Egg and Juvenile Development of the Australian Freshwater Crayfish, *Euastacus bispinosus* Clark (Decapoda; Parastacidae)

JODIE A. HONAN
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Box 205, Port Fairy, Victoria 3284, Australia (formerly School of Aquatic Science and Natural Resources Management, Deakin University, PO Box 423, Warrnambool, Victoria 3280)

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Aspects of egg attachment, embryogeny and development of early juvenile stages were investigated in *Euastacus bispinosus* from south-west Victoria. Shortly after spawning the eggs (4.0 x 2.9 mm) become attached in small groups to filamentous oosetae on the maternal pleopods. The egg nauplius takes two weeks to develop and at 90 days an egg mysis has formed, with eye pigmentation occurring at about 100 days.

The development of eggs takes about 140 days. Hatching takes 30–60 minutes and the embryo moults at the same time. The cast exoskeleton forms a temporary link to the mother's pleopod by adhering to the telson for 24–36 hours. The Stage 1 juveniles then grip the pleopods with their fourth and fifth pereiopods. After two more moults juveniles become independent at about 170 days. *Euastacus bispinosus* development is similar to other parastacids and key features are compared with those of other crayfish groups. Possible evolutionary relationships are also briefly discussed.

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KEYWORDS: Egg attachment, embryogeny, Euastacus bispinosus, juvenile stages, reproduction.

INTRODUCTION

As part of broader studies on reproductive cycles, growth and management of the Glenelg River crayfish, *Euastacus bispinosus* (Honan and Mitchell 1995a, b, c), observations were made on egg attachment, embryo development and early juvenile stages. This large species is endemic to the Glenelg River system (south-west Victoria) and coastal drainages of south-eastern South Australia (Morgan 1986).

Egg and juvenile development have been described for many freshwater crayfish (Hamr 1992). Eggs of northern and southern hemisphere species develop in similar ways, but juveniles differ in their method of attachment to the maternal pleopods (Gurney 1935, 1942) which indicates independent invasions of fresh water. The eggs and juveniles of many Australian genera have been described, but there is no full description for any *Euastacus* species. Clark (1937) and Turvey and Merrick (1997) include partial descriptions. *Euastacus* is a widespread genus endemic to the east, south-east and southern coastal areas of mainland Australia (Morgan 1997).

Objectives of this paper are: to describe the setal attachment of eggs to the maternal pleopods; to document embryo and larval development in the egg; to describe hatching and major changes in juvenile stages up to release; to compare and contrast developmental features of the species with other freshwater crayfish groups, and consider the evolutionary relationships between the superfamilies.

METHODS

Three egg-bearing females from the Glenelg River drainage were kept in 720 L stainless steel vats with near natural photoperiod and temperature changes (although the temperatures were about 5°C warmer than in the field). The warmer temperatures were likely to speed up development, but not alter the sequence (Wear 1974). They were fed a varied diet, and the water was changed monthly. Eggs or juveniles were removed from the females monthly, then weekly, then daily as hatching approached. The colour, texture and movement of live eggs and juveniles were noted and photographs were taken. Samples were preserved in 10% formalin and transferred to 90% ethanol. To observe hatching, a group of advanced eggs was carefully cut from a pleopod of one female and maintained in dechlorinated, aerated tap water. These eggs were checked frequently.

Two or three eggs or juveniles were removed from each female captured during monthly sampling in south-west Victoria (Honan and Mitchell 1995a). The samples were preserved in alcoholic Bouin's fluid and transferred to 70% ethanol after 24–48 hours (after Johnson 1979). This technique discoloured the eggs and juveniles, and distorted the carapace of juveniles. The preserved material was however valuable for examining setation and other fine detail and for following development in the field. Illustrations were constructed from a combination of photographs and sketches of fresh and preserved material.

RESULTS

The pleopods of *E. bispinosus* have an endopodite and exopodite of similar shape and size. They have three types of setae which are similar to those described by Thomas (1970). Pinnate setae (~4.6 mm long) fringe the margins of the exopodite and endopodite. Filamentous oosetae (~5.1 mm long) are only found on mature females. These setae grow in groups of 10–18 along all margins of the endopodite, except the tip. They also occur on the basal third of the outer edge of the exopodite, and mesially on the basipodite. Serrulate setae are short (0.5–1.2 mm) and sturdy and are found on the surface of the pleopods, rather than the margins. In males serrulate setae occur on the outer edges of the anterior face of the endopodite and exopodite, and on the posterior face of the exopodite. In females serrulate setae occur along all margins of the posterior faces of both podites.

Most eggs are attached to filamentous oosetae on the maternal pleopods (Fig. 1). On large females, eggs may also rarely attach to setae at the ventral junction of the abdomen and cephalothorax. Each egg is surrounded by a balloon-shaped membrane, with a twisted stalk at one end. The stalk is not in a constant position relative to the developing embryo. Groups of fifteen or more filamentous oosetae are gathered and their tips held twisted together by the egg stalk. Up to ten eggs have their stalks joined to a large twisted bunch of setae, although groups of two or three, or single eggs are more common. Occasionally the stalk envelops pinnate setae and produces a matted area rather than a distinct twisted cord. Some eggs have no stalk, instead the setae adhere to the side of the egg.

Incubation in the field lasted 18–20 weeks; eggs were spawned in early May, and hatched in October-November. Eggs in the laboratory were about 5°C warmer, and hatched about four weeks earlier. Egg-bearing females feed during incubation and are easily caught in the field (Honan and Mitchell 1995a). The approximate ages are for eggs developing in the field.

The eggs are pale burgundy, soft and elongate (4.0 x 2.9 mm) shortly after spawning. The first stage observed was an early gastrula with well developed blastopore. This invagination is about 200 μm in diameter. Surrounding the pore is a slightly raised area about 750 μm in diameter. Two days later the pore is much deeper (Fig. 2a). The rudiments of the protocerebra and the two thoracico-abdominal segments have started to develop. One day later the blastopore has begun to close over, forming an advanced gastrula (Fig. 2b). The embryonic area has differentiated into the cephalic regions, and the

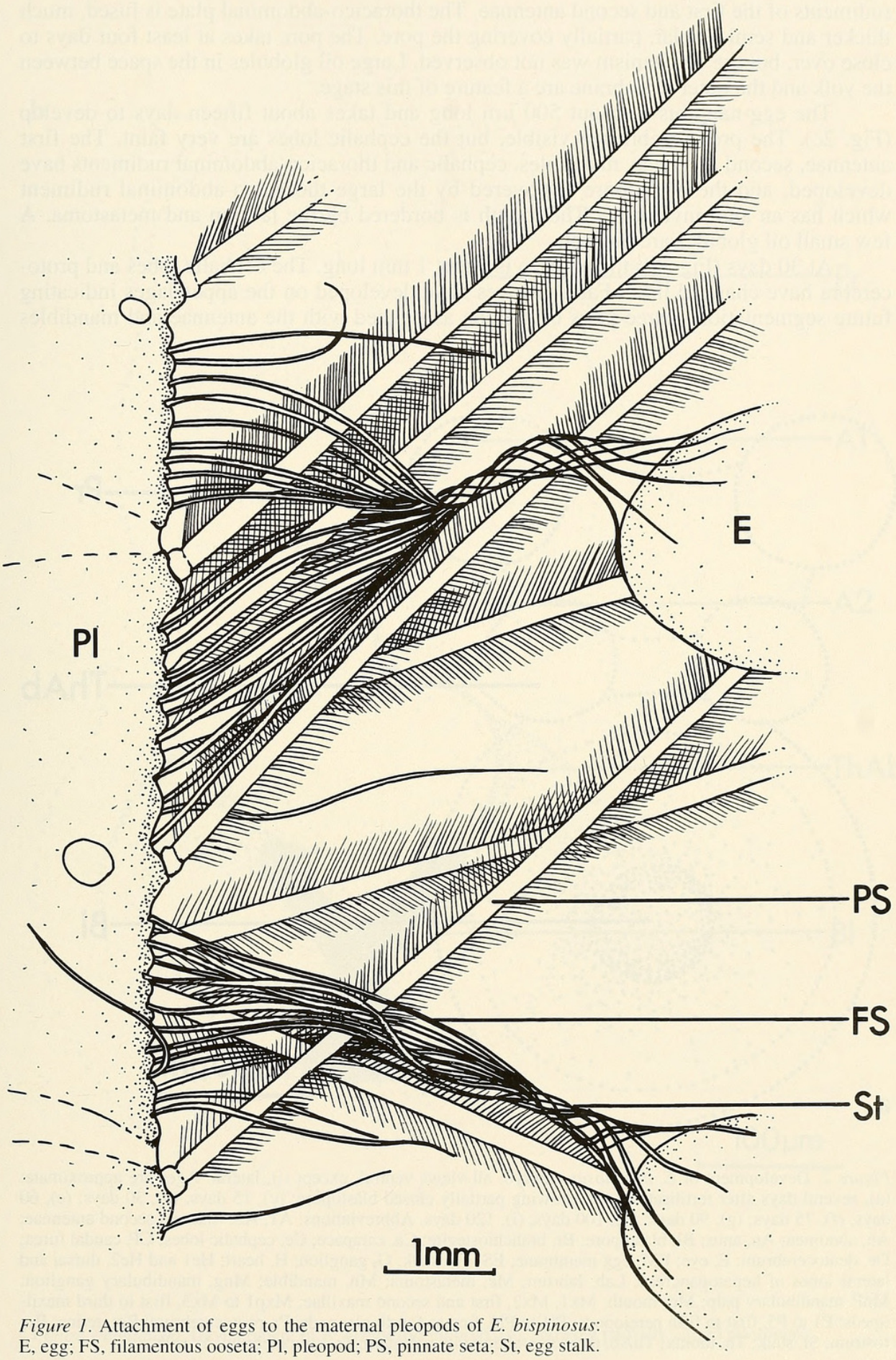


Figure 1. Attachment of eggs to the maternal pleopods of *E. bispinosus*: E, egg; FS, filamentous ooseta; Pl, pleopod; PS, pinnate seta; St, egg stalk.

rudiments of the first and second antennae. The thoracico-abdominal plate is fused, much thicker and semicircular, partially covering the pore. The pore takes at least four days to close over, but the mechanism was not observed. Large oil globules in the space between the yolk and the outer membrane are a feature of this stage.

The egg-nauplius is about 500 μm long and takes about fifteen days to develop (Fig. 2c). The protocerebra are visible, but the cephalic lobes are very faint. The first antennae, second antennae, mandibles, cephalic and thoracico-abdominal rudiments have developed, and the blastopore is covered by the large thoracico-abdominal rudiment which has an anal involution. The mouth is bordered by the labrum and metastoma. A few small oil globules are present.

At 30 days (Fig. 2d) the embryo is about 1 mm long. The cephalic lobes and protocerebra have changed little. Faint grooves have developed on the appendages indicating future segmentation. Three pairs of ganglia associated with the antennae and mandibles

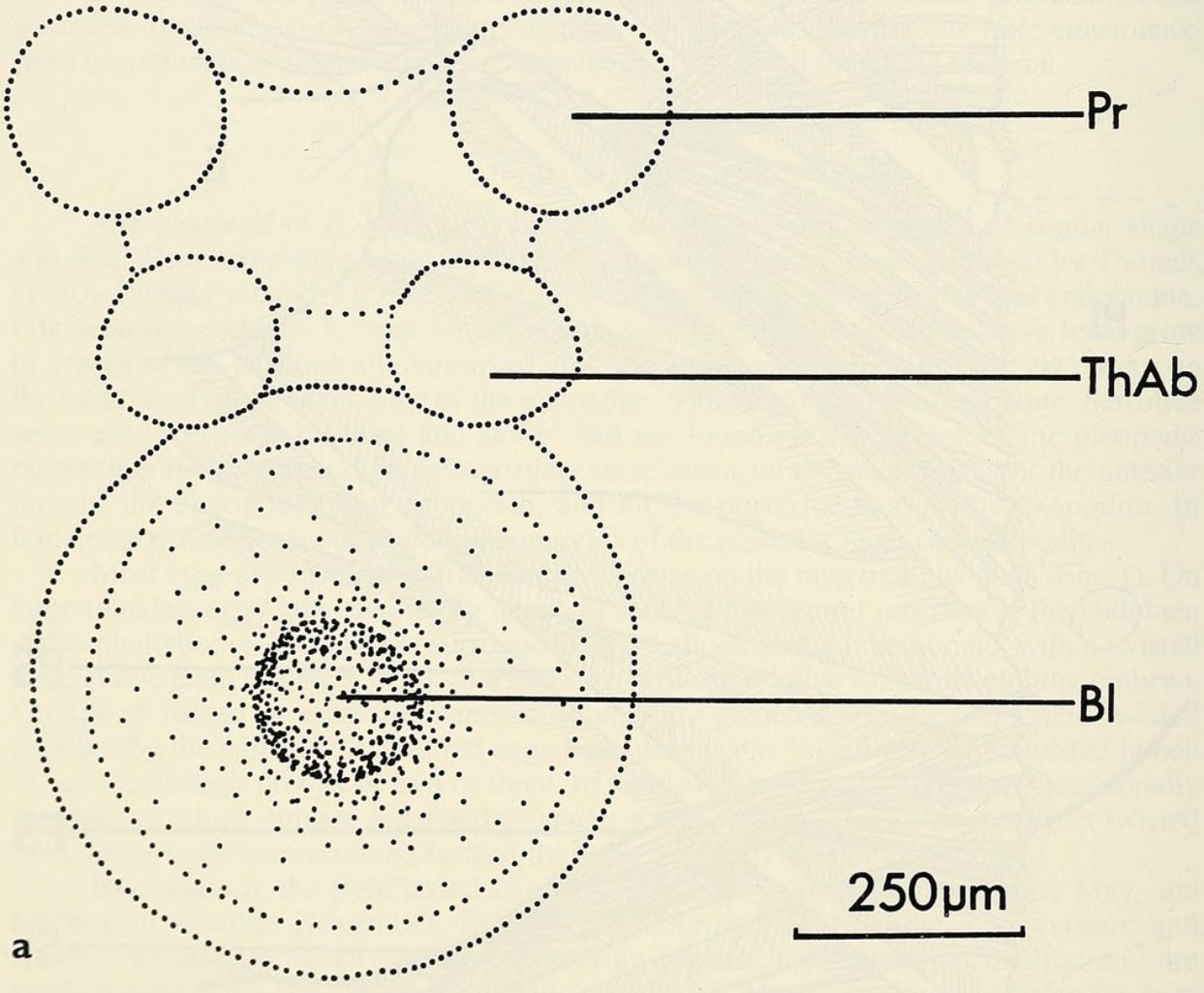


Figure 2. Development of *E. bispinosus* embryo, all views ventral, except (i), lateral. Ages are approximate: (a), several days after fertilisation; (b), showing partially closed blastopore; (c), 15 days; (d), 30 days; (e), 60 days; (f), 75 days; (g), 90 days; (h), 100 days, (i), 120 days. Abbreviations: A1, A2, first and second antennae; Ab, abdomen; An, anus; Bl, blastopore; Br, branchiostegite; Ca, carapace; Ce, cephalic lobes; CF, caudal furca; De, deutocerebrum; E, eye; EM, egg membrane; ES, eye stalk; G, ganglion; H, heart; He1 and He2, dorsal and lateral lobes of hepatopancreas; Lab, labrum; Me, metastoma; Mn, mandible; Mng, mandibulary ganglion; MnP, mandibulary palp; Mo, mouth; Mx1, Mx2, first and second maxillae; Mxp1 to Mx3, first to third maxillipeds; P1 to P5, first to fifth pereiopods; Pl1 to Pl4, first to fourth pleopods; Pr, protocerebrum; Ret, retina; Ro, rostrum; St, stalk; Th, thorax; ThAb, thoracico-abdominal rudiment; Tr, tritocerebrum; Y, yolk.

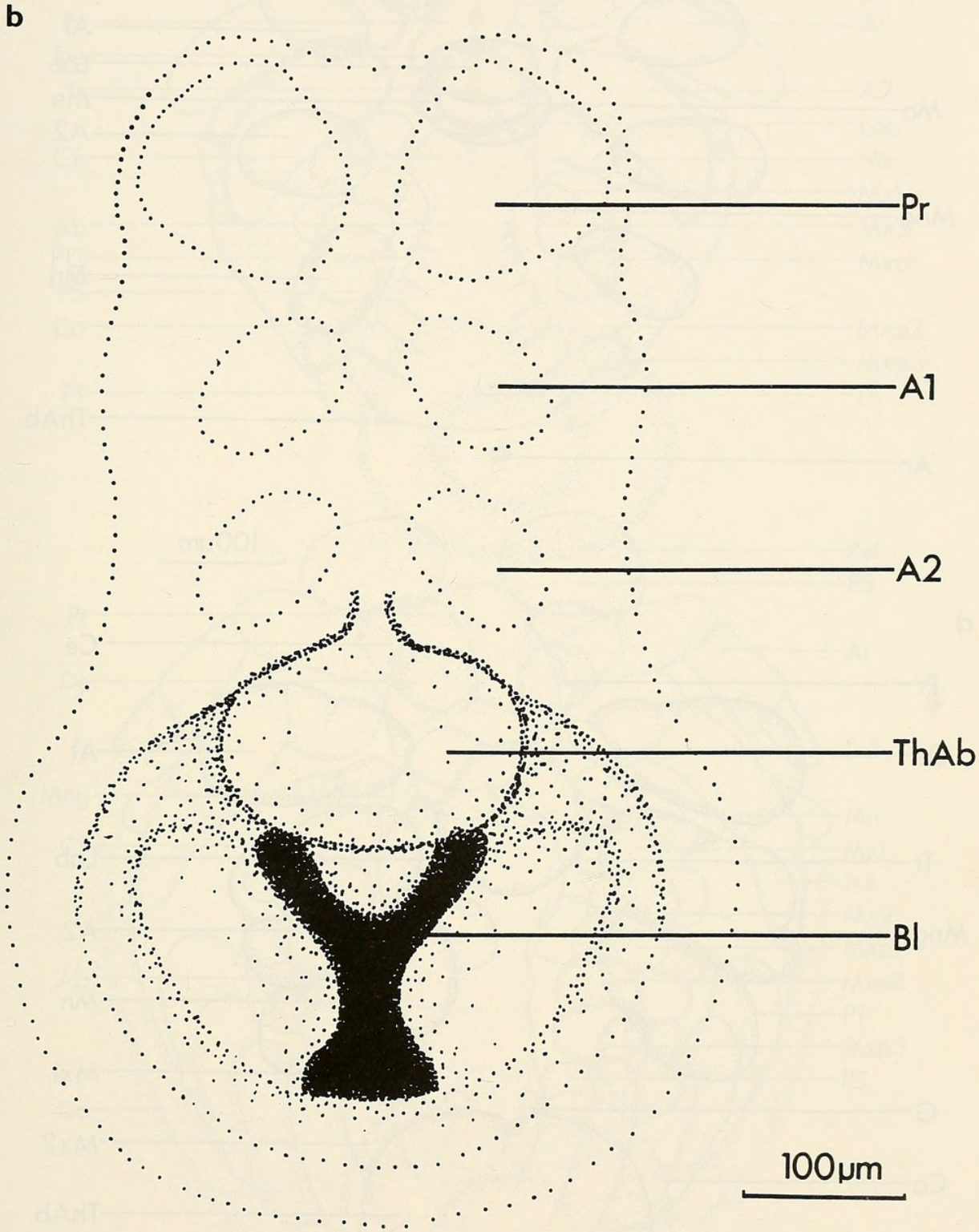
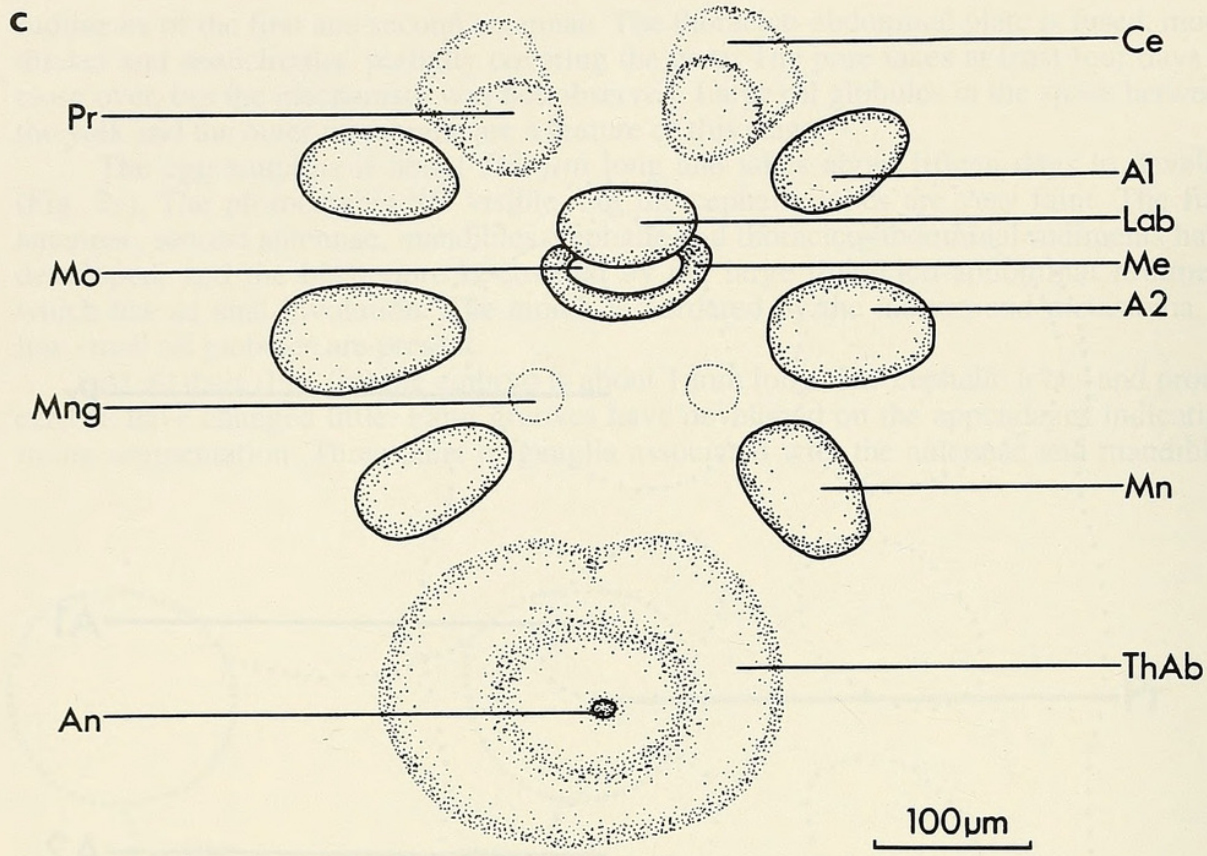


Figure 2 continued. Development of *E. bispinosus* embryo, (b), showing partially closed blastopore.



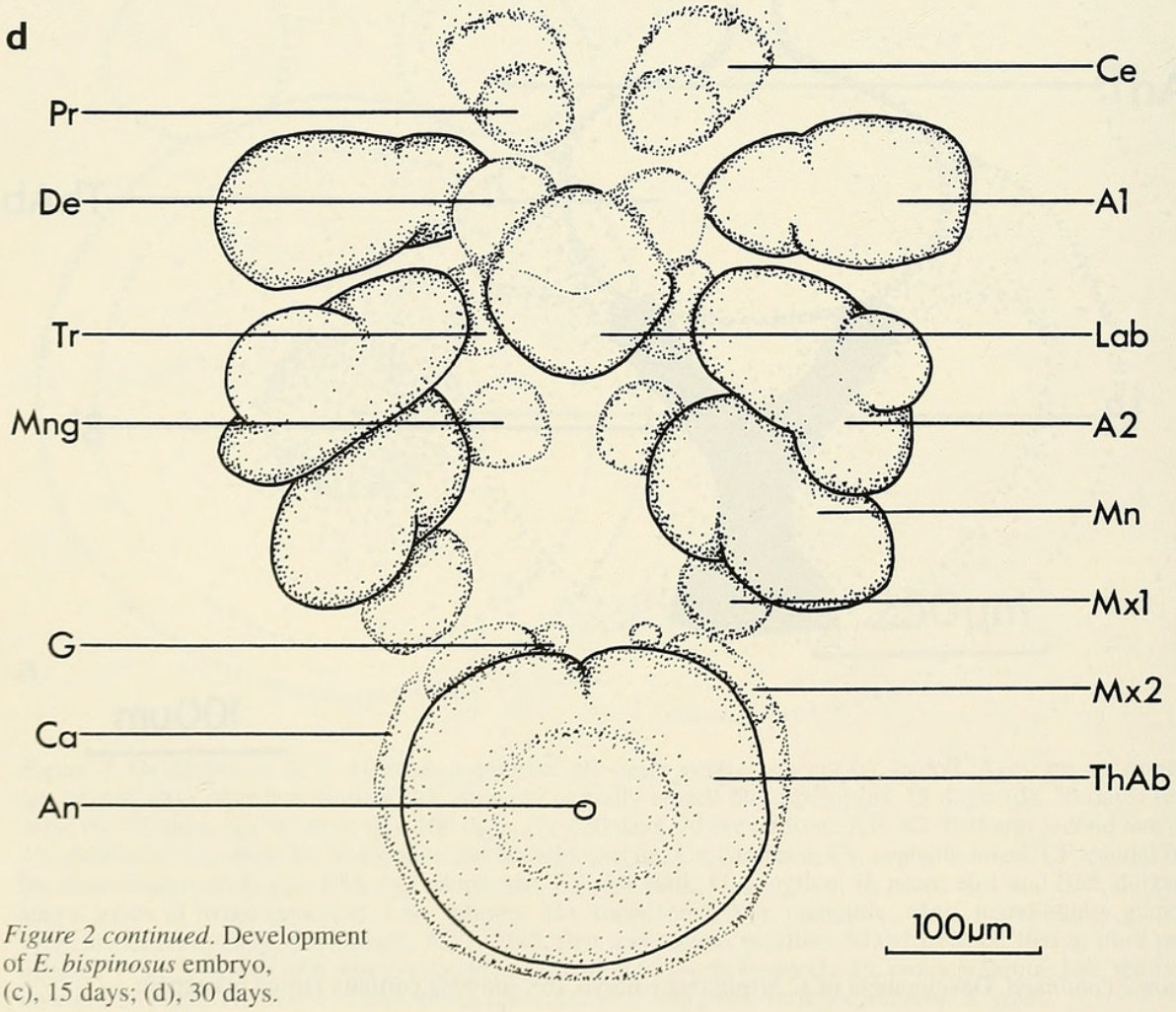
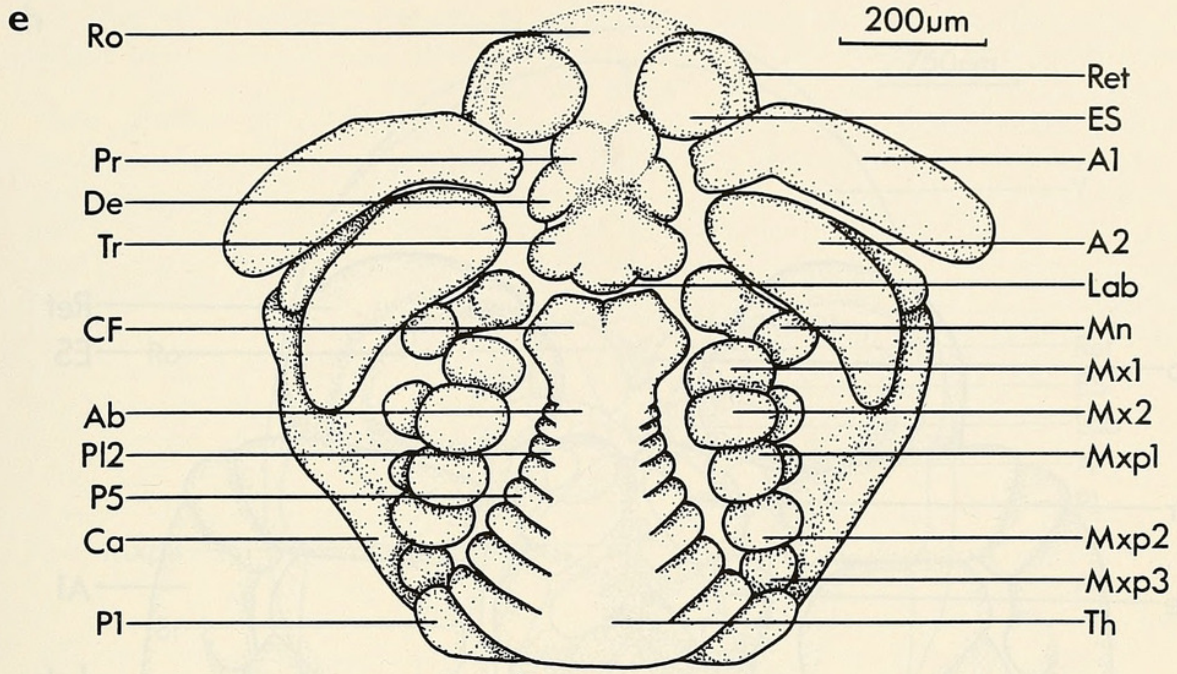


Figure 2 continued. Development of *E. bispinosus* embryo, (c), 15 days; (d), 30 days.



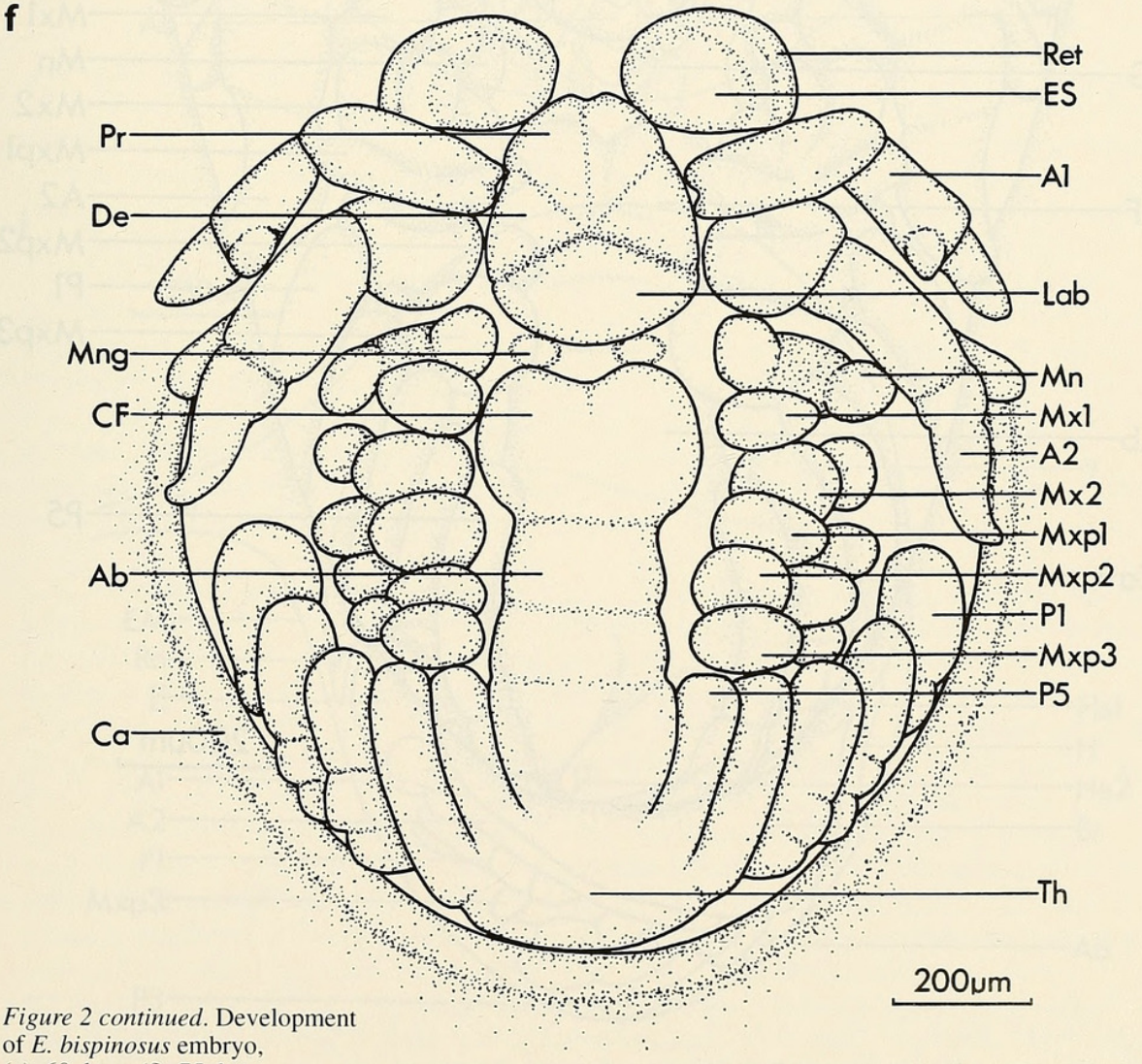


Figure 2 continued. Development of *E. bispinosus* embryo, (e), 60 days; (f), 75 days.

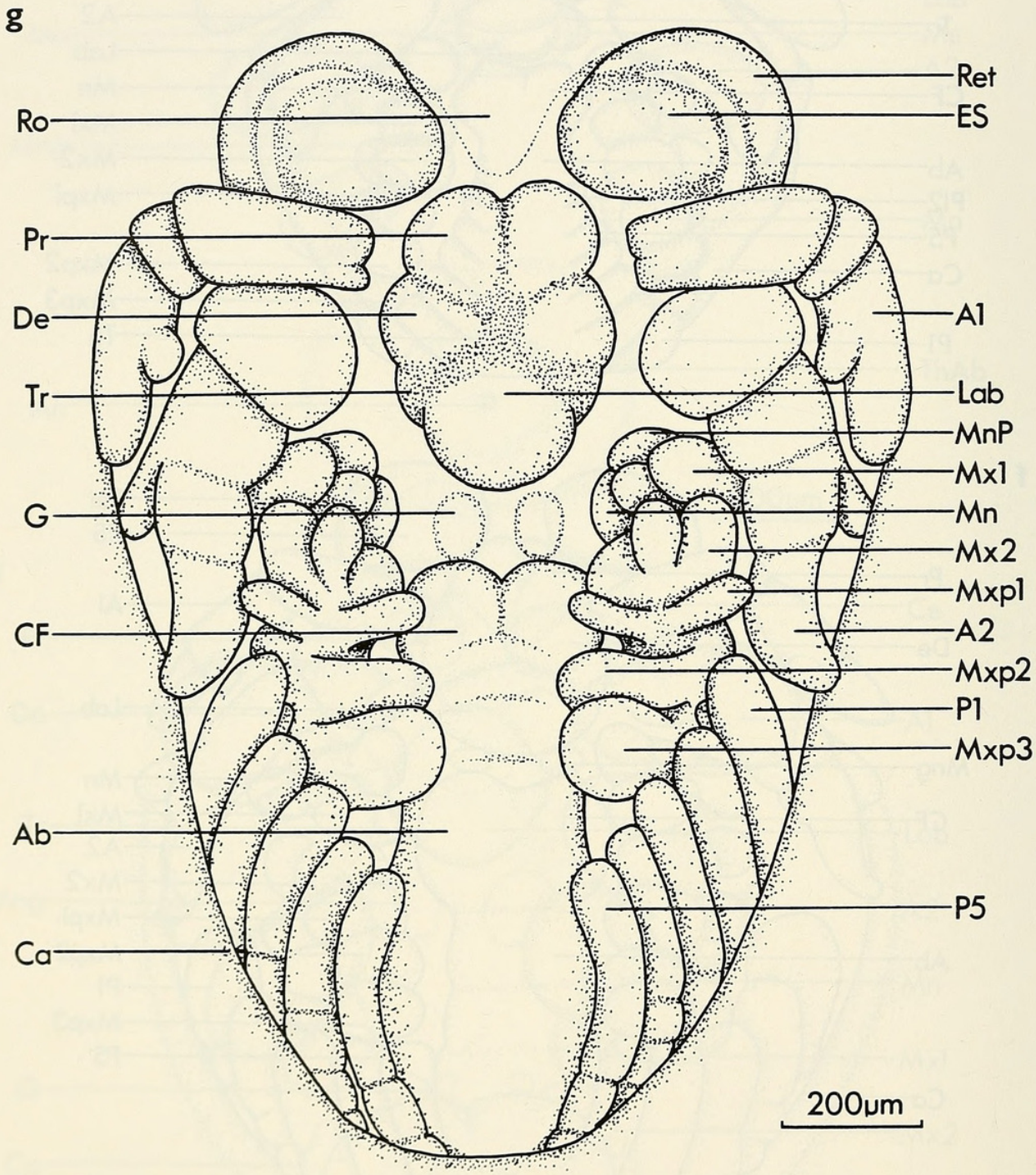


Figure 2 continued. Development of *E. bispinosus* embryo, (g), 90 days.

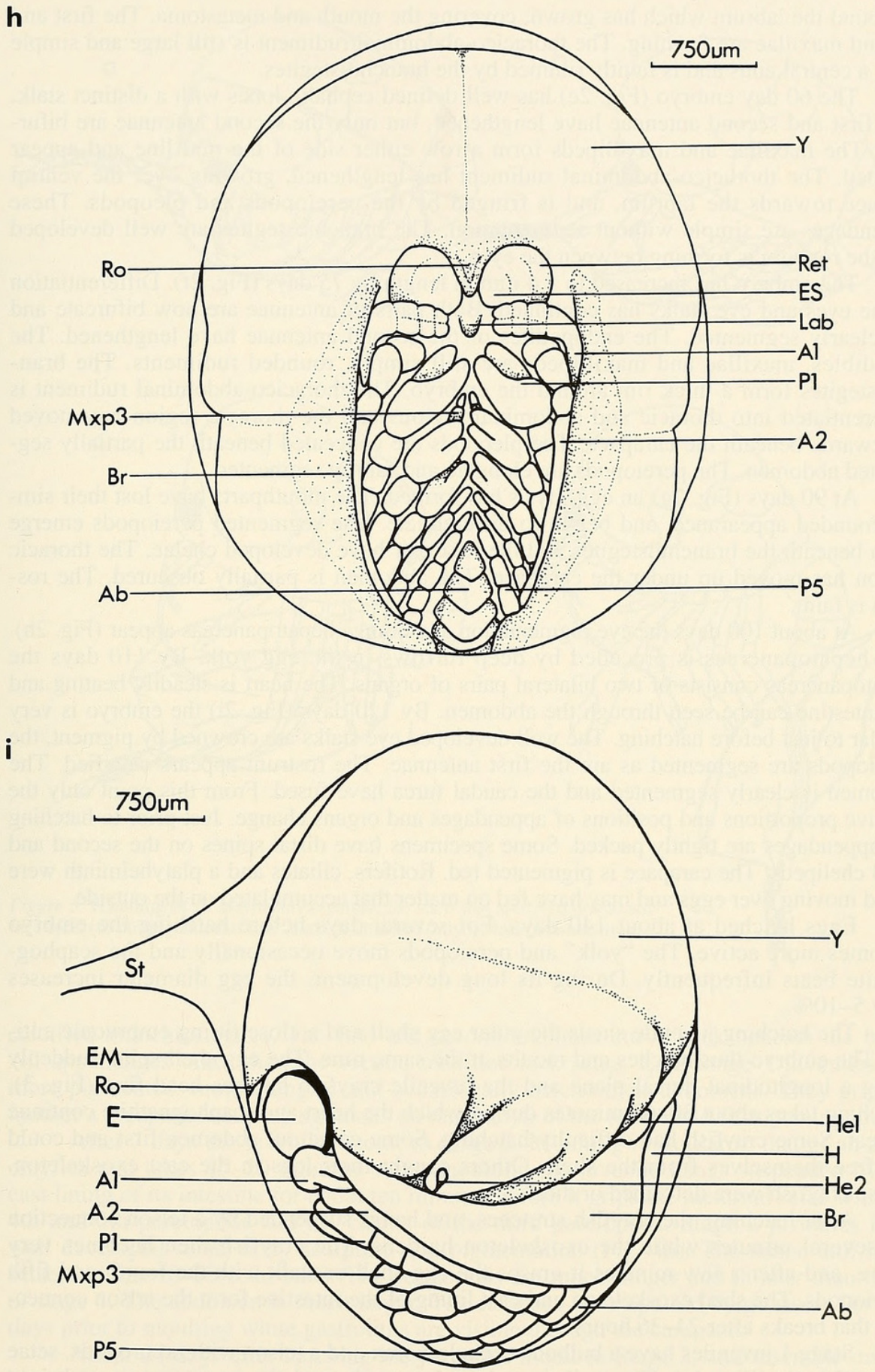


Figure 2 continued. Development of *E. bispinosus* embryo, (h), 100 days, (i), 120 days.

surround the labrum which has grown, covering the mouth and metastoma. The first and second maxillae are forming. The thoracico-abdominal rudiment is still large and simple with a central anus and is faintly rimmed by the branchiostegites.

The 60 day embryo (Fig. 2e) has well defined cephalic lobes with a distinct stalk. The first and second antennae have lengthened, but only the second antennae are bifurcate. The maxillae and maxillipeds form a row either side of the mid line and appear bilobed. The thoracico-abdominal rudiment has lengthened, growing over the ventral surface towards the labrum, and is fringed by the pereiopods and pleopods. These appendages are simple without segmentation. The branchiostegites are well developed and the rostrum is forming between the eyes.

The embryo has increased to 1.4 mm in length by 75 days (Fig. 2f). Differentiation of the eyes and eye stalks has continued. Both pairs of antennae are now bifurcate and are clearly segmented. The endopodites of the second antennae have lengthened. The mandibles, maxillae and maxillipeds are still simple, rounded rudiments. The branchiostegites form a thick rim around the embryo. The thoracico-abdominal rudiment is differentiated into thoracic and abdominal regions and the thoracic region has moved backwards beneath the carapace. The pleopods are concealed beneath the partially segmented abdomen. The pereiopods are elongate and faintly segmented.

At 90 days (Fig. 2g) an egg-mysis has formed. The mouthparts have lost their simple rounded appearance, and begun to differentiate. The segmented pereiopods emerge from beneath the branchiostegites and the first pair have developed chelae. The thoracic region has moved up under the carapace. The abdomen is partially obscured. The rostrum is faint.

At about 100 days the eye pigmentation and orange hepatopancreas appear (Fig. 2h). The hepatopancreas is preceded by deep furrows in the egg yolk. By 110 days the hepatopancreas consists of two bilateral pairs of organs. The heart is steadily beating and the intestine can be seen through the abdomen. By 120 days (Fig. 2i) the embryo is very similar to just before hatching. The well developed eye stalks are crowned by pigment, the pereiopods are segmented as are the first antennae. The rostrum appears calcified. The abdomen is clearly segmented and the caudal furca have fused. From this point only the relative proportions and positions of appendages and organs change. Just prior to hatching the appendages are tightly packed. Some specimens have distal spines on the second and third chelipeds. The carapace is pigmented red. Rotifers, ciliates and a platyhelminth were noted moving over eggs and may have fed on matter that accumulated on the outside.

Eggs hatched at about 140 days. For several days before hatching the embryo becomes more active. The "yolk" and pereiopods move occasionally and the scaphognathite beats infrequently. During its long development, the egg diameter increases only 5–10%.

The hatching juvenile sheds the outer egg shell and a close fitting embryonic cuticle. The embryo thus hatches and moults at the same time. The egg shell splits suddenly along a longitudinal dorsal plane and the juvenile crayfish hatches head first (Fig. 3). Hatching takes about 30–60 minutes during which the heart and scaphognathite continue to beat. Some crayfish had difficulty hatching. Some came out abdomen first and could not free themselves from the shell. Others caught their legs in the cast exoskeleton. These crayfish were deformed or died.

After hatching, the crayfish stretches, and hangs suspended by a telson connection for several minutes while the exoskeleton hardens. The crayfish then becomes very active, and after a few minutes it grasps the egg shell or stalk with the fourth and fifth pereiopods. The shed exoskeleton and cast lining of the intestine form the telson connection that breaks after 24–36 hours.

Stage 1 juveniles have a bulbous cephalothorax and a telson with no uropods, setae or setal buds (Fig. 4a). The yolk is a deep burgundy and the hepatopancreas bright orange. The rostrum is depressed between sessile eyes. The gills beat beneath the well

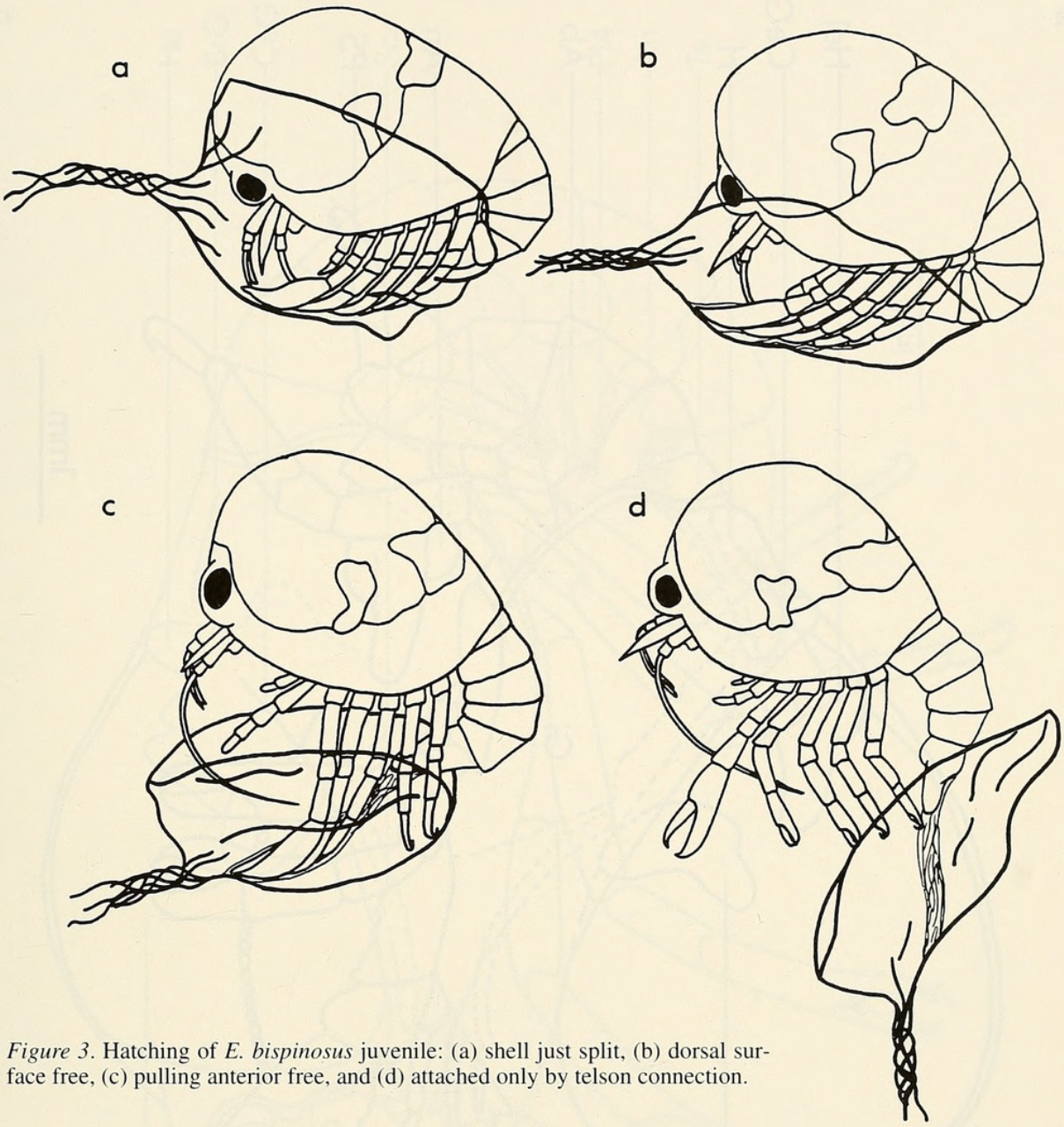


Figure 3. Hatching of *E. bispinosus* juvenile: (a) shell just split, (b) dorsal surface free, (c) pulling anterior free, and (d) attached only by telson connection.

calcified branchiostegites. The first and second antennae curve back beneath the body. All appendages other than the second maxillae lack setae. Late Stage 1 juveniles are more pigmented, more elongate and occasionally extend their abdomens. They grip the mother's pleopodal setae using hooks on the dactyli of the fourth and fifth pereiopods.

After 7 days the juveniles moult to Stage 2. Moulting is similar to that of an adult crayfish and takes 15–20 minutes. After moulting the juvenile hangs suspended by the cast lining of its intestine for about ten minutes before it grips the maternal setae with the 4th and 5th pereiopods and the chelae of the third pereiopods. Stage 2 juveniles have well developed setae, body sculpture and pigmentation (Fig. 4b). The telson still lacks setae, but has 18–20 setal buds. The pereiopods are much longer and thinner than those of stage 1. The abdomen is much larger. The carapace is sculptured by grooves. For 2–3 days prior to moulting white gastroliths are visible through the carapace.

About 24 days after hatching the juveniles moult to Stage 3, and resemble miniature adults with a complete tail fan, numerous setae and more pigmentation (Fig. 4c). The yolk is much reduced. Initially they continue to cling to the mother and each other.

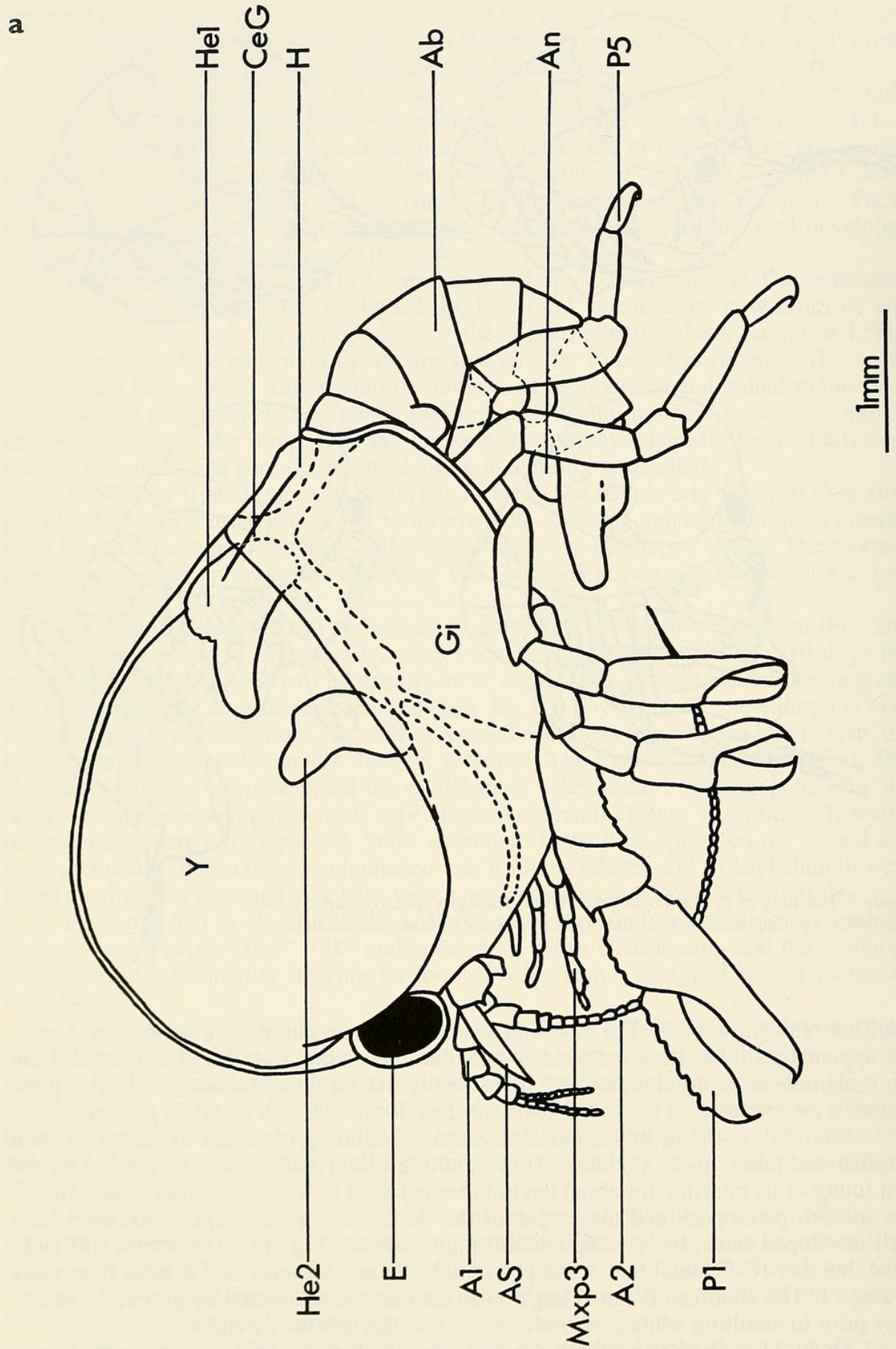


Figure 4. Juvenile stages of *E. bispinosus* after hatching: (a), Stage 1, one day after hatching; (b), Stage 2; (c), Stage 3. Abbreviations as per Figure 2. Also AS, antennal scale; BrG, branchiocardiac groove; CeG, cephalic groove; Gi, gills; Sc, scaphognathite; Ssp, suborbital spine; Te, telson; U, uropod.

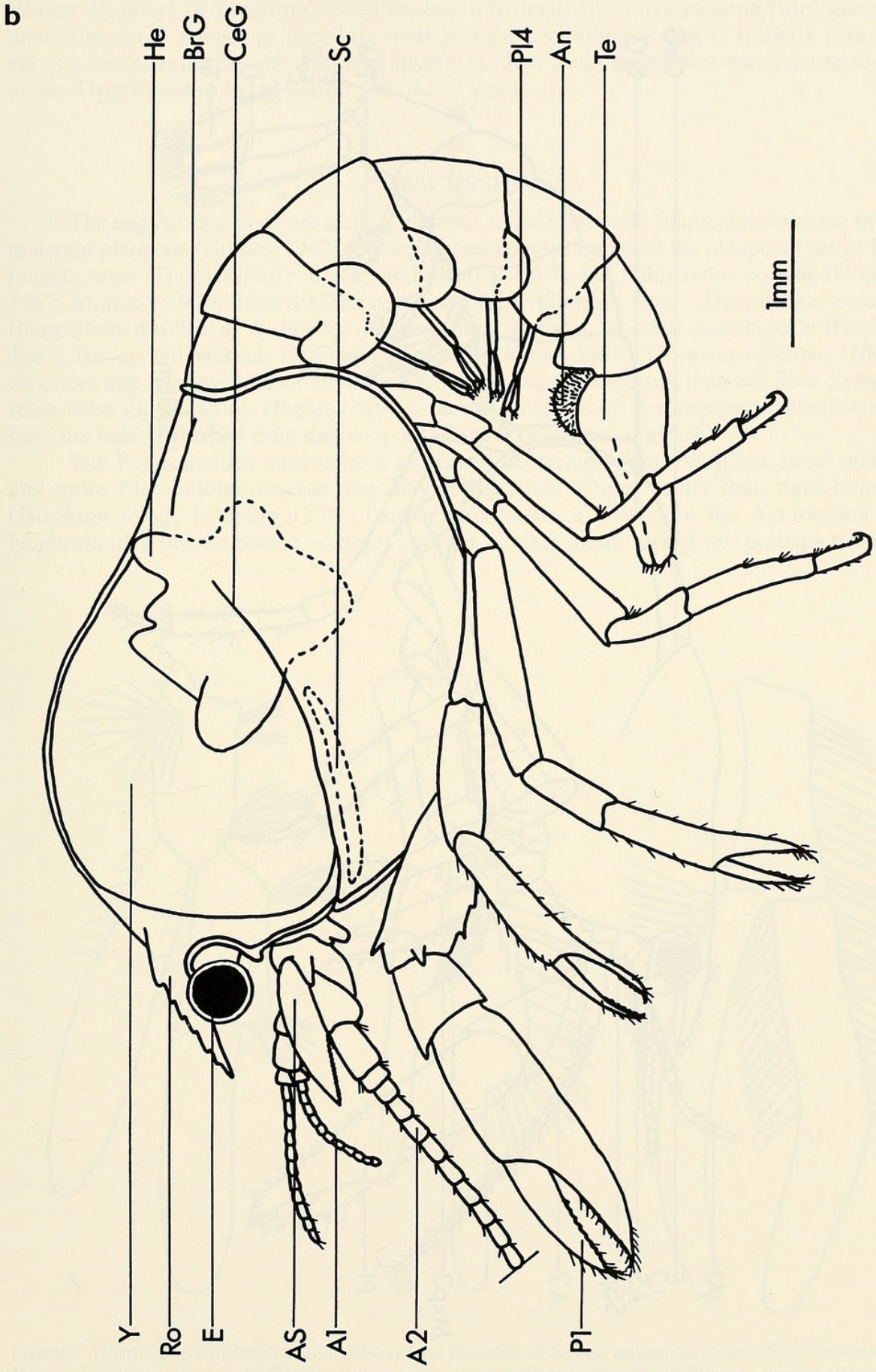


Figure 4 continued. Juvenile stages of *E. bispinosus* after hatching.

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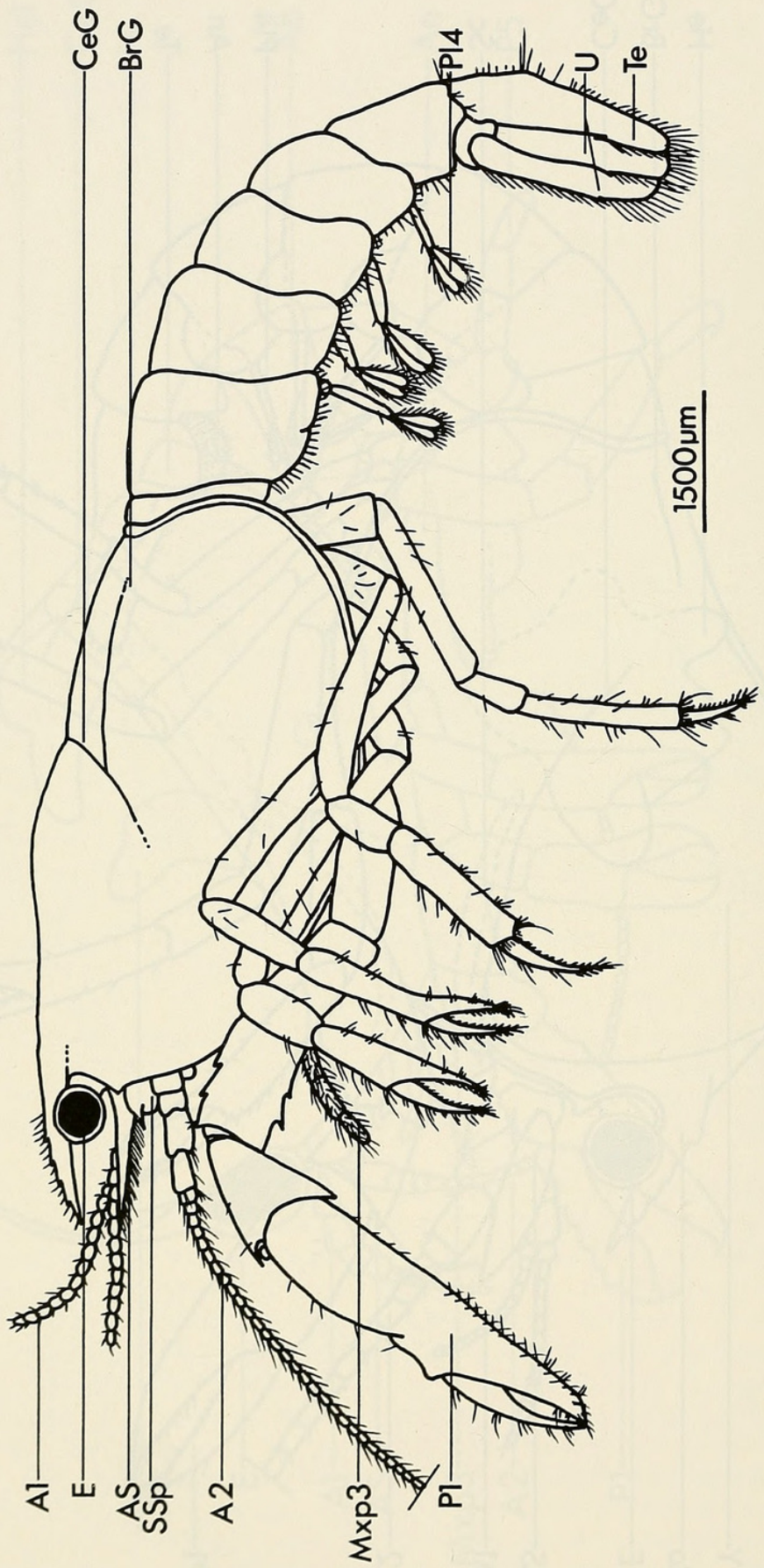

Figure 4 continued. Juvenile stages of *E. bispinosus* after hatching: (c), Stage 3.

Within 48 hours of moulting, juveniles begin to feed. Juveniles become fully independent after about a week as they lose their yolks and clinging instincts. Initially juveniles eat egg cases, exoskeletons and dead juveniles, then catch zooplankton and graze sessile algae. They moult to Stage 4 after a further 3 weeks.

DISCUSSION

The eggs of decapods are usually attached to long, smooth, filamentous oosetae on the maternal pleopods (Gurney 1942). There has been confusion about the pleopodal setae. Both pinnate setae (Thomas 1970; Turvey and Merrick 1997) and filamentous oosetae (Hopkins 1967; Morrissy 1970; Suter 1977) have been called "plumose setae". The pinnate setae and filamentous oosetae of *E. bispinosus* are similar to those of other parastacoids (Hopkins 1967; Turvey and Merrick 1997) and astacoids (Thomas 1970). However Andrews (1907b) describes egg-bearing setae of *Orconectes* as more like a bottlebrush than a feather. Serrulate setae were illustrated by Hopkins (1967) on the pleopods of *Paranephrops planifrons* but have not been described from the pleopods of other freshwater crayfish.

The Parastacoidea tend to have narrower pleopodal podites with less basal dilation and more filamentous oosetae that may form dense fringes rather than tight bunches (Hopkins 1967; Johnson 1979; Turvey and Merrick 1997). In the Astacoidea and Nephropoidea the exopodite is larger and has a basal dilation (Fig. 5), perhaps to aid in

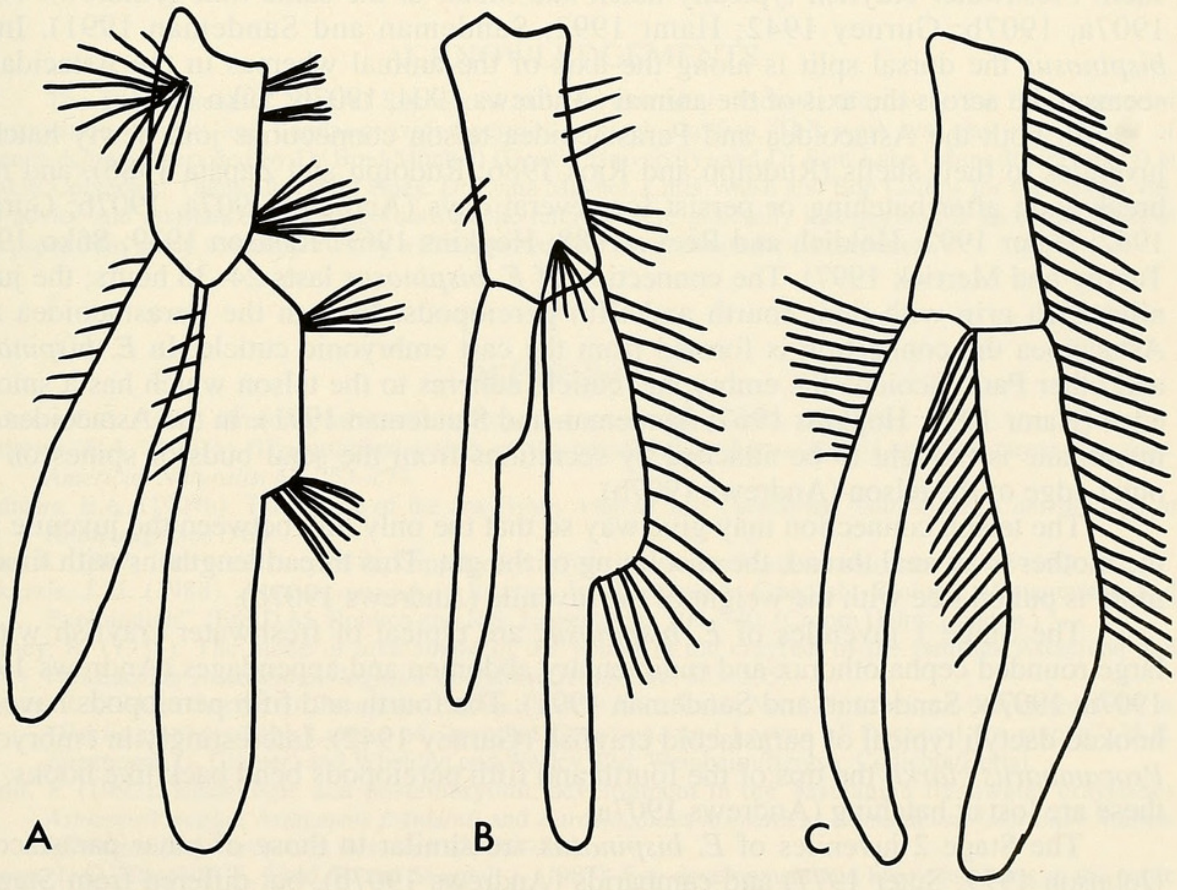

Figure 5. Distribution of filamentous oosetae on the pleopods of female astacurans in breeding condition: (a), *Homarus vulgaris* (Yonge 1937); (b), *Austropotamobius pallipes* (Thomas 1970); (c), *Euastacus spinifer* (Turvey and Merrick 1997). Diagrammatic, other types of setae not illustrated.

swimming. Burrowing parastacids may have even denser oosetae (Suter 1977), but the setation of the Cambaridae is unclear.

Euastacus bispinosus has a similar egg stalk to other parastacoids (Hamr 1992; Turvey and Merrick 1997) and astacoids (Thomas 1991). The egg stalk of some species is in a constant position relative to the embryo (Johnson 1979; Sûko 1962), but in *E. bispinosus*, *Astacopsis* and *Parastacoides* (Hamr 1992) this is not the case.

The morphological changes in the embryo of *E. bispinosus* are similar to those of other freshwater crayfish (Hamr 1992; Johnson 1979; Reichenbach 1877, cited in Huxley 1880; Reichenbach 1886, cited in MacBride 1914; Sandeman and Sandeman 1991). Both *Cherax destructor* (Sandeman and Sandeman 1991) and *E. bispinosus* take 10–15 days to reach egg-nauplius, despite very different incubation periods (40 versus 140 days). As development continued the larger *E. bispinosus* eggs developed more slowly. *Euastacus bispinosus* eggs continued to develop during winter, whereas in the Astacidae a winter diapause of 3–4 months occurs when low water temperatures inhibit development (Cukerzis 1988).

During development the egg diameter of *E. bispinosus* increased only 5–10%. The eggs of Astacoidea may increase by 13–27% (Hessen et al. 1987; Köksal 1988; Mason 1977). The eggs of *Procambarus clarkii* and *Astacus astacus* increase their diameters by 16–19% in the one or two days before hatching (Hessen et al. 1987; Sûko 1962).

Euastacus bispinosus split the egg dorsally and hatched legs last. Clark (1937), however, noted that *Euastacus* split the egg with its abdomen and rapidly hatched legs first. It is unlikely that members of the same genus would have very different methods of hatching. A few *E. bispinosus* did attempt tail first hatching, but it was slow, and deformities and mortality were high as the crayfish shed an exoskeleton as well as an egg shell. Freshwater crayfish typically hatch and moult at the same time (Andrews 1904, 1907a, 1907b; Gurney 1942; Hamr 1992; Sandeman and Sandeman 1991). In *E. bispinosus* the dorsal split is along the axis of the animal whereas in the Astacidae it seems to be across the axis of the animal (Andrews 1904, 1907b; Sûko 1962).

In both the Astacoidea and Parastacoidea telson connections join newly hatched juveniles to their shells (Rudolph and Rios 1986; Rudolph and Zapata 1986), and may break soon after hatching or persist for several days (Andrews 1907a, 1907b; Gurney 1942; Hamr 1992; Holdich and Reeve 1988; Hopkins 1967; Johnson 1979; Sûko 1962; Turvey and Merrick 1997). The connection of *E. bispinosus* lasts 24–36 hours; the juveniles then grip with their fourth and fifth pereiopods. In both the Parastacoidea and Astacoidea the connection is formed from the cast embryonic cuticle. In *E. bispinosus* and other Parastacoidea the embryonic cuticle adheres to the telson which has a smooth edge (Hamr 1992; Hopkins 1967; Sandeman and Sandeman 1991). In the Astacoidea the membrane is thought to be attached by secretions from the setal buds or spines on the outer edge of the telson (Andrews 1907b).

The telson connection may give way so that the only link between the juvenile and the mother is an anal thread, the cast lining of the gut. This thread lengthens with time as more is pulled free with the weight of the juvenile (Andrews 1907b).

The Stage 1 juveniles of *E. bispinosus* are typical of freshwater crayfish with a large rounded cephalothorax and rudimentary abdomen and appendages (Andrews 1904, 1907a, 1907b; Sandeman and Sandeman 1991). The fourth and fifth pereiopods have the hooked dactyli typical of parastacoid crayfish (Gurney 1942). Interestingly in embryonic *Procambarus clarkii* the tips of the fourth and fifth pereiopods bend back like hooks, but these are lost at hatching (Andrews 1907a).

The Stage 2 juveniles of *E. bispinosus* are similar to those of other parastacoids (Johnson 1979; Suter 1977) and cambarids (Andrews 1907b), but differed from Stage 2 astacids in being dependent on the mother. Stage 2 astacids have well developed setae, especially the dense fringe of telson setae and an elongate cephalothorax similar to Stage 3 parastacoid juveniles (Andrews 1907b; Köksal 1988; Lowery and Holdich 1988; Mason

1977). Stage 2 Cambaridae and Parastacoidea are more rotund, have poorly developed sensory setae, and small setal buds on the telson (Andrews 1904, 1907a, 1907b; Rudolph and Rios 1986; Rudolph and Zapata 1987). The exceptions to this are Stage 2 *Astacopsis gouldi* and *A. franklinii* juveniles which have rudimentary uropods (Hamr 1992).

Stage 3 *E. bispinosus* juveniles were independent and were similar to juveniles of other parastacoids (Johnson 1979; Suter 1977). They had similar heavy pigmentation and body sculpture to *Astacopsis* (Hamr 1992), reflecting the larger egg size, longer incubation time and heavier body sculpture of the adults.

Hatching, moulting and independence were all synchronous in *E. bispinosus* and in *E. spinifer* (Turvey and Merrick 1997); other genera are less so (Hopkins 1967; Suter 1977; Rudolph and Rios 1986; Rudolph and Zapata 1987), perhaps to avoid overcrowding and improve survival of the entire brood (Hopkins 1967).

The similarities and differences between the eggs, pleopods and juveniles of the astacuran superfamilies support the current phylogenetic relationships. The differences between the Astacoidea and Parastacoidea in the attachment of Stage 1 and 2 juveniles support independent invasions of fresh water by these two superfamilies (Gurney 1942). This is supported by the different egg shapes (Honan and Mitchell 1995a), hatching and telson connections. Within the Astacoidea there are significant differences between the Cambaridae and Astacidae, particularly the stage at which they become independent. Conversely the similarity of egg and juvenile development within the ecologically diverse Parastacidae indicates that these species probably had a common invasion of fresh water. An exception to this is the Tasmanian genus *Astacopsis* which warrants further investigation.

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