

Jengalpheops rufus gen. nov., sp. nov., a New Commensal Alpheid Shrimp from the Philippines (Crustacea: Decapoda)

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(Accepted July 4, 2006)

Arthur Anker and Peter C. Dworschak (2007) *Jengalpheops rufus* gen. nov., sp. nov., a new commensal alpheid shrimp from the Philippines (Crustacea: Decapoda). *Zoological Studies* **46**(3): 290-302. *Jengalpheops rufus* gen. nov., sp. nov., is described on the basis of several specimens collected on intertidal sand and mud flats of Panglao I., the Philippines. The uniformly reddish shrimps inhabit burrow mounds of the large callianassid mudshrimp, *Glypturus armatus* (A. Milne Edwards, 1870). *Jengalpheops* is defined mainly by the dorsally exposed eyestalks; the absence of orbital teeth; the short triangular rostrum; the unspecialized and feebly enlarged chelipeds, with comb-like rows of setae on the carpus and without snapping mechanism on the fingers; the 3rd maxilliped with styliform lateral plate; and the presence of strap-like epipods on the 1st to 4th pereiopods. The new genus appears to be relatively basal within the family, and is presumably most closely related to *Potamalpheops* Powell, 1979 and *Stenalpheops* Miya, 1997. http://zoolstud.sinica.edu.tw/Journals/46.3/290.pdf

Key words: Alpheidae, new genus, symbiosis, Callianassidae, Philippines.

Alpheid shrimps represent one of the most diverse decapod families. The numerous recently described genera and species (e.g., Anker and Iliffe 2000, De Grave and Anker 2000, Dworschak et al. 2000, Hayashi and Nagata 2000 2002, Anker 2001a 2003a b, Anker et al. 2001, Xuan 2001, Hayashi 2002, Wicksten and McClure 2003, Anker and Dworschak 2004, Anker and Komai 2004, Cai and Anker 2004, De Grave 2004a b, Anker and Felder 2005) show that this family is still far from being comprehensively known. This is particularly true for the so-called infaunal alpheids, i.e., those that live as associates ("commensals") in burrows of larger animals, such as stomatopods, mudshrimps, other alpheids, and echiurans (e.g., Williams 1965, Miya 1980, Felder and Manning 1986, Berggren 1991, Froglia and Atkinson 1998, Dworschak and Coelho 1999, De Grave and Anker 2000, Dworschak et al. 2000, Anker et al. 2001, Hayashi 2002).

During the Panglao Marine Biodiversity Project in May-July 2004, mollusks and crustaceans were extensively sampled around the island of Panglao, southwest of Bohol, the Philippines. During this survey, one of the authors (PCD) collected numerous small, reddish-coloured alpheid shrimps from burrow mounds of the large callianassid mudshrimp, *Glypturus armatus* (A. Milne-Edwards, 1870). A closer examination revealed that these shrimps belong to a hitherto undescribed species that could not be assigned to any of the previously described alpheid genera. Therefore, a new genus is established for the below-described new species.

MATERIALS AND METHODS

All specimens were collected on intertidal sand and mud flats with the aid of a bait suction

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pump ("yabby" pump) and preserved in 70% ethanol. One specimen was digitally photographed to illustrate the colour pattern. Drawings were made with the aid of a camera lucida. The carapace length (CL) and total length (TL) were measured with a micrometer along the mediodorsal line, from the tip of the rostrum to the posterior margin of the carapace and the telson, respectively. The holotype is deposited in the National Museum of the Philippines, Manila, the Philippines (NMCR). The paratypes are deposited in the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC), Museum national d'Histoire naturelle, Paris, France (MNHN), Naturhistorisches Museum in Wien, Vienna, Austria (NHMW), National Taiwan Ocean University Museum, Keelung, Taiwan (NTOUM), and Research Center for Biodiversity, Institute of Zoology, Academia Sinica, Taipei, Taiwan (ASIZ). Abbreviations used in the text: P, pereiopod; Mxp, maxilliped.

TAXONOMY

Family Alpheidae Rafinesque, 1815

Jengalpheops gen. nov.

Diagnosis: Carapace glabrous, with anterolateral suture; branchiostegial margin without notch or pronounced ventral lip; cardiac notch well developed. Frontal margin with broad, short, triangular rostrum; orbital teeth absent. Pterygostomial angle rounded. Eyes partly visible in dorsal view, exposed in lateral and frontal view. Antennular peduncle robust, 1st segment with ventromesial tooth; stylocerite not appressed, distally acute; 2nd segment longer than broad; lateral antennular flagellum with well-developed accessory branch. Antenna with robust basicerite; carpocerite not overreaching scaphocerite. Mouthparts typical for family; mandible with 2-segmented palp; 1st maxilliped with segmented palp and expanded caridean lobe; 2nd maxilliped with oval epipod. Third maxilliped pediform, lateral plate styliform; tip of ultimate segment armed with spines. First pereiopods (chelipeds) feebly enlarged, equal in size, symmetrical in shape, carried extended or flexed, in latter case without specific folding system; basis, ischium, and merus unarmed; carpus cup-shaped or subcylindrical, with comb-like rows of setae mesially; chela simple; palm smooth, linea impressa and adhesive discs absent; fingers without snapping mechanism, finger tips trifid. Second pereiopod with 5-segmented carpus; chela with ventrally excavated dactylus. Third pereiopod with ischium and merus bearing spines on ventrolateral margin; propodus with small spine-like setae on ventral margin, dactylus simple. Sixth abdominal somite with articulated plate at posterolateral angle. Male 2nd pleopod with appendix interna and appendix masculina. Uropod with unarmed protopod; diaeresis without specific modifications. Telson with 2 pairs of dorsal and 2 pairs of posterolateral spines; posterior margin rounded; anal tubercles absent. Gill/exopod formula: 5 pleurobranchs (P1-5), 1 arthrobranch (Mxp3), 0 podobranch, 2 lobe-shaped epipods (Mxp1-2), 5 strap-like epipods = mastigobranchs (Mxp3, P1-4), 5 sets of setobranchs (P1-5), 3 exopods (Mxp1-3).

Type species: Jengalpheops rufus sp. nov., by monotypy and present designation.

Gender: Masculine.

Etymology: This new genus is dedicated to Dr. Ming-Shiou Jeng (Research Center for Biodiversity, Academia Sinica, Taipei, Taiwan), who has published several studies on the shrimp family Alpheidae, including some in co-authorship with the senior author (Jeng and Chang 1985 1988, Jeng 1994 1997, Anker et al. 2001, Anker and Jeng 2002). The 2nd part is derived from the abbreviated generic name *Alpheopsis*.

Relationships: See below under "Remarks".

Jengalpheops rufus sp. nov.

Material examined: Holotype: NMCR 19111, male (CL 5.3), Panglao Marine Biodiversity Project, Sta. M11: Philippines, Panglao I., Sungcolan Bay, 9°38.3'N, 123°49.6'E, tidal flat, fringe mangrove and seagrass, from *Glypturus* armatus mound, P. C. Dworschak coll., 6 June 2004 (PD50). Paratypes: ZRC 2005.0081, 5 females (1 ovig.) and 4 males (CL 3.9-5.6) (1 female CL 5.6 dissected), same collection data as for holotype; NHMW 16794, 1 ovig. female (CL 4.4), same collection data as for holotype; ASIZ-73513, 1 male (CL 5.0), 1 ovig. female (CL 4.6), same collection data as for holotype; ZRC 2005.0082, 5 males, 1 female (CL 3.6-4.9) (1 male CL 3.9: P3 dissected), Panglao Marine Biodiversity Project, sta. M11: Philippines, Panglao I., Sungcolan Bay, 9°38.3'N, 123°49.6'E, tidal flat, fringe mangrove and seagrass, from *Glypturus* armatus mound, P.C. Dworschak coll., 7 June 2004 (PD34); NHMW 16823, 1 male (CL 3.8), 2 females (CL 4.4, 4.6), same data as for paratype ZRC 2005.0082; NTOUM 00663, 1 male (CL 4.1), 1 ovig. female (CL 4.5), same collection data as for paratype ZRC 2005.0082; ZRC 2005.0083, 1 female (CL 4.9) (photographed), Panglao Marine Biodiversity Project, sta. M8[M5]: Philippines, Panglao I., Doljo Point, 9°35.4'N, 123°44.3'E, mixed intertidal platform, fringe mangrove, sea-grass, from *Glypturus armatus* mound, P. C. Dworschak coll., 2 June 2004 (PD17); MNHN-Na 15772, 3 males, 2 females (CL 3.9-4.9), same data as for paratype ZRC 2005.0083; ZRC 2005.0084, 1 male (CL 5.5) (dissected), Panglao Marine Biodiversity Project, sta. M9: Philippines,

Panglao I., inside lagoon near Doljo Point, 9° 35.1'N, 123°43.6'E, muddy sand flat with seagrass, fringe mangrove, from *Glypturus armatus* mound, P. C. Dworschak coll., 4 June 2004 (PD20).

Description: Body moderately elongated (Fig. 1A, B), not particularly compressed laterally, glabrous. Carapace with distinct longitudinal suture laterally, proximal to base of antenna (Fig. 2A, B). Rostrum broadly triangular, broader than long (Fig. 2A, C), tip bearing minute setae (Fig. 2C); rostral carina absent. Orbital teeth absent (Fig. 2A, B). Pterygostomial angle rounded (Fig. 2B). Branchiostegial margin sparsely furnished



Fig. 1. Jengalpheops rufus gen. nov., sp. nov. (A) Male holotype (NMCR 19111); (B) ovigerous female paratype (NHMW 16794). Scale bar, 1 mm.

with setae (Fig. 2E). Cardiac notch well developed (Fig. 2E). Eyes partly exposed in dorsal view, almost completely exposed in frontal and lateral views (Fig. 2C, D), each with small anteromesial tubercle (Fig. 2C, D); cornea well developed. Ocellar beak not conspicuous. Epistomial sclerite unarmed.

Antennular peduncle moderately stout (Fig. 2A, B), 2nd segment shorter than visible portion of 1st segment and distinctly longer than 3rd segment; stylocerite not reaching distal margin of 1st

segment, distally acute (Fig. 2A, F); ventromesial carina with small acute tooth (Fig. 2F); lateral flagellum biramous, accessory branch composed of 5-6 free segments with groups of aesthetascs (Fig. 2G); proximal fused portion composed of 6-7 segments (Fig. 2G). Antenna with basicerite stout, armed with strong ventrolateral tooth (Fig. 2B); scaphocerite broadly oval, anterior margin of blade convex, not extending beyond distolateral tooth (Fig. 2H); carpocerite robust, exceeding distal margin of scaphocerite (Fig. 2B, H).



Fig. 2. Jengalpheops rufus gen. nov., sp. nov., male paratype (ZRC 2005.0084). (A) Frontal region, dorsal view; (B) same, lateral view; (C) details of rostrum and eyes, dorsal view; (D) same, lateral view; (E) carapace; (F) antennule, 1st segment, lateral view; (G) same, flagella; (H), antenna, dorsal view. Scale bars, 1 mm.

Mouthparts typical for family. Mandible (Fig. 3A, B) with 2-segmented palp; molar process as illustrated (Fig. 3A); incisor process distally with 6 subtriangular teeth, 3rd ventral tooth largest (Fig. 3B). Maxillule (Fig. 3C, D) with bilobed palp, dor-

sal and ventral lobes each with 1 slender seta (Fig. 3C); ventral endite with strong elongated spines (Fig. 3D). Maxilla (Fig. 3E) with moderately broad scaphognathite; endopod small, unsegmented; dorsal endite slightly subdivided. First maxilliped



Fig. 3. Jengalpheops rufus gen. nov., sp. nov., male paratype (ZRC 2005.0084). (A) Mandible, mesial view; (B) same, incisor process and palp, dorsal view; (C) maxillule, lateral view; (D), same, mesial view; (E) maxilla, lateral view; (F) 1st maxilliped, lateral view; (G) 2nd maxilliped, lateral view; (H) 3rd maxilliped, lateral view; (I), same, ventrolateral view; (J) same, tip of ultimate segment; (K) same, lateral plate and mastigobranch. Scale bars, 1 mm.

(Fig. 3F) with expanded caridean lobe on exopod; endopod 2-segmented; epipod large, subdivided into 2 lobes. Second maxilliped (Fig. 3G) with large ovate epipod; propodus with inconspicuous transverse-oblique suture. Third maxilliped (Fig 3H-K) pediform, moderately slender; lateral plate styliform (Fig. 3I, K); antepenultimate segment somewhat flattened; penultimate segment about 2.5 times as long as wide; tip of ultimate segment tapered, with 1 apical and 2 subdistal spines (Fig. 3J); arthrobranch well developed (Fig. 3H, I).

First pereiopods (chelipeds) (Fig. 4) equal in size, symmetrical in shape, carried extended or flexed without specific folding mechanism, not particularly robust or enlarged; coxa, basis, and ischium unarmed; merus not particularly swollen, about 4 times as long as wide; carpus varying from slightly elongated and cylindrical (Fig. 4A) in young adults to short and cup-shaped (Fig. 4H) in larger adults of both sexes, with comb-like rows of setae mesially (Fig. 4B, C, I); chela not enlarged in younger individuals, somewhat enlarged in larger individuals (Figs. 4I, 7); palm smooth, linea impressa and adhesive discs absent; fingers variable from slightly longer than palm (Fig. 4D) to distinctly shorter than palm (Fig. 4I), not gaping when closed (Fig. 4C, D, I); cutting edges of fingers usually unarmed, especially in younger individuals, in larger adults with pronounced tooth on pollex (Fig. 4C, I) and 2 subtriangular teeth near tips of pollex and



Fig. 4. *Jengalpheops rufus* gen. nov., sp. nov. (A-F, J, K) Male paratype (ZRC 2005.0084); (G) female paratype (ZRC 2005.0081); (H) male holotype (NMCR 19111); (I) female paratype (ZRC 2005.0081). (A) Right cheliped, lateral view; (B) left cheliped, carpus, mesial view; (C) same, chela, mesial view; (D) right cheliped, distal pollex detached to expose tip of dactylus, lateral view; (E) same, distal portion of pollex; (F) left cheliped, coxa, and basis, lateral view; (G) right cheliped, lateral view; (H) same, carpus, lateral view; (I) left cheliped, chela, lateral view; (J) 2nd pereiopod, lateral view; (K) same, detail of distal segment of carpus and chela. Scale bars, 1 mm.

dactylus (Fig. 4D, E); snapping mechanism absent.

Second pereiopod slender (Fig. 4J); ischium slightly shorter than merus; carpus with 5 segments, segment length ratio approximately equal to 6: 4: 5: 4.2: 4.5 (Fig. 4J); chela simple, fingers distinctly longer than palm, dactylus ventrally excavated (Fig. 4K). All pereiopods relatively slender. Third pereiopod (Fig. 5A-C) with ischium bearing 1 spine on ventrolateral margin; merus about 1.3 times longer than ischium, armed with 1 or 2 ventrolateral spines (Fig. 5A, C); carpus subequal in length to ischium, unarmed; propodus subequal in length to merus, armed with 2 small ventral spines and 1 slender distoventral spinule proximal to dactylus (Fig. 5A, B); dactylus (Fig. 5B) simple, slender, slightly curved, about 0.4 times length of propodus. Fourth pereiopod (Fig. 5D) similar to 3rd, merus with 1 spine. Fifth pereiopod (Fig. 5E, F) slightly longer than 3rd and 4th pereiopods; ischium unarmed; merus twice as long as ischium, armed with 1 ventrolateral spine (Fig. 5E); propodus about 1.2 times length of merus, distal portion with at least 10 rows of setae (Fig. 5F); dactylus slender, curved, slightly more than 0.3 times length of propodus.

Pleura of 1st to 5th abdominal somites with rounded to slightly angular posterolateral angles



Fig. 5. Jengalpheops rufus gen. nov., sp. nov. (A, B, D-I) Male paratype (ZRC 2005.0084); (C) male paratype (ZRC 2005.0082); (J) female paratype (ZRC 2005.0081). (A) Right 3rd pereiopod, lateral view (mastigobranch and setobranch accidentally detached); (B) same, dactylus; (C) left 3rd pereiopod, lateral view; (D) left 4th pereiopod, lateral view; (E) right 5th pereiopod, lateral view; (F) same, distal propodus and dactylus, mesial view; (G) male 1st pleopod, mesial view; (H) male 2nd pleopod, lateral view; (I) same, detail of appendix masculina and appendix interna; (J) female pleopod, lateral view. Scale bars, 1 mm.

(Fig. 1); 6th somite with well-developed articulated plate at posteroventral angle (Fig. 6G); posterior projection subrectangular, not acute (Fig. 6G); preanal plate posteriorly rounded. Endopod of male 1st pleopod less than 1/2 length of exopod (Fig. 5G). Male 2nd pleopod (Fig. 5H) with slender appendix masculina, more than twice as long as appendix interna, with slender setae on apex and along lateral margin (Fig. 5I). Female 2nd pleopod with short appendix interna; protopod and basal endopod with long setae in ovigerous females (Fig. 5J). Uropods distinctly exceeding telson (Fig. 6G); lateral lobe of protopod (= sympodite) distally rounded, without distinct tooth (Fig. 6A); endopod and exopod subequal in length; exopod with mostly straight diaeresis, slightly curved between mesial margin and feebly marked blunt lateral

tooth (Fig. 6A, B); distolateral spine slender, short (Fig. 6B). Telson (Fig. 6C) relatively slender, slightly tapering distally, about 1.5-2 times longer than wide proximally; proximal width about 1.5 times width of posterior margin; dorsal surface usually with 2 pairs of spines situated at some distance from lateral margin, 1 pair just anterior to mid-length and another pair at distal 1/3 of telson length (Fig. 6C), occasionally without spines (Fig. 6F); posterior margin rounded medially; each posterolateral angle usually with 1 pair of spines, lateral spines slightly shorter than mesial spines (Fig. 6D); sometimes more than 2 spines present at 1 or both posterolateral angles (Fig. 6E, F); median portion of posterior margin between mesial posterolateral spines with 8-12 plumose setae; anal tubercles absent. Gill/exopod formula as given for



Fig. 6. Jengalpheops rufus gen. nov., sp. nov. (A, B, G) Male paratype (ZRC 2005.0084) (C, D) female paratype (ZRC 2005.0084); (E) another female paratype (ZRC 2005.0084); (F) ovigerous female paratype (NHMW 16794). (A) Right uropod; (B) same, detail of lateral spine and diaeresis; (C) telson; (D), same, detail of posterior margin; (E) telson of another specimen, detail of posterior margin; (F) telson without dorsal spines; (G) posterior abdominal somites, uropods and telson, lateral view. Scale bars, 1 mm.

genus.

Color: Semitransparent, reddish; red colour more intense on antennular peduncles, basicerite and scaphocerite of antennae, tail fan, dorsal and anterolateral portions of carapace, and posterior portions of abdominal somites (forming diffuse transverse bands); chelipeds, walking legs, and antennular and antennal flagella semitransparent with pinkish tinge (Fig. 7); yellow-orange ovary visible through semitransparent carapace in females (Fig. 7).

Size: Small-sized shrimp; the largest specimen, a female, is 5.6 mm in CL and 15.3 mm in TL; the smallest specimen, a male, is 3.6 mm in CL and 11.1 mm in TL.

Etymology: The new species' name (*rufus* = red in Latin) refers to the characteristic reddish colour pattern (Fig. 7).

Ecology: All specimens of Jengalpheops rufus sp. nov., were collected with a "yabby" pump from mounds of the thalassinidean shrimp, Glypturus armatus (A. Milne-Edwards, 1870). These largesized (up to 140 mm in TL) mudshrimps live in spacious burrows. At the sediment surface, the burrows are characterized by a large mound with a nearby funnel. In Panglao, these mounds and funnels occur in high densities in the intertidal zone fringed by mangroves (Fig. 8A), and in lower densities within seagrass beds. In the intertidal, the mounds are flattened during low tide, are 5-15 cm high, and have a diameter of about 30 cm at their base. The funnel is always concealed by seagrass, consisting of a crater 5-10 cm in diameter and 5-10 cm deep. A sharp-edged hole, 2-3 cm in diameter, is present at the base of the funnel indicating the lined wall of the deeper-leading tunnel of the burrow. The tunnel itself is often blocked by sediment a few centimeters below the entrance. In the subtidal, mounds and funnels of *Glypturus* are found in water down to a depth of about 7 m, among seagrass (Fig. 8B), in coral rubble mixed with sand (Fig. 8C), and in the lagoon in sandy mud, among loose stands of Enhalus and Halimeda (Fig. 8D). However, no associated alpheids were captured from the subtidal sites.

Resin casts of *Glypturus* burrows show that they consist of a spiral with several radiating tunnels branching off the upper level, with one of them leading to a funnel and the other to a mound. The others are blocked and are either filled funnels or so-called irrigation tunnels. Deeper side branches are filled with coarse shell material. Burrows may reach a sediment depth of 180 cm (de Vaugelas 1990, Dworschak and Ott 1993). *Glypturus* feed on organic material that enters the funnel. Coarse particles are sorted out and stored in blind tunnels. Fine material is pumped out of the burrow by vigorous beating of the pleopods, and accumulates in the form of mounds at the surface.

Jengalpheops rufus sp. nov., was obtained mostly in pairs (1 pair per mound), always during the 1st sucking action exerted on the mound. This indicates that the associated shrimps live in the upper burrow layer, either freely in the host's tunnel underneath the mound or in self-constructed smaller burrows in the mound sediment, which often showed smaller (2-4 mm in diameter) burrow openings. In the intertidal zone, the coalescent mounds of Glypturus are often stabilized by microbial mats and thus provide a stable habitat for shallow-tier burrowers (Curran and Martin 2003). Morphologically, Jengalpheops rufus sp. nov., does not appear to have any particular adaptations for sediment digging. However, further observations are needed to elucidate whether this alpheid lives symbiotically ("commensally") in burrows of Glypturus (which is the more-likely possibility), or is able to dig its own small burrow in the mound of Glypturus.

Variability: The shape of the chelipeds and the armature of the 3rd pereiopod and telson of *Jengalpheops rufus* sp. nov., appear to be variable. The chelipeds of most of the larger adults differ from those of younger adults and immature individuals in that the carpus is much shorter and cup-shaped (vs. elongated and cylindrical, see Fig. 4A, G, H), and the chela is more enlarged and armed with distinctly larger teeth (see Fig. 4B, C,



Fig. 7. Jengalpheops rufus gen. nov., sp. nov. Colour pattern of female paratype (ZRC 2005.0083) (photograph by C.W. Lin).

I). The merus of the 3rd pereiopod may bear 1 (usually) or 2 (less frequently) spines, sometimes in the same individual. The usual telson spination includes 2 pairs of dorsal and 2 pairs of posterolateral spines (Fig. 6C, D); however, some individuals may have 3 or even 4 spines at 1 posterolateral angle of the telson (Fig. 6E, F), and no spines at all on the dorsal surface (Fig. 6F). Similar variations in the numbers of dorsal and posterolateral spines occur in some species of *Potamalpheops* (Bruce 1991 1993).

Distribution: Presently known only from the type locality, Panglao I., southwest of Bohol, the Philippines. The presumed host, *Glypturus armatus*, ranges from the Red Sea to French Polynesia (Sakai, 1999).

Remarks: Jengalpheops gen. nov., appears to be relatively basal within the family Alpheidae. The most important plesiomorphies include the unspecialized chelipeds, the partly exposed eyes,

(A)

the complete epipod set on the pereiopods, and the presence of spines on the ischium and merus of the 3rd and 4th pereiopods.

The chelipeds of Jengalpheops gen. nov., are equal in size and symmetrical in shape, which is clearly an ancestral condition within the family, although cheliped symmetry is also retained in some higher alpheid genera (Anker 2001b, Anker et al. 2006a). Furthermore, in Jengalpheops gen. nov., the chela is only feebly enlarged or not at all (Figs. 1A, B, 4), while the cheliped fingers are mostly unarmed, except for a few simple teeth (Fig. 4C, I). The finger tips are trifid, i.e., with 2 additional teeth near the tip (Fig. 4D). Bifid or trifid finger tips are also found on both chelipeds of Yagerocaris Kensley, 1988 (Anker 2001b), most species of Potamalpheops Powell, 1979 (e.g., Bruce and lliffe 1992, Yeo and Ng 1997), and on the minor cheliped of some Synalpheus Bate, 1888 (e.g., Dardeau 1984). According to Coutière



(B)

Fig. 8. Lebensspuren of the callianassid mudshrimp *Glypturus armatus* at Panglao, Bohol, the Philippines. (A) PCD at the intertidal of Doljo Point collecting associated alpheids; note the large mounds of *Glypturus* burrows in the background (photograph by Pierre Lozouet); (B) mounds of *Glypturus* burrows among seagrass in water about 4 m deep at Momo Beach (distance across foreground about 3 m); (C), mound (m) and funnel (f) of a *Glypturus* burrow in coral rubble in about 4 m of water at Momo Beach; scale bar, 50 cm; (D) mounds in about 3-4 m of water at Panglao Bay; scale bar, 50 cm.

(1899), chelipeds with bifid finger tips represent a "primitive" feature within the Alpheidae.

Another important feature of the chelipeds of Jengalpheops gen, nov., is the presence of several comb-like rows of setae on the mesial side of the carpus (Fig. 4B, C). The comb-like rows of setae are also found in most species of Potamalpheops (Powell 1979, Anker 2003a, Cai and Anker 2004), Stenalpheops Miya, 1997 (Miya 1997), Yagerocaris (Anker 2001b), Coutieralpheus Anker and Felder, 2005 (Anker and Felder 2005), and Leslibetaeus Anker, Poddoubtchenko and Wehrtmann, 2006 (Anker et al. 2006b), but are absent from other alpheid genera. These setae may be used for grooming and appear to be plesiomorphic within the Alpheidae (Anker 2001b, Anker et al. 2006a); similar grooming setae are present in some other caridean shrimps, including many of the Hippolytidae.

Jengalpheops gen. nov., is morphologically most similar and therefore probably most closely related to Potamalpheops. This is indicated by numerous features, such as the presence of an articulated plate on the 6th abdominal somite; the complete gill formula; the shape and armature of the 3rd maxilliped; the non-modified mouthparts; the spination of the 3rd to 5th pereiopods; the configuration of the frontal region, including the short rostrum and the partly exposed eyestalks; and the unspecialized chelipeds, with feebly enlarged chela and rows of setae on the carpus. However, the new genus differs from Potamalpheops by the styliform (needle-shaped) lateral plate on the coxa of the 3rd maxilliped (vs. ear-shaped in Potamalpheops); the absence of extra-orbital teeth; the much broader rostrum; and the uropodal exopod with a straight diaeresis (vs. finely toothed in Potamalpheops) (see Powell 1979, Hobbs 1983, Bruce 1991 1993, Bruce and Iliffe 1992, Anker 2003a, Cai and Anker 2004).

Potamalpheops darwiniensis Bruce, 1993 from northern Australia, differs from the other species of Potamalpheops by the chelipeds not being particularly enlarged, but with a noticeably swollen chela (Bruce 1993, fig. 1); reduced extracorneal teeth (idem, fig. 2A); and the presence of a small tubercle on the anteromesial margin of the eyestalks (idem, fig. 2B, C). These features make *P. darwiniensis* remarkably similar to *Jengalpheops rufus* sp. nov. Furthermore, the unique specimen of *P. darwiniensis* was collected from a "mud mound, amongst mangroves" (Bruce 1993), which could be a mound of a burrowing animal, e.g., a thalassinidean. However, *P. dar*-

winiensis differs from Jengalpheops rufus sp. nov., by the presence of a finely toothed diaeresis on the uropodal exopod (Bruce 1993, figs. 2L, 3H); the pterygostomial margin furnished with a row of plumose setae (idem, fig. 2B); the presence of a peculiar hook on the mastigobranch of the cheliped (idem, fig. 2G); and the presence of a strong acute tooth on the uropodal protopod (idem, fig. 2L). The presence of a finely toothed diaeresis and extra-corneal teeth (reduced but still recognizable in P. darwiniensis) are important diagnostic features of Potamalpheops, making it impossible to place the new species from Panglao into this genus without considerable emendation of its generic diagnosis. Nevertheless, Jengalpheops gen. nov., probably evolved from a Potamalpheops -like ancestor. It is not inconceivable that intermediate forms between Potamalpheops and Jengalpheops gen. nov. may be found, thus narrowing the gap between the 2 genera.

Jengalpheops gen. nov., also presents some similarities with Stenalpheops, which is presumably closely related to Potamalpheops (Miya 1997, Anker et al. 2001 2006a). Jengalpheops gen. nov., differs from Stenalpheops by the much less enlarged chelipeds with straight fingers (vs. strongly bent backwards in Stenalpheops); the branchiostegial margin without a deep sinus (vs. with sinus above the 2nd pereiopods in Stenalpheops); and the uropodal exopod with a non-modified diaeresis (vs. bearing large rounded teeth in Stenalpheops) and without a distal segmented appendix (vs. with a segmented appendix in Stenalpheops) (see Miya 1997, Hayashi 1998, Kim 1998, Anker et al. 2001).

Jengalpheops gen. nov. is probably only distantly related to the western Atlantic Coutieralpheus, characterized by the robust enlarged chelipeds; the dorsally concealed eyes, and the presence of 2 stiff setae on the tip of the rostrum (see Anker and Felder 2005); all these features are not present in Jengalpheops gen. nov. The new genus also differs in many respects from the eastern Pacific Leslibetaeus, e.g., by the presence of an articulated plate on the 6th abdominal somite (absent in Leslibetaeus); the 3rd maxilliped with a styliform lateral plate (vs. with a bluntly earshaped plate in Leslibetaeus); the presence of spines on the ischium and merus of the ambulatory pereiopods (absent in Leslibetaeus); the ventromesial carina of the 1st antennular segment bearing an acute tooth (unarmed in *Leslibetaeus*); and the much longer scaphocerite, almost reaching the distal end of the carpocerite (vs. reaching only 1/2 of the carpocerite in Leslibetaeus).

In summary, *Jengalpheops* gen. nov. appears to form a separate lineage among morphologically least derived alpheids. On the other hand, its association with callianassids indicates a specialized, possibly "commensal"-type life style. This type of ecology is also characteristic of two other basal alpheid lineages, *Stenalpheops* and *Coutieralpheus*, and is further suspected in *Leslibetaeus* (AA, pers. obs.), suggesting that symbiotic associations started to evolve early in the evolutionary history of the Alpheidae.

Acknowledgments: The material described herein was collected during the Panglao Marine Biodiversity Project 2004, made possible through grants from the Total Foundation, the French Ministry of Foreign Affairs, and the ASEAN Regional Centre for Biodiversity Conservation. PCD thanks the Principal Investigators, Dr. Philippe Bouchet (Muséum National d'Histoire Naturelle, Paris, France) and Dr. Danilo Largo (University of San Carlos, Cebu, the Philippines) for the invitation to participate in the fieldwork. AA is grateful to Dr. Peter K. L. Ng and Dr. Swee-Hee Tan (Department of Biological Sciences, National University of Singapore, Singapore) for the opportunity to study the alpheid shrimps collected during the Panglao project. Dr. M. S. Jeng (Research Center for Biodiversity, Academia Sinica, Taipei, Taiwan) generously sponsored AA's trip to Singapore, enabling a preliminary identification of the Panglao material. Tin-Yam Chan and Chia-Wei Lin (Taiwan National Ocean University, Keelung, Taiwan) photographed many alpheid specimens in Panglao, including the present new species. The present study was supported by a NSERC operating grant (A7245) to Dr. A. Richard Palmer (Department of Biological Sciences, University of Alberta, Edmonton, Canada). We also thank 2 anonymous reviewers for their useful comments on the manuscript.

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