateral hairs. Right side 2 large posterolateral bumps with long hairs; integumental ridges across ventrolateral face; scattered hairs dorsally. Ventral surface slightly produced into genital prominence with accentuating integumental ridges; large transverse ridge posteriorly, with associated hairs. Ur2&3 (Fig. 1a) with thin hairs scattered over entire segment; distinctly thicker hairs along posterodorsal margin. CR with hairs dorsally and laterally; first terminal setae reduced, originating from ventral surface; remaining terminal setae and dorsal seta long, thick and plumose; lateral seta small. A1 (Figs. 2c–e) 24 free segments, 8–9 fused. 1A1 with tiny spines; esthetes on 2,3,5,6,9,13,18,25. B1A2 (Fig. 2a) proximal comb of 6–7 setules; 1 distal seta. B2A2 2 distal setae. Re 7 segments; Re2–6 1 seta each; Re7 1 seta midlength, 3 distally. Ri1 2 distal setae; Ri2 separate group of setae on 2 distal edges, lateral edge 8 setae, medial 9. B1Md as shown (Fig. 3a); hairs of varying thickness on anterior surface. B2 3 medial setae. ReMd 5 segments; Re1–4 1 seta each Re5 with 2. Ri1Md 3 medial setae, thin hairs laterally; Ri2 10 distal setae. LeMx1 9 setae (Fig. 3c); Re 9 setae;

Ri 16 setae. B2 5 distal setae. Li3 4 setae; Le2 5 setae. Li1 10 anterior spines with long spinules; 4 posterior spines with short, thick spinules; hairs on anterior surface. B1Mx2 (Fig. 3e, f) with lateral spinules. L1–5Mx2 with small spines on posterior surface; each lobe 3 long spines with spinules or plumes. Ri 5 segments; Ri1–4 with large medial spine and reduced postero-lateral spine; Ri5 3 well-developed spines. B1&2Mxp with rows of spinules as illustrated (Fig. 4b). B1 3 groups of 3 spines. B2 2 medial spines with spinules and 3 plumose setae. Ri 5 segments; with 0,0,0,1,1 lateral setae and 3,4,3,3,3 medial spines with spinules. B1P1 (Fig. 5a) row of medial hairs; B2 row of medial hairs and strong curved distal spine extending over tubercule of Ri. Re 3 segments; articulation between Re1&2 incomplete. Re1 with medial hairs and 1 Se with spinules. Re2 medial hairs, tiny spines on anterodistal edge, 1 Se with spinules and 1 Si. Re3 hairs on anterior surface and along lateral edge, Se with spinules, 1 St plumose medially, spinules proximolaterally, serrate flange distolaterally, and 3 Si. RiP1 1 segment, forming medial tubercule on anterior face, with tiny spines (see Vaupel-Kline, 1972, for a more complete discussion of this structure in *Euchirella*), anterodistal hairs, 5 Si. B1P2 (Fig. 3h) medial hairs and 1 Si. B2 naked. ReP2 3 segments. Re1 medial hairs, 1 Se with serrate flange on both edges, 1 Si. Re2 similar to Re1 but with row of tiny anterodistal spines, lateral hairs, and lacking medial hairs. Re3 3 biflanged Se; St plumose medially, serrate flange laterally, and 4 Si. P3 (Fig. 3i) similar to P2 except Ri 3 segments. Ri1 1 Si. Ri2 lateral hairs and 1 Si. Ri3 posterior and lateral hairs, 1 Se, and 4 Si. P4 (Fig. 4a) similar to P3 except B1 medially formed lobe with comb of strong spines, 6–7 on left B1; 8–10 on right. B2 with posterior hairs. Ri2 with posterior hairs. P5 absent.

VI ♂: Length range 5.1–5.8 mm. Cph/Pg1 fused (Fig. 1d). Pg4/Pg5 fused; small unarticulated, slightly curved, posterodistal spine on each side. Ur1 (Fig. 1c) genital opening on left side. Ur2–5 posterodistal serrate fringe; without hairs on surface of segments. CR smaller than VI ♀ with fewer dorsal hairs; medial 2 setae longer than VI ♀. A1 (Figs. 2f–h) 24 free segments; 8&9 fused; articulation between 9&10 and 12&13 fused posteriorly; many more esthetes especially on proximal segments. B1A2 (Fig. 2b) distal seta reduced. B2 2 distal setae reduced. Re similar to VI ♀ but seta on Re2 and 1 on Re7 absent. Ri1 naked. Ri2 mediodistal series with 7 setae; latero-distal with 6. B1Md (Fig. 3b) gnathobase reduced to knob. B2 1 medial seta. Re all segments fused, with 6 setae. Ri1 lateral hairs and 2 medial setae. Ri2 9 distal setae. Mx1 (Fig. 3d) greatly reduced. Le 7 setae. Re 11 setae. Ri&B2 fused. Ri 10 setae; B2 with 5. Li3 2 small setae. Li1&2 naked. Mx2 (Fig. 3g) greatly reduced, all segments fused. L1–5 small knobs with 1,2,2,2,2 setae; L5 distal seta with swollen base. Ri 5 setae. Mxp (Fig. 4c) slightly reduced. B1 1 medial and 2 distal setae; small spines absent. B2 5 medial setae; no small spines. Ri with 3,3,2,2,3 medial spines; 0,0,0,1,1 lateral setae. P1 (Fig. 5f) slightly reduced, similar to VI ♀ but Re1&2 artic-

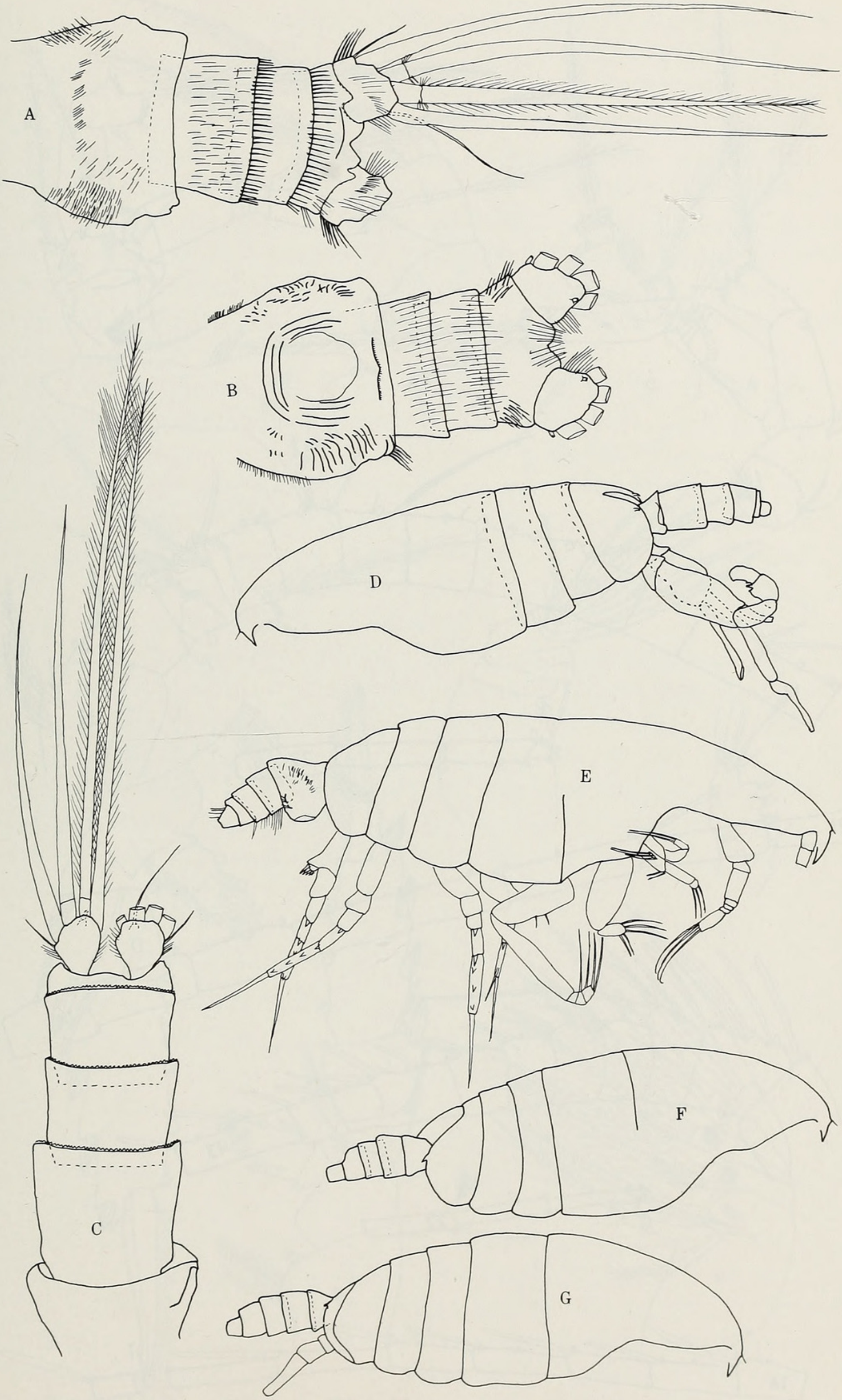

Fig. 1. *Pseudochirella squalida*: **a,** VI ♀ Ur, dorsal; **b,** VI ♀ Ur, ventral; **c,** VI ♂ Ur, dorsal; **d,** VI ♂ habitus, left lateral; **e,** VI ♀ habitus, right, lateral; **f,** V ♀ habitus, right lateral; **g,** V ♂ habitus, right lateral.

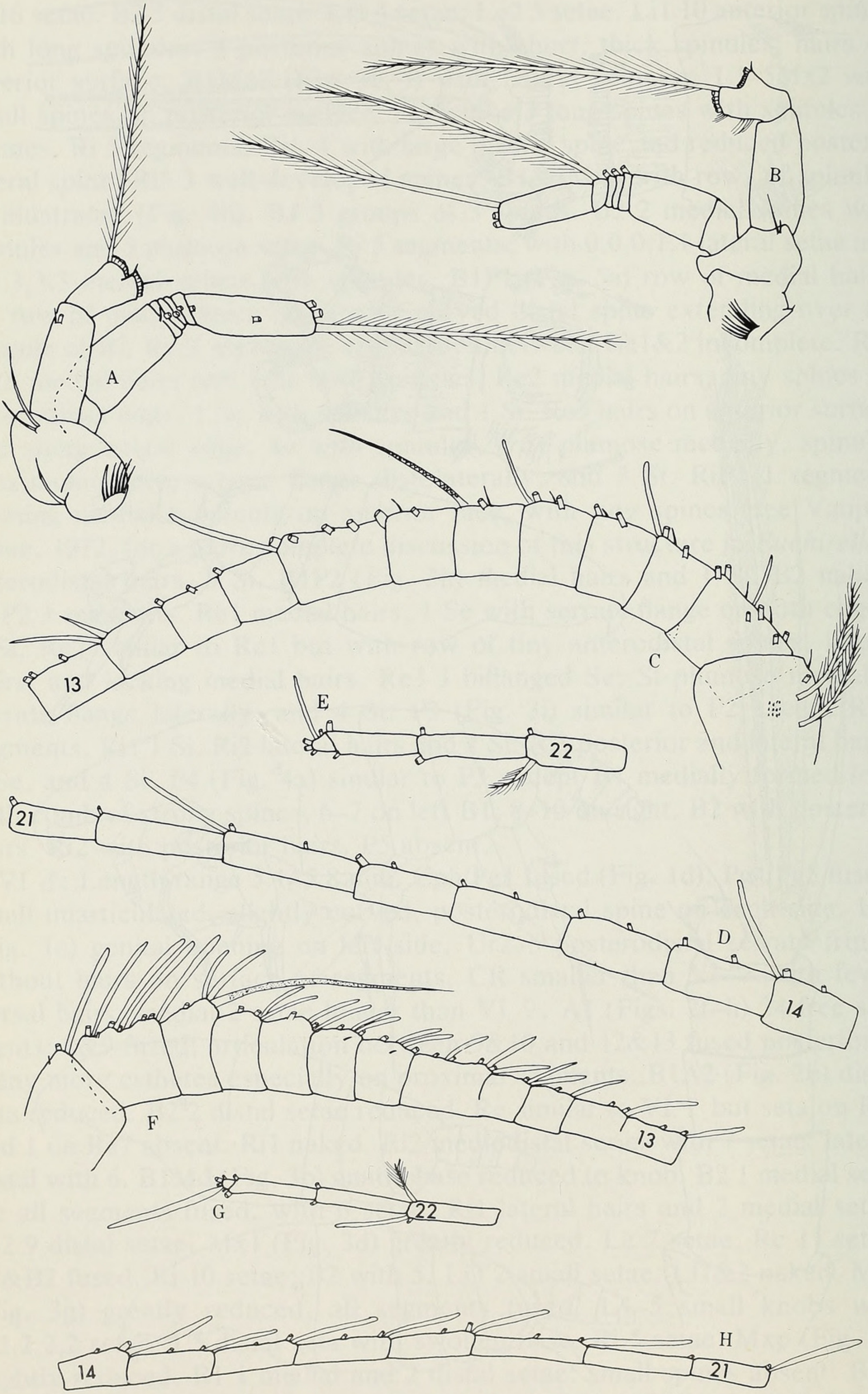

Fig. 2. *Pseudochirella squalida*: **a,** VI ♀ A2; **b,** VI ♂ A2; **c,** VI ♀ A1, 1–13; **d,** VI ♀ A1, 14–21; **e,** VI ♀ A1, 22–25; **f,** VI ♂ A1, 1–13; **g,** VI ♂ A1, 14–21; **h,** VI ♂ A1, 22–25.

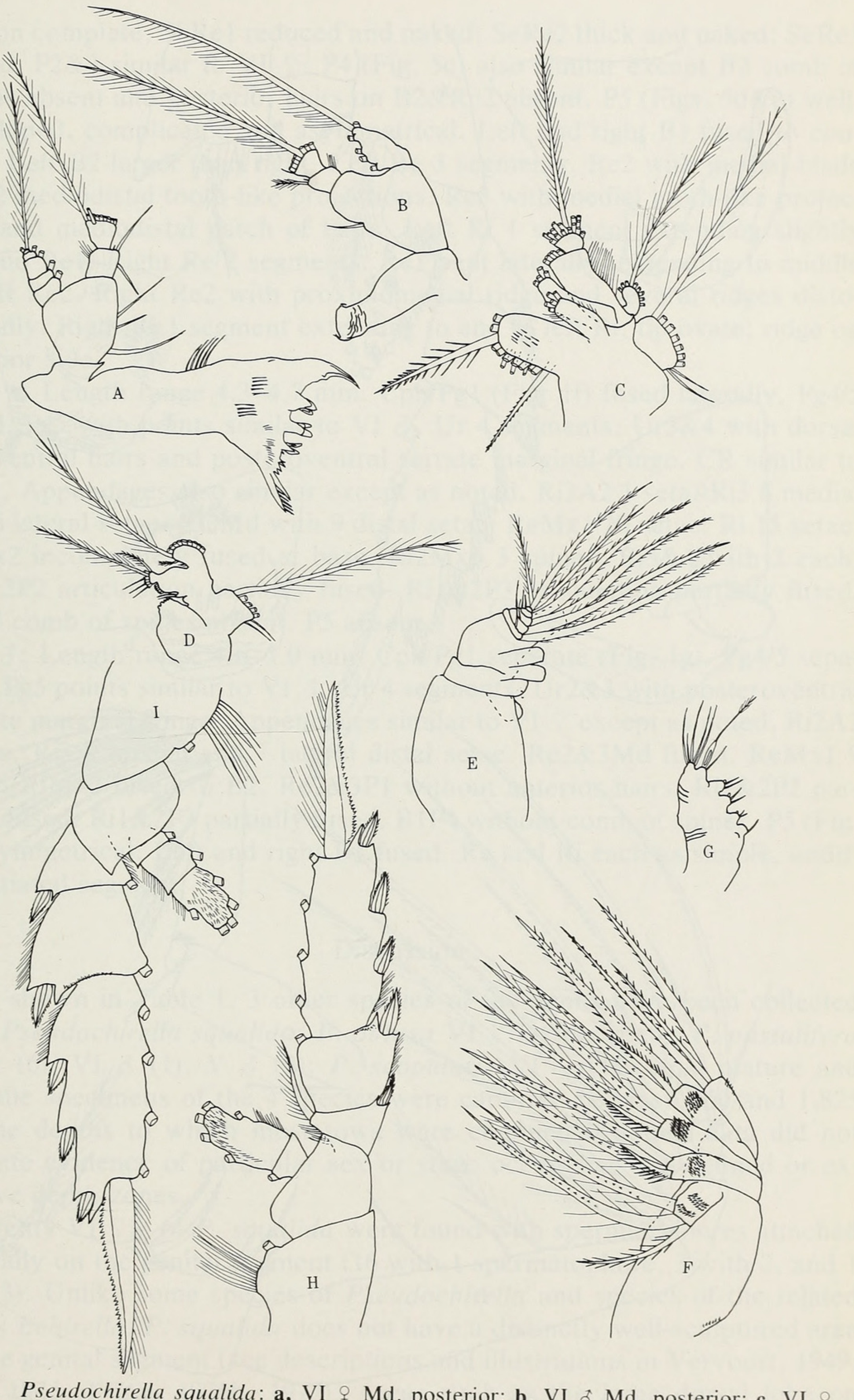

Fig. 3. *Pseudochirella squalida*: **a,** VI ♀ Md, posterior; **b,** VI ♂ Md, posterior; **c,** VI ♀ Mx1, posterior; **d,** VI ♂ Mx1, posterior; **e,** VI ♀ Mx2, posterior; **f,** VI ♀ Mx2, anterior; **g,** VI ♂ Mx2, posterior; **h,** VI ♀ P2, posterior; **i,** VI ♀ P3, posterior.

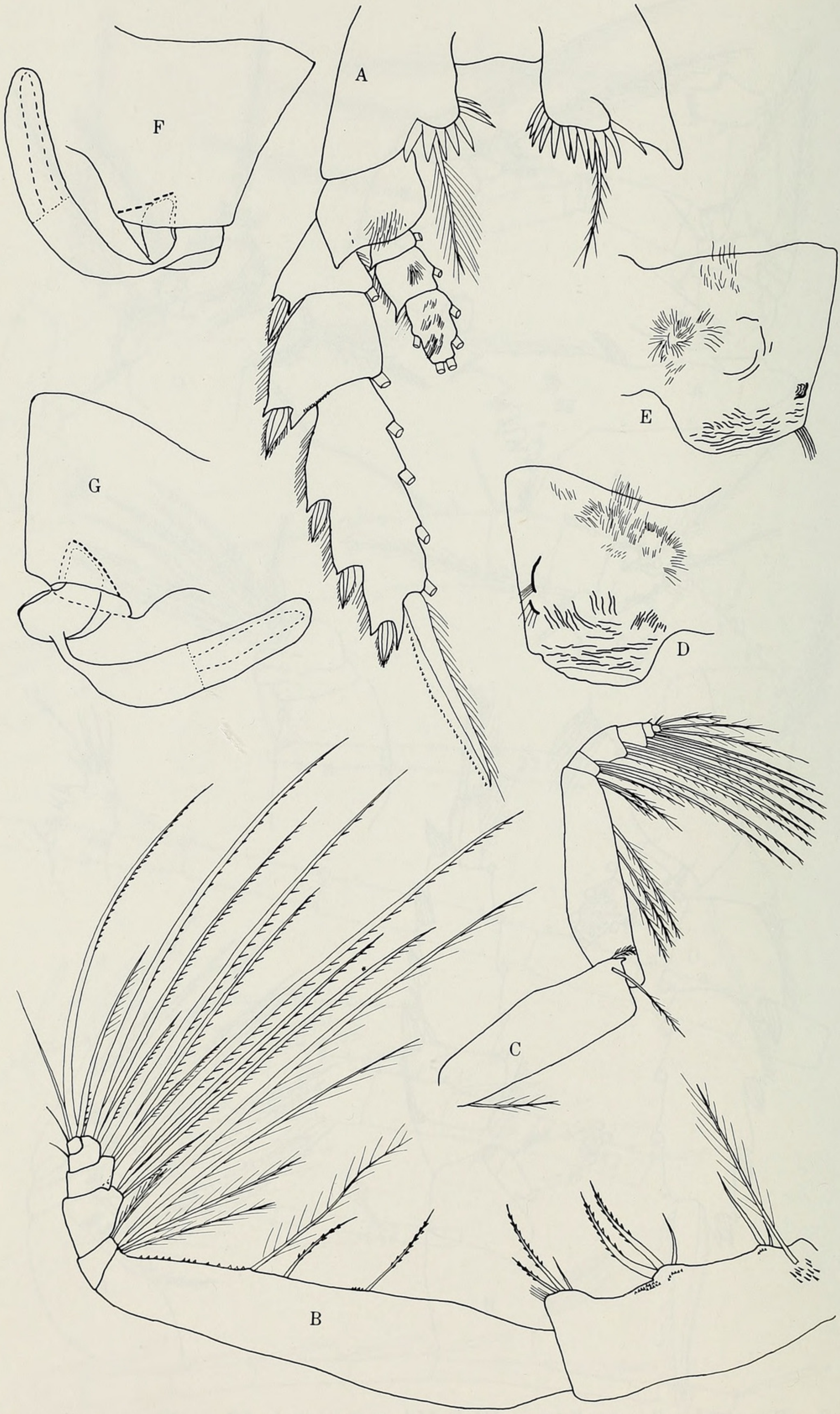

Fig. 4. *Pseudochirella squalida*: **a,** VI ♀ P4, posterior; **b,** VI ♀ Mxp, posterior; **c,** VI ♂ Mxp, posterior; **d,** VI ♀ genital segment, right lateral; **e,** VI ♀ genital segment, left lateral; **f,** VI ♀ genital segment with spermatophore, left lateral; **g,** VI ♀ genital segment with spermatophore, right lateral.

ulation complete; SeRe1 reduced and naked; SeRe2 thick and naked; SeRe3 naked. P2&3 similar to VI ♀. P4 (Fig. 5c) also similar except B2 comb of spines absent and posterior hairs on B2&Re2 absent. P5 (Figs. 5d&e) well-developed, complicated and asymmetrical. Left and right B1 fused to coupler. Left B2 larger than right. Left Re 3 segments. Re2 with medial blade and 2 mediodistal tooth-like projections. Re3 with medial tooth-like projection and mediodistal patch of hairs. Left Ri 1 segment extending slightly beyond Re1. Right Re 2 segments. Re1 bent laterally, extending to middle of left Re2. Right Re2 with proximomedial ridge and several ridges distolaterally. Right Ri 1 segment extending to end of left Ri; tip ovate; ridge on anterior side.

V ♀: Length range 4.3–4.7 mm. Cph/Pg1 (Fig. 1f) fused laterally. Pg4/5 fused. Pg5 with points similar to VI ♂. Ur 4 segments. Ur3&4 with dorsal and ventral hairs and posteroventral serrate marginal fringe. CR similar to VI ♀. Appendages also similar except as noted. Ri2A2 1 seta. Ri3 8 medial and 6 lateral setae. Ri2Md with 9 distal setae. ReMx1 10 setae; Ri 15 setae. RiMx2 incompletely fused at base. Ri2Mxp 3 spines; Ri3&4 with 2 each. Ri1&2P2 articulation partially fused. Ri1&2P3 articulation partially fused. B1P4 comb of spines absent. P5 absent.

V ♂: Length range 4.6–5.0 mm. Cph/Pg1 separate (Fig. 1g). Pg4/5 separate. Pg5 points similar to VI ♂. Ur 4 segments. Ur2&3 with posteroventral serrate marginal fringe. Appendages similar to VI ♀ except as noted. Ri2A2 1 seta. Ri3 8 medial and 7 lateral distal setae. Re2&3Md fused. ReMx1 9 setae. RiMx2 fused to B2. Re2&3P1 without anterior hairs. Ri1&2P2 partially fused. Ri1&2P3 partially fused. B1P4 without comb of spines. P5 (Fig. 5b) symmetrical. Left and right B1 fused. Re and Ri each as simple, undifferentiated segment.

Discussion

As shown in Table 1, 3 other species of the genus have been collected with *Pseudochirella squalida*: *P. obtusa* VI ♀ (1 specimen); *P. pustulifera* VI ♀ (6), VI ♂ (1), V ♂ (2); *P. scopularis* VI ♀ (1). Most mature and juvenile specimens of the 4 species were captured between 400 and 1,825 m, the depths to which most tows were confined. Capture data did not indicate evidence of particular sex or stage occupying well-defined or exclusive depth zones.

Twenty VI ♀♀ of *P. squalida* were found with spermatophores attached ventrally on the genital segment (16 with 1 spermatophore, 3 with 2, and 1 with 3). Unlike some species of *Pseudochirella* and species of the related genus *Echirella, P. squalida* does not have a distinctly well-sculptured area on the genital segment (see descriptions and illustrations in Vervoort, 1949; Park 1975, 1976a, 1976b, 1977). Areas such as the large dorsal lobe on *Euchirella messinensis* and the large protrusion on *E. truncata* serve as spermatophore attachment points away from the genital field. Fertilization

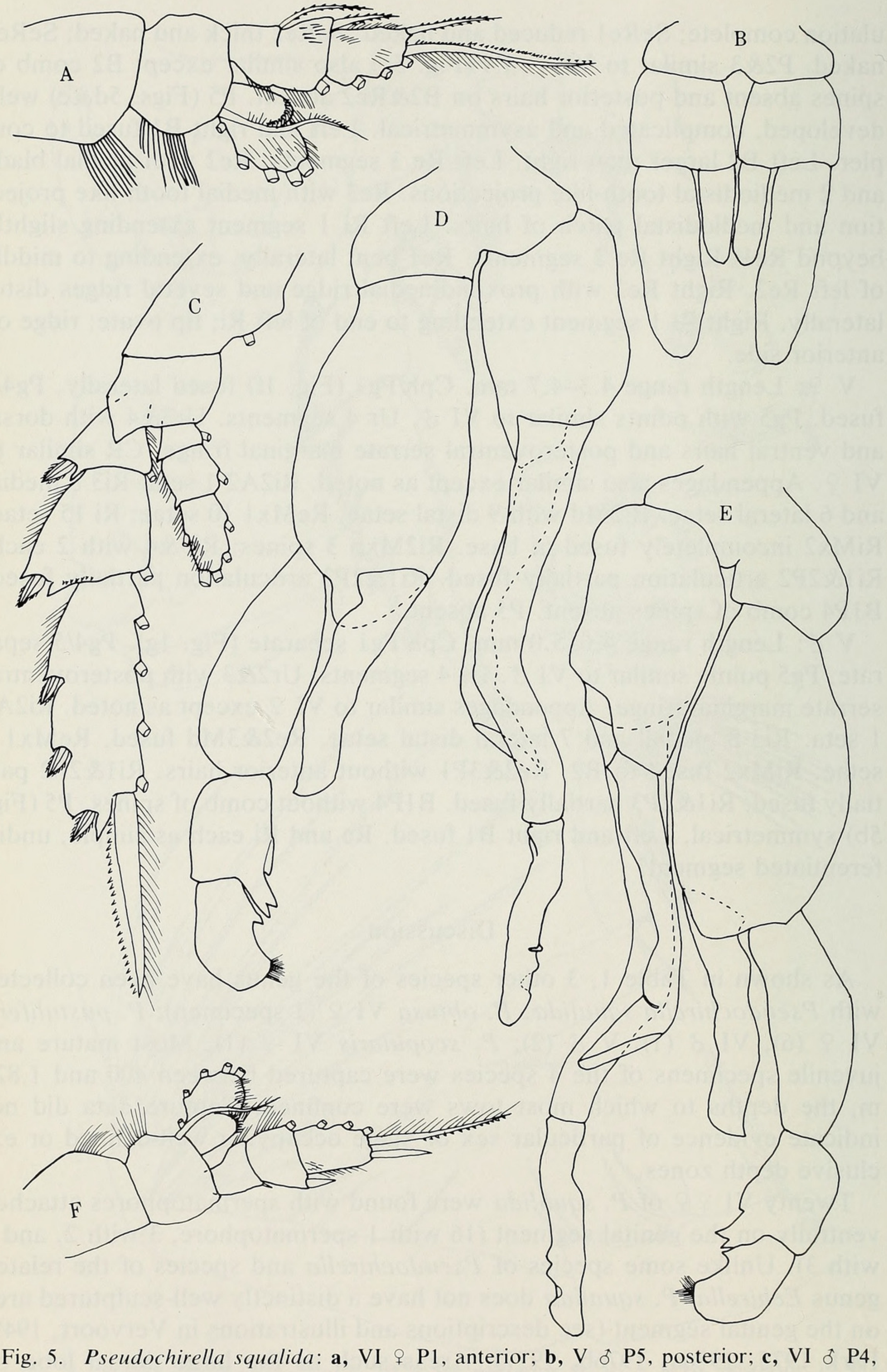

Fig. 5. *Pseudochirella squalida*: **a,** VI ♀ P1, anterior; **b,** V ♂ P5, posterior; **c,** VI ♂ P4, posterior; **d,** VI ♂ P5, posterior; **e,** VI ♂ P5, anterior; **f,** VI ♂ P1, anterior.

Table 1.—Samples from which *Pseudochirella squalida* were taken.

Cruise	Station	Date	Latitude (N)	Longitude (W)	Tow depth (m)	VI ♀	VI ♂	V ♀	V ♂	other *Pseudochirella*
2	7C	23 July 75	38°52′	072°04′	400–600				1	
2	14A	24 July 75	38°38′	072°03′	800–1,000	1				
2	17B	24 July 75	38°33′	072°10′	600–800				1	
2	23A	25 July 75	38°35′	072°08′	1,425–1,839					*pustulifera* 3 VI ♀, 2 V ♂ *obtusa* 1 VI ♀
2	24B	25 July 75	39°03′	072°04′	600–800	3	1	1	4	
2	24C	25 July 75	39°03′	072°04′	500–600	1		2	3	
2	25C	26 July 75	38°41′	072°02′	400–500	1		1		
2	45B	28 July 75	38°44′	072°02′	800–947					*pustulifera* 1 VI ♀
2	47B	28 July 75	38°56′	072°20′	600–700	2				
2	51B	29 July 75	38°51′	072°28′	700–800	1				
2	61A	30 July 75	38°52′	072°24′	900–1,085	1				
2	65B	31 July 75	38°46′	072°20′	600–700		1			
2	65C	31 July 75	38°46′	072°20′	500–600	1				
2	75A	1 August 75	38°38′	072°43′	700–800	2			1	
2	75C	1 August 75	38°38′	072°43′	500–600				1	*scopularis* 1 VI ♀
2	78A	1 August 75	38°43′	072°45′	700–800				1	
2	78C	1 August 75	38°43′	072°45′	500–600	2		2	6	
2	82A	2 August 75	38°48′	072°40′	700–800	2				
2	82B	2 August 75	38°48′	072°40′	600–700				4	
2	82C	2 August 75	38°48′	072°40′	500–600				1	
2	85C	2 August 75	38°57′	072°25′	800–1,000	1	1			
3	2A	20 February 76	37°01′	074°08′	400–500	28	6	15	30	
3	2B	20 February 76	37°01′	074°08′	300–400	8		3	5	
3	2C	20 February 76	37°01′	074°08′	200–300				1	
3	2M	20 February 76	37°01′	074°08′	0–200	1		1		
3	3A	21 February 76	37°09′	074°06′	700–800	1				*pustulifera* 3 VI ♀
3	3B	21 February 76	37°09′	074°06′	600–700	15	1	3	2	*pustulifera* 1 VI ♂

Table 2.—Characters which exhibit sexual dimorphism in stage V or stage VI and their state in the remaining stage.

Character	VI ♀	VI ♂	V ♀	V ♂
Cph/Pgl	fused dorsally	fused entirely	fused laterally	free
Pg4/Pg5	fused entirely	fused entirely	fused entirely	free
Pg5 points	absent	present	present	present
Ur	4 segments	5 segments	4 segments	4 segments
position, genital opening	ventral	lateral (left)	absent	absent
Ur marginal hairs	Ur 2&3	none	none	none
Ur marginal fringe	none	Ur 2–4	Ur 2&3	Ur 2&3
CR setae		longer than VI ♀	similar to VI ♀	similar to VI ♀
Al	8&9 fused 9&10 free 12&13 free	8&9 fused 9&10 part free 12&13 part free	similar to VI ♀	similar to VI ♀
A2 setae Re	9	7	9	9
Ri	19	15	15	16
Md gnathobase	well developed	reduced teeth absent	well developed	well developed
setae B2	3	1	3	3
segments Re	all free	all fused	all free	2&3 fused
setae Ri	13	11	12	12
Mx1 size		greatly reduced	similar to VI ♀	similar to VI ♀
spines Li1	14	0	14	14
setae Li2	5	0	5	5
setae Li3	4	2	4	4
setae Ri	16	10	15	15
setae Re	9	11	10	9
setae Le	9	7	9	9
Mx2 size		greatly reduced	similar to VI ♀	similar to VI ♀
spines L1	3	1	3	3
spines L2	3	2	3	3
spines L3	3	2	3	3
spines L4	3	2	3	3
spines L5	3	2	3	3
spines Ri	11	5	11	11
segments Ri	all free	all free	Ri1/B2 fused	all free
Mxp size		reduced slightly	similar to VI ♀	similar to VI ♀

Table 2.—Continued.

Character	VI ♀	VI ♂	V ♀	V ♂
spines B1	9	3	9	9
spines Ri	18	15	15	15
P1 size		reduced slightly	similar to VI ♀	similar to VI ♀
Ri1 & 2	partly fused	free	partly fused	partly fused
margin Se	spinules	smooth	spinules	spinules
P4 B1	spine comb	absent	absent	absent
P5	absent	large complex	absent	small simple

tubes serve to connect the sperm sac to the genital opening (unpublished observations).

Spermatophores of *P. squalida* were attached on the sternum to the left or right of the genital plate. Multiple spermatophores were also attached in this area. Figs. 4f, g show left and right lateral views of VI ♀ genital segment with the sperm sac narrowing to a short neck and attached to the left sternum by a simple plate. Several spermatophores including the one illustrated were partly empty, the distolateral areas absent. A similar situation was reported for *Euchaeta norvegica* and the implications discussed by Ferrari (1977). In the illustrated example the genital plate appears flexed up into the genital segment and a large mass of material seems to fill the vacated space below it. This mass was not detected on specimens with full spermatophores. Due to the thick cuticle and opaque structures associated with the spermatophore it was impossible to determine anything more of the relations of the mass, genital plate and pore, and seminal receptacle.

Characters which exhibit sexual dimorphism in either stages V or VI and their development in the remaining stage are described in Table 2. Very little is known of calanoid behavior in general or even of the function of various appendages, segments, or their armament. Nothing is known of the behavior of *P. squalida*. However some suggestions about the function of these sexually dirmorphic characters can be made based on studies of other calanoids. The characters can be artificially grouped into: those for which some information is available through behavioral observations of homologous morphological characters in other calanoids; those for which there is no homologous behavioral information but information about comparative morphology may permit some conjecture; those for which no statements can be made.

In the first group the reduction in size and/or ornamentation or A2, Md, Mx1, Mx2, and Mxp in VI ♂ indicates an inability of these animals to feed. This is further substantiated by the degenerate condition of the gut (unpub-

Table 3.—Comparison of sexual dimorphism (sd) and bilateral asymmetry (ba) for both sexes of stage V and stage VI.

	ba	sd
V	♀ None	Cph/Pg1 articulation Pg4/Pg4 articulation A2 Md Mx1 Mx2 P5
	♂ None	
VI	♀ Genital segment P4 comb of spines	Cph/Pg1 articulation Pg4 points Ur-shape and number of segments Ur-margin of segments CR-length of setae A1 A2 Md Mx1 Mx2 Mxp P1 P4 P5
	♂ Genital segment P5	

lished observations). Significant reductions occur in teeth of B1Md gnathobase and strong spines of LiMx1 and L1–5Mx2 which probably hold, tear, and crush the food prior to injestion.

Concerning the VI ♂ P5 and VI ♀ Ur1 (genital segment) much has been written about the Centropagidae (Lee, 1972, and Blades, 1977), *Labidocera* (Fleminger, 1975 and Blades & Youngbluth, 1979) and *Euchaeta norvegica* (Hopkins *et al.*, 1978). The VI ♂ uses his P5 to clasp the ♀ and position himself immediately prior to spermatophore transfer which is accomplished by his left ReP5. The shape of the VI ♀ genital segment may mirror the clasp of her mate as well as the position of the spermatophore.

Regarding the second group of characters, sexual dimorphism in A1 of VI ♀ and ♂ is manifested in greater number of esthetes of the ♂. Griffiths & Frost (1976) state that VI ♂ esthetes on *Calanus pacificus* and *Pseudocalanus* sp. may be chemoreceptors upon which dissolved organic matter produced by VI ♀ accumulates. They suggest this organic matter is a pheromone.

CR setae of VI ♀ are the initial contact point of VI ♂ during mating of the heterarthandrid copepods *Centropages typicus* and *Labidocera aestiva* (Blades, 1977, and Blades & Youngbluth, 1979). The VI ♂ grasps the VI

♀ CR setae with his geniculate right A1. Obviously this behavior does not occur during mating of *P. squalida* as VI ♂ lacks the geniculation. However such as function for the CR setae should not be precluded since another appendage could be used by the VI ♂ in the initial contact.

No direct information is available about the function of the comb of spines on B1P4 VI ♀. Considering the absence of P5 in VI ♀ and the position of the spines, it is possible that they function in an analogous manner to the reduced P5 in VI ♀ of other calanoid females. Lawson (1977) describes VI ♀ P5 of the Candaciidae as a "secondary sexual structure." Fleminger (1975) calls it a "sexually modified character" of *Labidocera*. Blades & Youngbluth (1979) have recently reported that *Labidocera aestiva* VI ♀ uses P5 to remove the spermatophore after sperm discharge.

P1 is morphologically similar to P2–4 but differs not only by the presence of the modified Ri and B2 setae but also in the ornamentation of SE Re1–3. The further sexual dimorphism in Se Re1–3 VI ♂, reduction in size and ornamentation (VI ♀ morphology is virtually identical to V ♀ and V ♂), would appear to follow the progression of such reductions in the feeding appendages anterior to it, as there are only minor morphological changes in swimming appendages posteriorly.

The functional significance of such sexually dimorphic characters as Cph/Pg1 articulation, Pg4/5 articulation, points on Pg5, number of Ur segments, position of genital opening, and posterior margins of Ur segments is not understood.

Table 3 briefly lists those external morphological characters which exhibit sexual dimorphism in either VI ♀&♂ or V ♀&♂ and compares these to characters exhibiting bilateral asymmetry. Bilateral asymmetry is apparent only in the adult, is not manifested in one sex more than the other and involves known primary or secondary sexual characters involved in reproduction.

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