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HAMALPHEUS ACANTHOPS, NEW GENUS, NEW SPECIES, A STYGIOPHILIC ALPHEID SHRIMP FROM A SAMOAN LAVA TUBE

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ABSTRACT

A new stygiophilic alpheid shrimp from Upolu, Samoa Islands, is described and illustrated. *Hamalpheus acanthops*, new genus, new species, is the only alpheid shrimp definitely known from a marine lava tube. The new genus is characterized by a conspicuous spiniform process of the anterior eyestalk and a modified caudal fan with unique holdfast adaptations. The new genus is most closely related to *Betaeopsis* Yaldwyn, from which it is distinguished by the presence of the above-mentioned features. A key is also provided to the 29 alpheid genera currently known from the Indo-West Pacific Region.

Alpheid shrimps are abundant in marine habitats, particularly in the tropics and on coral reefs. Few occur in brackish or fresh waters and their occurrence in troglobitic situations is particularly rare. *Potamalpheops stygicola* (Hobbs, 1973) has been reported from a fresh-water cave in Mexico and two species of *Metabetaeus*, *M. lohena* Banner and Banner, 1960, and *M. minutus* (Whitelegge, 1897) occur in anchialine lava and coral pools (Holthuis, 1986). The present shrimp appears to be the first alpheid shrimp to be found in a marine lava tube.

SYSTEMATIC ACCOUNT

Hamalpheus, new genus

Definition.—Body subcylindrical, feebly compressed, smooth, glabrous. Rostrum absent; carapace without supracorneal, supraorbital, extracorneal, or infracorneal spines; sixth abdominal segment with posteroventral angle nonarticulate; pleura of first 4 abdominal segments rounded, fifth posteroventrally acute; telson without dorsal spines, anal tubercles absent. Antennal peduncles robust; stylocerite well developed; basicerite with large lateral tooth, scaphocerite normal; antennal flagellum robust, semirigid proximally; eyes with cornea completely covered in dorsal view, stalk with stout, acute anterior tooth. Mouthparts normal; mandible with 2-jointed palp; molar process well developed, incisor process dentate; third maxilliped with slender endopod, not suboperculate. First pereiopods small, robust, subequal, similar; chelae carried extended (?), palm tuberculate medially, fingers without molar tooth and fossa. Second pereiopods slender, carpus 5-segmented. Ambulatory pereiopods robust, dactyls biunguiculate; first and second pereiopods with epipods. Uropod with protopod distolaterally acute, exopod with well-developed diaeresis, proximal margin with single lateral spine only; endopod with pair of stout spines distally.

Type Species.—*Hamalpheus acanthops*, new species.

Systematic Position.—*Hamalpheus* is most closely related to the genera *Betaeus* Dana, 1852, and *Betaeopsis* Yaldwyn, 1971. These three genera share the following features: rostrum absent; eyes completely covered by anterior carapace; carapace spines completely lacking; first pereiopods with chelae carried in extended position, with dactyl ventrally, fingers without molar process and fossa; second pereiopods with 5-segmented carpus; ambulatory pereiopods robust, only first and second with epipods; uropod with diaeresis of exopod nondenticulate. The closely related genera *Betaeus* and *Betaeopsis* are distinguished primarily by the presence of a moveable articulated plate at the posteroventral angle of the sixth abdominal segment in the former genus and its absence in the latter. In this feature, *Hamalpheus* resembles *Betaeopsis*. *Hamalpheus* may be distinguished from *Betaeopsis* by (1) the absence of dorsal telson spines, associated with (2) the recurved inner posterior telson spines and (3) the strong spines at tip of the exopod of the uropod, and (4) the acute spinous processes on the anterior aspect of the eye stalk. The mouthparts in the two genera are

essentially similar. In *Hamalpheus* the epipod of the first maxilliped is more triangular and bilobed than in *Betaeopsis* and that on the second maxilliped more triangular than oval. On the third maxilliped, the lateral plate of the coxa is distinctly acute in *Hamalpheus,* but blunt in *Betaeopsis.*

Etymology.—From *hamus,* Latin, a hook, referring to the spines on the caudal fan, and *Alpheus*, a generic name first used by Fabricius (1798).

Hamalpheus acanthops, new species
Figs. 1–5

Material Examined.—1 ♀, Station 83–034, Tosua-Tolesua lava tube cave located near Lotofaga village, south coast of Upolu Island, Western Samoa, 17 April 1988, collected by T. M. Iliffe and S. Sarbu.

Description.—Body form subcylindrical, slightly compressed (particularly carapace), smooth, glabrous.

Carapace with rostrum completely lacking, frontal region broad, feebly concave, completely covering eyes in dorsal view, without dorsal carina; supracorneal, extracorneal, and infracorneal spines or teeth absent; anterior margin of branchiostegite slightly produced, broadly rounded; cardiac notch distinct.

Abdomen with pleuron of first 3 segments broadly rounded, fourth slightly produced posteriorly, rounded, fifth strongly produced posteriorly, posteroventrally acute; sixth segment about 1.3 times length of fifth, 1.3 times longer than deep; posterolateral angle slender, acute; posteroventral angle blunt, nonarticulate. Telson subequal to sixth segment length, strongly convex dorsally, concave ventrally, without anal tubercles, about 1.6 times longer than anterior width, lateral margins feebly sinuous, convergent, without dorsal spines, posterior margin about 0.5 of anterior width, with small acute lateral tooth, convex, with small inner and outer spines laterally, inner spine smaller, curved dorsomedially, outer spine longer, straight, projecting posteriorly, lower convex margin with 13 long slender segmented plumose setae projecting posteriorly, upper margin with numerous shorter simple setae projecting dorsally.

Antennular peduncle, short, robust; proximal segment about 1.9 times longer than wide, with large ventromedial tooth, stylocerite well developed, slender, acute, reaching to about level of distal margin of intermediate segment; statocyst normal; intermediate segment subcylindrical, with feeble ventromedial lamina, about as long as wide; distal segment subcylindrical, slightly compressed, about 1.6 times longer than wide; upper flagellum feebly biramous, rami fused for proximal 11 segments, compressed, each segment with paired groups of aesthetascs ventrally; shorter free ramus with single incompletely free segment; longer free ramus slender, about 0.6 of carapace length; lower flagellum slender, filiform, subequal to carapace length.

Antenna with stout basicerite, with conspicuous triangular laminar tooth anterolaterally; carpocerite stout, far exceeding scaphocerite and antennular peduncle, subcylindrical, about 2.6 times longer than distal width; merocerite and ischiocerite normal; flagellum about 2.0 times carapace length, proximal segments fully fused, proximal half of flagellum semirigid, distal half more flexible; scaphocerite well developed, reaching to about middle of distal segment of antennular peduncle, broad, about 1.75 times longer than wide, lateral margin feebly convex, with strong distolateral tooth, reaching about to distal margin of lamella.

Eye completely concealed dorsally by carapace, cornea hemispherical, well pigmented, obliquely orientated on stalk; stalk ovoid, with large acute tooth projecting anteriorly from anterior margin adjacent to cornea, without setae.

Mandible (right) robust, with 2-segmented palp, proximal segment irregularly subcylindrical, slightly expanded distally, nonsetose, distal segment laminar, oval, with feebly plumose marginal setae; molar process well developed, subcylindrical, obliquely truncate distally, with dense tuft of longer setae proximoanteriorly; incisor process very stout, deeply concave medially, with 5 stout acute teeth distally. Maxillula with bilobed palp, upper lobe with 2 setae, lower lobe with 1 longer stouter seta; upper lacinia broad, with double row of 14 short stout spines distally, with numerous feebly setulose setae distodorsally, coarsely setulose setae distoventrally; lower lacinia slender, with 4 stout spines distally, numerous serrulate setae. Maxilla with short, tapering, angulate palp, with short simple

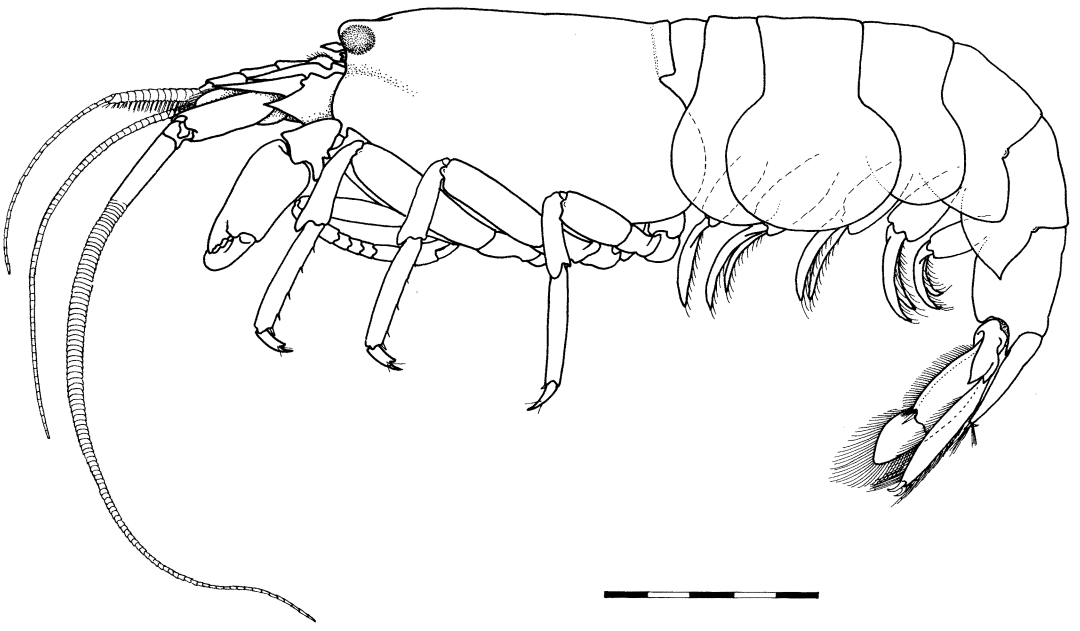

Fig. 1. *Hamalpheus acanthops,* new genus, new species, holotype female, Upolu, Samoa. Scale bar in mm.

distal setae, several short weakly plumose setae proximolaterally; basal endite large, bilobed, lobes subequal, broad, densely fringed with short setae medially; coxal endite reduced, angular, with few long setae; scaphognathite well developed, narrow, about 3.5 times longer than wide; anterior lobe 1.75 times longer than wide, distal half narrow; posterior lobe well developed, about 0.3 of scaphognathite length. First maxilliped with slender tapering simple palp, with slender feebly plumose setae along medial margin and distally, basal endite broad, with feebly plumose setae along anterodistal margin, dense fringe of short feebly setulose setae along medial margin; coxal endite weakly bilobed, sparsely setose; exopod well developed, flagellum slender, with numerous plumose setae distally, with small, narrow caridean lobe; epipod large, triangular, weakly bilobed. Second maxilliped of normal form, endopod with dactylar segment narrow, densely spinulate medially; propodal segment expanded anteromedially, anterior margin with feebly setulose setae and spiniform setae, medial margin with spines; ischiomerus with short, feebly setulose setae laterally; basis medially excavate; exopod slender, with numerous plumose setae distally, short, feebly setulose setae medially and laterally on proximal half; coxa without medial protuberance, sparsely setose, with large triangular simple epipod laterally, without podobranch. Third maxilliped with endopod slender, not suboperculate, ischiomerus and basis completely fused, about 5.6 times longer than central width, subuniform, with few short setae distally on lateral margin, medial margin generally sparsely setose; carpal segment short, 2.0 times longer than central width, about 0.23 of antepenultimate segment length, centrally slightly swollen, tapering distally, sparsely setose laterally, small groups of setae medially; terminal segment slender, about 0.5 of antepenultimate segment length, 6.0 times longer than wide, tapering distally, with subdivision into larger proximal and smaller distal segments, with single spine distally, with numerous groups of long slender finely serrulate setae on ventromedial margins, sparsely setose laterally, exopod well developed, not reaching to carpomeral articulation, with numerous plumose setae distally; coxa not medially produced, sparsely setose, with well-developed lateral plate, acutely produced anterolaterally, lateral margin with sparsely setulose setae, with epipod ventrolaterally; with small arthrobranch.

Thoracic sternites narrow, unarmed. Branchial formula:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	−	−	−	+	+	+	+	+
Arthrobranchs	−	−	+	−	−	−	−	−
Podobranchs	−	−	−	−	−	−	−	−
Mastigobranchs	−	−	−	+	+	+	−	−
Epipods	+	+	+	+	+	−	−	−
Exopods	+	+	+	−	−	−	−	−

First pereiopods small, robust, subequal, similar, reaching to about level of distal end of carpocerite, chela carried in extended position (?); chela stout, about 0.7 of carapace length, palm subcylindrical, slightly compressed, about 1.8 times longer than central width, slightly swollen centrally, generally smooth, with blunt tubercles ventromedially, with long simple setae; fingers robust, dactylus curved, about 0.7 of palm length, 4.0 times longer than proximal depth, with stout hooked tip, cutting edge slightly laterally situated, with 4 low teeth on proximal half, smaller, irregular, more acute teeth (damaged?) over distal half; fixed finger similar, with 4 low teeth over proximal 0.6 of cutting edge, with several small teeth and short sharp cutting edge distally, with stout acute hooked tip; carpus short, stout, about 0.4 of palm length, smooth, unarmed, deeply excavate distally; merus subequal to palm length, robust, about 2.5 times longer than distal width, slightly tapered proximally, deeply excavate distoventrally, lateral margin entire, medial margin with large blunt tubercles and setae; ischium short, stout, unarmed, about 0.4 of merus length, ventral margin feebly carinate, setose; ischium about 0.5 of merus length, 2.0 times longer than distal width, tapering proximally, unarmed; coxa robust, with small setose distoventral process, epipod, and trisetose setobranch.

Second pereiopods small, slender, subequal, similar, extending to slightly beyond carpocerite; chela small, about 0.33 of first pereiopod chela length, palm subcylindrical, slightly compressed, feebly tapering distally, 1.6 times longer than deep, fingers about 0.85 of palm length, slender, simple, with small, acute hooked tips, slightly laterally situated, entire cutting edges along distal 0.6 of opposing margins, numerous groups of setae; carpus about 2.0 times chela length; 5-segmented, segment lengths in ratio 4:1:1:1:2.5; merus about 1.75 times chela length, 5.0 times longer than central width; ischium subequal to meral length, about 5.0 times longer than distal width, tapering proximally; basis short, obliquely articulated with ischium, sparsely setose ventrally; coxa stout, sparsely setose ventrally, with trisetose setobranch and epipod dorsolaterally.

Ambulatory pereiopods robust; third pereiopod exceeding carpocerite by dactyl and 0.2 of propod; dactyl robust, strongly compressed, 3.0 times longer than proximal depth, distally acute, biunguiculate, with stout, blunt accessory tooth at 0.6 of ventral margin length, about 0.5 of distal tooth length, ventral border mainly convex, blunt, corpus with groups of setae distolaterally and medially; propod about 0.38 of carapace length, 3.5 times dactyl length, subuniform, 7.0 times longer than deep, with pair of short, stout, feebly hooked distoventral spines, ventral border with medial and lateral rows of sparse, short slender spines; carpus about 0.6 of propod length, 3.5 times longer than distal width, with strong distodorsal lobe, unarmed; merus about 1.2 times propod length, 3.7 times longer than wide, unarmed; ischium about 0.3 of merus length, 1.5 times longer than distal width, tapering proximally, unarmed; basis normal; coxa stout, with bisetose setobranch, without epipod. Fourth and fifth pereiopods similar; fifth pereiopod with propod about 0.9 of third propod length, with transverse rows of short setae distomedially.

Pleopods without special features; second pleopod with basipodite 2.0 times longer than distal width, with pair of short, rudimentary ovigerous setae (?) at 0.3 of medial margin length.

Uropod with protopodite robust, with stout acute distolateral lobe, smaller acute distomedial lobe; exopod broad, far exceeding telson, 1.2 times sixth abdominal segment length, 2.0 times longer than wide, ovoid, with very well-marked diaeresis at about 0.6 of length, proximal margin nonspinulate, distal portion of lamella highly flexible; lateral margin feebly convex, with dense row of short stiff plumose submarginal ventral setae, with small acute distal ventral tooth, with single well-developed mobile spine medially, separated by dense tuft of long simple setae projecting dorsolaterally, distolateral and medial margins

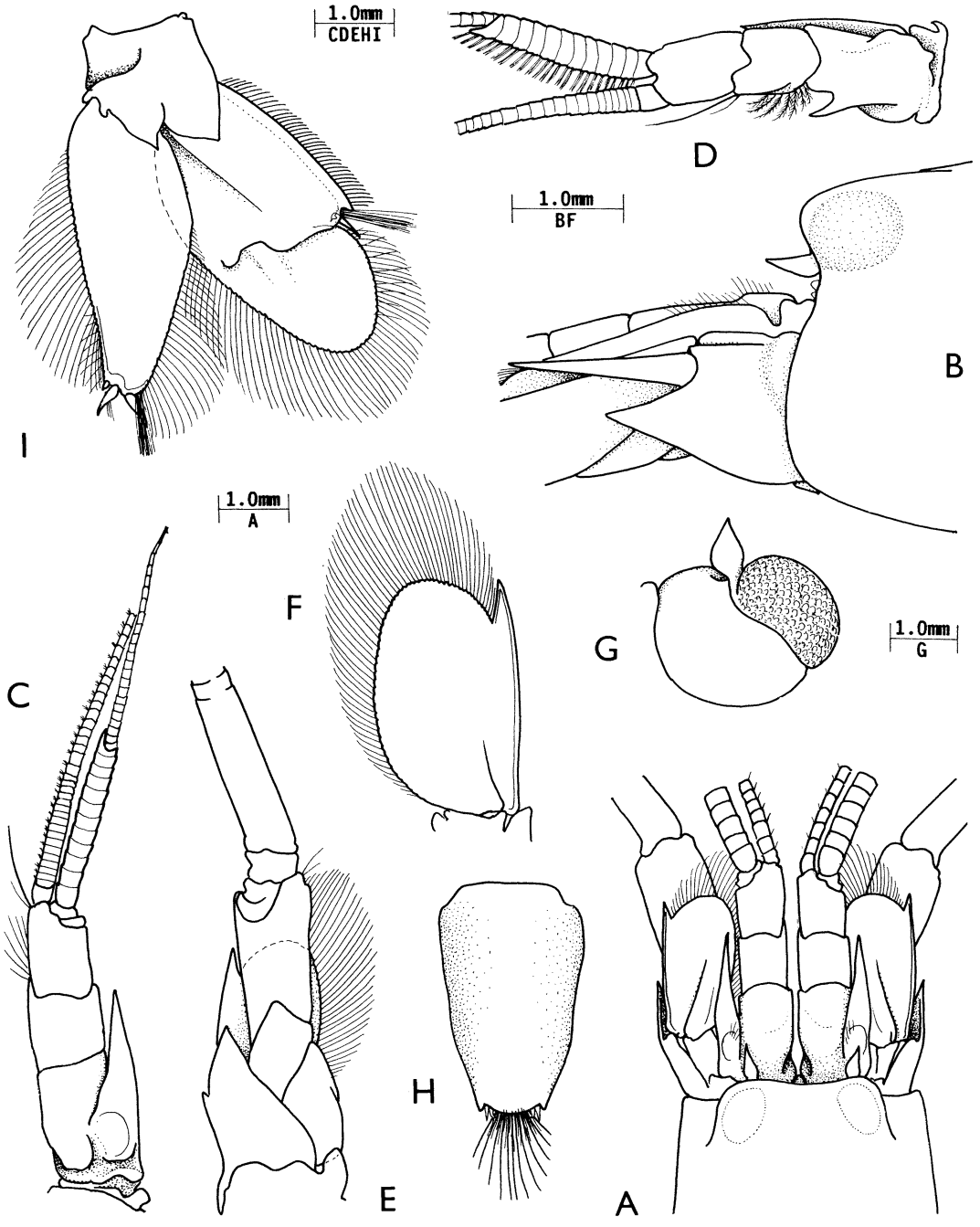

Fig. 2. *Hamalpheus acanthops,* new genus, new species, holotype female. A, anterior carapace and antennal peduncles, dorsal aspect; B, same, lateral aspect; C, antennule; D, antennular peduncle, medial aspect; E, antennal peduncle, ventral; F, scaphocerite, dorsal; G, eye, dorsal; H, telson; I, uropod.

densely fringed with long robust annulate plumose setae; endopod about 1.1 times exopod length, 2.7 times longer than wide, proximal half uniform, distal half tapering medially, posterior margin about 0.33 of width with 3 spines laterally and dense tuft of long simple setae medially, medial spine small, subconical, intermediate and lateral spines robust, about 0.12 of endopod length, divergent, strongly curved ventrally; medial and lateral margins fringed with long, robust annulate plumose setae.

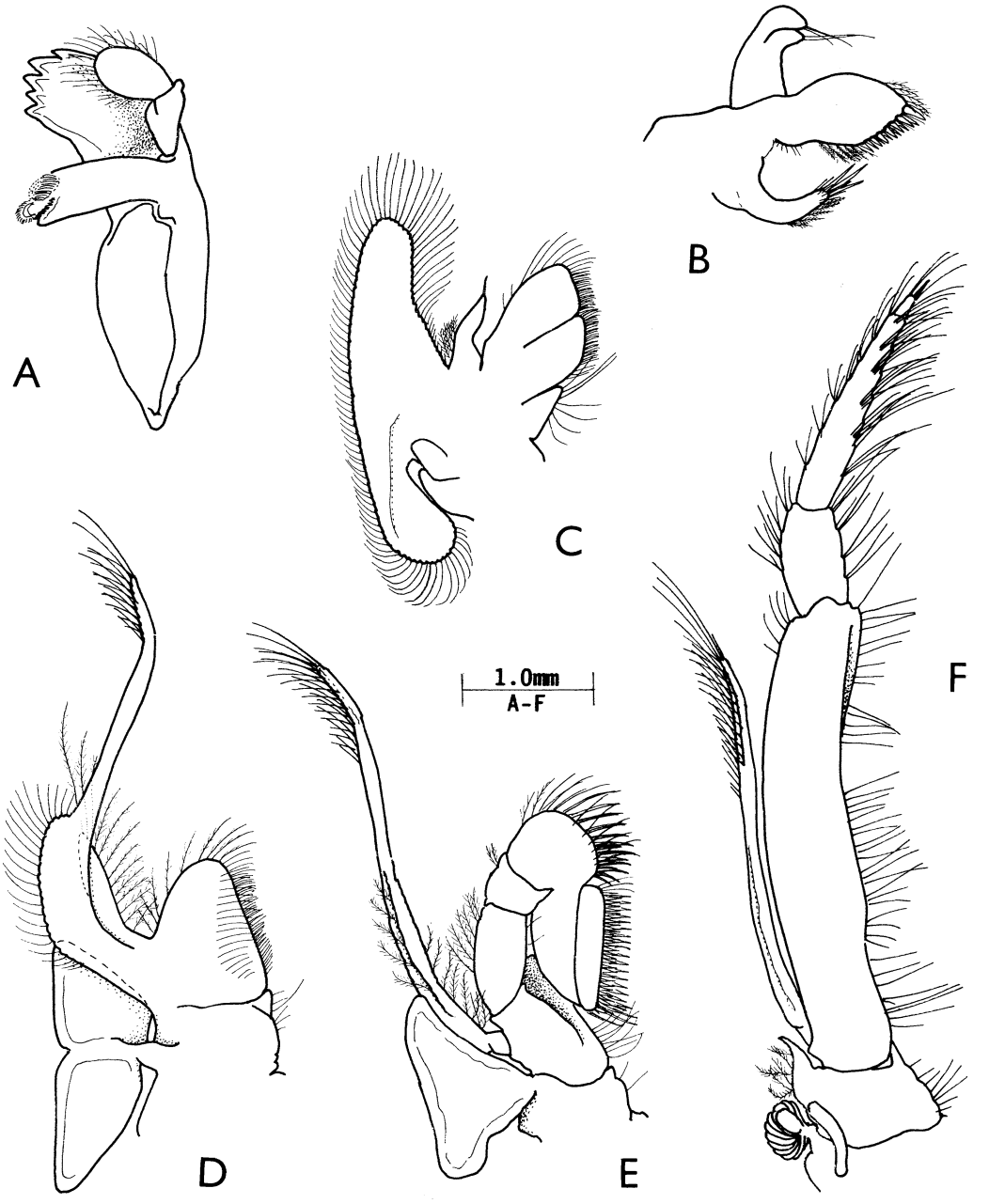

Fig. 3. *Hamalpheus acanthops,* new genus, new species, holotype female. A, right mandible, dorsal; B, maxillula, ventral; C, maxilla; D, first maxilliped; E, second maxilliped; F, third maxilliped.

Type.—The single available specimen is the holotype and is deposited in the collection of the Northern Territory Museum, Darwin, catalogue number NTM Cr.007421.

Measurements (mm).—Total body length (approximate), 27.3; carapace length, 7.7; second pereiopod chela, 4.5.

Coloration.—No data.

Habitat.—The Tosua-Tolesua lava tube consists of two large collapsed sinkholes, interconnected by a lava tube, but also directly connected with the sea. Salt water from the ocean extends most of the way back into the system. Beginning at the base of 15-m

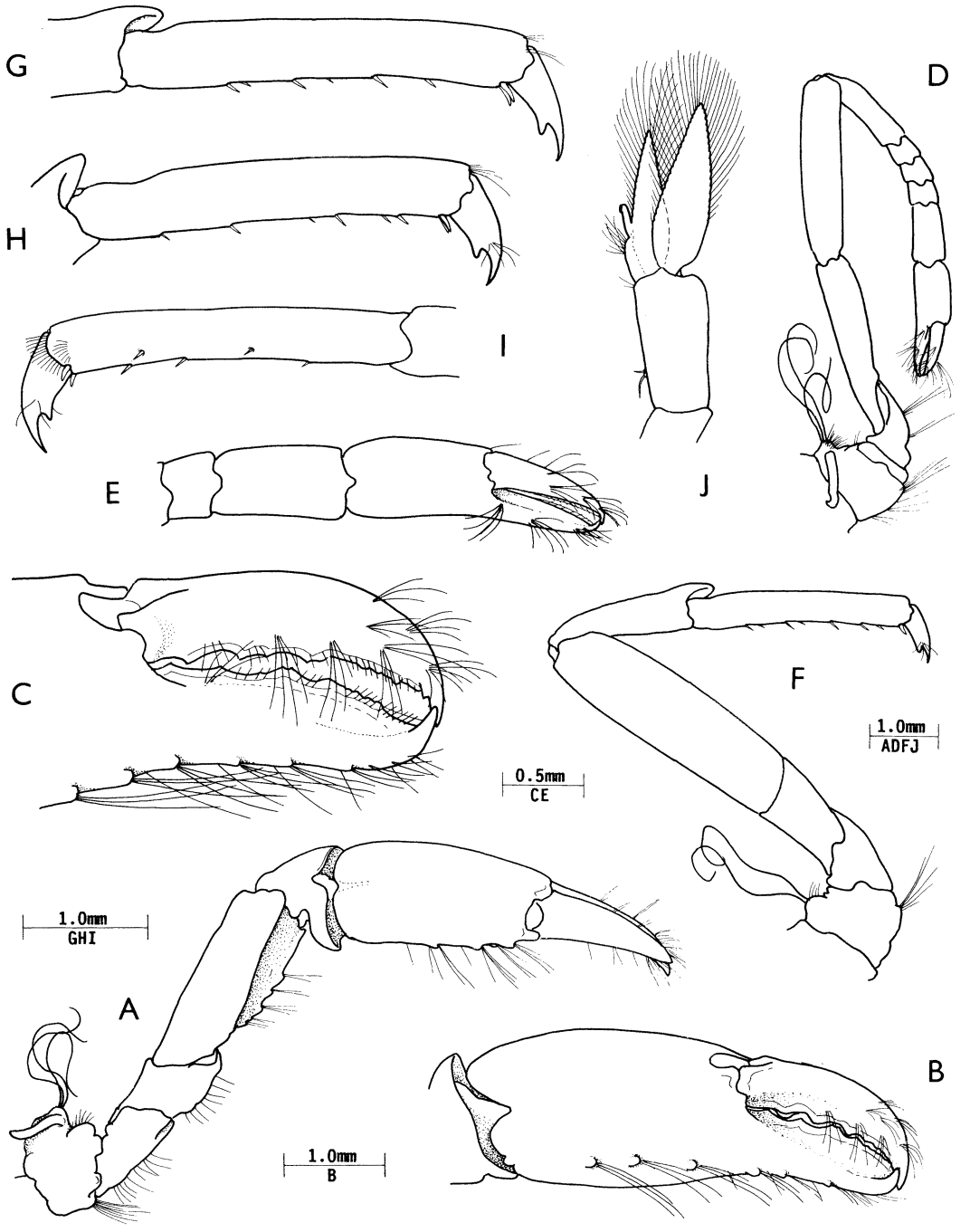

Fig. 4. *Hamalpheus acanthops,* new genus, new species, holotype female. A, first pereiopod, right, lateral aspect; B, same, chela; C, same, fingers; D, second pereiopod, right; E, same, chela and distal carpus; F, third pereiopod; G, same, propod and dactyl; H, fourth pereiopod, propod and dactyl; I, fifth pereiopod, propod and dactyl; J, second pleopod.

high coastal sea cliffs, an underwater passage continues inland for 20 m to a large pool situated directly beneath the Tosua entrance (30 m long by 20 m wide and 26 m deep). A further 30-m section of lake ends at a breakdown slope ascending to the Tolesua entrance (15-m diameter, 8-m depth). Brackish water emerging out of this break-

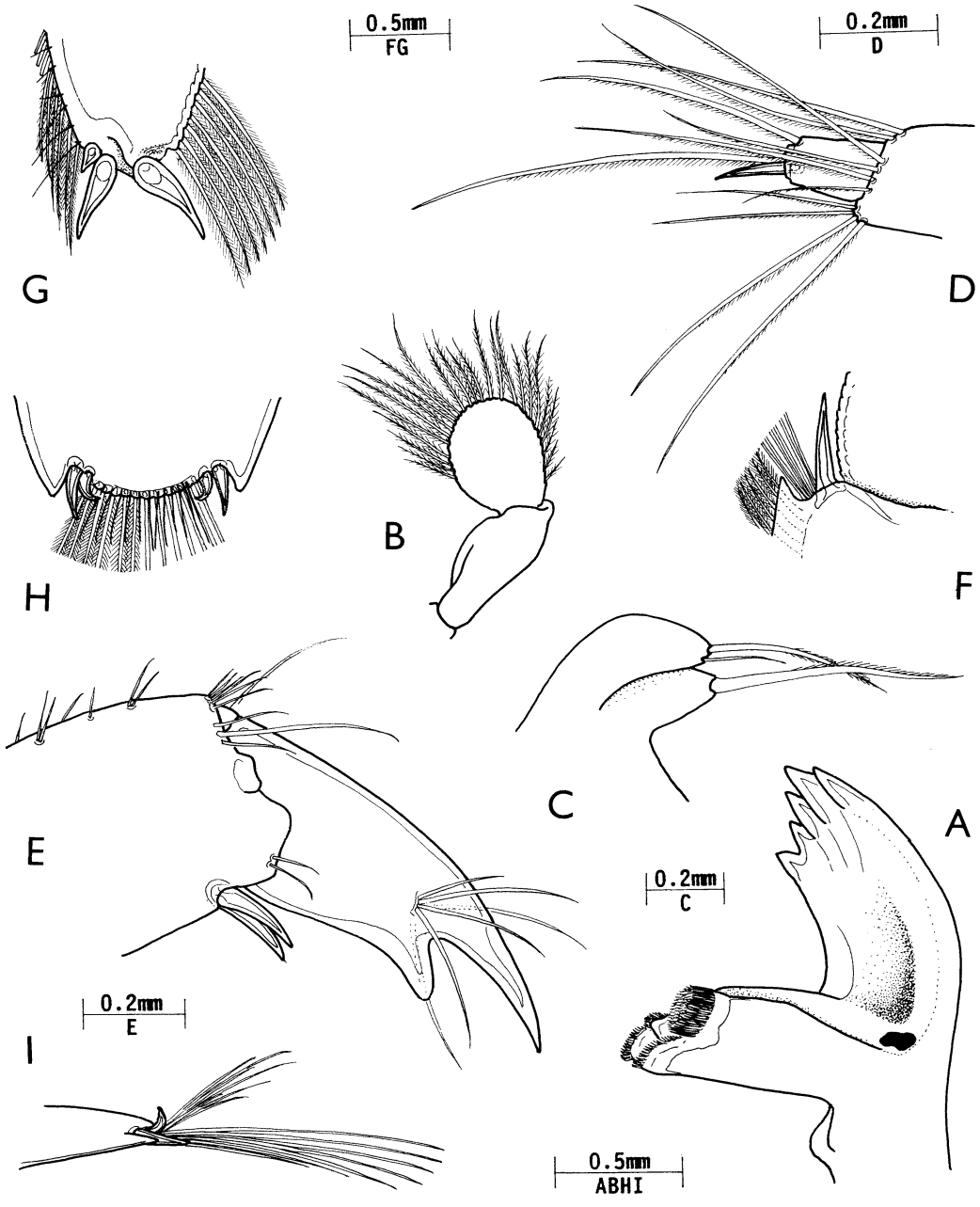

Fig. 5. *Hamalpheus acanthops,* new genus, new species, holotype female. A, mandible, molar and incisor processes, palp removed; B, same, palp; C, maxillula, distal palp; D, third maxilliped, distal endopod; E, third pereiopod, distal propod and dactyl; F, uropod, distolateral angle of exopod; G, same, distal endopod; H, telson, posterior margin; I, same, lateral aspect.

down suggests the presence of an inaccessible inland continuation of the cave under the collapse. The floor of most of the pool is coarse sand and rubble with very large sand ripples indicating the existence at times of strong currents within the cave. Total length of the cave is 181 m, with a maximum depth of 26 m.

The single specimen of *Hamalpheus acanthops* was collected by hand from a

shallow intertidal pool in the rear portion of a small side gallery of the cave, close to the sea.

Remarks.—The unusual acute process in the anterior aspect of the eye stalk in *H. acanthops* is unique and its functions are not immediately obvious. Other alpheid shrimps may also have small acute processes in this situation, among them *Alpheus brucei,* but in these the processes are comparatively small (Banner and Banner, 1981b). The caudal fan is also unique, with the lack of dorsal telson spines, of which two pairs are almost invariably present in the rest of the Alpheidae, and the dorsally recurved inner posterior marginal spines, together with the group of ventrally curved spines at the tip of the exopod of the uropod, a position devoid of spines in most other alpheid shrimps, although some species of *Alpheus,* such as *A. bucephalus* Coutière, may have numerous small spinules around the margin of the endopod of the uropod (Banner and Banner, 1981a). The morphology of the caudal fan suggests an adaptation to life in a rapidly fluctuating water current, possibly beneath stones, slabs, or rocks. Most shrimps actively face into a water current and retain their position by their walking legs. *Hamalpheus acanthops* may use its caudal fan as an anchor, in a reversing current, with the uropod spines attaching to the substrate and the inner telson spines possibly to the roof of the cavity occupied. The mode of carriage of the chelae of the first pereiopods is uncertain. The ventral merus is deeply excavate and can readily accommodate the flexed carpus and chela, but these appear to be naturally held in an extended position, with the dactyl ventrally, in the preserved specimen. The presence of biunguiculate dactyls and robust ambulatory pereiopods in alpheid and some other shrimps also generally suggests a commensal lifestyle, often in association with modifications of the caudal fan, all adaptations to retaining an association with the host animal. No such associations appear to have been possible in the case of *H. acanthops,* where the habitat was generally devoid of potential hosts. An alternative explanation is that the dactyls and pereiopods may also be developed as an independent adaptation to strong currents.

Etymology.—From *akantha,* Greek, a thorn or spine, and *ops,* Greek, an eye.

Discussion

Hamalpheops acanthops is the first alpheid definitely recorded from a lava tube. However, *Metabetaeus lohena* has also been recorded from a pool in a marine cave on Hawaii that may possibly also be the remains of a lava tube (Banner and Banner, 1960b).

A key to the then-known genera of the family Alpheidae was provided by Holthuis in his invaluable volume published in 1955. This included 19 genera, of which 16 were represented in the Indo-West Pacific region. Since then, *Arete* Stimpson has been synonymized with *Athanas* Leach (Banner and Banner, 1960a). The genus *Metalpheus* Coutière has also been resurrected (Chace, 1988). A further 9 genera have now been described which contain representatives in the Indo-West Pacific fauna, including the present genus *Hamalpheus*. There are 25 genera now reported from the Indo-West Pacific region. Johnson (1961) provided a key to eight genera known from the Indo-Australian region. Subsequently Banner and Banner (1973) published a key to nine genera from Australian waters. Recently, Chace (1988) provided a key to the 15 genera known from the Philippine Islands. To facilitate the identification of all Indo-West Pacific genera, the following key is provided.

Key for the Identification of the Indo-West Pacific Genera of the Family Alpheidae

1. Body very strongly flattened, first pleuron covering much of posterior carapace; eyes dorsally exposed; first pereiopods very feebly developed, smaller than second pereiopods ..... *Pterocaris* Heller, 1862
– Body not strongly depressed, first pleuron covering only posterior branchiostegite; first pereiopods larger than second pereiopods 2
2. Fingers of major first pereiopod with sound-producing molar process and fossa mechanism 3
– Fingers of major first pereiopod without sound-producing molar process and fossa mechanism 6
3. Body strongly bilaterally compressed; carapace and abdomen with strong median dorsal carina; chelae of first pereiopods strongly compressed ..... *Racilius* Paulson, 1875
– Body not strongly compressed; carapace with

at most feeble median carina, abdomen dorsally noncarinate; chelae of first pereiopods not strongly compressed 4
4. Antepenultimate segment of endopod of third maxilliped markedly broadened, flattened, suboperculate ..... *Metalpheus* Coutière, 1908
– Antepenultimate segment of endopod of third maxilliped subcylindrical, not suboperculate 5
5. Pereiopods without epipods ..... *Synalpheus* Bate, 1888
– First 4 pereiopods with straplike epipods ..... *Alpheus* Fabricius, 1798
6. Major chela with adhesive plaques adjacent to dactylar hinge; carpus subrectangular ..... *Nennalpheus* Banner and Banner, 1981
– Major chela without adhesive plaques; carpus not subrectangular 7
7. Posteroventral angle of sixth abdominal segment acute, nonarticulate 8
– Posteroventral angle of sixth abdominal segment with articulated triangular plate 14
8. Eyes completely covered by anterior carapace in dorsal view 9
– Eyes partially or completely exposed in dorsal view 13
9. Mandible with palp 10
– Mandible without palp 11
10. Telson with 2 pairs of dorsal spines; endopod unarmed; eye stalk unarmed ..... *Betaeopsis* Yaldwyn, 1971
– Telson without dorsal spines; endopod with strong terminal spines; eyestalk with conspicuous acute anterior process ..... *Hamalpheus,* new genus
11. Frontal margin entire, without rostrum; incisor process of mandible dentate ..... *Bannereus* Bruce, 1988
– Frontal margin with distinct rostrum and supracorneal teeth; incisor process of mandible nondentate 12
12. Pereiopods without epipods; exopod of uropod without distinct diaeresis ..... *Batella* Holthuis, 1955
– First 3 pairs of pereiopods with epipods; exopod of uropod with distinct diaeresis ..... *Vexillipar* Chace, 1988
13. Rostrum well developed, acute; eyes dorsally concealed, cornea well developed; chelae of first pereiopods carried flexed ..... *Salmoneus* Holthuis, 1955
– Rostrum markedly reduced; eyes fully exposed dorsally, cornea reduced; chelae of first pereiopods carried extended ..... *Automate* de Man, 1888
14. Rostrum absent (in Indo-West Pacific species) 15
– Rostrum present 18
15. Eyes dorsally exposed ..... *Metabetaeus* Borradaile, 1899
– Eyes concealed dorsally 16
16. Posterior margin of telson acutely produced (first pereiopods unknown) ..... *Parabetaeus* Coutière, 1897
– Posterior margin of telson convex 17
17. First pereiopods subequal, similar, carried in extended position; free-living or associated with gastropods ..... *Betaeus* Dana, 1852
– First pereiopods markedly unequal, dissimilar, carried in flexed position; associated with thalassinids ..... *Leptalpheus* Williams, 1965
18. Posterior margin of telson acutely produced ..... *Neoalpheopsis* Banner, 1953*
– Posterior margin of telson not acutely produced 19
19. Exopod of uropod with diaeresis strongly dentate or spinulate 20
– Exopod of uropod with diaeresis entire, distolateral tooth and spine only 22
20. Mandibles with molar process obsolete, incisor process greatly enlarged, without palp ..... *Prionalpheus* Banner and Banner, 1960
– Mandible normal, with palp 21
21. Eyes dorsally concealed ..... *Potamalpheops* Powell, 1979
– Eyes exposed dorsally ..... *Pseudathanas* Bruce, 1983
22. First 3 or 4 pairs of pereiopods with epipods ..... *Alpheopsis* Coutière, 1896
– At most, first 2 pairs of pereiopods with epipods (sometimes rudimentary) 23
23. Eyes fully concealed dorsally ..... *Athanopsis,* Coutière, 1897
– Eyes partly exposed dorsally 24
24. Rostrum short, blunt, carapace without periorbital teeth; major chela with palm strongly compressed, dorsally and ventrally carinate; mandible without palp; associated with pagurid crabs ..... *Aretopsis* de Man, 1910
– Rostrum long, acute, with periorbital teeth; chelae oval in section, noncarinate; mandible with palp; free-living or associated with echinoderms ..... *Athanas* Leach, 1814

* *Neoalpheopsis* is possibly a junior synonym of *Parabetaeus* (see Banner and Banner, 1985).

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