THE ATTACHMENT OF THE YOUNG IN THE NEW ZEALAND FRESHWATER CRAYFISH *PARANEPHROPS ZEALANDICUS* (WHITE, 1847) (DECAPODA, ASTACIDA, PARASTACIDAE)

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ABSTRACT

Scholtz, G. (1995). The attachment of the young in the New Zealand freshwater crayfish *Paranephrops zealandicus* (White, 1847) (Decapoda, Astacida, Parastacidae). *New Zealand Natural Sciences* 22: 81-89.

Some aspects of early postembryonic development of the New Zealand freshwater crayfish *Paranephrops zealandicus* are investigated. The main topic is the attachment of the juvenile crayfishes to their mothers. Three different mechanisms can be discerned: the telson thread, the hooks on pereiopods four and five, and the anal thread. All these characters protect the non-autonomous juvenile crayfish from being dislodged from the mother. The telson of the first juvenile stage bears some processes which might be involved in the attachment of the telson thread. A comparison is made between the modes of attachment in *Paranephrops* and in other freshwater crayfish. Evolutionary changes in attachment are discussed within the context of the phylogenetic systematics of freshwater crayfishes.

KEYWORDS: freshwater crayfish - development - brood care - phylogeny - evolution.

INTRODUCTION

In contrast to most other decapods, all freshwater crayfish (Astacida *sensu* Scholtz & Richter 1995) undergo direct development which is combined with unique features of maternal care for the early juvenile stages. These features include various modes of attachment of the juveniles to their mothers by special threads and hooks (*e.g.*, Wood-Mason 1876; Andrews 1907; Gurney 1935; Sandeman & Sandeman 1991; Hamr 1992). It has been shown that the different patterns of this attachment are crucial for the understanding of freshwater crayfish phylogeny and evolution (Scholtz 1995). For example, the monophyly of the Northern Hemisphere Astacoidea and the Southern Hemisphere Parastacoidea (*sensu* Hobbs 1988) respectively is supported by the occurrence of hooks on the 1st pereiopods of juveniles of the former and on the 4th and 5th pereiopods of juveniles of the latter. Furthermore, the existence of a telson thread connecting the telson of the early first juvenile stage and the maternal pleopods is shared by all freshwater crayfishes and has been taken as evidence for their monophyletic origin and their single invasion into freshwater (Scholtz 1995).

In addition to the postembryonic development of several Astacoidea (*e.g.*, Andrews 1907; Baumann 1932; Price & Payne 1984), that of some Australian and South American species of the Parastacoidea has been studied (*e.g.*, Suter 1977; Rudolph & Zapata 1986; Rudolph & Rios 1987; Sandeman & Sandeman 1991; Hamr 1992). Little is known, however, about the juvenile characters of the two New Zealand freshwater crayfish species of the genus *Paranephrops*. Wood-Mason (1876) described the hooks on the dactyls of the 4th and 5th pereiopods of the first juvenile stage of *Paranephrops zealandicus* (referred to as *Astacoides zealandicus*) and Hopkins (1967) reported corresponding structures for *Paranephrops planifrons*.

The present investigation deals with the different modes of attachment of the juvenile stages of *Paranephrops zealandicus*. The scanning electron microscope (SEM) is used to complement SEM-

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studies in representatives of Cambaridae (Price & Payne 1984) and Astacidae (Holdich & Reeve 1988). It is shown that a telson thread, an anal thread and hooks on pereiopods four and five occur. All of these structures are typical of the Parastacoidea. The functional and the phylogenetic aspects of these findings are discussed.

MATERIAL AND METHODS

Adult *Paranephrops zealandicus* obtained from a crayfish farm in Otago, New Zealand were kept in tanks. Females in berry were isolated and the juveniles of different stages removed. For SEM, the juveniles were fixed in either 5% formaldehyde or alcoholic Bouin's solution. After dehydration in an ethanol series they were critical point dried and sputter coated. Observations were made with a Leica scanning electron microscope.

RESULTS

General outline of early postembryonic development

In general, the early postembryonic development of *Paranephrops zealandicus* follows the mode described for *Paranephrops planifrons* (Hopkins 1967). One can discern three juvenile stages (see Holdich 1992). The 1st juvenile stage after hatching is characterized by a large amount of yolk, stalkless eyes, a roundish shape of the thoracic region, the presence of all appendages found in the adult except the uropods, special hooks on the dactyls of the 4th and 5th pereiopods, and absence of setae (Fig. 1). The 2nd juvenile stage is more elongated, the eyes are stalked, the antennae and legs are setose, and the uropods are still missing. The pereiopodal hooks persist (Fig. 2). The 3rd juvenile stage looks more or less like the adult crayfish with fully developed uropods. The pereiopodal hooks are no longer present. The modes of attachment of the juvenile stages are described in detail below.

The telson thread

Immediately after hatching, the 1st juvenile stage is connected to the mother by the telson thread formed by the embryonic cuticle which is shed during hatching. This thread is connected to the egg shell; in turn this is attached to the maternal pleopods (Figs. 1, 3). The telson thread covers the posterior dorsal part of the telson of the juvenile crayfish (Fig. 3B). The mode of attachment to the

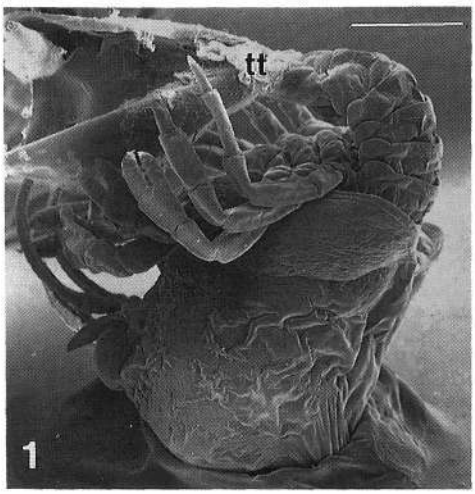

Fig. 1. The early 1st juvenile stage with the telson thread (tt). Scale bar 1mm.

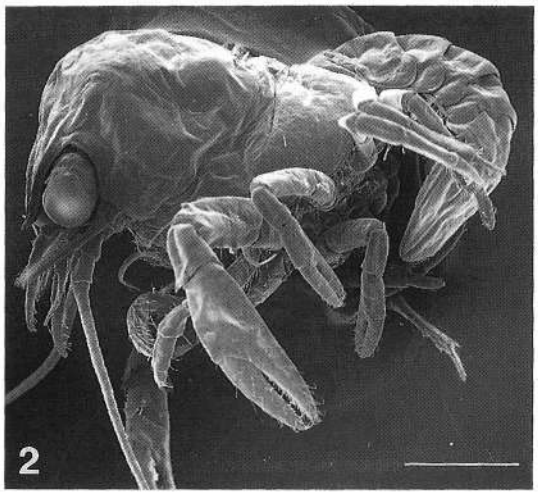

Fig. 2. The 2nd juvenile stage. Scale bar 1mm.

telson is unclear. Special hooks for this purpose which are found at the posterior margin of the telson in corresponding stages of Astacoidea (*e.g.* Price & Payne 1984; Holdich & Reeve 1988) are not differentiated. When the telson thread is removed, however, 5 to 7 small processes can be seen on either side dorsal to the posterior margin of the telson (Fig. 4).

THE PEREIOPODAL HOOKS

After a certain time the telson thread disappears (eaten?) and the juvenile crayfish cling to the pleopod setae of the mother using the pereiopodal hooks. These hooks are formed by the recurved and serrated tips of the dactyls of the 4th and 5th pereiopods (Fig. 5A). The fingers of the 1st pereiopods, the chelipeds,

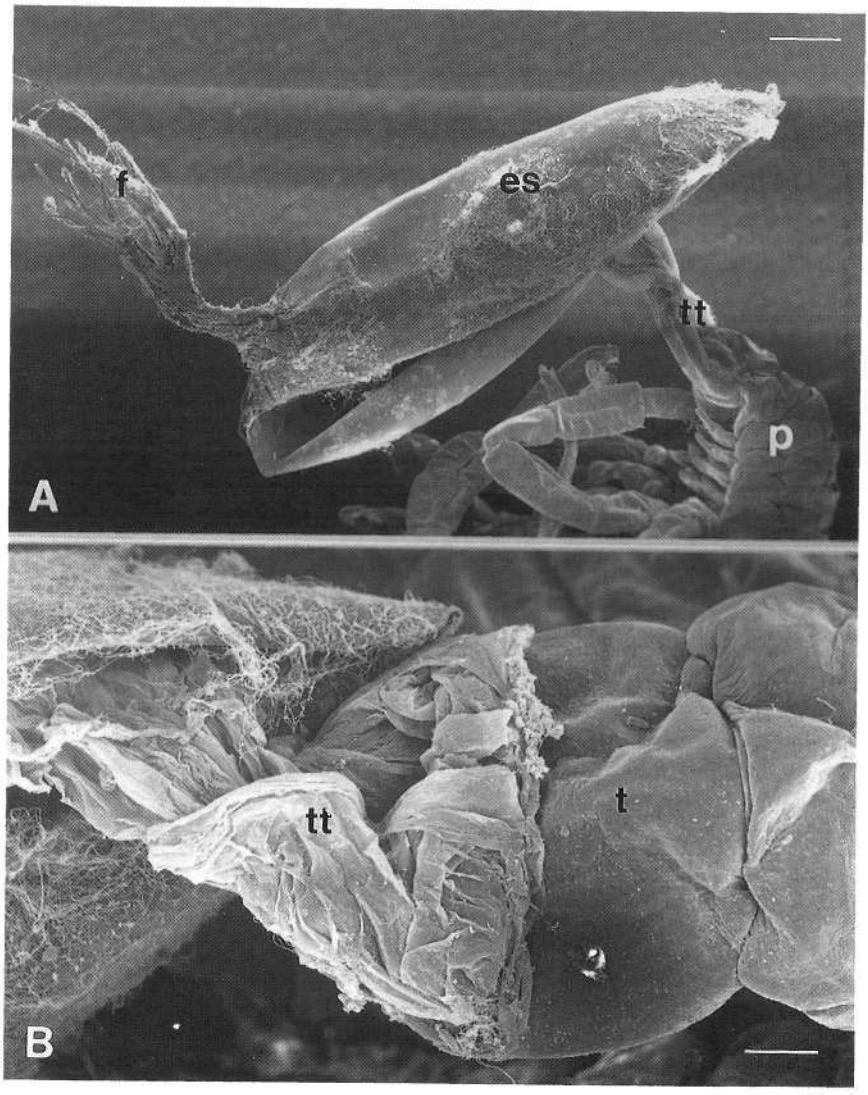

Fig. 3. The telson thread. A) Lateral view of the pleon (p) of the 1st juvenile stage and the telson thread (tt) consisting of the embryonic cuticle which is connected to the egg shell (es). The latter is attached to the maternal pleopods by a filamentous strand (f). Scale bar 300 μm. B) Dorsal view of the connection between the juvenile telson (t) and the telson thread (tt). Scale bar 100 μm.

do not form recurved spines or hooks (Fig. 5B), although the chelipeds are also used for grasping the setae of the mother's pleopods. In the 2nd juvenile stage the pereiopodal hooks are somewhat modified (Fig. 6). In particular that of the 5th pereiopod is now much shorter (Fig. 6B).

THE ANAL THREAD

For a short period after the 1st postembryonic moult, the early 2nd juvenile stage is connected to the mother via a so-called anal thread (see Andrews 1907; Hamr 1992). The anal thread is formed by the moulted cuticle of juvenile stage 1 (Fig. 7). The inner lining of the hindgut is still attached to the anus of the young crayfish. On the other end the pereiopodal hooks of the old cuticle cling to the pleopodal setae of the mother. The telson now shows hook-like setal precursors which, however, are not involved in the anal thread mechanism (Fig. 8). When the moulting process is completely finished the stage 2 juveniles again use the pereiopodal hooks for attachment to their mother (see Fig. 6). The occurrence of an anal thread during the 2nd postembryonic moult was not observed, but since this structure has been reported for other parastacid species (Hamr 1992) the possibility that it is also formed in *Paranephrops zealandicus* cannot be excluded.

DISCUSSION

All modes of attachment of the juveniles of *Paranephrops zealandicus*, the telson thread, the hooks on the dactyls of pereiopods 4 and 5, and the anal thread fulfil one main function: they act as mechanisms to protect the juvenile crayfishes from being dislogded from their mother by water currents. Therefore they have been interpreted as adaptations to life in freshwater (Scholtz 1995). Because of their restricted mobility, the juveniles are not autonomous at the two earliest stages. The telson thread is important during hatching and the first postembryonic period. The anal thread attaches the juvenile during moulting. In both phases the juveniles are very vulnerable and in particular danger of becoming separated from their mother. The occurrence of the pereiopodal hooks is correlated with the restricted mobility of the first two juvenile stages. The third stage during which parastacid crayfish normally begin their first excursions (see Hopkins 1967; Suter 1977; Rudolph & Zapata 1986; Rudolph & Rios 1987; Hamr 1992) is devoid of pereiopodal hooks.

In the following discussion, the evolution of the attachment mechanism within freshwater crayfishes is considered in the context of the phylogenetic

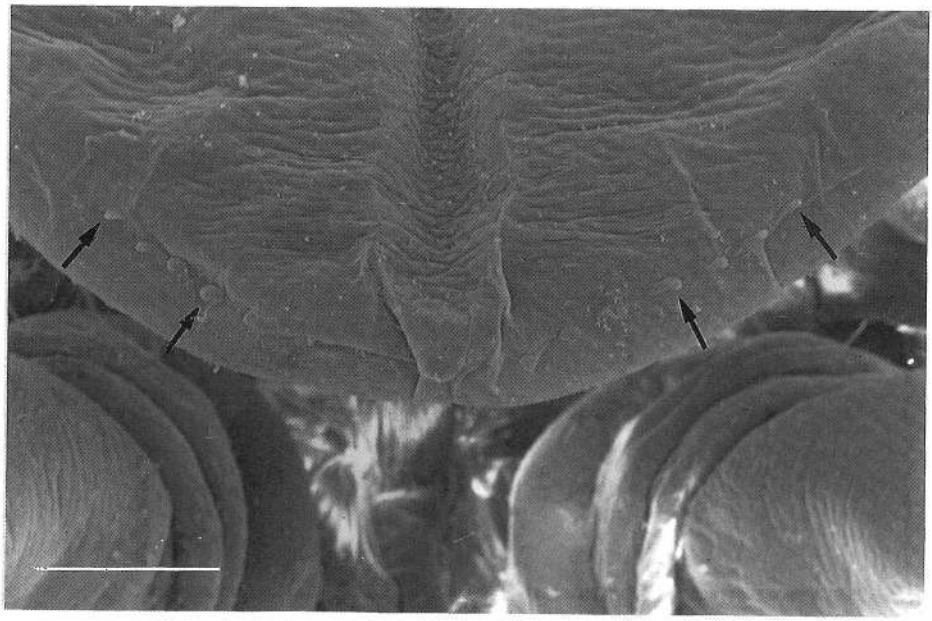

Fig. 4. The posterior margin of the telson of the 1st juvenile stage. Note the small processes on either side (arrows). Scale bar 100 μm.

systematics of the Astacida proposed by Scholtz (1993, 1995) (Fig. 9). The pattern of attachment of the juveniles of *Paranephrops zealandicus* corresponds to that reported for other parastacids (*e.g.* Hamr 1992). However, not all the attachment characters found are apomorphic for the Parastacidae. This is only true for the hooks on the dactyls of pereiopods 4 and 5 (Scholtz 1995). These have been reported for all early juvenile parastacids investigated (*e.g.*, Gurney 1935, 1942; Hopkins 1967; Suter 1977; Rudolph & Zapata 1986; Rudolph & Rios 1987; Sandeman & Sandeman 1991; Hamr 1992). In contrast, the juveniles of the Northern Hemisphere Astacoidea possess apomorphic recurved spines on the tips of the chelipeds and their pereiopods 4 and 5 are not specialised (*e.g.*, Huxley 1880;

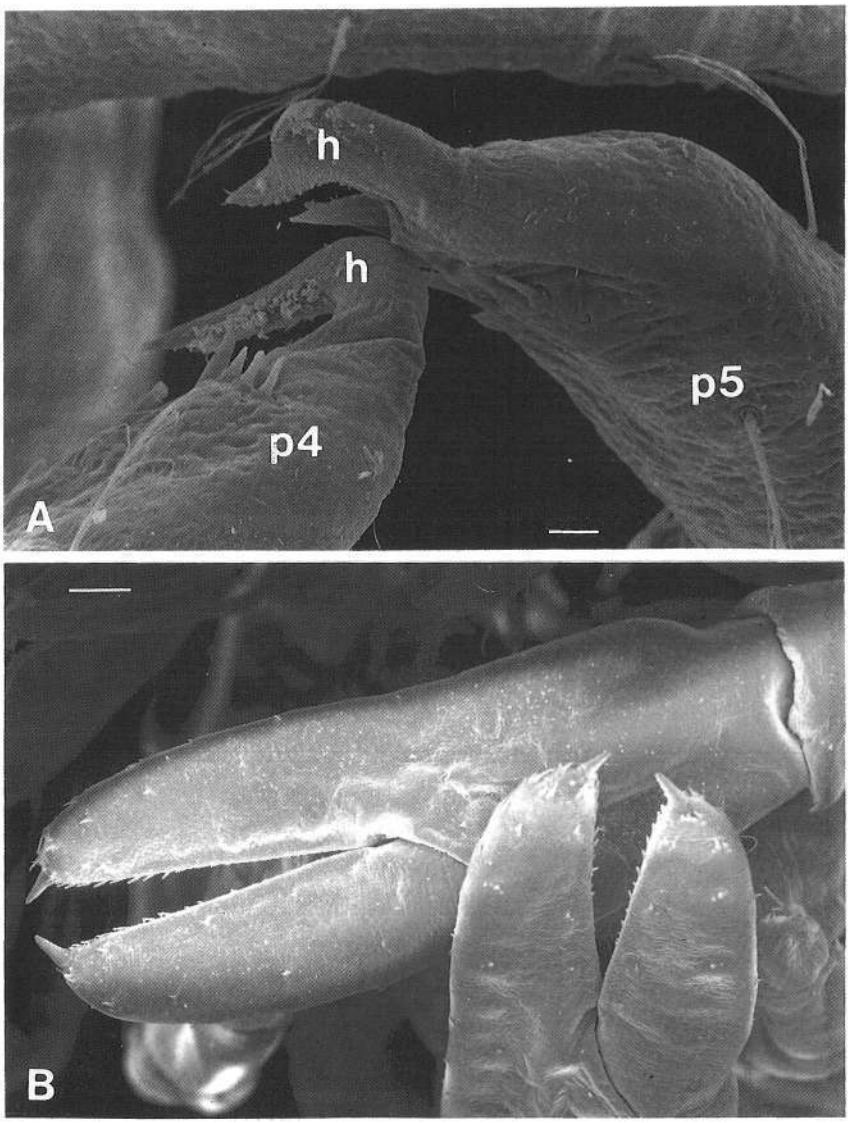

Fig. 5. Pereiopodal hooks. A) The hooks (h) on the dactyls of pereiopods 4 (p4) and 5 (p5) of the 1st juvenile stage. Note the serrated inner margin of the hooks and the supporting setae. Scale bar 20 μm. B) The chelipeds (1st pereiopods) of the 1st juvenile stage. Scale bar 100 μm.

Andrews 1907; Price & Payne 1984; Holdich & Reeve 1988). The hooks of pereiopods 4 and 5 in the Parastacoidea and the recurved spines on the chelipeds of Astacoidea seem to be convergent improvements for juvenile attachment and in the freshwater crayfish stem species both mechanisms were absent (Scholtz 1995).

The telson thread occurs in Astacoidea (*e.g.*, Andrews 1907; Skorikow & Redikorzew 1911; Thomas 1973) and Parastacoidea (*e.g.*, Gurney 1942; Suter 1977; Sandeman & Sandeman 1991; Hamr 1992) and is obviously an apomorphy of the Astacida (see Scholtz 1995). However, there are some contradictions about how it is formed. It has been suggested that the telson thread might be either the inner lining of the egg envelope (Andrews 1907; Suter 1977; Hamr 1992) or the embryonic cuticle (Andrews 1907; Price & Payne 1984; Rudolph & Zapata 1986; Rudolph & Rios 1987; the present investigation). Since it seems to be a general feature of freshwater crayfishes that hatching is accompanied by moulting (Andrews 1907; Price & Payne 1984; Sandeman & Sandeman 1991; present investigation) it is likely that the telson thread in all species is formed by the

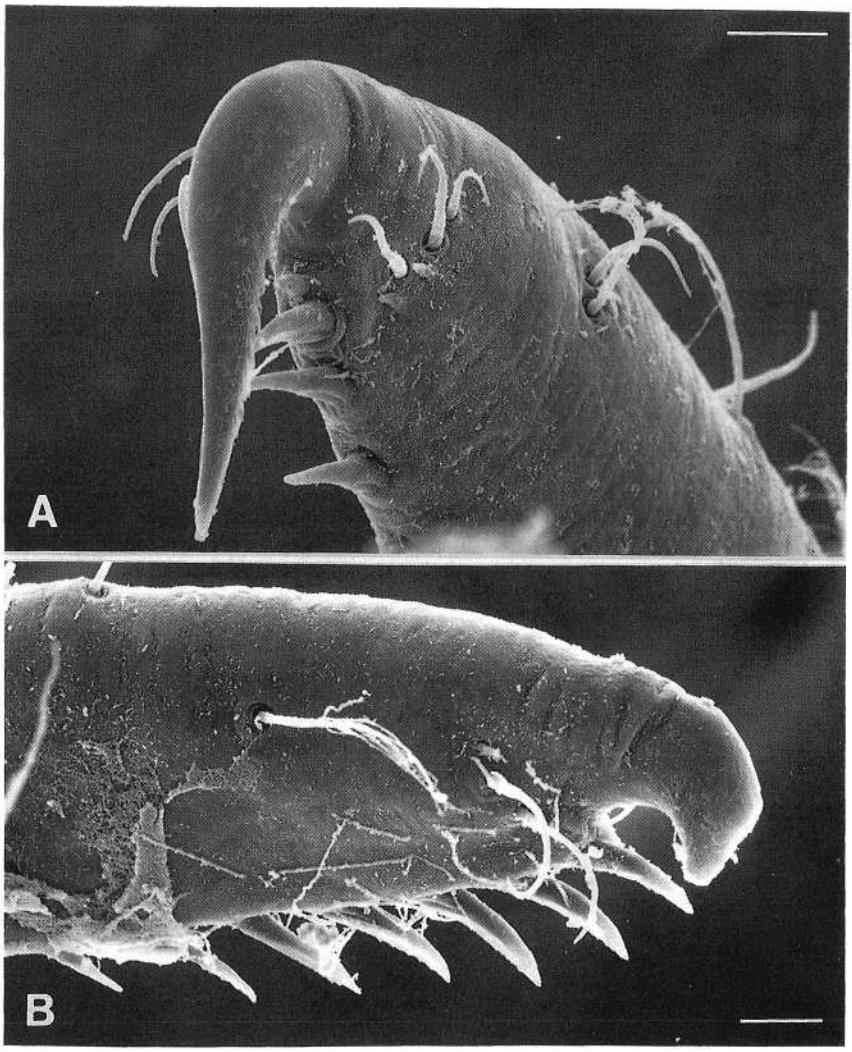

Fig. 6. Pereiopodal hooks of the 2nd juvenile stage. A) The hook on the dactyl of the 4th pereiopod. B) The hook on the dactyl of the 5th pereiopod. Compare with Fig. 5A. Scale bars 30 μm.

embryonic cuticle. In Astacoidea the telson thread is attached to the juvenile by special hook-like setal precursors at the posterior margin of the telson (*e.g.*, Andrews 1907; Baumann 1932; Price & Payne 1984; Holdich & Reeve 1988). Several authors have suggested that these hooks might bear glands that produce an adhesive fluid to attach the thread to the telson (Andrews 1907; Skorikow & Redikorzew 1911; Baumann 1932). Corresponding hooks are absent in the 1st juvenile stage of Parastacoidea (see Hamr 1992). It must remain an open question at present whether the telson hooks are apomorphic for the Astacoidea or whether they are reduced or lost in the lineage leading to the Parastacoidea. However, the present study shows the occurrence of processes at the posterior telson margin in a parastacid species. Whether these are only setal precursors (see Thomas 1973) or (in addition?) the openings of glands that produce some sort of "glue" requires further investigation. In any case these processes are too small to act in a comparable way to the telson hooks in the Astacoidea.

The formation of an anal thread has hitherto been reported for a cambarid (Andrews 1907) and several parastacid species (Hamr 1992). The lack of data for astacids might reflect incomplete observations. However, the postembryonic development of this group has been intensely studied and therefore it is likely that an anal thread is really absent in the Astacidae. From the distribution of the anal thread among the Astacida (Cambaridae and Parastacidae do not constitute a monophyletic taxon) it is concluded that this character was part of the ground plan of freshwater crayfishes. How then can the loss of the anal thread in the Astacidae be explained? Albrecht (1982) suggests that an advanced postembryonic development is an apomorphy of the Astacidae. In contrast to the 2nd stage juveniles of the Cambaridae and the Parastacidae, those of the Astacidae are morphologically and behaviourally more advanced. For instance, the telson is already equipped with long plumose setae at this stage and the young start their first excursions (see Holdich 1992). Since the anal thread serves as protection for relatively immobile juveniles that are still dependent on their mothers it apparently lost this function in the lineage leading to the Astacidae and eventually disappeared.

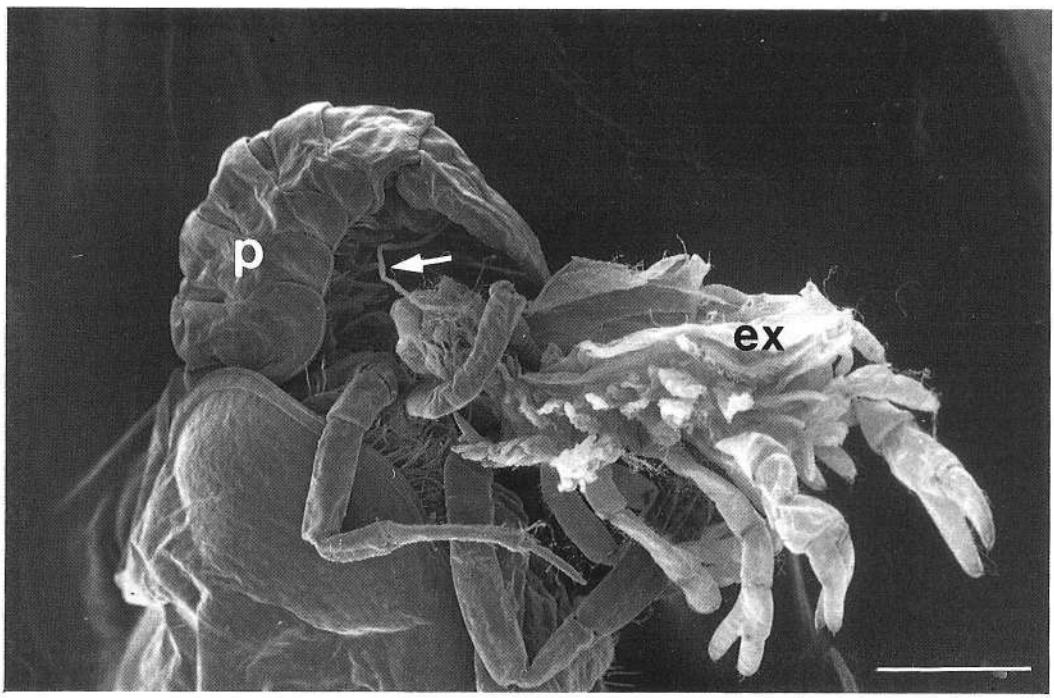

Fig. 7. Lateral view of the pleon (p) of the early 2nd juvenile stage and anal thread. The anal thread (arrow) is connected to the juvenile anus. (ex) exuviae of the 1st postembryonic moult. Scale bar 1 mm.

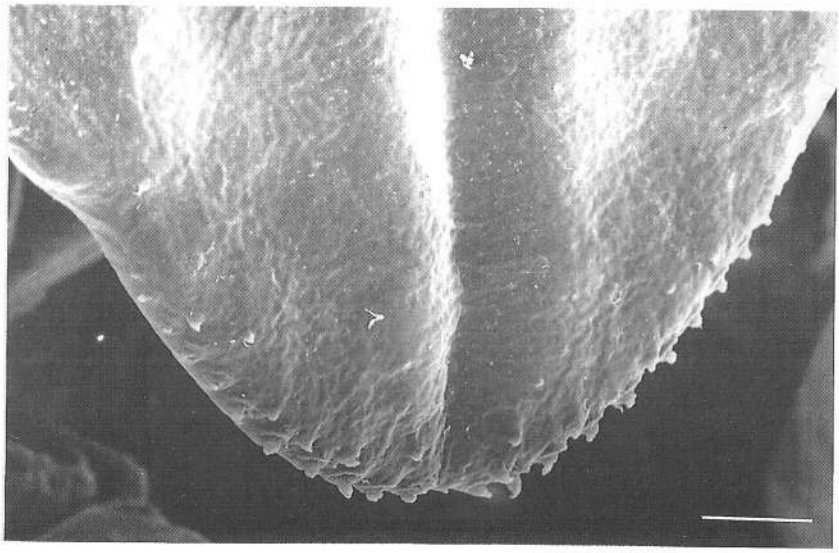

Fig. 8. The posterior margin of the telson of the early 2nd juvenile stage. Rows of hook-like setal precursors are recognizable. Compare with Fig. 4. Scale bar 100 μm.

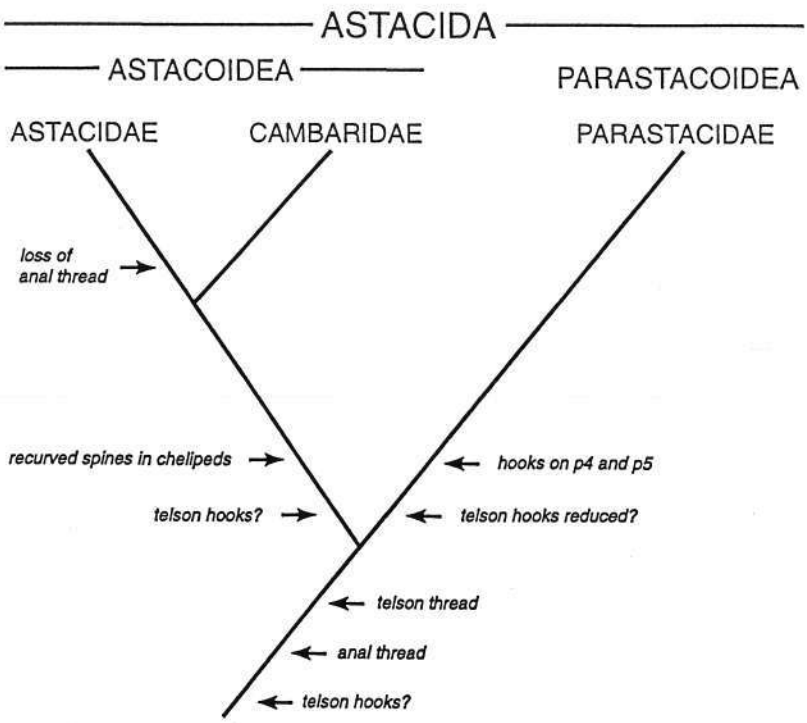

Fig. 9. Phylogenetic systematics of the Astacida as proposed by Scholtz (1995). The characters discussed in the present paper are mapped on the tree. The appearance of evolutionary novelties is marked with arrows.

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