

A new species of *Euryrhynchus* Miers, with a discussion of the systematic position of the Euryrhynchidae Holthuis (Crustacea, Decapoda)

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Abstract

A new species of the South American freshwater genus *Euryrhynchus*, *E. tomasi* sp. nov., is described on the basis of two specimens from French Guyana. The new species differs from all its congeners by the presence of two disto-lateral spines on the merus of the second pereopod, combined with the absence of any carpal spines. The recent elevation of the euryrhynchids to family status is supported, whilst a discussion is presented of their systematic position and affinities, emphasising the remote systematic affinity with the Typhlocarididae, previously assumed to be closely related. An appraisal of the systematically important characters in the Euryrhynchidae highlights the need for a reappraisal of the caridean superfamily Palaemonoidea.

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Keywords: *Euryrhynchus*; New species; French Guyana; Euryrhynchidae; Palaemonoidea; Caridea

1. Introduction

The caridean family Euryrhynchidae Holthuis, 1950, presently contains six species in three genera, all of which occur in freshwater. The genus *Euryrhynchus* Miers, 1877, presently contains four species, all from South America, whilst the monotypic genera *Euryrhynchoides* Powell, 1976, and *Euryrhynchina* Powell, 1976, are known from Sierra Leone and Nigeria respectively (Powell 1976), with both genera not having been reported upon since their original description.

Euryrhynchus wrzesniowksii Miers, 1877 (the type species of the genus) was described from a well in French Guyana (Miers 1877), and has since been reported from surface waters in Guyana, Suriname, and French Guyana (Tiefenbacher 1978). There is also a

single record from Brazil (Kensley and Walker 1982), and it is no longer considered a troglitic species (Holthuis 1986). The second species of the genus, *Euryrhynchus burchelli* Calman, 1907, was also initially described from a subterranean habitat (a well in the Brazilian state of Pará), but the species has since been recorded from surface waters across a large area in Brazilian Amazonia (Tiefenbacher 1978) and is also no longer considered a stygobiont (Holthuis 1986). Tiefenbacher (1978) described *Euryrhynchus amazoniensis*, a widespread species in Brazilian Amazonia, that also was recently recorded from the Peruvian Amazon (García-Dávila and Magalhães 2006). *E. amazoniensis* was eloquently illustrated and described by Holthuis (1966) under the name of *E. burchelli*. This species is the only one for which the ecology has been studied, with Kensley and Walker (1982) describing the habitat of the species as being restricted to submerged leaf litter in

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small streams within the inundated forests of the Rio Negro basin. The abbreviated larval development of these three species has been studied by Magalhães (1988). Finally, Pereira (1985) described *Euryrhynchus pemoni* Pereira from La Gran Sabana, Venezuela, a species which not been reported upon since.

Recently a collection of freshwater shrimps from French Guyana was submitted for identification by Mr. J. Tomas (Fulda, Germany). Amongst the specimens, two individuals were encountered which could not be assigned to any of the known species of *Euryrhynchus*, and these are herein described as a new species.

The systematic position of the Euryrhynchidae has been controversial for some time. The family has been variously treated as a subfamily or a family by different authors, and has been traditionally assigned to the superfamily Palaemonoidea. Prompted by the discovery of the new species, the systematic position of the genus/family is reviewed and their systematic status discussed. Type material of the new species has been deposited in the collections of the Natural History Museum, London (NHM), whilst other material is in the Zoological Collections of the Oxford University Museum of Natural History (OUMNH-ZC). Terminology for setae and spines follows Watling (1989).

2. Taxonomy

Family Euryrhynchidae Holthuis, 1950

Genus *Euryrhynchus* Miers 1877

Euryrhynchus tomasi sp. nov.

(Figs. 1–7).

Material examined: Male holotype (post-orbital carapace length 5.0 mm), Crique Timothy, near the N2 road from Régina to St Georges de l'Oyapock, 20 km NW of St Georges de l'Oyapock, French Guyana, approximately 4°00'N 51°52'W; leg. J. Tomas, 29.03.2006 (NHM 2007.62). Female paratype (pocl 4.3 mm), same data as holotype (NHM 2007.63).

Comparative material examined: *Euryrhynchus wrzesniowskii* Miers, 25 specimens, Cascades Fourgassier, French Guyana, 52°18'346 W 04°37'369 N; leg. O. Helker, 28.03.2006 (OUMNH-ZC 2006-21-001). *E. burchelli* Calman (holotype), well at Pará, Brazil; coll. Burchell, 04.09.1829 (specimen dried, in poor condition) (OUMNH-ZC 2006-21-002). *E. amazoniensis* Tiefenbacher, five specimens, from commercial import into Germany, probable origin Peruvian Amazonia, don J. Tomas, 26.10.2006 (OUMNH-ZC 2006-21-003). *Typhlocaris lethaea* Parisi, two specimens, Lethe Cave, Libya; leg. J. Cooke, 27.01.1960 (OUMNH 9528).

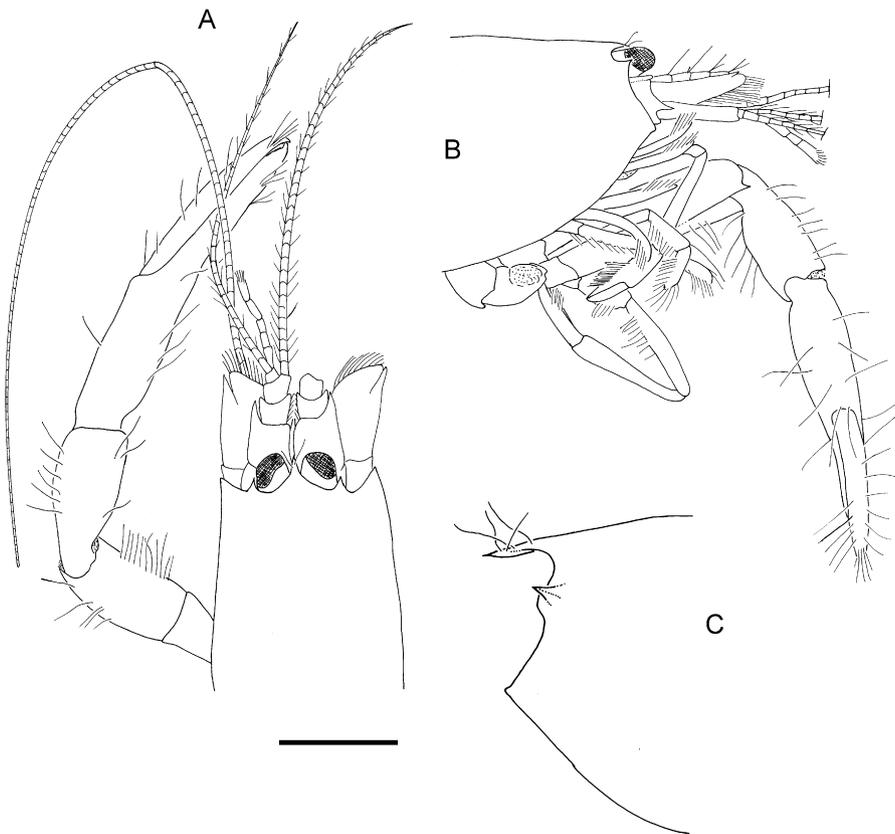


Fig. 1. *Euryrhynchus tomasi* sp. nov., holotype: (A) Frontal region, dorsal view; (B) lateral view; paratype: (C) frontal region, lateral view. Scale bar indicates 0.5 (A, B) or 1 (C) mm.

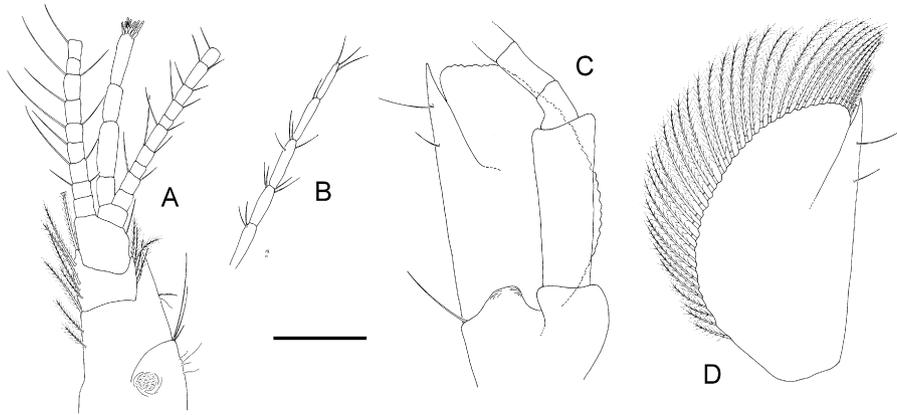


Fig. 2. *Euryrhynchus tomasi* sp. nov., paratype. (A) Antennule; (B) tip of upper, outer flagellum; (C) antennal peduncle (ventral view); (D) antennal scale. Scale bar indicates 0.35 (A) or 0.5 (B–D) mm.

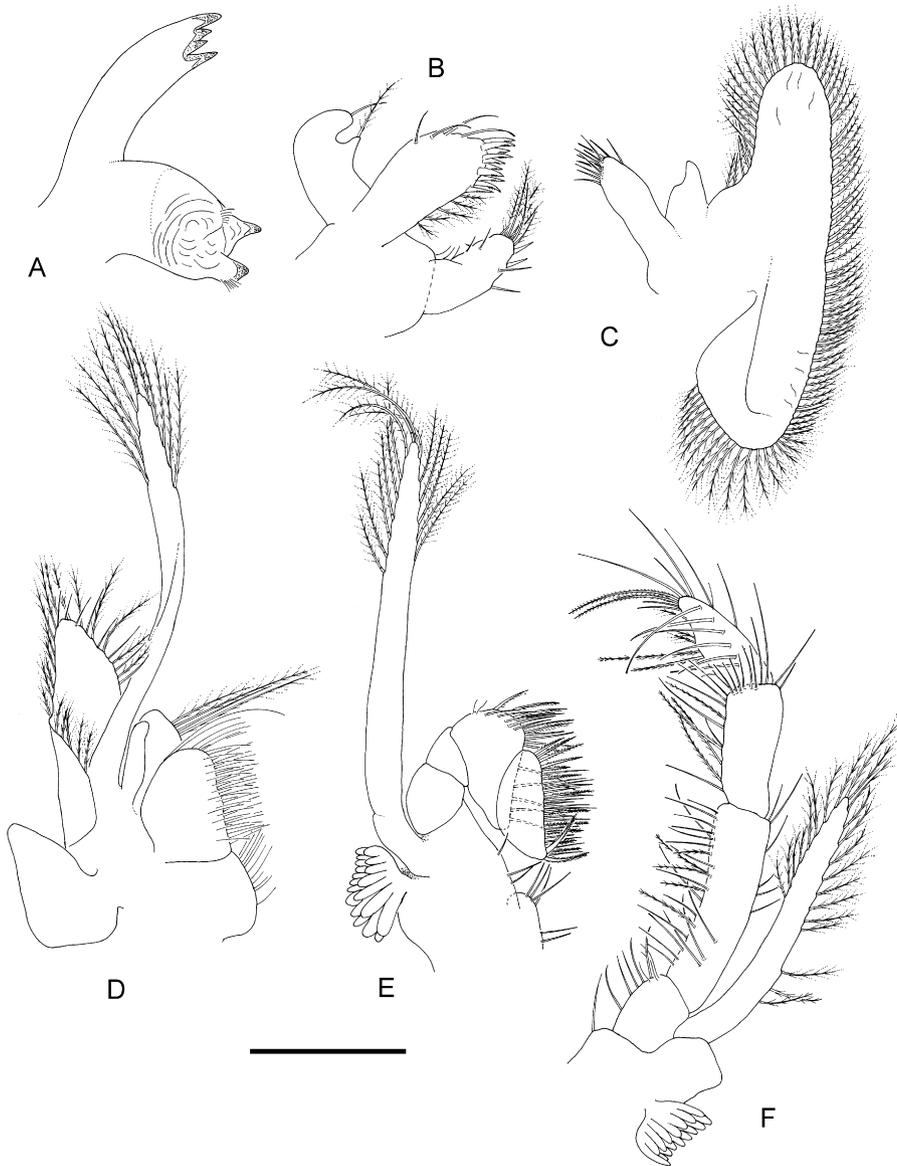


Fig. 3. *Euryrhynchus tomasi* sp. nov., paratype. (A) Left mandible, (B) maxillule, (C) maxilla, (D) maxilliped I, (E) maxilliped II, (F) maxilliped III. Scale bar indicates 0.5 (A, B), 0.75 (C–E) or 0.8 (F) mm.

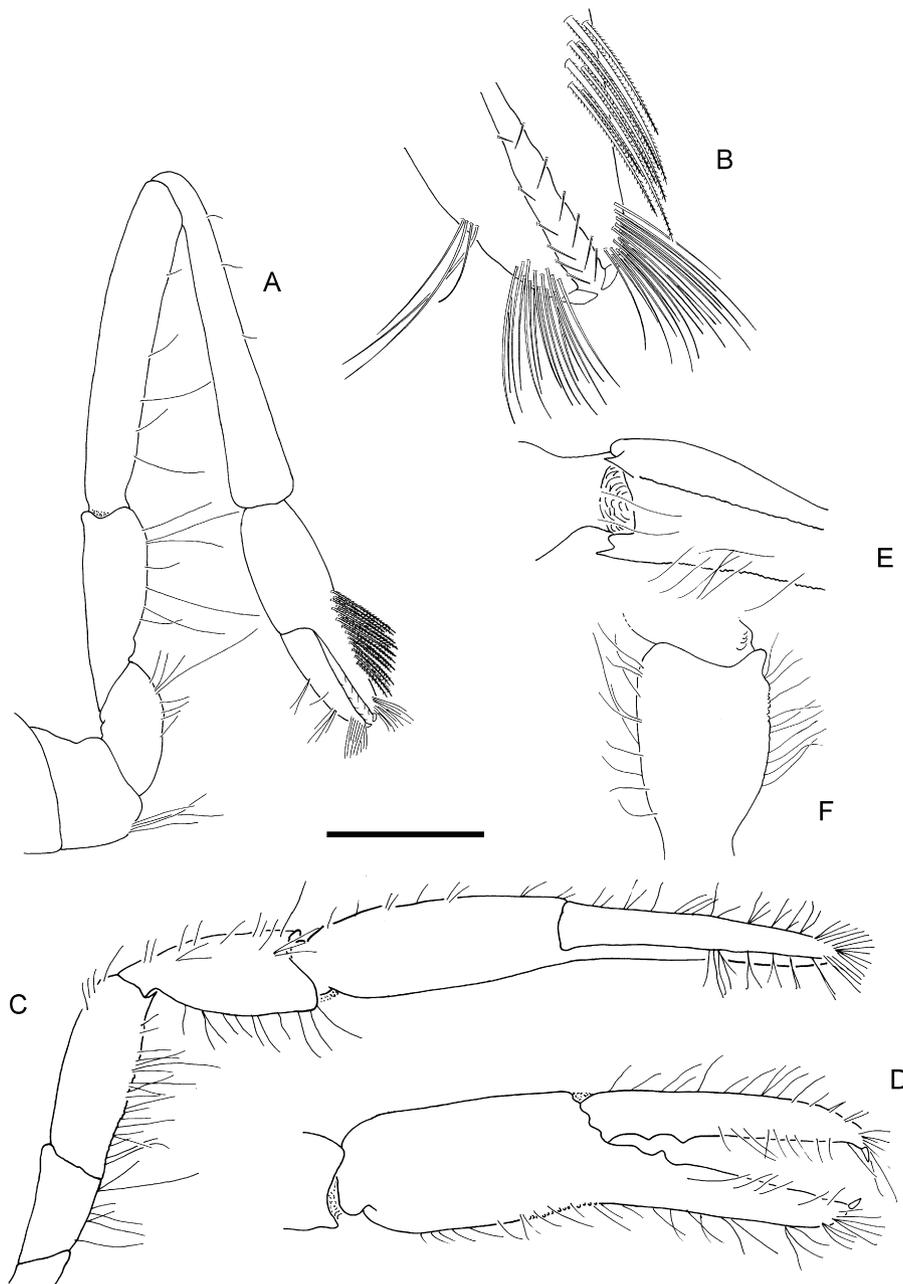


Fig. 4. *Euryrhynchus tomasi* sp. nov., paratype. (A) Right first pereiopod; (B) tip of chelae; holotype: (C) right second pereiopod; (D) chelae; (E) merus, ventral view, oblique; (F) carpus. Scale bar indicates 0.5 (A), 0.2 (B), 2 (C, D) or 1 (E, F) mm.

Description: Carapace smooth, without setae or grooves (Figs. 1A, B); rostrum triangular, depressed (Fig. 1C), falling short of distal margin of eyes; few long setae along lateral margin (Fig. 1C); sub-orbital angle poorly developed; antennal spine distinct, placed level with sub-orbital angle, over-reaching sub-orbital angle (Fig. 1C); pterygostomial angle protruding forward, angular, not over-reaching rostrum.

Fourth thoracic sternite in male with well developed transversal ridge, provided with median spine; fifth thoracic sternite with well developed transversal ridge, provided with broad median lobe; both ridges also

present in female, but without a spine on fourth thoracic sternite, and fifth one with narrower lobe.

Abdomen smooth, pleura 1–3 ventrally rounded, pleuron 2 greatly expanded in both female and male, overlapping both pleuron 1 and 3 by half; pleura 4–5 postero-lateral angle quadrate; lower margin of pleura 5–6 with fringe of plumose setae.

Antennular peduncle with stylocerite not laterally expanded (Figs. 1A, 2A); antero-lateral angle of basal segment produced into a sharply pointed tooth, over-reaching second segment; second segment short, with both antero-lateral and antero-medial angle bluntly



Fig. 5. *Euryrhynchus tomasi* sp. nov., paratype. (A) Right third pereopod; (B) right fourth pereopod, distal part; (C) right fifth pereopod, distal part. Scale bar indicates 0.8 (A) or 0.5 (B, C) mm.

produced (Fig. 2A); third segment quadrate; lower antennular flagellum long, 2.5 times as long as carapace, distal segments not appreciable shorter (Fig. 2B); upper antennular flagellum biramous (Fig. 2A), joint portion consisting of single segment, outer flagellum long, 1.2 times as long as carapace; inner flagellum short, broad, approximately 1.5 times as long as wide (Fig. 2A), consisting of 4 segments only, distal one longest, aesthetascs only present on distal article.

Scaphocerite broad, equal in length to antennular peduncle (Figs. 1A, 2C), fringed with annular plumose setae (Fig. 2D); outer margin straight, ending in a distal tooth, which slightly over-reaches the lamella (Fig. 2C); carapocerite approximately 0.7 times as long as scaphocerite; basicerite broadly rounded, bilobed distally, lateral spine present (Fig. 1B), latter not visible in dorsal view.

Mandible with incisor and molar processes widely separated (Fig. 3A), palp absent; incisor process ending in four teeth, outer ones larger; molar process distally bilobed, with numerous ridges. Maxilla I with two endites; upper endite broad, distally furnished with

cuspidate setae, lateral margin with several pappose setae (Fig. 3B); lower endite distally with several plumose setae, and finer cuspidate setae; palp bilobed, upper lobe larger, each lobe with single, terminal plumose seta (Fig. 3B). Maxilla II with single endite, furnished terminally with several simple setae; endopod short, proximally broadening (Fig. 3C); scaphognathite large, entire margin furnished with plumose setae. First maxilliped with well developed exopod; endites separated over their entire width, endopod well-developed, caridean lobe large, folded; epipod present (Fig. 3D). Second maxilliped with well developed pleurobranch; endopod without distinguishing features; exopod well developed (Fig. 3E). Third maxilliped pediform, elongate but stout; endopod consisting of four segments, proximal segment shortest, antepenultimate segment longest, penultimate segment about 0.6 times as long as antepenultimate segment; ultimate segment medio-distally with distinct concave margin exopod reaching past antepenultimate segment; single arthrobranch present (Fig. 3F).

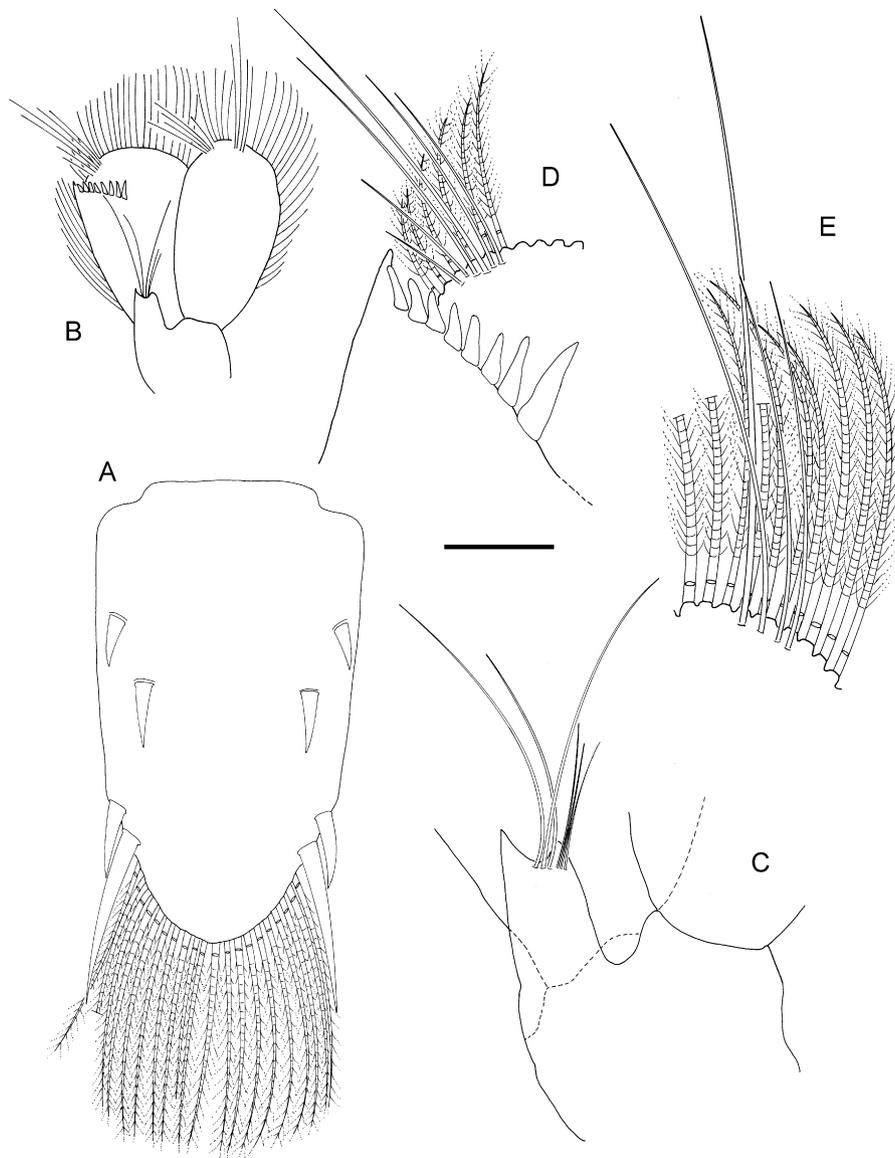


Fig. 6. *Euryrhynchus tomasi* sp. nov., paratype. (A) Telson; (B) right uropod; (C) protopod; (D) diaresis; (E) distal part of endopod. Scale bar indicates 1 (A), 0.5 (E), or 0.25 (B–D) mm.

First pereiopod slender, reaching with basal part of propodus past scaphocerite (Fig. 1B); merus about 1.8 times as long as ischium; carpus of equal length to merus; chelae about 0.75 times as long as carpus; fingers of chelae of equal length to palm (Fig. 4A), both fixed and movable finger furnished distally with strong tooth (Fig. 4B), lower surface of palm and fixed finger with well-developed, medial tuft of serrate setae, tips of fingers each with tuft of simple setae (Fig. 4B).

Second pereiopod robust, equal, reaching with the larger part of the carpus beyond the scaphocerite (Fig. 1A); merus twice as long as ischium (Fig. 4C), lower margin rugose, antero-lateral margin with two sharp spines (Fig. 4E); carpus equal in length to merus, minute tuberculation on lower surface, anterior margin without

spines (Fig. 4F); chelae about 2.75 times as long as carpus, fingers slightly longer than palm (Fig. 4D), lower surface of palm medially rugose, both fixed finger and movable finger ending in single fixed tooth, proximal margin of cutting edges with two low teeth on both fixed and movable finger (Fig. 4D).

Third to fifth pereiopods similar in shape and size. Third pereiopod (Fig. 5A) basis short, merus about 1.5 times as long as ischium; carpus about 0.5 times as long as ischium, upper corner of distal margin furnished with single, long, simple seta, reaching nearly to 0.3 of length of propodus; propodus about 1.7 times as long as carpus, lower margin with six clusters of cuspidate setae (Fig. 5A); dactyl bifid, about 0.5 times as long as propodus, upper margin indented, furnished with two

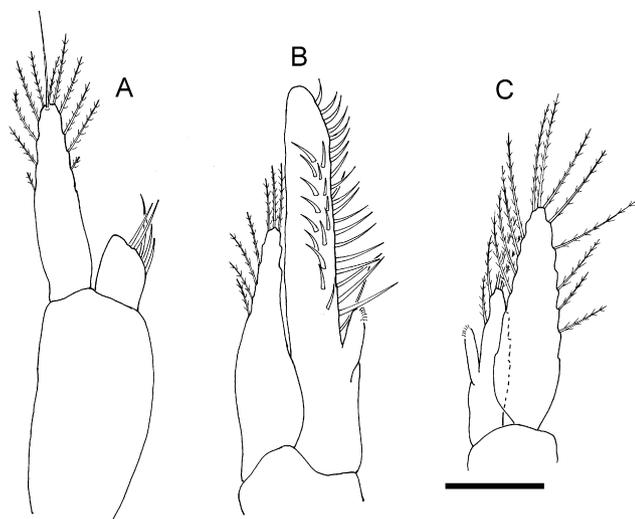


Fig. 7. *Euryrhynchus tomasi* sp. nov., holotype. (A) First pleopod; (B) second pleopod. Scale bar indicates 0.3 mm.

simple setae, unguis not demarcated; fourth pereopod similar to third, lower margin of propodus with four clusters of cuspidate setae, and two single cuspidate setae along upper margin (Fig. 5B); fifth pereopod similar to third, lower margin of propodus with six clusters of cuspidate setae, disto-laterally furnished with four rows of pappose setae (Fig. 5C), terminal setae on carpus proportionally much longer.

Telson broad, about 1.9 times as long as wide (Fig. 6A), dorsal surface with two pairs of spine-like setae, anterior pair situated about 0.3 of telson length, posterior pair larger in size, situated at about 0.4 telson length, placed more medially than anterior pair; posterior margin broadly rounded, laterally furnished with two pairs of spine-like setae, inner pair twice as long as outer pair; margin furnished with numerous long, annulate, plumose setae.

Uropod broad; protopod with lateral expansion (Figs. 6B, C), tip furnished with long simple setae; endopod and exopod subequal in length; diarsis on exopod incomplete, furnished with eight cuspidate setae, increasing in length medially (Fig. 6D); margins of exopod and endopod furnished with long, plumose, annulate setae; in addition three clusters of longer, simple setae are present, one on the exopod above the diarsis, two along the distal margin of the endopod (Figs. 6D, E).

Male first pleopod (Fig. 7A) with well developed protopod, exopod three times as long as endopod, furnished with five cuspidate setae; male second pleopod (Fig. 7B) with endopod longer than exopod, endopod with lateral and two partial medial rows of cuspidate setae, appendix interna reduced, appendix masculina absent; male third to fifth pleopod with well developed endopod, appendix interna shorter than endopod

(Fig. 7C). Female second to fifth pleopod without appendix interna.

Colour description: Body tinted brown-orange, on a grey-blue background, numerous small red dots present; chelipeds greyish-blue, chelae tinted with brown; ambulatory pereopods greyish-blue (after an aquarium colour photo by J. Tomas).

Derivation of name: Named after the collector of the type series, Mr. Joachim Tomas. The name is a genitive.

Ecology: Both specimens were collected from leaf litter in a slow flowing creek.

Distribution: Presently known only from the type locality.

Remarks: The known species of *Euryrhynchus* are very similar in their morphology, with identification primarily based on the number of meral and carpal spines on the second pereopod. In this respect, *Euryrhynchus tomasi* sp. nov. harbours two meral spines and no carpal spine (instead a carpal lobe is present), distinguishing it immediately from all other known species. These characters are distributed as follows in the other species: *E. amazoniensis* (0 meral spines, 1 carpal spine), *E. wrzesniowskii* (0, 0), *E. burchelli* (2, 1) and *E. pemoni* (1, 0). **Kensley and Walker (1982)** drew attention to the structure of the male second pleopod in *E. amazoniensis*, which differs greatly from that of *E. wrzesniowskii* and *E. burchelli* (see Figs. 2, 3 in **Kensley and Walker, 1982**). *E. tomasi* sp. nov. has a very similar male second pleopod to *E. wrzesniowskii* and *E. burchelli*, and is thus presumed to be more closely related to the latter two species. The post-embryonic development of the species studied by **Magalhães (1988)** supports this, with the development of *E. amazoniensis* differing from the other two species. Although the postembryonic development of *E. pemoni* is not known, the similarity of the male second pleopod (**Pereira 1985**) suggests a close affinity to *E. wrzesniowskii* and *E. burchelli* and indeed *E. tomasi* sp. nov. *Euryrhynchus tomasi* sp. nov. differs from *E. pemoni* primarily by having more slender chelae of the second pereopod, in the relative size of the inner pair of postero-lateral telson spine-like setae, and less cuspidate setae along the lower margin of the propodus of the third and fifth pereopod, which are arranged in *E. tomasi* sp. nov. in clusters, rather than as a continuous series as in *E. pemoni* (compare Fig. 5 with Fig. 5 in **Pereira, 1985**). Although **Pereira (1985)** does not mention the presence of a setal brush on the fifth pereopod, it is assumed this is an oversight, as it is present in all other species, and this would not distinguish both species. *Euryrhynchus tomasi* sp. nov. remains difficult to separate from the two remaining species, *E. wrzesniowskii* and *E. burchelli*, with the main distinction among these three species being the above mentioned meral and carpal spines on the second pereopod. In addition, the second sternal ridge in male *E. wrzesniowskii* harbours a median spine (pers. obs.),

whilst a broad lobe is present in *E. tomasi* sp. nov. Further, the endopod of the third to fifth male pleopod in *E. wresniowskii* is reduced and shorter than the appendix interna (see Fig. 20c-e in Gordon 1935); in contrast the endopod is of a normal size in *E. tomasi* sp. nov. (see Fig. 7C). These latter two characters are presently unknown for *E. burchelli*.

3. Discussion

The systematic position of the euryrhyndids has been controversial over the years. They have been variously treated as a subfamily or a family within the Palaemonoidea. When the genus *Euryrhyndus* was erected, Miers (1877) simply assigned it to the family Palaemonidae, an action followed by Calman (1907). Bals (1957) recognised four subfamilies within the Palaemonidae: Desmocaridinae, Palaemoninae, Pontoniinae and Typhlocaridinae, the latter consisting of the single troglobitic genus *Typhlocaris* Calman (Calman 1909), with *Euryrhyndus* again being assigned to the Palaemoninae. Holthuis (1950) did not recognise the subfamily Desmocaridinae, but he erected a new subfamily, Euryrhyndinae, for the then only known genus *Euryrhyndus*, and he defined the subfamily as follows: (1) upper antennular flagellum with two rami free throughout their length, (2) male second pleopod without appendix masculina, (3) female second pleopod without appendix interna, and (4) pleurobranch absent from third maxilliped. Further, Holthuis (1951) mentioned that the Euryrhyndinae are most closely related to the Typhlocaridinae, as they share the shape of the rostrum, the telson, the eyes and features of the mouthparts, as well as a common branchial formula, and he separated them on the basis of the presence of a longitudinal suture on the carapace (see Calman 1907). In fact, prior to Holthuis (1951), Annandale and Kemp (1913) had already remarked upon the similarity between the two genera but stated that the resemblance was, in their opinion, a convergence, rather than of genetic origin (i.e., a result of convergent evolution rather than common ancestry), probably influenced by the fact that both the then known species of *Euryrhyndus* were still known only from subterranean habitats. Powell (1976), when describing *Euryrhyndoides* and *Euryrhyndina*, supported Holthuis's (1950) decision of a separate subfamily but at the same time discussed the invalidity of two of the defining characters of the subfamily: male second pleopod without appendix masculina (present in both *Euryrhyndina* and *Euryrhyndoides*, although much modified in the latter, see below) and female second pleopod without appendix interna (present in both *Euryrhyndina* and *Euryrhyndoides*). At the same time Powell (1976) considered the systematic relationship between the Euryrhyndinae and Typhlocaridinae re-

mote, mainly based on reduced features (rostrum, eyes, mouthpart, gill formula) or features common in many other genera (e.g., broad posterior lobe of telson). Following on from this, Bruce (1986) considered the Euryrhyndinae and the Typhlocaridinae as separate subfamilies within the Palaemonidae. In his key, in addition to the upper antennular flagellum distinct throughout their length, Bruce (1986) used the male second pleopod without appendix masculina and the female one without appendix interna, an error in light of the two other genera included in the family/subfamily. In a major review of caridean systematics, Chace (1992) finally elevated several of the subfamilies of Palaemonidae to family status and proposed six families within the superfamily Palaemonoidea, these being Anchistioididae, Desmocarididae, Gnathophyllidae, Hymenoceridae, Palaemonidae, and Typhlocarididae. Within the Typhlocarididae, Chace (1992) recognised two subfamilies: Euryrhyndinae and Typhlocaridinae, separated by the presence of a longitudinal suture on the carapace in *Typhlocaris* and the third antennular flagellum entirely non-fused with either of the other two flagella in the euryrhyndid genera. Combining all four genera into a single family was based on the nearly identical mouthparts in *Typhlocaris* and the euryrhyndid genera, with the Typhlocarididae defined by the acutely produced caridean lobe on the first maxilliped. This action was followed by Chace and Bruce (1993), although they hinted that the virtually single character which distinguishes *Typhlocaris* and *Euryrhyndus* may be important enough to justify familial recognition of each genus. Holthuis (1993), in his review of all caridean families and genera, equally maintained two subfamilies within the Typhlocarididae. In contrast, Bruce (1993) considered both genera not closely related, and suggested that each receive family status, again emphasising the two main characters that distinguish both taxa, but still mentioning the lack of an appendix masculina on the male second pleopod (see below). In the most recent classification of Crustacea (Martin and Davis 2001), eight families are recognised within the superfamily Palaemonoidea. In addition to those mentioned in the Chace (1992) classification (see above), the Kakaducarididae are recognised following Bruce (1993), whilst the Euryrhyndinae are finally elevated to full family status (at the recommendation of L.B. Holthuis as a pers. com.).

Full family status of the euryrhyndid genera is herein supported. Of the previously suggested shared characters between the euryrhyndid genera and *Typhlocaris*, some clearly do not hold true, such as the eye, which in the troglobitic *Typhlocaris* species is reduced and without a cornea, whilst it is relatively normally developed in euryrhyndids, but not globular as in many other palaemonoids. Other characters, such as the broadly rounded posterior margin of the telson furnished with numerous plumose setae, are a neotenic character,

present in the larvae of many palaemonoids (see Fig. 10K in Bruce 1993) and cannot be interpreted as a symplesiomorphic character state. Although there is a general similarity in mouthpart structure, this is equally shared with many genera presently in the Palaemonidae and is perhaps better considered as the plesiomorphic state in Palaemonoidea. In contrast, both taxa differ in some fundamental characters. The upper antennular flagellum is divided into two branches in all euryrhyndids, with the inner flagellum being well developed; in contrast in *Typhlocaris* (like in many genera in the Palaemoninae) it is jointed for a considerable distance, with in addition the inner flagellum being rudimentary (Calman 1909). Both taxa have a partial diaresis on the uropodal exopod, but in the euryrhyndids it is provided with a row of large, cuspidate setae (unique within Palaemonoidea), which are absent in *Typhlocaris*. *Typhlocaris* harbours a complete post-antennal suture (Calman 1909), in a position similar to the linea thalassica in Thalassinidea, possibly an adaptation to low oxygen environments (D. Felder, pers. comm.), which is completely absent in the euryrhyndids. In view of these differences, a close relationship between the Euryrhyndidae and Typhlocarididae does not seem likely.

The family Euryrhyndidae can be characterised by the following characters: upper antennular flagellum divided throughout its length into two rami, segments of inner rami flattened, uropodal protopod with well-developed postero-lateral extension and exopodal diaresis with series of large cuspidate setae. Holthuis (1950) also characterised the family by the male second pleopod having no appendix masculina and the female second pleopod having no appendix interna, but both these characters are present in *Euryrhyndina* and *Euryrhyndoides* (Powell, 1976). In addition, Holthuis (1950) used the absence of a pleurobranch on the third maxilliped as a defining character. The interpretation of the branchial formulae as a phylogenetically informative character must however await more detailed descriptions of many palaemonoid genera (see Bruce 1993), especially regarding the number of arthrobranches and pleurobranches on the third maxilliped, considered an important character within Palaemonoidea. Much confusion is present in the literature on this. For instance Bruce (1993), in a discussion of this character in Kakaducarididae, states that the Euryrhyndinae only possess a single arthrobranch, which only holds for *Euryrhyndus* (Fig. 3F), as *Euryrhyndoides* has two (Powell, 1976), and *Euryrhyndina* none (Powell, 1976). The development of the appendix masculina in euryrhyndids is of particular interest, as it varies considerably amongst the three constituent genera. The appendix masculina in *Euryrhyndina edingtonae* is of the usual caridean form (see Figs. 7J, K in Powell 1976), but the interpretation of the male second pleopod in *Euryrhyndoides holthuisi* is more problematic. Powell (1976) interprets the flattened, curled structure originat-

ing from the endopod as an appendix masculina, with no trace of an appendix interna. However, as this structure is unique within caridean shrimp (and perhaps reminiscent of Brachyura) and bears no similarity to any other described caridean appendix masculina, its true nature is unknown, and this may well be a modified appendix interna or even coalesced appendices interna and masculina. Powell (1976), reprised by Kensley and Walker (1982), also suggested that the endopod in *Euryrhyndus* actually represents a true appendix masculina on an endopod lacking its distal part, supported by the fact that the more posterior pleopods lack distal parts (see Powell 1976), for which he referred to the description of *E. wresniowskii* in Gordon (1935). However, the posterior pleopods of *E. tomasi* sp. nov. are of the usual caridean form with the endopod being well-developed, surpassing the appendix interna, and perhaps representing a more ancestral state.

The affinities of the Euryrhyndidae within the Palaemonoidea and indeed Caridea in general are at present difficult to establish. Chace (1992) defined the Palaemonoidea as follows: pereopods without arthrobranches, dorsal (i.e., upper) antennular flagellum with accessory branch, incisor process of mandible (if present) distinctly separated from molar process, prominent caridean lobe on first maxilliped, and scaphognathite of maxilla rounded, not produced far into branchial chamber. Christoffersen (1990), in a cladistic revision of caridean superfamilies, identified a single synapomorphy for the Palaemonoidea: the basal segment of the antennular peduncle with a disto-lateral tooth. But he also noted that at sub-ordinate levels character reversals and homoplasies are present. Given the variability of this character in, for instance, Pontoniinae (see Bruce 1995), it is clear that this is not a defining synapomorphy. The Euryrhyndidae do indeed fit within the diagnosis of Palaemonoidea as currently defined (Chace 1992), but differ in some fundamental characters from all other included families, notably the upper antennular flagellum, diaresis armed with cuspidate setae and the postero-lateral extension of the uropodal protopod. Within the superfamily their affinities are unclear, with their remote relationship to the Typhlocarididae already discussed. The vestigial incisor process and the broadened segments of the third maxilliped in the Gnathophyllidae and Hymenoceridae indicates a remote systematic affinity with the Euryrhyndidae. Equally, a remote affinity with the Anchistioideidae can be inferred, due to the flared molar process and the unique larval history of the latter family. Any systematic relationship with the Pontoniinae (family Palaemonidae) is difficult to assess, given the extensive modifications of the basic bauplan in that subfamily, but there appears little reason to suggest a systematic affinity. The deep separation of the mandibular incisor and molar, coupled with the presence of a

setal brush on the fifth pereopod, as well as the structure of the antennular peduncle suggests a systematic affinity with the Palaemoninae (family Palaemonidae), Kakaducarididae and Desmocarididae. Clearly all three taxa can be separated by a score of characters (branchial formulae, antennule, mouthparts, uropods, etc.), but the Euryrhyndidae appear more closely related to these taxa, rather than the other constituent taxa within the Palaemonoidea. In addition to these similarities, the appendix masculina in *Desmocaridis* (family Desmocarididae) harbours similar rows of cuspidate setae, but at least in this genus clearly is separate from the endopod (see Fig. 4 in Powell 1977). Interestingly, the appendix masculina in two genera of the Kakaducarididae also is provided with cuspidate setae (*Kakaducaris glabra* Bruce, 1993; *Leptopalaemon gadjui* Bruce and Short, 1993), rather than the more usual compliment of long, simple setae. However, in both these cases, the appendix masculina is elongate and distinct from the appendix interna and endopod (Bruce 1993; Bruce and Short 1993). The third genus within the Kakaducarididae, *Calathaeon holthuisi* (Strenth, 1976) harbours a more traditional appendix masculina, and although this species has a filtratory apparatus similar to *Kakaducaris* and *Leptopalaemon*, doubt has been expressed whether it should be included in the Kakaducarididae, based on its branchial formula (Bruce and Short 1993) and biogeography (De Grave et al. in press).

It is interesting to note that all species of Desmocarididae and Kakaducarididae, as well as the majority of Palaemoninae are freshwater animals (De Grave et al. in press), in common with Euryrhyndidae, whilst all species in the other families/subfamily are marine animals (with the exception of the freshwater troglobitic Typhlocarididae). A unique character of the Euryrhyndidae (diarsis with well several developed cuspidate setae) is shared with two subfamilies within the Atyidae (Caridellinae, Atyinae), and although it is not suggested that the Euryrhyndidae are related to the Atyidae, a fresh appraisal of palaemonoid relationships (and indeed caridean family level relationships in general) appears long overdue. It should be noted that some species of Pontoniinae, for instance *Periclimenaeus truncatus* (Rathbun, 1906) and *Paraclimenaeus fimbriatus* (Borradaile, 1915) also harbour more than one cuspidate seta on the external margin of the diarsis, but this does not appear to be as developed as is the case in Euryrhyndidae and Atyidae, where the row of setae is also medially developed. Although the presently included families are seemingly united by several synapomorphies, the diverse nature of many other characters (e.g. longitudinal suture on the carapace in Typhlocarididae, mouthparts modified into filtratory basket in Kakaducarididae, operculate third maxilliped in Hymenoceridae, molar process flared in Anchistoididae to name but a few) may suggest a lower taxonomic affinity

than presently assumed. Of course, the extra-ordinarily variation of character states within the Pontoniinae (see Chace and Bruce 1993; Bruce 1995) makes such an assessment an arduous task.

The Euryrhyndidae are clearly an ancient lineage, with their present day distribution pattern suggesting a Gondwanaland origin. In view of their morphologically conservative bauplan, their evolutionary pathway is difficult to ascertain. However, based on the structure of the second pleopods and accepting the interpretation of Powell (1976), the following hypothesis is put forward. It is postulated that *Euryrhyndina edingtonae* is close to the ancestral stock, as the species still has an appendix interna on the female second pleopod, and with the appendix masculina being of the usual caridean form. If indeed the second male endopod represents a modified appendix masculina, then the next evolutionary stage would be represented by *E. tomasi* sp. nov., as the posterior pleopods still have well developed endopods. *E. wrzesniowskii*, and presumably the closely related *E. burchelli* and *E. pemoni*, present a further development with a reduction in the endopod of the posterior pleopods. The unique development of the male second pleopod in *Euryrhyndoides holthuisi* can be relatively easily derived from the structure seen in *E. amazoniensis*, thus providing an evolutionary link between both genera, with the latter representing a more advanced stage within the genus *Euryrhyndus*. If this theory is indeed correct, then all three genera (or their ancestral stock) would have been present before the break-up of Gondwana and the emergence of the Atlantic Ocean (130–110 million years ago), making them of one oldest freshwater shrimp lineages, as the origin of the freshwater Atyidae is assumed to be in the Cretaceous, whilst the earliest date for the genus *Macrobrachium* (Palaemoninae) is set at the late Oligocene–early Miocene (see De Grave et al. in press)

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