Description of a new species of commensal alpheid shrimp (Crustacea, Decapoda) from the southern Caribbean Sea

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ABSTRACT

Leptalpheus felderi n. sp., a commensal alpheid shrimp, is described from two localities in the southern Caribbean Sea: Isla Margarita, Venezuela and Bahía Cispata, Colombia. All specimens of *L. felderi* n. sp. were collected with the aid of a suction pump; the Venezuelan specimens came from burrows of the upogebiid mudshrimp *Upogebia omissa* Gomes Corrêa, 1968. The new species is unique among species of Leptalpheus Williams, 1965 in having small triangular crests on the orbital hoods; a dense row of long, flexible setae on the dactylus of the major chela; two subacute distal processes on the carpus of the major chela; minute, saw-like teeth on the pollex of the minor chela; and only four instead of the usual five segments in the carpus of the second pereiopod. The new species is also characterized by the pinkish-red colour. The diagnosis of the genus Leptalpheus is significantly emended, to accommodate L. felderi n. sp. The taxonomy and intra-generic relationships of *Leptalpheus* species are discussed, and a table of all species of *Leptalpheus*, with information on the distribution and hosts, is provided. Because of the invalid description, L. petronii Ramos-Porto & Souza, 1994 is placed in synonymy of L. axianassae Dworschak & Coelho, 1999. Three preliminary species groups, based mainly on the features of the major cheliped and frontal region, are established.

KEY WORDS
Alpheidae,
Leptalpheus,
Upogebia,
commensal shrimp,
infauna,
western Atlantic,
genus emendation,
new species.

RÉSUMÉ

Description d'une nouvelle espèce de crevette alphéidée commensale (Crustacea, Decapoda) du sud de la mer Caraïbe.

Leptalpheus felderi n. sp., une espèce nouvelle commensale, est décrite de deux localités dans le sud de la mer Caraïbe: Isla Margarita au Vénézuela et Bahía Cispata en Colombie. Tous les spécimens de L. felderi n. sp. ont été récoltés à l'aide d'une pompe à succion ; les spécimens vénézuéliens ont été trouvés dans les terriers de la crevette-taupe Upogebia omissa Gomes Corrêa, 1968. La nouvelle espèce est unique dans le genre Leptalpheus Williams, 1965 par la possession de deux crêtes triangulaires sur les voûtes orbitaires, d'une rangée très dense de soies fines et longues sur le dactyle de la grande pince, de deux processus aigus distaux sur le carpe du grand chélipède, de petits denticules en forme de scie sur le pollex de la petite pince, et de seulement quatre articles dans le carpe du deuxième péréiopode, au lieu de cinq habituellement présents. La nouvelle espèce est également caractérisée par la coloration rose-rougeâtre. La diagnose du genre Leptalpheus est considérablement modifiée, pour y placer L. felderi n. sp. La taxonomie et les relations intra-génériques des espèces de Leptalpheus sont brièvement discutées; un tableau de référence résume toutes les espèces connues de Leptalpheus, avec les données disponibles sur la distribution et les hôtes. La description de L. petronii Ramos-Porto & Souza, 1994 est considérée comme invalide, ce binom est alors placé en synonymie de L. axianassae Dworschak & Coelho, 1999. Trois groupes d'espèces fondés sur les caractères du grand chélipède et de la région frontale sont définis.

MOTS CLÉS
Alpheidae,
Leptalpheus,
Upogebia,
crevette commensale,
faune endogène,
Atlantique occidental,
redéfinition du genre,
espèce nouvelle.

INTRODUCTION

The members of the alpheid genus Leptalpheus Williams, 1965 are rarely collected and therefore among the least known of caridean shrimp. This is due mainly to their small size (most measure 5-15 mm in total length) and very cryptic habits: all known species live in burrows of thalassinidean mudshrimps (e.g., Williams 1965a; Dawson 1967; Saloman 1971; Simon & Dauer 1977; Ríos & Carvacho 1983; Ríos 1992; Felder & Rodriguez 1993; Ramos-Porto & Souza 1994; Felder et al. 1995, 2003; Campos et al. 1995; Felder & Manning 1997a, b; Dworschak & Coelho 1999; D. Felder pers. comm.). The genus is presently defined by the absence of teeth on the orbital hoods; the rostrum absent or reduced to a median projection; the very asymmetrical and unequal chelipeds, carried folded at rest, and with the major chela lacking snapping mechanism; the presence of a triangular plate on the sixth abdominal somite; and several more subtle features.

Until the present study, Leptalpheus contained five nominal species. Three of them – the type species L. forceps Williams, 1965, L. petronii Ramos-Porto & Souza, 1994 and L. axianassae Dworschak & Coelho, 1999 - are patchily distributed in the tropical-subtropical Western Atlantic, from North Carolina to southern Brazil (Williams 1965a; Dawson 1967; Saloman 1971; Ramos-Porto & Souza 1994; Christoffersen 1998; Dworschak & Coelho 1999). The fourth species, L. mexicanus Ríos & Carvacho, 1983, is found in the tropical Eastern Pacific, from the Gulf of California to Colombia (Ríos & Carvacho 1983; Ramos 1995), while the fifth, L. pacificus Banner & Banner, 1974, is the only presently known Indo-West Pacific member of this genus (Banner & Banner 1974, 1983).

In December 2003 we were able to collect several interesting shrimp specimens from burrows of upogebiid mudshrimp, close to the village of Guamache, situated on the southern shore of Isla Margarita, Estado Nueva Esparta, Venezuela. Close

examination of these specimens revealed that they belong to a hitherto unknown species of *Leptalpheus*, which is described as new herein.

The original diagnosis of *Leptalpheus* (Williams 1965a: 192) was subsequently modified by Ríos & Carvacho (1983: 312) to accommodate *L. mexicanus*, the only species of the genus bearing a rostral projection. Several specific features of the new species from Venezuela make a second emendation of the generic diagnosis of *Leptalpheus* necessary. The genus is redefined and the taxonomy and intra-generic relationships of *Leptalpheus* species are discussed. Three preliminary species groups, based mainly on features of the major cheliped and frontal region, are proposed.

MATERIAL AND METHODS

All specimens were collected in water depth of 0.5-1 m, with the aid of Alvey bait pump ("yabby pump") and a self-made, fine-meshed (about 2 mm) sieve. The specimens were brought alive to the laboratory at the Universidad de Oriente, Boca del Río, Isla Margarita, photographed, and then preserved in 70% ethanol. All drawings were made with the aid of a camera lucida. The carapace length (CL) and the total length (TL) are given in mm, and were measured with a micrometer, along the mediodorsal line from the frontal to the posterior margin of the carapace (CL), and from the frontal margin of the carapace to the posterior margin of the telson (TL). The type specimens are deposited in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN), the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) and the Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela (IVIC). Other abbreviations used in the text: Mxp, maxilliped; P, pereiopod.

SYSTEMATICS

Genus Leptalpheus Williams, 1965

Type species. — Leptalpheus forceps Williams, 1965.

SPECIES INCLUDED. — Leptalpheus forceps Williams, 1965, L. pacificus Banner & Banner, 1974, L. mexicanus Ríos & Carvacho, 1983, L. axianassae Dworschak & Coelho, 1999 (synonym: L. petronii Ramos-Porto & Souza, 1994), L. felderi n. sp. (see below).

DISTRIBUTION. — Western Atlantic from North Carolina, USA, through Caribbean and Gulf of Mexico to São Paulo, Brazil; Eastern Pacific from Gulf of California to Colombia; Indo-West Pacific from Madagascar to Hawaii.

DIAGNOSIS. — Carapace glabrous, with more or less conspicuous longitudinal anterolateral suture; branchiostegial margin with pronounced lip. Frontal margin rounded, without rostrum, or with acute median rostral projection; orbital teeth absent; orbital hoods with or without small crests above eyes. Pterygostomial angle rounded. Eyes completely concealed in dorsal view, visible in frontal view, eyestalk with more or less developed rounded anteromesial process. Antennular peduncle slender to relatively stout; first segment with strong tooth on ventromesial carina; stylocerite more or less apressed to first segment; second segment sometimes elongated, much longer than visible portion of first; lateral antennular flagellum biramous, shorter ramus with at least two free segments. Antenna with basicerite robust; carpocerite exceeding scaphocerite; flagellum robust, compressed. Mandible with bisegmented palp; incisor process usually with five to seven triangular distal teeth, molar process with distal rows of setae and lamellae. First maxilliped with palp (endopod) elongated and caridean lobe greatly expanded. Second maxilliped with epipod elongated. Third maxilliped pediform; lateral plate conspicuously elongated, acute or subacute; ultimate segment with rows of long, distally thickened setae, tip unarmed. First pereiopods (chelipeds) enlarged, very unequal in size, asymmetrical in shape, carried flexed; major cheliped on left or right side (chelipeds antisymmetrical). Major cheliped slender, smooth or with small rugosities on ischium, merus and chela; ischium with or without tooth on ventromesial margin; merus slender, elongated, more or less flattened or shallowly excavated on ventral margin; carpus cup-shaped, sometimes ventrally depressed and with distal processes or lobes; palm with or without small tubercles or granules, with broad, shallow ventromesial groove, linea impressa absent; fingers often strongly curved or forceps-shaped, sometimes gaping, cutting edges usually armed with variously shaped teeth, snapping mechanism absent; dactylus with or without dense rows of filtering setae; adhesive discs present or absent. Second pereiopod with five- or four-segmented carpus. Third and fourth pereiopods compressed; third pereiopod with ischium unarmed or armed with one spine on ventral margin; carpus armed with spine on distoventral margin; propodus armed with three to five spines on ventral margin; dactylus simple, conical.

Table 1. — Preliminary list of species of *Leptalpheus* Wiiliams, 1965 and *Fenneralpheus* Felder & Manning, 1986. Abbreviations: **CAL**, Thalassinidea, Callianassidae; **LAO**, Thalassinidea, Laomediidae; **LYS**, Stomatopoda, Lysiosquillidae; **UPO**, Thalassinidea, Upogebiidae.

Species	Locality	Host species (family)	Reference
L. axianassae	São Paulo, Brazil	Axianassa australis (LAO)	Dworschak & Coelho 1999
	Fort Pierce, Florida	Axianassa australis (LAO)	Felder et al. 2003
	Itamaraca, Pernambuco, Brazi	l "Thalassinidea"	Ramos-Porto & Souza 1994
			(as L. petronii)
	Paripe, Pernambuco, Brazil	No data	Coelho dos Santos & Coelho 2001
	•		(as L. petronii)
L. felderi n. sp.	Isla Margarita, Venezuela	Upogebia omissa (UPO)	present study
•	Bahía de Cispata, N Colombia	a No data	present study
L. forceps	North Carolina	Upogebia affinis (UPO)	Williams 1965a, b, 1984
	Mississippi	Lepidophthalmus Iouisianensis (CAL)	Dawson 1967
	Old Tampa Bay, Florida	Upogebia affinis (UPO)	Saloman 1971
	Old Tampa Bay, Florida	Upogebia affinis (UPO)	Simon & Dauer 1977
	Florida	No data	Abele & Kim 1986
	Fort Pierce, Florida	Upogebia cf. affinis (UPO)	A. Anker pers. obs.
	E Gulf of Mexico (Florida)	No data	Posey et al. 1998
	NW Florida	Lepidophthalmus Iouisianensis (CAL)	Felder & Rodriguez 1993
	Bay St. Louis, Mississippi	Lepidophthalmus Iouisianensis (CAL)	Felder & Rodriguez 1993
	Tamaulipas, Mexico	Lepidophthalmus Iouisianensis (CAL)	Felder & Rodriguez 1993
	Veracruz, Mexico	Neocallichirus grandimana (CAL)	Hermoso Salazar 2001
	Sacrificios, Veracruz, Mexico	No data	McClure 2005
	Cahuita, Costa Rica	Lepidophthalmus sp.	A. Anker pers. obs.
L. cf. forceps A	Sergipe, Brazil	Lepidophthalmus siriboia (CAL)	Christoffersen 1980, 1998
	31		(as L. forceps, host as
			Callianassa jamaicensis)
L. cf. forceps B	Obispo, Cariaco, Venezuela	Upogebia omissa (UPO)	Muñoz Alcala & Blanco Rambla 2000
L. sp. 1 aff. forceps	Florida	No data	D. Felder pers. comm.
	Fort Pierce, Florida	Neocallichirus grandimana (CAL)	A. Anker pers. obs.
L. sp. 2 aff. forceps	Florida	No data	Felder & Manning 1997a, b; Felder &
			Staton 2000
	Belize	Lepidophthalmus richardi (CAL)	Felder & Manning 1997a
	E Mexico	Lepidophthalmus manningi (CAL)	Felder & Staton 2000
	N Colombia	No data	A. Anker pers. obs.
	Isla Tortuga, Venezuela	Glypturus acanthochirus	A. Anker & C. Lira pers. obs.
	3.,	or Neocallichirus grandimana (CAL)	
L. sp. 3 aff. forceps	N Colombia	No data	A. Anker pers. obs.
L. sp. 4 aff. forceps	N Panama (Caribbean coast)	Neocallichirus sp. (?) (CAL)	A. Anker, pers. obs.
L. mexicanus	Mulegé, Baja California	Upogebia sp. (UPO)	Ríos & Carvacho 1983
	Mulegé, Baja California	Upogebia dawsoni (UPO)	Ríos 1992
	La Paz, Baja California	Upogebia dawsoni (UPO)	Campos et al. 1995
L. sp. 5 aff. mexicanus	Bahía Málaga, W Colombia	No data	Ramos 1995 (as L. mexicanus)
L. sp. 6 aff. mexicanus	Nicaragua (Pacific coast)	No data	Felder et al. 2003 (as L. nov. sp. D)
L. pacificus	Oahu, Hawaii	No data	Banner & Banner 1974
L. cf. pacificus A	Toliara, SW Madagascar	No data	Banner & Banner 1983 (as L. pacificus)
L. cf. pacificus B	Viti Levu, Fiji	Neocallichirus sp.	A. Anker pers. obs.
	-	or Callianassa sp. (CAL)	•
L. cf. pacificus C	Nhatrang, S Vietnam	Glypturus cf. armatus (CAL)	A. Anker pers. obs.
L. sp. 7 aff. pacificus	Panglao, Philippines	Glypturus sp. (CAL)	A. Anker pers. obs.
L. sp. 8	Nicaragua (Pacific coast)	No data	Felder et al. 2003 (as L. nov. sp. A)
L. sp. 9	Nicaragua (Pacific coast)	No data	Felder et al. 2003 (as L. nov. sp. B)
<i>L.</i> sp. 10	Nicaragua (Pacific coast)	No data	Felder et al. 2003 (as L. nov. sp. C)
<i>L.</i> sp. 11	Costa Rica (Pacific coast)	No data	A. Anker pers. obs.
F. chacei	Indian River, Florida	?Lysiosquilla scabricauda (LYS)	Felder & Manning 1986
	Key West, Florida	?Lysiosquilla scabricauda (LYS)	Felder & Manning 1986
F. sp. 1	Florida	No data	Felder et al. 2003 (as F. nov. sp. E)

Fifth pereiopod with propodus bearing well developed brush of setae. Sixth abdominal somite with articulated plate at posteroventral angle. Male second pleopod with appendix interna and appendix masculina. Uropod with posterior margin of exopod truncate; diaeresis with deep

incision proximal to mesial margin of exopod; lateral spine strong. Telson with two pairs of dorsal spines and two pairs of posterolateral spines; posterior margin rounded; anal tubercles absent or poorly developed. Gill formula: five pleurobranchs (P1-5); one well developed

or hypertrophied arthrobranch (Mxp3); Mxp2 without podobranch; two lobed epipods (Mxp1-2); five strap-like epipods or mastigobranchs (Mxp3, P1-4); five sets of setobranchs (P1-5); three exopods (Mxp1-3).

REMARKS

The emended diagnosis of *Leptalpheus* includes features of all described and several undescribed species known to the senior author. In view of the increasing morphological heterogeneity of *Leptalpheus* s.l., several species may be subsequently assigned to other genera (D. Felder pers. comm.). In this case, the diagnosis of *Leptalpheus* s.s. will be restricted to the type species, *L. forceps*, and several closely related species. As a first step to the general revision of *Leptalpheus* s.l. and pending generic rearrangements, we define three morphologically distinctive species groups.

Leptalpheus forceps species group

This species group corresponds to *Leptalpheus* s.s. (sensu Williams 1965a) and includes at least 10 species from the western Atlantic and eastern Pacific: L. forceps, L. mexicanus, L. felderi n. sp. and several undescribed species (L. spp. 1-4 aff. forceps, L. spp. 5-6 aff. mexicanus, and L. sp. 11 in Table 1). In the western Atlantic, the *L. forceps* group is represented by at least six species and ranges from North Carolina (one species) to Florida (three species), Gulf of Mexico (at least three species) and Caribbean (at least four species), extending further south to Brazil (one or more species). In the eastern Pacific, it is represented by at least four species ranging from the central Gulf of California (one species) to Nicaragua (three species) and further south to Colombia (one species).

DEFINITION

Frontal margin without (most species) or with (*Leptalpheus mexicanus*) median rostral projection; orbital hoods without (most species) or with (*L. felderi* n. sp. and *L.* sp. 3 aff. *forceps*) small crests. Antennular peduncle usually slender, with each segment longer than wide, second segment

considerably (most species) or slightly (L. felderi n. sp.) elongated; stylocerite apressed against first segment of antennular peduncle, not reaching distal margin of first segment. Major cheliped with ischium bearing blade-shaped or triangular tooth on ventromesial margin; surface (especially chela and margins of merus and ischium) more or less rugose, covered by granules or minute tubercles; major chela without adhesive discs; dactylus of major chela without (most species) or with (L. felderi n. sp., L. sp. 11) dense row of long filtering setae; cutting edges armed with variously shaped teeth. Second pereiopod with five (most species) or four (L. felderi n. sp.) carpal segments. Third pereiopod without (most species) or with (*L. felderi* n. sp.) ventral spine on ischium. Uropodal exopod with subtriangular posterolateral margin.

REMARKS

Within the *L. forceps* group, *L. felderi* n. sp. is clearly the most aberrant species, differing from other species by the stouter less elongated antennular peduncles; the longer stylocerite, almost reaching the distal margin of the first segment of the antennular peduncle, less apressed and with a more individualized tip; the second pereiopod with four-segmented carpus; the ischium of the third pereiopod armed with spine; and the serrated fingers of the minor cheliped. These differences could be sufficient for a placement of this species in a separate species group. However, the characteristic orbital crests and the long setae on the dactylus of the major chela are also present in two undescribed species with clear affinities to *L. forceps*. Furthermore, *L. forceps*, L. mexicanus and L. felderi n. sp. share the presence of a triangular or blade-like tooth on the ventromesial side of the ischium of the major chelipeds, which is in our opinion a very good phylogenetic character. Therefore, *L. felderi* n. sp. seems appropriately placed in the *L. forceps* group.

Leptalpheus pacificus species group

This species group includes *L. pacificus* and several closely related forms (*L.* cf. *pacificus* A-C and *L.* spp. 7 aff. *pacificus* in Table 1). All members of this group

occur in the Indo-West Pacific: Madagascar, Vietnam, Philippines, Fiji and Hawaii (see Table 1).

DEFINITION

Frontal margin without rostrum; orbital hoods without crests. Antennular peduncle slender, with each segment longer than wide, second segment moderately elongated; stylocerite laterally convex, only slightly apressed against first segment of antennular peduncle, reaching or overreaching distal margin of first segment. Major cheliped with ischium lacking tooth on ventromesial margin; surface smooth, without granules or tubercles; major chela with large adhesive discs; dactylus of major chela without dense row of long filtering setae; cutting edge of pollex armed with only two large teeth; dactylus distoventrally thickened, with one or two teeth. Second pereiopod with five carpal segments. Third pereiopod with unarmed ischium. Uropodal exopod with bluntly angular posterolateral margin.

Remarks

The *L. pacificus* group differs from the *L. forceps* group (*Leptalpheus* s.s.) mainly by three characters on the major cheliped: the chela, merus and ischium smooth, without granules or tubercles; the presence of well developed adhesive discs; and the pollex armed with two peculiar teeth, a larger proximal tooth and a smaller subdistal tooth (Banner & Banner 1974; Anker 2001).

Leptalpheus axianassae species group

This species group includes the remaining species, *L. axianassae* (= *L. petronii*, see below) from the western Atlantic (Florida to Brazil), and possibly three further *Leptalpheus* spp. from the Pacific coast of Nicaragua (Felder *et al.* 2003; *L.* spp. 8-10 in Table 1).

Definition (based on features of *L. axianassae*)

Frontal margin without rostrum; orbital hoods without crests. Antennular peduncle stout, with each segment about as long as wide, second segment not elongated; stylocerite laterally convex, not apressed

against first segment of antennular peduncle, reaching distal margin of first segment. Major cheliped with ischium lacking tooth on ventromesial margin; surface smooth, without granules or tubercles; major chela with large adhesive discs; dactylus of major chela without dense row of long filtering setae; cutting edge of pollex with obtuse ridge proximally, without pronounced teeth; dactylus ventrally thickened, without teeth. Second pereiopod with five carpal segments. Third pereiopod with ischium unarmed. Uropodal exopod with bluntly angular posterolateral margin.

REMARKS

Leptalpheus axianassae differs from all the other species of Leptalpheus by the much stouter antennular peduncles (with segments only slightly longer than wide); the presence of a small tubercle on the eyestalk; and the absence of a well defined teeth armature on the fingers of the major chela (Dworschak & Coelho 1999). The *L. axianassae* group is possibly more closely related to the *L. pacificus* group. Both species groups share the presence of adhesive discs on the major chela; the general shape of the fingers of the major chela; the laterally convex stylocerite (less apressed to the segment compared to species of the *L. forceps* group), reaching to or slightly beyond the distal margin of the first segment of the antennular peduncle (vs. not reaching this margin in species of the *L. forceps* group); and the major cheliped lacking granules or tubercles, and without tooth on the ventromesial side of the ischium (both features present in the *L. forceps* group).

Leptalpheus forceps species group

Leptalpheus felderi n. sp. (Figs 1-5; 6A, B)

Type Material. — Holotype: Venezuela, Estado Nueva Esparta, Isla Margarita, southern shore near Guamache, sandy, slightly muddy substrate, near shore, close to mangrove and sea grass beds, with yabby pump, depth 0.5-1 m, from burrow of *Upogebia omissa*, 13.XII.2003, coll. A. Anker & J. A. Vera Caripe, 1 ovigerous \$\forall\$, CL 6.0, TL 20.0 (MNHN-Na 13620).

Paratypes: same locality and collectors as for holotype,

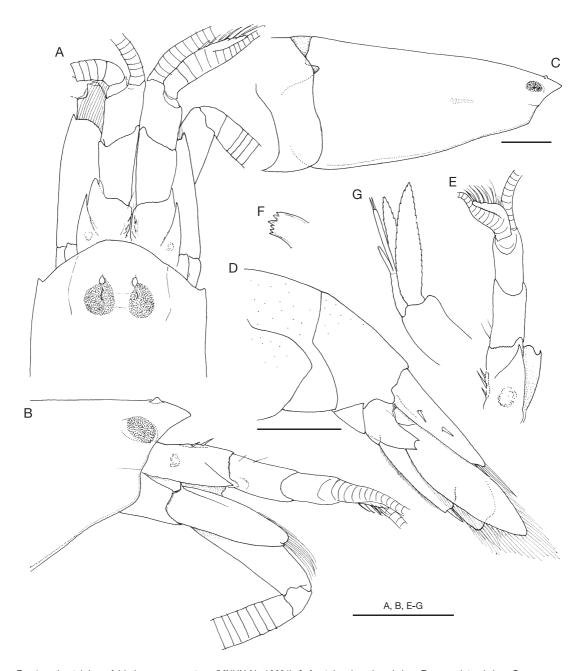


Fig. 1. — Leptalpheus felderi n. sp., & paratype (MNHN-Na 13621): **A**, frontal region, dorsal view; **B**, same, lateral view; **C**, carapace, lateral view; **D**, posterior abdominal segments and tail fan, lateral view; **E**, antennule, lateral view; **F**, mandible, incisor process; **G**, second pleopod. Scale bars: 1 mm.

depth 0.5 m, from burrow of *Upogebia omissa* (host deposited under MNHN-Th 1460), 14.XII.2003, 1 σ (photographed, dissected), CL 5.2, TL 16.4 (MNHN-Na

13621). — Same locality and collectors as for holotype, depth 0.5-1 m, from burrow of *Upogebia omissa* (host deposited under MNHN-Th 1461, two parasitic bopyrids,

1 σ and 1 φ , detached from host and deposited under MNHN-Ep 1007), 13.XII.2004, 1 σ , CL 5.8, TL 18.6, 1 φ , CL 7.6, TL 23.8 (both specimens photographed, female with all pereiopods regenerating on left side) (MNHN-Na 13679). — Same locality and collectors as for holotype, depth 0.5 m, from burrow of *Upogebia omissa* (host deposited under USNM 1073867), 14.XII.2003, 1 φ , CL 5.8, TL 16.5 (USNM 1073866). — Same locality as for holotype, depth 0.5 m, from burrow, 5.II.2004, coll. C. Lira, 1 σ , CL 5.2, TL 16.1 (photographed) (IVIC 1128).

Type Locality. — Venezuela: Estado Nueva Esparta, Isla Margarita, southern shore, Guamache.

ETYMOLOGY. — We are pleased to name this remarkable new species in honour of Dr Darryl L. Felder (University of Louisiana, Lafayette), a renowned carcinologist and world authority of infaunal decapods.

OTHER MATERIAL EXAMINED. — Colombia. Caribbean coast, Bahía Cispata, mouth of Río Sinú, Cienaga Soledad, among mangrove roots, with yabby pump, 8.I.1995, coll. D. L. Felder, R. Lemaitre and S. F. Nates, 1 immature \mathfrak{P} , CL 3.3, TL 9.4 (identified as *Leptalpheus* "nov. sp. C" [DLF]) (USNM 1022183).

DISTRIBUTION. — Presently known from two localities in the southern Caribbean Sea: Isla Margarita, Venezuela (type locality) and Bahía Cispata, Colombia.

DESCRIPTION

Body elongate, carapace and abdomen somewhat compressed laterally, glabrous (Fig. 1C), with very short, scarce setae. Carapace with inconspicuous suture proximal to base of antenna (Fig. 1A, B). Frontal margin rounded, without rostrum and orbital teeth; orbital hood with two small, triangular crests above each eye (Fig. 1A-C). Pterygostomial angle rounded, not protruding (Fig. 1B). Eyes completely covered by carapace, not visible in dorsal view, with feebly marked anteromesial process; cornea well developed. Ocellar beak not conspicuous.

Antennular peduncle relatively stout (Fig. 1A), second segment longer than dorsally visible portion of first segment; stylocerite not reaching distal margin of first segment, distally subacute (Fig. 1A, E); dorsomesial carina with slender spinules (Fig. 1E); ventromesial carina with strong tooth (Fig. 1E); lateral flagellum biramous, with shorter ramus well developed, situated at third-fourth segment (Fig. 1B, E). Antenna with basicerite bearing strong

ventrolateral tooth (Fig. 1B); scaphocerite broad, anterior margin of blade not protruding anteriorly, not reaching level of distolateral spine (Fig. 1A); carpocerite long, robust, reaching far beyond scaphocerite (Fig. 1B).

Mouthparts typical for genus. Mandible with incisor process bearing six teeth, third largest (Fig. 1F). Maxillule bilobed with palp, both lobes with one seta. First maxilliped with greatly expanded caridean lobe on exopod. Second maxilliped with elongated epipod; propodus without distinct transverse suture. Third maxilliped relatively slender (Fig. 4A); lateral plate produced towards exopod, acute; ultimate segment with rows of long, distally thickened setae, tip unarmed; arthrobranch well developed (Fig. 4A).

First pereiopods (chelipeds) very asymmetrical, unequal (Figs 2; 3), carried flexed ventrally or ventromesially; major cheliped (either on left or on right side) robust, elongated; ischium short, ventromesial margin with subtriangular tooth (Figs 2A, F; 3A); merus elongate, distally slightly widening, with two rounded lobes ventrally depressed (Fig. 2A, G), lateral margin slightly rugose (Fig. 2A, G), mesial margin almost straight (Figs 2A; 3A); carpus short, more or less cup-shaped, ventrally depressed, distally with two very strong, subacute ventral processes (Fig. 2A, C, E); chela subcylindrical; palm ventromesially with shallow groove (Fig. 2B, C), ventral margin with irregular granules and small tubercles (Fig. 2); adhesive discs absent; fingers about as long as palm, gaping proximally when closed (Fig. 2B, D), tips distally crossing (Fig. 2C, E); pollex ventrally rugose, distally strongly curved mesially (Figs 2C, E; 5A), distomesially with dense row of setae (Figs 2B, E; 3A); cutting edge armed with teeth as illustrated (Figs 2B, D; 3B): one small and one larger proximal teeth, one very large subtriangular tooth at mid-length and one large subdistal tooth; dactylus massive, distally curved ventrally (Fig. 2C, D); dorsolateral distal half with dense rows of fine, long setae (Figs 2; 3A); cutting edge armed with teeth as illustrated (Figs 2B, D; 3B): two large proximal teeth, one very large subtriangular tooth at mid-length, followed by one smaller tooth and small irregular, rounded subdistal teeth; largest tooth of pollex juxtaposed by mesial surface with that of dactylus when fingers

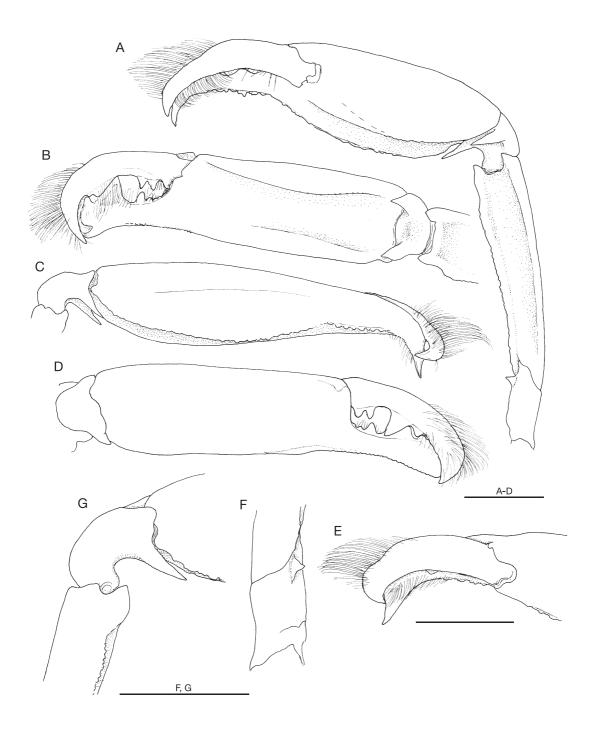


Fig. 2. — Leptalpheus felderi n. sp., & paratype (MNHN-Na 13621), right major cheliped: **A**, general aspect, ventromesial view; **B**, chela, mesial view; **C**, same, ventral view; **D**, same, lateral view; **E**, fingers of chela, dorsal view; **F**, ischium, ventrolateral view; **G**, distal merus and carpus, lateral view. Scale bars: 1 mm.

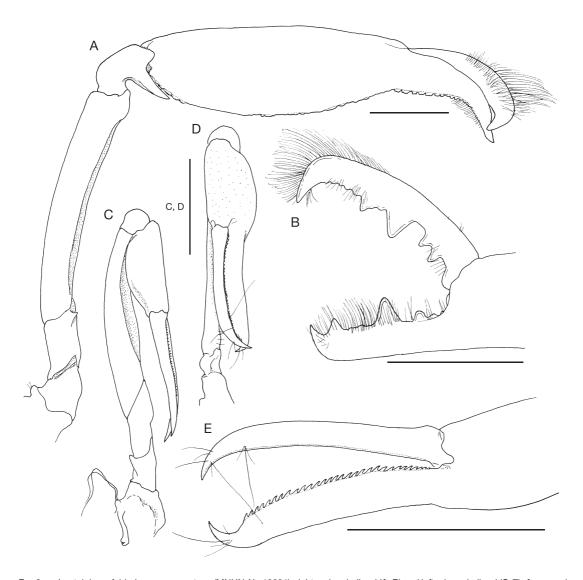


Fig. 3. — Leptalpheus felderi n. sp., σ paratype (MNHN-Na 13621), right major cheliped (**A**, **B**) and left minor cheliped (**C**-**E**): **A**, general view, lateral view; **B**, fingers of chela opened, mesial view; **C**, general aspect, lateral view; **D**, same, ventral view; **E**, fingers of chela. Scale bars: 1 mm.

closed (Fig. 2D). Minor cheliped much smaller than major cheliped, slender, carried flexed (Fig. 3C, D); ischium short, unarmed, merus ventrally shallowly depressed; carpus very short, cup-shaped; chela strongly flattened on mesial side (Fig. 3D), fingers 1.5 times longer than palm, distally curved, with tufts of elongated setae (Fig. 3E), tips crossing (Fig. 3D); cutting edge of pollex serrated with

proximally directed, acute teeth; cutting edge of dactylus unarmed (Fig. 3E).

Second pereiopod slender; ischium about 3/4 length of merus; carpus four-segmented, segments with ratio approximately equal to 4/1/1/2 (Fig. 4B); chela simple, fingers robust, longer than palm (Fig. 4C). Third and fourth pereiopods very robust, flattened on mesial side; third pereiopod

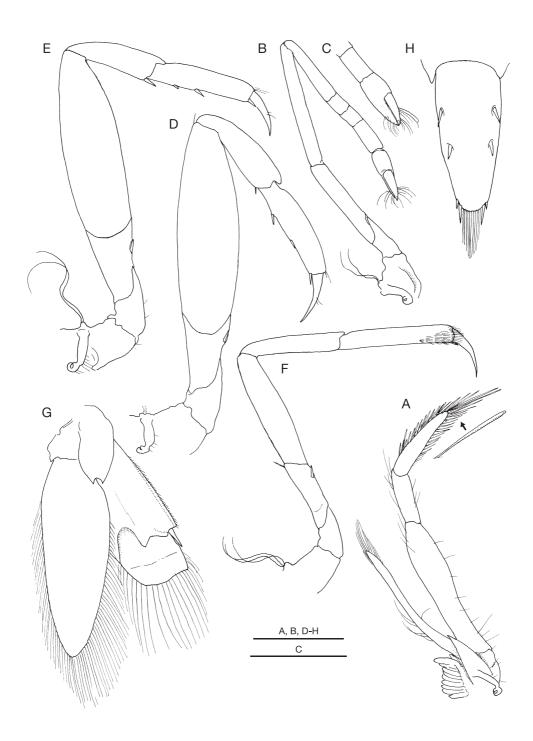


Fig. 4. — Leptalpheus felderi n. sp., σ paratype (MNHN-Na 13621): **A**, third maxilliped, lateral view; **B**, second pereiopod, lateral view; **C**, same, distal segment of carpus and chela; **D**, third pereiopod, lateral view; **E**, fourth pereiopod, lateral view; **F**, fifth pereiopod, lateral view; **G**, uropod, dorsal view; **H**, telson, dorsal view. Scale bars: 1 mm.

with ischium bearing one spine situated in a small pit on ventral margin (Fig. 4D); merus inflated, about 2.5 times as long as ischium, and more than twice as long as carpus, unarmed; carpus with small distoventral spine (Fig. 4D); propodus longer than carpus, ventrally with two spines + one distoventral spine proximal to dactylus; dactylus simple, robust, about half length of propodus, curved (Fig. 4D); fourth pereiopod (Fig. 4E) very similar to third. Fifth pereiopod much more slender than third and fourth (Fig. 4F); ischium armed with one spine on ventral margin, distodorsal margin with one long slender spine-like seta; merus only 1.5 times as long as carpus; carpus slender, unarmed; propodus about 1.5 length of carpus, unarmed, distally with five or six rows of setae; dactylus similar to that of third and fourth pereiopods (Fig. 4F).

Abdominal segments I-V with posteroventral angles rounded (Fig. 1D); segment VI with rounded posterior projection and with articulated plate ventroposteriorly (Fig. 1D); preanal plate posteriorly rounded. Male second pleopod with appendix masculina and appendix interna; appendix masculina slender, twice as long as appendix interna, almost reaching distal margin of endopod, distally with two slender spines (Fig. 1G). Uropods distinctly exceeding telson (Figs 1D; 5C); lateral lobe of sympodite distally with two acute tooth; endopod much longer than exopod (Fig. 4G); exopod posteriorly truncate, laterally angular and slightly protruding (Fig. 4G); diaeresis laterally straight, mesial portion deeply incised forming a triangular tooth proximal to mesial margin; lateral spine well developed (Fig. 4G). Telson relatively slender, about 2.5 times as long as wide proximally (Fig. 4H); dorsal surface with two pairs of spines situated more or less close to lateral margin, at about proximal 1/3 length and slightly posterior to mid-length of telson, respectively (Figs 1D; 4H); posterior margin rounded, with two pairs of posterolateral spines, lateral much shorter than mesial (Fig. 4H); anal tubercles absent.

Gill formula typical for genus: pleurobranchs above first to fifth pereiopods; arthrobranch above third maxilleped; podobranch absent; lobed epipods on first and second maxillipeds; mastigobranchs (strap-like epipods) on third maxilliped and first

to fourth pereiopods; sets of setobranchs on first to fifth pereiopods; exopods on first to third maxillipeds.

Size

CL ranges from 3.3 to 7.6 mm, TL ranges from 9.4 to 23.8 mm. Diameter of eggs in ovigerous female (holotype) about 0.5×0.7 mm.

Colour

General appearance pinkish-red (Fig. 6A, B); lateral carapace and most ventral portions of pleura pale or whitish semitransparent; dorsal carapace, most of abdomen, telson, endopod of uropod, antennular and antennal peduncles pinkish red due to numerous reddish chromatophores arranged in more or less distinct broad transverse bands on abdomen and longitudinal bands on carapace; chromatophores more dense on antennular peduncles and endopod of uropod; chelipeds whitish, opaque, with pinkish tinge; walking legs, exopod of uropod and antennal flagella semitransparent; eyes dull green; eggs or gonad egg mass (visible by transparence) dull green.

Variability

The uropodal endopod is posteriorly rounded in most specimens (Fig. 4G). Remarkably, in one of the male paratypes (MNHN-Na 13679), the uropodal endopods are considerably elongated posteriorly, and at least the right endopod presents traces of segmentation in the most distal part of the elongation (Fig. 5C). The largest female specimen appears to have a less developed, lateral cornea and somewhat protruding anteromesial process on the eyestalks. The dorsal part of the eyestalks is not accessible without the total destruction of the frontal region of the carapace. The young female from Colombia (USNM 1022183) differs slightly in the armature of the fingers of the major cheliped (Figs 3B; 5B).

Ecology

Similar to the other species of *Leptalpheus*, *L. felderi* n. sp. appears to be an obligate commensal associate of thalassinidean mudshrimps. All Venezuelan specimens of *L. felderi* n. sp. were collected from

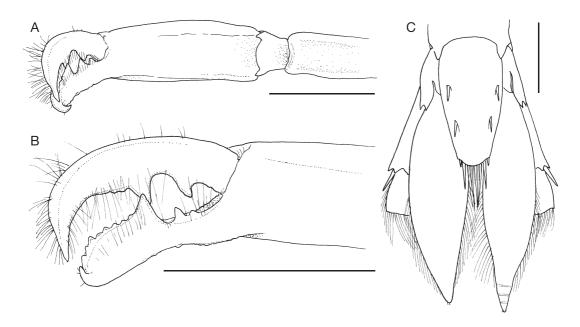


Fig. 5. — Leptalpheus felderi n. sp.: **A**, **B**, young ♀ from Colombia (USNM 1022183); **A**, right major cheliped, distal merus, carpus and chela, mesial view; **B**, same, fingers slightly opened; **C**, ♂ paratype from Venezuela (MNHN-Na 13679), telson and uropods, dorsal view. Scale bars: 1 mm.

thalassinidean burrows with the aid of a suction pump, although at only two occasions, the shrimps were obtained together with the host, the fairly large (adult specimens 4-5 cm TL) upogebiid mudshrimp Upogebia omissa Gomes Corrêa, 1968 (Fig. 6C). On two occasions, the alpheids were collected as cohabiting pairs from the same mudshrimp burrow. The burrow openings were situated a few meters from the shore, at a depth of 0.5-1 m, in purely marine water. The substrate was fine sand, patchily either firmer or muddier, with small stones and shell debris, and a few meters away from mangrove trees and sea grass beds. The burrow openings did not have conspicuous mounds and were rather small (diameter from a few mm to 1 cm), contrasting with the much larger (diameter up to 3 cm) openings of the lined spacious tunnels of the large callianassid mudshrimp Glypturus acanthochirus Stimpson, 1866 (one captured specimen measured 15 cm TL) (see Dworschak & Ott 1993 for description of burrows of G. acanthochirus). The only other crustacean collected from a burrow at this site was a single specimen of Alpheus cf. armillatus H. Milne Edwards,

1837. The immature specimen from Colombia was collected from a burrow of an undetermined host among mangrove roots.

The captured individuals of *L. felderi* n. sp. and other species of *Leptalpheus* are very agile and move (crawl or swim) very quickly (A. Anker pers. obs.). Williams (1984) reported that specimens of *L. forceps* "have been often taken at night in surface plankton inside inlets and in tidal currents in the sounds of North Carolina". Thus, it is likely that these commensal shrimps leave the burrow and forage outside during the night.

BIOLOGY AND TAXONOMY OF HOST

Upogebia omissa is widely distributed in Brazil and throughout the Caribbean region (Williams 1993). The feeding and burrowing behaviour and the burrow morphology of *U. omissa*, the host of *L. felderi* n. sp., were studied in Brazil by Coelho *et al.* (2000). Most burrows of *U. omissa* were Y- or U-shaped, but several consisted of a single, oblique tunnel. The burrows spread vertically rather than horizontally and were occasionally interconnected.

The mudshrimp filtered suspended particles, and also fed directly on the sediment. Filter-feeding occurred mainly within U-shaped tunnels, while deposit-feeding was observed in association with the oblique tunnels of the burrow (Coelho *et al.* 2000). In Brazil, *U. omissa* is sometimes infested by the bopyrid isopod *Parione tropica* Lemos de Castro & Brasil-Lima, 1975 (Brasil-Lima 1998). Two of our specimens were also infested by branchiostegial bopyrids.

Upogebia omissa is presently believed to be a morphologically variable species. The variation affects the number of the post-orbital spines on the carapace (one or two) and distodorsal spines on the merus of the second pereiopod (one or two), the development of spines on the abdominal sternites and some other features (Williams 1993). Most specimens from Isla Margarita have two post-orbital spines, one distodorsal spine on the merus of the second pereiopod and only a few lateral spines on the anterior abdominal sternites. The presence of only one distodorsal spine on the merus of the second pereiopod characterizes U. omissago Williams, 1993, which is also present in Venezuela (Williams 1997). Both *U. omissa* and U. omissago are probably two complexes with unappreciated variation that departs from the key characters presently in use (D. Felder pers. comm.), and would need a thorough revision.

REMARKS

The new species can be separated from all other species of the genus by the presence of small triangular crests on the orbital hoods; the dense row of long, flexible setae on the dactylus of the major chela; the unique armature on the cutting edges of the fingers of the major chela; two subacute processes on the carpus of the major chela; the minute, saw-like teeth on the pollex of the minor chela; and the carpus of the second pereiopod bearing only four instead of five segments.

The long filtering setae on the dactylus of the major cheliped are also present in an undescribed species of *Leptalpheus* from the Pacific coast of Costa Rica (A. Anker pers. obs.); however, this species (*Leptalpheus* sp. 11 in Table 1) lacks orbital crests and has a somewhat different armature on the cutting edges of the major chela. Neverthe-

less, it is possible that this eastern Pacific species (known from Costa Rica and possibly Nicaragua, cf. Table 1) is the closest relative of the western Atlantic *L. felderi* n. sp.

The posterior elongation of the uropods, as found in one of the male paratypes, is also observed in three other alpheids, Stenalpheops anacanthus Miya, 1997, S. crangonus (Anker, Jeng & Chan, 2001) and Mohocaris bayeri Holthuis, 1973. In S. anacanthus and S. crangonus, these caudal appendices are also segmented, but situated on the exopod (Miya 1997; Kim 1998; Hayashi 1998), while in *M. bayeri* they are not segmented and situated on the endopod (Holthuis 1973), as in the male paratype of *L. felderi* n. sp. Interestingly, both species of Stenalpheops are also associated with thalassinideans: S. anacanthus with *Upogebia major* (De Haan, 1939) and *Nihonot*rypaea japonica Ortmann, 1891 (Hayashi 1998; see Manning & Tamaki 1998; Wardiatno & Tamaki 2001 and Tamaki 2003 for taxonomy of *N. japonica*), and S. crangonus with Austinogebia edulis (Ngoc-Ho & Chan, 1992) (Anker et al. 2001; see Ngoc-Ho 2001 for taxonomy of *A. edulis*). The morphology of *M. bayeri* (especially the highly specialized chelipeds and the elongated uropodal endopod) suggests that it is probably associated with burrows of larger crustaceans or other organisms in deeper waters. The function of the elongated caudal appendices, if there is any, remains unknown (see also Hayashi 1998; Anker et al. 2001), as remains unanswered the question why these appendices are present in one specimen of *L. felderi* n. sp. and absent in others.

The reddish longitudinal banding of *L. felderi* n. sp. (Fig. 6A, B) may prove to be another species-diagnostic feature. The only other species for which the live colour description was published is *L. forceps*, described as "translucent, colourless in life" (Williams 1984). In reality, this species has very pale greenish transverse bands on the abdomen, while the antennules and the antennae are pale lettuce-greenish, and the tail fan has locally pinkish, bluish and greenish tinge (A. Anker pers. obs.). *Leptalpheus* spp. from the Indo-West Pacific (Vietnam, Philippines, Fiji) are colourless (with pink tinge) or uniform pink-reddish, sometimes with a diffuse transverse banding on the abdomen (A. Anker pers. obs.).



Fig. 6. — Leptalpheus felderi n. sp. (**A**, **B**) and host *Upogebia omissa* Gomes Corrêa, 1968 (**C**), habitus and colour patterns in life: **A**, *♂* paratype (IVIC 1128), dorsal view; **B**, ♀ paratype (MNHN-Na 13679), lateral view; **C**, *U. omissa*, lateral view.

DISCUSSION

With *L. felderi* n. sp., the genus *Leptalpheus* contains six nominal species, the others being *L. forceps, L. pacificus, L. mexicanus, L. axianassae* and *L. petronii*. The latter two species have

been suspected to be synonymous (D. Felder pers. comm.; see below), while numerous other species are undescribed (Felder *et al.* 2003; Anker 2001; see Table 1). The presently monotypic genus *Fenneralpheus* Felder & Manning, 1986 is closely related to *Leptalpheus* (Felder & Manning

1986; Anker 2001; Felder *et al.* 2003) and also contains undescribed species (Felder *et al.* 2003). The American species of *Leptalpheus* and *Fenneralpheus* are currently under study by D. Felder and R. Robles, while two Indo-West Pacific species, including an undescribed species from the Philippines, are currently under study by the first author. Three literature records of *Leptalpheus* species, the taxonomic status of *L. petronii* and the relationships between *Leptalpheus* and *Fenneralpheus* are briefly discussed here.

LEPTALPHEUS FORCEPS

Muñoz Alcala & Blanco Rambla (2000) reported L. forceps from burrows of Upogebia omissa in the Ensenada Grande del Obispo, Golfo de Cariaco, Estado Sucre (mainland Venezuela, south of Isla Margarita). The identity of the specimens from Obispo remains uncertain, as they could belong to L. forceps, L. felderi n. sp. or to one of the several undescribed Caribbean species (*Leptalpheus* spp. 1-3 aff. forceps in Table 1). One of these undescribed species (Leptalpheus sp. 2 aff. forceps in Table 1) was recently collected on the island of La Tortuga by one of us (CL). This specimen was associated with a large callianassid, probably Glypthurus acanthochirus Stimpson, 1866 or Neocallichirus grandimanus (Gibbes, 1850) (C. Lira pers. obs.). Thus, at least two species of Leptalpheus are present in Venezuelan waters.

LEPTALPHEUS MEXICANUS

The record of *L. mexicanus* from Bahía Málaga, Pacific coast of Colombia (Ramos 1995), is doubtful. The illustrated specimen (Ramos 1995: fig. 1) shows clear differences with the type specimen of *L. mexicanus* from Río Mulegé, Baja California Sur, Mexico (cf. Ríos & Carvacho 1983). The most important differences are the much narrower and elongated frontal margin, the juxtaposed eyestalks (separated in *L. mexicanus*) and the stylocerite distinctly overreaching the distal margin of the first segment of the antennular peduncle (not even reaching this margin in *L. mexicanus*). In our opinion, Ramos' specimen certainly represents an undescribed species closely related to *L. mexicanus* (*Leptalpheus* sp. 5 aff. *mexicanus* in Table 1).

LEPTALPHEUS PACIFICUS

This species is presently known only from Oahu, Hawaii (type locality: Pearl Harbor) (Banner & Banner 1974), and from Toliara (Tuléar), Madagascar (Banner & Banner 1983). The latter record needs confirmation. The authors stated that the chelipeds of the single female (TL 7 mm) were more slender, with the large cheliped being 6.3 times as long as broad (4.4 times in the types of *L. pacificus*) and the small chela 5.6 times as long as broad (5.0 in the types), and suggested that "the small size of the specimen probably account for the different proportions". Unfortunately, this specimen (*L. cf. pacificus* A in Table 1) was not located in the collections of the MNHN, where it was originally deposited (Banner & Banner 1983).

Leptalpheus axianassae and L. Petronii

The taxonomic identity of *L. petronii*, described from Ilha de Itamaracá, Pernambuco, northeastern Brazil (Ramos-Porto & Souza 1994), is problematic. The original description of this species was published as an abstract in a publication with very limited distribution (Abstracts of the XXth Brazilian Congress of Zoology), without illustrations and proper diagnosis, and was not republished in a more complete form elsewhere. This description is clearly not in accordance with the standards of the *International Code of* Zoological Nomenclature (ICZN 1999). According to the very short morphological notes provided by Ramos-Porto & Souza, L. petronii matches L. axianassae, described and illustrated properly by Dworschak & Coelho (1999). The type locality of *L. axianassae* is São Sebastião, São Paulo, Brazil, situated approximately 2000 km south of the type locality of *L. petronii*. The recollections at the type locality of *L. petronii* confirmed that *L. petronii* is the same species as *L. axianassae* (D. Felder pers. comm.). Therefore, the inadequate description of L. petronii should be invalidated, and L. axianassae should take the nominal priority over *L. petronii*, despite the fact that the latter was described five years earlier. Leptalpheus axianassae appears to be distributed throughout Brazil, Florida, the Gulf of Mexico and the Caribbean Sea (D. Felder pers. comm.), and is associated with the same host, the laomediid mudshrimp Axianassa australis Rodrigues

& Shimizu, 1992 (Rodrigues & Shimizu 1992; Dworschak & Rodrigues 1997).

FENNERALPHEUS

Fenneralpheus chacei Felder & Manning, 1986 from Florida is closely related to *Leptalpheus*, as indicated by numerous features on the carapace, antennules, antennae, mouthparts, chelipeds, third to fifth pereiopods and uropods (Felder & Manning 1986; Anker 2001). Fenneralpheus can be distinguished from Leptalpheus by the major cheliped having a stouter merus and longer fingers; the cutting edges of the major chela fingers armed with particular teeth, described as "rounded, cuspate, obliquely oriented ridges, intermeshing near mid-length of fingers" (Felder & Manning 1986; Anker 2001); the pterygostomial angle anteriorly produced (vs. rounded in Leptalpheus); the scaphocerite of the antenna with reduced distolateral tooth; and the third maxilliped with penultimate segment more elongated, almost as long as antepenultimate segment, the latter divided in two sub-segments by a suture. Felder & Manning (1986) listed other differences, most of which however, e.g., the more pronounced ventral lip on the carapace and much larger size, are clearly not of generic importance.

Remarkably, Fenneralpheus shares some features with the L. forceps group (Leptalpheus s.s.), e.g., the stylocerite tightly appressed and not reaching the distal margin of the first segment of the antenular peduncle; the carpus of the major cheliped bearing distally two rounded processes (feature shared with at least two undescribed species and L. felderi n. sp.); and the cutting edges of the major chela armed with (somewhat modified) teeth. Although the host of E. chacei remains unknown, Felder & Manning (1986) assumed that this species may be associated with burrows of the lysiosquillid stomatopod Lysiosquilla scabricauda (Lamarck, 1818), and not with thalassinideans, as presumably all Leptalpheus species (see Table 1).

The present taxonomic situation of the generic complex *Leptalpheus-Fenneralpheus*, with numerous species remaining to be described (Table 1), does not allow hypotheses on the intra-generic relationships among the species of *Leptalpheus*, and a more conclusive definition of *Leptalpheus* s.s.

The preliminary phylogeny of the generic complex Leptalpheus-Fenneralpheus, based on the analysis of 16s mDNA of selective species (Felder et al. 2003: fig. 9), shows that Fenneralpheus forms a sister-group to Leptalpheus s.l., whereas Leptalpheus s.s. [L. forceps + L. sp. 6 aff. mexicanus] forms a sister group to [L. axianassae + L. spp. 8-10]. Unfortunately, L. pacificus and L. mexicanus were not included in this analysis. The presently available molecular data appear to contradict the morphological data, which supports the clade [Fenneralpheus-Leptalpheus s.s.] and thus results in the paraphyly of *Leptalpheus* (A. Anker unpubl. data). A more complete molecular and morphological analysis of Leptalpheus and Fenneralpheus is being prepared by D. Felder and R. Robles.

The biology of the associations between the alpheid shrimps of the genus Leptalpheus and the various mudshrimps from the infra-order Thalassinidea remains for the most part unknown, with the notable exception of Saloman's (1971) study of the ecology and reproductive biology in the type species of the genus, L. forceps Williams, 1965. The relationships between the shrimps and their hosts can be best described as commensal, although at least occasionally they may become mutualistic, for example, when the shrimp clean the burrow and/or the host. The dense, long, very fine setae on the fingers of the major chela of *L. felderi* n. sp. are probably used as a filtering brush. Such a filtering apparatus is also present in several other burrow-dwelling commensal alpheids, e.g., Athanas squillophilus Hayashi, 2002, associated with stomatopods, and A. dentirostris Anker, Jeng & Chan, 2001, associated with upogebiids (Anker et al. 2001; Hayashi 2002).

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