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RICHALPHEUS PALMERI, N. GEN., N. SP., AN INFAUNAL ALPHEID SHRIMP FROM THE PHILIPPINES, WITH REDESCRIPTION OF *AMPHIBETAEUS JOUSSEAUMEI* (COUTIÈRE, 1896) (DECAPODA: CARIDEA)

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A B S T R A C T

A new alpheid shrimp genus, *Richalpheus*, new genus, is established for *R. palmeri*, new species, from Panglao, Philippines, and based on a single specimen collected from a presumed thalassinidean burrow in a shallow lagoon. *Richalpheus* appears to be most closely related to *Amphibetaeus* Coutière and *Leptalpheus* Williams (sensu lato). *Richalpheus* and *Amphibetaeus* share the presence of a non-functional fossa-tooth system on the fingers of the major cheliped, but the new genus differs from *Amphibetaeus* by the absence of pereiopodal epipods and the presence of only four segments in the carpus of the second pereiopod. The syntypes of *Amphibetaeus jousseaumei*, a species not collected since the original description by Coutière, remain untraceable except for one major cheliped. *Amphibetaeus jousseaumei* is redescribed based on the original descriptions and illustrations of Coutière scattered in older French publications, and on the newly rediscovered, diagnostic major cheliped, which is designated as lectotype of *A. jousseaumei*.

Introduction

The shrimps of the family Alpheidae are commonly called "snapping shrimps" because of the snapping sound they produce with their voluminous major claw. However, members of only five genera, including the two largest, *Alpheus* Fabricius, 1798 and *Synalpheus* Bate, 1888, possess a complex socket-plunger system on the major claw, which is responsible for snapping. Species from the remaining 33 alpheid genera are unable to snap; in most the cheliped fingers are unarmed or armed with various types of teeth, and lack a socket-plunger system. However, simple and apparently non-functional fossa-tooth systems, more or less reminiscent of the socket-plunger of *Alpheus* and *Synalpheus*, evolved independently in four alpheid genera: *Vexillipar* Chace, 1988, *Bannereus* Bruce, 1988, *Nennalpheus* Banner and Banner, 1981, and *Amphibetaeus* Coutière, 1896.

During the international Panglao Marine Biodiversity Project in May-July 2004, Dr. Peter C. Dworschak (Naturhistorisches Museum in Wien, Vienna, Austria) extensively collected infaunal decapods, including alpheid shrimps, around the island of Panglao, situated southwest of Bohol, Philippines. Among them was a single female specimen collected from a presumed thalassinidean burrow in a shallow lagoon and initially labeled as "*Leptalpheus* sp." This specimen was examined and identified as a hitherto undescribed genus and species with affinities to *Amphibetaeus* and *Leptalpheus* Williams, 1965. (sensu lato). The three most diagnostic features of this new species were the absence of strap-like epipods (mastigobranchs); the four-segmented carpus of the second pereiopod; and the presence of a thick bulge on the dactylus fitting into a shallow fossa on the pollex, thus superficially resembling the tooth-fossa of *A. jousseaumei*, as it was illustrated and described by Coutière (1899). The new genus and species is described and illustrated below, and contrasted to *Amphibetaeus* and *Leptalpheus*.

Amphibetaeus is a monotypic genus, and includes *Amphibetaeus jousseaumei* (Coutière, 1896), described as *Betaeus jousseaumei* on the basis of three specimens from Djibouti and southern Yemen in the Gulf of Aden (Coutière, 1896a, 1896c). These three specimens (syntypes) were most likely deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Judging from Coutière's (1899) drawings and descriptions, at least one syntype must have been completely dissected, and therefore, was heavily damaged or even completely destroyed (Coutière also investigated internal anatomy). The whereabouts of the other two syntypes remain unknown. On the other hand, Coutière's detailed descriptions of the colour pattern and ecology of *A. jousseaumei* were based on his personal observations in Tadjourah, Djibouti (summarized in Coutière, 1899), but it remains unclear whether he preserved and deposited some of these specimens in the MNHN or elsewhere.

After an extensive search for specimens of *A. jousseaumei* in the collections of the MNHN and other world museums, one of us (AA) was able to locate only the major cheliped of one of the three syntypes in the MNHN. It was precisely the cheliped illustrated by Coutière in his famous monograph (Coutière, 1899, p. 181, fig. 218). Therefore, this major cheliped is designated as the lectotype of *A. jousseaumei* (MNHN-Na 13677). To our best knowledge, *A. jousseaumei* was not collected or reported since the original description by Coutière (1896a, 1896b, 1899).

Because of great interest of *Amphibetaeus* for the Alpheidae, underlined by Coutière (1899), and its affinities to the new genus from Panglao, we provide a redescription of *Amphibetaeus* and its type species, *A. jousseaumei*, based on Coutière's descriptions and illustrations previously

scattered in older French publications (Coutière, 1896a, 1896b, 1896c, 1897, 1898, 1899). We also provide detailed illustrations of the newly rediscovered major cheliped of *A. jousseaumei*.

Material and Methods

The material used in the present study is deposited in the collections of the Muséum National d'Histoire Naturelle, Paris, France (MNHN) and National Museum of the Philippines, Manila, Philippines (NMCR). All drawings were made with the help of a camera lucida. The carapace length (CL) and total length were measured in mm along the mediodorsal line from the tip of the rostrum to the posterior margin of the carapace or telson, respectively. Abbreviations used in the text: P - pereiopod; Mxp - maxilliped.

Systematics

Family Alpheidae Rafinesque, 1815

Richalpheus, new genus

Diagnosis.—Carapace glabrous, with anterolateral suture; branchiostegial margin with pronounced ventral lip and with rounded notch; cardiac notch well developed. Frontal margin without rostrum or orbital teeth. Pterygostomial angle rounded. Eyes concealed in dorsal and lateral view; anteromesial margin of eyestalk bluntly projecting. Antennular peduncle robust, first segment with ventromesial tooth; stylocerite appressed, distally blunt; second segment longer than wide; lateral antennular flagellum indistinctly biramous, shorter ramus mostly fused to main ramus. Antenna with basicerite moderately robust; carpocerite overreaching scaphocerite. Mouthparts fairly typical for family; mandible with two-segmented palp; first maxilliped with greatly elongated palp and expanded caridean lobe; second maxilliped with elongated epipod. Third maxilliped pediform; lateral plate elongated, distally acute; tip of ultimate segment unarmed. First pereiopods (chelipeds) enlarged, very unequal in size, asymmetrical in shape, carried flexed; major cheliped with basis and ischium unarmed; merus slender, unarmed, ventral surface depressed; carpus short, cup-shaped; chela moderately large, subcylindrical; palm depressed longitudinally on ventromesial side, linea impressa absent; adhesive discs present; fingers with shallow fossa on pollex and flat bulge on dactylus, without additional teeth. Second pereiopod with carpus four-segmented; chela simple, with dense rows of stiff setae. Third pereiopod with ischium and merus unarmed, carpus armed with distal spine on ventral margin; propodus armed with spines on ventral margin, dactylus simple, conical. Fifth pereiopod with propodus unarmed, distally bearing well-developed brush of setae. Sixth pleomere with inconspicuous suture, but without articulated plate, at posteroventral angle. Uropod with sympod unarmed; exopod distally truncated, diaeresis with deep incision and triangular tooth near mesial margin of exopod. Telson with two pairs of dorsal spines and two pairs of posterolateral spines; posterior margin rounded; anal tubercles present. Gill/exopod formula as following: 5 pleurobranchs (P1-5), 1 arthrobranch (Mxp3), 0 podobranch, 2 lobe-like epipods (Mxp1-2), 0 strap-like epipods = mastigobranchs, 0 sets of setobranchs, 3 exopods (Mxp1-3).

Type Species.—*Richalpheus palmeri*, new species (see below).

Etymology.—We are pleased to dedicate this interesting new alpheid genus and species to Dr. A. Richard Palmer (Department of Biological Sciences, University of Alberta, Edmonton, Canada) for his invaluable support of the taxonomic and phylogenetic research on the shrimp family Alpheidae.

Distribution.—Western Pacific Ocean, presently known only from the Philippines.

Phylogenetic Affinities.—*Richalpheus* appears to be most closely related to *Amphibetaeus* and *Leptalpheus* (sensu lato), and more distantly to *Fenneralpheus*. In all these genera, the frontal margin of the carapace is devoid of rostrum and orbital teeth; the stylocerite is more or less apressed to the first segment, laterally not convex; the chelipeds are very asymmetrical and carried folded when not in use; and the minor cheliped has a very characteristic shape, with slender merus and elongated fingers. Further, the third and fourth pereiopod are strikingly similar among these genera in that all articles are flattened; the ischium is unarmed; the merus is unarmed and has conspicuously inflated (convex) dorsal and ventral margins; the carpus is armed with distoventral spine; the propodus armed with spines; the dactylus is simple and conical (cf. Williams, 1965; Banner and Banner, 1974; Felder and Manning, 1986; Dworschak and Coelho, 1999; Anker et al., 2006). *Richalpheus* shares with *Leptalpheus* and *Fenneralpheus* several features on the uropodal exopod (presence of a deep incision and a triangular tooth on the diaeresis, posterior margin truncate and angular laterally) and third maxilliped (lateral plate elongated, distally acute; comparatively large arthrobranch); these features remain unknown in *Amphibetaeus* (see below).

Richalpheus may be distinguished from *Amphibetaeus*, *Leptalpheus* and *Fenneralpheus* by the presence of characteristic dense stiff setae on the chela of the second pereiopod; the absence of strap-like epipods (mastigobranchs) on the third maxilliped and pereiopods (present on P1-4 in *Amphibetaeus*, *Leptalpheus* and *Fenneralpheus*); and the ultimate segment of the third maxilliped without dense thickened, bluntly ending setae (vs. with such setae in *Leptalpheus*, *Fenneralpheus* and *Amphibetaeus*) (cf. Williams, 1965; Banner and Banner, 1974; Ríos and Carvacho, 1983; Felder and Manning, 1986; Dworschak and Coelho, 1999; Anker et al., 2006).

The new genus differs from *Amphibetaeus* by the four-segmented carpus of the second pereiopod (vs. five-segmented in *Amphibetaeus*); the unarmed propodus of the fifth pereiopod (vs. armed with spines in *Amphibetaeus*); and the more slender antennular peduncles, with second segment distinctly elongated, twice as long as wide (vs. stout, as long as wide in *Amphibetaeus*) and with shorter, more apressed stylocerite (cf. Coutière, 1896a, 1899 and Fig. 8).

As mentioned above, *Richalpheus* and *Amphibetaeus* share the presence of a tooth on the dactylus and a fossa on the pollex of the major cheliped. However, the tooth-fossa systems of *Richalpheus* and *Amphibetaeus* are different. In *Richalpheus*, the dactylar tooth is flat and more bulge- than tooth-like, and both fingers lack additional teeth (Fig. 4),

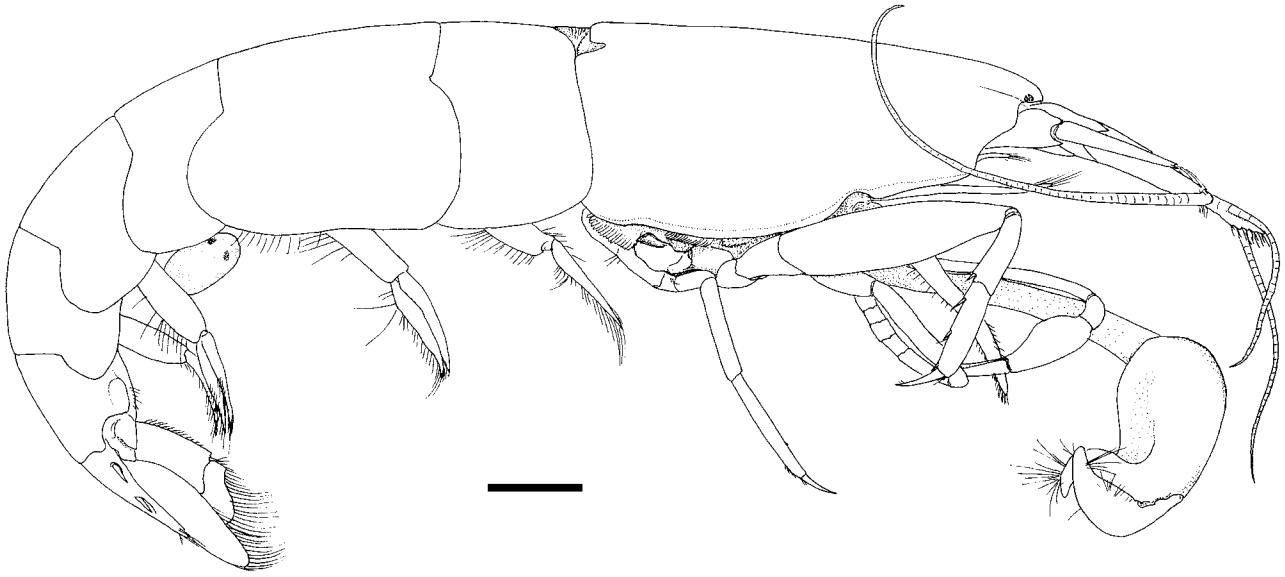

Fig. 1. *Richalpheus palmeri*, n. gen., n. sp., holotype, ovigerous female (NMCR 16202), habitus. Scale bar 1 mm.

whereas in *Amphibetaeus*, the dactylar tooth is more pronounced, and the dactylus and pollex bear one and two additional small teeth, respectively (Fig. 9). Further, in *Richalpheus*, the fingers are subequal in length and much shorter than the palm (Fig. 9), while in *Amphibetaeus*, the fingers are unequal in length (pollex reaching far beyond dactylus) and much longer than the palm (Fig. 9). The major chela is also comparatively much larger in *Amphibetaeus* than in *Richalpheus* (cf. Figs. 4, 9).

Richalpheus can be separated from *Leptalpheus* and *Fenneralpheus* by the presence of a fossa-bulge on the fingers of the major chela (vs. armed with variously shaped teeth in *Leptalpheus* and *Fenneralpheus*); the sixth abdominal somite with inconspicuous suture, but without distinct subtriangular articulated plate (vs. with subtriangular plate in *Leptalpheus* and *Fenneralpheus*); and the four-segmented carpus of the second pereiopod (vs. five-segmented in *Fenneralpheus* and most *Leptalpheus*, except for one undescribed species in press (cf. Williams, 1965; Banner and Banner, 1974; Ríos and Carvacho, 1983; Felder and Manning, 1986; Dworschak and Coelho, 1999; Anker et al., 2005).

Interestingly, three species of *Leptalpheus* (sensu lato), *L. axianassae* Dworschak and Coelho, 1999, *L. pacificus* Banner and Banner, 1974 and *L.* n. sp. aff. *pacificus* (Anker et al., in prep.), share with *Richalpheus* and *Amphibetaeus*, the presence of adhesive discs on the major chela (cf. Banner and Banner, 1974; Dworschak and Coelho, 1999). These two species also markedly differ from other species of *Leptalpheus* and may be transferred to other genera (D. L. Felder, personal communication). Furthermore, in *Richalpheus*, *Amphibetaeus*, *L. pacificus*, and *L.* sp. aff. *pacificus*, the major chela is transversely constricted near the propodo-dactylar articulation. These features may indicate that *L. axianassae* and the Indo-West Pacific members of *Leptalpheus* are perhaps more closely related to *Richalpheus* and *Amphibetaeus* than to other species of *Leptalpheus*.

Richalpheus palmeri, new species
Figs. 1-6

Material Examined.—Holotype: 1 ovig. female (CL 5.1, TL 17.6), NMCR 16202, Panglao Marine Biodiversity Project, Philippines, Panglao Island, Pontod Islet lagoon, Sta. R32, 9°33.1′N, 123°44.0′E, mud-sand with extensive seagrass, few coral heads, depth: 3-4 m, 10 June 2004, coll. P. C. Dworschak [PD81].

Description.—Body elongate, relatively slender (Fig. 1); carapace and abdomen slightly compressed laterally, glabrous. Carapace with suture proximal to base of antenna (Fig. 2b). Frontal margin broadly rounded, not greatly protruding, without rostrum and orbital teeth (Fig. 2a, c); orbital hoods feebly inflated. Pterygostomial angle rounded, not protruding (Fig. 2b). Branchiostegial margin with rounded incision above first pereiopods (Fig. 1), without setae. Eyes completely covered by carapace, not visible in dorsal and lateral view (anterior portion visible in antero-lateral view) (Fig. 2a-c), with feebly protruding antero-mesial process, cornea mostly lateral, relatively small; area laterally adjacent to eyestalk with short, blunt process. Ocellar beak not protruding. Epistomial sclerites unarmed.

Antennular peduncle relatively slender (Fig. 2a, b), flattened, second segment almost twice as long as wide, shorter than dorsally visible portion of first segment; stylocerite reduced, apressed, not reaching distal margin of first segment, distally blunt (Fig. 2a, c); dorsomesial carina of first segment with minute, slender spinules (Fig. 2c); ventromesial carina of first segment with strong subacute tooth (Fig. 2d); lateral flagellum indistinctly biramous, shorter ramus partly fused to main ramus, without segments, basal fused portion composed of three segments; distal portion of main ramus and shorter ramus bearing groups of aesthetascs (Fig. 2e). Antenna with stout basicerite, bearing strong, acute ventrolateral tooth (Fig. 2b); scaphocerite oval-shaped, anterior margin of blade not protruding beyond stout distolateral tooth, latter separated from blade by deep

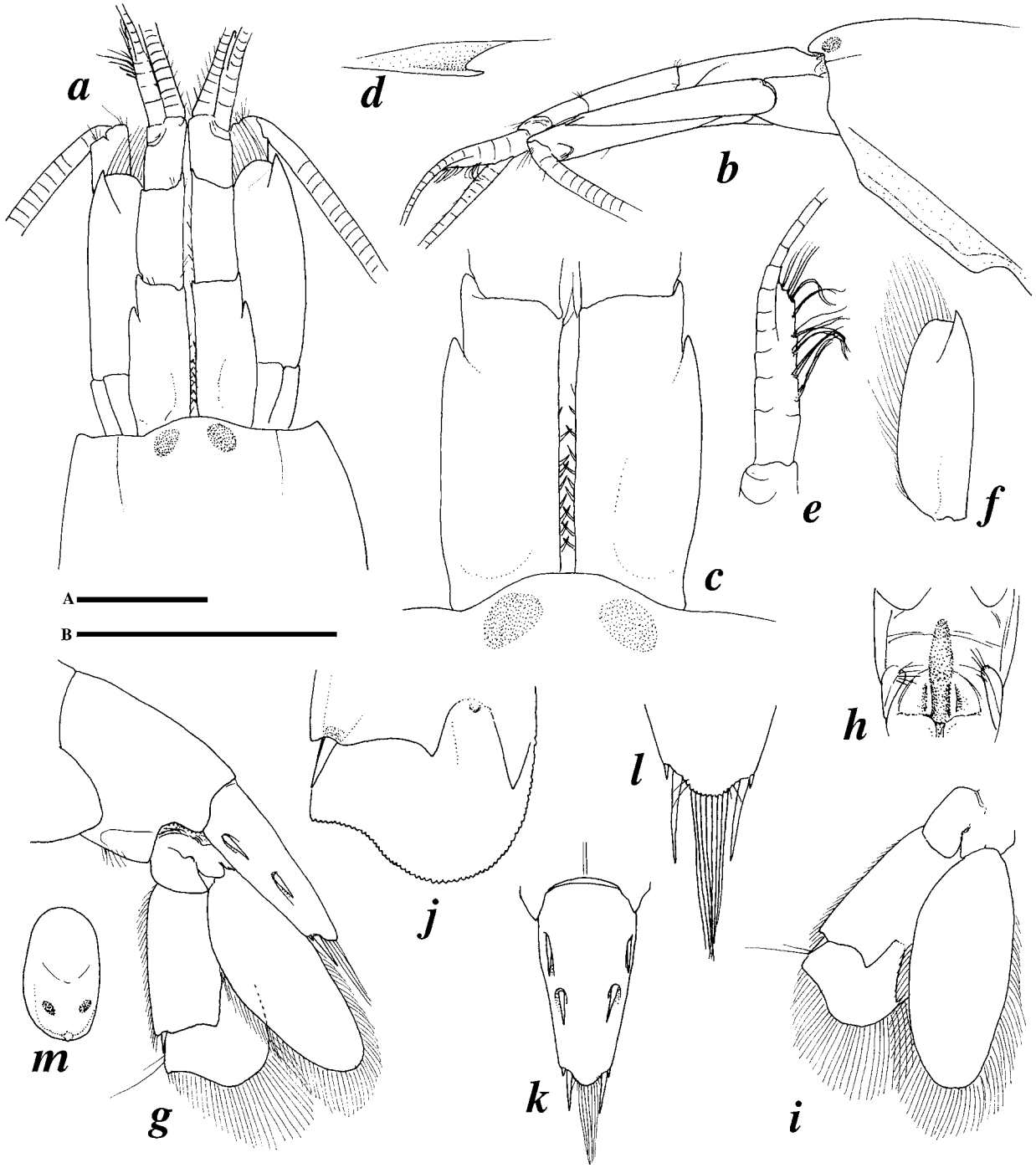

Fig. 2. *Richalpheus palmeri*, n. gen., n. sp., holotype, ovigerous female (NMCR 16202), a - frontal region, dorsal view; b - same, lateral view; c - frontal margin and base of antennules, dorsal view; d - antennule, first segment, tooth of ventromesial carina; e - same, lateral flagellum; f - antenna, scaphocerite; g - posterior pleomeres and tail fan, lateral view; h - sixth pleomere, sternal view; i - uropod; j - same, detail of exopod; k - telson; l - same, detail of posterior margin; m - egg. Scale bars 1 mm: A (a, b, f, g, h, i, k, m), B (c, d, e, j, l).

incision (Fig. 2a, f); carpocerite elongated, robust, overreaching distolateral tooth of scaphocerite (Fig. 2a, b); tubercle of antennal gland not protruding.

Mouthparts fairly typical for family. Mandible with two-segmented palp; molar process comparatively small; incisor process bearing nine teeth, three most lateral teeth slightly larger than remaining teeth (Fig. 3a). Maxillule with palp bilobed, each lobe furnished with one seta (Fig. 3b). Maxilla with dorsal endite deeply incised; scaphognathite relatively broad (Fig. 3c). First maxilliped with conspicuously elongated and broadened endopod (palp); caridean lobe on exopod greatly expanded; epipod ear-shaped, with indistinct lobes (Fig. 3d). Second maxilliped with elongated, sausage-shaped epipod; propodus without transverse suture (Fig. 3e).

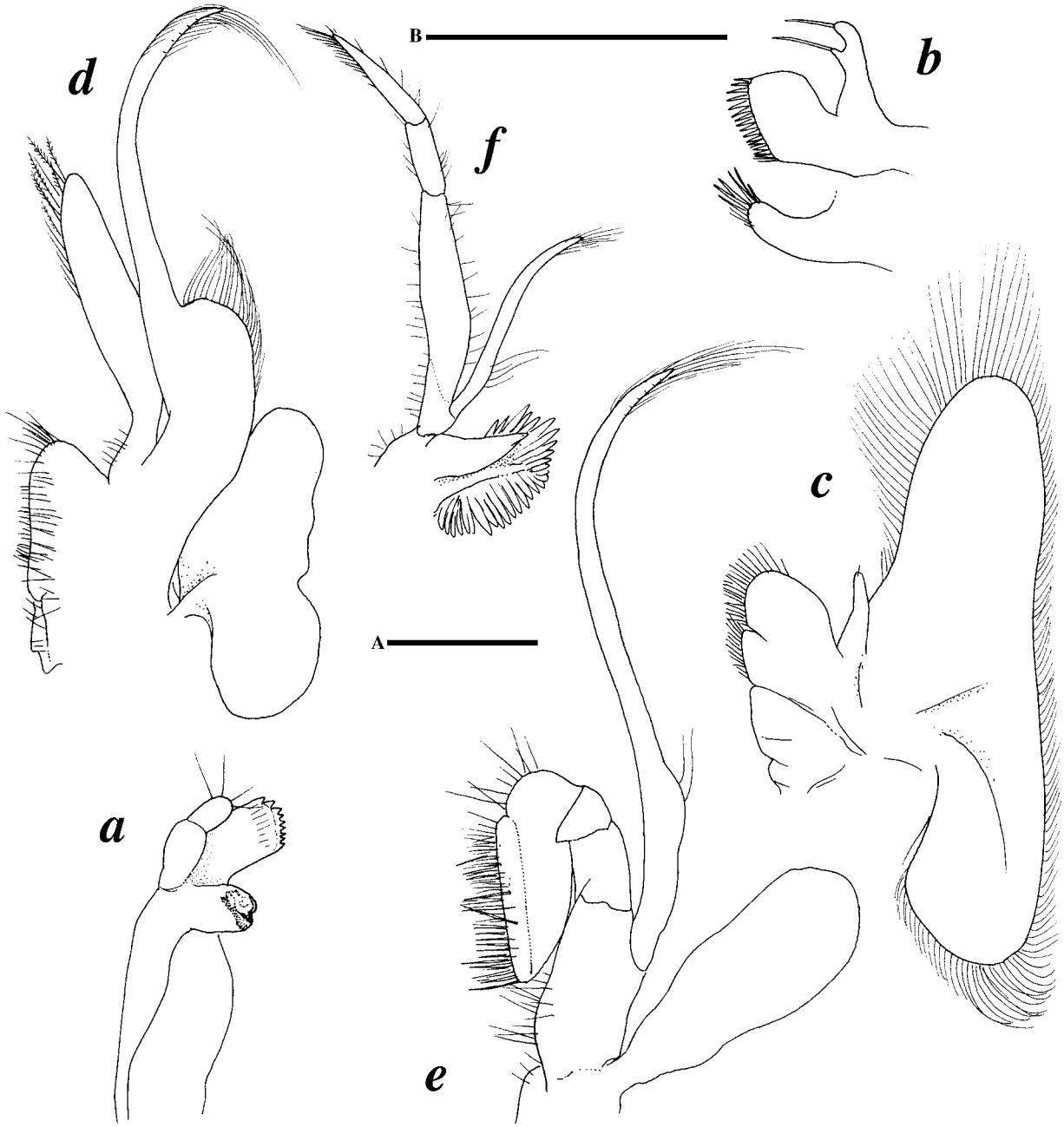

Fig. 3. *Richalpheus palmeri*, n. gen., n. sp., holotype, ovigerous female (NMCR 16202), a - mandible; b - maxillule; c - maxilla; d - first maxilliped; e - second maxilliped; f - third maxilliped (all in lateral view). Scale bars 1 mm: A (a-e), B (f).

Third maxilliped relatively slender; ultimate segment distally tapering, with rows of long setae, tip unarmed; penultimate segment more than twice as long as wide; antepenultimate segment with oblique basal suture near insertion of exopod; lateral plate large, produced into acute lobe; strap-like epipod absent (Fig. 3f); exopod with flexible setae on posterior margin, not overreaching distal margin of antepenultimate segment; arthrobranch well developed (Fig. 3f).

First pereiopods (chelipeds) very asymmetrical in shape and unequal in size (Fig. 1), carried flexed ventromesially (Fig. 1), probably ventrally in life. Major cheliped (on left side in the only available specimen) slender, elongated; ischium short, unarmed (Fig. 4a, b); merus elongated, slender, ventrally depressed, distally not widening, with smooth margins (Fig. 4a, b), carpus very short, cup-shaped (Fig. 4a, b, d); chela large, subcylindrical; palm depressed longitudinally on ventromesial side (Fig. 4a, c, e) and transversely constricted on dorsal margin near propodo-dactylar articulation (Fig. 4a, c, e, f); palmar surface smooth, linea impressa absent; adhesive discs large (Fig. 4a, g); fingers twisted mesially, about 0.6-0.7 times as long as palm, not gaping when closed (Fig. 4a); finger tips distally strongly curved and crossing, with tufts of setae (Fig. 4a, f);

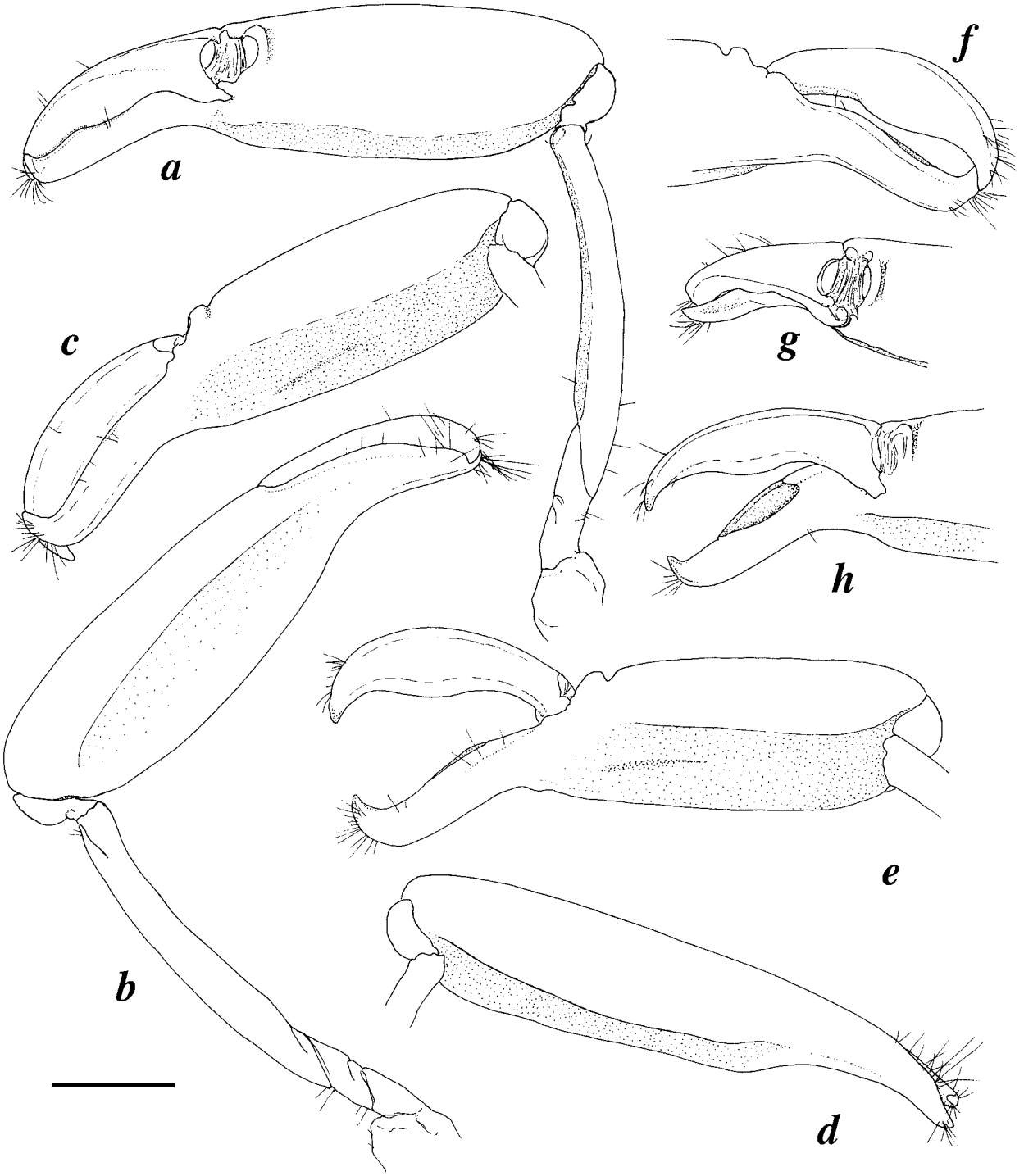

Fig. 4. *Richalpheus palmeri*, n. gen., n. sp., holotype, ovigerous female (NMCR 16202), major (left) cheliped: a - general aspect, ventrolateral view; b - same, dorsolateral view; c - chela, fingers closed, mesial view; d - same, dorsal view; e - same, fingers slightly opened, mesial view; f - chela fingers, lateral view; g - same, dorsal view; h - same, dorsomesial view. Scale bar 1 mm.

cutting edge of pollex with shallow fossa at about 2/3 pollex length (Fig. 4f, h), without additional teeth; cutting edge of dactylus with thickened bulge-like tooth at mid-length, fitting into fossa on pollex (Fig. 4e, f, h), without additional teeth.

Minor cheliped considerably smaller than major cheliped, slender, carried flexed (Fig. 1); ischium unarmed, merus ventrally depressed, dorsal margin with regularly spaced setae (Fig. 5a, b); carpus short, cup-shaped; chela flattened ventromesially (Fig. 5a, c); fingers about 1.8 times as long as palm; finger tips distally strongly curved, crossing, with a few tufts of setae (Fig. 5c); cutting edges of pollex and dactylus mostly straight, except for two small, irregular teeth at proximal 1/3 of finger length (Fig. 5d).

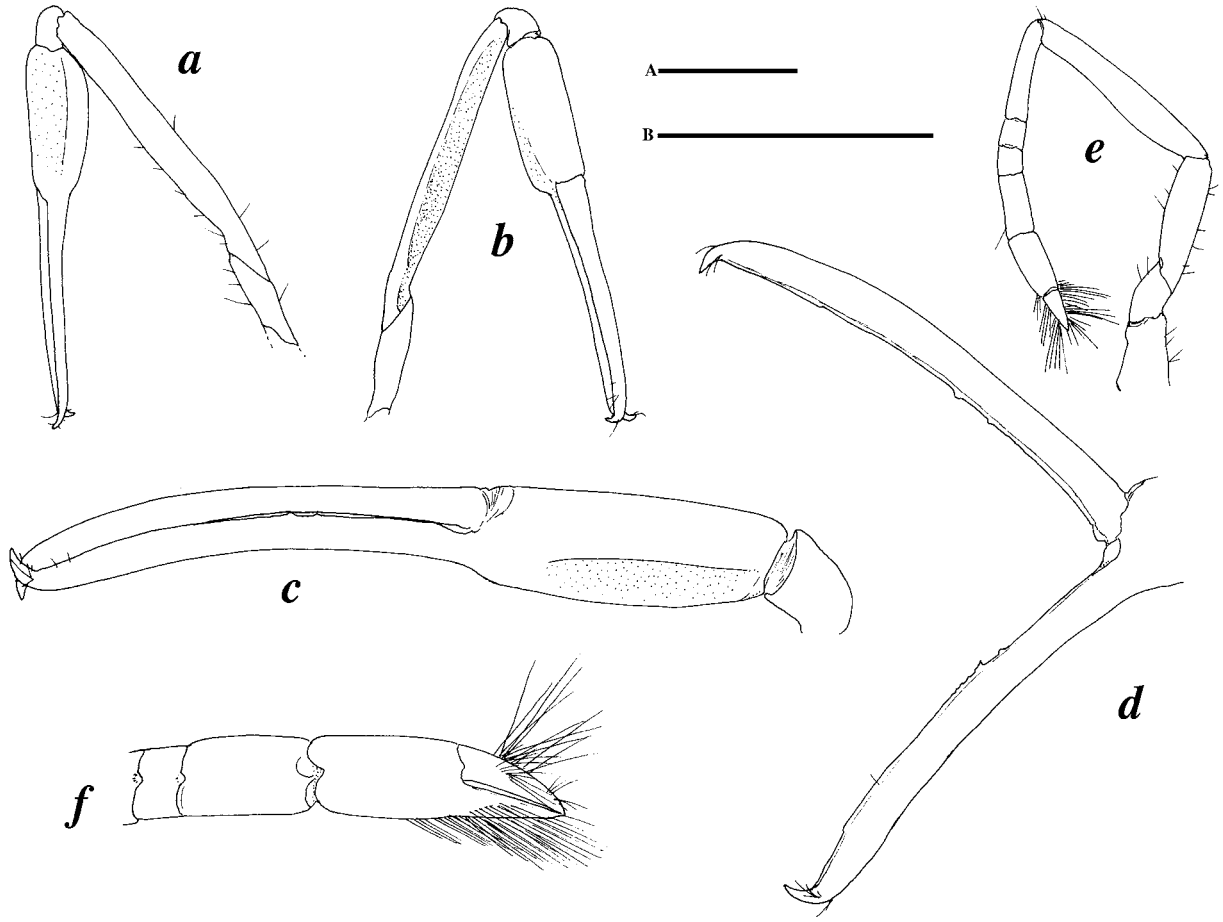

Fig. 5. *Richalpheus palmeri*, n. gen., n. sp., holotype, ovigerous female (NMCR 16202): a - minor cheliped, general aspect, ventrolateral view; b - same, lateral view; c - same, chela, mesial view, fingers closed; d - same, fingers opened; e - second pereiopod, lateral view; f - same, distal carpus and chela. Scale bars 1 mm: A (a, b, e), B (c, d, f).

Second pereiopod moderately slender; ischium about 0.7 times as long as merus; carpus four-segmented, segments with ratio approximately equal to 3/1/1/2 (Fig. 5e); chela with fingers stout, shorter than palm; distoventral portion of palm, pollex and dactylus with very dense rows or tufts of setae (Fig. 5f). Third and fourth pereiopods robust, flattened on mesial side; third pereiopod with ischium unarmed; merus about four times as long as ischium, broad, ventral and dorsal margins convex, unarmed (Fig. 6a); carpus with slender distoventral spine; propodus as long as carpus, with three slender spines on ventral margin, including distal spine near articulation with dactylus (Fig. 6a, b); dactylus simple, subconical, slightly less than 1/2 as long as propodus, feebly curved (Fig. 6a, b). Fourth pereiopod similar to third pereiopod, slightly more slender (Fig. 6c). Fifth pereiopod shorter and more slender than third and fourth pereiopods (Fig. 6d); ischium unarmed; merus 2.5 times as long as ischium, with margins feebly convex, unarmed; carpus slender, unarmed; propodus slender, about 1.5 times length of carpus, without spines on ventral margin, distally with four rows of setae (Fig. 6e); dactylus similar to that of third and fourth pereiopods, slightly more curved (Fig. 6e).

Pleomeres I-V with posteroventral angles rounded; segment II greatly expanded in female (Fig. 1); segment VI with rounded posterior lobe (Fig. 2g) and feeble mediodorsal keel (Fig. 2k); posteroventral angle with inconspicuous, almost complete suture, but without individualized articulated plate (Fig. 2g); preanal plate with median groove bordered by slight ridges, posteriorly rounded (Fig. 2h). First pleopod with small endopod fringed with setae distally (Fig. 6f). Female second pleopod with slender appendix masculina (Fig. 6g); male second pleopod unknown. Uropods distinctly exceeding telson (Fig. 2g); lateral lobe of sympod distally rounded (Fig. 2g, i); endopod slightly longer than exopod; exopod posteriorly truncate, lateral angle slightly protruding (Fig. 2i); diaeresis laterally sinuous, mesially deeply incised and with large triangular tooth near mesial margin of exopod (Fig. 2i, j); distolateral spine slender, not reaching distal margin of exopod. Telson moderately slender, less than twice as long as wide at base, distally tapering (Fig. 2k); dorsal surface with two pairs of strong, slender spines inserted in deep pits, first pair closer to lateral margin, at about proximal 1/3 length of telson, second pair at some more distantly from lateral margin, at about 1/2 length of telson (Fig. 2g, k); posterior margin rounded medially, with two pairs of posterolateral spines, lateral very short, slender; mesial elongated, slender, about five times as long as lateral (Fig. 2l); margin between mesial spines with eight slender setae; anal tubercles present, moderately developed. Gill/exopod formula as given for

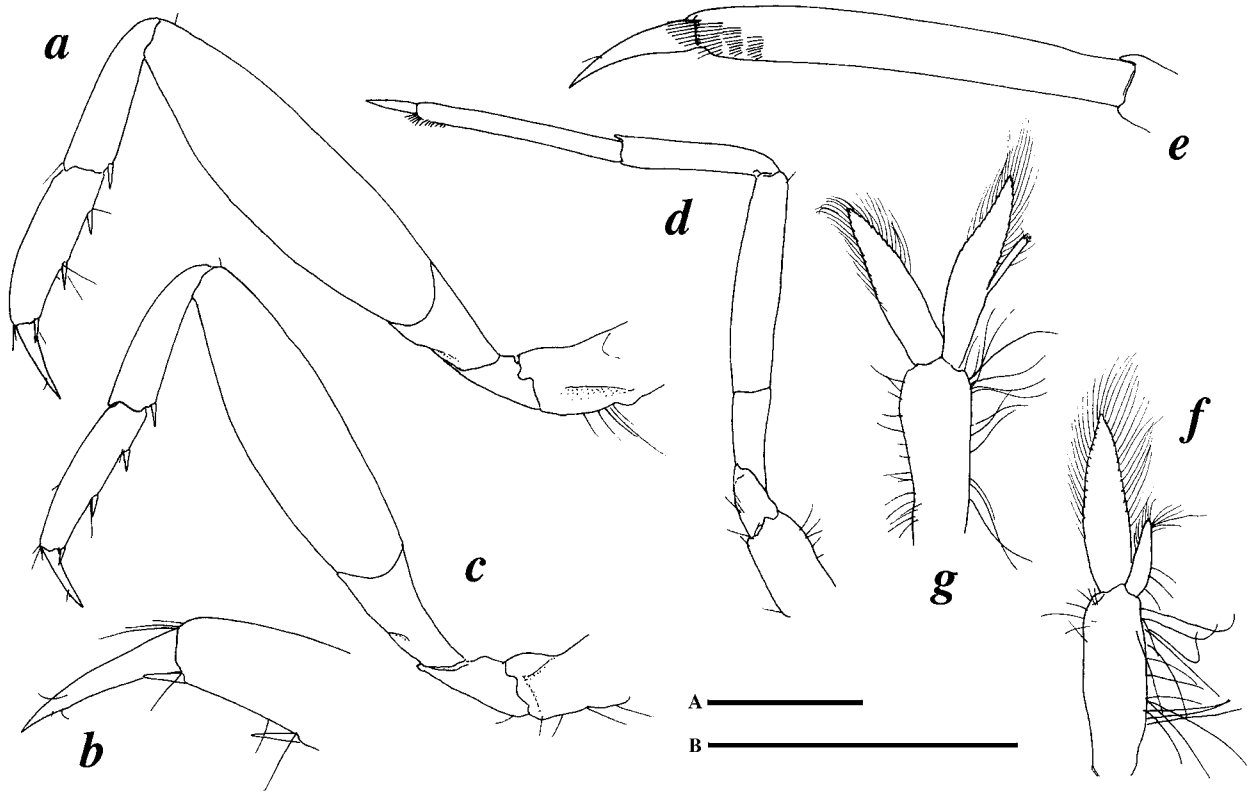

Fig. 6. *Richalpheus palmeri*, n. gen., n. sp., holotype, ovigerous female (NMCR 16202): a - third pereiopod, lateral view; b - same, distal propodus and dactylus; c - fourth pereiopod, lateral view; d - fifth pereiopod, lateral view; e - same, propodus and dactylus; f - first pleopod, mesial view; g - second pleopod, mesial view. Scale bars 1 mm: A (a, c, d, f, g), B (b, e).

genus. Eggs fairly large (most eggs shed, only two remaining, diameter approximately 0.9 × 0.5 mm), with distinct eyespots of developing embryos Fig. 2m).

Colour Pattern.—Unknown.

Size.—The CL and TL of the single specimen are 5.1 mm and 17.6 mm, respectively.

Etymology.—See under *Richalpheus*, new genus.

Habitat.—The single holotype was collected with the aid of a suction pump from a burrow of unknown (possibly thalassinidean) host, in a shallow lagoon, at a depth of about 3-4 m, on mud sand bottom with seagrass and some coral heads. The bottom was heavily disturbed by various burrowing organisms, with predominance of large mounds of the callianassid *Glypturus* sp. (P. C. Dworschak, personal communication). Other macrocrustaceans collected at this station were the callianassids, *Neocallichirus* sp., *Callianassa* cf. *acutirostrella* Sakai, 1988 and *Calliaxina* (*Paraglypturus*) sp., the burrowing alpheid shrimp, *Alpheus* sp., and small burrowing stomatopods (P. C. Dworschak, personal communication). Although the host of *R. palmeri*, new species remains unknown, the most likely candidates are the thalassinideans, and in particular *Glypturus* sp.

Distribution.—Presently known only from the type locality, Panglao, southwest off Bohol, Republic of the Philippines.

Genus *Amphibetaeus* Coutière, 1896

Amphibetaeus Coutière, 1896c: 384.

Redefinition.—Carapace glabrous. Branchiostegial margin without pronounced ventral lip; cardiac notch well developed. Frontal margin without rostrum or orbital teeth. Pterygostomial angle rounded. Eyes concealed in dorsal and lateral view; anteromesial margin of eyestalk bluntly projecting. Antennular peduncle robust, first segment with ventromesial tooth; stylocerite somewhat appressed, distally blunt; second segment as long as wide; lateral antennular flagellum indistinctly biramous, shorter ramus mostly fused to main ramus. Antenna with robust basicerite; carpocerite overreaching scaphocerite. Mouthparts fairly typical for family; mandible with two-segmented palp; first maxilliped with elongated palp and expanded caridean lobe. Third maxilliped pediform, tip of ultimate segment unarmed. First pereiopods (chelipeds) enlarged, very unequal in size, asymmetrical in shape, carried flexed; major cheliped with basis and ischium unarmed; merus slender, unarmed, ventral surface not depressed; carpus short, cup-shaped; chela very large, subcylindrical; palm depressed proximally on ventromesial side, linea impressa absent; adhesive discs present; fingers with non-snapping fossa-tooth system on cutting edges, with additional teeth. Second pereiopod with carpus five-segmented. Third pereiopod with ischium and merus unarmed, carpus with distal spine on ventral margin; propodus with spines on ventral margin, dactylus simple, conical. Fifth pereiopod with propodus armed with spines

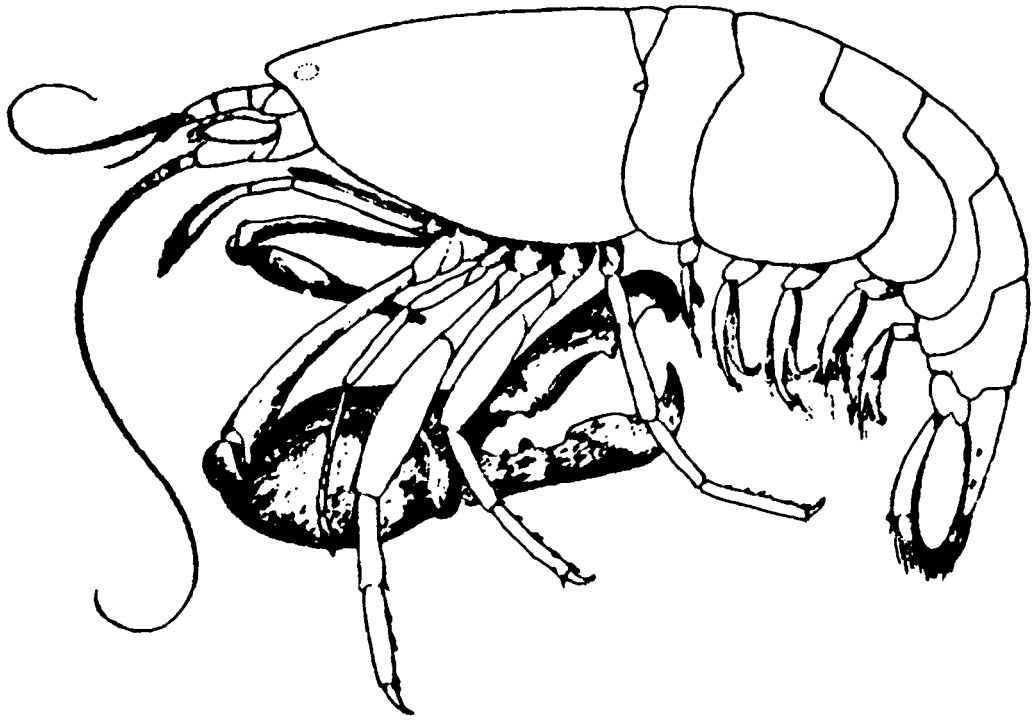

Fig. 7. *Amphibetaeus jousseaumei* (Coutière, 1896), syntype, habitus (from Coutière, 1896a).

and distally bearing well-developed brush of setae. Pleomere without articulated plate at posterolateral angle. Male second pleopod with appendix interna and appendix masculina. Uropod with sympod unarmed. Telson with two pairs of dorsal spines and two pairs of posterolateral spines; posterior margin rounded; anal tubercles present. Gill/exopod formula as following: 5 pleurobranchs (P1-5), 1 rudimentary pleurobranch (Mxp3), 1 arthrobranch (Mxp3), 0 podobranch, 2 lobe-like epipods (Mxp1-2), 5 strap-like epipods = mastigobranchs (Mxp3, P1-4), 5 sets of setobranchs (P1-5), 3 exopods (Mxp1-3).

Type Species.—*Amphibetaeus jousseaumei* (Coutière, 1896) [originally as *Betaeus jousseaumei* Coutière, 1896a: 236]; designated by monotypy (Holthuis, 1993).

Other Species Included.—None. The western Atlantic "*Amphibetaeus simus*" reported by Verrill (1922: 123) is not a species of *Amphibetaeus*, but most likely refers to *Alpheus simus* Guérin, 1857.

Distribution.—Northwestern Indian Ocean, presently known only from the western Gulf of Aden.

Phylogenetic Affinities.—*Amphibetaeus* is presumably closely related to *Leptalpheus* Williams, 1965 (sensu lato), *Fenneralpheus* Felder & Manning, 1986 and *Richalpheus*, new genus; this is supported by the general shape of the frontal margin and the chelipeds, in particular the minor cheliped. Unfortunately, two features that could confirm the closeness of *Amphibetaeus* to these three genera, viz., the elongated lateral plate of the third maxilliped, and the deep incision and tooth on the uropodal diaeresis, were not described or illustrated by Coutière (1896a, 1896b, 1899). Coutière (1896a, 1896b) only noted that the third maxilliped and the tail fan (including uropods) of *Amphibetaeus jousseaumei* are essentially similar to those of *Alpheus edwardsii* (Audouin, 1826).

Amphibetaeus jousseaumei (Coutière, 1896)
Figs. 7-9

Betaeus jousseaumei Coutière, 1896a: 313, figs. 1-12; Coutière, 1896b: 236.

Amphibetaeus jousseaumei Coutière, 1896c: 384; Coutière, 1897: 234; Coutière, 1898: 39; Coutière, 1899: 52, 53, 74 (figs. 24, 25), 114 (fig. 93), 124, 129 (fig. 113), 133 (figs. 118, 122), 146 (fig. 143), 156 (figs. 149, 150), 158 (figs. 159, 160), 166 (fig. 182), 181 (fig. 218), 184 (fig. 217), 259 (figs. 314, 323), 262 (fig. 330), 462, 486, 493-494, 545; Banner & Banner, 1981: 40; Holthuis, 1993: 195 (figs. from Coutière, 1899).

Material Examined.—1 major cheliped, lectotype, MNHN-Na 13677, specimen from Coutière's syntype series, either from Tadjourah, Djibouti or Perim, Yemen, Gulf of Aden.

Description.—[Based on description and illustrations in Coutière (1896a, 1896c, 1899) and major cheliped of syntype] Body moderately elongated and slender (Fig. 7); carapace and abdomen not particularly compressed laterally (Fig. 8q), glabrous. Frontal margin broadly rounded, protruding, without rostrum and orbital teeth (Fig. 8a, b); orbital hoods not inflated. Pterygostomial angle rounded, not protruding (Fig. 8b). Eyes completely covered by carapace, not visible in dorsal or lateral view (Fig. 8a, b), with broadly rounded, protruding anteromesial process, cornea mostly lateral, relatively small (Fig. 8d, f); lateral area adjacent to eyestalk with conspicuous elongated process (Fig. 8e, f). Ocellar beak not protruding.

Antennular peduncle relatively stout (Fig. 8d, e), somewhat flattened, second segment almost slightly shorter than

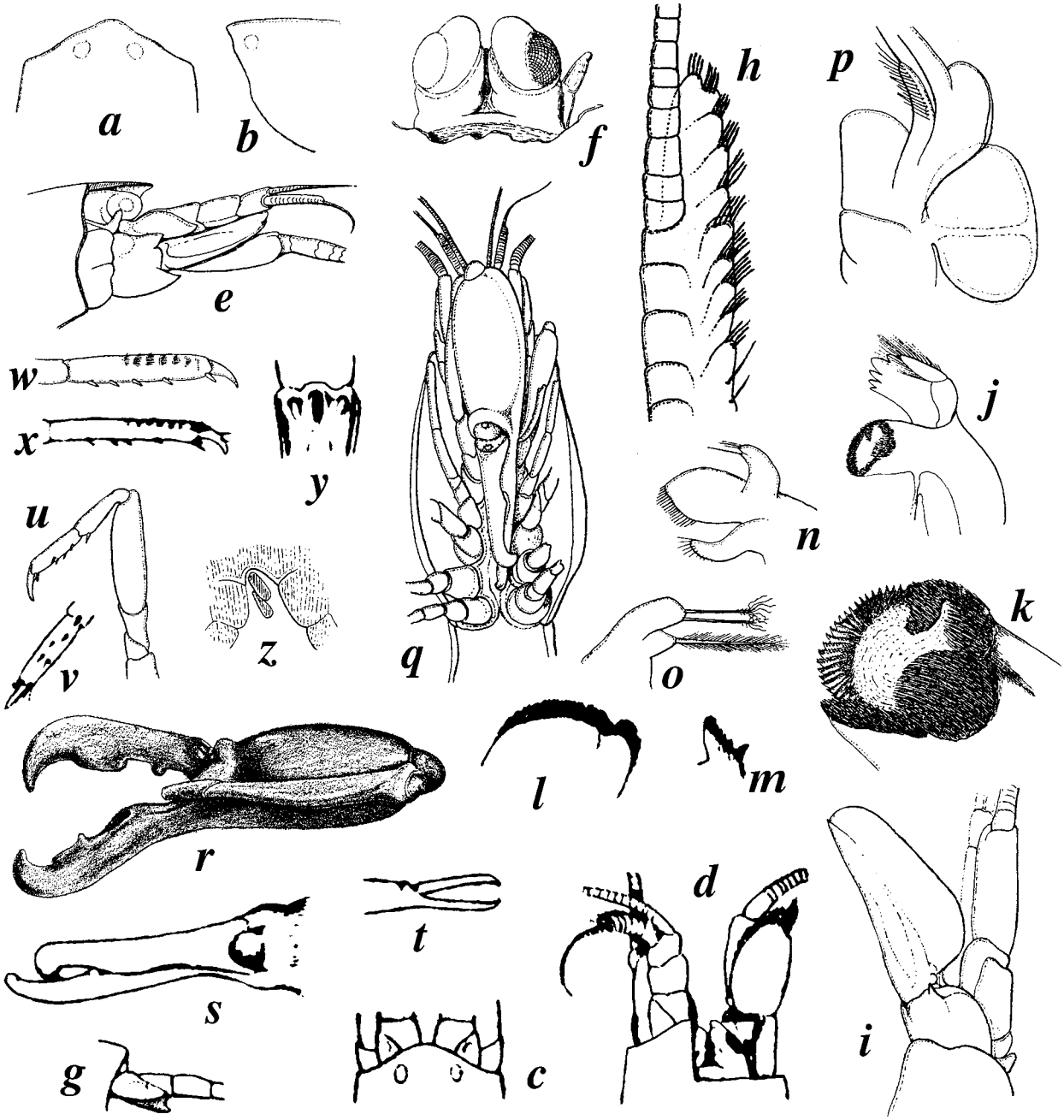

Fig. 8. *Amphibetaeus jousseaumei* (Coutière, 1896), syntypes, a - frontal margin of carapace, dorsal view; b - same, lateral view; c - frontal margin of carapace and base of antennules, dorsal view; d - frontal margin of carapace and frontal appendages, right portion of orbital hood and right antennule dissected; e - frontal region in lateral view, right portion of orbital hood dissected; f - eyestalks (carapace removed); g - antennule, lateral view showing tooth on ventromesial carina; h - antennular flagellum; i - antenna, ventral view; j - mandible; j - same, molar process, detail; k - same, detail; l, m - same, different aspects; n - maxillule; o - same, distal portion of palp; p - first maxilliped (distal exopod and endite setae omitted); q - cephalothorax and appendages, ventral view showing position of major and minor chelipeds; r - major cheliped, lateral view; s - same, distal portion of chela, dorsal view; t - minor chela, distal palm and fingers; u - third pereiopod; v - same, propodus and dactylus, ventral view; w - fifth pereiopod, propodus and dactylus; x - same, slightly different angle; y - ventroproximal portion of telson showing anal tubercles; z - transverse section through cephalothorax showing sternal depression and fingers of major cheliped (from Coutière, 1896a, 1899).

wide, equal to dorsally visible portion of first segment; stylocerite somewhat apressed, falling short of distal margin of first segment, distally subacute or blunt (Fig. 8c, e); ventromesial carina of first segment with strong subacute tooth (Fig. 8g); lateral flagellum indistinctly biramous, shorter ramus partly fused to main ramus, composed of several segments, fused portion (including short ramus) composed of eight to ten segments, distal six segments furnished with groups of aesthetascs (Fig. 8h). Antenna with large, stout basicerite, bearing strong, acute ventrolateral tooth (Fig. 8e); scaphocerite ovate, anterior margin of blade protruding beyond reduced distolateral tooth (Fig. 8d, i);

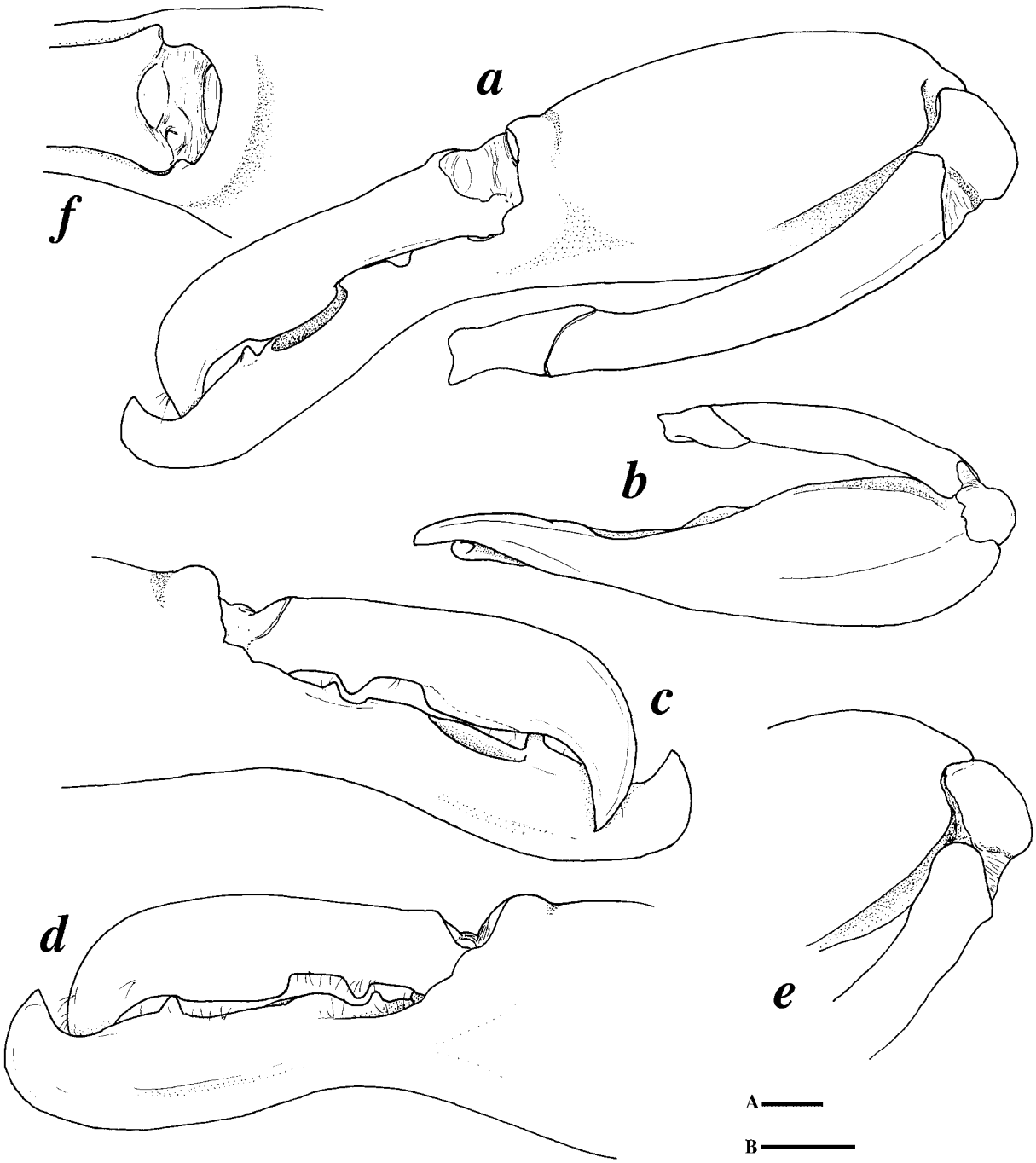

Fig. 9. *Amphibetaeus jousseaumei* (Coutière, 1896), major (left) cheliped of lectoype (MNHN-Na 13677), same cheliped as on fig. 1p: a - general aspect, dorsolateral view; b - same, ventral view; c - distal palm and fingers, mesial view; d - same, lateral view; e - distal merus and carpus, lateral (slightly oblique) view; f - distal palm and proximal fingers, dorsal view showing adhesive discs. Scale bars 1 mm: A (b), B (a, c, d, f).

carpocerite elongated, robust, reaching slightly past disto-lateral tooth of scaphocerite (Fig. 8d, e); tubercle of antennal gland protruding (Fig. 8i).

Mouthparts fairly typical for family. Mandible (Fig. 8j-m) with two-segmented palp; molar process comparatively large, with row of lamellar teeth (Fig. 8k); incisor process bearing five stout subtriangular teeth, second lateral tooth largest (Fig. 8j). Maxillule (Fig. 8n) with palp bilobed, dorsal lobe furnished with two distally plumose setae, ventral lobe with one stiff plumose seta (Fig. 8o). First maxilliped with somewhat elongated endopod (palp) fringed with row of long setae (Fig. 8p); caridean lobe on exopod expanded; epipod oval, with two similarly shaped lobes (Fig. 8p). Third maxilliped slender; ultimate segment distally tapering, with rows of long thick setae; penultimate segment more about twice as long as wide (Fig. 7); shape of lateral plate unknown; arthrobranch present.

First pereiopods (chelipeds) very asymmetrical in shape and unequal in size, carried flexed ventrally (Figs. 7, 8q), major chela fitting into sternal depression (Fig. 8z). Major

cheliped (either on left or right side, cf. Figs 7, 8q) slender, elongated; ischium relatively short, unarmed (Figs. 8r, 9a, b); merus elongated, slender, subcylindrical, ventrally not depressed, distally slightly widening, with smooth margins (Figs. 8r, 9a), carpus very short, cup-shaped (Figs. 8r, 9a, b, e); chela large, subcylindrical; palm depressed proximally on ventromesial side (Fig. 9a, e) and transversely constricted on dorsal margin near propodo-dactylar articulation (Figs. 8r, 9a, c); palmar surface smooth, linea impressa absent; adhesive discs large (Figs. 8s, 9c, d, f); fingers slightly twisted mesially, almost as long as palm, slightly gaping when closed; finger tips distally strongly curved and crossing; fingers unequal: tip of pollex reaching far beyond tip of dactylus (Figs. 8r, 9a, c, d); cutting edge of pollex with small subproximal tooth followed by relatively deep hiatus, large shallow fossa at about mid-length of pollex, and small rounded tooth distal to this fossa (Figs. 8r, 9a, c, d); cutting edge of dactylus with subproximal tooth fitting into hiatus of pollex and large, flattened tooth distal to mid-length, fitting into fossa on pollex (Figs. 8r, 9a, c, d); fingers furnished with small tufts of setae.

Minor cheliped considerably smaller than major cheliped, slender, carried flexed (Fig. 7z); ischium unarmed, merus ventrally depressed; carpus short, cup-shaped; chela with slight transverse constriction on dorsal margin near propodo-dactylar articulation (Fig. 7r); fingers longer than palm; finger tips distally curved; cutting edges of pollex and dactylus mostly straight, except for small irregular teeth (Fig. 7r).

Second pereiopod moderately slender; ischium about 0.7 times as long as merus; carpus five-segmented, segments with ratio approximately equal to 6/1/1/1/2 (Fig. 7), i.e., $1 = (2 + 3 + 4 + 5) + 4$, $2 = 3 = 4$, $5 = 3 + 4$; chela small, equal to length of three distal carpal segements. Third and fourth pereiopods robust, flattened on mesial side; third pereiopod (Fig. 8u) with ischium relatively long, unarmed; merus about 2.5-3 times as long as ischium, broad, ventral and dorsal margins convex, unarmed (Fig. 8u); carpus with distoventral spine (Fig. 8u, v); propodus slightly longer than carpus, with six spines on ventral margin, including pair of distal spines near articulation with dactylus (Fig. 8u, v); dactylus simple, subconical, slightly more than 1/2 as long as propodus, feebly curved (Fig. 8u). Fourth pereiopod similar to third, more slender (Fig. 7). Fifth pereiopod shorter and more slender than third and fourth pereiopods (Fig. 7); ischium unarmed; merus about twice as long as ischium, with margins not convex, unarmed; carpus more slender, unarmed; propodus about 1.5 times length of carpus, with five spines on ventral margin, including distal spine near articulation with dactylus, distally with seven-eight rows of setae (Fig. 8w, x); dactylus similar to that of third and fourth pereiopods, shorter, less than 1/3 length of propodus (Fig. 8w).

Pleomeres I-V with posteroventral angles rounded; segment II relatively expanded (Fig. 7); segment VI with rounded posterior lobe; posteroventral angle without articulated plate (Fig. 7); preanal plate posteriorly rounded. Male second pleopod with appendix interna and appendix masculina. Uropods distinctly longer than telson (Fig. 7); lateral lobe of sympod distally rounded; endopod slightly longer than exopod; distolateral spine slender, not reaching distal margin of exopod; shape of diaeresis unknown. Telson moderately slender, distally tapering; dorsal surface with two pairs of spines, first pair at about 1/2 length of telson, second pair between 1/2 and 1/4 length of telson (Fig. 7); posterior margin broadly rounded medially, with two pairs of posterolateral spines, lateral shorter than mesial; anal tubercles present (Fig. 8y). Gill/exopod formula as given for genus. Ovigerous females with numerous comparatively small-sized (diameter 0.8 mm) eggs.

Colour.—Whitish, with slight pinkish tinge on distal portion of the major chela; eyes visible as small black spots (Coutière, 1899, original statement: ''incolore, à peine lavée de rose à l'extrémité de la grande pince, les yeux sont visibles comme deux faibles points noirs''); uniform intensive orange in formalin (Coutière, 1896a).

Size.—The largest original syntype measured 11.0 mm CL, and 36.3 mm TL (Coutière, 1896a).

Habitat.—Mixed sand-mud flats close to coral reefs, compact sand and mud with rocks and coral debris, in horizontal galleries under boulders, probably associated with the callianassid ghost shimp *Neocallichirus mucronatus* (Strahl, 1862), sipunculans and echiurans (Coutière, 1899, original statement: ''vit également dans la des galeries horizontales, plus spacieuses, en compagnie des mêmes Thalassiniens [*Callianassa mucronauta*] et de Géphyriens, Phascolosomes et Échiures''); another alpheid frequently found in this habitat was *Automate dolichognatha* De Man, 1888 (Coutière, 1899).

Biology.—According to observations of Coutière (1899), the shrimps usually hold their very massive major cheliped folded beneath the body, with the major chela fitting in a special depression on the sternum (see Fig. 8q, z). To extend the major cheliped the shrimp twists it slowly, first sidewards, then horizontally making approximately 180°, thus placing the major chela in front of the body. The shrimps appear to be quite aggressive, attacking everything placed in front of them (Coutière, 1899). However, despite the presence of a plunger-fossa-like system on the major chela (consisting of a truncate tooth on the dactylus, a shallow fossa on the pollex, and adhesive discs on the distal palm and base of the dactylus, Fig. 9a, f), *A. jousseaumei* is apparently unable to snap and produce audible sounds (Coutière, 1899). The small size and the great number of eggs, as well as the fact that the first zoea resembles that of a typical *Alpheus* sp. suggest that the larval development of *A. jousseaumei* is extended (Coutière, 1899).

Distribution.—Presently known only from Tadjourah, the Republic of Djibouti, and Perim, off southwestern coast of the Republic of Yemen, two localities in the area of Bab al Mandab Strait, between the Red Sea and the Gulf of Aden. The species has not been reported since the original description by Coutière (1896a, 1896b, 1899).

Remarks.—Coutière (1896a, 1896b) noted that the major cheliped of the three original syntype specimens was on the left side (see Fig. 7), but in the specimen illustrated in his

monograph (Coutière, 1899) the major cheliped was on the right side (Fig. 8q). Therefore, the major cheliped in *Amphibetaeus* may be on either side, i.e., the chelipeds are antisymmetrical (Palmer, 1996).

Coutière (1899) obviously made a clear distinction between pleurobranchs and arthrobranchs. He noted that a rudimentary pleurobranch, composed of only a few leaflets, is inserted well above the arthrobranch of the third maxilliped. Therefore, the actual number of pleurobranchs in *Amphibetaeus* is six. Interestingly, a rudimentary pleurobranch above the third maxilliped is also present in a number of species of *Alpheus* (Coutière, 1899).

The mandibular palp was described and illustrated as three-segmented in the original description (Coutière, 1896a: fig. 5). However, in his monograph, Coutière (1899) illustrated a two-segmented palp (cf. Fig. 8j) for *A. jousseaumei*, and stated that generally in the Alpheidae the palp ("synaphipode") is composed of two segments. Therefore, we assume that the mandibular palp of *A. jousseaumei* is indeed two-segmented, like in most Alpheidae.

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