AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Balanoid Barnacles of the Genus *Hexaminius* (Archaeobalanidae: Elminiinae) from Mangroves of New South Wales, including a Description of a New Species.

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ABSTRACT. *Hexaminius foliorum* n.sp. is described and separated from *H. popeiana* Foster on differences in adult and larval anatomy, supported by differences in cirral activity, copulatory activity and breeding. Structure, function and reproduction in *H. foliorum* are more specialised than in *H. popeiana*. The differences are related adaptively to the occupancy by *H. popeiana* of a variety of hard substrata, but not mangrove leaves, and the confinement of *H. foliorum* to the ephemeral habitat of immersible mangrove leaves. *Hexaminius foliorum* may be a specialised descendant of *H. popeiana*.

Foster (1982) revised the taxonomy of the high shore estuarine barnacles of New South Wales, hitherto referred to as *Elminius modestus* Darwin (Pope, 1945). The majority of the four–plated specimens were referred by Foster to a new species, *Elminius covertus*. Foster also observed that *E. covertus* is intermingled with a six–plated archaeobalanid which he described and named as *Hexaminius popeiana*. An archaeobalanid subfamily Elminiinae was erected by Foster in recognition of the close relationship between *Hexaminius* and *Elminius*, a concept further supported by Buckeridge (1983) and by Egan & Anderson (1985), who described the larval development of *H. popeiana* and *E. covertus*. The larvae of *E. covertus* are close to but different from those of *E. modestus*. The larvae described by Egan & Anderson (1985) under the name *H. popeiana* are more like those of the *Conopea* group of archaeobalanines, but also share sufficient features in common with the larvae of *Elminius* to lend further weight to the Elminiinae as a distinct subfamily.

During their study of larval development, Egan and Anderson noted that *H. popeiana* were to be found at their study site (Iron Cove, Port Jackson, NSW) on two distinct surfaces, rocks and the lower leaves of the mangrove *Avicennia marina*. The settlement of this species on mangrove leaves was not mentioned by Foster (1982), nor, indeed has this part of the mangrove surface been recorded as a habitat for other balanomorphs in Australia, although a number of species are known to inhabit mangrove trunks and pneumatophores (Hutchings & Recher, 1982; Achituv, 1984). The observation was therefore of sufficient interest to prompt Egan and Anderson to make parallel studies during 1982–1984 of the seasonal breeding of populations of *H. popeiana* from rocks and mangrove leaves at the Iron Cove site, while utilising the mangrove leaf individuals as a source of nauplii for larval culture. Initially it was assumed that the differences in external appearance between the mangrove leaf and rock populations were a consequence of a greater level of erosion of the rock-dwelling individuals. However, a study of seasonal cycles during 1982–1984 showed that the two populations had different breeding patterns. The mangrove leaf population, as illustrated by Egan & Anderson (1985), bred throughout the year, with
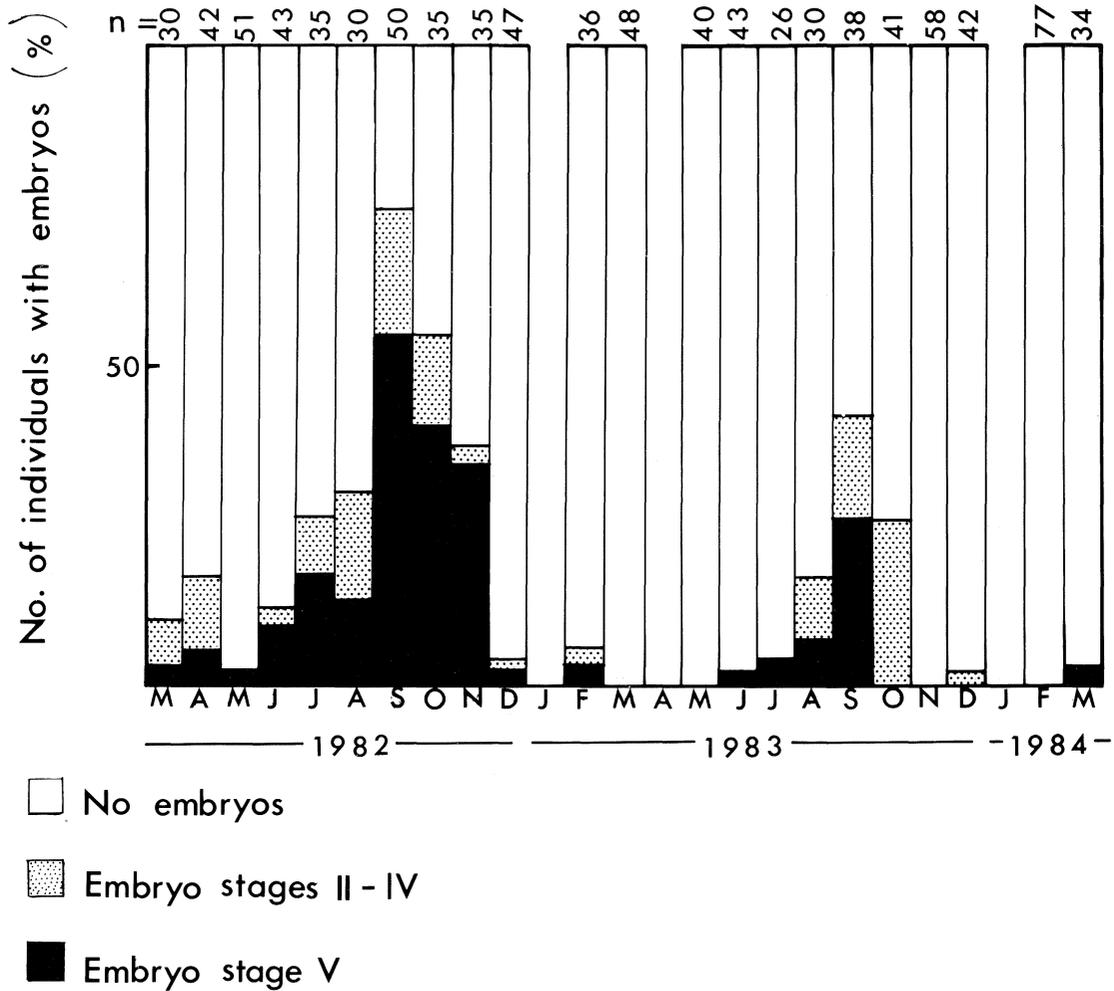
Fig.1. Percentages of individuals of rock-dwelling *Hexaminius popeiana* brooding embryos of different developmental stages, in monthly samples from Iron Cove, Port Jackson, NSW from 1982 to 1984. Sample size is given at the top of each column. The embryo stages are those of Sandison (1954).

some reduction in the autumn months. The rock population, in contrast, built up through the winter to a spring breeding peak, and showed little or no breeding during the summer and autumn (Fig. 1).

The question therefore arose, whether the external differences between the leaf-dwelling and rock-dwelling animals were indicative of separate breeding populations. We have now made a thorough morphological comparison of animals from the two substrata, utilising animals from a number of sites along the New South Wales coast, some of which were also used as collection sites by Foster (1982). In view of the apparent association of one of our breeding populations with the leaves of *Avicennia marina*, we took particular care also to collect specimens from the trunks of mangroves as well as from the leaves, and from rock surfaces in each locality.

This comparison has shown that there are two species of *Hexaminius* in the estuaries of the central coast of New South Wales. One of them, referable to

H. popeiana Foster, inhabits surfaces of a permanent or semipermanent nature on the upper shore of sheltered estuarine locations, including rocks, wooden structures and the trunks of mangrove bushes. The other species, newly described here, is confined to the leaves of *Avicennia marina*. Much of the present paper is devoted to a description of the new species. We also provide a more extended description of *H. popeiana* than was given by Foster (1982). Many of the features which differ between the two species were not mentioned in the initial description by Foster.

The description of the larval stages of *H. popeiana* given by Egan & Anderson (1985) was based on larvae obtained from mangrove leaf populations, and is therefore referable to the new species. As supplementary evidence of the differences between the species, we include in this paper a comparative account of the larvae of *H. popeiana* (s.s.), which are similar in general but different in detail from those of *H.* n. sp. We conclude our account with an analysis of

the cirral activities and copulatory activities of *H. popeiana* and *H.* n. sp. These activities also differ in ways that support the morphological analysis.

Materials and Methods

All specimens used for anatomical studies were collected in August and September 1984, at the height of the breeding season for *H. popeiana* and within the long period of maximum breeding activity of *H.* n.sp. All specimens were therefore sexually mature. Observations on cirral activity and copulatory activity (see below) were also made at the time. Larval cultures of *H. popeiana* (see below) were reared in August and September 1984.

Thirty individuals of each species, collected from Iron Cove, NSW, were investigated anatomically by the dissection of fresh specimens and specimens preserved in 5% formalin in seawater (V/V). Limbs and mouthparts were mounted in polyvinyl lactophenol after staining in lignin pink. Wall plates and opercular plates were disarticulated and cleared using sodium hypochlorite. Podomere counts were made for all limbs.

During or subsequent to each dissection, measurements were taken as follows: basal length and width; orifice length and width; scutum length (along occludent margin) and height (from occludent margin to basitergal angle); tergum length (from apex to tip of spur) and width (from scutal margin to carinobasal angle); ramal length for cirri III, IV–VI; length (from second tooth to base) and width (across cutting edge) of the mandible; length (from middle of cutting edge to base) and width (across cutting edge) of the maxillule; length (from base to tip) and width of the maxilla. These measurements were used to calculate the various ratios given in the results.

The larvae of *H. popeiana* described in this paper were reared and studied by the methods of Egan & Anderson (1985). Gravid specimens collected from Iron Cove and Folly Point, Port Jackson, NSW were used as a source of stage I larvae.

Cirral activity and copulatory activity were analysed from videotape records. Animals were filmed using a Sony video camera fitted with a Vivitar 90 mm macrolens, and a Sony U-matic portable videorecorder. Freshly collected animals were immersed in seawater at 23–25°C in a small perspex tank and illuminated by a Volpi fibre-optic lamp. Numerous sequences of cirral activity and copulatory activity were recorded and compared. Only general features of these activities are reported here. A detailed analysis will be presented elsewhere.

Hexaminius foliorum n.sp.
Figs 2–4

Hexaminius popeiana.—Egan & Anderson, 1985: 383.

Type material. HOLOTYPE hermaphrodite, 7.0 mm basal length, sexually mature, AM P37462 (spec. D26, Fig. 2a, complete shell 190). PARATYPES hermaphrodite, sexually mature, AM P (spec. D25, Fig. 2e, coll. 14 May 1984, 189), from Sisters Bay, Iron Cove, NSW, 33°51.5'S 151°09.5'E, on leaves of *Avicennia marina*, collected by D.T. Anderson, Aug 1984.

Additional material examined. Part specimens: DA bleached plates (Fig. 2b,c,d), 212; body (Fig. 2f), 59; spec. D1, oral cone (Fig. 4a), 54A; labrum (Fig. 4b), 65; DB penis (Fig. 4g), 217. Slides: cirri I–VI, D22, 13 May 1983, right cirri, 85; spec. D5, right palp and right mandible (Fig. 4c,d), 19; spec. D5, left maxillule and left maxilla (fig. 4e,f), 17. *Hexaminius foliorum* was also collected from the lower (immersible) leaves of *Avicennia marina* at Gosford and Woy Woy, on Brisbane Waters, and at Hawks Nest, Port Stephens; all localites on the Central Coast of NSW between 33–34°S.

Diagnosis. *Hexaminius* of low conical form; basal margin ovoid with bluntly protruding ribs; conspicuous reddish brown radial bands externally. Wall plates and opercular plates thin, fragile. Wall plates with thin basal margins; basis membranous, thick, semiopaque. Tergoscutal flaps with shallow carinal fold. Scutal depressor muscles thin. Prosoma elongate, fusiform; cirri IV–VI with long rami and long setae. Pedicel of penis not enlarged.

Description. The following description is based on 30 additional specimens from Iron Cove, NSW, which were destroyed during the course of the study.

EXTERNALS. Shell (Fig. 2a) to 7.0 mm in rostrocarinal basal length, low conical, even when crowded; basal length markedly greater than width, basal margin ovoid. Colour when live, pale brown, with darker reddish brown radial bands between low ribs. Preserved, cream with brown radial bands. Growth lines with conspicuous white spines. Ribs protruding bluntly around basal margin.

WALL. 6 plates, thin, fragile; rostrum (Fig. 2b) large, ovoid; carinolaterals narrow, width about ½ of laterals; radii moderate, leaving part of alae exposed.

ORIFICE. Pentagonal, width about ¾ length; rostral side short, straight.

OPERCULUM. Colour when live, brown, with white patches at rostral and lateral scutal angles; lateral patches extend toward apex as less conspicuous, whitish chevron. Preserved, greyish brown with whitish chevron on tergal edges of scuta. Opercular membrane pale brown. Tergoscutal flaps not deeply folded carinally; live, beige with cream edges, paired dark brown patches centrally, paired pale brown patches rostrally. Preserved, pale brown with cream edges; paired dark brown patches centrally.

BASIS. Membranous, thickish, semiopaque; ovaries creamy white to yellowish.

INTERIOR OF WALL. Mantle cream to brownish purple, dark brown beneath operculum. Exposed inner surfaces of wall plates cream, with reddish brown radial bands; basal margins (Fig. 2e) thin, sharp, sometimes with slight development of radial teeth. From basal margin to perimeter of sheath, internal surface of parietes gently sloping, not conspicuously hollowed out.
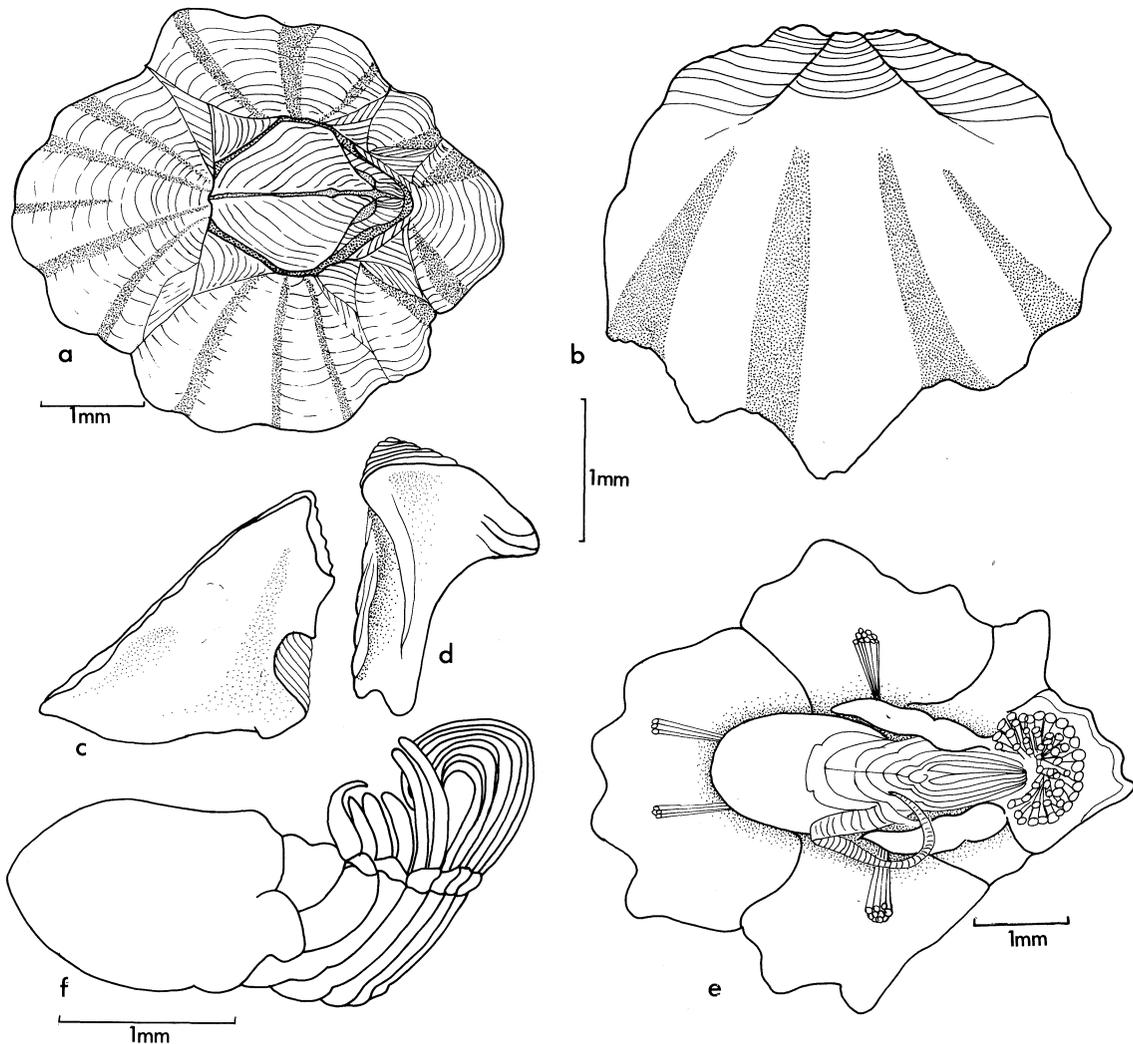
Fig.2. *Hexaminius foliorum.* **a,** apical view; **b,** rostrum, internal view; **c,** left scutum, internal view; **d,** left tergum, internal view; **e,** basal view with basis removed; **f,** body and limbs in right lateral view.

OPERCULAR PLATES. Thin, translucent, like wall plates. Scutum (Fig. 2c) slightly longer than high; articular ridge and furrow of approximately equal length, articular furrow shallow; adductor scar faint; depressor muscle scars very faint or absent. Tergum (Fig. 2d) hatchet shaped, frequently narrow; articular margin straight, with shallow articular furrow; basal margin straight, except apically, where it curves to join occludent margin as projection bearing 3–4 prominent muscle crests; tergal spur close to but separate from basiscutal angle, forming an acute angle with the short part of the basal margin and merging into the straight longer part of this margin; spur longer than basiscutal angle, concave internally.

OPERCULAR DEPRESSOR MUSCLES. Cloudy white in fresh specimens, brown when preserved. Tergal depressors (Fig. 2e) large, with distinct, large fibres; lateral scutal depressors thin; rostral scutal depressors very thin.

BODY. Prosoma (Fig. 2e,f) elongate and fusiform; postprosomal leg bases in paired linear array. Protopod of cirrus I just overlapping oral cone; protopods of II and III more posterior.

BRANCHIAE. Long, moderately wide (Fig. 2e), thin, smooth, semiopaque, white.

CIRRI. Cirrus I (Fig. 3a). Exopod, with 12–15 podomeres, half as long again as endopod; proximal podomeres of exopod broad, with setal bunches directed posteriorly; distal podomeres narrow, with setae directed apically. Endopod, with 6–7 podomeres, broad throughout; podomeres with anteriomedian cushions bearing bunches of anteroapically directed setae, some stout. Coxal setae pappose, other setae serrulate.

Cirrus II (Fig. 3b). Rami subequal, endopod slightly the longer; podomere numbers 8–9 and 7–10; both rami broad, tapering, with setae dense, anteriorly pointing, serrulate. Coxal setae pappose.
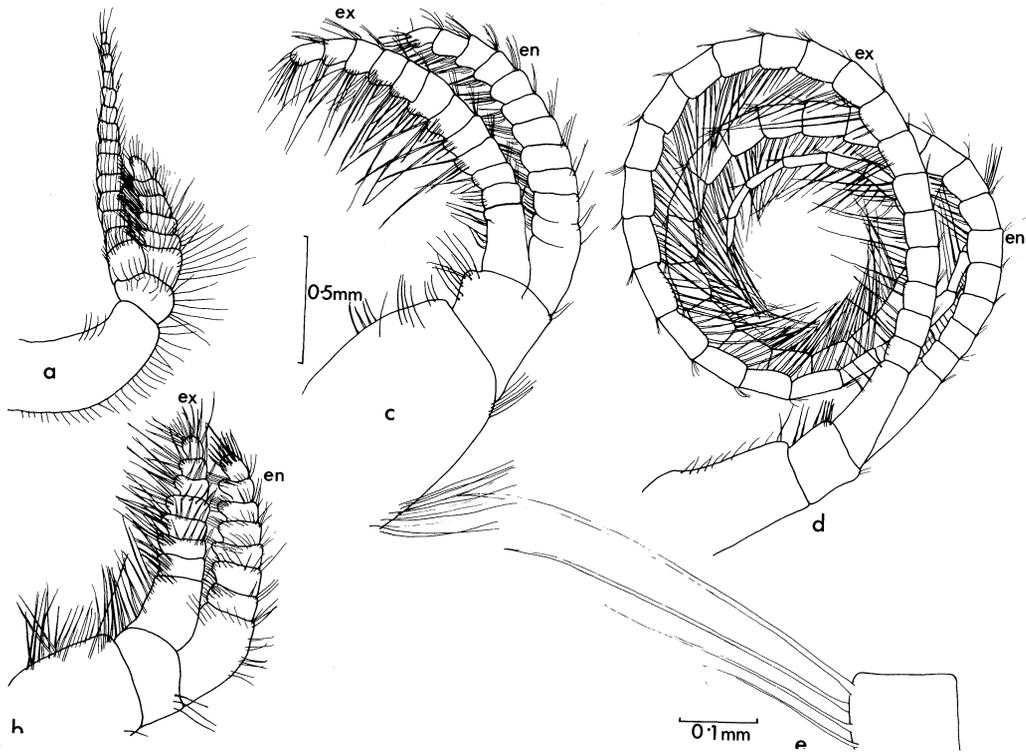
Fig.3. *Hexaminius foliorum.* **a,** cirrus I left, median view; **b,** cirrus II right, lateral view; **c,** cirrus III right, lateral view; **d,** cirrus V right, lateral view; **e,** podomere of endopod of cirrus V; **en,** endopod; **ex,** exopod.
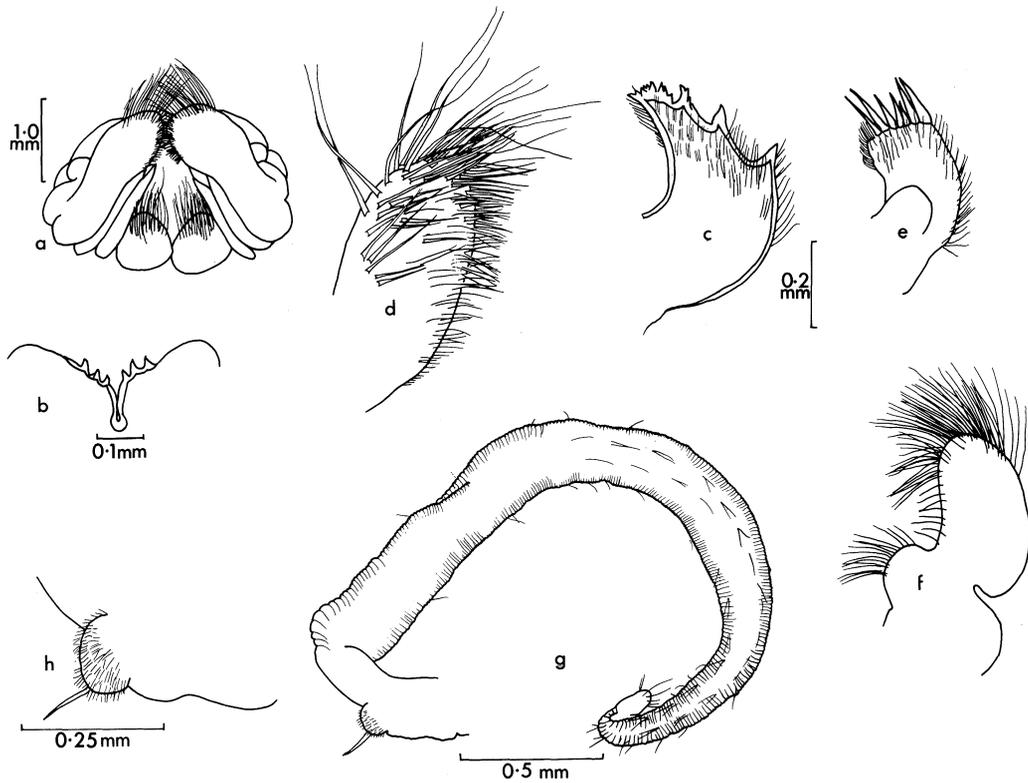
Fig.4. *Hexaminius foliorum.* **a,** oral cone in posterior view; **b,** labrum; c–f, mouthparts of right side; **c,** mandible; **d,** mandibular palp; **e,** maxillule; **f,** maxilla; **g,** penis in left lateral view; **h,** basidorsal point of penis.

Cirrus III (Fig. 3c). Rami equal, cylindrical, podomere numbers 11–13 and 10–12; mixed serrate and serrulate setae pointing anteriorly. Coxal setae pappose.

Cirri IV–VI (Figs 3d,e). Rami equal, 2.4, 3.4 and 3.8 times as long as those of cirrus III; podomere numbers 18–25 (IV), 23–29 (V) and 25–30 (VI). Anterolateral setae, 2 pairs per podomere proximally to 7 pairs distally, some reduction apically. Setae very long relative to ramal length. Protopods and rami slender.

MOUTHPARTS. Oral cone (Fig. 4a) slightly broader than high in posterior view, with palps set obliquely and conspicuous maxillae projecting posteriorly. Labrum (Fig. 4b) deeply notched, with 3 prominent teeth on either side. Mandible (Fig. 4c) quadridentoid, broad, ratio of length to width 0.98; incisor tooth separated from second tooth by half length of cutting edge; second to fourth teeth with subsidiary cusps; fourth tooth close to molar process. Molar process blunt, with low teeth, the first larger than the remainder; distal surfaces of mandible setose, setae set in palmate groups. Palp (Fig. 4d) with median edge straight, apex steeply convex. Apical fringe of long serrulate setae, median fringe of evenly spaced, short, jointed setae. Maxillule (Fig. 4f) long and narrow, ratio of length to width 1.7; with 2 spines at lateral angle, slight notch followed by 3 shorter and 2 longer spines; median angle with 4 pairs of small spines. Fringe of setae along almost entire lateral edge. Maxilla about half as broad as long, with dome-shaped end; apical setae long, fine serrulate; distoventral setae shorter, serrulate; proximoventral setae short, jointed, densely packed.

PENIS (Fig. 4g). Long, annulated throughout; pedicel little greater in diameter than base of penis, clothed in short spines; small basidorsal protuberance (Fig. 4h) covered with short setae, bearing 0, 1 or 2 longer, serrulate spines.

Etymology. Noun in apposition (*L. folium* = leaf), named after habitat: leaves on mangrove, *Avicennia marina*.

Distribution. Estuaries of central coast of New South Wales.

Hexaminius popeiana Foster
Figs 5–7

Hexaminius popeiana Foster, 1982: 28.
Not *Hexaminius popeiana*.—Egan & Anderson, 1982: 383 (= *H. foliorum*).

Material examined. Whole specimen: body in shell showing gills and muscles (Fig. 5a,e), 90. Part specimen: EA bleached plates (Fig. 5b–d), 206; spec. E12, whole body (Fig. 5f), 114; spec. E11, oral cone (Fig. 7a), 99; labrum (Fig. 7b), 117; EA penis (Fig. 7g), 208. Slides: spec. E6, right cirri I (Fig. 6a), right cirri II (Fig. 6b); spec. E6, right cirri III (Fig. 6c), right cirri IV; spec. E6, right cirri V (Fig. 6d,e), right cirri VI; spec. E6, left palp (Fig. 7c), left mandible (Fig. 7d); spec. E6, left maxillule (Fig. 7e), left

maxilla (Fig. 7f). *Hexaminius popeiana* was collected from rocks and jetsam, wooden structures and the trunks and branches of *Avicennia marina* at Iron Cove (AM P37464), Rose Bay, Vaucluse and Folly Point, Port Jackson, NSW; Taren Point, NSW; Nelson Bay, Lemon Tree Passage, Tanilba Bay and Karuah, Port Stephens, NSW; all between lat. 33°–34°S; and at Magnetic Island, north Qld, lat. 19°S, long. 147°E. The latter is a first record of the species beyond the coast of New South Wales and indicates a distribution of *H. popeiana* in estuaries along a major part of the coast of eastern Australia.

Diagnosis. Conical form; basal margin circular, lacking protruding ribs; reddish brown radial bands weak or absent. Wall plates and opercular plates thick, heavy. Wall plates with broad basal margins; basis membranous, thin, transparent. Tergoscutal flaps with deep carinal fold. Scutal depressor muscles thick. Prosoma short and round; cirri IV–VI of moderate length, with moderate length setae. Pedicel of penis enlarged.

Description. In this section we draw attention to those anatomical features in which *H. popeiana* (s.s.) differs from *H. foliorum*. The description is based on 30 specimens taken from rocks at Iron Cove, NSW.

EXTERNALS. Shell (Fig. 5a) up to 10.2 mm in rostrocarinal basal length, conical, tall when crowded; basal length only slightly greater than width, basal margin almost circular. Colour when live, greyish cream, uneroded specimens with darker radial bands between broad, low ribs. Preserved, grey. Growth lines in uneroded specimens with small white spines. Basal margin smooth to irregular, ribs not protruding.

WALL. 6 plates, solid and heavy; rostrum (Fig. 5b) large, squareish; carinolaterals narrow, width about ¼ of laterals; carina narrow, width about ⅓ of rostrum; radii moderate, leaving part of alae exposed.

ORIFICE. Pentagonal, width about ¾ length; rostral side concave.

OPERCULUM. Colour when live, purple brown, with conspicuous white chevron on tergal edges of scuta. Preserved, greyish brown, with white chevron unless eroded. Opercular membrane midbrown. Tergoscutal flaps deeply folded carinally; live, pale cream with white edges; with paired, very small, dark brown patches centrally and paired, dark brown patches rostrally and tergally, the latter pair deep within the tergal folds of the flaps; preserved, pale brown with cream edges, paired dark brown patches centrally and rostrally.

BASIS. Membranous, thin, transparent; ovaries creamy white to yellowish.

INTERIOR OF WALL. Mantle dark purple with brown edge marginally, dark brown beneath operculum. Exposed inner surface of wall plates pinkish mauve, becoming whitish when preserved; basal margins (Fig. 5e) flattened, broad, sometimes with single row of small radial teeth. From basal margin to perimeter of sheath, surface of parietes
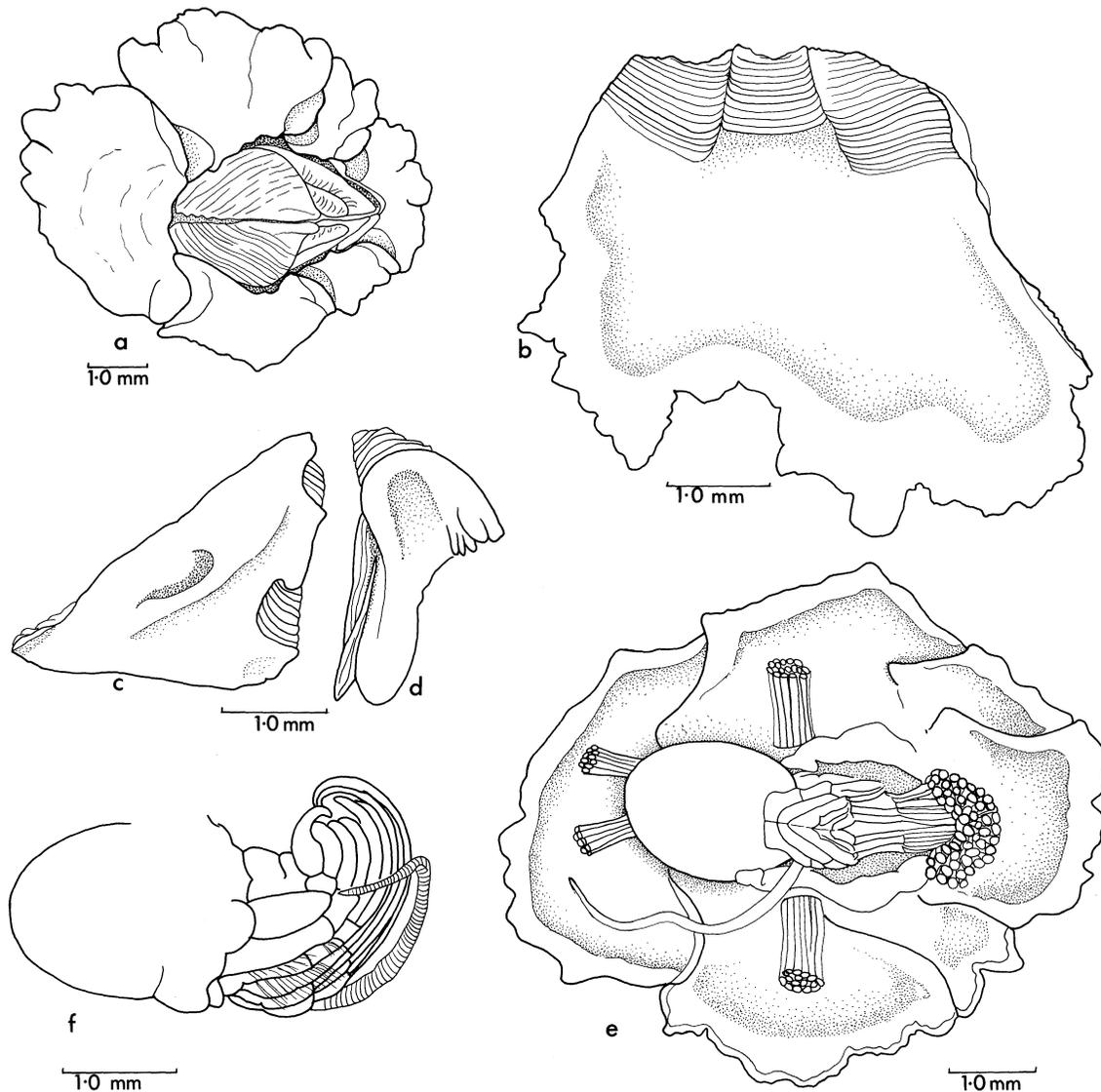
Fig.5. *Hexaminius popeiana.* **a,** apical view; **b,** rostrum, internal view; **c,** left scutum, internal view; **d,** left tergum, internal view; **e,** basal view with basis removed; **f,** body and limbs in right lateral view.

concave, conspicuously hollowed out.

OPERCULAR PLATES. Thick, opaque, like wall plates. Scutum (Fig. 5c) longer than high; articular ridge long, articular furrow short and deep; adductor ridge faint or absent; depressor muscle scars very faint or absent. Tergum (Fig. 5d) with occludent margin broad and obvious in apical view; club shaped, frequently broad; articular margin straight, with deep articular furrow; basal margin concave, curving apically to join occludent margin as projection bearing 4–5 irregular muscle crests; tergal spur located as in *H. foliorum* but not longer than basiscutal angle, flat internally.

OPERCULAR DEPRESSOR MUSCLES. Translucent white in fresh specimens, brown when preserved. Tergal depressors large (Fig. 5e), lateral scutal depressors moderately large, rostral scutal depressors thin.

BODY. Prosoma rounded, broad (Fig. 5e,f); postprosomal leg bases compacted together and overlapping. Protopods of cirri I–III curved around oral cone.

BRANCHIAE. As in *H. foliorum* but translucent white.

CIRRI. Cirrus I (Fig. 6a). As in *H. foliorum* but exopod nearly twice as long as endopod; podomere numbers 13–18 and 6–7; setae of endopod cushions a mixture of serrate, serrulate and simple. Coxal setae mixed pappose and serrulate.

Cirrus II (Fig. 6b). As in *H. foliorum* but rami slightly longer, podomere numbers 8–10 and 8–11.

Cirrus III (Fig. 6c). As in *H. foliorum*.

Cirri IV–VI (Fig. 6d,e). Rami equal, 2.4, 2.9 and 3.6 times as long as those of cirrus III, thus relatively shorter than in *H. foliorum*; podomere numbers 16–22 (IV), 21–25 (V) and 19–27 (VI). Anterolateral
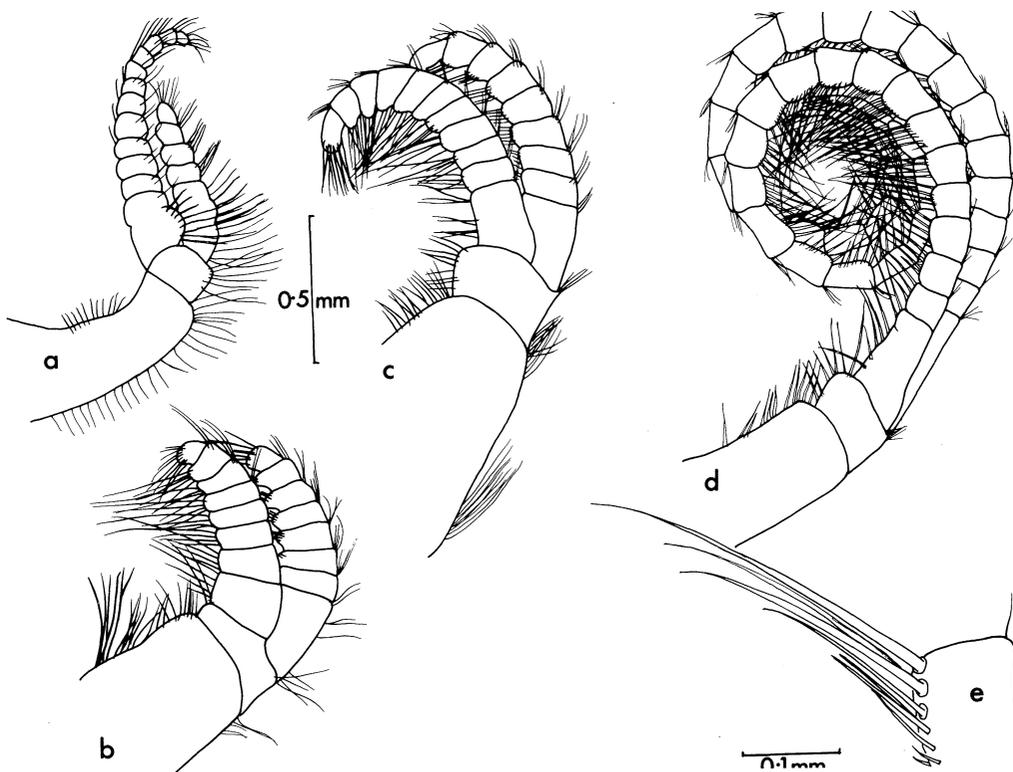
Fig.6. *Hexaminius popeiana.* **a,** cirrus I left, median view; **b,** cirrus II right, lateral view; **c,** cirrus III right, lateral view; **d,** cirrus V right, lateral view; **e,** podomere of endopod of cirrus V.
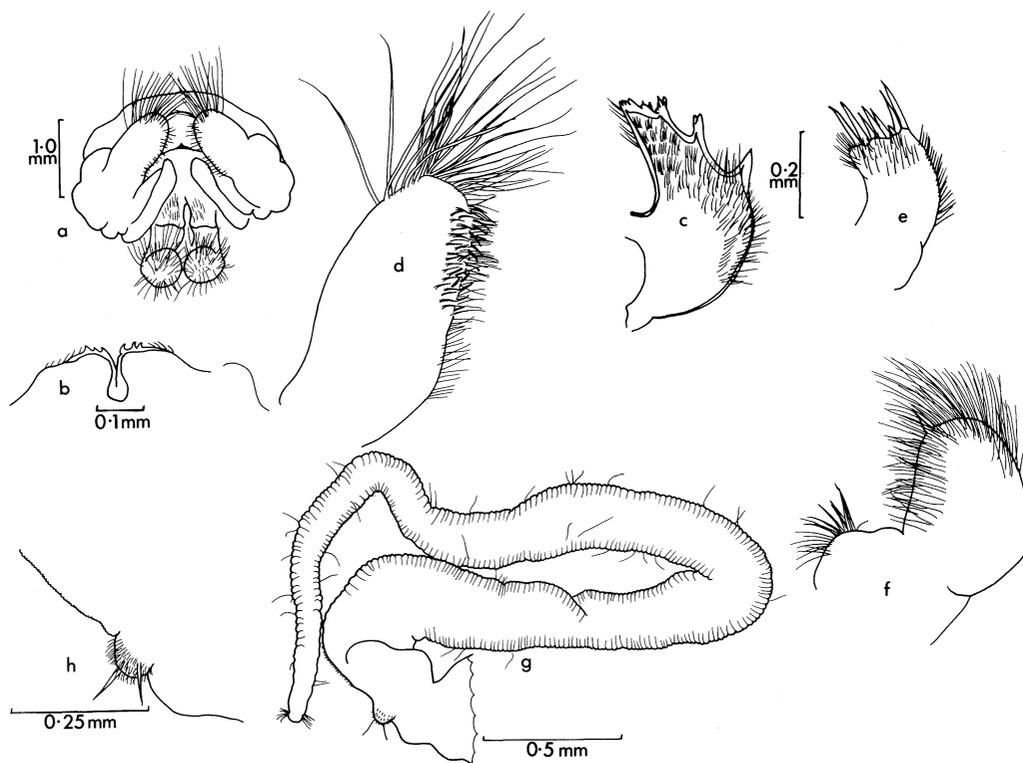
Fig.7. *Hexaminius popeiana.* **a,** oral cone in posterior view; **b,** labrum; c–f, mouthparts of right side; **c,** mandible; **d,** mandibular palp; **e,** maxillule; **f,** maxilla; **g,** penis in left lateral view; **h,** basidorsal point of penis.

setae 2 pairs per podomere proximally to 8 pairs distally, some reduction apically. Setae long relative to ramal length. Protopods and rami quite stout.

MOUTHPARTS. Oral cone (Fig. 7a) as in *H. foliorum* but teeth small. Labrum (Fig. 7b) as in *H. foliorum*. Mandible (Fig. 7c) as in *H. foliorum*, but narrower, ratio of length to width 1.42. Palp (Fig. 7d) as in *H. foliorum*, but apex roundly convex, median fringe of short, jointed setae massed towards apex. Maxillule (Fig. 7e) as in *H. foliorum*, but broader, ratio to length to width 1.3; median angle with 2 pairs of small spines. Maxilla (Fig. 7f) about half as broad as long, with blunt end; setation as in *H. foliorum*, but apical setae supplemented by blunt spine; jointed proximoventral setae sparse.

PENIS (Fig. 7g). Very long, annulated throughout; pedical broad, conspicuous; basidorsal protuberance (Fig. 7h) smaller than in *H. foliorum*.

Remarks. These morphological characteristics define sharply a species which occupies rock surfaces, wooden surfaces and the trunks and stems of the mangrove *Avicennia marina* in the upper intertidal of estuarine and sheltered waters, but does not inhabit the leaves of *A. marina*.

Distribution. Estuaries of New South Wales; Magnetic Island, north Qld.

The larval development of *H. popeiana*. As pointed out in the introduction, the larval development described by Egan & Anderson (1985) is that of *H. foliorum*. The present investigation has shown that the larvae of *H. popeiana* (Figs 8–12 and Tables 1–4) differ from those of *H. foliorum* in ways that allow each larval stage of the two species to be distinguished. There are also differences in the rate of larval development, compared under similar culture conditions at 20°C (Table 1 of this account and Table 1 of Egan & Anderson, 1985). Naupliar stages I–III develop at similar rates, but stages IV–VI proceed more slowly in *H. popeiana*. The cyprid stage is first reached in *H. foliorum* at 9 days, and in *H. popeiana* at 15 days.

The general dimensions of the naupliar stages and cyprid (Table 2) are similar in both species, as are many features of the dorsal shield, labrum and caudal papilla at each naupliar stage (Figs 8, 9). The differences between corresponding stages are set out in Table 3. Stages II–V (Fig. 8c,e,g,i) are more heavily spined in *H. foliorum*, while stage VI (Fig. 8k) is less spined. The cyprid of *H. foliorum* is also more sharply pointed at the anterior end in dorsal view than that of *H. popeiana* (Fig. 8m,n). There are no significant differences in the setal formulae of the naupliar limbs (Figs 10–12 and Table 4), but the naupliar plumose setae of *H. popeiana* have longer and more conspicuous setules than those of *H. foliorum*.

Functional morphology. CIRRAL ACTIVITIES. *Hexaminius popeiana* displays the full range of balanoid cirral activities described by Crisp &

Southward (1961) and redefined by Anderson & Southward (1987). On immersion, the animals briefly perform testing activity, accompanied by the release of bubbles of air from the mantle cavity. They then usually enter into pumping beat followed by normal beat, and variously alternate between these or between normal beat and fast beat. In any group of individuals, all of these levels of cirral activity can be observed, with some individuals showing withdrawal and closure of the operculum. Rocking of the closed operculum is a conspicuous activity. Prolonged cirral extension is rarely seen, and persists only for 1–2 seconds. Typical rates of cirral activity in *H. popeiana* are, pumping beat 5–6, normal beat 8–12 and fast beat 16–20 beats per 10s.

During normal beat and fast beat, the raised cirral fan achieves a less than vertical posture on each beat, always leaning slightly in a rostral direction. At the apex of cirral extension, the third maxillipeds are directed laterorostrally at the margins of the cirral fan.

Hexaminius foliorum, in contrast, is faster and more restricted in its range of cirral activities. Newly immersed animals release air bubbles in the usual way, but then enter directly into fast beat, with the operculum raised and open and the cirri fully exposed. Normal beat is rarely observed except as a brief preliminary to fast beat. Pumping beat and rocking of the closed operculum do not occur in this species. The rate of beating during fast beat is 18–23 per 10s and the cirral fan swings through a wide arc on each beat, leaning slightly carinally at the apex of the beat. The third maxillipeds remain more raised and rostrally directed than in *H. popeiana*, even at the apex of the beat.

COPULATORY ACTIVITIES. The difference in cirral activities between *H. popeiana* and *H. foliorum* is accompanied by a difference in the copulatory action of functional "males". In general, the copulatory action in both species follows the typical mode for small estuarine balanoids, the penis being extended after cirral beating has commenced, and the cirri then being held extended while penis extension and probing occur.

In *H. popeiana*, when extension of the penis has been achieved, the extended rami of cirri IV–VI show a slight increase in curvature (Fig. 13) indicative of contraction of their retractor muscles. Functionally, this presumably increases the hydraulic pressure of the haemocoelic fluid in the extended penis. The extended maxillipeds also exhibit bouts of rapid muscular twitching coincident with the maxima of penis extension, perhaps further augmenting the enforcement of fluid into the penis.

In *H. foliorum*, copulatory activity is pursued very vigorously and it is usual to find several functional "males" simultaneously probing a functional "female". In each "male", when full penis extension is achieved, the distal ends of the rami of the long cirri curl up strongly (Fig. 14) and the extended

Table 1. Time taken at 20°C for the appearance of the larval stages in the most productive cultures of *H. popeiana* — No larvae detected. Blank space, time unknown.

| Adult locality | Algal Food* | Time (No. of days) to appearance of naupliar stage | | | | | | |
		I	II	III	IV	V	VI	Cyprid
Folly Point	*P.l., C.c., S.c.*	1	1	2		10	11	15
Iron Cove	*P.l., C.c., S.c.*	1	1	2	3		9	—

P.l., Pavlova lutheri; C.c., Chaetoceros calcitrans (Minutecellus polymorphys); S.c., Skeletonema costatum.

Table 2. Mean size of the cultured larval stages of *Hexaminius popeiana*

Stage	n	TL(mm)	SL(mm)	SP(mm)	W or D (mm)
I	5	0.22+0.01	—	—	0.12+0.01
II	14	0.33+0.002	—	—	0.15+0.004
III	12	0.40+0.02	—	—	0.17+0.01
IV	11	0.46+0.03	0.27+0.02	0.07+0.01	0.22+0.01
V	10	0.53+0.03	0.35+0.01	0.08+0.01	0.27+0.01
VI	5	0.62+0.03	0.44+0.02	0.09+0.01	0.33+0.01
Cyprid	1	0.47	—	—	0.23

n. Sample number; TL, total length; SL, shield length; SP, posterior shield spine length; W or D, shield width or cyprid depth. Confidence limites are 95%.

Table 3. Morphological differences between the naupliar stages of *H. popeiana* (this account) and *H. foliorum* (from Egan and Anderson 1985).

Stage	*H. popeiana*	*H. foliorum*
I	Anterior shield margin domed	Anterior shield margin convex
II	Anterior shield margin smooth. Lateral shield margin with fine spines.	Anterior shield margin spined. Lateral shield margin with coarse spines.
III	Lateral shield margin with few spines. Setae on median labral lobe serrate.	Lateral shield margin with many spines. Setae on median labral lobe simple.
IV	Frontolateral horns with large and small spines, not heavily ornamented. Setae on median labral lobe serrate.	Frontolateral horns with large spines, heavily ornamented. Setae on median labral lobe simple.
V	Frontolateral horns not heavily ornamented. One pair of long. slender dorsal shield spines, one short pair.	Frontolateral horns heavily ornamented. One pair of long, thick dorsal shield spines.
VI	Frontolateral horns heavily ornamented. One pair of long, slender dorsal shield spines, two short pairs. Posterior shield spines long (0.09+0.01 mm)	Frontolateral horns with short spines only. One pair of short dorsal shield spines. Posterior shield spines short (0.06+0.01 mm)

Table 4. Setal formulae for the nauplii of *Hexaminius popeiana*

| Nauplius stage | Antennule | Antenna | | Mandible | |
		Exopodite	Endopodite	Exopodite	Endopodite
VI	*S:P:P:*PSPP:SP:P:SP:S	PPPP:8P	PPSPP:SPP:PD:SPPC:G	P:5P	SSSS:SSDD:SP^{D}CP:$_{sp}$PP^{D}C:G
V	*S:P:P:*PSPP:SP:S:P:S	PPP:8P	PPSPP:SPP:PD:SP^{S}PC:G	P:SP	SSSS:SSDD:SP^{D}CP:$_{sp}$PP^{D}C:G
IV	*S:P:*PSPP:SP:P:S	PP:7P	PPPSS:SPS:PD:SPC:G	P:4P	SSSS:SDD:SP^{D}S:PCP:$_{sp}$PP^{D}C:G
III	*S:*PSPP:SP:P:S	PP:5P	PPPst^S:SP:PD:SPC:G	P:3P:S	SSS:SP^{D}S:PCP:$_{sp}$PP^{D}C:G
II	SSPS:SP:P:S	SP:4P:S	PPS:SP:PD:SPC:G	P:3P:Sst	SSS:SP:SCP:PC:G
I	SSSS:SS:S:S	S:S:S:S:S	SSS:SS:SS:SS:G	S:S:S:S	SSS:SS:SS:SS:G

Setal types: S, simple; P, plumose; D, plumodenticulate; C, cuspidate; G, gnathobase; $_{sp}$, spine; S^P, simple, sometimes plumose; P^S, plumose, sometimes simple; P^D, plumose, sometimes plumodenticulate; st, setal stub; st^S, stub, sometimes short simple seta; Sst, simple seta, sometimes short simple seta, Pre-axial setae on the antennule are given in italics.
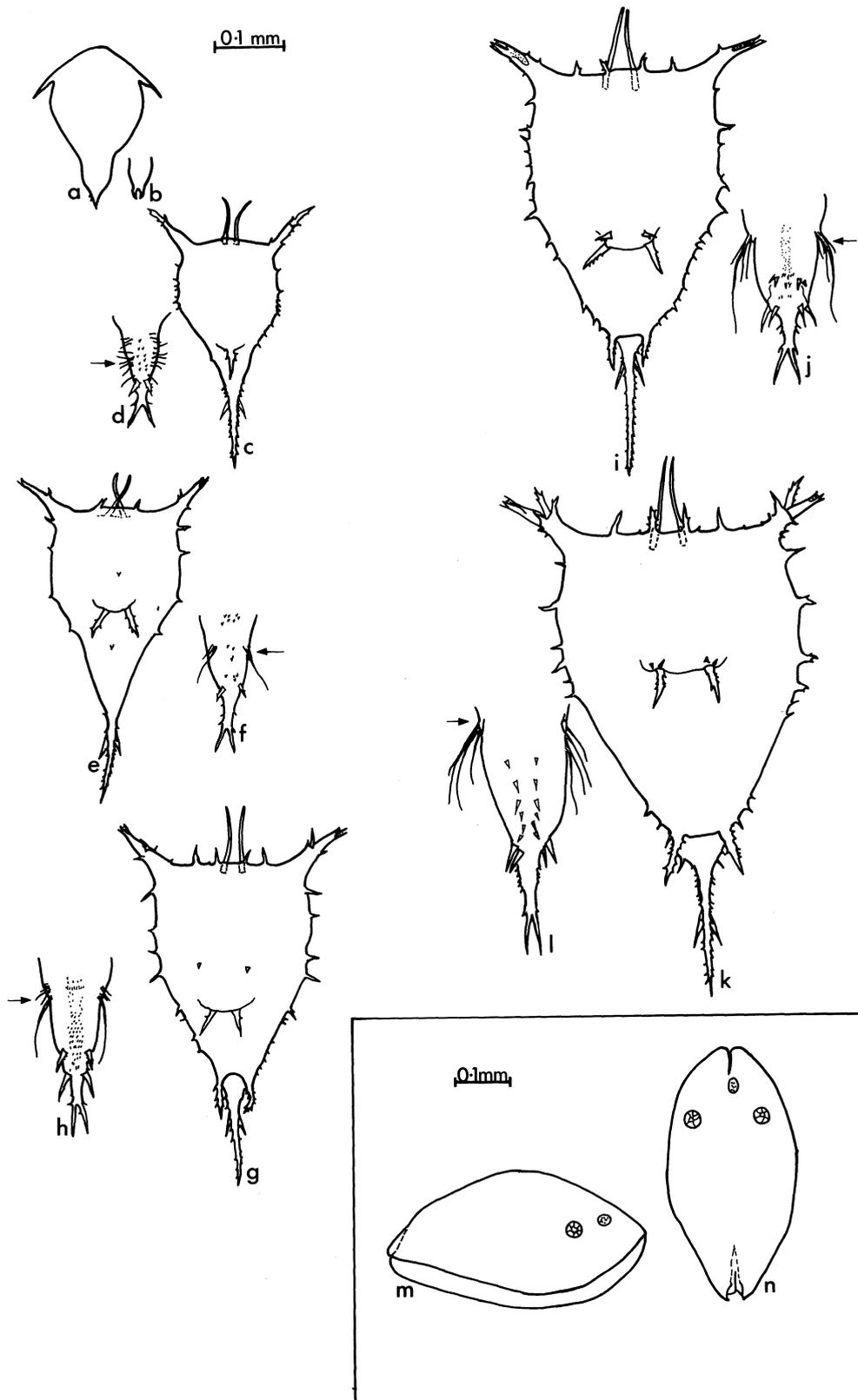
Fig.8. *Hexaminius popeiana.* **a,c,e,g,i,k,** dorsal shield outlines of nauplius stages I–VI; **b,d,f,h,j,l,** ventral views of thoracoabdominal process of naupliar stages I–VI; **m,** cyprid in lateral view; **n,** cyprid in dorsal view. Arrows indicate the position of the maxilla for each naupliar stage. Scale 0.1 mm.

Fig.9. *Hexaminius popeiana.* **a,b,d,f,h,j** lateral view of thoracoabdominal process of naupliar stages I–VI; **c,e,g,i,k** labrum of naupliar stages I–VI, ventral (outer) surface. Arrows indicate the position of the maxilla for each naupliar stage. Scale 0.1 mm.
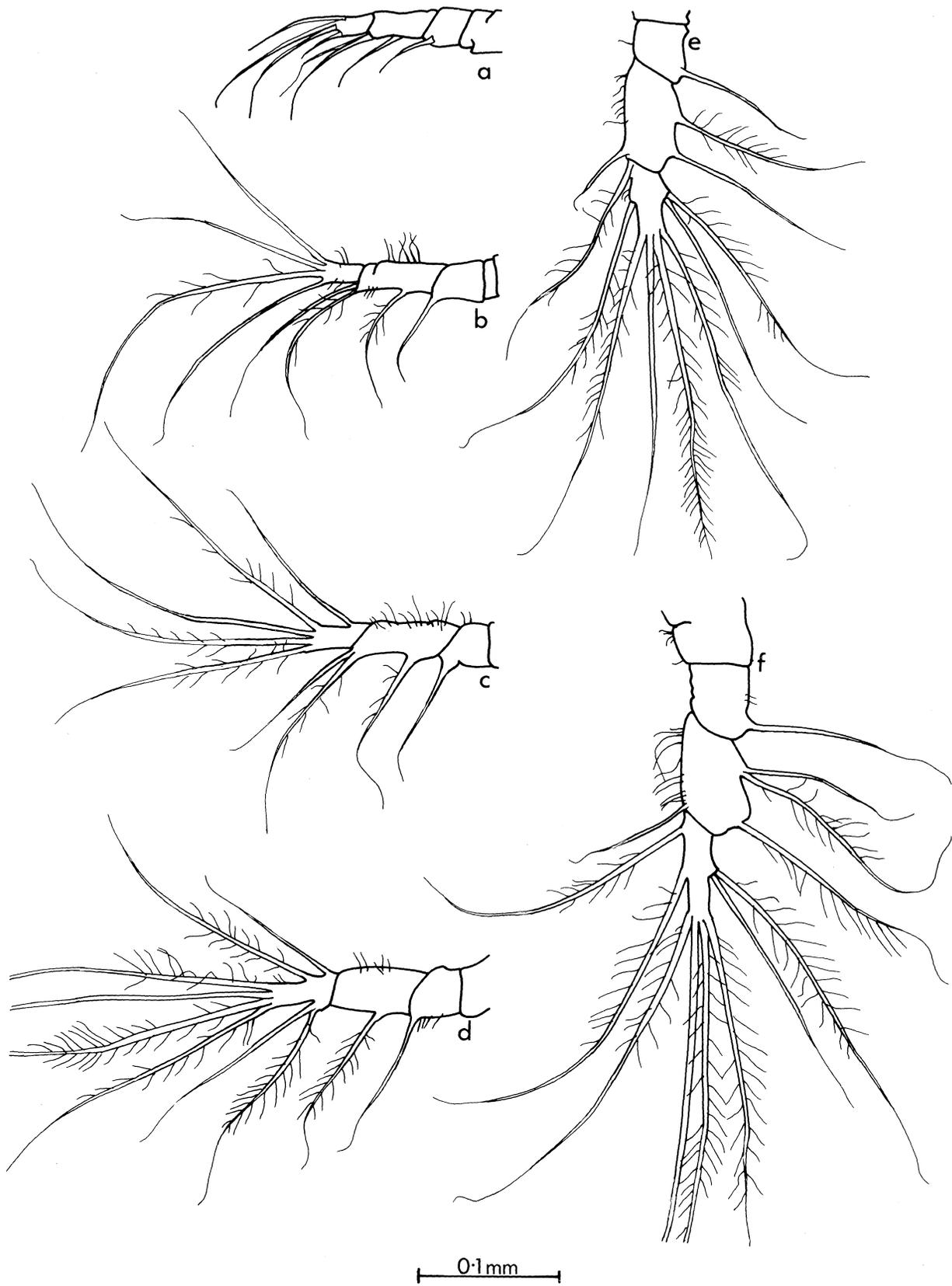
Fig.10. *Hexaminius popeiana.* **a–f,** antennule of naupliar stages I–VI. Scale 0.1 mm.

Fig.11. *Hexaminius popeiana.* **a–f,** antenna of naupliar stages I–VI. Scale 0.1 mm.

0·1 mm

Fig.12. *Hexaminius popeiana.* **a–f,** mandible of naupliar stages I–VI. Scale 0.1 mm.

Fig.13. *Hexaminius popeiana.* "Male" posture during copulation.
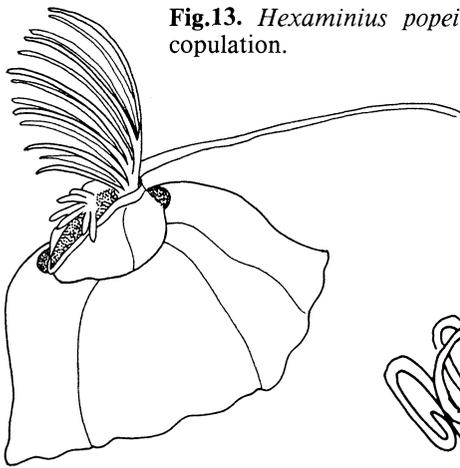
Fig.14. *Hexaminius foliorum.* "Male" posture (left) and "female" posture (right) during copulation.

maxillipeds beat together in continuous rapid motion, all indicative of the involvement of the whole body in a powerful copulatory effort. The copulatory intensity of *H. foliorum* is much higher than in *H. popeiana.* The recipient functional females also show a higher level of response, with gaping opercular valves and a partially extended, passive posture. The "females" of *H. popeiana*, in contrast, are more active and show a greater tendency to opercular closure in response to incipient probing.

Discussion

Balanomorphs on mangroves. The occupancy of mangrove surfaces by balanomorph barnacles is recorded for mangroves from most parts of their world range (Achituv, 1984), but barnacles have rarely been recorded on mangrove leaves. The usual surfaces to be encrusted are the trunks, stems, rhizophores and pneumatophores. Leaf occupancy has been noted only for *Euraphia withersi* in southern India (Daniel, 1972), some unspecified

chthamalids in South China (Wei & Lin, reported in Achituv, 1984) and *Elminius modestus* in northern New Zealand (Moore, 1944). All of these are species known to settle and grow on a variety of surfaces. We have also observed this phenomenon of settlement on different surfaces, including mangrove leaves, for *Balanus variegatus* and for *Elminius covertus* in New South Wales. The identification of *Hexaminius foliorum* as a species limited to the occupancy of mangrove leaves therefore appears to represent a unique level of restriction to this ephemeral habitat. It is made the more interesting by the sympatric existence of *Hexaminius popeiana*, whose larvae have access to but do not occupy the same leaves.

Functional morphology and reproduction of *H. foliorum.* The anatomical and functional differences between *H. foliorum* and *H. popeiana* are consistent with the view that *H. foliorum* is specialised as compared with *H. popeiana*. 1. The wall plates of *H. foliorum* are thinner and more fragile. 2. The basis of *H. foliorum* is thicker. 3. The tergoscutal flaps of *H. foliorum* are more superficial and less deeply folded. 4. The opercular plates of *H. foliorum* are thinner,
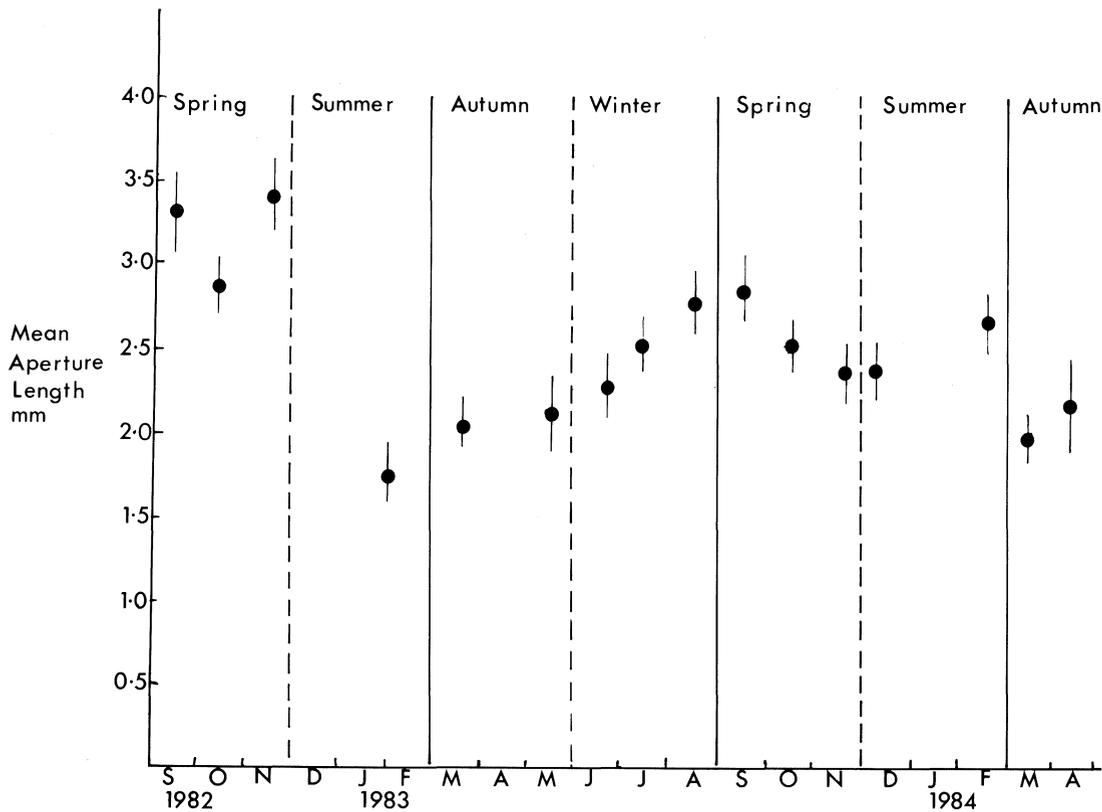
Fig.15. *Hexaminius foliorum.* Mean size of individuals in the population at Iron Cove, NSW, based on monthly samples of 50 individuals. Bars indicate standard error.

with weaker articulation of the scutum and tergum; the terga have fewer depressor muscle crests; the adductor muscle scar is less prominent on the scuta but the spur is longer on the terga. Opercular depressor muscles are also thinner. 5. The body of *H. foliorum* is longer and more streamlined, with thoracic limb bases more spread anteroposteriorly. 6. Cirrus I in *H. foliorum* has a shorter exopod and simplified setation; cirrus II has shorter rami; cirri IV–VI contrast in being longer and thinner, with more podomeres and longer setae. 7. Mandibles in *H. foliorum* are broader; maxillules narrower; maxillae are more prominent and setose. 8. The penis is shorter in *H. foliorum*, with reduced development of the pedicel.

Interpreting these differences in relation to habitat, the key factor may be that mangrove leaves are subject to leaf fall. Most of the leaf fall of *Avicennia marina* in the Sydney region occurs during the summer months (December–February), coincident with the major production of new leaves. There is an abrupt decrease in leaf fall during autumn (March–May) and little leaf fall during the winter months (June–August). An increase in leaf fall and leaf replacement occurs each spring (Goulter & Allaway, 1979).

Measurements of the mean size of individuals in

the population of *H. foliorum* at Iron Cove, NSW during 1983 and 1984 (Fig. 15) revealed a minimum mean size in late summer/early autumn, followed by a gradual increase in mean size during the autumn and winter months, commensurate with the relative stability of the substratum during that time. During the spring and summer, the high leaf fall and replacement was associated with fluctuations in mean size of *H. foliorum* as the population progressed once again to a minimum mean size. This is in accord with the loss of large adults due to leaf fall and the recruitment of young individuals onto new leaves. The life cycles of *H. foliorum* is thus an annual one, with population replacement mainly occurring each summer. At the same time, breeding and recruitment occur throughout the year (Egan & Anderson, 1985), with a reduction only in the autumn when the adult mortality resulting from the summer leaf fall is followed by a high incidence of immaturity in the succeeding generation. The continuous breeding of *H. foliorum* can be interpreted as an adaptation to maintenance of the species on a substratum that peaks in instability in the summer but is always ephemeral. *H. popeiana*, in contrast, inhabiting more stable and permanent substrata, shows a typical seasonal breeding pattern with a spring peak and little or no breeding during the

remainder of the year (Fig. 1). It seems likely that individuals of *H. popeiana* may live for more than one year, but this has yet to be tested.

In view of the similarities in body size, egg number and egg size in the two species, it is evident that *H. foliorum* releases more broods of larvae per individual per year and thus has a higher and more continuous reproductive effort than *H. popeiana.* The functional morphological modifications of *H. foliorum* are correlated with this reproductive difference. The thinner plates are indicative of more rapid growth. The longer, thinner captorial cirri with their longer setae imply a more rapidly acting cirral fan, achieving a faster feeding rate as a basis for faster growth and more sustained reproduction. The maxillipeds and mouthparts are modified in ways which suggest a more rapidly acting ingestive mechanism. The shorter penis, with reduced pedicel, may be correlated with a more rapid and intensive copulatory activity of *H. foliorum* as compared with *H. popeiana.*

Of these interpretations, two have been subjected to direct testing in the present investigation. The cirral mechanism is faster acting and more specialised in *H. foliorum* than in *H. popeiana.* The latter species displays the entire range of balanoid cirral activities, testing, pumping beat, normal beat and fast beat. *Hexaminius foliorum* displays only fast beat, which it performs more rapidly, with a greater sweep of the captorial cirri, than in *H. popeiana.* The copulatory mechanism in *H. foliorum* is also more specialised and more vigorous than in *H. popeiana.* Penis extension in functional "males" is frequent and rapid, and involves an intense effort in cirral curling and maxilliped beating. Functional "females" are passively receptive to probing by several males. In *H. popeiana*, these reproductive events are less intense and more leisurely in expression. The action of the species thus support the interpretation, based on morphology, that *H. foliorum* is specialised in ways that relate to the hazards of life on an ephemeral leaf habitat.

Larval development of *H. foliorum.* The morphological differences between the larvae of *H. foliorum* and *H. popeiana* are sufficient to support the separation of the two species, but do not offer any information on the relationship between them. Rates of larval development, however, are in accord with the concept that *H. foliorum* has higher rates generally than *H. popeiana* (nine days to cyprid as compared with 15).

Evolution of *H. foliorum.* We therefore conclude that *H. popeiana* is a six–plated elminiine as proposed by Foster (1982), but is confined to rocks, wood and mangrove trunks in the upper littoral of eastern Australian sheltered waters. Among mangroves of the central coast of New South Wales, another species, *H. foliorum*, occurs as an inhabitant of mangrove leaves, mainly occupying the underside of lower leaves subject to tidal immersion. The functional morphology and reproductive biology of *H. foliorum* are specialised in ways related to the ephemerality of the leaf habitat. It seems likely that *H. popeiana* and *H. foliorum* have an ancestor-descendant relationship. Apart from the genetic questions raised by this interpretation, an ecological question is also presented. What are the settlement and recruitment patterns that lead the cyprids of *H. popeiana* to successful settlement on many surfaces, but not mangrove leaves, and *H. foliorum* to successful settlement on mangroves leaves only, thus resulting in populations of the two species that abut, but do not overlap, even on the same mangrove plant?

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