

The shrimp genus *Leptalpheus* Williams, 1965 in the southwestern Caribbean Sea, with description of one new species from Panama (Crustacea, Decapoda, Alpheidae)

Arthur ANKER

Instituto Smithsonian de Investigaciones Tropicales,
apartado 0843-03092, Balboa, Ancón, Panamá (Panama)
Current address: Florida Museum of Natural History, University of Florida,
250A Dickinson Hall, Gainesville, FL 32611-7800 (USA)
aanker@flmnh.ufl.edu

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ABSTRACT

Two species of the alpheid shrimp genus *Leptalpheus* Williams, 1965 are reported from the southwestern Caribbean Sea. *Leptalpheus pierrenoeli* n. sp. is described on the basis of a single male specimen collected from a burrow of unknown, presumably callianassid host on Isla Grande, Panama. This species differs from all other species of *Leptalpheus* by the dentition on the fingers of the major cheliped and the elongate stylocerite. *Leptalpheus* cf. *forceps* is recorded for the first time from Cahuita, Costa Rica, representing a considerable range extension of *L. forceps* Williams, 1965, previously known from North Carolina to the Gulf of Mexico, into the southern Caribbean Sea. The Cahuita specimens bear a peculiar segmented filament on the uropodal endopod (caudal filament), a feature not observed in the type specimens. Furthermore, they were found in association with the callianassid ghostshrimp, *Lepidophthalmus richardi* Felder & Manning, 1997. This finding represents a new host record for *L. forceps* and a significant range extension of *L. richardi*, previously known only from the type locality in Belize.

KEY WORDS

Crustacea,
Decapoda,
Alpheidae,
Leptalpheus,
Callianassidae,
Lepidophthalmus,
Caribbean,
western Atlantic
infaunal shrimp,
burrow,
commensalism,
new species.

RÉSUMÉ

Le genre de crevettes Leptalpheus Williams, 1965 dans le sud-ouest de la mer des Caraïbes, et description d'une nouvelle espèce du Panama (Crustacea, Decapoda, Alpheidae).

Deux espèces de crevettes alphéidées du genre *Leptalpheus* Williams, 1965 sont signalées du sud-ouest de la mer des Caraïbes. *Leptalpheus pierrenoeli* n. sp. est décrite d'après un unique spécimen mâle trouvé dans un terrier d'un hôte inconnu, probablement une crevette-taupe (Callianassidae), à Isla Grande au Panama. Cette espèce se distingue des autres espèces du genre *Leptalpheus* par la dentition sur les doigts de la grande pince et un stylocérite allongé. *Leptalpheus* cf. *forceps* est signalé pour la première fois de Cahuita au Costa Rica, ce qui représente une extension considérable de l'aire de distribution de *L. forceps* Williams, 1965, précédemment connue de la Caroline du Nord jusqu'au Golfe du Mexique, au sud de la mer des Caraïbes. Les deux spécimens mâles de *L. cf. forceps* de Cahuita possèdent un filament segmenté sur l'endopodite de l'uropode (filament caudal), celui-ci faisant défaut chez les spécimens types. En outre, ils ont été trouvés en association avec un callianassidé, *Lepidophthalmus richardi* Felder & Manning, 1997, ce qui représente une nouvelle association pour *L. forceps*, mais aussi un élargissement considérable de l'aire de distribution de *L. richardi*, qui auparavant n'était connue que de la localité type au Belize.

MOTS CLÉS

Crustacea,
Decapoda,
Alpheidae,
Leptalpheus,
Callianassidae,
Lepidophthalmus,
Caraïbe,
Atlantique occidental,
crevette,
faune des terriers,
commensalisme,
espèce nouvelle.

INTRODUCTION

The genus *Leptalpheus* Williams, 1965 was established for the peculiar alpheid shrimp *Leptalpheus forceps* Williams, 1965 originally described from North Carolina in the southeastern USA. Since then several species were described in this genus, two of them in the western Atlantic: *L. axianassae* Dworschak & Coelho, 1999 (subjective junior synonym *L. petronii* Ramos-Porto & Souza, 1994; see Anker *et al.* 2006b) from Brazil, and *L. felderi* Anker, Vera Caripe & Lira, 2006 from Venezuela and Colombia (Dworschak & Coelho 1999; Anker *et al.* 2006b). Anker *et al.* (2006b) provided a table with all known records of *Leptalpheus* species, showing presence of at least three undescribed taxa in the western Atlantic, defined three species groups within *Leptalpheus*, based mainly on the features of the major cheliped.

All species of *Leptalpheus* appear to be associated with burrows of thalassinidean mudshrimps belonging to the families Callianassidae Dana, 1852, Upogebiidae Borradaile, 1903 and Laomediidae

Borradaile, 1903 (see Anker *et al.* 2006b). Between October and November 2005, the author investigated various types of burrows and mounds at two localities in the southwestern Caribbean Sea: Isla Grande, Panama, and Cahuita, Costa Rica. At Isla Grande, a single specimen of *Leptalpheus* was collected in the shallow subtidal, from a burrow of an unknown (presumably callianassid) host. This specimen was immediately recognized to represent an undescribed species of *Leptalpheus*, but all subsequent attempts to collect more *Leptalpheus* specimens at this locality ended unsuccessfully. Fortunately, the Isla Grande specimen was a complete adult male with several unique features separating its species from all other species of *Leptalpheus* thus fully justifying the below description of the new species based on a single specimen. At Cahuita, three specimens of *Leptalpheus* were collected, two of them together with their callianassid hosts. They were identified as *Leptalpheus* cf. *forceps*, a species that was not previously reported from the southwestern Caribbean. Because of some differences observed between the Cahuita specimens and the type of *L. forceps* from

North Carolina, detailed drawings of one of the Cahuita specimens are provided. The species groups of *Leptalpheus* proposed by Anker *et al.* (2006b) are briefly discussed.

MATERIAL AND METHODS

All specimens were collected from burrows with the aid of Alvey bait suction (“yabby”) pump. Most were photographed alive after capture and preserved in 75% ethanol; one specimen was preserved in Ambion RNA-later for genetic studies. The holotype of the new species is deposited in the collections of the Muséum national d’Histoire naturelle, Paris (MNHN). The material of *L. forceps* is deposited in the MNHN and the Universidad de Costa Rica, Museo de Zoología, San José (UCRMZ). The hosts were identified using Manning & Felder (1991) and Sakai (1999). Carapace length (CL) and total length (TL) were measured in mm from the anterior margin of the carapace (or tip of the rostral projection) to the posterior margin of the carapace and telson, respectively.

OTHER ABBREVIATIONS

fcn field collection number;
Mxp maxilliped;
P pereopod.

SYSTEMATICS

Family ALPHEIDAE Rafinesque, 1815

Genus *Leptalpheus* Williams, 1965

Leptalpheus pierrenoeli n. sp.

(Figs 1; 2; 3A, B)

Leptalpheus sp. 4 aff. *forceps* – Anker *et al.* 2006b: 686.

TYPE MATERIAL. — Holotype: Panama, Caribbean coast, Isla Grande, southern shore, village, near Cabañas Super Jackson, from burrow, bait suction pump, depth 0.5–1 m, coll. A. Anker and C. Hurt, 6.X.2005, fcn 05-105, 1 ♂, CL 4.5, TL 14.6 (MNHN-Na 17067).

ETYMOLOGY. — This new species is named after Dr Pierre Y. Noël (MNHN), who directed the author’s Ph.D. thesis on the taxonomy and phylogeny of the

Alpheidae (Anker 2001), and also in recognition of his numerous contributions to the biology and taxonomy of caridean shrimps.

TYPE LOCALITY. — Isla Grande, Caribbean coast of Panama.

DISTRIBUTION. — Tropical western Atlantic: presently known only from the type locality: Isla Grande, Caribbean coast of Panama.

DESCRIPTION

Body moderately slender (Fig. 3A, B), carapace and abdomen slightly compressed laterally, glabrous. Carapace with hardly visible anterolateral suture proximal to base of antenna (Fig. 1B). Frontal margin with broad, subtriangular, bluntly ending rostral projection, without orbital teeth or crests (Fig. 1B). Pterygostomial angle bluntly protruding anteriorly; branchiostegial region with pronounced lip anteriorly (Fig. 1B); cardiac notch deep. Eyes not visible in dorsal view, anterior portion visible in lateral view (Fig. 1A, B); anteromesial process bluntly subtriangular, feebly protruding (Fig. 1B); cornea small, lateral, pigmented (Fig. 1B). Ocellar beak not conspicuous.

Antennular peduncle relatively stout (Fig. 1A), second segment about 1.5 times as long as broad, longer than dorsally visible portion of first segment; stylocerite slightly exceeding distal margin of first segment, acute distally (Fig. 1A); ventromesial carina of first segment with very strong, anteriorly acute tooth; lateral flagellum biramous, with shorter ramus distinct, inserted at fourth segment (Fig. 1B). Antenna with basicerite bearing strong ventrolateral tooth (Fig. 1B); scaphocerite broadly ovate, anterior margin of blade slightly convex, not protruding beyond distolateral tooth (Fig. 1A); carpuccerite long, stout, reaching far beyond scaphocerite (Fig. 1A, B).

Mouthparts not dissected, appearing typical for genus in external view. Third maxilliped moderately slender, elongate; lateral plate acutely produced (Fig. 1C); ultimate segment with rows of long, distally thickened setae, tip unarmed; arthrobranch well developed (Fig. 1C).

Chelipeds strongly asymmetrical in shape, unequal in size (Fig. 2), carried folded (Fig. 3A). Major cheliped moderately enlarged; ischium without subtriangular

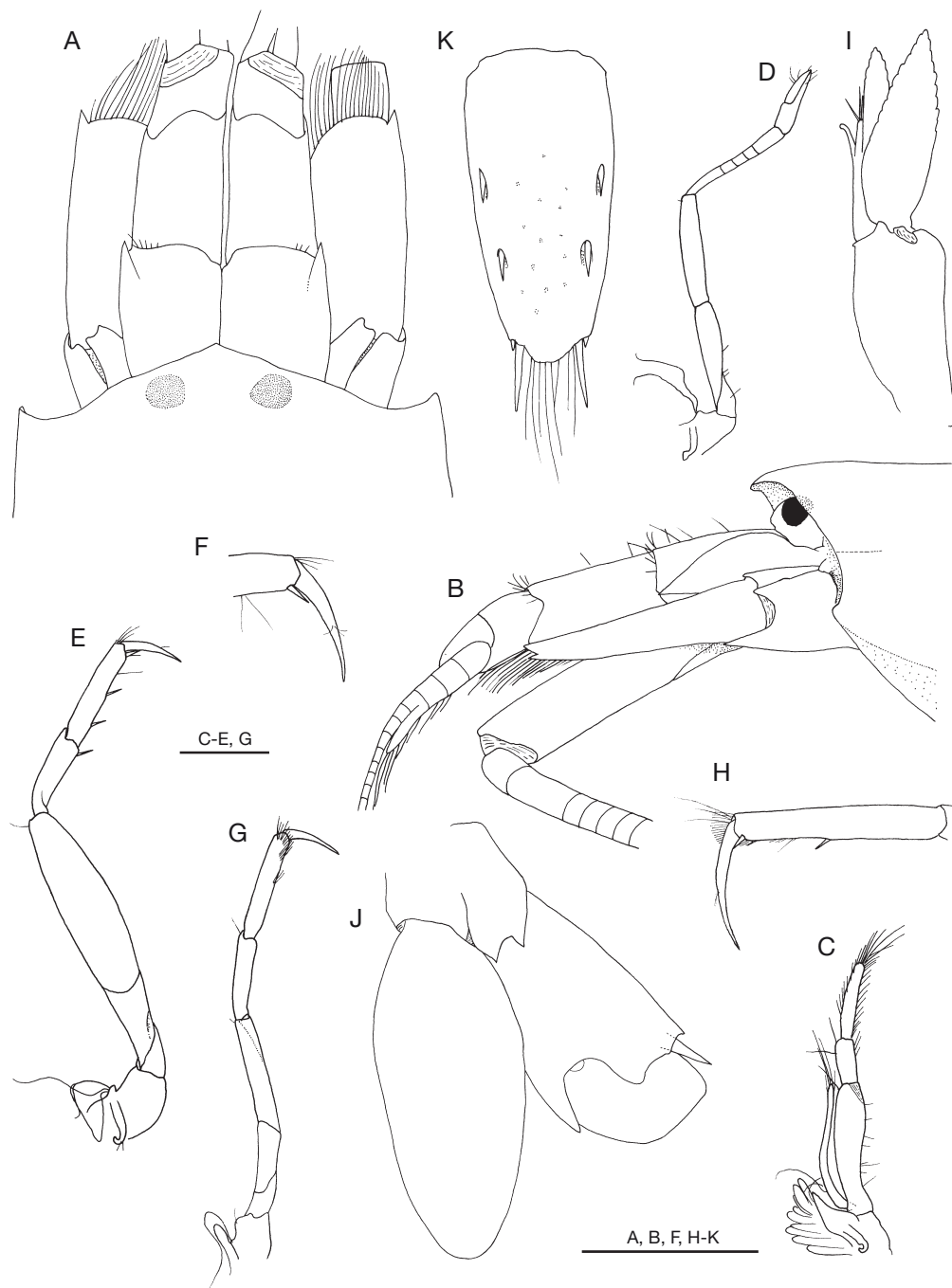


FIG. 1. — *Leptalpheus pierrenoeli* n. sp., ♂ holotype from Isla Grande, Caribbean coast of Panama (MNHN-Na 17067): **A**, frontal region, dorsal view; **B**, same, lateral view; **C**, third maxilliped, lateral view; **D**, second pereopod, lateral view; **E**, third pereopod, lateral view; **F**, same, detail of propodus and dactylus; **G**, fifth pereopod, lateral view; **H**, same, detail of propodus and dactylus, mesial view; **I**, second pleopod, mesial view; **J**, uropod, dorsal view; **K**, telson, dorsal view. Scale bars: 1 mm.

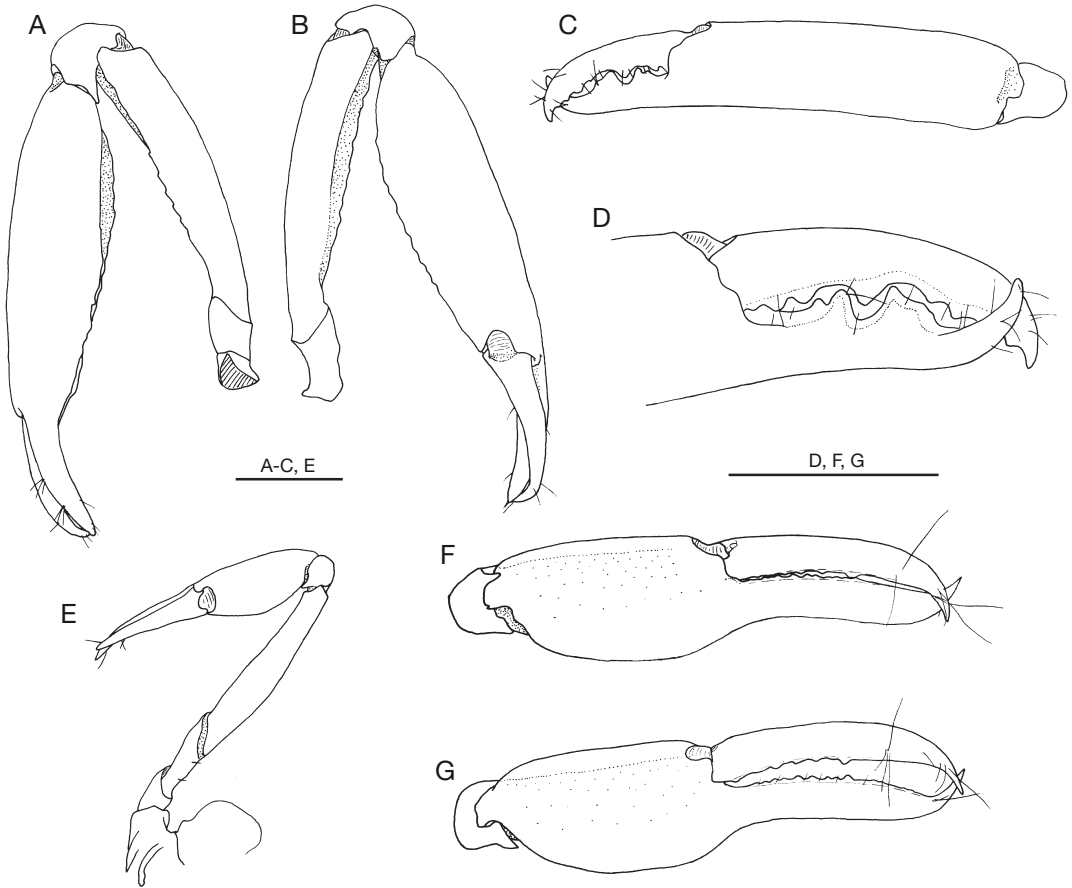


FIG. 2. — *Leptalpheus pierrenoeli* n. sp., ♂ holotype from Isla Grande, Caribbean coast of Panama (MNHN-Na 17067): **A**, major (right) cheliped, mesial view; **B**, same, lateral view; **C**, same, chela, ventrolateral view; **D**, same, chela fingers, ventromesial view; **E**, minor (left) cheliped, lateral view; **F**, same, chela and carpus, ventromesial view; **G**, same, slightly more ventral and fingers opened. Scale bars: 1 mm.

tooth on ventromesial margin (Fig. 2A); merus moderately slender, elongate, ventrally depressed, with rugose ventromesial margin (Fig. 2A, B), blunt distally; carpus short, cup-shaped, with large blunt distomesial tooth (Fig. 2A); chela subcylindrical, palm ventromesially excavated (Fig. 2A), about three times as long as high (Fig. 2C), smooth except for a somewhat rugose ventral margin (Fig. 2A); adhesive discs absent (Fig. 2B); fingers about half as long as palm, moderately curved (Fig. 2B), finger tips crossing when chela closed (Fig. 2C); pollex with two smaller proximal teeth and one larger distal tooth separated by large hiatus (Fig. 2C, D); dactylus

with two smaller proximal teeth, one larger median tooth opposed to hiatus of pollex, and two smaller distal teeth (Fig. 2C, D). Minor cheliped (Fig. 2E) with unarmed ischium; merus slender, ventrally slightly depressed; carpus very short, cup-shaped, with subacute distolateral tooth (Fig. 2E, G); chela smooth, flattened on mesial side (Fig. 2E, F), fingers slightly longer than palm, tips crossing when chela closed; cutting edge of pollex with small irregularly subtriangular teeth on proximal half, most distal tooth largest, situated slightly beyond mid-length of pollex; dentition of dactylus nearly identical to that of pollex (Fig. 2G).

Second pereopod small, slender; ischium slightly shorter than merus; carpus five-segmented, segment ratio approximately: 2.5/1/1/1/2 (Fig. 1D); chela simple, slender, much longer than first carpal segment; fingers longer than palm (Fig. 1D). Third pereopod with unarmed ischium; merus flattened mesially, more than twice as long as ischium, about five times as long as wide (Fig. 1E), ventral margin convex; carpus less than half length of merus, with distoventral spine; propodus longer than carpus, with two ventral spines and one distoventral spine proximal to dactylus; dactylus simple, slender, about 3/5 length of propodus, curved (Fig. 1E). Fourth pereopod similar to third. Fifth pereopod much more slender than third and fourth pereopods (Fig. 1F), not flattened mesially; ischium, merus and carpus unarmed; merus not convex ventrally; propodus as long as merus, without spines, distolaterally with three rows of setae; dactylus similar to that of third and fourth pereopods (Fig. 1F).

First to fifth abdominal somites with minute pits; posteroventral angles rounded; sixth somite with articulated plate posteroventrally. Male second pleopod (Fig. 1I) with appendix interna and appendix masculina, latter slightly longer than former and with three slender spine-like setae on apex (Fig. 1I). Uropod with lateral lobe of protopod (sympodite) bearing two small acute teeth distally (Fig. 1J); endopod longer than exopod, without specific features; exopod with truncate posterior margin, with distolateral tooth adjacent to distolateral spine (Fig. 1J); lateral half of diaeresis shallowly concave, mesial half deeply incised forming large triangular tooth proximal to mesial margin (Fig. 1J). Telson moderately large, more than twice as long as wide proximally (Fig. 1K); dorsal surface covered with minute pits and bearing two pairs of spines inserted at some distance from lateral margin, at about 2/5 and 2/3 length of telson, respectively (Fig. 1K); posterior margin feebly rounded, with two pairs of spines at posterolateral angles: long mesial and very short lateral spines (Fig. 1K); anal tubercles not distinct. Gill/exopod formula typical for genus: 5 pleurobranches (above P1-5); 1 arthrobranch (above Mxp3); 0 podobranch; 2 lobe-shaped epipods (Mxp1-2); 5 mastigobranchs or strap-like epipods

(Mxp3, P1-4); 5 sets of setobranchs (P1-5); 3 exopods (Mxp1-3).

Size

The holotype is 4.5 mm CL and 14.6 mm TL.

Colour pattern

Semitransparent with patches of red chromatophores over most of the body and particularly dense (and therefore more intense red) on dorsal and dorsolateral areas of the carapace, tail fan, antennular peduncles, orbital area and along posterior margin of abdominal somites thus forming diffuse transverse bands on the abdomen; walking legs, second pereopod and antennular/antennal flagella semitransparent, colourless; major cheliped hyaline-white (chromatophore pattern visible in Figure 3A, B).

ECOLOGY

The single specimen was collected from a burrow of unknown host in about knee-deep water. The substrate was fine sand with some shell debris and patches of seagrass (more extensive seagrass beds nearby). Although the host was not collected several specimens of the callianassid ghostshrimps, *Neocallichirus grandimana* (Gibbes, 1850) (Fig. 3C) and *N. rathbunae* (Schmitt, 1935) (Callianassidae), collected at the same site (including some on the same day and a few meters away from the collection site of *L. pierrenoeli* n. sp.) suggest that one of them may be the host of this species. *Neocallichirus* species were previously reported as hosts of *Leptalpheus* (see Anker *et al.* 2006b: table 1).

REMARKS

Leptalpheus pierrenoeli n. sp. appears to be morphologically closest to the heterogeneous *L. forceps* species group, which also includes *L. forceps* and *L. felderi* from the western Atlantic, and *L. mexicanus* Ríos & Carvacho, 1983 from the eastern Pacific, as well as at least three undescribed taxa in the western Atlantic and eastern Pacific (see Anker *et al.* 2006b: table 1). However, the new species is not closely related to any of the aforementioned described species, being separated from all of them by the unique dentition on the cutting edges of the fingers of the major chela; the absence of a mesial tooth on the

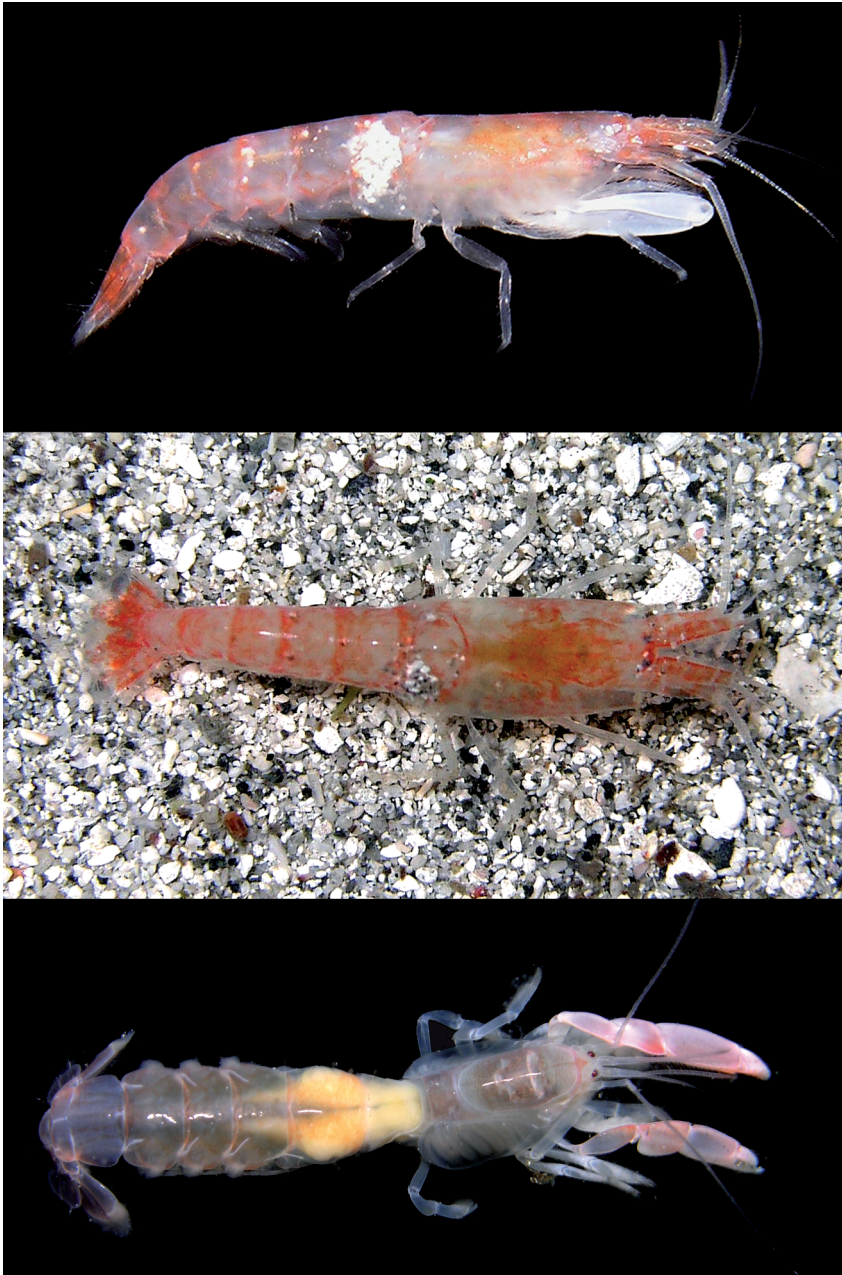


FIG. 3. — **A, B**, *Leptalpheus pierrenoeli* n. sp.; **A**, ♂ holotype from Isla Grande, Caribbean coast of Panama (MNHN-Na 17067), habitus in lateral view; **B**, same in dorsal view (photos taken immediately after collection, note sand grains sticking to a small wound on the right side of the first pleuron); **C**, *Neocallichirus* cf. *grandimana* (Gibbes, 1850) (Callianassidae), habitus in dorsolateral view, specimen collected within a few meters from the collection site of *L. pierrenoeli* n. sp.

ischium of the major cheliped; and the distinctly longer stylocerite (overreaching the distal margin of the first antennular peduncle vs. not reaching this margin in the other three species).

The new species differs more specifically from *L. forceps* (cf. Williams 1965, see also Figs 4; 5) by the much shorter antennular peduncles; the stouter major chela, with comparatively longer fingers; the anterior margin of the carapace with a blunt rostral projection (vs. rounded in *L. forceps*); and in life, also by the more intense red colour (compare Figs 3A, B and 6A, B). It can be distinguished from *L. felderi* (cf. Anker *et al.* 2006b) by the absence of orbital crests (present in *L. felderi*); the unarmed ischium of the third pereopod (vs. with spine in *L. felderi*); the absence of a brush of long flexible setae on the dactylus of the major chela (present in *L. felderi*); the different arrangement of teeth on the cutting edges of the fingers of the major and minor cheliped; the five-segmented carpus of the second pereopod (vs. four-segmented in *L. felderi*); and the colour pattern (cf. Fig. 3A, B [black-and-white photographs] and Anker *et al.* 2006b: fig. 6A, B). Finally, *L. pierrenoeli* n. sp. differs in several respects from *L. mexicanus* (cf. Ríos & Carvacho 1983), including the much less produced rostral projection; the major cheliped with shorter, less twisted, less gaping and differently armed fingers; the much shorter antennular peduncles; and the colour pattern (A. Anker pers. obs.).

Leptalpheus cf. *forceps* Williams, 1965
(Figs 4; 5; 6A, B)

Leptalpheus forceps Williams, 1965: 194; 1984: 101. — Dawson 1967: 224. — Saloman 1971: 67. — Chace 1972: 77. — Abele & Kim 1986: 194, 228. — Felder & Rodrigues 1993: 366. — Holthuis 1993: 203. — Anker *et al.* 2006b: 686.

(?) *Leptalpheus forceps* – Christoffersen 1980: 135; 1998: 361. — Hermoso-Salazar 2001: 1278.

MATERIAL EXAMINED. — **Costa Rica.** Caribbean coast, Cahuita, Punta Uva, small mangrove river, coarse sand, from burrow of *Lepidophthalmus richardi* (host fcn 05-118, will be deposited in MNHN), bait suction pump, depth 10-30 cm, coll. A. Anker, I. Wehrtmann and L. Harris, 26.XI.2005, fcn 05-119, 1 ♂, CL 8.2, TL 22.2

(MNHN-Na 17066). — Same collection data, from burrow of *Lepidophthalmus richardi* (host fcn 05-120, UCRMZ 2420-02), fcn 05-121, 1 ♂, CL 6.1, TL 15.3 (UCRMZ 2420-01); 1 specimen (CL and TL not measured, sex not determined) preserved in Ambion RNA-later for molecular studies (fcn 05-006).

DESCRIPTION

For complete description see Williams (1965, 1984). Detailed drawings of Cahuita specimens are provided in Figures 4 and 5.

Size

The two Costa Rican male specimens were 6.1 mm CL, 15.3 mm TL, and 8.2 mm, 22.2 mm TL. Williams' (1965) type specimens were 7.8 mm CL (female holotype) and 5.2 mm CL (male paratype).

Colour pattern

Semitransparent with yellowish and reddish chromatophores, more intense on tail fan, antennular peduncles, eyestalk and along posterior margins of the carapace and abdominal somites, forming transverse bands; some pale blue and greenish chromatophores present on the antennal scaphocerite and antennular peduncle; merus and carpus of major cheliped with reddish and some bluish chromatophores, major chela hyaline-whitish. The above-described pattern is much less conspicuous on a dark background: the shrimp appears as uniform whitish, with pale reddish bands on the abdomen and tail fan (see black-and-white photographs in Figure 6A, B). The specimens from Fort Pierce, Florida (previously deposited in the MNHN) had pale greenish transverse bands on the abdomen; the antennules and the antennae were pale lettuce-greenish; the tail fan had locally pinkish, bluish and greenish tinge (Anker *et al.* 2006b). Williams (1984) described the colour of *L. forceps* as "translucent, colorless in life; eggs light green in formalin".

ECOLOGY

The present specimens were collected from burrows along the sea-side of a small river estuary, about 5 m wide, fringed with mangrove. Two specimens were collected together with their hosts, the callianassid ghostshrimp *Lepidophthalmus richardi* Felder &

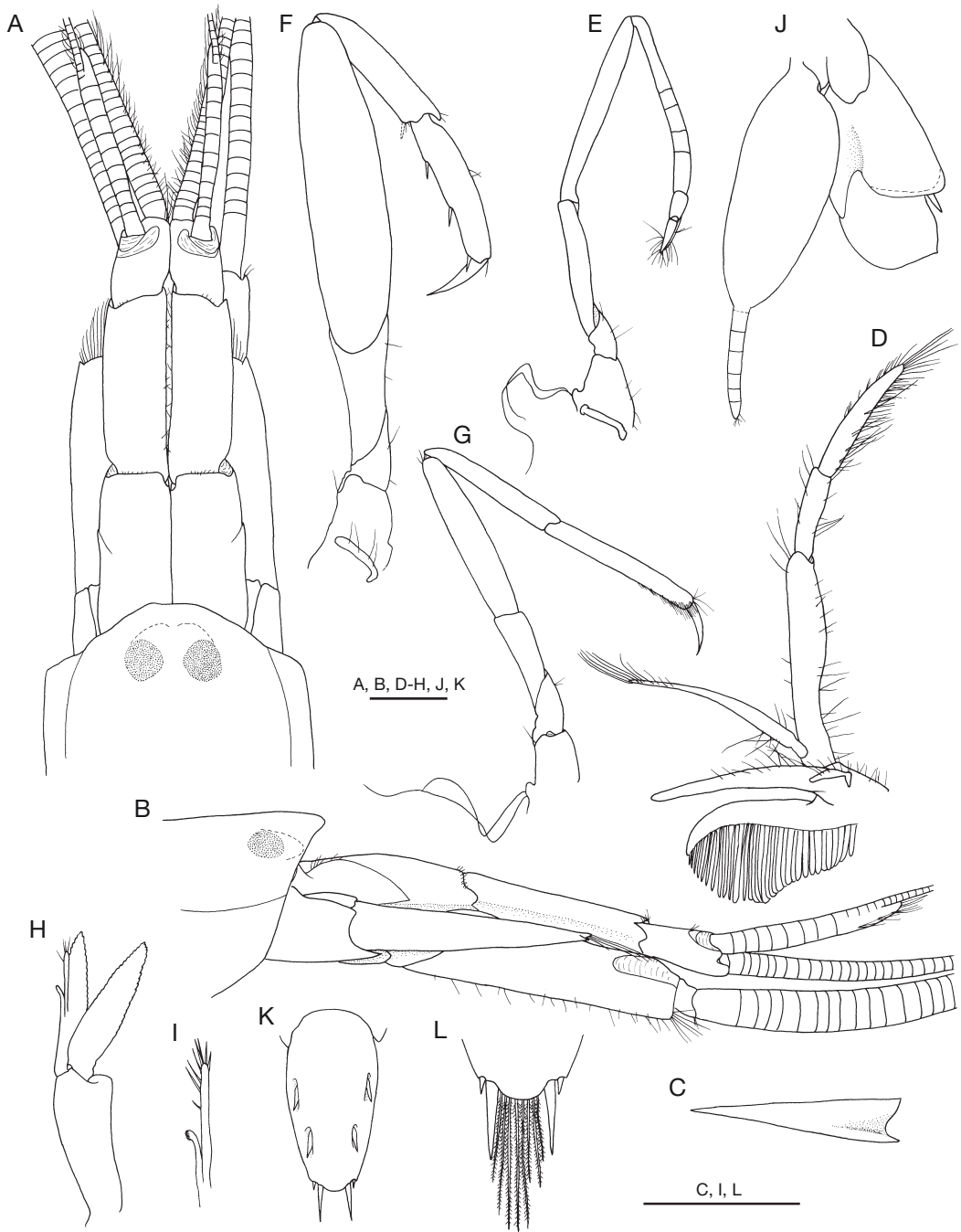


FIG. 4. — *Leptalpheus* cf. *forceps* Williams, 1965, larger ♂ from Cahuita, Caribbean coast of Costa Rica (MNHN-Na 17066): **A**, frontal region, dorsal view; **B**, same, lateral view; **C**, tooth on ventromesial carina of first segment of antennular peduncle, lateral view; **D**, third maxilliped, lateral view; **E**, second pereopod, lateral view; **F**, third pereopod, lateral view; **G**, fifth pereopod, lateral view; **H**, second pleopod, mesial view; **I**, same, detail of appendix masculina and appendix interna; **J**, uropod, dorsal view; **K**, telson, dorsal view; **L**, same, detail of posterior margin. Scale bars: 1 mm.

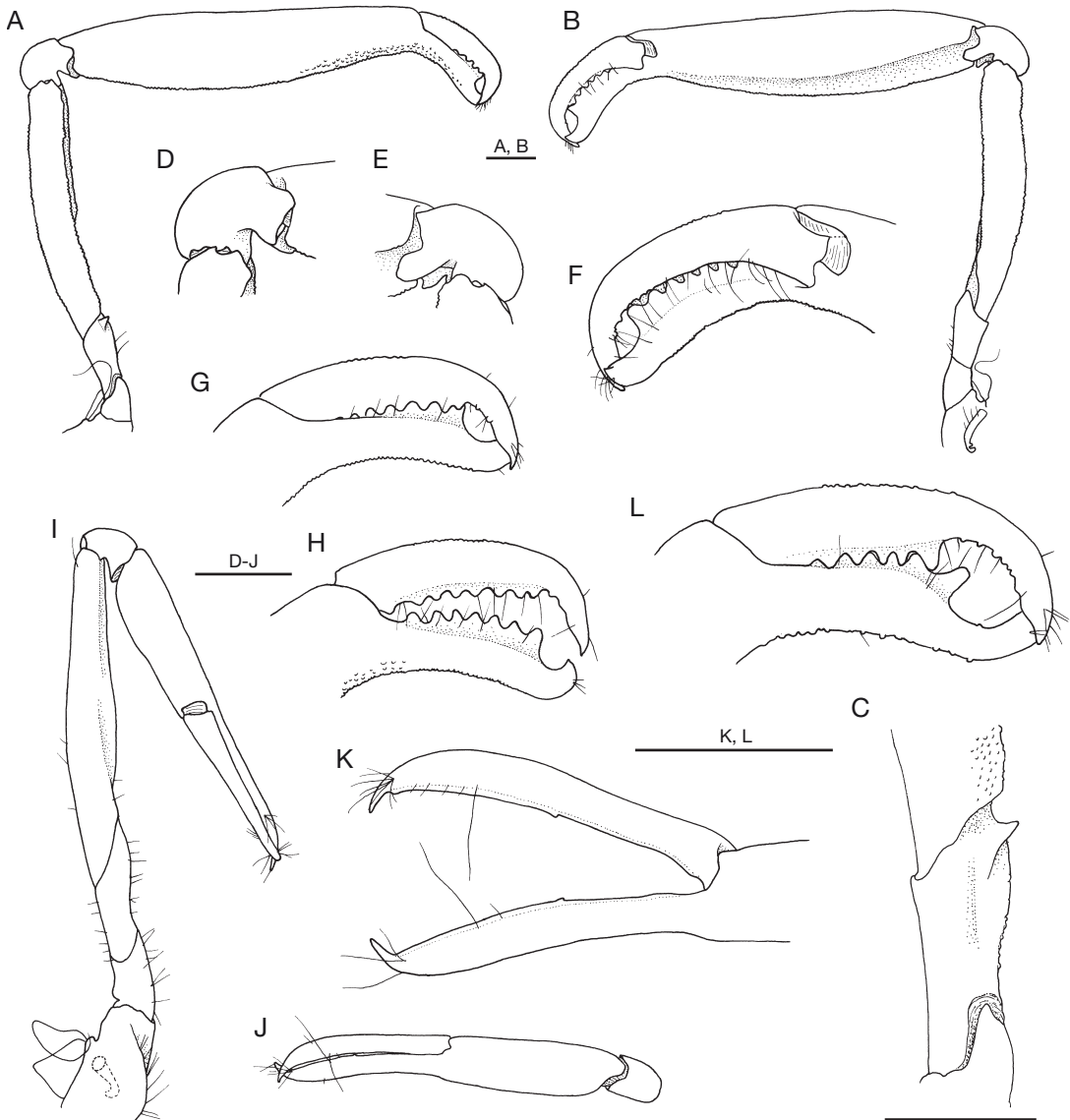


FIG. 5. — *Leptalpheus* cf. *forceps* Williams, 1965, larger ♂ (A–K) from Cahuita, Caribbean coast of Costa Rica (MNHN-Na 17066), smaller ♂ (L) from the same locality (UCRMZ 2420-01): **A**, major (left) cheliped, mesial view; **B**, same, lateral view; **C**, same, detail of ischium, mesial view; **D**, same, detail of carpus, mesial view; **E**, same, lateral view; **F**, same, chela fingers, lateral view; **G**, same, mesial view; **H**, same, fingers opened; **I**, minor (right) cheliped, lateral view (mastigobranch accidentally detached); **J**, same, chela and carpus, ventrolateral view; **K**, same, chela fingers opened; **L**, major (left) cheliped of smaller male, chela fingers, mesial view. Scale bars: 1 mm.

Manning, 1997 (Fig. 6C). Elsewhere, *L. forceps* was found in burrows of the present host's congeners, *L. siriboia* Felder & Rodrigues, 1993 (Christoffersen

1980, as *Callianassa jamaicensis*) and *L. louisianensis* (Schmitt, 1935) (Felder & Rodrigues 1993), as well as the upogebiid mudshrimp, *Upogebia affinis*

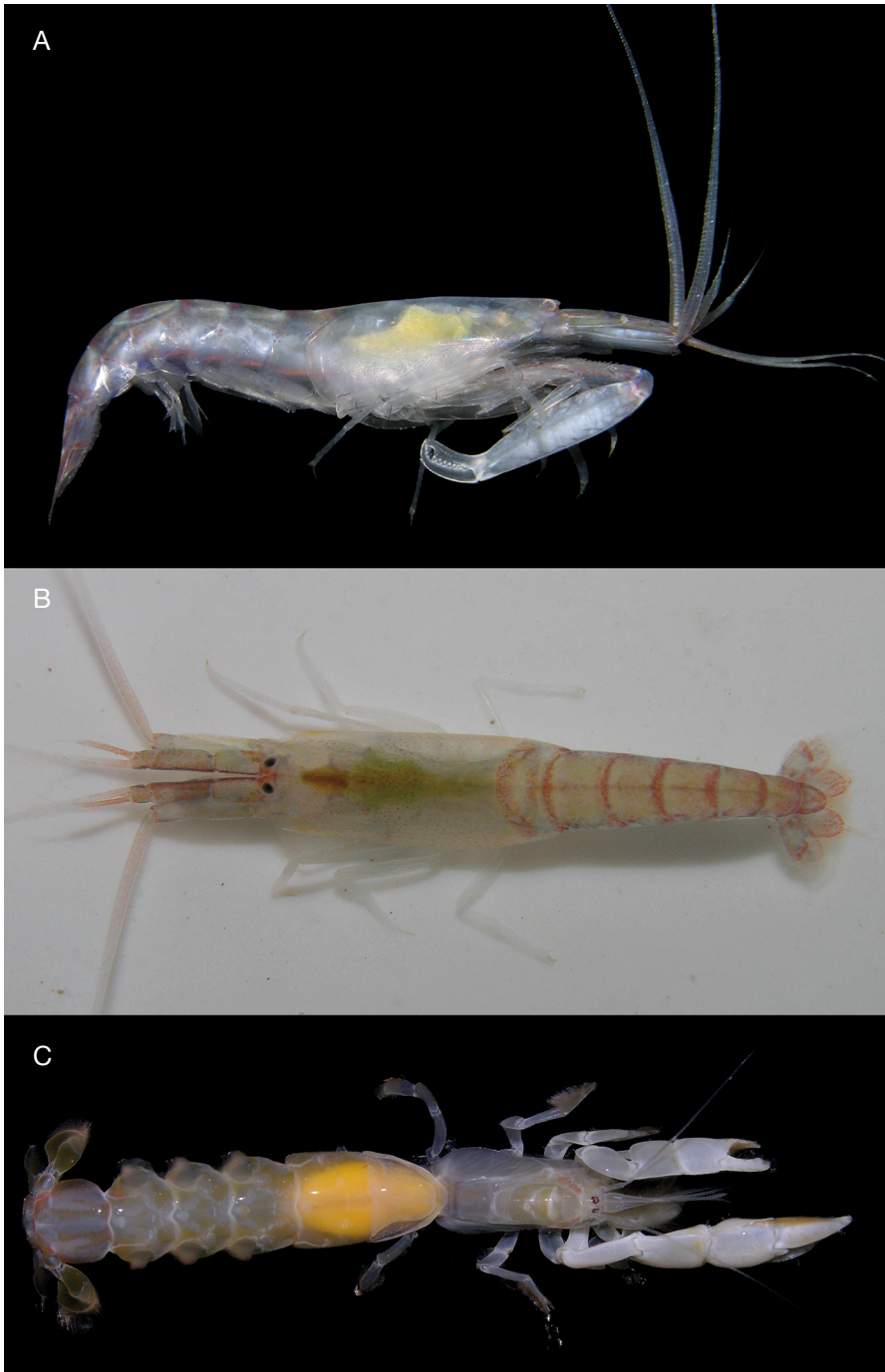


FIG. 6. — **A, B**, *Leptalpheus* cf. *forceps* Williams, 1965, larger ♂ from Cahuita, Caribbean coast of Costa Rica (MNHN-Na 17066); **A**, habitus in lateral view; **B**, same in dorsal view; **C**, *Lepidophthalmus richardi* Felder & Manning, 1997 (Callinassidae), host (UCRMZ 2420-02) of smaller ♂ from Cahuita (UCRMZ 2420-01), habitus in dorsal view.

(Say, 1818) (Williams 1965). Williams (1965, 1984) provided a brief summary of the biology of *L. forceps*.

HOST

Lepidophthalmus richardi (Fig. 6C) was previously known only from the type locality in Belize (Felder & Manning 1997). The record from Cahuita represents a second finding of this species and a considerable extension of its distribution range from Belize southward to Costa Rica.

REMARKS

The two male specimens from Costa Rica (Figs 4; 5) agree reasonably well with the illustrated female holotype from North Carolina (cf. Williams 1965), except for the more robust antennular peduncles (compare Fig. 4A and Williams 1965: fig. 1B); the slightly shorter scaphocerite, reaching to about 2/3 length of the second segment of the antennular peduncle (Fig. 4A) vs. reaching almost to the end of this segment in the type (Williams 1965: fig. 1B); and the more elongate lateral plate on the coxa of the third maxilliped (compare Fig. 4D and Williams 1965: fig. 2F). Williams (1965) noted that “the fingers of the major chela are slightly less gaping in females than in males” and that “there is a slight variation in the number of teeth on the fingers of the major cheliped”, however, without providing the exact range of this variation. The dentition of the type includes six teeth (Williams 1965: fig. 1G), whereas the two examined Costa Rican specimens have six and seven teeth, respectively (not counting the small most proximal tooth visible only when chela is widely opened) (Fig. 5F-H, L). The most distal tooth on the pollex may be more protruding than the others (Fig. 5L). However, the most important difference between the specimens from Costa Rica and North Carolina lies in the development of a segmented appendix on each uropodal endopod. These appendices (caudal filaments) are present in both males from Cahuita (Fig. 4J), and absent in the female holotype and apparently also in all paratypes of *L. forceps* (Williams 1965: fig. 2L). Similar caudal filaments were observed in one male specimen of *L. felderi* from Isla Margarita, Venezuela (Anker *et al.* 2006b: fig. 5C); however, in other males and

in females of this species, the distal margin of the uropodal endopod was rounded. The function of these structures, if there is any, as well as their occurrence in some individuals and absence in others remain unexplained. Thus *L. felderi* appears to be a highly variable species, but more specimens and DNA sequencing are needed to determine the full extension and the genetic base of this variation, and to decide whether *L. cf. felderi* from Costa Rica is conspecific with *L. felderi* from North Carolina and Florida.

DISCUSSION

Leptalphes s.l. was divided into three informal species groups: the amphi-American (eastern Pacific-western Atlantic) *L. forceps* and *L. axianassae* groups, and the Indo-West and Central Pacific *L. pacificus* group (Anker *et al.* 2006b). The above-described *L. pierrenoeli* n. sp. appears to be closest to the morphologically heterogeneous *L. forceps* group, which includes *L. forceps*, *L. mexicanus*, *L. felderi*, as well as several undescribed taxa (see Anker *et al.* 2006b). This group is defined by the presence of a mesial tooth on the ischium of the major cheliped and the stylocerite not reaching the distal margin of the first segment of the antennular peduncle (Anker *et al.* 2006b). However, in *L. pierrenoeli* n. sp., the mesial side of the major cheliped ischium lacks a protruding tooth (Fig. 2A), and the stylocerite slightly overreaches the distal margin of the first segment of the antennular peduncle (Fig. 1A). This suggests that *L. pierrenoeli* n. sp. may represent a distinct lineage within *Leptalphes* s.l., and therefore, should be placed in its own species group allied to the *L. forceps* group.

The increasing diversity within *Leptalphes* s.l. may result into splitting of this genus into two or more genera (D. Felder pers. comm.). This is also true for the *L. forceps* species group, which may be subdivided into several smaller, better defined units (species complexes, subgroups). However, more formal subdivisions of either *Leptalphes* s.l. or the *L. forceps* species group are presently impossible because of more than a dozen undescribed taxa (Anker *et al.* 2006b, A. Anker pers. obs.) and the

absence of a solid phylogenetic hypothesis based on morphological or molecular characters. Preliminary insights into the morphological diversity of *Leptalpheus* s.l. indicate that some features present in undescribed taxa (e.g., setal brush on the dactylus of the major cheliped, orbital crests, caudal filaments, adhesive disks on the major chela, mesial tooth on the ischium of the major cheliped, etc.) could represent important synapomorphies, while others could reveal as homoplasies. Only a combined morphological and molecular treatment of all species of *Leptalpheus* s.l. and the allied leptalpheoid genera (i.e. the ALF clade in Anker *et al.* [2006a] and the recently described *Richalpheus* Anker & Jeng, 2006 [Anker & Jeng 2006]) will possibly allow to make more conclusive phylogenetic and taxonomic statements.

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REFERENCES

- ABELE L. G. & KIM W. 1986. — An illustrated guide to the marine decapod crustaceans of Florida. *Technical Series Department of Environmental Regulations* 8, parts 1 and 2: 1-760.
- ANKER A. 2001. — *Taxonomie et évolution des Alpheidae* (Crustacea, Decapoda). Thèse de Doctorat, Muséum national d'Histoire naturelle, Paris, France, 2 vols, 547 + 331 p.
- ANKER A. & JENG M. S. 2006. — *Richalpheus palmeri*, n. gen., n. sp., an infaunal alpheid shrimp from the Philippines, with redescription of *Amphibetaeus jousseumei* Coutière, 1896 (Decapoda: Caridea). *Journal of Crustacean Biology* 26: 379-391.
- ANKER A., AHYONG S. T., PALMER A. R. & NOËL P. Y. 2006a. — Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. *Evolution* 60: 2507-2528.
- ANKER A., VERA CARIFE J. A. & LIRA C. 2006b. — Description of a new species of commensal alpheid shrimp (Crustacea, Decapoda) from the southern Caribbean Sea. *Zoosystema* 28 (3): 683-702.
- CHACE F. A. JR. 1972. — The shrimps of the Smithsonian-Bredin Caribbean expeditions with a summary of the West Indian shallow water species (Crustacea Decapoda: Natantia). *Smithsonian Contributions to Zoology* 98: i-x + 1-179.
- CHRISTOFFERSEN M. L. 1980. — *Taxonomia e distribuição geográfica dos Alpheoidea* (Crustacea, Decapoda, Natantia) do Brasil, Uruguay e norte da Argentina, incluindo considerações sobre a divisão do sul do continente em províncias biogeográficas marinhas. Ph.D. Thesis, Universidade do São Paulo, São Paulo, Brazil, 467 p.
- CHRISTOFFERSEN M. L. 1998. — Malacostraca. Eucarida. Caridea, Crangonoidea and Alpheoidea (except Glyphocrangonidae and Crangonidae), in YOUNG P. S. (ed.), *Catalogue of Crustacea of Brazil*. Museu Nacional, Rio de Janeiro: 351-372.
- DAWSON C. E. 1967. — Notice of the occurrence of alpheid shrimp *Leptalpheus forceps* Williams in the northern Gulf of Mexico. *Crustaceana* 12: 224.
- DWORSCHAK P. C. & COELHO V. R. 1999. — On two alpheids from Araçá (Sao Paulo, Brazil) with a description of a new species of *Leptalpheus* (Decapoda: Caridea: Alpheidae). *Annalen des Naturhistorischen Museums in Wien* 101B: 475-488.
- FELDER D. L. & MANNING R. B. 1997. — Ghost shrimps of the genus *Lepidophthalmus* from the Caribbean region, with description of *L. richardi*, new species, from Belize (Decapoda: Thalassinidea: Callianassidae). *Journal of Crustacean Biology* 17: 309-331.
- FELDER D. L. & RODRIGUES S. A. 1993. — Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to *L. siriboia*, new species from Brazil (Decapoda: Thalassinidea: Callianassidae). *Journal of Crustacean Biology* 13: 357-376.
- HERMOSO-SALAZAR A. M. 2001. — Ampliación de ámbito de *Leptalpheus forceps* (Caridea: Alpheidae) al Golfo de México. Range extension of *Leptalpheus forceps* (Caridea: Alpheidae) to the Gulf of Mexico. *Revista de Biología Tropical* 49: 1278.
- HOLTHUIS L. B. 1993. — *The Recent Genera of the Caridean and Stenopodidean Shrimps* (Crustacea, Decapoda). With an Appendix on the Order Amphionidacea. National Natuurhistorisch Museum, Leiden, 328 p.
- MANNING R. B. & FELDER D. L. 1991. — Revision of

- the American Callianassidae (Crustacea: Decapoda: Thalassinidae). *Proceedings of the Biological Society of Washington* 104: 764-792.
- RÍOS R. & CARVACHO A. 1983. — *Leptalpheus mexicanus*, new species (Crustacea, Decapoda, Alpheidae). Caridean shrimps of the Gulf of California III. *Journal of Crustacean Biology* 3: 306-313.
- SAKAI K. 1999. — Synopsis of the family Callianassidae, with keys to subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea). *Zoologische Verhandelingen* 326: 1-152.
- SALOMAN C. H. 1971. — The shrimp *Leptalpheus forceps* in Old Tampa Bay, Florida. *Quarterly Journal of Florida Academy of Sciences* 34: 66-67.
- WILLIAMS A. B. 1965. — A new genus and species of snapping shrimp (Decapoda, Alpheidae) from the southeastern United States. *Crustaceana* 9: 192-198.
- WILLIAMS A. B. 1984. — *Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, DC, 550 p.

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