

The developmental stages of *Pseudodiaptomus hessei* (Copepoda: Calanoida)

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Nauplii and copepodid developmental stages of the estuarine copepod, *Pseudodiaptomus hessei*, are described and illustrated. Five post-embryonic naupliar and five copepodid stages (excluding adults) are distinguished. Diagnostic characteristics separating stages are also tabulated.

Nauplius- en kopepodiet-ontwikkelingsstadia van die getyrvier Copepoda-spesie, *Pseudodiaptomus hessei*, word beskryf en geïllustreer. Vyf nauplius- en vyf kopepodiet-stadia (volwassenes uitgesluit) is uitgekien. Diagnostiese kenmerke wat die stadia van mekaar onderskei, word getabuleer.

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The genus *Pseudodiaptomus* is to date represented by 70 species worldwide (Walter 1984). Of these, the naupliar and copepodid stages of only five have been described. They are *P. euryhalinus* from the coast of California (Johnson 1948), *P. aurivilli* from the Gulf of Mannar, India (Ummerkutty 1964), *P. coronatus* from Woods Hole, Massachusetts (Grice 1969), *P. marinus* from the Inland Sea of Japan (Uye & Onbe 1975) and *P. richardi inaequalis* from the La Plata River, Argentina (Cicchino 1975). The naupliar development of a sixth species, *P. ardjuna*, occurring along the coast of Bombay, has also been documented (Alvarez & Kewalramani 1969). Although Hart (1973) listed criteria to aid identification of the different stages of *P. hessei*, no formal description has been published to date.

Pseudodiaptomus hessei is widely distributed in estuaries in southern Africa (Grindley 1963). This species attains high population densities and may dominate zooplankton biomass, particularly after fluvial flooding (Wooldridge & Bailey 1982). Five post-embryonic naupliar development stages of *P. hessei* are evident. Eggs hatch into Stage 2 nauplii, the first stage being completed before hatching. This was also reported for most other pseudodiaptomids, although Uye & Onbe (1975) reported a first naupliar stage for *P. marinus*.

Methods

Developmental stages were first identified from animals reared in the laboratory. These were correlated with animals collected in the field. Nauplii were measured from the anterior margin to the tip of the caudal region, excluding spines. Copepodids were measured from the anterior border to the end of the caudal rami. The upper size limit reported for each stage represents animals sampled in winter (water temperature of 13°C), while lower range limits are representative for summer animals (26°C) (Table 1). Thirteen to 42 individuals of each stage were measured to determine average lengths.

Animals were sampled with a modified WP2 plankton net and preserved in approximately 5% estuarine water formalin. Different appendages were removed and drawn with the aid of a camera lucida.

Since adults (copepodid Stage 6) were adequately described by Grindley (1963) only copepodid Stages 1 to 5 are described.

Nauplius larvae

The body is pear-shaped becoming more elongated after each moult. Body lengths and diagnostic characteristics are indicated in Table 1.

Caudal region of N2 (Figure 1A) bearing one strong and one fragile spine. Fine hairs present in horizontal rows just anterior to caudal armature. Caudal region of third naupliar stage (Figure 2A) bilobed. A strong spine present on the right lobe while the other bears a slender,

Table 1 Sizes and diagnostic characteristics separating developmental stages of *Pseudodiaptomus hessei*. In the nauplii stages, data refer to the number of setae in the group. a = aesthetask; C5M and C5F = copepodid Stage 5 male and female respectively

	Nauplii stages					
	N2	N3	N4	N5	N6	
Size range (mm)	0,168 – 0,181	0,216 – 0,234	0,269 – 0,275	0,308 – 0,328	0,360 – 0,390	
Setal arrangement on terminal antennule segment	2 a 1	3 a 3	5 a 5	6 a 7	6 a 9	
	Copepodid stages					
	C1	C2	C3	C4	C5M	C5F
Size range (mm)	0,508–0,541	0,628–0,688	0,791–0,888	1,064–1,065	1,131–1,283	1,376–1,580
Number of prosomal segments	4	5	6	6	6	6
Number of urosomal segments	2	2	2	3	4	3
Number of leg pairs	2	3	4	5	5	5

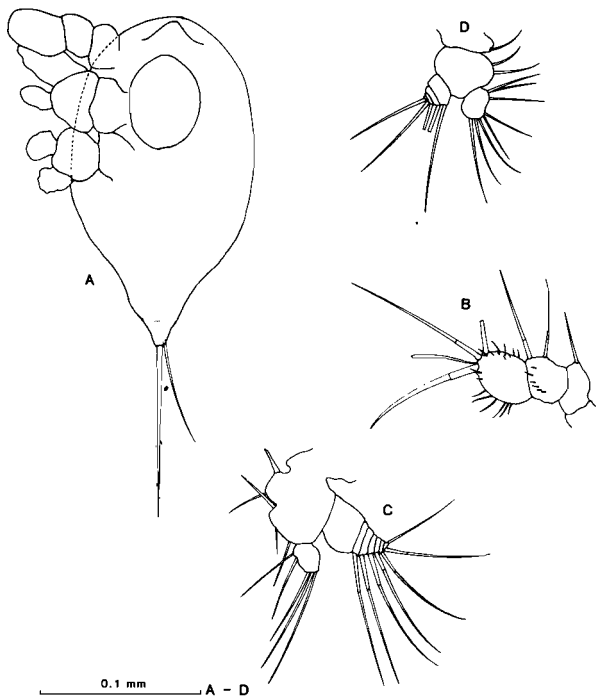


Figure 1 Nauplius Stage 2. A. Body in ventral view; B. Antennule; C. Antenna; D. Mandible.

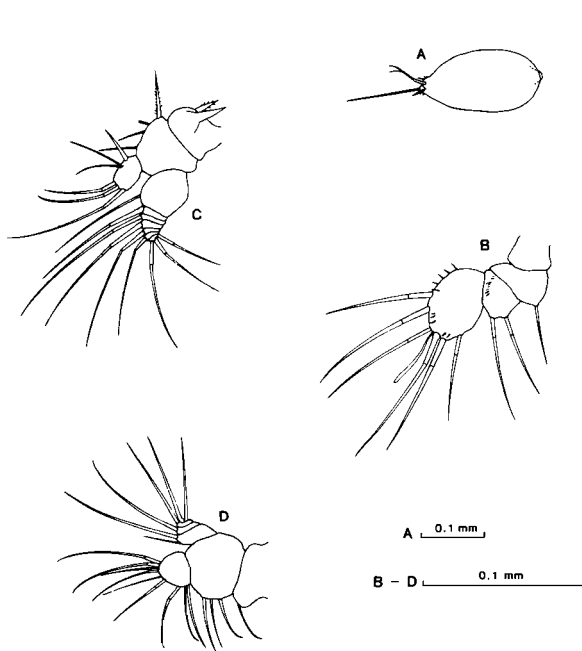


Figure 2 Nauplius Stage 3. A. Body in dorsal view; B. Antennule; C. Antenna; D. Mandible.

dorsally directed spine. The slender spine bifurcate. A short spine present at the base of each of the longer spines. Short spines becoming larger and more conspicuous in Stage 4 (Figure 3A). One extra spine on each caudal lobe in Stage 6 (Figure 5A).

Antennule (Figures 1B, 2B, 3B, 4B, 5B) four segmented. Basal segment non-setose, the second and third with one and two setae respectively. Setation on the terminal segment increases with each instar (Table 2).

Antenna (Figures 1C, 2C, 3C, 4C, 5C). Stage 2 has

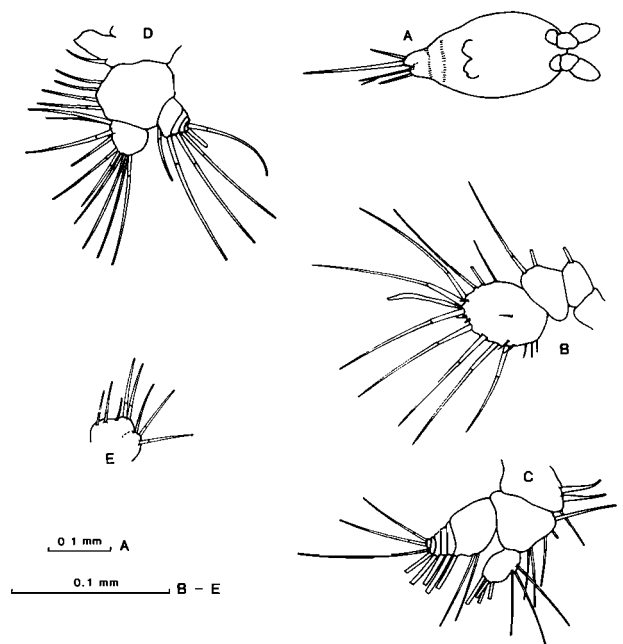


Figure 3 Nauplius Stage 4. A. Body in ventral view; B. Antennule; C. Antenna; D. Mandible; E. Maxillule.

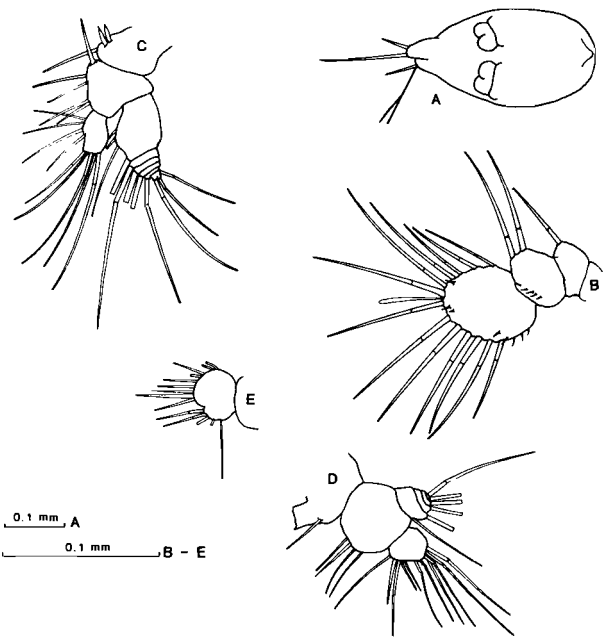


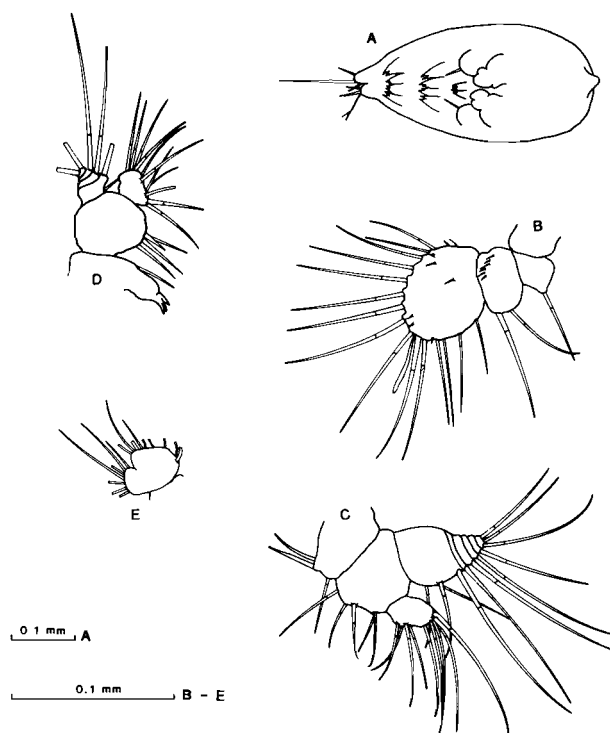
Figure 4 Nauplius Stage 5. A. Body in ventral view; B. Antennule; C. Antenna; D. Mandible; E. Maxillule.

one basipodite segment bearing a strong masticatory process and four setae. Subsequent stages have two basipodite segments. Two strong spines are present on the first with the addition of one seta in Stages 4 to 6. Stage 3 has four setae on the second basipodite segment while the remaining stages bear five. Armature of the endo- and exopodites are indicated in Table 2.

Mandible (Figures 1D, 2D, 3D, 4D, 5D) consisting of two basal segments, a single-segmented endopodite and a four-segmented exopodite. Stage 2 bears one seta on the first and two on the second basipodite. In the third

Table 2 Setation of naupliar appendages, a = aesthetask

Stage	Antennule (Terminal segment)	Antenna		Mandible		Maxillule	
		Endopodite	Exopodite	Endopodite	Exopodite	Inner lobe	Outer lobe
2	3 (2 a 1)	5	7	8	5	–	–
3	6 (3 a 3)	6	9	9	6	–	–
4	10 (5 a 5)	7	10	10	6	5	3
5	13 (6 a 7)	9	11	11	6	9	5
6	14 (6 a 9)	9	11	11	6	9	7

**Figure 5** Nauplius Stage 6. A. Body in ventral view; B. Antennule; C. Antenna; D. Mandible; E. Maxillule.

naupliar instar the second basipodite bears three setae. The first basipodite of the remaining stages armed with a blade and one seta while the second basipodite bears four setae. Endo- and exopodite armed as shown in Table 2.

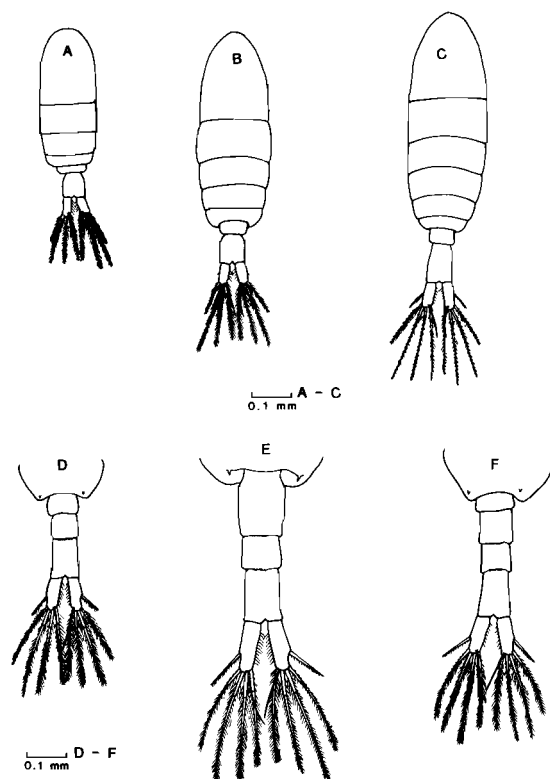
Maxillule (Figures 3E, 4E, 5E) present from Stage 4. Maxilla represented by a single seta in Stages 5 and 6. Rudimentary maxillipeds present in Stage 6 (Figure 5A).

Copepodid stages

Body lengths for the respective stages are indicated in Table 1.

Prosomal and urosomal segments increase in number during development (Table 1). In the first three stages lateral margins of the last prosomal segments are rounded whereas in Stages 4 and 5 these segments carry a short spine on the posteriodorsal corners (Figures 6A–F).

A row of teeth present on posteriodorsal margin of the second urosomal segment of Stage 4; on the first and

**Figure 6** A. Copepodid Stage 1, dorsal. B. Copepodid Stage 2, dorsal. C. Copepodid Stage 3, dorsal. D. Urosome, Copepodid Stage 4. E. Urosome, Copepodid Stage 5 female. F. Urosome, Copepodid Stage 5 male.

second urosomal segments of Stage 5 in the female and the two middle urosomal segments of Stage 5 in the male (Figures 6D–F).

Caudal rami symmetrical, bearing four terminal setae on each ramus. A small seta present dorsally near inner distal angle. Fine seta present along inner margin of the caudal rami. Hair-like rudimentary setae present on the outer margins of the caudal rami of C2. These setae become more prominent with each instar.

Antennular segmentation increases with each instar (Table 3), armature as illustrated (Figures 7A, 8A, 9A, 11A, 13A, 13B).

Antenna (Figures 7B, 8B, 9B, 11B, 13D) consisting of basipodite, four-segmented endopodite and a two-segmented exopodite. Setation given in Table 3.

First mandibular basipodite bearing teeth and a single

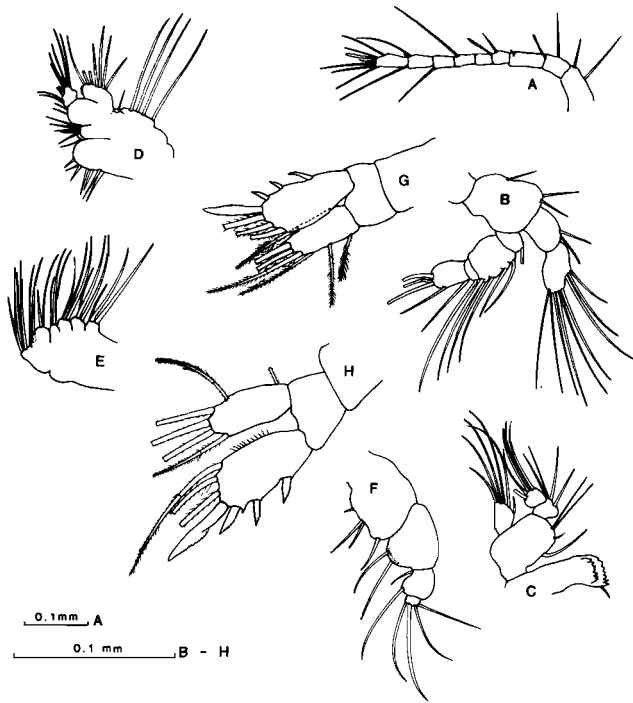


Figure 7 Copepodid Stage 1. A. Antennule; B. Antenna; C. Mandible; D. Maxillule; E. Maxilla; F. Maxilliped; G. First swimming leg; H. Second swimming leg.

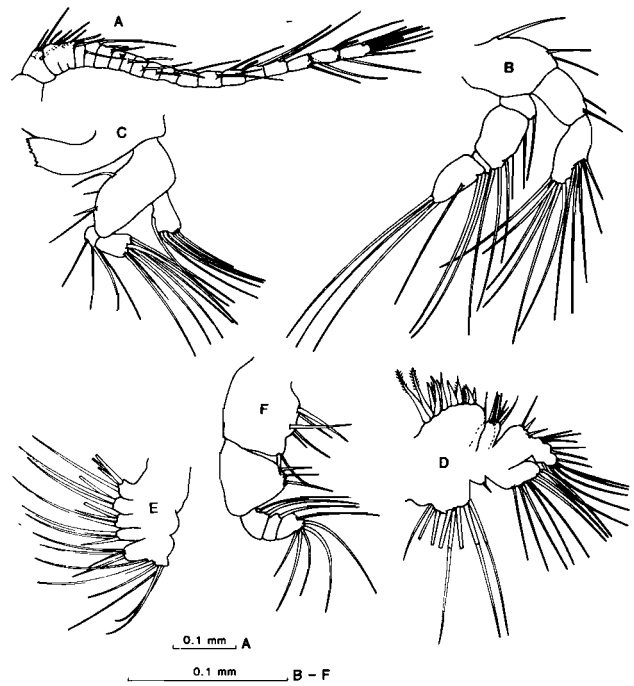


Figure 9 Cephalosome, Copepodid Stage 3. A. Antennule; B. Antenna; C. Mandible; D. Maxillule; E. Maxilla; F. Maxilliped.

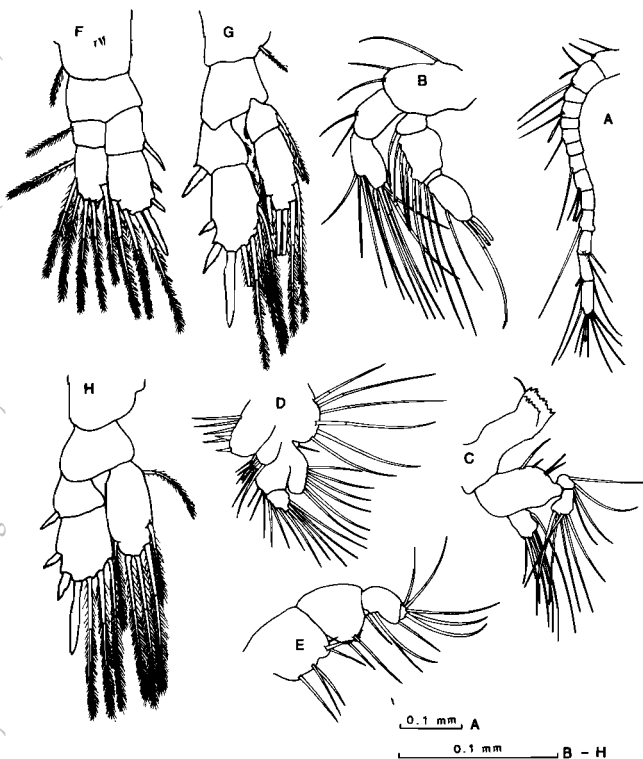


Figure 8 Copepodid Stage 2. A. Antennule; B. Antenna; C. Mandible; D. Maxillule; E. Maxilliped; F. First swimming leg; G. Second swimming leg; H. Third swimming leg.

seta (Figures 7C, 8C, 9C, 11C). Setation on second basipodite, endo- and exopodite described in Table 3.

Maxillule (Figures 7D, 8D, 9D, 11D, 13E) consisting

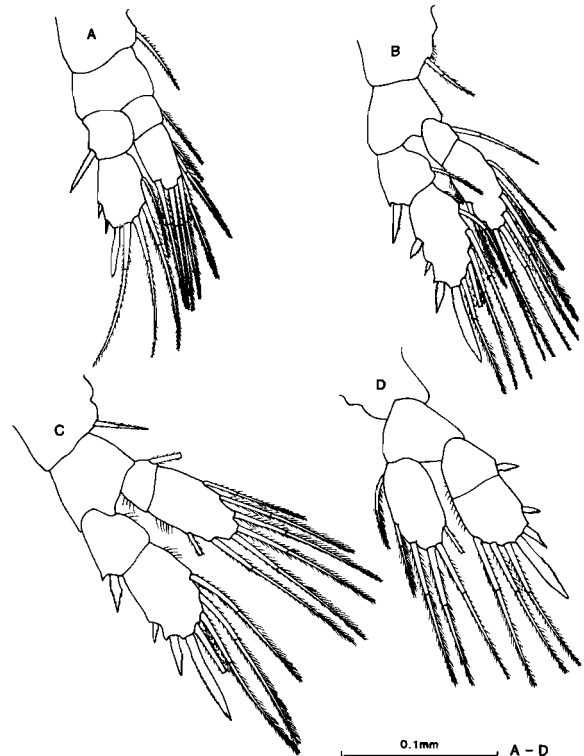


Figure 10 Copepodid Stage 3. A. First swimming leg; B. Second swimming leg; C. Third swimming leg; D. Fourth swimming leg.

of three inner and two outer lobes as well as an exo- and endopodite. Setation as in Table 3.

Maxilla (Figures 7E, 9E, 13F) with five setose endites (Table 3).

Table 3 Segmentation and setation of copepodid cephalosomatic appendages. Setae – arabic numerals, spines – roman numerals

Stage	Antennule segmen- tation	Antenna		Mandible		Maxillule		Maxilla		Maxilliped		
		Segment	Setation	Segment	Setation	Segment	Setation	Segment	Setation	Segment	Setation	
C1	9	Basipodite	3	2nd basipodite	4	1st outer lobe	4	Endite	1	3	1	4
		Endopodite	1	Endopodite	1	2nd outer lobe	1		2	3	2	2
			2		2	1st inner lobe	VII		3	3	3	2
			3	Exopodite	6	2nd inner lobe	3		4	3	4	4
			4			3rd inner lobe	3		5	2		
		Exopodite	1			Exopodite	7	Distal				
			2			Endopodite	11	end		6		
C2	14	Basipodite	3	2nd basipodite	4	1st outer lobe	6	Endite	1	3	1	5 I
		Endopodite	1	Endopodite	1	2nd outer lobe	1		2	3	2	2
			2		2	1st inner lobe	VII		3	3	3	4
			3	Exopodite	6	2nd inner lobe	3		4	3	4	5
			4			3rd inner lobe	3		5	2		
		Exopodite	1			Exopodite	6	Distal				
			2			Endopodite	11	end		6		
C3	19	Basipodite	3	2nd basipodite	4	1st outer lobe	6	Endite	1	4	1	6 I
		Endopodite	1	Endopodite	1	2nd outer lobe	1		2	3	2	3
			2		2	1st inner lobe	VII		3	3	3	2
			3	Exopodite	6	2nd inner lobe	3		4	3	4	1
			4			3rd inner lobe	3		5	4	5	6
		Exopodite	1			Exopodite	8	Distal				
			2			Endopodite	14	end		6		
C4	22	Basipodite	3	2nd basipodite	4	1st outer lobe	9	Endite	1	4	1	8 I
		Endopodite	1	Endopodite	1	2nd outer lobe	1		2	3	2	3
			2		2	1st inner lobe	IX 2		3	3	3	4
			3	Exopodite	6	2nd inner lobe	3		4	3	4	4
			4			3rd inner lobe	3		5	4	5	2
		Exopodite	1			Exopodite	8	Distal			6	6
			2			Endopodite	15	end		7		
C5	21	Basipodite	3	2nd basipodite	4	1st outer lobe	9	Endite	1	5	1	8 I
		Endopodite	1	Endopodite	1	2nd outer lobe	1		2	3	2	3
			2		2	1st inner lobe	IX 2		3	3	3	6
			3	Exopodite	6	2nd inner lobe	3		4	3	4	4
			4			3rd inner lobe	3		5	4	5	2
		Exopodite	1			Exopodite	9	Distal			6	7
			2			Endopodite	20	end		8		

In Stages 1 and 2, maxilliped four-segmented (Figures 7F, 8E). Segmentation increases to five in Stage 3 (Figure 9F) and six in remaining stages (Figures 11E, 13G). Branched setae, as noted by Grindley (1963) for adults, occur on the third and fourth segments in Stage 4 and on the third, fourth and fifth segments in Stage 5. Setation as in Table 3.

Swimming legs (Figures 7G, 7H, 8F, 8G, 8H, 10, 12, 14). Leg pairs increase in number from two in Stage 1 to five in Stages 4 and 5 (Table 1). Each swimming leg consists of a two-segmented basipodite, the first basipodite segment non-setose in Stage 1 and in the last pair of legs of remaining stages. All other legs with one seta on inner margin. Segmentation and armature of endo- and exopodite of each leg given in Table 4. The spines on all

the legs, except for the fifth pair, are blade-like and serrated.

Fifth pair legs (Figures 12E, 12F, 14E, 14F) first appear in Stage 4. Endopodite represented by a short protrusion which is larger in male left leg. Exopodite spines increase from two terminal and one on outer margin in Stage 4 to two terminal and two lateral spines in Stage 5.

Remarks

Small differences are apparent between the developmental stages of *P. hessei* and those described for other members of the genus. In the nauplii, the caudal armature is asymmetrically bilobed with the right lobe larger than the left. This asymmetry is also reported for *P. ardjuna*.

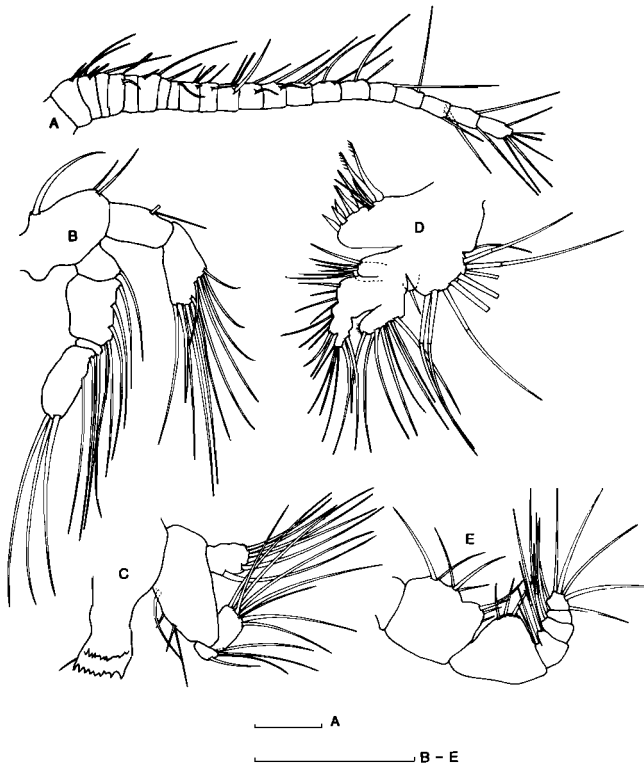


Figure 11 Cephalosome, Copepodid Stage 4. A. Antennule; B. Antenna; C. Mandible; D. Maxillule; E. Maxilliped.

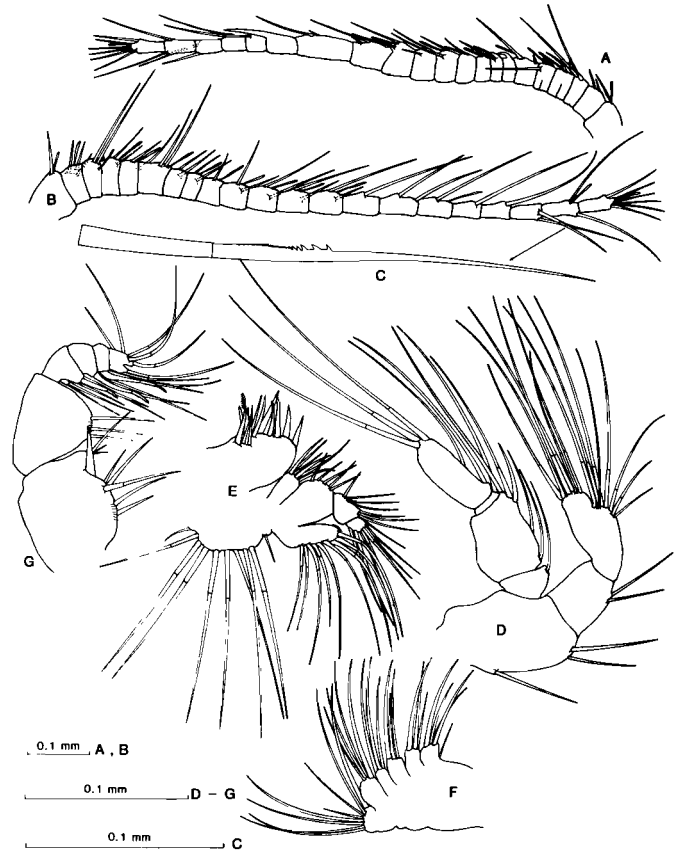


Figure 13 Cephalosome, Copepodid Stage 5. A. Right antennule, male; B. Antennule, female; C. Comb-like seta of female antennule; D. Antenna; E. Maxillule; F. Maxilla; G. Maxilliped.

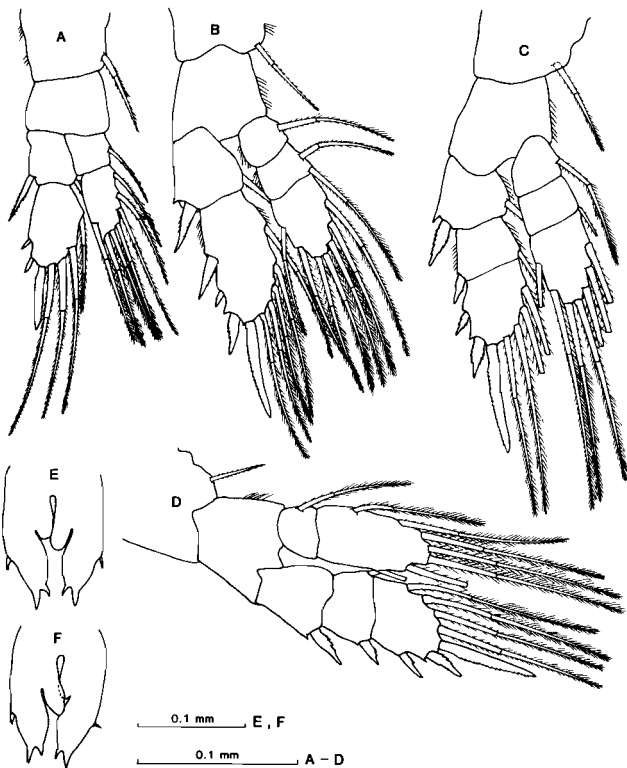


Figure 12 Copepodid Stage 4. A. First swimming leg; B. Second swimming leg; C. Third swimming leg; D. Fourth swimming leg; E. Fifth swimming legs, copepodid Stage 4 female; F. Fifth swimming legs of copepodid Stage 4 male in posterior view.

The slender dorsally directed seta on the smaller lobe differs from other species in that it is split at the end.

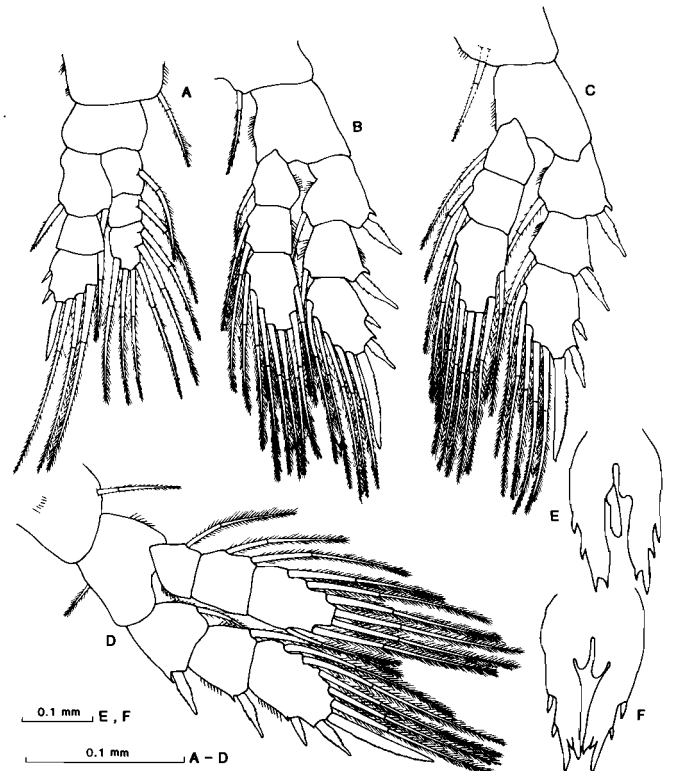


Figure 14 Copepodid Stage 5. A. First swimming leg; B. Second swimming leg; C. Third swimming leg; D. Fourth swimming leg; E. Fifth swimming legs, copepodid Stage 5 male in posterior view; F. Fifth swimming legs of copepodid Stage 5 female.

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Table 4 Segmentation and setation of the swimming legs of *Pseudodiaptomus hessei*. Setae – arabic numerals, spines – roman numerals

Stage	Legs															
	1st pair				2nd pair				3rd pair				4th pair			
	Endopodite		Exopodite		Endopodite		Exopodite		Endopodite		Exopodite		Endopodite		Exopodite	
segment	setae	segment	setae	segment	setae	segment	setae	segment	setae	segment	setae	segment	setae	segment	setae	
C1	1	7	1	3 IV	1	6	1	3 IV								
C2	1	1	1	I	1	1	1	I	1	6	1	I				
	2	6	2	3 III	2	7	2	4 III			2	3 III				
C3	1	1	1	I	1	1	1	1 I	1	1	1	I	1	6	1	I
	2	7	2	4 III	2	8	2	5 IV	2	7	2	4 III			2	3 III
C4	1	1	1	1 I	1	1	1	1 I	1	1	1	1 I	1	1	1	I
	2	7	2	4 III	2	2	2	5 IV	2	1	2	1 I	2	7	2	1 I
					3	7			3	7	3	4 III			3	4 III
C5	1	1	1	1 I	1	1	1	1 I	1	1	1	1 I	1	1	1	1 I
	2	1	2	1	2	2	2	1 I	2	2	2	1 I	2	2	2	1 I
	3	6	3	3 III	3	8	3	5 III	3	8	3	5 III	3	7	3	5 III

This phenomenon is also apparent in *Diaptomus* sp. (Johnson 1948).

On the terminal antennal segment the number of setae increases with each naupliar development stage, an important feature in distinguishing different stages (Table 1).

Segmentation of the prosome and urosome of copepods can be used to distinguish between the various developmental stages (Table 1). On the posteriodorsal corners of the prosome short spines occur after third stage, resembling *P. aurivilli*. The rows of teeth on some of the urosomal segments from Stage 4 onwards are not described for the other species.

Sexual differences are first noted in the fourth copepodid stage. In the male the endopodite of the left fifth leg is larger than that of the right. This difference is further enhanced in the fifth copepodid stage. There is also a noticeable body size difference between sexes which is most marked in the adult (Grindley 1963).

Although there are no marked size differences between the naupliar stages of different *Pseudodiaptomus* species, *P. hessei* is larger than the other reported species with respect to total length during copepodid stages.

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