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Minibrachium, a new subgenus of *Rhamphobrachium* (Annelida: Onuphidae) from Australia with the description of three new species

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Abstract

This study describes a new subgenus of miniature, progenetic *Rhamphobrachium* species from eastern Australia. *Minibrachium*, n. subg. is characterised by such paedomorphic features as lack of peristomial cirri and branchiae, possession of only two pairs of modified parapodia with spiny recurved hooks and very early onset of subacicular hooks. Three new species are described, of which at least *R.* (*Minibrachium*) *nutrix* n. sp., the type species (from Lizard Island, Great Barrier Reef), is a fully grown adult, brooding several 16- to 20-chaetiger juveniles in the parental tubes. *Rhamphobrachium* (*M*.) *talboti* n. sp. (from off Sydney) and *R.* (*M.*) *fractum* n. sp. (from Bass Strait), although twice as large as the type species, have only partially developed frontal lips, indicating either incomplete growth or presenting an additional paedomorphic character. We discuss the position of the new subgenus in the *Rhamphobrachium* complex and present a key to the subgenera of *Rhamphobrachium* and species of *R.* (*Minibrachium*).

Key words: polychaetes, taxonomy, brooding, juveniles, Lizard Island, progenesis

Introduction

The genus *Rhamphobrachium* was erected by Ehlers, 1887 for his previously described *Onuphis brevibrachiatum* Ehlers, 1875 and a new species, *Rhamphobrachium agassizii* Ehlers, 1887, for onuphids with three prolonged anterior pairs of parapodia with long, spiny, distally recurved hooks. Subsequently the definition was broadened to include species with two to five pairs of modified parapodia and spineless recurved as well as spiny tridentate hooks (Monro 1937), Day (1960), Estcourt (1966) and Kucheruk (1979). In her generic revision of Onuphidae, Paxton (1986a) revised *Rhamphobrachium*, demonstrated that some species with two pairs of modified parapodia were juveniles, and that several species with four or five pairs of modified parapodia differed also in a number of additional important characters. She restricted the definition of *Rhamphobrachium* to species with three pairs of modified parapodia with hooks with moveable spines and long chaetal sacs, described two new genera *Brevibrachium* Paxton, 1986 and *Longibrachium* Paxton, 1986 to accommodate the pre-empted species, and regarded the group as a complex of related genera, the *Rhamphobrachium* complex. Furthermore, Paxton (1986b) showed that *Rhamphobrachium agassizii* (type species) and *R. chuni* Ehlers, 1908, differed in a number of characters from the remaining species and erected the subgenus *R. (Rhamphobrachium*) for the former two and *R. (Spinigerium*) for the species possessing spinigers in anterior parapodia.

Small specimens, lacking frontal lips, peristomial cirri and branchiae, possessing two pairs of modified parapodia with internal to protruding spiny hooks and peculiar wing-shaped subacicular hooks with spiny hoods, were reported as *R*. (*Rhamphobrachium*) sp. because of their lack of spinigers (Paxton 1986a, b). These small specimens, collected off southeast Australia in depths of 31-126 m, ranged in size from 10-22 mm in length and were regarded as juveniles, but despite continued vigilance over almost thirty years, adult *R*. (*Rhamphobrachium*) species have never been reported from these waters.

Whilst sorting previously collected onuphids from Lizard Island we came across three samples of very small *Rhamphobrachium* specimens that resembled the specimens reported as *R. (Rhamphobrachium)* sp. juveniles mentioned above, but upon closer examination were found to belong to a different species. However, to our great surprise, they were not juveniles but tiny adults, some still in their tubes together with developing juveniles. The apparent juvenile characteristics such as absence of peristomial cirri, branchiae, only two pairs of modified parapodia and the very small size are here interpreted as a result of progenesis, the acceleration of sexual maturation in the sense of Gould (1977).

The aim of this paper is to erect a new subgenus for the three miniature new species, describe the new species and their developing juveniles, and discuss their position in the *Rhamphobrachium* complex.

Material and methods

Collected specimens were fixed in 4% formalin and later transferred to 75% ethanol. For light and scanning electron microscopy (SEM) examination, specimens were extracted from their tubes. Overall morphology was examined under a stereomicroscope; small specimens and body parts as temporary mounts in diluted glycerine or permanent slides embedded in the mounting medium Hydro-Matrix (Micro-Tech-Lab, Graz, Austria) were examined under a compound light microscope.

For SEM studies, specimens were dehydrated in a graded ethanol series, critical-point dried, sputter coated with gold and examined with a ZEISS Supra 55VP/EVO LS15 scanning electron microscope.

Terminology of prostomial appendages and chaetae follows Paxton (1986a; 1998). Materials are deposited in the Australian Museum, Sydney (AM) and in the Museum Victoria, Melbourne (MV).

Taxonomic account

Family Onuphidae Kinberg, 1865

Genus Rhamphobrachium Ehlers, 1887, emend.

Rhamphobrachium Ehlers, 1887: 70.—Paxton 1986a: 44. *Paranorthia* Moore, 1903: 448.

Type-species. Rhamphobrachium agassizii Ehlers, 1887: 70, by subsequent designation of Hartman, 1944: 47. Gender: neuter.

Diagnosis. The definition given by Paxton (1986a) is here emended as follows: peristomial cirri present or absent; anterior two or three pairs of parapodia modified, moderately prolonged, hooks with two rows of moveable spines, chaetal sacs extending to chaetiger 20–60; branchiae present or absent.

Remarks. The genus was previously defined as having peristomial cirri, branchiae, and three anterior pairs of modified parapodia with chaetal sacs extending to chaetiger 30–60. The erection of a new subgenus for the three progenetic new species described below necessitated the present emendation. With the description of the new subgenus, *Rhamphobrachium* includes three subgenera which can be distinguished as outlined in the key at the end of the paper.

Minibrachium n. subgen.

Type-species. Rhamphobrachium (Minibrachium) nutrix n. sp. Gender: neuter.

Diagnosis. Antennae on median part of prostomium. Frontal lips present or absent. Upper lips globular without median section, lower lips rectangular to crescentic. Nuchal grooves with narrow middorsal separation. Peristomial cirri absent. Branchiae absent. Recurved hooks uni- or bidentate, pseudocompound. Limbate chaetae simple, spinigers and falcigers absent. Two or more subacicular hooks with spiny hoods from chaetiger 3 or 5; hoods initially almost enclosing distal part of hooks, gradually opening up, becoming less spiny and changing to divided

hoods, one on either side of distal part of hook by about chaetiger 20, resembling typical subacicular hooks. One or two pairs of anal cirri.

Size. Very small; largest complete specimen 22 mm for 110 chaetigers; width to 1 mm.

Remarks. The new subgenus is characterised by its paedomorphic features that will be explored more fully in the Discussion. Two pairs of anal cirri has been a characteristic for the subfamily Onuphinae whilst members of Hyalinoeciinae have only one pair of anal cirri. *Rhamphobrachium* (M.) *nutrix* n. sp. is the first onuphine species reported to lack the second pair.

Etymology. The name refers to the small size of the animals and particularly their extremely short modified parapodia: Latin *mini* (small) and *brachium* (arm).

Distribution. Pacific Ocean: Australia, Lizard Island, Queensland to Bass Strait, Victoria; 9–126 m depth.

Rhamphobrachium (Minibrachium) nutrix n. sp.

(Figs 1–4)

Type material. Holotype: AM W.46046, Queensland, Lizard Island, outer Yonge Reef, 14°36'S, 145°28'E, dead coral, 10 m, coll. P.A. Hutchings & P.B. Weate, 25 Jan 1977, Collection Event Code 77 LIZ 56-2. Paratypes: AM W.47873 (3), same data as holotype; AM W.46045 (9), Queensland, Lizard Island, outer Yonge Reef, 14°36'S, 145°28'E, dead coral, 9 m, coll. P.A. Hutchings & P.B. Weate, 15 Jan 1977, Collection Event Code 77 LIZ 48-4.

Other material examined. AM W.47874 (35, 1 on slide, 1 on SEM stub), same data as holotype; AM W.47875 (28, 1 on slide, 2 and 1 juvenile on SEM stub), Queensland, Lizard Island, outer Yonge Reef, 14°36'S, 145°28'E, dead coral, 9 m, coll. P.A. Hutchings & P.B. Weate, 15 Jan 1977, Collection Event Code 77 LIZ 48-4; AM W.46043(1), Queensland, Yonge Reef, outer slope, 14°36'S, 145°38'E, reef rock with *Halimeda* and *Lithothamnion*, 36 m, coll. P.A. Hutchings & P.B. Weate, 9 Jan 1975, Collection Event Code 75 LIZ D-1.

Diagnosis. Very small, up to 0.5 mm wide. Diagnosis and description based on holotype and paratypes wider than 0.2 mm at chaetiger 10 excluding parapodia. Bidentate distally recurved spiny hooks on chaetigers 1 and 2; two subacicular hooks with spiny hoods from chaetiger 5, hoods becoming gradually less spiny, resembling typical subacicular hooks by about chaetiger 20; pectinate chaetae with 12–14 moderately long teeth. Pygidium with one pair of anal cirri.

Description. Holotype incomplete, measuring 16 mm in length for 55 chaetigers, 0.55 mm wide; largest complete specimens 9.4–11.0 mm long for 40–54 chaetigers, 0.4–0.5 mm wide. Alcohol stored specimens overall cream-coloured, lacking colour pattern.

Prostomium anteriorly rounded, wider than long, with paired globular frontal lips (Fig. 1A–C). Ceratophores of palps and antennae with one proximal ring and one longer distal ring; ceratostyles short and subulate, palps reaching to peristomium, lateral and median antennae reaching to chaetiger 1. Nuchal grooves curved laterally, with small middorsal separation. One pair of small eyespots at bases of lateral antennae. Peristomium shorter than first chaetiger; peristomial cirri absent.

First two pairs of parapodia modified, projecting anterolaterally, directed ventrally (Fig. 1B). Each of parapodia 1 and 2 with three short papilliform lobes and one ovate postchaetal lobe (Fig. 1E, F). Unmodified parapodia lacking distinct parapodial lobes. Dorsal cirri subulate on chaetiger 1 and 2, then becoming digitate. Ventral cirri subulate on chaetiger 1 and 2, replaced by rounded ventral pads from chaetiger 3. Branchiae absent.

Modified parapodia with three long, pseudocompound recurved hooks (Figs 1D, 2A), each projecting from a papilliform lobe (Fig. 1C, E). Shafts of hooks with two rows of long moveable spines below pseudoarticulation and irregularly distributed small spines; slight swelling before distal curvature of hook and small secondary hook, resulting in bifid recurved hook (Figs 2A, 3A–C). Internal chaetal sacs to chaetiger 20–22.

Unmodified parapodia from chaetiger 3, supported by two to three very thick aciculae (Fig. 3D, F). Limbate chaetae from chaetiger 3, decreasing in length from upper to lower position (Fig. 3D). Spinigers absent. Two bidentate subacicular hooks with spiny hoods from chaetiger 5 (Figs 2B, 3F); hoods initially almost enclosing distal part of hooks, gradually opening up, becoming smoother and changing to divided hoods, one on either side of distal part of hook by about chaetiger 20, resembling typical subacicular hooks (Fig. 3G–I). Slightly oblique pectinate chaetae with 12–14 moderately long teeth from chaetiger 12 (Fig. 3E). Pygidium with one pair of anal cirri. Fragile mucous tube without incrustations. Mandibles and maxillae extremely small and fragile, not clearly visible.



FIGURE 1. *Rhamphobrachium (Minibrachium) nutrix* n. sp., AM W.47875. A. Lateral view; B. Anterior part of body, lateral view; C. Prostomium and chaetigers 1–2, ventral view; D. Recurved hooks from chaetiger 1; E. Parapodium from chaetiger 1; F. Parapodium from chaetiger 2. Abbreviations: dc = dorsal cirrus, fl = frontal lip, la = lateral antenna, ll = lower lip, ma = median antenna, p = palp, per = peristomium, psl = postchaetal lobe, ul = upper lip, pl = papilliform lobe, vc = ventral cirrus.

Remarks. *Rhamphobrachium (M.) nutrix* n. sp. differs from *R. (M.) fractum* n. sp. and *R. (M.) talboti* n. sp. in being much smaller, having bidentate instead of unidentate distally recurved hooks, having two subacicular hooks per parapodium from chaetiger 5 instead of multiple hooks from chaetiger 3, and having one pair of anal cirri instead of two. Furthermore, *R. (M.) nutrix* has pectinate chaetae with 12–14 moderately long teeth while the other two new species have pectinate chaetae with 9–13 very long and 8–10 long teeth respectively.

Etymology. The species name *nutrix* (nurse) in Latin refers to the ability of the individuals of the new species to brood their young.

Biology. Despite their small size the specimens of the new species brood their young and thus are considered fully grown individuals. The holotype and several paratypes have two to four juveniles inside their tubes. Several similarly sized juveniles are present in the examined samples; presumably they have detached from their parents because of the destruction of the very fragile tubes. None of the specimens has an intact tube and the number of

juveniles per parent could not be established with certainty; however, judging from the size of the juveniles, only few of them (possibly not more than 10) could fit with a single brooding parent.



FIGURE 2. *Rhamphobrachium (Minibrachium) nutrix* n. sp. (A, B), *R. (M.) fractum* n. sp., (C–G) and *R. (M.) talboti* n. sp., (H–I). A. Distal part of recurved hook from chaetiger 1; B. Subacicular hook from chaetiger 20; C. Anterior part of body; D. Distal part of recurved hook from chaetiger 1; E. Compound subacicular hook from chaetiger 3; F. Pseudocompound subacicular hook from chaetiger 3; G. Simple subacicular hook from chaetiger 4; H. Mandibles; I. Part of maxillary apparatus (MxI, MxII and MxIII are shown).

Examined juveniles have about 16–20 chaetigers and are about 1 mm long, 0.2 mm wide, with developed palps and antennae but lacking fully formed frontal, upper and lower lips (Fig. 4A, B). The anterior two pairs of parapodia have subulate dorsal and ventral cirri but are not enlarged and lack chaetal lobes and recurved hooks. Limbate chaetae are present from chaetiger 3 (Fig. 4C); pectinate chaetae are absent. Subacicular hooks with spiny hoods number up to three per parapodium from chaetiger 3 (Fig. 4D, E). In posterior chaetigers hoods on subacicular hooks become smaller and less spiny (Fig. 4F).

Type locality. Pacific Ocean, Outer Yonge Reef, Lizard Island, Queensland; 14°36'S, 145°28'E.



FIGURE 3. *Rhamphobrachium (Minibrachium) nutrix* n. sp., AM W.47875. A–B. Distal bidentate parts of the recurved hooks from chaetiger 1; C. Spiny shaft of recurved hook from chaetiger 1; D. Parapodium from chaetiger 3; E. Pectinate chaeta from chaetiger 25; F. Parapodium from chaetiger 5; G. Subacicular hooks from chaetiger 6; H. The same from chaetiger 14; I. The same from chaetiger 22.

Distribution. This species is only known from Lizard Island, Great Barrier Reef, Queensland, Australia; in 9–36 m depth.

Rhamphobrachium (Minibrachium) fractum n. sp.

(Figs 2, 5)

Rhamphobrachium (Rhamphobrachium) sp.—Paxton 1986a: 19; 1986b: 87.

Type material. Holotype: AM W.198965, Victoria, 112 km S of Lakes Entrance, 39°00'00"S, 148°24'50"E, sta. 20 'Esso-Gipps', sand, 95 m, coll. C. Phipps, May 1969. Paratypes: AM W.47833 (2); AM W.47834.001, W.47835.001, W.47836.001, 3 specimens on SEM pins, same data as holotype; AM W.198964 (2), Bass Strait, 39°00'00"S, 148°30'00"E, sta. 19 'Esso-Gipps', 126 m, coll. C. Phipps, 7–9 May 1969.

Other material examined. MV F43626(1), Tasmania, eastern Bass Strait, 42 km SW of Babel Island, 40°14.4'S, 148°40.0'E, sta. BSS 165 'Tangaroa', fine sand, 60 m, Smith-McIntyre grab, coll. R. Wilson, 14 Nov 1981; MV F43628 (9), Tasmania, eastern Bass Strait, 63 km E of North Point, Flinders Island, 39°44.8'S, 148°40.6'E, sta. BSS 167 'Tangaroa', muddy sand, 124 m, Smith-McIntyre grab, coll. R. Wilson, 14 Nov 1981; MV F43629 (13), Tasmania, eastern Bass Strait, 63 km E of North Point, Flinders Island, 39°44.8'S, 148°40.6'E, sta. BSS 167 'Tangaroa', muddy sand, 124 m, Smith-McIntyre grab, coll. R. Wilson, 14 Nov 1981; MV F43629 (13), Tasmania, eastern Bass Strait, 63 km E of North Point, Flinders Island, 39°44.8'S, 148°40.6'E, sta. BSS 167 'Tangaroa', muddy sand, 124 m, WHOI epibenthic sled, coll. R. Wilson, 14 Nov 1981.



FIGURE 4. Juvenile of *Rhamphobrachium (Minibrachium) nutrix* n. sp., AM W.47875. A. Ventral view; B. Anterior part of body, ventral view; C. Parapodia from chaetigers 3 and 4; D. Parapodium from chaetiger 6; E. Subacicular hooks from chaetiger 9; F. The same from chaetiger 12. Abbreviations: fl = frontal lip, la = lateral antenna, ll = lower lip, ma = median antenna, p = palp, ul = upper lip.

Diagnosis. Small, up to 1.0 mm wide; diagnosis and description based on holotype and paratypes wider than 0.4 mm at chaetiger 10 excluding parapodia. Unidentate distally recurved spiny hooks on chaetigers 1 and 2; four to eight compound to pseudocompound subacicular hooks with spiny hoods on chaetiger 3, five to eight simple subacicular hooks from chaetiger 4, hoods becoming gradually less spiny, resembling typical subacicular hooks by about chaetiger 20; pectinate chaetae with 8–10 long teeth. Pygidium with two pairs of anal cirri.

Description. Holotype incomplete, measuring 11.5 mm in length for 38 chaetigers, 0.8 mm in width; only complete paratype 10 mm long for 58 chaetigers, 0.5 mm wide, incomplete paratypes 0.5–0.9 mm wide. Complete non-type specimens 4–20 mm long for 35–77 chaetigers, 0.3–1.0 mm wide. Alcohol stored specimens overall cream-coloured, lacking colour pattern.

Prostomium (Fig. 5A) of holotype and most paratypes anteriorly shovel-nosed, two paratypes with indented frontal margin, representing partly formed frontal lips (Fig. 2C). Ceratophores of palps and antennae with one to two proximal rings and one longer distal ring; ceratostyles short and subulate, palps reaching to peristomium or chaetiger 1, lateral and median antennae reaching to chaetiger 1. Nuchal grooves curved laterally, with narrow middorsal separation. One pair of small eyespots between bases of palps and lateral antennae. Peristomium slightly shorter than first chaetiger; peristomial cirri absent.



FIGURE 5. *Rhamphobrachium (Minibrachium) fractum* n. sp., AM W.47834.001. A. Anterior part of body, lateral view; B. Parapodia from chaetigers 3-5; C. Compound subacicular hooks from chaetiger 3; D. Simple subacicular hooks from chaetiger 4; E. Parapodium from chaetiger 19; F. Simple subacicular hook from chaetiger 23; G. Pectinate chaeta from chaetiger 13; H. Posterior end, dorsolateral view, showing pygidium with anus and anal cirri. Abbreviations: ac = anal cirrus, dc = dorsal cirrus, la = lateral antenna, ma = median antenna, p = palp, vgp = ventral glandular pad.

First two pairs of parapodia modified, projecting anterolaterally, directed ventrally (Fig. 5A). Neither of parapodia 1 and 2 fully extended, anterior ends inverted, hiding parapodial lobes. Unmodified parapodia lacking distinct parapodial lobes. Dorsal cirri subulate on anterior chaetigers, more posteriorly becoming digitate. Ventral cirri subulate on chaetiger 1 and 2, replaced by rounded ventral pads from chaetiger 3. Branchiae absent.

Modified parapodia with three long, pseudocompound recurved hooks (Figs 2D, 5A). Shafts of hooks with two rows of long moveable spines below pseudoarticulation and irregularly distributed small spines along whole length of shaft, but more dense above pseudoarticulation; slight swelling before distal curvature of hook. Internal chaetal sacs to chaetiger 30.

Unmodified parapodia from chaetiger 3, supported by two to three very thick aciculae. Limbate chaetae from chaetiger 3, decreasing in length from upper to lower position (Fig. 5B). Spinigers absent. Four to eight compound

(Fig. 2E) to pseudocompound (Fig. 2F) subacicular hooks with spiny hoods on chaetiger 3 (Fig. 5C) (holotype with five compound and two pseudocompound hooks); five to eight simple subacicular hooks from chaetiger 4 (Figs 2G, 5D) (except in juveniles, measuring less than 0.3 mm in width). Hoods initially enclosing distal part of hooks more closely, gradually opening up, becoming smoother and changing to divided hoods, one on either side of distal part of hook by about chaetiger 20, resembling typical subacicular hooks; concurrent with morphological change, number of hooks becoming gradually reduced to two by chaetiger 20–25 (Fig. 5E, F). Slightly oblique pectinate chaetae from chaetiger 13; with 8–10 long teeth, one lateral tooth twice as long, as other teeth (Fig. 5G). Pygidium with two pairs of anal cirri; dorsal pair longer than ventral one (Fig. 5H). Fragile mucous tube without incrustations.

Mandibles decalcified, only protomandibles visible. Maxillae very delicate, elements transparent, attachment areas between plates only areas of slight sclerotisation. Maxillary formula: MxI = 1+1; MxII = 5+8; MxIII = 6+0; MxIV = 7+10; MxV = 1+1.

Remarks. *Rhamphobrachium* (M.) *fractum* n. sp. and R. (M.) *talboti* n. sp. are much more similar to each other than to R. (M.) *nutrix* n. sp. described above. They are almost twice as large as the latter, have unidentate instead of bidentate distally recurved spiny hooks, multiple subacicular hooks from chaetiger 3 instead of only two from chaetiger 5, have two pairs instead of one pair of anal cirri and have pectinate chaetae with much longer teeth. The former two species differ from each other in that the subacicular hooks of chaetiger 3 are always simple in R. (M.) *talboti* n. sp. (Fig. 6F) but compound to pseudocompound in R. (M.) *fractum* n. sp. (Fig. 5C). This is a consistent characteristic that is not growth dependent as the smallest R. (M.) *talboti* n. sp. (11 mm for 67 chaetigers, 0.45 mm wide) presented only simple subacicular hooks on chaetiger 3. Furthermore, the pectinate chaetae of R. (M.) *talboti* n. sp. have 9–13 very long teeth (Fig. 6K), while those of R. (M.) *fractum* n. sp. have 8–10 long teeth instead (Fig. 5G).

Etymology. The name is derived from *fractus* (break) in Latin and refers to the characteristic compound subacicular hooks on chaetiger 3.

Biology. No brooding specimens were encountered. The smallest specimens in the mixed samples measured 3–4 mm in length for 35–40 chaetigers, 0.3 mm in width and are considered to be recently settled juveniles. These juveniles differ from the larger specimens described above in having compound to pseudocompound subacicular hooks not only on chaetiger 3, but also up to about chaetiger 20, and thereafter only simple ones. In other characteristics they are like larger specimens, except for having even less developed frontal lips and shorter modified parapodia. The distally recurved spiny hooks are not visible externally but are present internally with the chaetal sacs reaching to about chaetiger 20.

Type locality. Pacific Ocean, 110 km S of Lake Entrance, Victoria; 39°00'00"S, 148°24'50"E.

Distribution. Bass Strait, Victoria and Tasmania, Australia; in 60–126 m depth.

Rhamphobrachium (Minibrachium) talboti n. sp.

(Figs 2, 6)

Rhamphobrachium (Rhamphobrachium) sp.—Paxton 1986a: 19, fig. 13c; 1986b: 87.

Type material. Holotype: AM W.198967, New South Wales, Sydney, off Palm Beach, 33°35'03"S, 151°21'30"E, 31 m, coll. F. Talbot *et al.*, 17 Mar 1978; Paratypes: AM W.47837(1), same data as holotype; AM W.47838.001, W.47839.001, 2 specimens on SEM pins, same data as holotype; AM W.198966 (14), New South Wales, Sydney, off Palm Beach, 33°35'03"S, 151°21'30"E, 31 m, coll. F. Talbot *et al.*, 10 Dec 1977.

Diagnosis. Small, width up to 1.0 mm wide. Unidentate distally recurved spiny hooks on chaetigers 1 and 2; six to ten simple subacicular hooks with spiny hoods from chaetiger 3, hoods becoming gradually less spiny, resembling typical subacicular hooks by about chaetiger 20; pectinate chaetae with 9–13 very long teeth. Pygidium with two pairs of anal cirri.

Description. Holotype incomplete, measuring 27 mm in length for 72 chaetigers, 1.0 mm wide; complete paratypes ranging from 11–21 mm long for 67–110 chaetigers, 0.45–1.0 mm wide. Alcohol stored specimens overall cream-coloured, lacking colour pattern.

Anterior part of prostomium shovel-nosed, representing partly formed frontal lips (Fig. 6A, B). Ceratophores of palps and antennae with one to two proximal rings and one longer distal ring; ceratostyles short and subulate,

palps reaching to peristomium or chaetiger 1, lateral and median antennae reaching to chaetiger 1. Nuchal grooves curved laterally, with narrow middorsal separation. One pair of small eyespots between the bases of palps and lateral antennae. Peristomium shorter than first chaetiger; peristomial cirri absent.



FIGURE 6. *Rhamphobrachium (Minibrachium) talboti* n. sp., AM W.47838.001. A. Anterior part of body, ventral view; B. The same, lateral view; C. Parapodium from chaetiger 3; D. The same, enlarged; E. Parapodium from chaetiger 9; F. The same, enlarged; G. Distal part of recurved hook from chaetiger 1; H–J. Shafts of recurved hooks with movable spines; K. Pectinate chaeta from chaetiger 13. Abbreviations: la = lateral antenna, ll = lower lip, ma = median antenna, mx = maxillae, p = palp, per = peristomium, ul = upper lip, vc = ventral cirrus.

First two pairs of parapodia modified, projecting anterolaterally, directed ventrally (Fig. 6B). Neither of parapodia 1 and 2 fully extended, anterior ends inverted, hiding parapodial lobes. Unmodified parapodia lacking distinct parapodial lobes. Dorsal cirri subulate on anterior chaetigers, more posteriorly becoming digitate. Ventral cirri subulate on chaetiger 1 and 2, replaced by rounded ventral pads from chaetiger 3 (Fig. 6A, B). Branchiae absent.

Modified parapodia with three long, pseudocompound recurved hooks. Shafts of hooks with two rows of long moveable spines below pseudoarticulation and irregularly distributed small spines along whole length of shaft, but more dense above pseudoarticulation; slight swelling before distal curvature of hook (Fig. 6G–J). Internal chaetal sacs to chaetiger 30.

Unmodified parapodia from chaetiger 3, supported by two to three very thick aciculae (Fig. 6C, D). Limbate chaetae from chaetiger 3, decreasing in length from upper to lower position. Spinigers absent. Six to ten bidentate subacicular hooks with spiny hoods from chaetiger 3 (Fig. 6E, F); hoods initially enclosing distal part of hooks more closely, gradually opening up (Fig. 6C, D), becoming smoother and changing to divided hoods, one on either side of distal part of hook by about chaetiger 20, resembling typical subacicular hooks; concurrent with morphological change, number of hooks becoming gradually reduced to two per parapodium by chaetiger 20–30. Slightly oblique pectinate chaetae (Fig. 6K) from chaetiger 13; with 9–13 extremely long teeth, gradually decreasing in length from one side of comb to other. Pygidium with two pairs of anal cirri; dorsal pair longer than ventral one. Fragile mucous tube with attached sand grains.

Jaws very delicate and fragile. Mandibles (Fig. 2H) with long, slender shafts; cutting plates relatively small, covered with thin layer of calcium, protomandibles clearly visible. Maxillae (Fig. 2I) extracted only partially due to their delicate nature; elements almost transparent, hardly sclerotised. Incomplete maxillary formula: MxI = 1+1; MxII = 9+10; MxIII = 7+0; other elements not observed.

Remarks. *Rhamphobrachium* (M) *fractum* n. sp. is most similar to *R*. (M) *talboti* n. sp. described above, where the relationships of the two species have been discussed.

Etymology. It is a pleasure to dedicate this new species to Dr. Frank Talbot, former Director of the Australian Museum, under whose tenure Lizard Island Research Station was established, and who collected the material with his students.

Biology. No brooding specimens were encountered and hence we have no evidence that the specimens examined are adults. However, since they were collected at the same site three months apart with a similar size distribution and the chaetal characteristics showed no size dependent variations, we feel justified to assume that the larger specimens were fully grown.

Type locality. Pacific Ocean, off Palm Beach, Sydney, New South Wales; 33°35'03"S, 151°21'30"E.

Distribution. This species is only known from off Palm Beach, Sydney, New South Wales, Australia; in 31 m depth.

Key to subgenera of Rhamphobrachium and species of R. (Minibrachium) n. subg.

1	Peristomial cirri absent; branchiae absent; lower limbate chaetae simple, spinigers absent; subacicular hooks with spiny hoods
	from chaetiger 3–5, gradually changing to typical subacicular hooks by about chaetiger 20R. (Minibrachium) n. subg3
-	Peristomial cirri and branchiae present; subacicular hooks from chaetiger 10–16
2. (1)	Peristomial cirri inserted far apart; lower limbate chaetae pseudocompound to compound (= spinigers); maximum of two sub-
	acicular hooks per parapodium; Mx VI absent
-	Peristomial cirri inserted close together; all limbate chaetae simple; maximum of three to six subacicular hooks on chaetigers
	15–30 <i>R.</i> (<i>Rhamphobrachium</i>)
3. (1)	Bidentate distally recurved spiny hooks (Figs 2A, 3A–C); two subacicular hooks per parapodium from chaetiger 5
-	Unidentate distally recurved spiny hooks (Figs 2B, 6G–J); 4–10 subacicular hooks per parapodium from chaetiger 34
4. (3)	Subacicular hooks of chaetiger 3 simple (Fig. 6D, F); pectinate chaetae with 9–13 very long teeth (Fig. 6K)
-	Subacicular hooks of chaetiger 3 compound to pseudocompound (Figs 2D, E, 5C); pectinate chaetae with 8–10 long teeth (Fig.
	5G)

Discussion

The *Rhamphobrachium* complex includes three genera: *Rhamphobrachium*, *Brevibrachium* and *Longibrachium*. The three new species described above are clearly members of *Rhamphobrachium* for sharing the specialised spiny, distally recurved hooks of the anterior modified parapodia. These hooks bear moveable spines that have been considered as an apomorphic character for the genus (Paxton 1986a).

Species	Authority	Distribution	Depth	Reference
R. (Rhamphobrachium) agassizii	Ehlers, 1887	E N Atlantic: Florida and Puerto Rico; W N Atlantic: Azores Morocco, Ivory Coast	?40–2165 m	Paxton 1986b
R. (Rhamphobrachium) chuni	Ehlers, 1908	Indo-Pacific: E. Africa, India, Indonesia, Philippines, ?New Zealand	?64–1362 m	Paxton 1986b
R. (Spinigerium) averincevi	Kucheruk, 1979	S Pacific: S of New Zealand	134–1400 m	Paxton 1986b
R. (Spinigerium) brevibrachiatum	(Ehlers, 1875)	WN Atlantic: English Channel to Mediterranean; w N Atlantic: N. and S. America; Pacific: Japan	35–1470 m	Paxton 1986b; Imajima 1999
R. (Spinigerium) diversosetosum	Monro, 1937	Indian Ocean: Maldives	183–274 m	Paxton 1986b
R. (Spinigerium) ehlersi	Monro, 1930	S Atlantic: S. Shetlands, S. Orkneys, S. Georgia, Antarctica; ?S.Pacific: Chathams	199–935 m	Paxton 1986b
R. (Spinigerium) hutchingsae	Paxton, 1986	S Pacific: Solomons, Australia; Suruga Bay, Japan	110–400 m	Paxton 1986b; Imajima 1999
R. (Spinigerium) longisetosum	Berkeley & Berkeley, 1938	Pacific: S. California to Mexico; Galapagos Isl.	20–730 m	Paxton 1986b
R. (Spinigerium) noeli	Paxton, 1986	S Pacific: Australia	6.4–9.5 m	Paxton 1986b
R. (Spinigerium) pettiboneae	Paxton, 1986	N Atlantic: USA, off Georgia	495 m	Paxton 1986b
R. (Spinigerium) pyriforme	Paxton, 1986	Pacific: E Australia	800 m	Paxton 1986b
R. (Spinigerium) verngreni	Kinberg, 1865	S Atlantic: Brazil, Uruguay	72–115 m	Paxton 1986b
?R. (Spinigerium) bipes*	Monro, 1937	Indian Ocean: Gulf of Aden	91 m	Paxton 1986b
?R. (Spinigerium) brevicornutum*	Moore, 1903	EN Pacific: Japan	82-88	Paxton 1986b
?R. (Spinigerium) cristobalensis*	Fauchald, 1968	Pacific Ocean: Baja California	75 m	Paxton 1986b
R. (Minibrachium) nutrix	n. sp.	Pacific: Lizard Island, Australia	9–36 m	present study
R. (Minibrachium) talboti	n. sp.	Pacific: Sydney, Australia	31 m	present study
R. (Minibrachium) fractum	n. sp.	Pacific: Bass Strait, Australia	60–126 m	present study

TABLE 1. List of Rhamphobrachium species. *corresponds to incertae sedis.

The genus *Rhamphobrachium* contains 12 recognised species with three pairs of modified anterior parapodia and three species with two pairs of modified parapodia determined as *incertae sedis* by Paxton (1986b) (Table 1). This decision was based on a study of ontogenetic changes in *R. ehlersi* Monro, 1930. Paxton (1986a) studied a large number of specimens (juveniles from 0.7 mm to adults of 3.5 mm width), was able to divide them into several growth stages and clearly demonstrate that parapodia became successively modified during development until

three pairs of parapodia were modified when the animals reached a width of 1.8 mm and adult characteristics. Other early juvenile characters were absence of frontal lips, peristomial cirri and branchiae, and a much earlier appearance of subacicular hooks (chaetiger 7–8 in the youngest juveniles vs. 15–16 in adults). The three species determined as *incertae sedis* (Table 1) ranged in width from 1.0–1.5 mm and all possessed peristomial cirri and branchiae. We still consider them as advanced juveniles that have not developed the third pair of modified parapodia yet and are unable to place them confidently with any described species.

The chaetal complement of onuphids is size-dependent and this is particularly obvious with the occurrence of subacicular hooks (SAHs). The first SAHs commence more anteriorly in juveniles and the most anterior are gradually lost as the animals grow as in the case of *R. ehlersi* discussed above. However, the juvenile SAHs may also be of a different form and are referred to as "provisional SAHs" that are replaced progressively by "permanent SAHs" as the animal grows (Paxton 1986a). These provisional SAHs are compound and differ in shape from the compound bidentate falcigers with the appendage resembling the terminal part of the SAHs.

Rhamphobrachium (*Minibrachium*) spp. represent a previously unreported SAH replacement pattern. Subacicular hooks, the distal part almost enclosed by spiny hoods, start on chaetigers 3 or 5 and gradually change their form by becoming less spiny, the hoods open up more to become divided hoods, one on either side of the distal part by about chaetiger 20, resembling typical SAHs. Since there is no abrupt change, and since this pattern is not size-dependent, we refrain from terming the anterior hooks as provisional SAHs. This pattern was observed for *R*. (*M*.) *nutrix* n. sp. and *R*. (*M*.) *talboti* n. sp. However, in *R*. (*M*.) *fractum* n. sp. the SAHs of chaetiger 3 are compound to pseudocompound while those of the following chaetigers are simple. Furthermore, juvenile specimens presented compound to pseudocompound SAHs up to about chaetiger 20, thus clearly indicating that the compound to pseudocompound SAHs are provisional. Although the compound SAHs resemble the falcigers that are found in some species of *R*. (*Spinigerium*) on chaetigers 3 and 4, the two forms may not be homologous.

Furthermore, the three new *R*. (*Minibrachium*) species lack peristomial cirri, branchiae, have only two modified pairs of parapodia, and are of a very small size. In effect, these are the characteristics of early juveniles. Yet, *R*. (*M.*) *nutrix* n. sp. includes reproducing adults and we assume that the retention of juvenile characters by adult stages has arisen as a result of progenesis in the sense of Gould (1977) by an acceleration of the sexual maturation. We have not been able to find any reproducing adults of the other two new species. However, since the three species are obviously closely related, sharing the unusual subacicular hooks with spiny hoods, we feel justified to assume that *R*. (*M.*) *talboti* n. sp. and *R*. (*M.*) *fractum* n. sp. are also valid species. The shovel-nosed frontal lips of the former and the shovel-nosed to partly developed frontal lips of the latter may suggest that the specimens examined are not fully grown. However, the stabilised chaetal distribution of the larger specimens, with *R*. (*M.*) *fractum* n. sp. having lost the provisional SAHs, and the fact that specimes of both species were collected in different areas at different times as the only *Rhamphobrachium* species collected in the samples, indicate otherwise. Furthermore, *R*. (*M.*) *nutrix* n. sp. which has completely formed, globular frontal lips rather represent another paedomorphic character for *R*. (*M.*) *talboti* n. sp. and *R*. (*M.*) *fractum* n. sp., as may the most unusual possession of only one pair of anal cirri in *R*. (*M.*) *nutrix* n. sp.

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