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The evolutionary significance of heterochrony in the abbreviated zoeal development of pilumnine crabs (Crustacea: Brachyura: Xanthoidea)

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The zoeal development of *Pilumnus hirtellus* (Linnaeus, 1761) is redescribed and the four stages are compared with the abbreviated development of *Actumnus setifer* (de Haan, 1835) with three stages, and *Pilumnus sluiteri* De Man, 1892 with two stages. A number of characters are not affected by abbreviated zoeal development and do not change during successive stage moults. Of these, some traits remain conservative at higher taxonomic level, whereas others varied between closely related pilumnid taxa, but neither provided phylogenetic information within the three pilumnines studied. However, abbreviated zoeal development affected 23 pilumnine characters that change with successive stage moults. Their timing of appearance and rate of development occur at different stages relative to the homologous process in an ancestral sequence with more zoeas, and can be attributed to three heterochronic mechanisms; postdisplacement, predisplacement and acceleration. These processes collectively appear to provide the predominant mechanism underlying the evolution of oligomerization within pilumnine zoeas.

ADDITIONAL KEYWORDS: abbreviated development – acceleration – brachyuran zoeas – paedomorphosis – peramorphosis – Piluminae – postdisplacement – predisplacement.

INTRODUCTION

Clark (2001) analysed patterns in chaetotaxy and segmentation associated with abbreviated zoeal development in three higher taxa of brachyuran crabs, comprising two portunids, two xanthoids and a number of majoids. He examined the abbreviated development of larvae reared in the laboratory from species that exhibit life cycles containing six zoeal stages [*Charybdis helleri* (A. Milne Edwards, 1867) by Dineen *et al*., 2001], five stages [*Liocarcinus arcuatus* (Leach, 1814) by Clark, 1984], four stages [*Lophozozymus pictor* (Fabricius, 1798) by Clark & Ng, 1998], three stages [*Actumnus setifer* (de Haan, 1835) examined specifically for Clark, 2001, described by Clark & Ng, 2004a) and two stages [*Macrocheira kaempferi* (Temminck, 1836), by Clark & Webber, 1991, *Libinia spinosa* H. Milne Edwards, 1834, by Clark, Clazans & Rodrigues, 1998b, *Inachus dorsettensis* (Pennant, 1777) and *Inachus leptochirus* Leach, 1817, both by Clark, 1980, 1983]. Comparing these life cycles, Clark (2001) concluded that development of different characters/structures occurred at different times and/or rates, suggesting that evolutionary histories of brachyuran zoeas were robust examples of heterochrony.

Clark & Ng (2004a, b) described the zoeal development of *Actumnus setifer* (de Haan, 1835) with three zoeal stages and *Pilumnus sluiteri* De Man, 1892 with two zoeal stages. The four zoeal stages of *Pilumnus hirtellus* (Linnaeus, 1761) were described by Salman (1982), but his study does not conform to modern standards. The aim of this present study is to redescribe the zoeal development of *Pilumnus hirtellus* in accordance with modern standards (Clark, Calazans & Pohle, 1998a) and examine the patterns of zoeal character expression associated with abbreviated development, in the larvae of *Pilumnus hirtellus*, *Actumnus setifer* and *Pilumnus sluiteri* for evidence of mosaic heterochrony within a subfamily, namely the Pilumninae.

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Abbreviations

NHM The Natural History Museum, London
ZRC Zoological Reference Collection, Raffles Museum, National University of Singapore
coll. collected by
reg. registration
PZ prezoea
ZI first-stage zoea
ZII second-stage zoea
ZIII third-stage zoea
ZIV fourth-stage zoea
Meg. megalop
Cr. crab stage.

Endopod/antennal protopod ratio: endopod was measured from approximate base of the antenna to its tip.

MATERIAL AND METHODS

Material examined

Pilumnus hirtellus – Falmouth Harbour, England, coll. R. Lincoln, 15 April 1975, Hatched in NHM, 4–5 June 1975 and laboratory reared in the Department of Zoology, NHM. NHM reg. 1998: 600. Specimens examined, 5 × ZI, 5 × ZII, 4 × ZIII, 4 × ZIV.

Actumnus setifer – Siloso Beach, Sentosa Island, Singapore, coll. Peter Ng, 10–12 May 1982. Hatched 14 May 1982 and laboratory reared in the Department of Biological Sciences, National University of Singapore. Specimens examined: 5 × ZI, 6 × ZII, 6 × ZIII.

Pilumnus sluiteri – shore at low tide, west of Alona Beach, Panglao Island off Bohol, Philippines; coll. Paul Clark & Peter Ng, 29 July, 2003; hatched in the Systematics and Ecology Laboratory, Department of Biological Sciences, Singapore University, 1 August 2003; spent female and larvae ZRC reg. 2003: 281. Specimens examined, 5 × ZI, 6 × ZII.

Methods

The zoeal development of *Pilumnus hirtellus* was redescribed from material reared in the laboratory of the Zoology Department, NHM. Hatched zoeas were reared in transparent plastic, 18-compartmented boxes, one to a single compartment. The larvae were maintained at about 18 °C, fed *Artemia* nauplii and reared in natural sea-water without additives. The sea-water was changed every second day and the larvae were preserved in 70% industrial methylated spirits.

The zoeas were dissected on glass slides in polyvinyl lactophenol under a Leica MZ16 microscope and the appendages were allowed to clear for 24 h before examination. Cover-slips were sealed with clear nail varnish. Appendages were drawn using an Olympus BH-2 compound microscope equipped with differential interference contrast (DIC) and a camera lucida. Setal ambiguities were resolved using a Zeiss Axioskop or a Leica DMR HC compound microscopes each with DIC. The sequence of the zoeal descriptions is based on the malacostracan somite plan and described from anterior to posterior. Setal armature of appendages was described from proximal to distal segments and in order of endopod to exopod (see Clark *et al*., 1998a). The long antennular aesthetascs and long plumose natatory setae of the first and second maxillipeds were drawn truncated. The mandible is not fully described or illustrated because the only significant character of this appendage is the appearance of the palp in the zoeal phase; this character is figured. The approximate length of the antennal endopod (for its ratio with the protopod) was measured from its base to the tip.

RESULTS

Description of zoeal stages

Pilumnus hirtellus (Linnaeus, 1761)
Figures 1–15

Pilumnus hyrtellus – Williamson, 1915: 490, figs 314–316, 317 (ZI, Cr.).
Pilumnus sp. – Williamson, 1915: 492, figs 318, 319 (ZI, II).
Pilumnus hirtellus – Boraschi, 1921: 9, Tav. 1, fig. 14 (ZI); Lebour, 1928: 532, fig. 1(18), pl. II, fig. 5, pl. X, figs 6–8, pl. XI, figs 1–4 (PZ, ZI-IV, Meg., Cr.I); Bourdillon-Casanova, 1960: 172, fig. 54 (PZ, ZI, Cr.I); Salman, 1982: 113, figs 1–7 (ZI-IV, Meg.); Ingle, 1983: 973, fig. 15a,b,f (Meg., Cr.I); Hong, 1988: 1019, fig. 12 (ZI-IV, Meg.); Ingle, 1991: 232–234, figs 1.13k, 1.18b, 1.23c, 1.25g, 1.29b, 1.32c, 1.34o, 1.36h, 1.38d, 2.30b–t (ZI-IV, Meg.); Ng & Clark, 2000: 228–231, figs 20–23 (Z1).

Zoea I

Carapace (Fig. 1A): dorsal spine smooth, curved distally, approximately twice as long as rostral spine; rostral spine smooth, shorter than antennal protopod; lateral spines unarmed; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Fig. 4A): uniramous, endopod absent; exopod unsegmented with 4 terminal aesthetascs (2 broad and long, 2 shorter and slender) plus 2 terminal setae of unequal length.

Antenna (Fig. 5A): protopod distally spinulate, longer than rostral spine but slightly shorter than exopod;

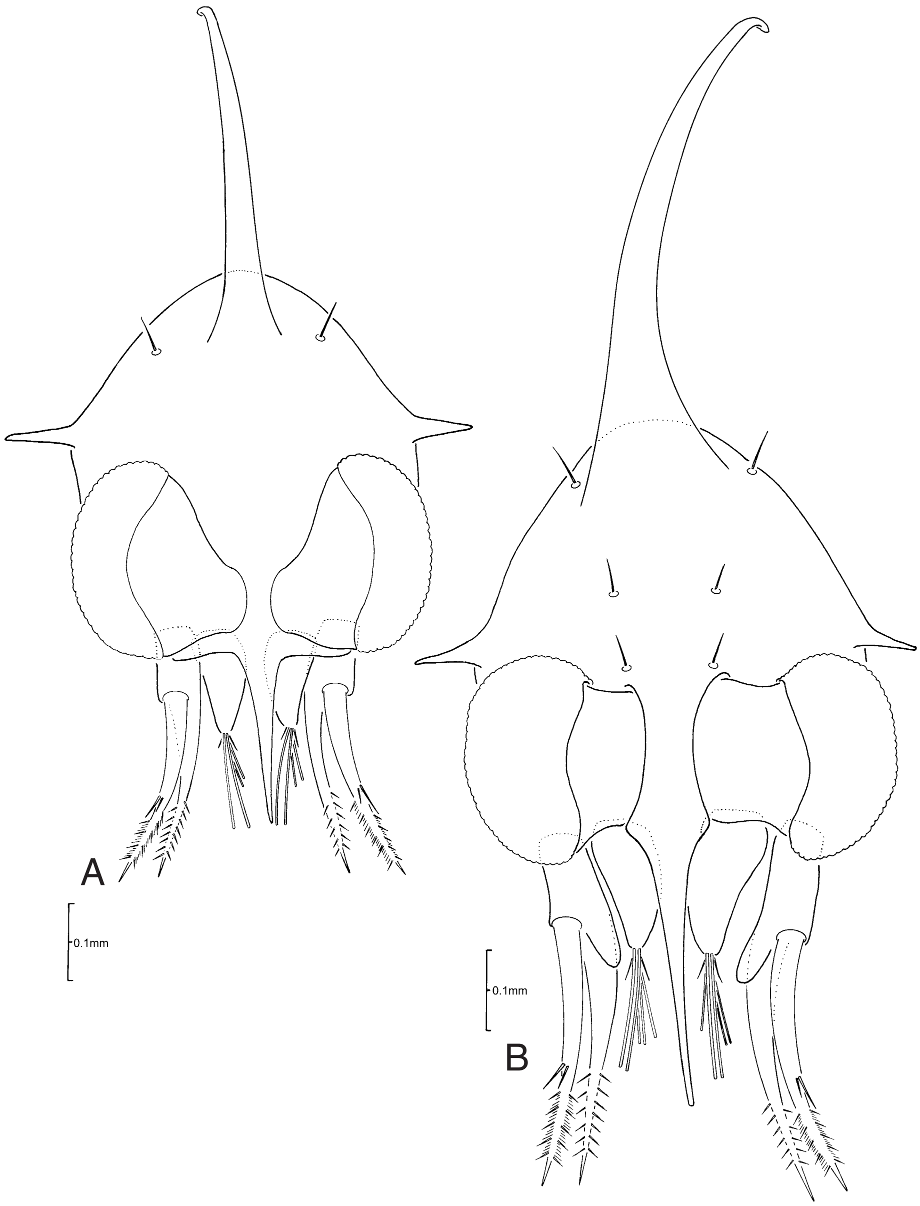

Figure 1. *Pilumnus hirtellus* (Linnaeus, 1761), anterior view of the carapace: A, zoea I; B, zoea II.

endopod absent; exopod longer than protopod, unsegmented, distally spinulate with 2 medial setae of unequal length.

Mandible: endopod palp absent.

Maxillule (Fig. 6A): epipod seta absent, coxal endite with 7 setae; basial endite with 5 terminal setal processes and 2 small teeth; endopod 2-segmented, proximal segment with 1 seta; distal segment with 6 (2 subterminal, 4 terminal) setae; exopod seta absent.

Maxilla (Fig. 7A): coxal endite bilobed with 5 + 4 setae; basial endite bilobed with 5 + 4 setae; endopod bilobed with 3 + 5 (2 subterminal, 3 terminal) setae; exopod (scaphognathite) margin with 4 setae and 1 long distal plumose stout process.

First maxilliped (Fig. 8A): coxa without setae; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,5 (1 subterminal, 4 terminal setae), respectively; exopod 2-segmented, distal segment with 4 long-terminal plumose natatory setae.

Second maxilliped (Fig. 9A): coxa without setae; basis with 4 setae arranged 1,1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae,

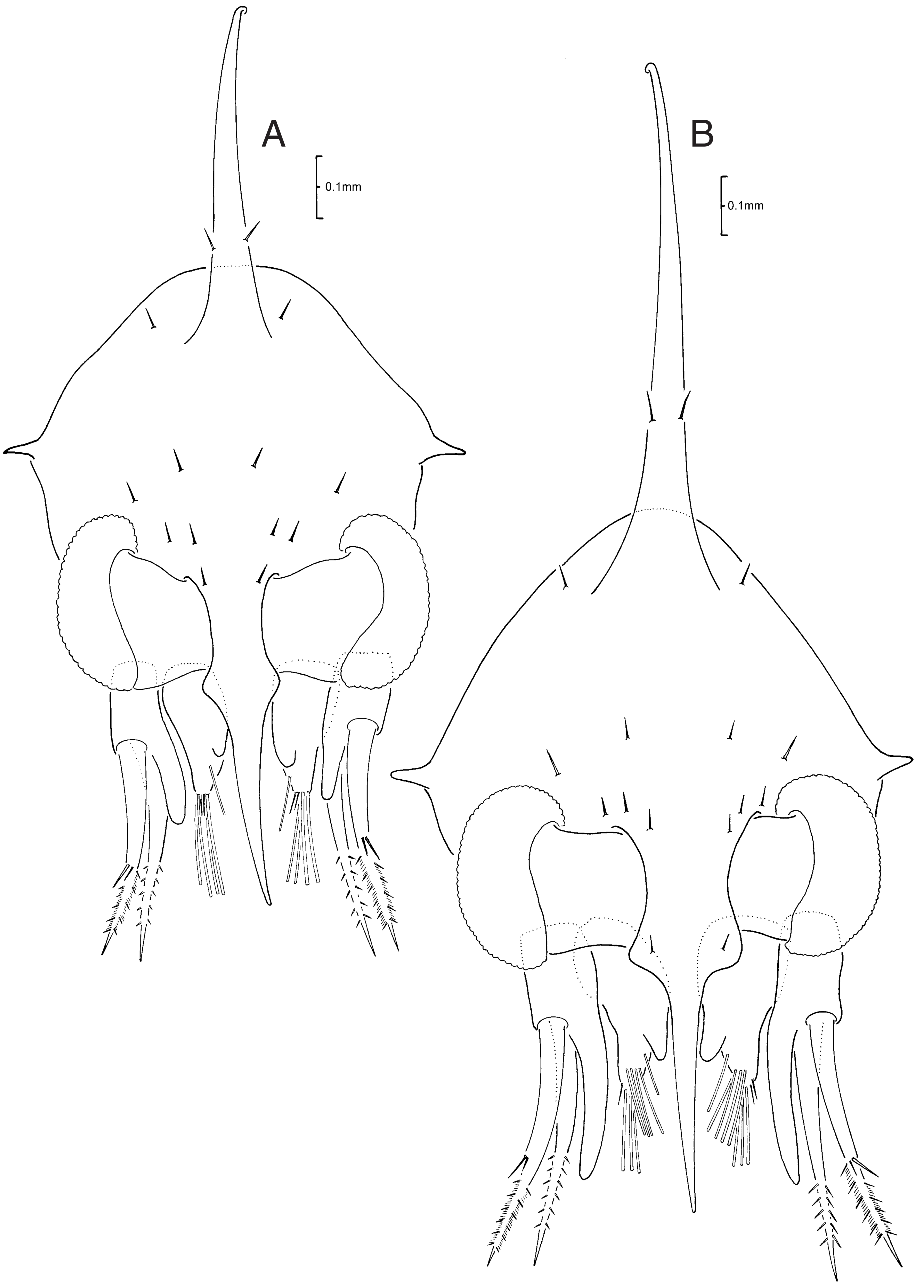

Figure 2. *Pilumnus hirtellus* (Linnaeus, 1761), anterior view of the carapace: A, zoea III; B, zoea IV.

respectively; exopod 2-segmented, distal segment with 4 long-terminal plumose natatory setae.

Third maxilliped: absent.

Pereiopods: absent.

Abdomen (Figs 12A, 14A): 5 somites; somite 2 with pair of dorsolateral processes directed anteriorly; somite 3 with pair of dorsolateral processes directed ventrally; somites 1–2 with rounded posterolateral processes and 3–5 with spinous posterolateral processes; somite 1 without setae; somites 2–5 with 1 pair of posterodorsal setae; posterior margin of somites 2–5 spinulate; pleopod buds absent.

Telson (Figs 12A, 14A, 15A): each telson fork long, spinulate and gradually curved distally; 1 long spinulate and 1 small lateral spine; dorsal medial spinulate spine present; posterior margin with 3 pairs of stout spinulate setae.

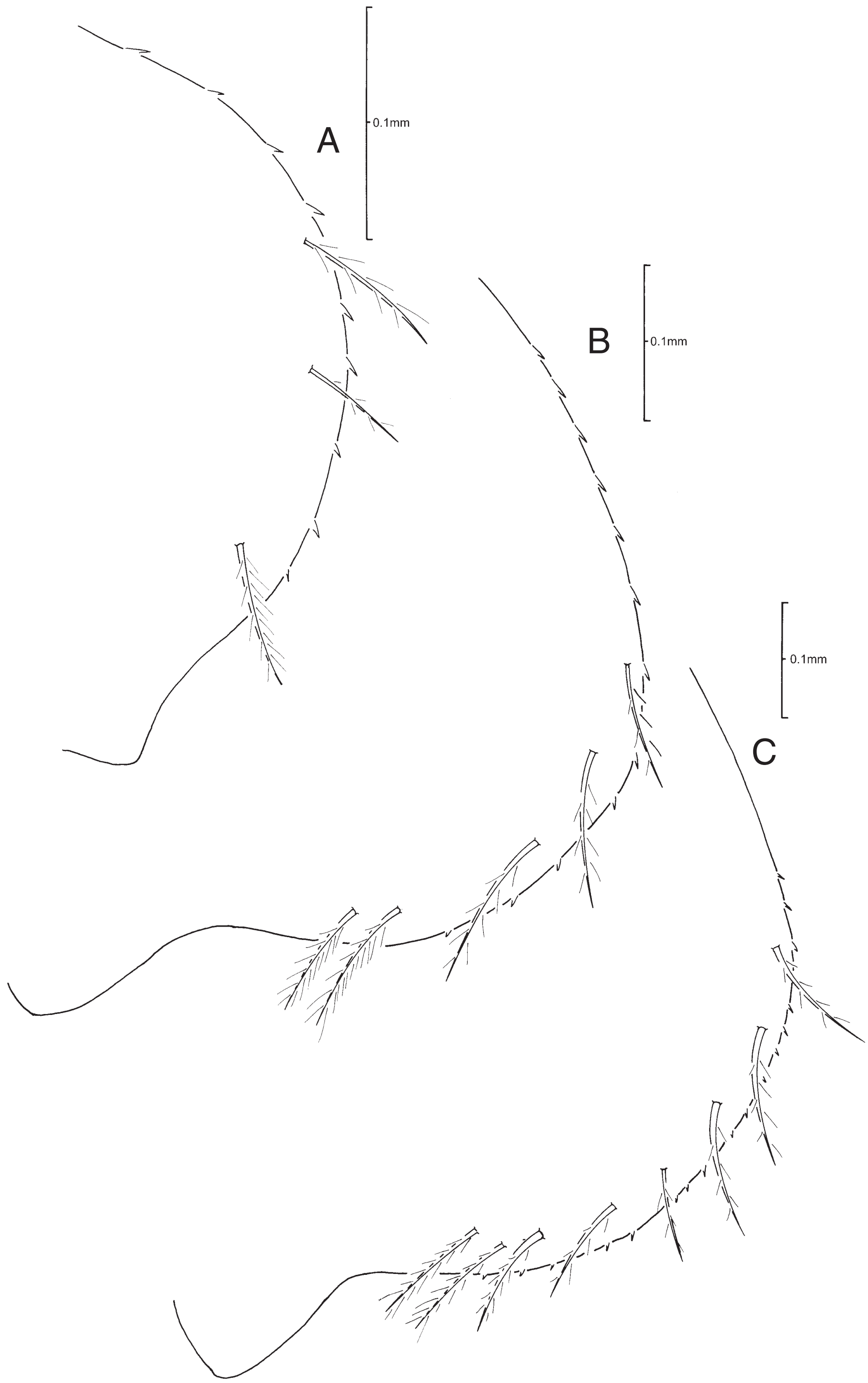

Figure 3. *Pilumnus hirtellus* (Linnaeus, 1761), ventral carapace margin: A, zoea II; B, zoea III, C, zoea IV.

Zoea II

Carapace (Figs 1B, 3A): now 2 pairs of anterodorsal setae; ventral margin with 1 anterior seta plus 2 posterior seta; eyes stalked, otherwise unchanged.

Antennule (Fig. 4B): now with 2 stout and 3 slender aesthetascs plus 2 setae, otherwise unchanged.

Antenna (Fig. 5B): endopod bud present, *c.* 43% of protopod; otherwise unchanged.

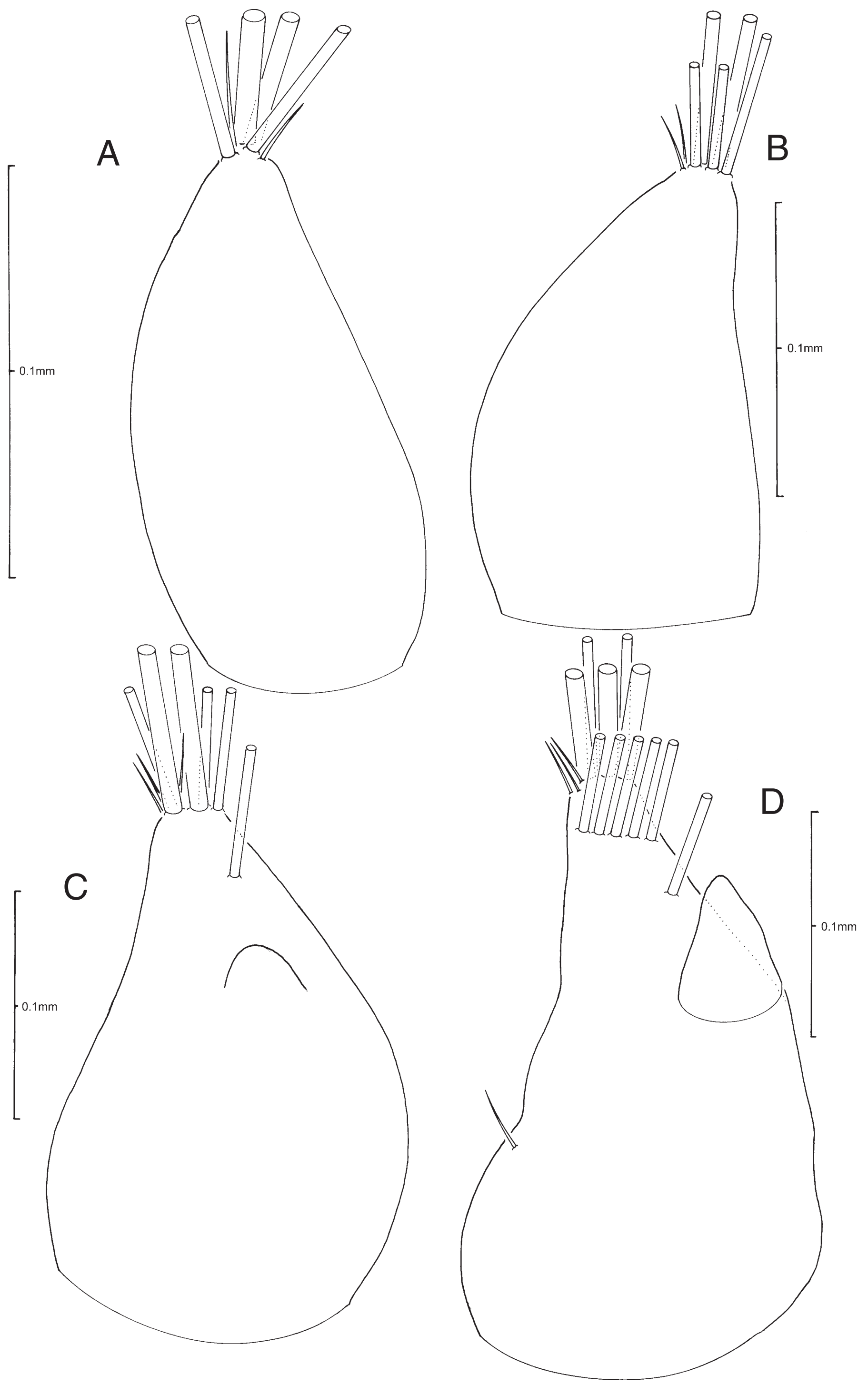

Figure 4. *Pilumnus hirtellus* (Linnaeus, 1761), antennule: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

Mandible: unchanged.

Maxillule (Fig. 6B): epipod seta present; basial endite with 8 setal processes, teeth no longer apparent; exopod seta present; otherwise unchanged.

Maxilla (Fig. 7B): basial endite now with 5 + 5 setae; exopod margin with 11 setae and stout process no longer prominent; otherwise unchanged.

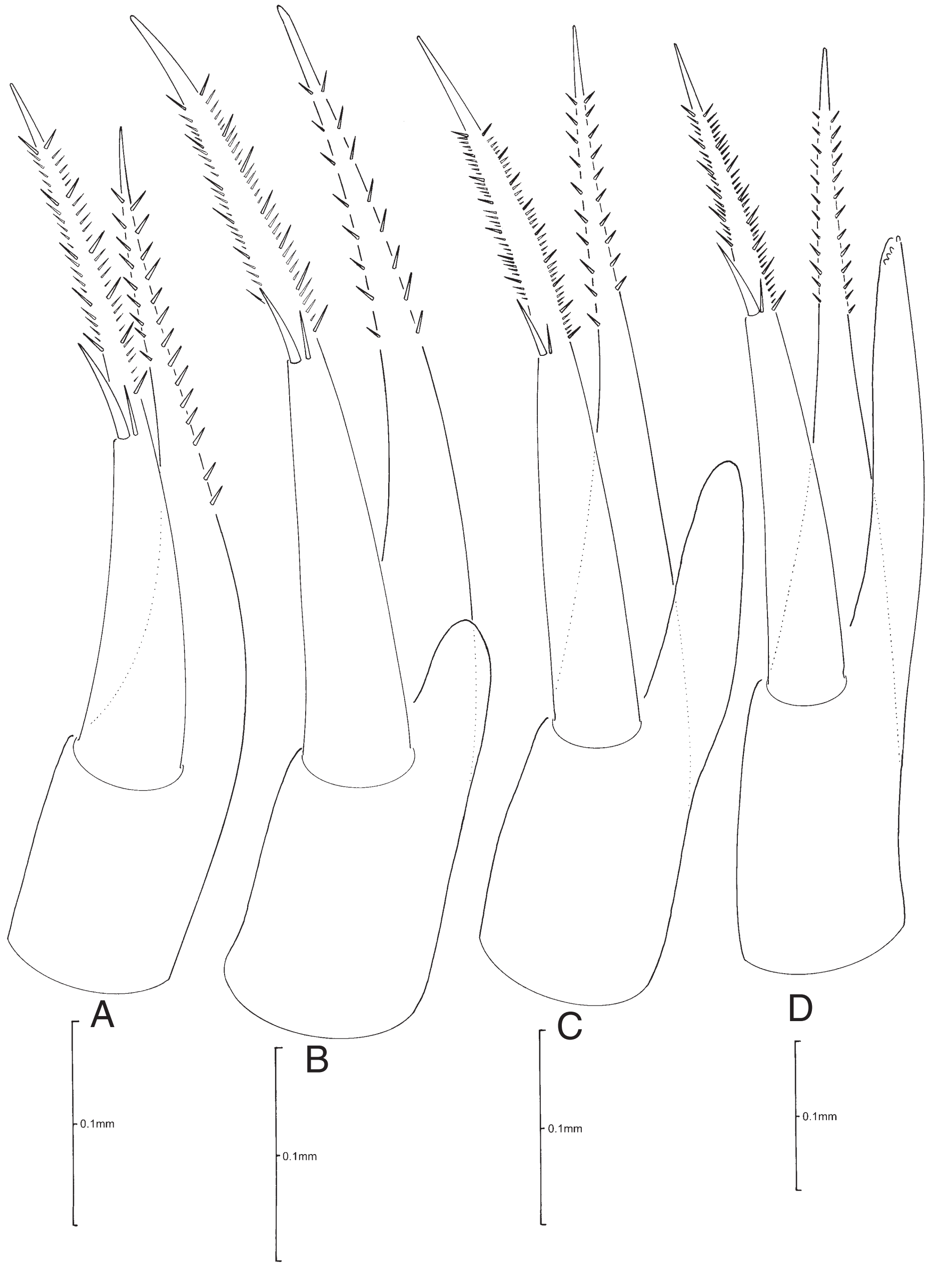

Figure 5. *Pilumnus hirtellus* (Linnaeus, 1761), antenna: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

First maxilliped (Fig. 8B): exopod distal segment now with 6 long-terminal plumose natatory setae; otherwise unchanged.

Second maxilliped (Fig. 9B): exopod distal segment now with 6 long-terminal plumose natatory setae; otherwise unchanged.

Third maxilliped (Fig. 10B): present, rudimentary, biramous, endopod longer than exopod.

Pereiopods (Fig. 11A): present, rudimentary and chela bilobed.

Abdomen (Figs 12B, 14B): somite 1 with 1 medial seta.

Telson (Figs 12B, 14B, 15B): unchanged.

Zoea III

Carapace (Figs 2A, 3B): dorsal spine with 1 pair of setae; now with 5 pairs of anterodorsal setae; ventral margin with 1 anterior seta plus 4 posterior setae; otherwise unchanged.

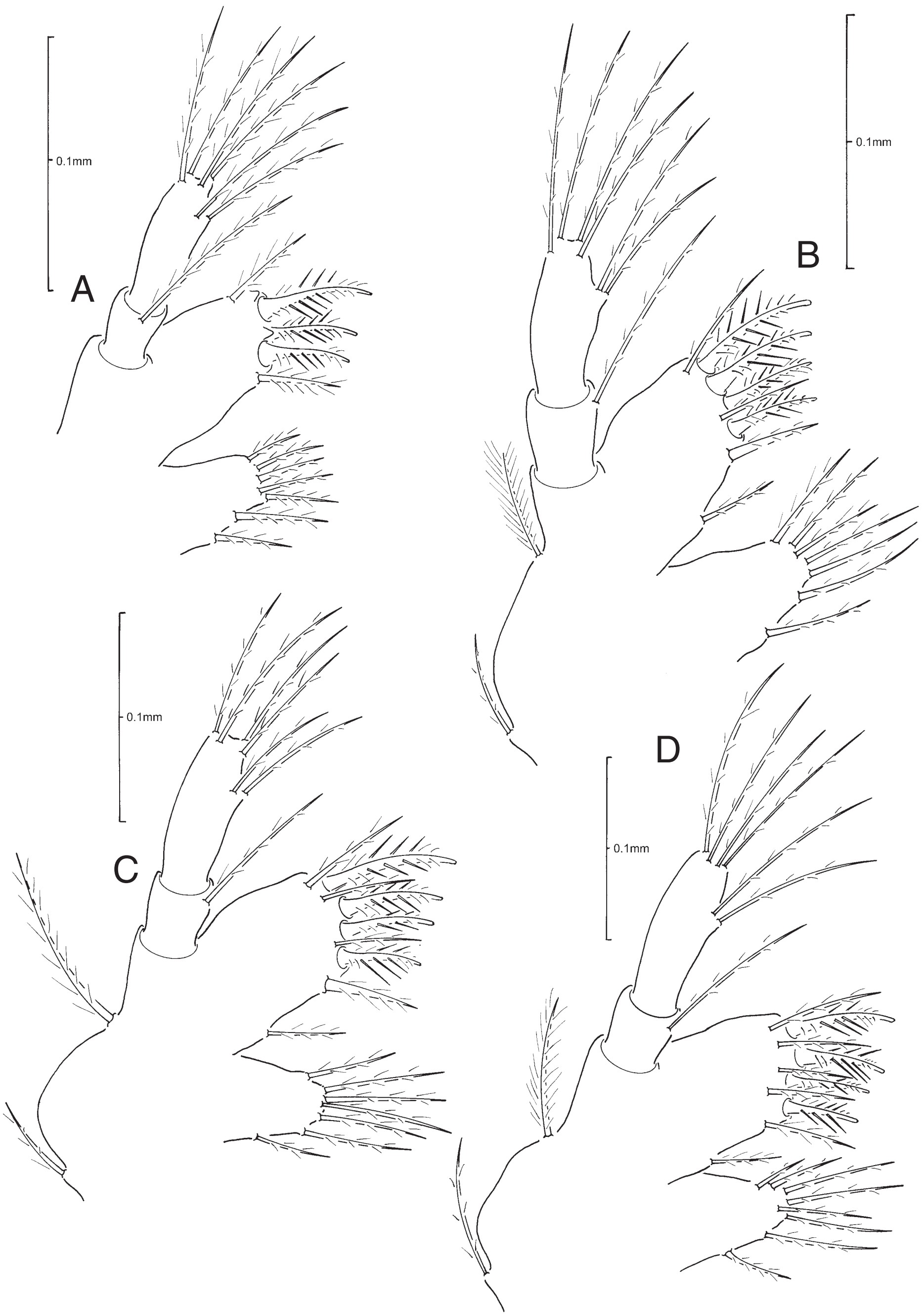

Figure 6. *Pilumnus hirtellus* (Linnaeus, 1761), maxillule: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

Antennule (Fig. 4C): biramous; endopod bud swollen and developing; exopod now with 1 subterminal seta plus 2 broad and long, 3 shorter and slender aesthetascs plus 3 setae, all terminal.

Antenna (Fig. 5C): endopod more developed *c.* 58% of protopod; otherwise unchanged.

Mandible: unchanged.

Maxillule (Fig. 6C): basial endite now with 9 setal processes; otherwise unchanged.

Maxilla (Fig. 7C): basial endites with 6 + 6 setae; exopod margin with 18 setae of equal length; otherwise unchanged.

First maxilliped (Fig. 8C): endopod distal segment now with 6 (2 subterminal, 4 terminal) setae; exopod

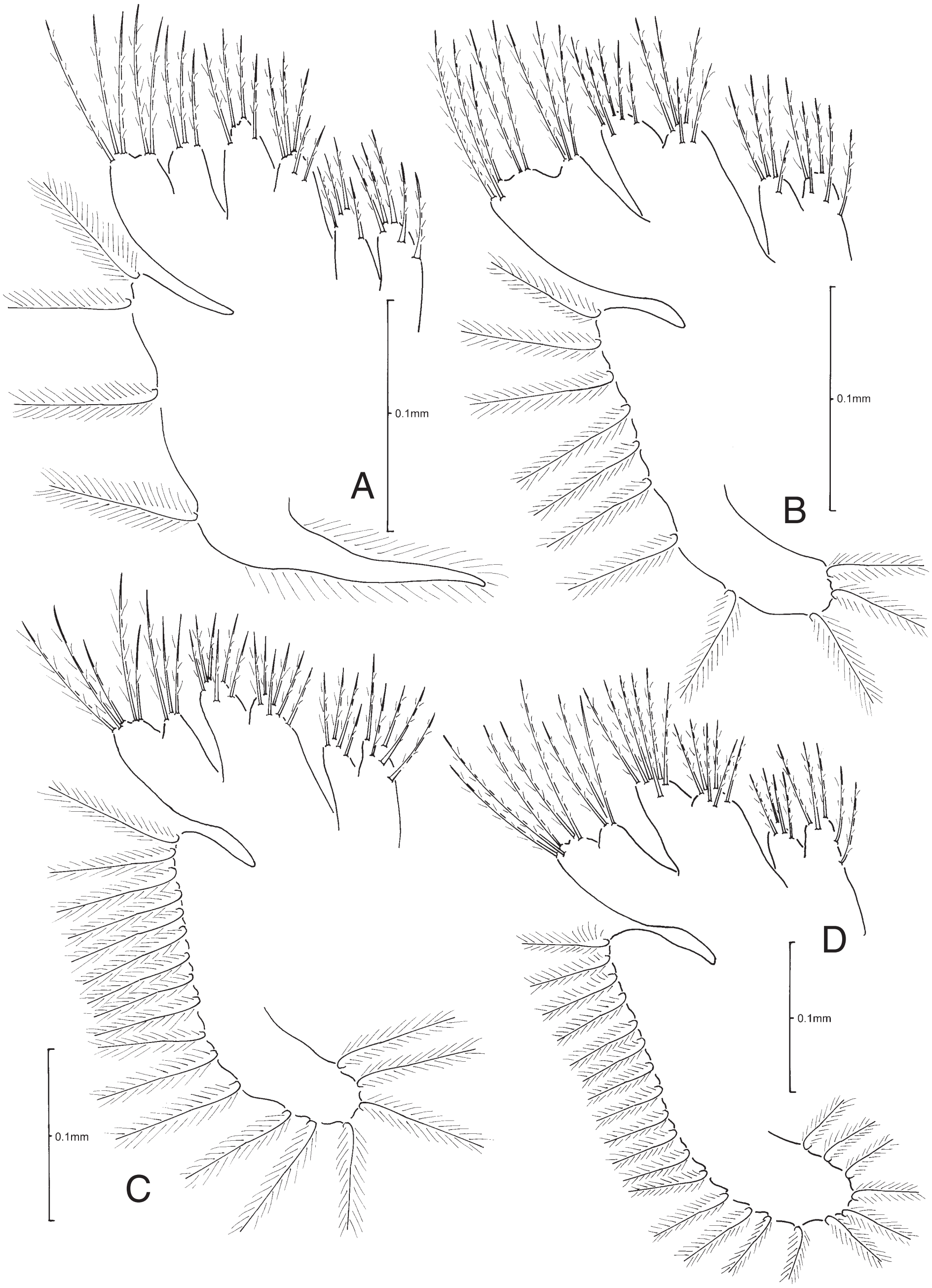

Figure 7. *Pilumnus hirtellus* (Linnaeus, 1761), maxilla: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

distal segment now with 8 long-terminal plumose natatory setae; otherwise unchanged.

Second maxilliped (Fig. 9C): exopod distal segment now with 8 long-terminal plumose natatory setae; otherwise unchanged.

Third maxilliped (Fig. 10C): developing, epipod bud present.

Pereiopods (Fig. 11B): developing with some cheliped segmentation.

Abdomen (Figs 13A, 14C): now with 6 somites; somite 1 with 1 pair of dorsal medial setae plus 1 posterodorsal seta; somite 6 without setae; somites 2–6 with uniramous pleopod buds present without endopods; otherwise unchanged.

Telson (Figs 13A, 14C, 15C): unchanged.

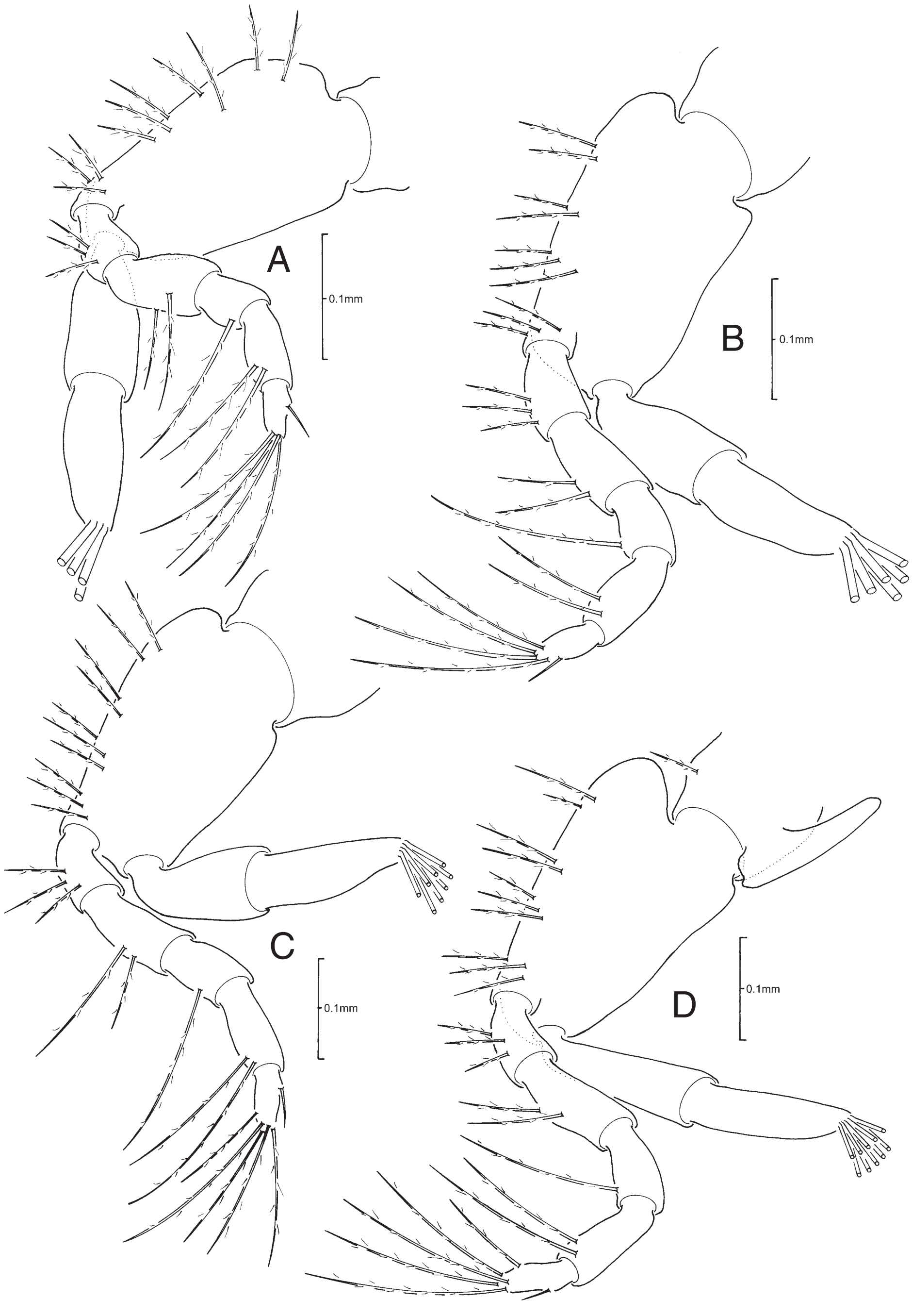

Figure 8. *Pilumnus hirtellus* (Linnaeus, 1761), first maxilliped: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

Zoea IV

Carapace (Figs 2B, 3C): 6 pairs of anterodorsal setae; ventral margin with 1 anterior seta plus 7 posterior setae; otherwise unchanged.

Antennule (Fig. 4D): protopod with 1 seta; endopod bud now developed; exopod now with 1 proximal subterminal aesthetasc, 5 distal subterminal aesthetascs; 3 stout and long, 2 shorter and slender aesthetascs plus 3 setae, all terminal.

Antenna (Fig. 5D): endopod more developed *c.* 80% of protopod and with minute terminal setal buds; otherwise unchanged.

Mandible (Fig. 10A): palp present.

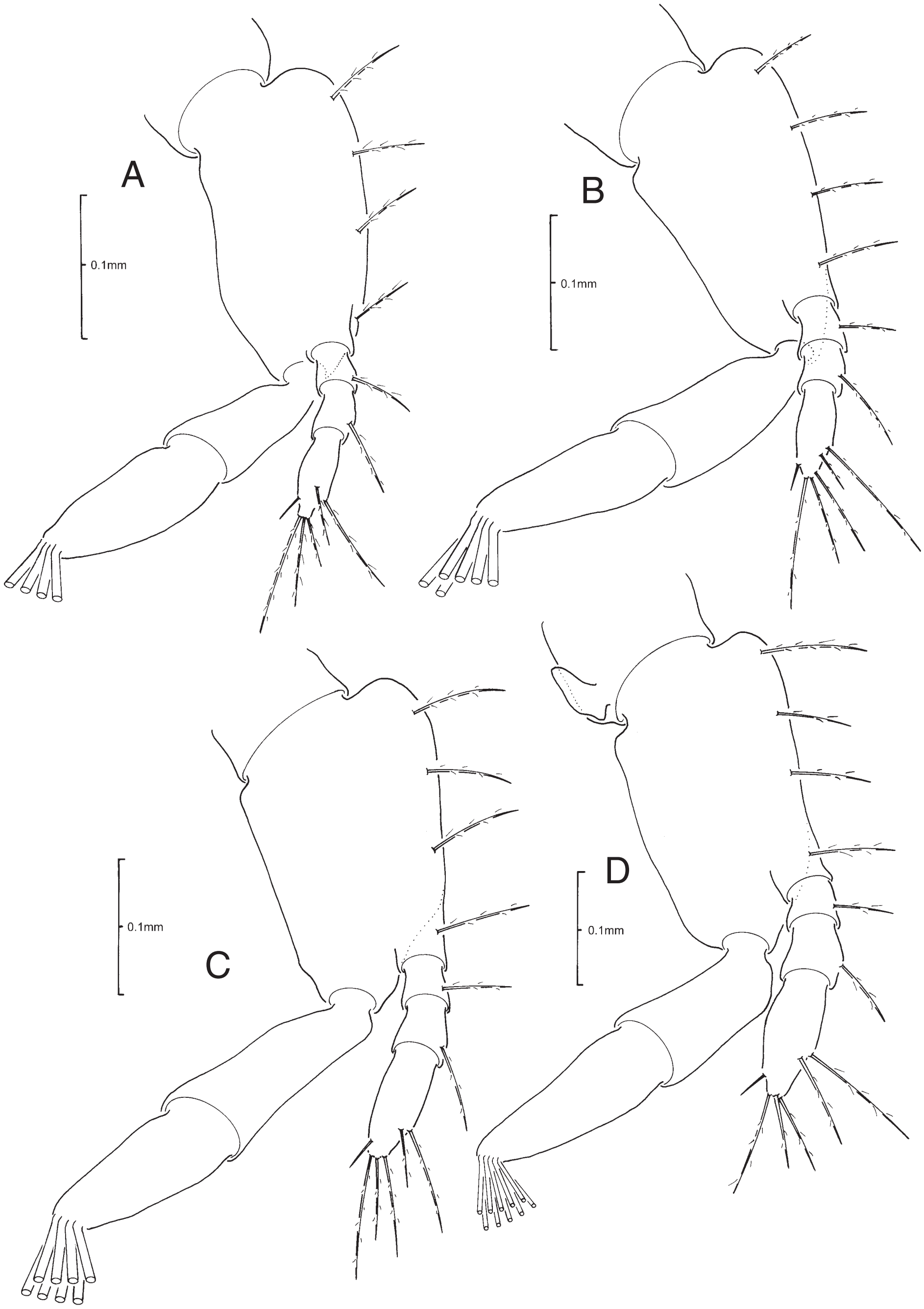

Figure 9. *Pilumnus hirtellus* (Linnaeus, 1761), second maxilliped: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

Maxillule (Fig. 6D): coxal endite with 8 setae; basial endite with 10 setal processes; otherwise unchanged.

Maxilla (Fig. 7d): exopod margin with 22 setae of equal length; otherwise unchanged.

First maxilliped (Fig. 8D): coxal segment with epipodal bud; exopod distal segment with 10 long-terminal plumose natatory setae.

Second maxilliped (Fig. 9D): coxal segment with epipodal bud; exopod distal segment with 10 long-terminal plumose natatory setae.

Third maxilliped (Fig. 10D): arthrobranch gill bud developing.

Pereiopods (Fig. 11C): developing with some segmentation.

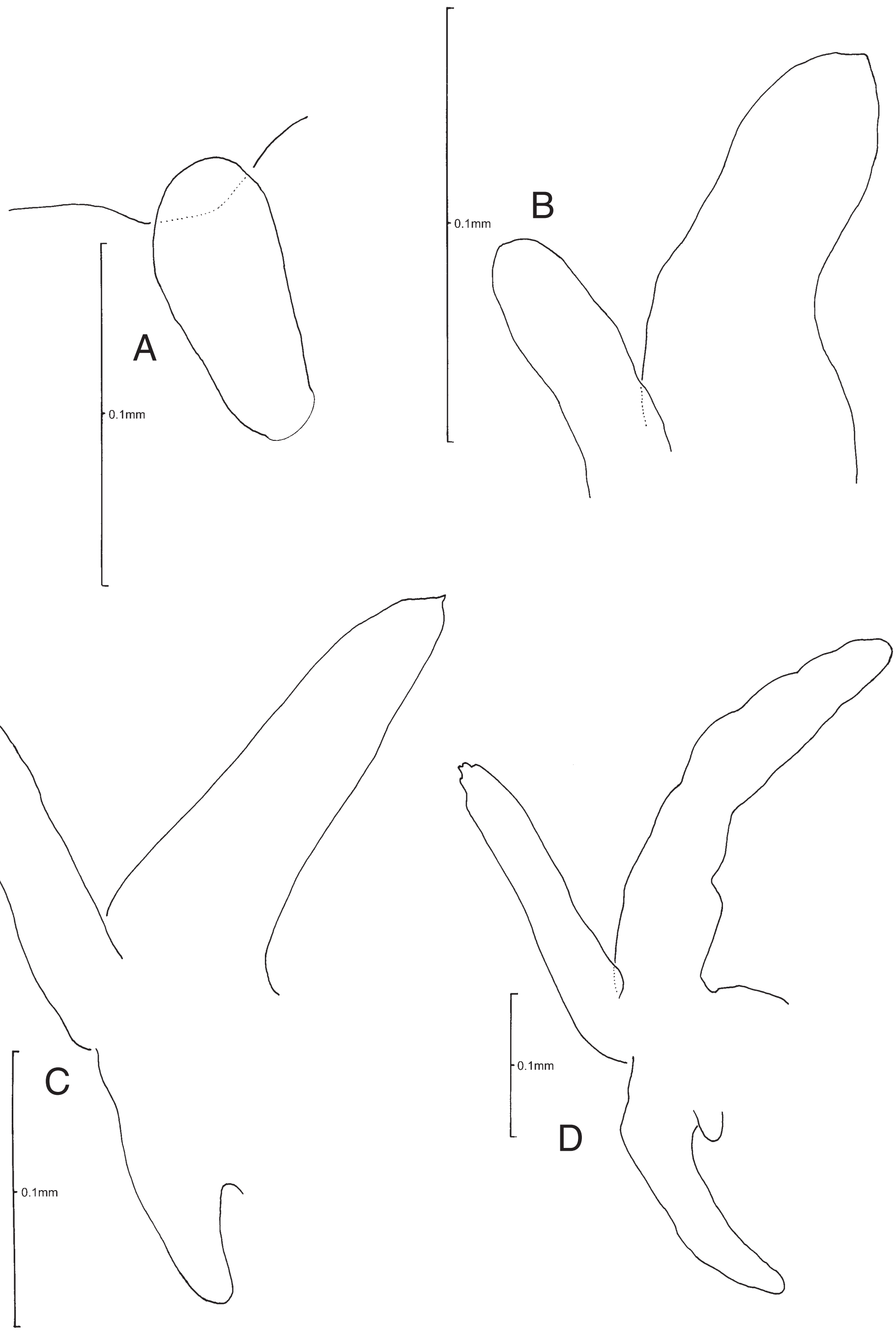

Figure 10. *Pilumnus hirtellus* (Linnaeus, 1761), mandibular palp: A, zoea IV; third maxilliped: B, zoea II; C, zoea III; D, zoea IV.

Abdomen (Figs 13B, 14D): somite 1 with 2 pairs of dorsal medial setae plus 1 posterodorsal seta; pleopods with endopod buds present (biramous); otherwise unchanged.

Telson (Figs 13B, 14D, 15D): 1 pair of dorsal medial setae; otherwise unchanged.

Variability

The setation of the maxillule coxal endite, fourth zoeal stage, varied and of the six appendages examined they scored 1×7; 3×8; 1×9; 1×10 setae. In other descriptions of *Pilumnus hirtellus*, Salman (1982) recorded 7–8 setae and Ingle (1991) eight setae for this character.

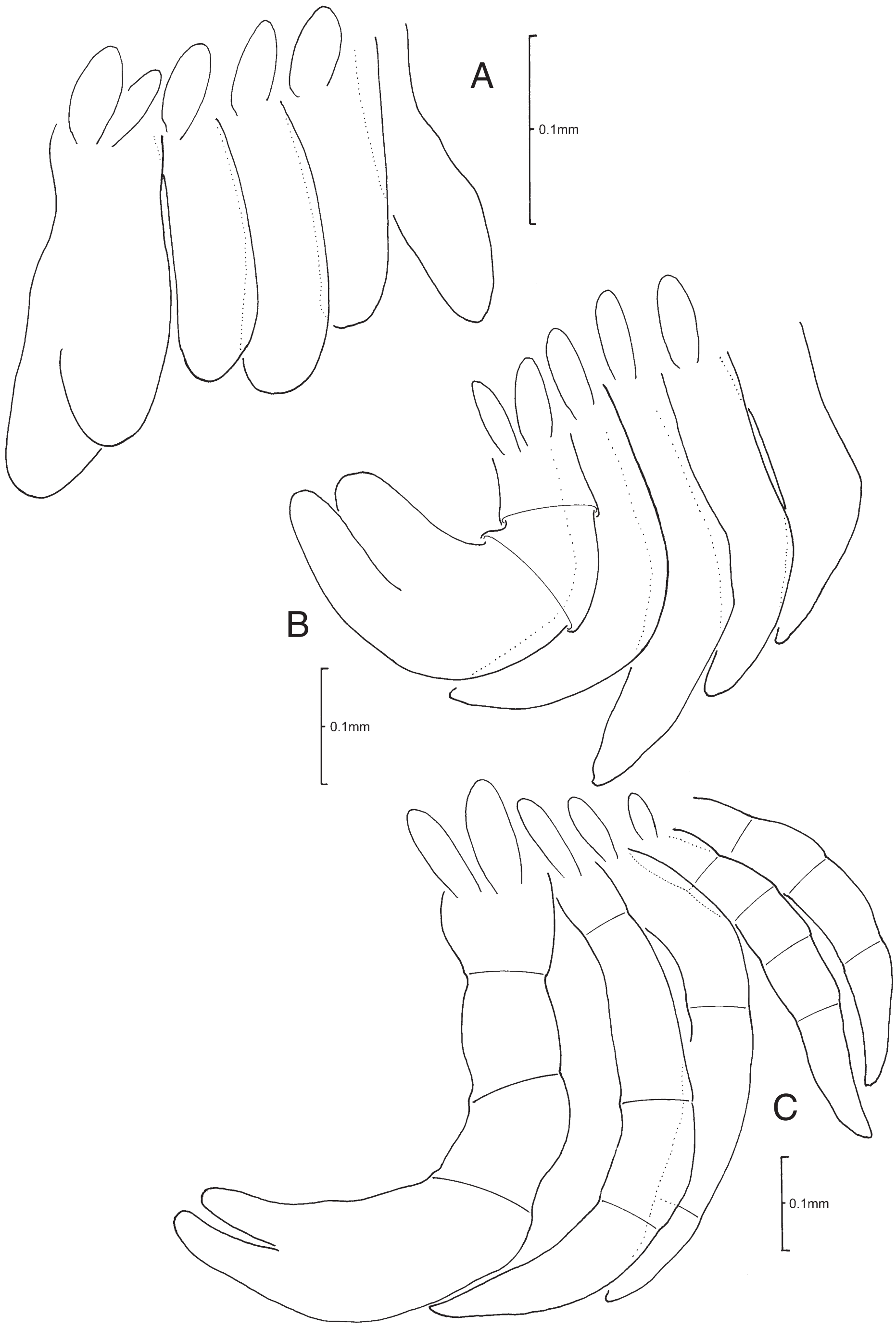

Figure 11. *Pilumnus hirtellus* (Linnaeus, 1761), pereiopods: A, zoea II; B, zoea III; C, zoea IV.

Previous descriptions

Although nine larval references are listed in the synonymy for *P. hirtellus* only the study of Salman (1982) appears to be complete. However, a number of characters in his zoeal description are problematical because some setal counts remain conservative throughout development. For example, the number of anterodorsal setae on the carapace remains at two pairs of setae for ZII–ZIV and the setation of the ventral carapace margin is four in all zoeal stages. In contrast, the setae for these two characters in the present study are shown to increase in number with successive moults (see Figs 1–3). Furthermore, a number of characters are not fully described such as the appearance of the

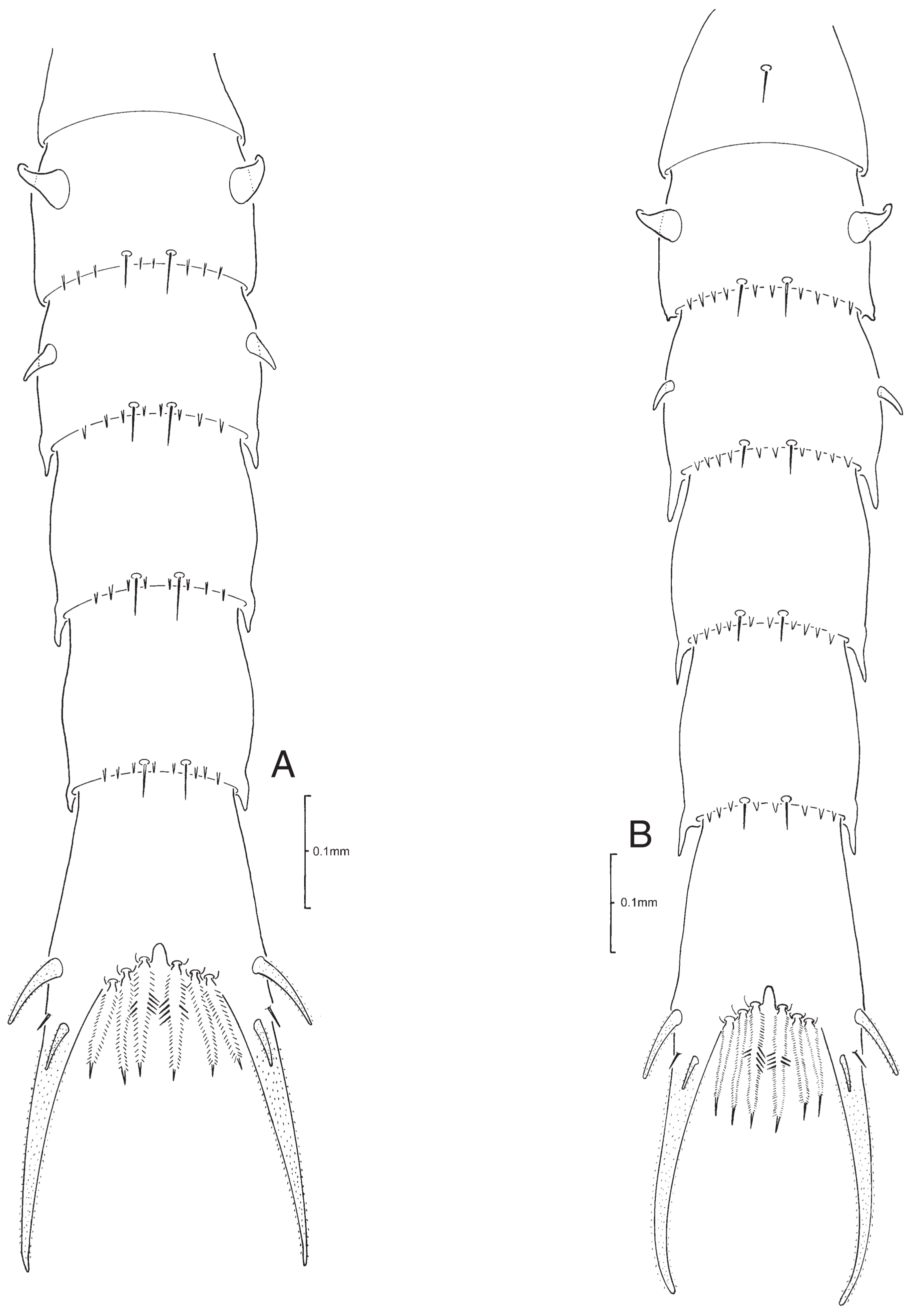

Figure 12. *Pilumnus hirtellus* (Linnaeus, 1761), dorsal view of abdomen: A, zoea I; B, zoea II.

mandibular palp and the development of the third maxilliped. Table 1 lists the differences between the zoeal description of *Pilumnus hirtellus* by Salman (1982) and the present study.

Comparative zoeal development

The timing of expression of ontogenetic characters was analysed from the zoeal development of *Pilumnus hirtellus* (the present study), *Actumnus setifer* (by Clark & Ng, 2004a) and *P. sluiteri* (by Clark & Ng, 2004b). Characters relating to number of zoeal stages; appearance of sixth somite division; appearance of appendages; appearance of endopod buds; appearance of the epipod on the first maxilliped and appearance of setae were compared and are summarized in Tables 2–24.

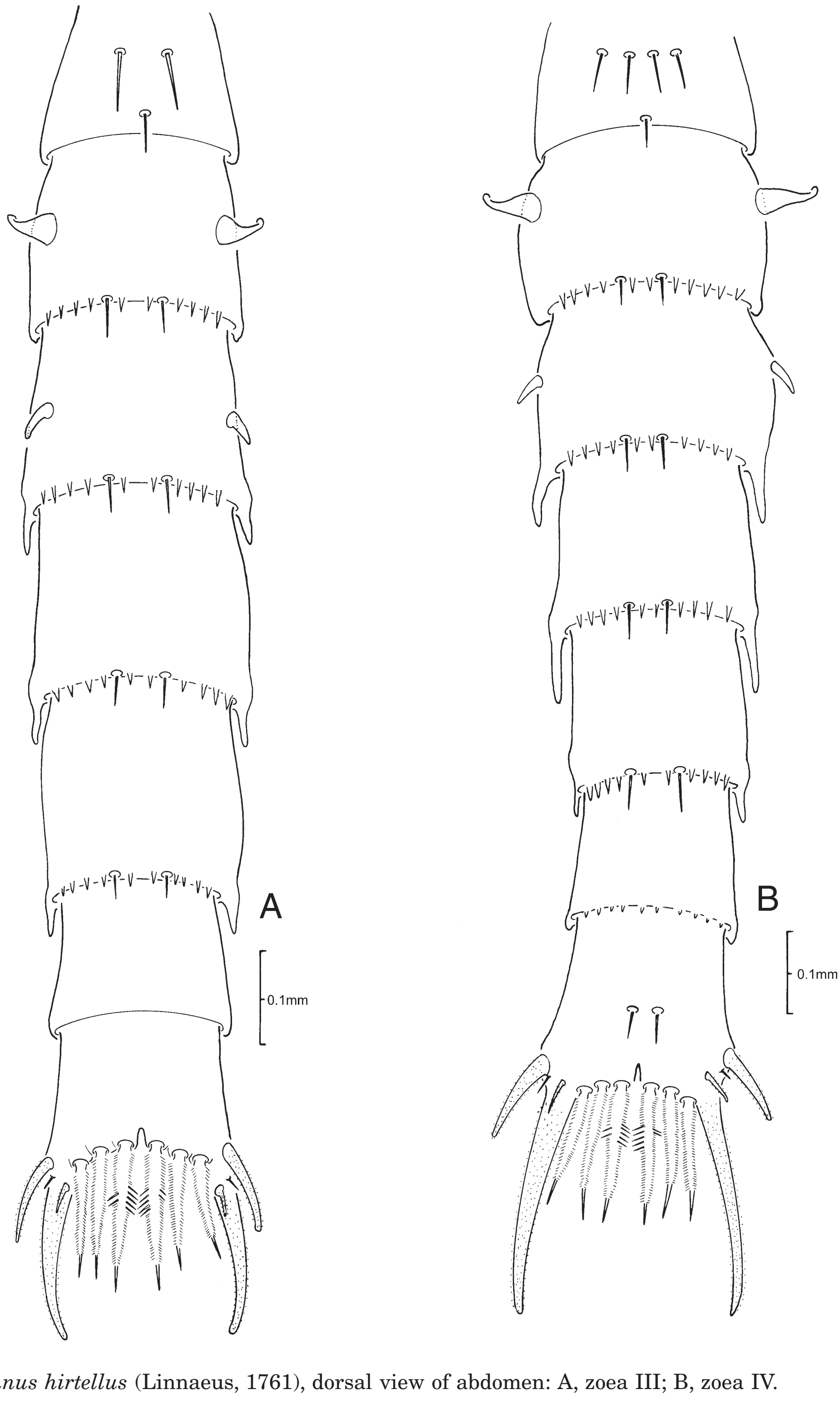

Figure 13. *Pilumnus hirtellus* (Linnaeus, 1761), dorsal view of abdomen: A, zoea III; B, zoea IV.

Number of zoeal stages

Defining each zoeal stage (see Figs 8A–D, 9A–D, Table 2): Each zoeal stage can be unequivocally defined by the number of terminal plumose natatory setae on the distal exopod segment of the first and second maxillipeds. This number is 4 in ZI, 6 in ZII, 8 in ZIII and 10 in ZIV.

Number of zoeal stages (see Table 3): Within the pilumnines there is a reduction (abbreviation) in the

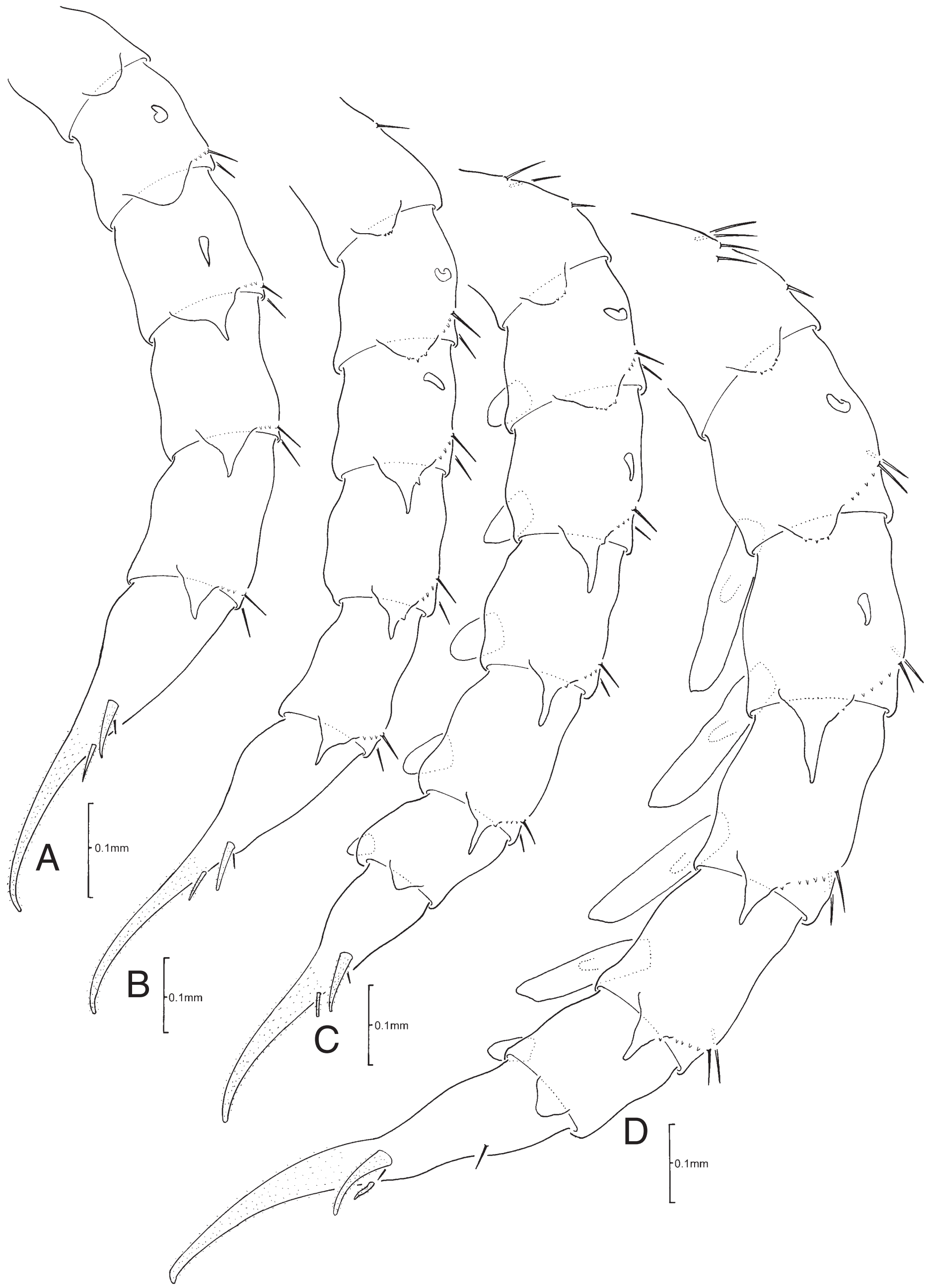

Figure 14. *Pilumnus hirtellus* (Linnaeus, 1761), lateral view of abdomen: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

number of zoeal stages expressed during larval development; for example *Pilumnus hirtellus* has four zoeal stages; *Actumnus setifer* has three (see Clark & Ng, 2004a) and *P. sluiteri* has two (see Clark & Ng, 2004b). The extreme case is exemplified by *P. novaezealandiae* Filhol, 1885, which hatches directly as a megalop (see Wear, 1967; Wear & Fielder, 1985) and lacks a zoeal phase altogether.

Appearance of 6th abdominal somite division

Abdominal somite division (see Figs 12A, B, 13A, B, 14C, D, Table 4): The adult crab abdomen comprises six somites, but in *P. hirtellus* and *A. setifer* first-stage zoeas possessed only five somites. The sixth somite appears at ZIII in *P. hirtellus*, at ZII in *A. setifer* and at ZI in *P. sluiteri*.

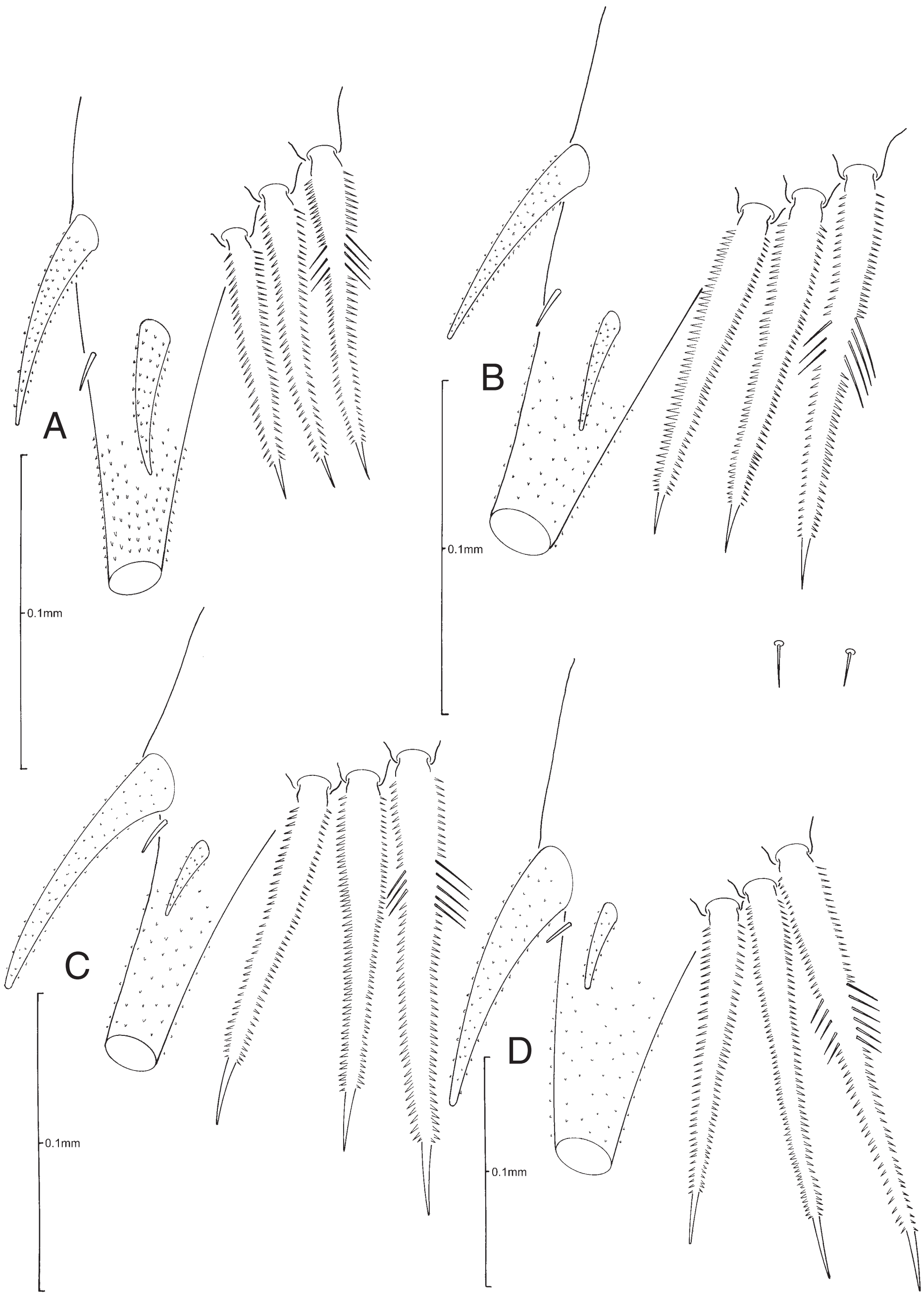

Figure 15. *Pilumnus hirtellus* (Linnaeus, 1761), telson: A, zoea I; B, zoea II; C, zoea III; D, zoea IV.

Appearance of appendages

During the zoeal phase in pilumnines three appendages appear, develop and have no apparent function until the metamorphosis to megalop. These are the third maxillipeds, pereiopods and pleopods.

Third maxillipeds (see Fig. 10B–D, Table 5): In adult brachyurans the third maxillipeds are the outermost thoracic feeding appendages. In pilumnine zoeal stages these first appear as biramous unsegmented appendages comprising a longer endopod and a shorter exopod (see Fig. 10B). In later stages the epipod (see Fig. 10C) and the arthrobranch gill bud appear (see Fig. 10D). The third maxilliped may not be functional in zoeal stages and is a rudimentary developing structure before the metamorphosis to megalop when it will be transformed into a thoracic feeding appendage.

Table 1. The differences between the description of *Pilumnus hirtellus* zoeal stages by Salman (1982) and the present study

Characters	*Pilumnus hirtellus* (Salman, 1982)	*Pilumnus hirtellus* (present study)
Zoea I		
CARAPACE	fig. 1A	Fig. 3
setation of posterior margin	4 setae	absent
MAXILLULE	text	Fig. 6A
setation of coxal endite	6–7	7
Zoea II		
CARAPACE	fig. 2A	Fig. 3A
setation of ventral margin	4 setae	3 setae
ANTENNULE	text	Fig. 4B
terminal setation	2 stout, 3 slender aesthetascs plus 1 hair	2 stout, 3 slender aesthetascs plus 2 setae
MAXILLULE	fig. 2E, text	Fig. 2B
epipod seta	absent	present
setation of coxal endite	6–7	7
PEREIOPODS	text	Fig. 11A
cheliped	rudimentary	bilobed
ABDOMEN	text	Fig. 14B
pleopods	just present	absent
Zoea III		
CARAPACE	fig. 3A, text	Fig. 2A
dorsal spine	1 fine seta	1 pair of setae
anterodorsal setation	2 pairs of setae	5 pairs of setae
setation of ventral margin	4 setae	5 setae
ANTENNULE	fig. 3C, text	Fig. 3C
setation	1 subterminal; 2 stout & 3 slender aesthetascs plus 1 seta all terminal	1 subterminal; 2 stout & 3 slender aesthetascs plus 3 setae all terminal
MAXILLULE	fig. 2F, text	Fig. 6C
epipod seta	absent	present
coxal endite setation	6–7	7
basial endite setation	8–9	9
MAXILLA	fig. 3F, text	Fig. 7C
basial endite setation	6 + 5–6	6 + 6
THIRD MAXILLIPED		Fig. 10C
epipod bud	not described	present
PEREIOPODS		Fig. 11B
cheliped	not described	bilobed
ABDOMEN	fig. 3C, text	Figs 13A, 14C
somite 1 setation	2 long and 2 small medial setae + 1 medial postero-dorsal seta	2 long setae + 1 medial postero-dorsal seta
Zoea IV		
CARAPACE	fig. 4A, B	Fig. 2B
dorsal spine	1 fine seta	1 pair of setae
anterodorsal setation	2 pairs of setae	7 pairs
setation of ventral margin	4 setae	8 setae
MANDIBLE		Fig. 10A
mandibular palp	not described	present
MAXILLULE	fig. 4F, text	Fig. 6D
epipod seta	absent	present
coxal endite setation	7–8	7–10
basial endite setation	10–12	10
MAXILLA	fig. 4G, text	Fig. 7D
basial endite setation	5–6 + 6	6 + 6
FIRST MAXILLIPED	fig. 4H	Fig. 8D
coxal segment	not figured	epipodal bud present + 1 seta
SECOND MAXILLIPED	fig. 4I	Fig. 9D
coxal segment	not figured	epipodal bud present
ABDOMEN	text	Fig. 14D
pleopods with endopods	not described	present

Table 2. Number of terminal plumose natatory setae on distal exopod segment of first and second maxillipeds

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	4	6	8	10
Actumnus setifer	4	6	8	
Pilumnus sluiteri	4	6		

Table 3. Number of zoeal stages expressed in pilumnines

Species	Larval stages				
Pilumnus hirtellus	ZI	ZII	ZIII	ZIV	Meg.
Actumnus setifer	ZI	ZII	ZIII	Meg.	
Pilumnus sluiteri	ZI	ZII	Meg.		
Pilumnus novaezealandiae	Meg.				

Table 4. Appearance of 6th somite division

	No. of abdominal somites			
Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	5	5	6	6
Actumnus setifer	5	6	6	
Pilumnus sluiteri	6	6		

Table 5. Appearance and development of third maxilliped

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	+	++	+++
Actumnus setifer	+	++	+++	
Pilumnus sluiteri	++	+++		

–, absent; +, biramous unsegmented rudimentary appendage comprising a longer endopod and a shorter exopod (see Fig. 10B); ++, biramous unsegmented with epipod present (see Fig. 10C); +++, biramous unsegmented appendage comprising a longer endopod with a degree of segmentation plus a shorter exopod, and epipod with arthrobranch gill bud developing (see Fig. 10D).

Pereiopods (see Fig. 11A–C, Table 6): Pereiopods develop simultaneously with the third maxillipeds. The cheliped is normally bilobed and is expressed without segmentation. In later zoeal stages segmentation is expressed in both claw and walking legs. The pereiopods are probably not functional during the zoeal phase and are just developing prior to the metamorphosis to the transitional (becoming benthic from planktonic) phase of the megalop.

Table 6. Appearance of the pereiopods

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	+	++	+++
Actumnus setifer	+	++	+++	
Pilumnus sluiteri	++	+++		

–, absent; +, rudimentary appendage comprising a bilobed chela, not segmented (see Fig. 11A); ++, developing (see Fig. 11B); +++, with some appendage segmentation (see Fig. 11C).

Table 7. Development of the pleopods

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	+	++
Actumnus setifer	–	+	++	
Pilumnus sluiteri	+	++		

–, absent; +, rudimentary buds without endopods (see Fig. 14C); ++, with endopods (see Fig. 14D).

Table 8. Development of antennulary endopod bud

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	+	++
Actumnus setifer	–	+	++	
Pilumnus sluiteri	+	++		

–, absent; +, rudimentary swelling (see Fig. 4C); ++, pronounced bud (see Fig. 4D).

Pleopods (see Fig. 14C, D, Table 7): In the megalop, pleopods are biramous, plumose, natatory appendages, but during the zoeal phase they are developing and non-functional. In pilumnines the pleopods first appear as uniramous buds and at the following moult they become biramous with distinct endopod buds.

Appearance of endopod buds

The endopod buds of the antennule, antenna and mandible all appear during the zoeal phase. They do not become functional or segmented until the metamorphosis to megalop.

Antennulary endopod (see Fig. 4C, D, Table 8): The antennulary endopod bud in pilumnids first appears as a rudimentary swelling (see Fig 4C) but in the subsequent moult it becomes pronounced with a defined shape (see Fig. 4D).

Antennary endopod (see Fig. 5A–D, Table 9): In the zoeal phase the antennary endopod bud is developing and its length can be represented as an approximate percentage of the length of the protopod. After metamorphosis to megalop, the endopod becomes segmented and functional as the sensory flagellum while the protopod becomes reduced in size and the exopod is lost.

Mandibular palp (Fig. 10A, Table 10): The mandibular palp is expressed in the ultimate zoeal stage and appears to have no function during this phase.

Appearance of epipod

First maxilliped: epipod (see Fig. 8A–D, Table 11): In the last zoeal stage an epipod appears on the coxal segment of the first maxilliped.

Appearance of setae

Dorsal spine setation (see Fig. 2A, B, Table 12): A pair of setae appears on the dorsal carapace spine in later zoeal stages, but these are absent in the zoeal development of *P. sluiteri*.

Anterodorsal carapace setae (see Figs 1A, B, 2A, B, Table 13): Anterodorsal carapace setae are paired and increase in number with successive zoeal moults.

Ventral carapace marginal setae (see Fig. 3A–C, Table 14): Clark *et al.* (1998a) presented a brief account of ventral carapace marginal setae. These increase in number with successive zoeal moults.

Antennulary protopod seta (see Fig. 4A–D, Table 15): In the last zoeal stage a seta appears on the proximal (protopod) part of the antennule. It appears earlier in taxa with abbreviated development.

Table 9. Length of antennary endopod bud represented as an approximate percentage of protopod length

SPECIES	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	43%	58%	80%
Actumnus setifer	60%	66%	84%	
Pilumnus sluiteri	56%	75%		

–, absent.

Table 10. Appearance of the mandibular palp

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	–	+
Actumnus setifer	–	–	+	
Pilumnus sluiteri	–	+		

–, absent.

Table 11. Appearance of epipod on first maxilliped

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	–	+
Actumnus setifer	–	–	+	
Pilumnus sluiteri	+	+		

–, absent.

Table 12. Paired setae on the dorsal carapace spine

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	+	+
Actumnus setifer	–	–	+	
Pilumnus sluiteri	–	–		

–, absent.

Table 13. Appearance and number of pairs of anterodorsal carapace setae

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	2	5	6
Actumnus setifer	–	2	6	
Pilumnus sluiteri	1	3		

–, absent.

Table 14. Appearance and number of ventral carapace marginal setae

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	3	5	8
Actumnus setifer	–	4	6	
Pilumnus sluiteri	1	8		

–, absent.

Table 15. Appearance of antennulary protopod seta

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	–	+
Actumnus setifer	–	–	+	
Pilumnus sluiteri	–	+		

–, absent.

Antennulary aesthetascs (see Fig. 4A–D, Table 16): Antennulary aesthetascs are extremely difficult to examine and count without the use of a suitable compound microscope. During zoeal development the number of terminal aesthetascs increases and in later zoeal stages subterminal aesthetascs appear.

Maxillule: coxal endite setae (see Fig. 6A–D, Table 17): Coxal endite setae increase in number during zoeal development.

Maxillule: basial endite setation (see Fig. 6A–D, Table 18): The setae of the basial endite comprise two distinct types, plumodenticular and plumodenticulate cuspidate. For the present study they have been combined in a joint setal count and they increase in number during zoeal development.

Maxilla: basial endite setation (see Fig. 7A–D, Table 19): The basial endites of the maxilla are bilobed; their setae increase in number during zoeal development.

Maxilla: exopod setation (see Fig. 7A–D, Table 20): The first-stage zoeal setation of the exopod (scaphognathite) margin with 4 setae and 1 long distal stout process in pilumnids is typical of many brachyuran species. After the moult to second stage the distal stout process is reduced and no longer prominent, becoming similar in size to the other marginal setae. The number of scaphognathite marginal setae increases during development.

First maxilliped: setation of distal endopod segment (see Fig. 8C, D, Table 21): In *P. hirtellus* and *A. setifer* a second subterminal seta appears later in zoeal development. This seta is absent in *Pilumnus sluiteri*.

Abdomen: dorsomedial setae on somite 1 (see Figs 12A, B, 13A, B, 14A–D, Table 22): The dorsomedial setae increase in number during zoeal development.

Table 16. Number of antennulary aesthetascs

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	4 t	5 t	1 st 5 t	1 ps, 5 ds, 5 t
Actumnus setifer	4 t	1 st, 6 t	1 ps, 4 ds, 4 t	
Pilumnus sluiteri	5 t	1 ps, 5 ds, 8 t		

ds, distal subterminal; ps, proximal subterminal; st, subterminal; t, terminal.

Table 17. Number of coxal endite setae on maxillule

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	7	7	7	8
Actumnus setifer	7	7	8	
Pilumnus sluiteri	7	9		

Table 18. Number of basial endite setae on the maxillule

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	5	8	9	10
Actumnus setifer	5	9	9	
Pilumnus sluiteri	5	9		

Table 19. Number of basial endite setae on the maxilla

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	5+4	5+5	6+6	6+6
Actumnus setifer	5+4	5+5	6+6	
Pilumnus sluiteri	5+4	5+6		

Table 20. Number of marginal scaphognathite setae

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	4+1	11	18	22
Actumnus setifer	4+1	11	21	
Pilumnus sluiteri	4+1	19		

4+1, four setae and one long distal stout process, the latter is reduced in the moult to ZII.

Table 21. The appearance and number of a second subterminal seta on the distal endopod segment of the first maxilliped

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	1+4	1+4	2+4	2+4
Actumnus setifer	1+4	1+4	2+4	
Pilumnus sluiteri	1+4	1+4		

Table 22. Number of dorsomedial setae on the first abdominal somite

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	1	2	4
Actumnus setifer	–	3	3	
Pilumnus sluiteri	1	3		

–, absent.

Table 23. Appearance of the dorsomarginal seta on the first abdominal somite

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	+	+
Actumnus setifer	–	+	+	
Pilumnus sluiteri	+	+		

–, absent.

Table 24. Appearance of paired dorsomedial setae on the telson

Species	ZI	ZII	ZIII	ZIV
Pilumnus hirtellus	–	–	–	+
Actumnus setifer	–	–	+	
Pilumnus sluiteri	–	–		

–, setae absent.

Abdomen: dorsomarginal seta on somite 1 (see Figs 12A, B, 13A, B, 14A–D,Table 23): A single dorsomarginal seta appears at some stage in zoeal development; this does not increase in number. It appears earlier in taxa with abbreviated development.

Telson: dorsomedial setae (see Figs 14D, 15D, Table 24): During the zoeal development of *P. hirtellus* and *A. setifer* a pair of dorsomedial setae appears on the dorsal surface of the telson. This pair of setae does not appear in the zoeal development of *P. sluiteri*.

DISCUSSION

Heterochrony

Decapoda larval stage moults are associated with body growth, division of somites, appearance and development of appendages, and expression of setae. However, the phylogenetic interpretation of these patterns within the zoeal development of the pilumnines under study is problematical. By comparing the zoeal stages of these pilumnines a number of characters appear at an earlier zoeal stage in *A. setifer*, with three zoeal stages, than in *P. hirtellus* with four stages. Similarly, the same characters appear earlier in *P. sluiteri* with two stages, than in *A. setifer* (e.g. the mandibular palp, Table 10). Moreover, some characters appear more developed in *P. sluiteri* as compared with the zoeal sequence of *A. setifer* and in turn with those of *P. hirtellus* (e.g. the pleopods, Table 7). This complex phenomenon, in which the timing of appearance and/or rate of character development occurs at different stages in the zoeal sequence of these three pilumnines, is known as heterochrony. Correct interpretation of these developmental processes and the extraction of reliable phylogenetic information can only be achieved by comparing homologous developmental processes between the descendant and its ancestor. There are two possible ways in which heterochrony can influence the number of zoeal stages in the developmental sequence of these pilumnines under study. One interpretation is by 'terminal addition'; a lengthening process by additions of zoeal stages ($0 \rightarrow 1 \rightarrow 2 \rightarrow 3 \rightarrow 4$). This would infer that *P. novaezealandiae* (see Table 3) is the ancestral condition with total loss of all the zoeal stages and that *P. hirtellus* with an increase of four zoeal stages is the derived sequence. The converse situation is also possible in that 'condensation' (reduction or abbreviation) of larval stages ultimately results in terminal delay of the zoeal phase ($4 \rightarrow 3 \rightarrow 2 \rightarrow 1 \rightarrow 0$). In this instant, the zoeal sequence of four stages in *P. hirtellus* would be the ancestral condition and the development of *P. novaezealandiae* hatching larvae directly as a megalop, without passing through the pelagic zoeal phase, would be the derived condition. In the absence of any known pilumnid ancestor it is important to determine correctly the polarity of the ontogenetic changes observed in the three pilumnines under study.

Plesiomorphic development sequence

The Dendrobranchiata is widely regarded as the most basal taxon within the decapods and their origins, according to Schram (1982), date back to the upper Palaeozoic. Extant relatives (Penaeoidea and Sergestoidea) of this 'plesiomorphic' group typically have an extensive life history. Eggs are released into the water column and hatch out as lecithotropic naupliar larvae. Their larval development consists of up to eight naupliar, eight zoeal and a number of decapodid (megalop) stages. The Pleocyemata (higher Decapoda), however, retain their eggs on pleopods, the naupliar phase has been lost and the larvae hatch out at a more advanced condition directly as zoea. According to Schram (1982), the Stenopodidea and the Caridea date back to at least the Jurassic and are geologically younger than the Dendrobranchiata. The larval development of the caridean *Palaemon serratus* (Pennant, 1777) by Fincham (1983) is perhaps representative of this infraorder. He describes eight zoeal stages and two decapodid (megalop) stages for which the latter represents a gradual transition between the planktonic and demersal periods. Stenopodid and caridean decapodids are morphologically similar to the preceding zoeal stage. The Brachyura also appeared in the Jurassic (Schram, 1982); their zoeas are spherical in contrast to the shrimp-like carapaces of the previous two taxa. The brachyuran moult to megalop (decapodid) is dramatic;

there is only one stage, it is not a gradual process and the results of this metamorphosis is a crab-like larva completely different to the zoeal phase and more like the adult except that the abdomen is still extended. Within the Pleocyemata decapods, abbreviated larval development frequently occurs with reduction in the number of zoeal stages and ultimately direct development with a benthic juvenile hatching directly from the egg.

This study considers that the larval development sequence within the Decapoda has shortened (abbreviated) when compared with the more primitive Dendrobranchiata. As a result the larval sequence of the higher decapods has lost the naupliar phase and the number of zoeal and decapodid (megalop) stages has become reduced (the derived condition). The latter represents the derived state of the Brachyura. The reverse condition to shortening is lengthening the larval developmental sequence, but the intercalation of additional stages and phases does not seem plausible. Consequently, the developmental sequence of four zoeal stages as described for *P. hirtellus* is considered to be the ancestral condition (see Table 3). The derived condition is the three zoeal stages of *A. setifer* and the two zoeal stages of *P. sluiteri* is considered to be further derived. Wear (1967) and Wear & Fielder (1985) reported the total loss of the zoeal stage for *P. novaezealandiae* and this is considered here as the ultimate terminal delay ($4 \rightarrow 3 \rightarrow 2 \rightarrow 1 \rightarrow 0$).

There are just three kinds of basic heterochronic change – changes in rate, onset time and offset time (McNamara, 1986; McKinney & McNamara, 1991). Each change can be either decreased (paedomorphosis) or increased (peramorphosis) in a descendant when the homologous condition is compared with its ancestor. Underdevelopment (paedomorphosis) can be produced by earlier onset (progenesis), reduced rate of morphological development (neoteny) and delayed onset (postdisplacement). By contrast, delayed offset (hypermorphosis), increased rate of morphological development (acceleration) and earlier onset (predisplacement) can produce overdevelopment (peramorphosis). These heterochronic changes can affect the entire organism (global heterochrony) – but these are rare – or, more commonly, individual characters or growth fields (dissociated or local heterochrony).

Four heterochronic processes were identified within the zoeal development sequence of pilumnines, namely global postdisplacement, and local postdisplacement, acceleration and postdisplacement.

Paedomorphosis

Abbreviated zoeal development, as in the two zoeal stages of *P. sluiteri*, can be associated with the underdevelopment of a character to a reduced state or even loss (terminal delay) when compared with its homologous condition in the ancestor *P. hirtellus* with four zoeal stages. This underdevelopment or paedomorphosis is produced by the processes of delaying the onset time (postdisplacement) of the character compared with its first appearance in the ancestor. In the present study, the process of postdisplacement was identified globally and locally in some developing characters.

Global postdisplacement: The onset of the moult to fourth zoeal stage expressed in *P. hirtellus* was terminally delayed in the developmental sequence of *A. setifer*. A shortening in the pilumnine developmental sequence occurred when the onset of the moult to third zoeal stage expressed in *P. hirtellus* and *A. setifer* was terminally delayed in *P. sluiteri* (see Table 3). This global postdisplacement resulted in abbreviated development and consequently affected the development of all the characters that normally change during the fourth and third zoeas in *A. setifer* and *P. sluiteri*, respectively, when compared with the developmental sequence of *P. hirtellus*.

Local postdisplacement: Some setal characters that appeared in the third and fourth zoeal stages of *P. hirtellus* were not expressed at all in the final zoeal stage (ZII) of *P. sluiteri*. Their onset is delayed (postdisplacement) when associated with abbreviated development. Postdisplaced characters include the pair of setae on the dorsal carapace spine (Table 12), the second subterminal seta on the distal endopod segment of the first maxilliped (Table 21) and the dorsomedial setae on the telson (Table 24).

Comparison of setal numbers in the last zoeal stage before the metamorphosis to megalop (i.e. ZIV in *P. hirtellus*, ZIII in *A. setifer* and ZII in *P. sluiteri*) demonstrates that in pilumnines reduced setal counts (late onset) are sometimes exhibited in association with abbreviated zoeal development. Thus, first and second maxilliped (Table 2) exopods are characterized by ten setae for ZIV, eight for ZIII and six for ZII. The number of paired anterodorsal setae (Table 13) is also reduced, ZIV and ZIII with six pairs, and ZII with three pairs. Similarly, the basal endite of the maxilla (Table 19) scores $6 + 6$ in ZIV and ZIII, and $5 + 6$ in ZII. However, although the marginal setae on the scaphognathite appear to demonstrate a reduction in numbers of setae from 22 in ZIV, 21 in ZII to 19 in ZII (Table 20), these marginal setae are known to vary. This character, unlike others examined, may not be a robust example of setal reduction associated with abbreviated zoeal development.

Peramorphosis

Abbreviated zoeal development, as in the two zoeal stages of *P. sluiteri*, can also be associated with overdevelopment of a character to a state beyond that of the homologous condition in *P. hirtellus* with four zoeal stages. In pilumnines this overdevelopment or peramorphosis is produced by two processes, advancing the onset time (predisplacement) or increasing the rate of development (acceleration) of a character compared with its state in the ancestor. In the present study predisplacement and acceleration were only identified locally in some developing zoeal characters.

Predisplacement: Some setal characters are not conservative and increase in number with successive zoeal stage moults. Furthermore, their onset of appearance becomes earlier (predisplacement) when associated with abbreviated zoeal development. These pilumnine characters include various setae on carapace (Tables 13, 14), antennule (Tables 15, 16), maxillule (Tables 17, 18), maxilla (Tables 19, 20), first maxilliped (Table 21), abdomen (Tables 22, 23) and telson (Table 24). The appearance of coxal endite setae on the maxillule (Table 17) is of interest as there are nine setae in ZII of *P. sluiteri*, which is an increase in number compared with the eight for *P. hirtellus* and *A. setifer*. However, Clark & Ng (2004b) noted variation in *P. sluiteri* for this character; of 11 second-stage zoeal maxillules examined coxal endites were found with seven (two), eight (four) and nine (five) setae. Clark & Ng (2004b) redescribed the only other pilumnid with two zoeal stages, *P. kempi*, which always carries nine setae on this endite. This suggests that pilumnines with two zoeal stages, unlike others with more stages, may have up to nine setae.

Somite and appendage onset of growth (timing of appearance) becomes earlier relative to the four-stage ancestral condition when associated with abbreviated zoeal development. Examples of such predisplacement within the pilumnines include the appearance of the sixth abdominal somite division (Table 4), third maxillipeds (Table 5), pereiopods (Table 6) pleopods (Table 7), antennulary endopod bud (Table 8), antennary endopod bud (Table 9), mandibular palp (Table 10) and epipod on the first maxilliped (Table 11).

With regard to the development of the antennulary endopod, Clark (2001) stated, that 'In all known brachyuran ZI, the antennule is uniramous – the endopod is absent. The endopod appears as an unsegmented bud in later stages. However, the absence of the character has gone unremarked in a number of descriptions.' Examination of the pilumnine antennule in *P. hirtellus* for this present study, *A. setifer* by Clark & Ng, 2004a) and *P. sluiteri* by Clark & Ng (2004b), suggests a two-stage development of the endopod. It first appears as a weakly defined swollen area on the antennule that from some views under the microscope is difficult to observe. However, in the last zoeal stage before the metamorphosis to megalop, the endopod is well defined (Fig. 4). In contrast, the endopod is present in *P. sluiteri* first-stage zoeas and provides to date the only known exception to the original statement of Clark (2001).

Acceleration: During the zoeal phase, in addition to an earlier onset of growth (predisplacement), some appendages continue to develop after their appearance. The rate of morphological development (acceleration) appears to be increased relative to the homologous condition in the ancestor. The third maxilliped for example takes three moults to express the epipod and arthrobranch gill in *P. hirtellus* with four zoeal stages and *A. setifer* with three. In contrast, the developmental rate of the epipod and arthrobranch gill has been accelerated (see Fig. 16, Table 5) in *P. sluiteri*, taking only two moults to attain the equivalent condition compared with the three in *A. setifer* and *P. hirtellus*. The pereiopods (Table 6) also show an accelerated rate of development in *P. sluiteri*.

Interpretation of other characters

The phylogenetic information available from some zoeal characters is difficult to analyse, for example the carapace surface ornamentation of brachyuran zoeas (see Fig. 17). Clark & Galil (1998, fig. 1A) illustrate the anterodorsal carapace surface of *Pseudoliomera speciosa* (Dana, 1852), [a xanthid], sparsely covered with small spines and Ng & Clark (2001) report a similar character for *Harrovia albolineata* Adams & White, 1849 and *Rhabdonotus pictus* A. Milne Edwards, 1879 [both pilumnids]. The first-stage zoeas of *Carpilius convexus* (Forskål, 1775) and *C. maculatus* (Linnaeus, 1758) recently described by Clark *et al.* (2005) have a densely spinulated carapace. This character has rarely been recorded in xanthoid zoeal descriptions. In fact examination of nearly 120 xanthoid first-stage zoeas and related taxa, including the pilumnines under study here, revealed that only six species have spinulated carapace ornamentation (my unpublished data). The evolution of carapace ornamentation within the xanthoids is not well understood and therefore difficult to polarize. Such characters appear not to be affected by abbreviated zoeal development.

Some setal characters are highly conservative throughout the zoeal phase and do not change during development within a taxon or between higher taxa. For example, the basis on the first maxilliped (see Fig. 8A–D) carries ten setae arranged 2,2,3,3. This character is constant for all the following xanthoid zoeas; *Epixanthus frontalis* (H. Milne Edwards, 1834), *Lydia annulipes* (H. Milne Edwards, 1834), *Eriphia scabricula* Dana, 1852, *Lybia plumosa* Barnard, 1947,

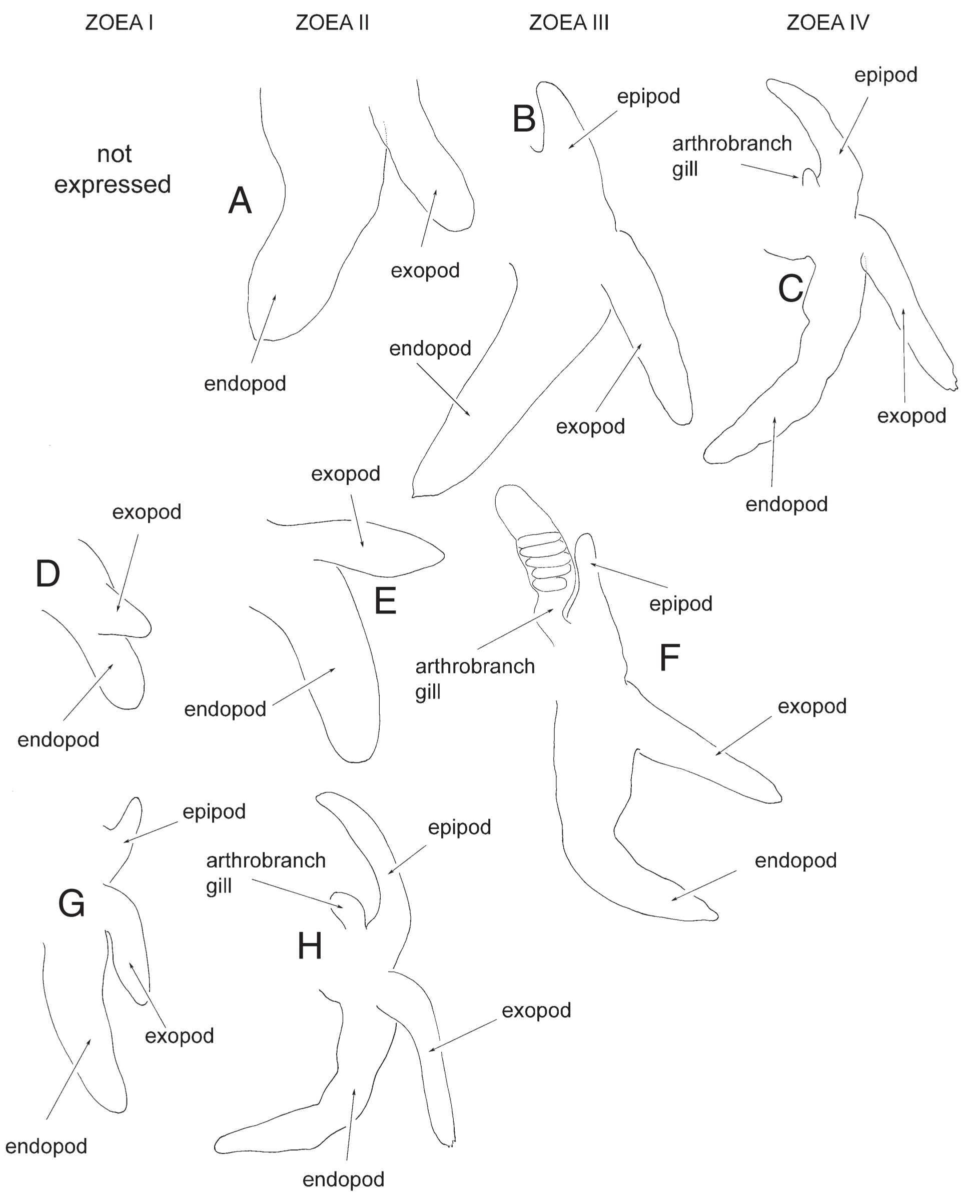

Figure 16. The peramorphic development of the third maxilliped; the ancestral condition in *Pilumnus hirtellus* (Linnaeus, 1761); A, zoea II; B, zoea III; C, zoea IV; predisplacement in *Actumnus setifer* (de Haan, 1835); D, zoea I; E, zoea II; F, zoea III; combined predisplacement and acceleration in *Pilumnus sluiteri* De Man, 1892; G, zoea I; H, zoea II (not drawn to scale).

Pilodius paumotensis Rathbun, 1907, *Zozymodes xanthoides* (Krauss, 1843), *Eurycarcinus natalensis* (Krauss, 1843), *Leptodius exaratus* (H. Milne Edwards, 1834), *Pilumnus longicornis* Hilgendorf, 1879 and *Pilumnus vespertilio* (Fabricius, 1793) (see Clark & Paula, 2003); the pilumnines examined for the present study; the majoid *Macrocheira kaempferi* (see Clark & Webber, 1991) and the portunid *Charybdis helleri* (see Dineen *et al.*, 2001). Such characters may not be phylogenetically informative within a discrete analysis, but may still be important in wider systematic issues and may not be affected by abbreviated zoeal development. Furthermore, abbreviated zoeal development does not appear to affect this particular character.

Another set of setal characters also remains conservative throughout the zoeal phase. They also do not change during development within a taxon, but provide information of phylogenetic significance between xanthoid taxa. For example, there are six distal setae on the third endopod segment of the second maxilliped and these can be identified individually (setae 3.1–3.6

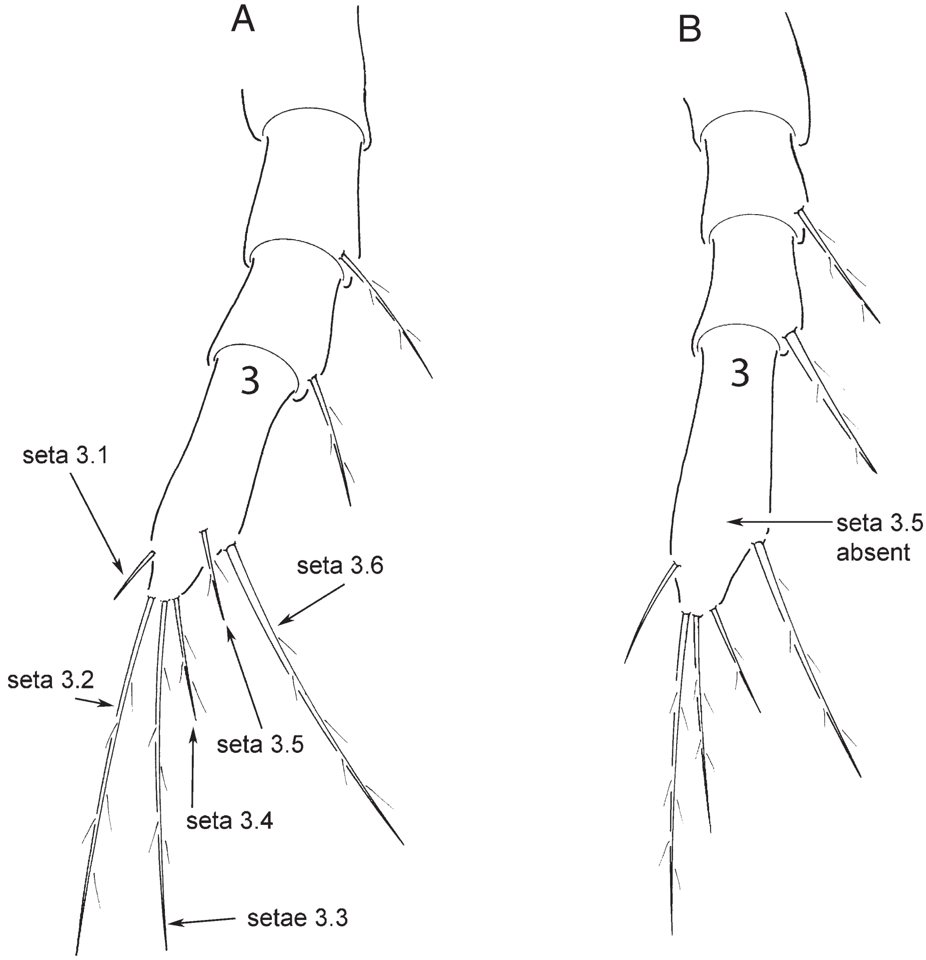

Figure 18. The third endopod segment of the second maxilliped showing: A, seta 3.5 present; B, seta 3.5 absent.

lopment can also advance the time of onset (predisplacement) and/or increase the rate of development (acceleration) of a character relative to its condition in the ancestral larval sequence, resulting in peramorphosis (overdevelopment). Furthermore, with reference to an ancestral developmental sequence heterochronic larval characters can provide valuable phylogenetic information. Finally, this pilumnine zoeal study appears to demonstrate that a mosaic of several heterochronic processes provides a dominant evolutionary mechanism influencing oligomerization within brachyuran zoeas.

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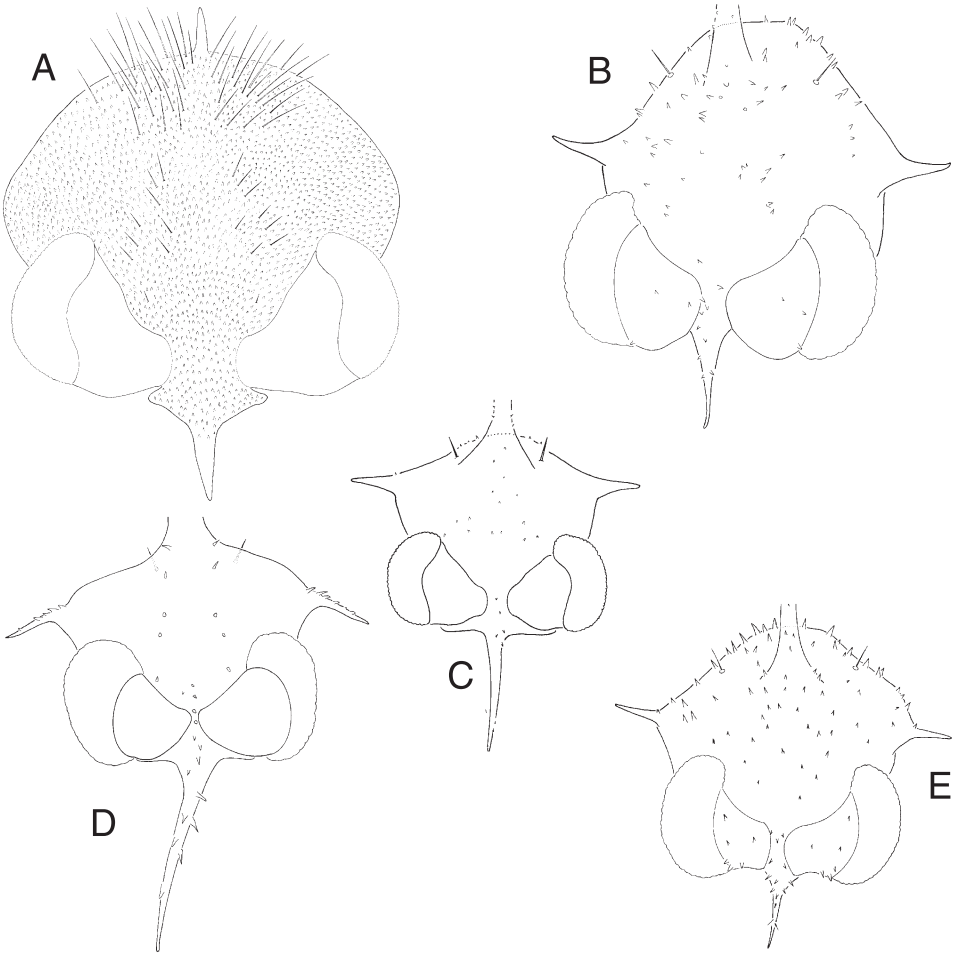

Figure 17. Carapace; ornamentation; A, *Carpilius convexus* (Forskål, 1775); B, *Harrovia albolineata* Adams & White, 1849; C, *Liomera laevis* (A. Milne-Edwards, 1873); D, *Pseudoliomera speciosa* (Dana, 1852); E, *Rhabdonotus pictus* A. Milne Edwards, 1879. The dorsal carapace spine has been drawn truncated in B, C, D, E.

in Fig. 18). Seta 3.5 is expressed (present) in xanthoid taxa *Atergatis subdentatus* (de Haan, 1835), *Chlorodiella nigra* (Forskål, 1775) and *Epiactaea nodulosa* (White, 1848) and the pilumnines of the present study, but it is absent in *Banareia subglobosa* (Stimpson, 1858), *Cataleptodius floridanus* (Gibbes, 1850) and *Monodaeus couchi* (Couch, 1851) (my personal data). Polarizing the presence or absent of seta 3.5 is difficult. Abbreviated zoeal development does not appear to affect seta 3.5 because it is present in all the pilumnines under study here. Furthermore, *A. subdentatus*, *C. nigra*, *B. subglobosa*, *C. floridanus* and *M. couchi* all have four zoeal stages, and this developmental sequence at this instant is regarded as the ancestral condition. If the general rule of oligomerization (loss or reduction) were applied to seta 3.5, its loss would be considered to be the derived condition. A number of brachyuran larvae workers have assumed that zoeal evolution has proceeded by loss or reduction of setae, these include: Lebour, 1928, 1931; Bourdillon-Casanova, 1960; Kurata, 1969; Clark, 1980, 1983; Rice, 1980, 1983, 1988; Clark & Webber, 1991 and Ng & Clark, 2001.

CONCLUSION

During the present study 23 pilumnine characters appeared to be influenced by abbreviated zoeal development (see Tables 2–24). The timing of appearance and rates of character development occur at different stages in abbreviated zoeal development relative to the same process in an ancestral sequence with more stages (heterochrony). Abbreviated zoeal development can delay the onset time (postdisplacement) of characters compared with its appearance in the ancestral larval sequence, resulting in paedomorphosis (underdevelopment). However, abbreviated zoeal deve-

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