

Proposal of *Marbefia*, gen. n. and *Inermiphonte*, gen. n., including updated keys to the species of *Pseudonychocamptus* Lang, 1944 and *Paralaophonte* Lang, 1948 (Copepoda, Harpacticoida, Laophontidae)

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Abstract

Both sexes of the enigmatic laophontid species *Pseudonychocamptus carthyi* Hamond, 1968 (Copepoda, Harpacticoida) are redescribed in detail based on type and other material from Norfolk, England. The species exhibits marked differences with other *Pseudonychocamptus* species and is consequently fixed as the type of a new genus *Marbefia*, **gen. n.**, being defined by the following autapomorphies: (1) P2–P4 enp-2 (except P4 enp-2 in ♂) inflated, with two parallel rows of flimsy setular extensions; (2) P4 with sexually dimorphic setation on enp-2 (outer distal seta reduced in ♀, very long in ♂); and (3) antennule ♀ with spinules along posterior margins of segments 1–6. *Laophonte danversae* Hamond, 1969, “Laophontid male, ?gen., ?sp.” *sensu* Hamond (1969) [renamed as *Inermiphonte hamondi*, **sp. n.**] and *Laophonte ?drachi* Médioni & Soyer, 1966 are collectively placed in a new genus *Inermiphonte*, **gen. n.** which shares as sistergroup relationship with *Harrietella* T. Scott, 1906. *Marbefia*, **gen. n.** is considered sister to a clade comprising the genera *Pseudonychocamptus* Lang, 1944, *Pilifera* Noodt, 1952, *Inermiphonte*, **gen. n.** and *Harrietella*. *Pseudonychocamptus kolarovi* Apostolov, 2008 is transferred to *Paralaophonte* whereas Chislenko’s (1967) record of *P. koreni* Sars, 1908a is considered doubtful. Willey’s (1935) variety “*fissirostris*” of *Paralaophonte brevisrostris* (Claus, 1863) is rejected pending a thorough analysis of the variability in the *P. brevisrostris* complex of species. *P. congenera mediterranea* Lang, 1948 appears to be more closely related to *P. lacerdai* Jakobi, 1953 than to its nominotypical subspecies *P. congenera congenera* (Sars, 1908b) whereas

P. pacifica galapagoensis Mielke, 1981 (here upgraded to full specific rank) is more similar to *P. brevirostris* than to its nominotypical subspecies *P. pacifica pacifica* Lang, 1965. A new species, *Paralaophonte pallaresae*, sp. n. is proposed for *P. gracilipes* Brady, 1910 *sensu* Pallares (1968). The potentially paraphyletic status of the genus *Paralaophonte* is discussed. Dichotomous identification keys are provided for the valid species of *Pseudonychocamptus* Lang, 1944 and *Paralaophonte* Lang, 1948.

Keywords

Copepoda, Laophontidae, *Inermiphonte*, gen. n., *Loureiophonte*, *Marbefia*, gen. n., *Paralaophonte*, *Pseudonychocamptus*, *Paralaophonte kolarovi*, comb. n., *P. pallaresae*, sp. n., *Inermiphonte hamondi*, sp. n., identification keys

Introduction

In one of his papers dealing with the Laophontidae from Norfolk, Hamond (1968) described a new species in the genus *Pseudonychocamptus* Lang, 1944 for a single female found in washings of intertidal colonies of the hydroid *Hartlaubella gelatinosa* (Pallas, 1766) (as *Laomedea gelatinosa*) collected under the Hunstanton pier. *Pseudonychocamptus carthyi* Hamond, 1968 has been recorded in the literature only once since its original description and the male has remained unknown. The only other record is that by Holmes and Minchin (2000) who collected a single female from a *Serpula vermicularis* L. reef at 4 m depth near the ferry pier on the south side of Killary Harbour, Co. Galway, Ireland.

In their review of the genus *Paronychocamptus* Lang, 1948, Lee and Huys (1999) identified a lineage within the subfamily Laophontinae, consisting of the genera *Pseudonychocamptus*, *Pilifera* Noodt, 1952, *Weddellaophonte* Willen, 1996 and *Heteronychocamptus* Lee & Huys, 1999. This “PWPH-clade” is primarily characterized by a distinctive type of swimming leg sexual dimorphism. In all four genera, females possess a seta on the proximal endopod segment of P3 and P4 but males consistently lack this armature element (Table 1). Lee and Huys (1999) also recognized a close relationship between *Pilifera* and *Pseudonychocamptus* but remarked that *P. carthyi*, by virtue of its primitive swimming leg armature, probably occupies a position close to the ancestor of the PWPH-clade. Pending the discovery of the unknown male, they refrained from attributing the species to a new genus. In this paper we have re-examined additional material of *P. carthyi* from Norfolk, which had been deposited in the collections of the Natural History Museum by Dr Richard Hamond. These specimens, representing both sexes, form the basis for a redescription of the female and the first description of the male, providing morphological evidence for its assignment to a new genus *Marbefia*.

Material and methods

Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the dissected parts were mount-

Table 1. Comparison between *Harrietella* and laophontid genera/species displaying sexual dimorphism in setation of P3–P4 enp-1 (exp = exopod; enp = endopod; benp = baseoendopod; A1 = number of antennular segments; P3 ♂ = number of endopodal segments); losses in males indicated in boldface; species here reassigned to *Inermiphonte* gen. n. marked by *.

		A1	P2		P3		P4		P5		P3 ♂
		exp	enp	exp	enp	exp	enp	exp	enp	benp	
<i>Weddella</i>	♀	0.1.1.23	0.220	0.1.223	1.121	0.1.223	1.120	5	5	5	–
	♂	0.1.1.23	0.220	0.1.223	0.0.120	0.1.223	0.120	4	2	2	3
<i>Heteronychocampus</i>	♀	0.1.1.23	[0–1].120	0.1.123	1.121	0.1.12[2–3]	1.121	4–5	5	5	–
	♂	0.1.1.23	[0–1].120	0.1.123	0.0.020	0.1.12[2–3]	0.121	4	2	2	3
<i>Marbefia</i> , gen. n.	♀	0.1.1.23	0.220	0.1.223	1.321	0.1.223	1.121	6	5	5	–
	♂	0.1.1.23	0.220	0.1.223	0.220	0.1.223	0.121	4	2	2	2
<i>Pilifera</i>	♀	0.1.1.23	0.120	0.1.123	1.221	0.1.122	1.121	5	5	5	–
	♂	0.1.1.23	0.120	0.1.123	0.020	0.0.022	0.020	4	2	2	2
<i>Pseudonychocampus</i>	♀	0.1.1.23	0.220	0.1.123	1.1[–2]21	0.1.123	1.121	5–6	5	5	–
	♂	0.1.1.23	0.120	0.1.123	0.120	0.1.123	0.020	3–4	2	2	2
<i>*Laophonte danversae</i> ^a	♀	0.1.0.23	0.120	0.1.023	0.121	0.0.022	1.021	6	5	5	–
	♂	0.1.0.23	0.120	0.1.023	0.020	0.0.022	0.021	5	2	2	2
<i>*Laophontid</i> male, ?gen., ?sp. ^b	♂	0.1.0.23	0.220	0.1.023	0.120	0.0.023	0.021	4	2	2	2
	♀	0.0.0.23	0.120	0.0.023	0.021	0.0.022	0.021	6	4	4	–
<i>*Laophonte drachi</i> ^c	♂	0.0.0.23	0.120	0.0.023	0.020	0.0.022	0.021	4	2	2	2
	♀	0.1.0.23	0.020	1.0.023	0.121	0.02[3–4]	0.020	4–5	3–4	3–4	–
<i>Harrietella</i>	♂	0.1.0.23	0.020	1.0.023	0.121	0.02[3–4]	0.020	4	1	1	2
	♀	0.1.0.23	0.020	1.0.023	0.121	0.02[3–4]	0.020	4	1	1	2

^a Hamond (1969) noted variability in the armature of P4 endopod ♀ (1.021 or 0.020 or 1.020); examination of additional material showed 1.021 to be the normal condition (as figured by Hamond 1969; his Fig 14).

^b *sensu* Hamond (1969: 9) = *Inermiphonte hamondi*, sp. n.

^c Note that Médioni and Soyer's (1966: 1057) armature formula is given in corrected format here to account for the small inner distal seta on P2–P4 exp-3 (figured by the authors for P3 but omitted in their formula; overlooked in P4; P2 was not figured). Wells (2007: 436, 458) had already amended the setal counts for P2–P3.

ed in lactophenol mounting medium. Broken glass fibres were added to prevent the animal and appendages from being compressed by the coverslip and to facilitate rotation and manipulation, allowing observation from all angles. Preparations were subsequently sealed with Glyceel or transparent nail varnish. All drawings were prepared using a camera lucida on a Zeiss Axioskop differential interference contrast microscope. Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Measurements were made with an ocular micrometer. Scale bars in illustrations are in μm . The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: ae, aesthetasc; P1–P6, for swimming legs 1–6; exp, enp and benp for exopod, endopod and baseoendopod, respectively; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus; NHM, Natural History Museum (London). The term ‘acrothek’ denotes the trifid setal structure found primitively on the apical margin of the distal antennular segment (Huys and Iliffe 1998).

Results

Order Harpacticoida Sars, 1903

Family Laophontidae T. Scott, 1905

Marbefia, gen. n.

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Diagnosis. Laophontidae. Body linear, not dorsoventrally depressed. Integument of cephalothorax and body somites covered with tiny spinules; posterior margins of somites smooth, with spinule rows dorsally and ventrally. Rostrum delimited at base; broadly triangular, prominent. Genital double-somite ♀ with lateral incisions and ventrolateral internal chitinous ribs marking original segmentation. Pleural extensions of ♀ abdominal somites well developed. Caudal ramus cylindrical, subrectangular and as long as wide; inner margin with long spinules; with 7 setae; setae IV and V well developed, pinnate; seta VI reduced, setiform. Anal operculum spinulose.

Sexual dimorphism in antennule, P3–P4 endopods, P5, P6 and in genital segmentation.

Antennule slender and 7-segmented in ♀; 8-segmented and subchirocer with 3 segments distal to geniculation in ♂; segments with spinular ornamentation along anterior margin of segments 1–4 in ♀ and 1–3 in ♂; segments 1–2 without processes; with aesthetasc on segment 4 (♀) or 5 (♂); acrothek on apical segment consisting of 2 setae and one aesthetasc. Antenna with 4 setae on exopod; allobasis with abexopodal seta. Mandibular palp elongate, 1-segmented; with one basal, one exopodal and 3 endopodal setae. Maxillule with defined exopod bearing 2 setae. Maxilla with 3 endites on syncoxa; endopod represented by 4 setae. Maxilliped elongate; syncoxa with 2 setae; basis without distinct ornamentation; endopodal claw long and curved, with one accessory seta.

P1 long, with elongate coxa and basis; with 3-segmented exopod, exp-2 1.6 times as long as exp-1, exp-3 with 2 short and 2 geniculate setae; endopod stout, enp-1 without inner seta, enp-2 with minute seta and long minutely denticulate claw. Swimming legs P2–P4 with 3-segmented exopods and 2-segmented endopods. P2–P4 enp-2 swollen, with double row of flimsy setular extensions along outer lateral margin (except for P4 in ♂); inner seta of P3–P4 enp-1 present in ♀ but absent in ♂. P3 enp-2 produced into straight spiniform apophysis in ♂ (homologous with outer spine of enp-2 in ♀). Armature formula of swimming legs 2 to 4 (P2–P4) as follows:

	Exopod	Endopod
P2	0.1.123	0.220
P3	0.1.223	1.321 [0.220 in ♂]
P4	0.1.223	1.121 [0.121 in ♂]

P5 with separate exopod and baseoendopod. Exopod elongate with 6 setae in ♀ and 4 setae in ♂. Endopodal lobe well developed in ♀, subrectangular, with 5 setae. Baseoendopods fused medially in ♂; endopodal lobes rudimentary, with 2 setae each.

P6 forming well developed operculum with 2 small setae in ♀; asymmetrical in ♂ (with dextral or sinistral configuration), with outer distal corner produced into conical process bearing 2 well developed elements.

Type and only species. *Pseudonychocamptus carthyi* Hamond, 1968 = *Marbefia carthyi* (Hamond, 1968), comb. n.

Etymology. The name of the new genus honours the advances in our understanding of marine ecosystem functioning stimulated by the MarBEF Network of Excellence in Marine Biodiversity and Ecosystem Functioning. Gender: feminine.

Marbefia carthyi (Hamond, 1968), comb. n.

Figs 1–6

Pseudonychocamptus carthyi Hamond, 1968

Type locality. England, Norfolk, Hunstanton; in washings of colonies of *Hartlaubella* (as *Laomedea*) *gelatinosa* (Pallas, 1766) (Hydrozoa, Campanulariidae) attached to concrete lumps found in little shallow pools under the pier; for associated fauna see Hamond (1968: 176).

Material examined. (1) **Holotype.** ♀ dissected on one slide (reg. no. NHM 1967.10.2.2), from type locality, collected on 2 April 1957 by R. Hamond;

(2) one ♀ dissected on 12 slides, one ♂ dissected on 9 slides, one ♀ and one ♂ used for SEM examination, and two ♂♂ in 70% ethanol; all specimens collected from Station MB.17 (53°10.34'N, 00°56.34'E) on 6 May 1992 by R.

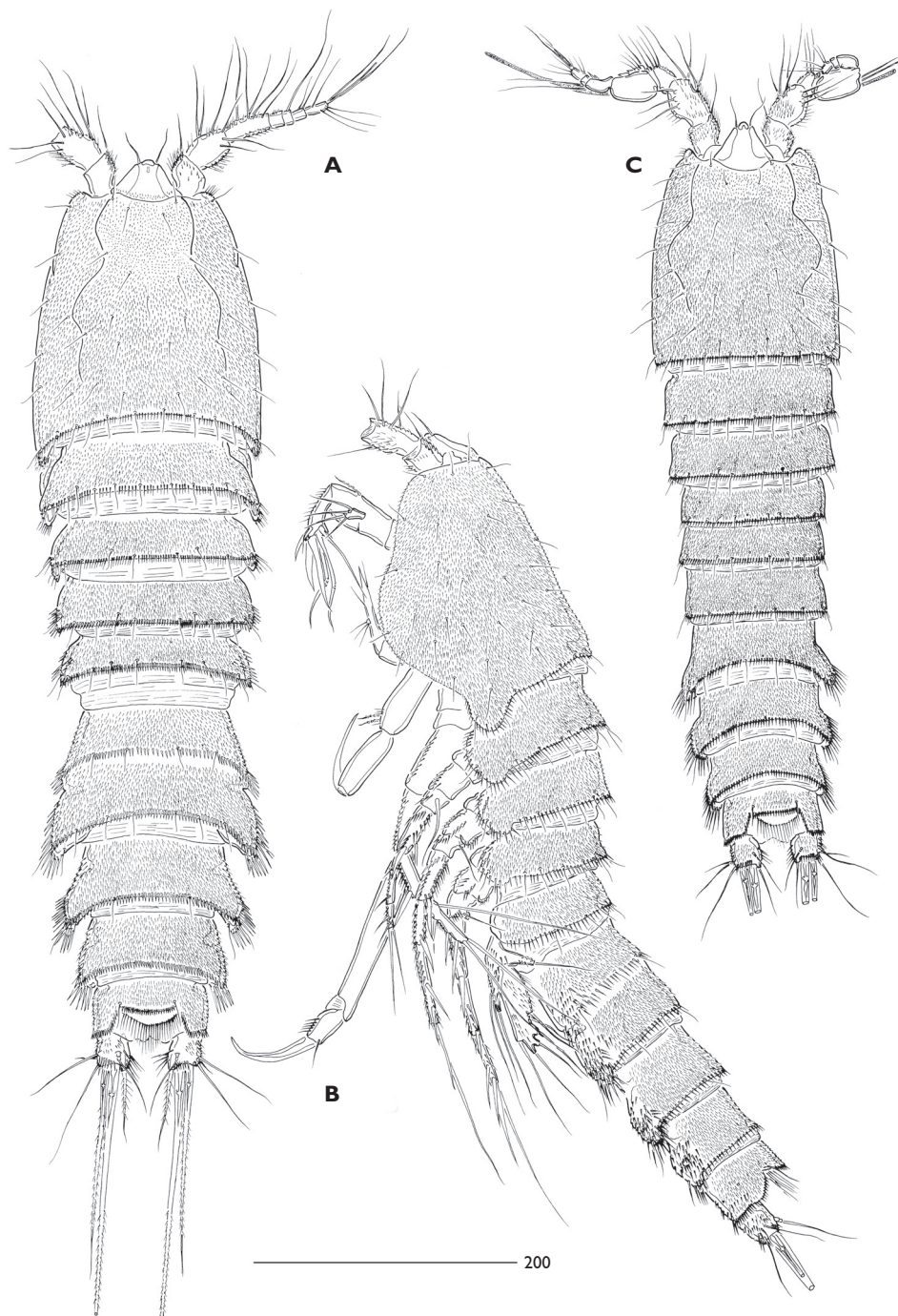


Figure 1. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** habitus ♀, dorsal **B** habitus ♀, lateral **C** habitus ♂, dorsal.

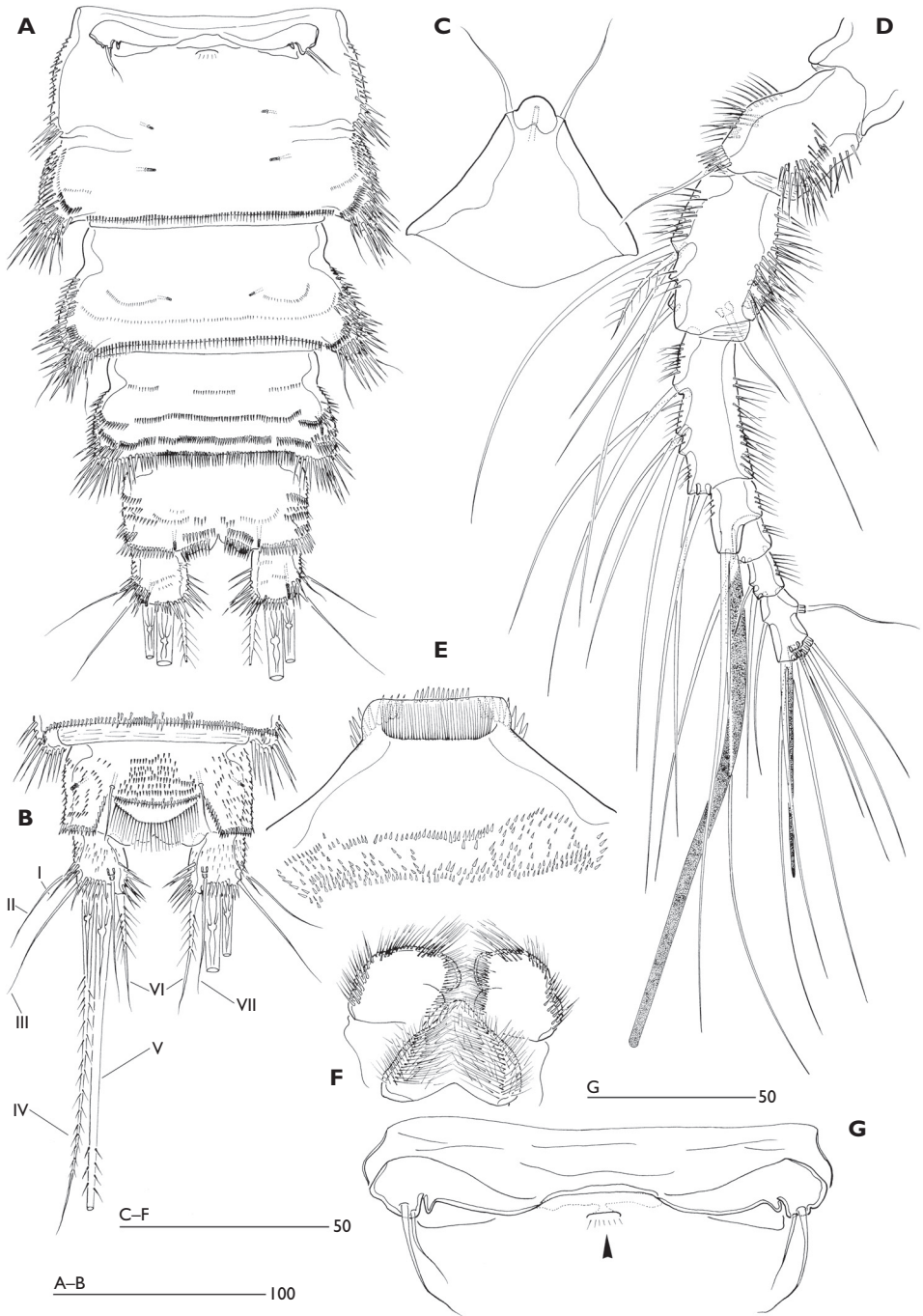


Figure 2. *Marbefia carthyi* (Hamond, 1968), comb. n. (♀): **A** urosome, ventral [excluding P5-bearing somite] **B** anal somite and caudal rami, dorsal **C** rostrum, dorsal **D** antennule, ventral **E** labrum, anterior **F** paragnaths, anterior **G** genital area with P6 [copulatory pore arrowed].

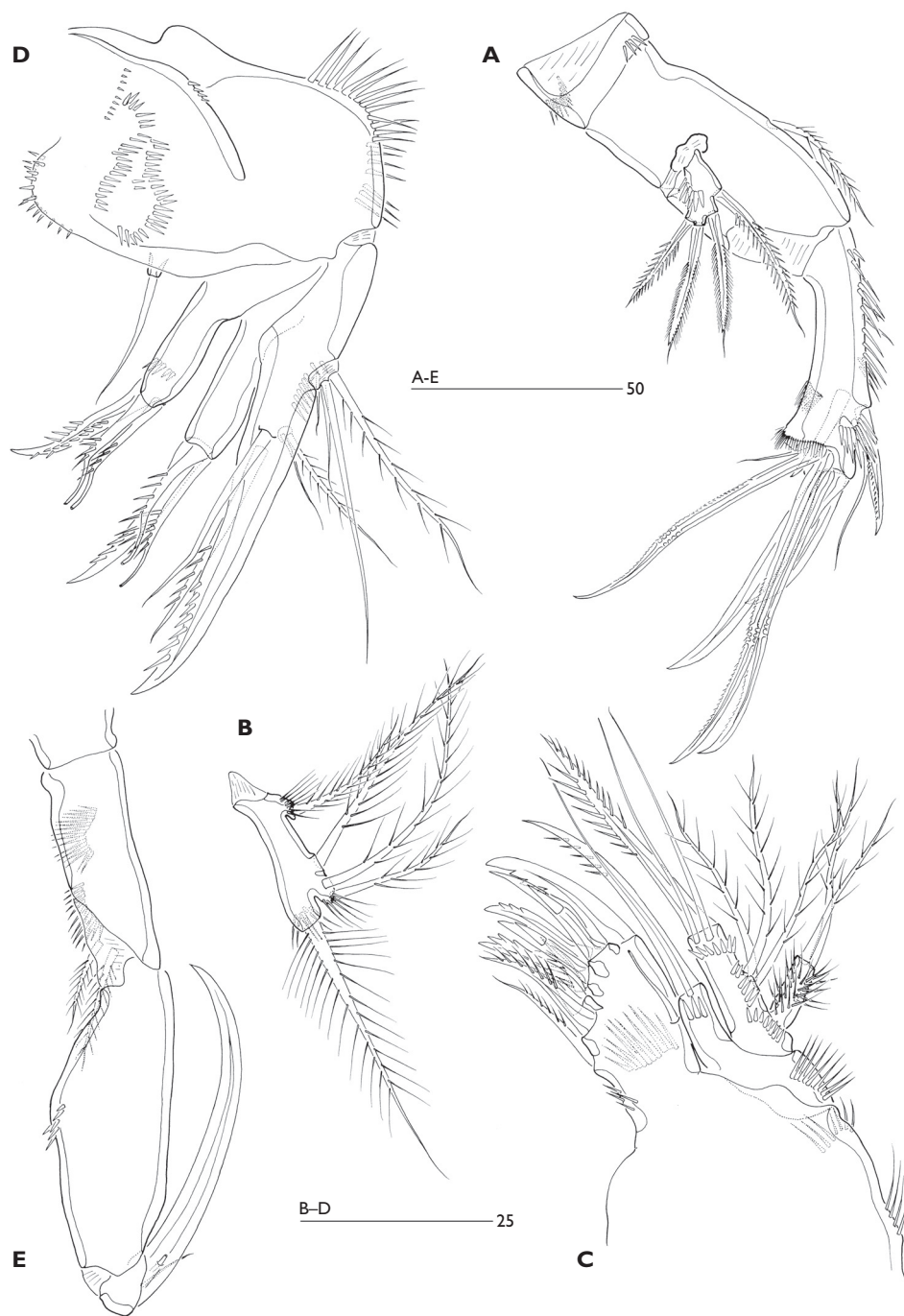


Figure 3. *Marbefia carthyi* (Hamond, 1968), comb. n. (♀): **A** antenna **B** mandibular palp **C** maxillule, anterior **D** maxilla, posterior **E** maxilliped, posterior.



Figure 4. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** P1 ♀, anterior **B** P4 ♀, anterior [inner seta on enp-1 arrowed] **C** P4 endopod ♂, anterior [spinular rows on enp-1 arrowed] **D** distal part of P4 endopod ♀, posterior.

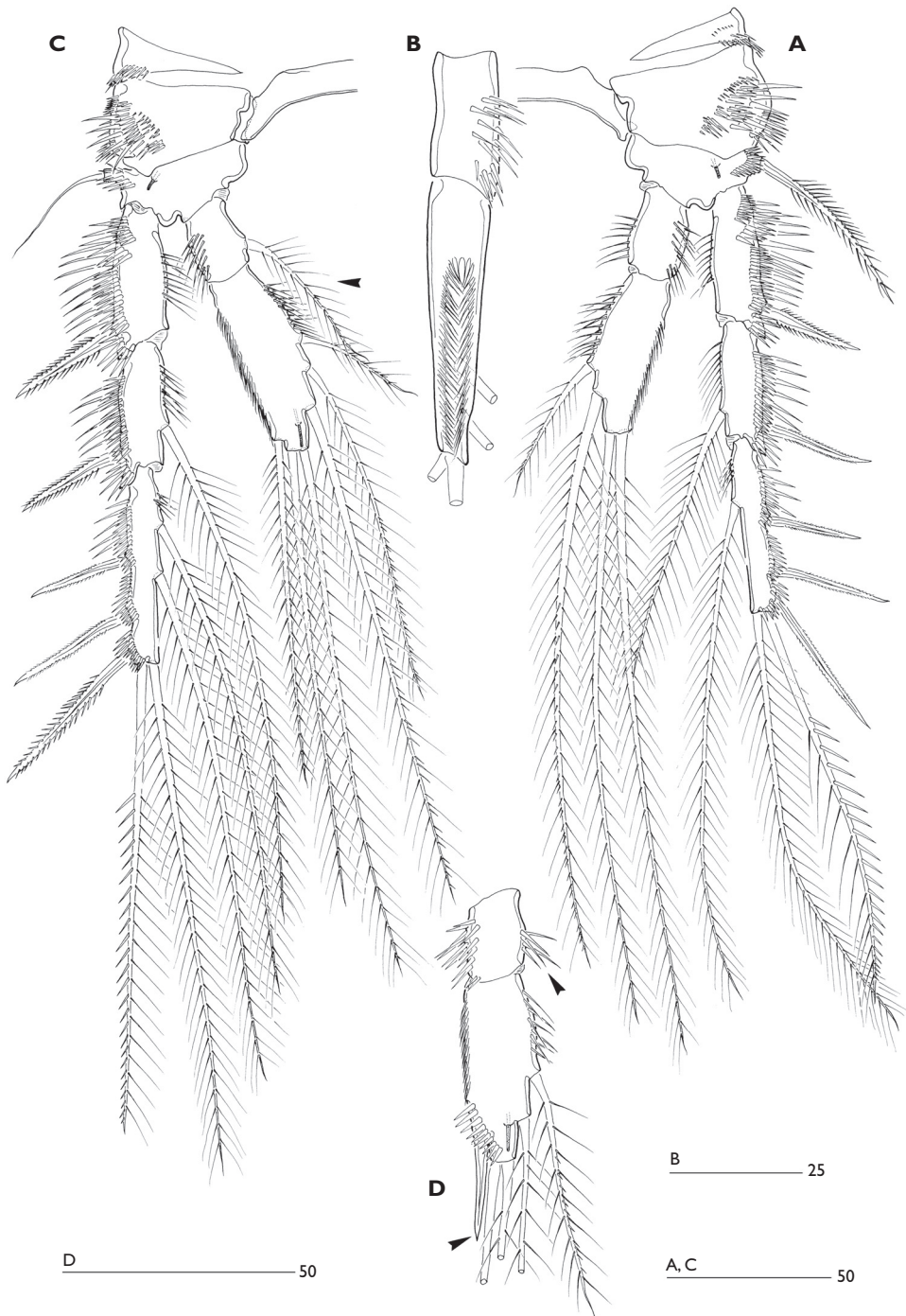


Figure 5. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** P2 ♀, anterior, **B** P2 endopod ♀, outer lateral **C** P3 ♀, anterior [inner seta on enp-1 arrowed] **D** P3 endopod ♂ [spinules on enp-1 and apophysis on enp-2 arrowed].

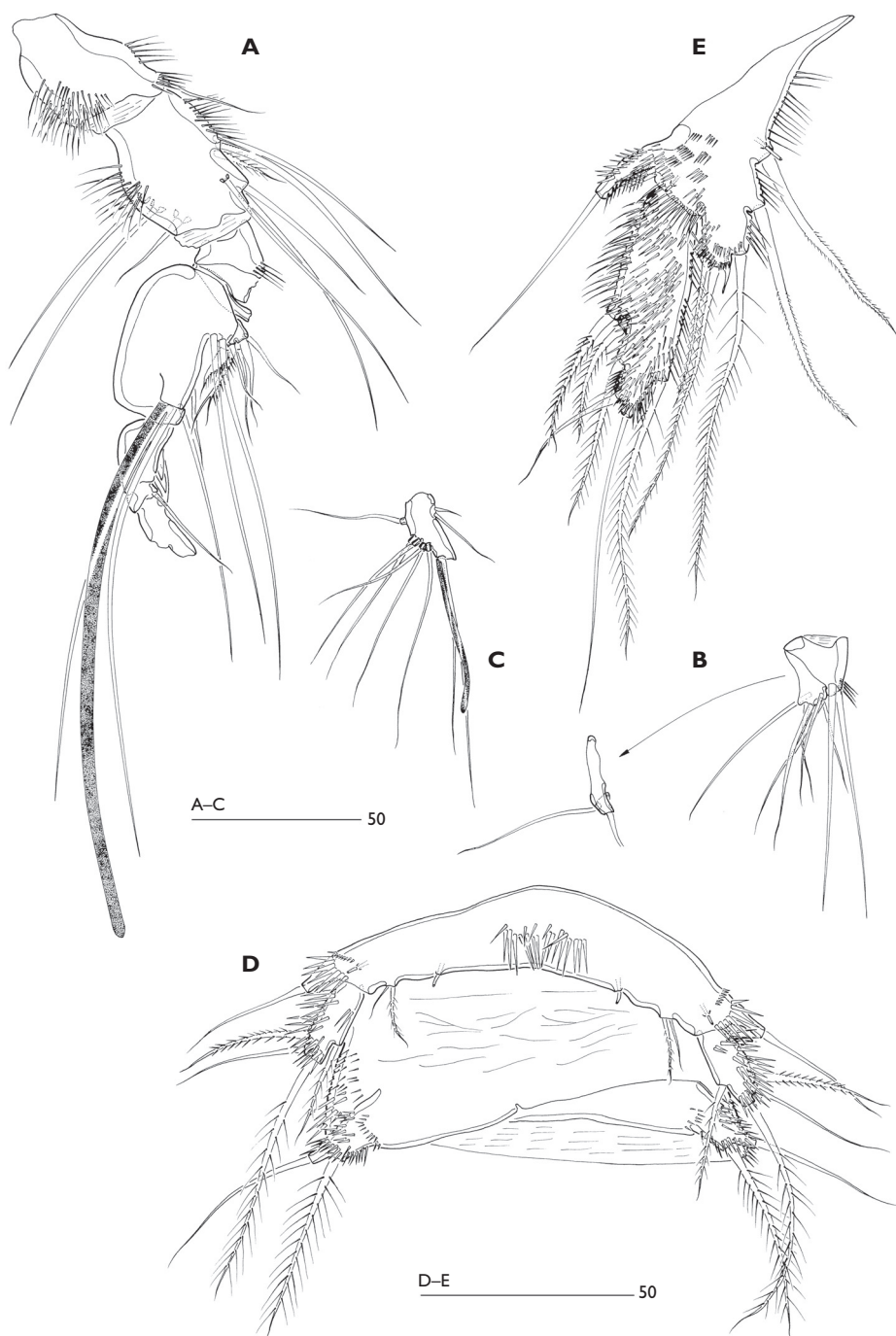


Figure 6. *Marbefia carthyi* (Hamond, 1968), comb. n.: **A** antennule ♂, ventral [armature on segments 3, 4 and 8 omitted] **B** antennular segments 3 (right) and 4 (left) ♂ **C** antennular segment 8 ♂ **D** P5 and P6 ♂, anterior **E** P5 ♀, anterior.

Hamond (reg. nos. NHM 1993.312–321); depth 12–13 m; fine sand with high silt content;

(3) one ♀ (reg. no. NHM 1998.588) re-identified by F. Fiers in 1998, found among *Pseudonychocamptus koreni* (Boeck, 1873) specimens (reg. no. NHM 1967.10.31–70) collected during the 1966 University of London Sub-Aqua Club expedition to the Isles of Scilly; Great Britain Rock, off St Mary's; algal debris at LWN, among bryozoans (*Cellaria*, *Lepralia*) and hydroids (*Sertularia*), 27 m; July 1966 (cf. Wells 1970: 267).

Description. Female. *Body* (Figure 1A, B). Total body length 696–738 µm (n=2; mean 717 µm). Largest width at posterior margin of cephalic shield (174 µm). Urosome gradually tapering posteriorly (Figure 1A). Rostrum triangular (Figure 2C), with pair of sensilla near apex; midventral tube-pore in subapical position; completely defined at base. Cephalothorax with posterior margin fringed with small spinules; pleural areas well developed and rounded with lobate posterolateral angles; entire surface covered with tiny spinules as illustrated in Figure 1A, B; sensilla and few pores present as illustrated in Figure 1A, B. Pedigerous somites covered with minute spinules. All prosomites without defined hyaline frills; posterior margins fringed with small spinules. Body constricted between individual somites. Urosome (Figures 1A, B; 2A) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. Abdominal half of genital double-somite and second abdominal somite with lateral lobate extensions. All urosomites with surface ornamentation consisting of small spinules dorsally and laterally; ventral surface largely naked except for few rows of spinules and paired tube-pores; ventral hind margin with large spinules laterally and small spinules medially (Figure 2A). Hyaline frills of urosomites not distinct. Genital double-somite (Figures 1A; 2A) with transverse, surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally. Genital field (Figure 2G) with medium-sized copulatory pore (arrowed in Figure 2G) located in median depression; gonopores fused medially forming single genital slit covered on either side by operculum derived from sixth leg; P6 with small protuberance bearing 2 bare setae; small triangular process located on medial side adjacent to protuberance. Anal somite (Figure 2B) with spinular ornamentation and pair of dorsal tube-pores; anal operculum well developed, bearing row of minute spinules and flanked by pair of sensilla; anal opening bordered by well developed frill bearing long setular extensions.

Caudal rami (Figure 2A, B). Short, cylindrical, as long as wide; each ramus with 7 setae: seta I subventral, bare and shortest; setae II and III bare; setae IV and V bipinnate, fused basally, and with predesigned fracture planes [seta V presumably longest but incomplete in all specimens examined including holotype, cf. Hamond (1968: Fig. 3)]; seta VI bipinnate; seta VII tri-articulate at base. Each ramus with spinules on outer dorsal surface; additional spinular ornamentation present along inner and outer margins and around ventral and dorsal hind margins; long tube-pore present near ventral hind margin.

Antennule (Figure 2D). Seven-segmented, slender; with well developed sclerite around base of segment 1; several rows of long spinules present along posterior margins of all segments except for apical segment, and along anterior margins of segments 1–4. Segments 1–2 without spinous processes. Segment 2 largest; segment 4 with aesthetasc fused basally to seta and arising from distinct pedestal. Armature formula: 1-[1], 2-[7

+ 1 pinnate], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[2], 7-[7 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 2 bare setae.

Antenna (Figure 3A). Three-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with 2 rows of spinules. Allobasis not elongate; without distinct surface suture marking original segmentation but with membranous insert around base of exopod; with one abexopodal bipinnate seta in distal half. Exopod small, twice longer than width, with 4 well developed pinnate setae (2 laterally, 2 apically), distal lateral and inner distal ones with finer spinules; one row of coarse spinules on anterior surface. Endopod shorter than allobasis; lateral armature arising in distal half, consisting of one bare seta flanked by 2 strong pinnate spines; apical armature consisting of 2 strong spines and 3 geniculate setae (one geniculate seta fused basally to short seta). Endopod with 2 rows of long spinules laterally and 2 transverse hyaline frills subapically.

Labrum. Well developed; spinular ornamentation on anterior surface as in Figure 2E.

Mandible (Figure 3B). With well developed gnathobase bearing several multicuspitate teeth around distal margin and one pinnate spine at dorsal corner as in original description (Hamond 1968: Fig. 6). Palp (Figure 3B) small; endopod and exopod fused to basis, represented by small peduncles bearing 3 plumose and one pinnate seta(e), respectively. Basal armature represented by one plumose seta.

Paragnaths (Figure 2F). Strongly developed paired lobes with medially directed hair-like setules, separated by medial lobe covered by dense pattern of short setules.

Maxillule (Figure 3C). Praecoxa with few long spinules around outer margin; arthrite strongly developed, with a tube-seta on anterior surface and 8 spines/setae around distal margin; one transverse row of long spinules on posterior surface, and one row of small spinules along inner margin of arthrite. Coxa with cylindrical endite bearing a naked seta and a curved, pinnate spine; with spinular row on anterior surface. Basis with cylindrical endite bearing 2 naked setae and a pinnate spine; with several spinular rows on anterior surface. Endopod completely incorporated into basis, forming cluster of 3 plumose setae; exopod 1-segmented, with 2 plumose setae and several rows of fine spinules on surface.

Maxilla (Figure 3D). Syncoxa with 3 endites; with a row of long spinules along outer margin, several rows of spinules on posterior surface, and several spinules along inner margin; praecoxal endite small and cylindrical, with one bare seta; both coxal endites with a strong pinnate spine and 2 pinnate setae with subapical tubular extension; proximal coxal endite with one row of spinules anteriorly. Allobasis drawn out into strong, slightly curved, distally pinnate claw; accessory armature consisting of 2 pinnate and 2 naked setae. Endopod represented by one bipinnate and 3 naked setae, surrounded by spinules at base.

Maxilliped (Figure 3E). Syncoxa elongate, with 2 plumose setae and two rows of spinules. Basis with one row of spinules along outer margin, palmar margin completely bare. Endopod drawn out into long claw; with one short accessory seta anteriorly, and one tube-pore posteriorly.

Swimming legs. *P1–P4* (Figures 4A, B; 5A–C). With wide intercoxal sclerites and well developed praecoxae. Praecoxae, coxae and bases with anterior rows of surface spinules as figured. Exopods 3-segmented, endopods 2-segmented.

P1 (Figure 4A). Coxa large; with several spinular rows and patches as figured. Basis with bipinnate seta on distal pedestal near insertion of endopod, long setules along inner margin and one bipinnate spine and several spinules along outer margin; anterior tube-pore near articulation with coxa. Exp-1 with one bipinnate seta; exp-2 with one naked outer seta; exp-3 with 2 virtually naked and 2 geniculate setae. Enp-1 1.8 times as long as exopod, with long spinules along proximal half of inner margin; enp-2 with one strong, minutely denticulate claw, and one small naked seta; several spinules along outer margin and around inner distal corner.

P2–P4 (Figures 4B; 5A, B). Coxae and bases with spinular rows along outer margin and on anterior surface; basis with tube-pore on anterior surface; outer margin of basis with bipinnate spine (*P2*) or naked seta (*P3–P4*); exopodal and endopodal segments with elaborate spinular/setular ornamentation as figured. *P4* outer exopodal spines with long spinules. *P2–P4* endopods with short enp-1 and long, inflated enp-2; outer margin of enp-2 weakly chitinized, with 2 parallel rows of flimsy setular extensions, possibly surrounding glandular structure (Figure 5B). *P3–P4* enp-2 with tube-pore near distal margin. *P2* enp-2 twice times longer than enp-1; endopod reaching to distal margin of exp-2; exp-3 longest. *P3* enp-2 2.5 times longer than enp-1; endopod reaching to distal margin of exp-2; exp-3 longest. *P4* enp-2 2.6 times longer than enp-1, posterior distal margin with spinular row (Figure 4D); endopod reaching to about distal margin of exp-2; exp-3 subequal to exp-1. Outer distal seta of *P4* enp-2 clearly shorter than others; inner seta of enp-1 very long (arrowed in Figure 4B) and much longer than in *P3* enp-1 (arrowed in Figure 5C). Spine and setal formulae of swimming legs as for genus.

Fifth pair of legs (Figure 6E). Baseoendopods not medially fused, with distinct medial extension. Exopod and baseoendopod discrete, each with pattern of spinules as figured; spinular pattern on exopod denser than on baseoendopod. Baseoendopod forming long, outer setophore bearing basal seta and rows of spinules; with 3 tube-pores on anterior surface; endopodal lobe just extending to proximal area of exopod, with 2 apical and 3 lateral bipinnate setae, proximal and inner middle ones minutely pinnate. Exopod elongate, about 3 times longer than wide; with one naked terminal seta, one bipinnate inner seta, and one bare and 3 pinnate setae along outer margin; terminal seta arising from short cylindrical process.

Egg-sac. Number of eggs and arrangement unknown.

Description. Male. *Body* (Figure 1C). Body length 570–587 μm ($n=3$; mean 579 μm). Largest width at posterior margin of cephalic shield (144 μm). Urosome narrower than prosome. Prosome (Figure 1C) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Cephalothorax with smooth posterior margin; pleural areas well developed and rounded, with lobate posterolateral angles; whole surface covered with tiny spinules as in ♀. Rostrum as in ♀. Pedigerous somites covered with minute spinules as in ♀. Urosome (Figure 1C) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. All urosomites with surface ornamentation consisting of tiny spinules dorsally and laterally; ventral surface smooth except for few rows of small spinules as in ♀; ventral posterior margin with large spinules laterally and minute spinules medially. Hyaline frills of urosomites not distinct.

Antennule (Figure 6A-C). Eight-segmented; subchirocer with geniculation between segments 5 and 6. Segments 1 and 2 with several rows of long spinules along anterior and posterior margins; without protuberances. Segment 3 (Figure 6B) with few spinules along anterior margin. Segment 4 represented by small U-shaped sclerite around anterior margin (see insert in Figure 6B). Segment 5 swollen. Segment 8 triangular (Figure 6C). Segmental homologies: 1-(I), 2-(II-VIII), 3-(IX-XII), 4-(XIII), 5-(XIV-XX), 6-(XXI-XXII), 7-(XXIII), 8-(XXIV-XXVIII). Armature formula: 1-[1], 2-[1 pinnate + 8], 3-[8], 4-[2], 5-[9 + 1 pinnate + 1 modified + (1 + ae)], 6-[3 modified spinous elements], 7-[1], 8-[8 + acrothek]. Apical acrothek consisting of minute aesthetasc and 2 naked setae.

Swimming legs. P2-P4 (Figures 4C; 5D). Shape and surface ornamentation of intercoxal sclerites and protopods as in ♀. P2-P3 enp-2 with double row of setular extensions along outer lateral margin as in ♀ (absent in P4; Figure 4C). No sexual dimorphism on P2. Endopodal segments of P3-P4 modified.

P3 (Figure 5D). Exopod as in ♀. Endopod 2-segmented, modified, not reaching to distal margin of exp-2. Enp-1 with several spinules on inner distal margin (arrowed in Figure 5D); inner seta absent. Enp-2 produced distally into short, straight, spiniform apophysis (homologous with outer spine of enp-2 in ♀; arrowed in Figure 5D) surrounded at base by row of coarse spinules.

P4 (Figure 4C). Exopod as in ♀. Endopod relatively shorter than in ♀. Enp-1 with several spinules along inner margin (arrowed in Figure 4C); inner seta absent; outer lateral margin without setular extensions found in ♀. Enp-2 twice longer than enp-1; both apical setae about equally long and longer than in ♀.

Fifth pair of legs (Figure 6D). Baseoendopods fused medially, with spinular patch medially. Baseoendopod with large setophore bearing outer basal seta; endopodal lobe vestigial bearing one pinnate and one bare seta; with one tube-pore along medial margin, and one tube-pore near articulation with exopod; with few coarse spinules at base of setophore. Exopod about twice as long as maximum width; with one inner, one apical and 2 outer setae; all setae pinnate except for distal outer one being smooth; anterior surface with several large spinules.

Sixth pair of legs (Figure 6D). Asymmetrical; represented on both sides by small plate (fused to ventral wall of supporting somite on one side; articulating at base and covering gonopore on other side; dextral and sinistral configurations observed); outer distal corner produced into cylindrical process bearing several spinules, one bipinnate inner and one naked outer seta.

Discussion. Hamond's (1968) original description of the female of *Pseudonychocamptus carthyi* is detailed by contemporary standards. Our redescription revealed some minor observational errors: (1) the entire body is covered by fine spinules instead "... a few long limp hairs, widely scattered here and there"; (2) the third antennular segment has 7 setae instead of 5; (3) the distal lateral and inner distal setae of the antennary exopod have fine spinules instead of membranous laminae; (4) the antennary endopod has an additional subdistal spine and the outermost geniculate seta is fused at the base to a minute seta; (5) the basis and coxal endite of the maxillule have an ad-

ditional seta; (6) the maxilla has a unisetose praecoxal endite and the endopod 4 setae instead of 2; (7) the P1 displays distinct spinule rows along the outer margin of the praecoxa and coxa, and enp-2 has a minute accessory seta at the base of the claw; (8) the outer spines of P2–P3 exp-2 and -3 are bipinnate instead of smooth; and (9) the caudal ramus has 7 setae (seta I was overlooked).

The discovery of the male of *P. carthyi* provides conclusive evidence not only for the inclusion of this species in Lee and Huys' (1999) *PWPH*-clade (grouping the genera *Pilifera*, *Pseudonychocamptus*, *Weddellaophonte* and *Heteronychocamptus*) but also for its exclusion from the genus *Pseudonychocamptus*. The sexual dimorphism in swimming leg armature (the inner seta of P3–P4 enp-1 being absent in the male) unequivocally links this species to the *PWPH*-clade (Table 1). The sexually dimorphic P4 endopod, being 2-segmented in the female but reduced to a minute bisetose segment in the male, is the most significant apomorphy of the genus *Pseudonychocamptus*, however, no such reduction is displayed by the male of *P. carthyi*. This species also displays the most primitive armature on P2–P5 within the *PWPH*-clade (Table 1), lending additional support to a different generic assignment. The only other genus exhibiting two inner setae on P3–P4 exp-3 is *Weddellaophonte*, however, in *P. carthyi* two additional setae are found on P3 enp-2 (formula 321). *Pseudonychocamptus carthyi* is here fixed as the type of a new genus, *Marbefia*, gen. n., which can be defined by the following autapomorphies: (1) P2–P4 enp-2 (except P4 enp-2 in ♂) inflated, with weakly chitinized outer margin bearing two parallel rows of flimsy setular extensions, possibly surrounding a glandular structure; a similar but non-homologous structure is found on the P4 endopod of species of *Corbulaseta* Huys & Lee, 2000 (Huys and Lee 2000; Gómez and Boyko 2006); (2) P4 with sexually dimorphic setation on enp-2 (outer distal seta reduced in ♀, very long in ♂); and (3) antennule ♀ with spinules along posterior margins of segments 1–6.

Fiers (1992: 213) hinted at a relationship between *Pseudonychocamptus* and the monotypic genus *Harrietella* T. Scott, 1906 (type: *Laophonte simulans* T. Scott, 1894a) but provided no supporting evidence for this claim. Presumably his assertion was adopted from Lang (1948: 1449) who recognized a similar relationship based on the shared more or less dorsoventrally flattened body and the 2-segmented P3 endopod and 1-segmented P4 endopod in the male, in addition to the overall similarity in the maxilliped, P1 and male P3 exopod. Most *Pseudonychocamptus* species, however, do not have a dorsoventrally depressed body and the general habitus is considerably different from that of *Harrietella simulans* (T. Scott 1894a; Sars 1920b). In *Pseudonychocamptus* the P4 endopod is suppressed during development in the male but not in the female, resulting in different segmentation and setation patterns, whereas in *Harrietella* both sexes display a 1-segmented endopod and no sexual dimorphism in setation is discernible (e.g. Vervoort 1950; Hicks 1989). The 2-segmented P3 endopod in the male, displaying a straight spinous outgrowth on the distal segment, is indicative of a relationship with *Pseudonychocamptus*, *Pilifera*, *Inermiphonte*, gen. n. (see below) and *Marbefia*, gen. n., however, *Harrietella* does not display the sexual dimorphism

(on P3–P4 enp-1) that defines Lee and Huys' (1999) *PWPH*-clade. Although this absence is conceivably secondary as a result of the loss of the inner seta on P3 enp-1 in the female, confirmation of its membership of this clade will probably have to await the arrival of molecular sequence data. *Harrietella* is here tentatively regarded as the sistergroup of *Inermiphonte*, gen. n. (see below).

Although the mosaic distribution of unique plesiomorphies in single species [e.g. *Heteronychocamptus exiguus* (Sars, 1905) with inner seta on P2 enp-1 (*cf.* Sars 1905: Fig. 125); *Laophonte danversae* Hamond, 1969 with 5 elements on ♂ P5 exopod (*cf.* Hicks 1982: Fig. 6); *P. carthyi* with 3 inner setae on ♀ P3 enp-2 (Figure 5C)] hampers the analysis of the basal relationships within the *PWPH*-clade, a well defined group of five genera can be distinguished based on the sexual dimorphism of the P3 endopod. In males of *Marbefia*, gen. n., *Pseudonychocamptus*, *Pilifera*, *Inermiphonte*, gen. n. and *Harrietella* the ramus is 2-segmented (instead of 3-segmented), bearing a straight (rather than a sigmoid) apophysis on the outer margin of the distal endopod segment (Table 1). Within this lineage, *Marbefia* is considered to be the basal offshoot, the other four genera sharing a suite of synapomorphic reductions on the swimming legs: (1) P3–P4 exp-3 with 1 inner seta, (2) P2 enp-1 with 1 inner seta, and (3) P3 enp-2 ♀ with at most 2 inner setae.

Key to the species of *Pseudonychocamptus* Lang, 1944

Lang (1944, 1948) proposed the genus *Pseudolaophonte* for four species previously allocated to the genus *Laophonte* Philippi, 1840: *Laophonte koreni* Boeck, 1873 (type by original designation), *L. gracilis* T. Scott, 1903, *L. proxima* Sars, 1908a and *L. abbreviata* Sars, 1920a. Noodt (1952) removed *L. gracilis* and designated it as the type (by original designation) of a new genus *Pilifera* Noodt, 1952 which has remained monotypic since its proposal. New species were added to *Pseudonychocamptus* by Lang (1965: *P. paraproximus* and *P. spinifer*), Hamond (1968: *P. carthyi*), Apostolov and Petkovski (1980: *P. marinovi*), Ceccherelli (1988: *P. colomboi*) and Apostolov (2008: *P. kolarovi*).

Both Sars (1908a) and Wilson (1932) described *Laophonte proxima* on the basis of females only (the latter author from a freshwater locality!) whereas Klie (1929) provided the first illustrations of the male, including the P5 which he figured with one seta on the endopodal lobe. Lang (1965) distinguished the closely related *Pseudonychocamptus proximus* and *P. paraproximus* on the basis of morphometric differences in the distal segment of the P4 exopod and P5 baseoendopod in the female and the P5 exopod in the male. An additional differentiating character used in his key referred to the number of setae on the male P5 baseoendopod. Hamond (1968) and Ceccherelli (1988) followed Lang's judgement, however Mielke (1975), in his redescription of the male of *P. proximus*, pointed out that the latter has two setae on the P5 baseoendopod (as in all other congeners), rendering the distinctiveness of *P. paraproximus* doubtful. Although we have followed Bodin (1997) and Wells (2007) in considering the latter a species of uncertain status (here ranked as *species inquirenda*), we have nevertheless included it in the key below, based on the inter-specific differences displayed in the length/width ratio of the male P5 exopod (Table 2).

Recently, Apostolov (2008) added a new species, *P. kolarovi*, based on two males collected from the Kavala beach (Greece) in the Aegean Sea. The author claimed that the species occupied an isolated position in the genus on account of the structure of the caudal rami and P1–P5. The 2-segmented P4 endopod (with one inner and two distal setae), the presence of 5 setae on the P5 exopod and the sexually dimorphic distal inner spine on the P2 endopod clearly exclude *P. kolarovi* from the genus *Pseudonychocamptus* and particularly the latter character unequivocally points to a relationship with the genera *Paralaophonte* Lang, 1944 and *Loureiophonte* Jakobi, 1953. The species is here formally placed in the genus *Paralaophonte* as *Paralaophonte kolarovi*, comb. n. (see below). The six valid species currently recognized in the genus, and the problematic species *P. paraproximus*, can be differentiated by the key below and the character states tabulated in Table 2.

- | | | |
|----|---|-------------------------------------|
| 1. | P3 enp-2 with 4 setae in ♀ and 2 setae in ♂ | 2 |
| – | P3 enp-2 with 5 setae in ♀ and 3–4 setae in ♂ | 3 |
| 2. | P5 exopod ♀ at least twice longer than wide, with 5 setae; P5 exopod ♂ with straight outer margin | <i>P. koreni</i>^a |
| – | P5 exopod ♀ about 1.3 times longer than wide, with 6 setae; P5 exopod ♂ with convex outer margin | <i>P. spinifer</i> |
| 3. | Caudal ramus longer than wide | 4 |
| – | Caudal ramus wider than long | <i>P. marinovi</i> |
| 4. | P5 exopod ♀ with 1 naked and 5 pinnate setae; P2 enp-2, P3 enp-2 and P5 exopod of ♂ with 4 setae | 5 |
| – | P5 exopod ♀ with 6 naked setae; P2 enp-2, P3 enp-2 and P5 exopod of ♂ with 3 setae | <i>P. colomboi</i> |
| 5. | Body elongate, length 3–4 times maximum width of cephalothorax; all setae of P5 exopod ♀ marginal | 6 |
| – | Body short, length about 1.85 times maximum width of cephalothorax; P5 exopod ♀ with 4 marginal and 2 surface setae | <i>P. abbreviatus</i> |
| 6. | P5 exopod ♂ about 2.7 times longer than wide | <i>P. proximus</i> |
| – | P5 exopod ♂ about 3.25 times longer than wide | <i>P. paraproximus</i> |

Proposal of *Inermiphonte*, gen. n.

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The taxonomic position of *Laophonte danversae* Hamond, 1969 has been surrounded by controversy since its original description. Hamond (1969) suggested a close rela-

^a Chislenko's [1967 – reproduced in Kornev and Chertoprud (2008)] female from the White Sea shows a P5 exopod ♀ with length/width ratio 1.64 and a P1 endopod which is distinctly more slender than in Sars' (1908a) material; this record is considered doubtful and may well refer to another as yet undescribed species.

Table 2. Setal number and morphometric differences between species of *Pseudonychocamptus* (CR = caudal ramus; exp = exopod; enp = endopod; benp = baseoendopod). Length/width ratios based on Chislenko (1967)^a, Sars (1908a)^b, Sars (1920a)^c, Lang (1965)^d, Letova (1982)^e, Apostolov and Petkovski (1980)^f and Ceccherelli (1988)^g.

species		P2 enp	P3 enp	P5		P5 exp ♀ L/W	CR L/W
				exp	benp		
<i>P. koreni</i>	♀	0.220	1.121	5	5	1.64 ^a –2.36 ^b	1.36 ^b
	♂	0.220	0.020	4	2	–	–
<i>P. proximus</i>	♀	0.220	1.221	6	5	1.64 ^b	1.80 ^b
	♂	0.220	0.220	4	2	–	–
<i>P. abbreviatus</i>	♀	0.220	1.221	6	5	1.25 ^c	1.38 ^c
	♂	0.220	0.220	4	2	–	–
<i>P. paraproximus</i>	♀	0.220	1.221	6	5	1.44 ^d	1.65 ^d
	♂	0.220	0.220	4	2	–	–
<i>P. spinifer</i>	♀	0.220	1.121	6	5	1.22 ^d –1.27 ^c	1.14 ^e –1.23 ^d
	♂	0.220	0.020	4	2	–	–
<i>P. marinovi</i>	♀	0.220	1.221	6	5	2.1 ^f	0.85 ^f
<i>P. colomboi</i>	♀	0.220	1.221	6	5	1.84 ^g	1.12 ^g
	♂	0.120	0.120	3	2	–	–

tionship with *L. cesareae* Por, 1964 (currently placed in *Loureirophonte*; cf. Fiers 1993 – see below) without giving any compelling evidence for this affiliation. Although his description of *L. danversae* was based solely on females from West Runton the author also illustrated a single male from the same locality under the nondescript name “Laophontid male, ?gen., ?sp.”. Hamond (1969) suggested that the latter might have been the unknown male of *L. danversae*, were it not for the marked differences observed in the rostrum, caudal rami and the armature on the P2–P4 exopods. In an addendum to his paper he also remarked that “Laophontid male, ?gen., ?sp.” and the male of *Laophonte ?drachi* Médioni & Soyer, 1966 shared the same type of sexual dimorphism on the P3 endopod and that the latter species was obviously closely related to *L. danversae*. As pointed out by Hicks (1982), Bodin (1971) clearly misinterpreted Hamond’s remarks when he suggested conspecificity between *L. danversae* and *L. ?drachi*. This misconception was perpetuated in the literature by Wells (1976) who considered Hamond’s “Laophontid male, ?gen., ?sp.” the true male of *L. danversae* and subsequently by Bodin (1979) who regarded both female and male *L. danversae* as junior synonyms of *L. ?drachi*. The issue of the unknown male of *L. danversae* was finally resolved by Hicks (1982) who provided its first description based on material from Robin Hood’s Bay (England). Hicks demonstrated that Hamond’s (1969) “Laophontid male, ?gen., ?sp.” and the males of *L. danversae* and *L. ?drachi* were significantly different in the swimming legs, leg 5 and caudal rami, corroborating their distinct specific identity but his comparative analysis did not, however, contribute

anything new to elucidating the relationships of this species group within the Laophontidae. Hamond (1969) had previously suggested that *L. danversae* might best be classified as an “anomalous species” of *Laophonte*, which does not fit into any of the species groups proposed by Lang (1948). Médioni and Soyer (1966) tentatively assigned *L. ?drachi* to the *inopinata*-group of *Laophonte* and noted some similarities with *L. ?platychelipusoides* Noodt, 1958 (currently placed in *Coullia* Hamond, 1973; cf. Hamond 1973; Huys 2009a). Lee and Huys (1999) instead recognized a relationship between *L. danversae* and the laophontid genera that display a similar type of setal sexual dimorphism on the endopods of P3–P4 (Table 1) but neither formally included the species in the *PWPH*-clade or removed it from its floating status in the genus *Laophonte*. *Laophonte danversae* is here fixed as the type species of a new genus *Inermiphonte*, gen. n. which also includes Hamond’s (1969) “Laophontid male, ?gen., ?sp.”. *Inermiphonte* is provisionally regarded as the sistergroup of *Harrietella* based on the following synapomorphies: (1) P2–P4 exp-3 ♀/♂ without inner setae, (2) P4 exp-2 without inner seta (exp-2 not expressed in *Harrietella* but inner margin of distal exopod segment without inner setae), (3) P3 enp-1 ♀ without inner seta, (4) P3 enp-2 ♀ with 0–1 seta, and (5) P4 enp-2 ♀ without inner setae.

Diagnosis. Laophontidae. Body linear or dorsoventrally depressed. Posterior margins of abdominal somites usually with spinule rows dorsally and ventrally. Rostrum delimited at base; broadly triangular, prominent. Genital double-somite ♀ with lateral incisions and ventrolateral internal chitinous ribs marking original segmentation. Pleural extensions of ♀ abdominal somites moderately developed. Caudal ramus rectangular or conical, longer than wide; inner margin with spinules; with 7 setae; setae IV and V well developed, pinnate; seta VI reduced, setiform. Anal operculum finely spinulose or smooth.

Sexual dimorphism in antennule, P3 (and occasionally P4) endopods, P5, P6 and in genital segmentation.

Antennule relatively short and 6- or 7-segmented in ♀; 6- or 7-segmented and (sub)chirocer with 1–2 segments distal to geniculation in ♂; segments with spinular ornamentation along anterior margin of segments 1–4 in ♀ and 1–3 in ♂; segments 1–2 without processes; dorsal surface of segment 1 with 2 thick pinnate spines; with aesthetasc on segment 4 (♀) or 5 (♂). Antenna with 4 setae on exopod; allobasis with abexopodal seta. Mandibular palp elongate, 1-segmented; with one basal, one exopodal and 3 endopodal setae. Maxillule with defined exopod bearing 2 setae. Maxilla with 3 endites on syncoxa; endopod represented by 3 setae. Maxilliped elongate; syncoxa with 2 setae; basis without distinct ornamentation; endopodal claw long and curved, with one accessory seta.

P1 long, with elongate coxa and basis; with 2- or 3-segmented exopod, distal exopod segment with 2 short and 2 geniculate setae; endopod stout, enp-1 without inner seta, enp-2 with minute seta and long minutely denticulate claw. Swimming legs P2–P4 with 3-segmented exopods and 2-segmented endopods. P2–P4 exp-3 and P4 enp-2 without inner setae; inner seta of P4 enp-1 occasionally present in ♀ but always absent in ♂. P3 enp-2 produced into straight spiniform apophysis in ♂ (homologous with

outer spine of enp-2 in ♀). Inner distal seta of P2–P4 exp-3 reduced in ♂. Armature formula of swimming legs 2 to 4 (P2–P4) as follows:

	Exopod	Endopod
P2	0.(0–1).023	0.(1–2)20
P3	0.(0–1).023	0.(0–1)21 [0.(0–1)20 in ♂]
P4	0.1.02(2–3)	(0–1).021 [0.021 in ♂]

P5 with separate exopod and baseoendopod. Exopod ovoid or elongate with 6 setae in ♀ and 4–5 setae in ♂. Endopodal lobe well developed in ♀, subtriangular, with 4–5 setae. Baseoendopods fused medially in ♂; endopodal lobes rudimentary, with 2 setae each.

P6 forming well developed operculum with 2 small setae in ♀; asymmetrical in ♂ (with dextral or sinistral configuration), with outer distal corner produced into process bearing 2 well developed elements.

Type species. *Laophonte danversae* Hamond, 1969 = *Inermiphonte danversae* (Hamond, 1969), comb. n.

Other species: *Inermiphonte hamondi*, sp. n.

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Species incertae sedis. *Laophonte* ? *drachi* Médioni & Soyer, 1966 = *Inermiphonte drachi* (Médioni & Soyer, 1966), comb. n.

Etymology. The generic name refers to the absence of inner setae on P2–P4 exp-3 and P4 enp-2 (Table 1). Gender: feminine.

Following Hicks' (1982) comparative analysis Hamond's (1969) "Laophontid male, ?gen., ?sp." is here assigned to a new species *Inermiphonte hamondi*, sp. n., which can be differentiated from the type species by the characters listed in Table 1 and Hicks' (1982: 306) Table II. *Laophonte* ? *drachi* shows some important differences with the other two species such as the 6-segmented antennule in the female, the 2-segmented P1 exopod, the reduced inner distal setae on the female P2–P4 exp-3 (a character typical for male *Inermiphonte*), and the presence of three strong spines on the male P4 endopod. *L.* ? *drachi* resembles *I. danversae* in the presence of only one inner seta on P2 enp-2, no inner setae on ♂ P3 enp-2 and only three outer spines on P4 exp-3; it is similar to *I. hamondi* in the presence of only four elements on the male P5 exopod. It is here placed as *species incertae sedis* in *Inermiphonte* as *I. drachi*, comb. n.

Inermiphonte danversae is thus far known only from two localities in England. Hamond (1969) recorded three females from the shore at West Runton (Norfolk) and Hicks (1980, 1982) reported the species from a range of littoral algae in Robin Hood's Bay (North Yorkshire) where it attained highest densities on *Corallina officinalis* L. and *Cladophora rupestris* (L.) Kutz. *Inermiphonte hamondi* and *I. drachi* are known only from their respective type localities, the former from the intertidal zone at West Runton (Hamond 1969) where it may co-exist with *I. danversae*, the latter from colonies of the bryozoan *Schismopora armata* (Hincks, 1860) near Racou (Roussillon, France) (Médioni and Soyer, 1966).

Key to the species of *Paralaophonte* Lang, 1948

Included species: *Paralaophonte pallaresae*, sp. n.

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The genus-group name *Paralaophonte* was first published by Lang (1944) who subdivided the genus in four species-groups and designated a type species for three of them: (1) *brevirostris*-group (no type designated), (2) *perplexa*-group (type: *Laophonte perplexa* T. Scott, 1899), (3) *gracilipes*-group (type: *Laophonte gracilipes* Brady, 1910), and (4) *karmensis*-group (type: *Laophonte karmensis* Sars, 1911). The artificiality of this system was subsequently exposed by the discovery of “transitionary” species which blurred the boundaries of some of the species groups (e.g. Vervoort 1962); consequently, Lang’s (1944, 1948) subdivision was finally disposed off by Wells (2007). Vervoort (1964) remarked that *Paralaophonte* Lang, 1944 is an unavailable generic name which was subsequently validated by Lang (1948) by the indication of a type species (*Cleta brevisrostris* Claus, 1863) and the provision of an accompanying generic diagnosis. The authorship and date of this genus should, therefore, be attributed as *Paralaophonte* Lang, 1948 (Huys 2009b).

According to the latest checklist (Wells 2007), the genus *Paralaophonte* currently includes 33 valid species and one *species incertae sedis* (*Laophonte lamellipes* Nicholls, 1944). Various authors (e.g. Willey 1935; Nicholls 1945; Yeatman 1970; Hamond 1973; Wells and Rao 1987; Wells 2007) have commented on the difficulties in separating the two most widely distributed species, *P. brevisrostris* (Claus, 1863) and *P. congenera* (Sars, 1908b), and some of them have casted doubt on the validity of this separation. Both species have also been reported to display a great deal of variability in the rostrum, antennule, leg 5 and caudal rami (e.g. Wells and Rao 1987) but it is unclear to what degree this pertains to genuine intra- or interpopulation variability or whether this is a reflection of allopatric or sympatric closely related species (as hinted at by Mielke 1981). The further subdivision of both species in subspecies has also led to taxonomic confusion. For example, Willey’s (1935) variety “*fissirostris*” of *P. brevisrostris* was upgraded to subspecies level by Lang (1965) (and accepted by most subsequent authorities: e.g. Wells et al. 1982; Wells 2007) but allegedly differs from the nominotypical subspecies only in the shape of the rostrum. Given the reported variability in this structure in other species it seems impractical to maintain Willey’s (1935) subspecies at present and hence they are here formally declared invalid. Similarly, *P. congenera mediterranea* Lang, 1948 appears to be more closely related to *P. lacerdai* Jakobi, 1953 than to its nominotypical subspecies *P. congenera congenera*. In fact both taxa can only be separated by subtle differences in the caudal ramus, length of endopodal setae in the female P5 and shape of the endopodal margin in the male P5. Likewise, *Paralaophonte pacifica galapagoensis* Mielke, 1981 is more similar to *P. brevisrostris* than to its nominotypical subspecies *P. pacifica pacifica* Lang, 1965 (see also Wells 2007); the first two taxa differ primarily in details of the female antennule, P4 endopod and the male P3 exopod. Mielke’s (1981) subspecies is here upgraded to full species rank since it differs sufficiently from Lang’s (1965) population to warrant such status: (a) second antennary segment with blunt protuberance instead of spinous projection; (b) P1 enp-1 10

times instead 8 times as long as wide; (c) P2–P3 exopods ♀ distinctly shorter; (d) P3 exp-3 ♂ inner distinctly longer instead of shorter than outer distal spine; (e) baseoendopod P5 ♂ with strongly developed seta instead of tiny reduced seta; and (f) caudal ramus 1.3 times as long as maximum width instead of quadratic.

Brady's (1910) original description of *P. gracilipes* (as *Laophonte gracilipes*) from the Kerguelen Islands (Grande Terre, Baie de l'Observatoire) is fragmentary and lacking in detail. Lang (1936) redescribed the species based on material from the Falklands and Pallares (1968) did the same using material from Puerto Deseado (Santa Cruz, Argentina). However, both redescriptions differ significantly in the number of inner setae on P3–P4 exp-3, the morphology of the female P5, the size of P1 exopod (relative to the endopod) and the length of the apophysis on the male P3, strongly suggesting that the Falklandian and Argentinian populations belong to different species. Wells et al. (1982) and Wells (2007) adopted Lang's (1936) swimming leg armature pattern in their respective identification keys, however, both incorrectly stated that the male P5 endopodal lobe lacked setae. Although Lang (1936) showed an endopodal seta, their error presumably stemmed from a misinterpretation of Brady's (1910) original figure of the male P5 which also shows the endopodal seta but not the typical outer basal one. Although the supporting evidence is admittedly slim (morphometric differences in P1 exopod and P2 endopod ♂) we have elected to attribute the Falklandian material to *P. gracilipes* and to propose a new species, *P. pallaresae*, sp. n., for the specimens illustrated by Pallares (1968). It should be noted that Pallares figured the female antennule as 8-segmented but stated in the text that it consists of only 7 segments (which is conceivably the correct number). *Paralaophonte obscura* Vervoort, 1962 from New Caledonia appears to be most closely related to *P. pallaresae*, sp. n. but differs from the latter in the female by the presence of a small conical protuberance on the second antennular segment and the semicircular P5 exopod in which the inner distal seta is only slightly longer than proximal inner one, and in the male by the presence of only 4 elements on the P5 exopod. *Paralaophonte pallaresae*, sp. n. can be characterized by the following differential diagnosis:

Paralaophonte. Abdominal somites without a middorsal spinous process. Caudal rami cylindrical, about 1.5 times as long as maximum width; with seta V elongate. Antennule ♀ 7-segmented; segment 2 without horn, spinous process or protuberance. P1 exopod 3-segmented. P3–P4 exp-3 with 1 inner seta. P3 enp-2 ♀ with 5 elements. P3 endopod ♂ 3-segmented with apophysis on enp-2 and 4 elements on enp-3; apophysis distinctly longer than endopodal segments combined. P4 enp-2 with 4 elements. P5 exopod ♀ longer than wide, inner distal seta twice the length of proximal inner one; baseoendopod with 4 elements. P5 exopod ♂ with 5 elements; longest seta at most 2.5 times the length of segment; endopodal margin with 1 long seta. Body length: 590–670 µm (♀), 500–510 µm (♂).

The original material collected by Dr Rosa Pallares is no longer available for re-examination (Dr S. Ménu-Marque, Universidad de Buenos Aires, pers. commn). In accordance with ICZN Arts 16.4 and 72.5.6 the male specimen illustrated by Pallares (1968: 87) in her plate XXXII (Figs 1, 5, 9, 12, 15) is here fixed as the holotype of *P. pallaresae*, sp. n. Type locality: Puerto Deseado, Santa Cruz Province (Argentina), plankton.

Jakobi (1953) proposed the genus *Loureiophonte* for two new species from Southern Brazil, *L. catharinensis* (type by original designation) and *L. paranaensis* and claimed a close relationship with the *inopinata*-group of *Laophonte*. Both Vervoort (1964) – who favoured a relationship with the *inornata*-group of *Laophonte* – and Lang (1965) questioned the accuracy of Jakobi's illustrations and generic diagnosis and doubted the validity of *Loureiophonte* until Mielke (1981) confirmed its separate identity by providing a detailed description of a third species, *L. isabelensis* Mielke, 1981. This course of action was corroborated by Fiers (1993) in his revision of the genus which saw the addition of five new species and another two which were transferred from other genera (*Laophonte caesarea* Por, 1964; *Paralaophonte subterranea* Lang, 1965). With the recent addition of *L. psammophila* Mielke, 2001 and *L. minutum* Gómez & Boyko, 2006 the genus now includes 12 species (Mielke 2001; Gómez and Boyko 2006) (Table 3) although it is known that other as yet undescribed species occur in the Galapagos (Mielke 1981). Fiers (1993) provided a key to species which was recently updated by Gómez and Boyko (2006). Fiers was also the first to claim a sistergroup relationship between *Paralaophonte* and *Loureiophonte* based on the sexual dimorphism of the P2 endopod, the presence of 5 setae on the P5 exopod of both sexes, and the presence of 4 setae and one seta on the P5 endopodal lobe in females and males, respectively. He also listed a suite of characters that serves to distinguish *Loureiophonte* from its sistertaxon: (a) P2 enp-2 ♀ with 1 distal and 2 inner setae (0.210); (b) bulbous appearance of the sexually dimorphic distal inner seta of P2 enp-2 (with a lamellar structure in the distal third); and (c) 1-segmented P4 endopod. Characters (a) and (c) are autapomorphies of *Loureiophonte* (although Fiers (1993) did report specimens of *L. mediterranea* that displayed a 2-segmented P4 endopod) supporting the monophyly of the genus. Both *Paralaophonte* and *Loureiophonte* display a homologous sexual dimorphism on the P2 endopod, involving the modification of the distal inner seta on enp-2. In the former genus the seta has attained a further derived state of modification (as described under character (b) above), raising the suspicion that *Loureiophonte* is merely nested within *Paralaophonte*. Indeed, at present there is not a single apomorphy supporting the monophyly of *Paralaophonte*, potentially rendering the latter paraphyletic exclusive of *Loureiophonte*. In addition, the dichotomy between the two genera that was traditionally based on different types of P2 endopod sexual dimorphism appears to be false since it is neither jointly exhaustive nor mutually exclusive. The evolutionary transition between both genera is best demonstrated by the modification in male *Paralaophonte macera* Sars, 1908b and *P. asellopsiformis* Lang, 1965 which is virtually identical to the *Loureiophonte* condition and, similarly, the state of the inner distal seta in male *L. furcata* Fiers, 1993 which resembles the *Paralaophonte* condition (Sars 1908b; Fiers 1993). Although the presence of such intermediate taxa casts further doubt on the validity of the basal split between *Loureiophonte* and *Paralaophonte* we have refrained from synonymizing these genera pending a thorough phylogenetic analysis at species level.

Five species have been added to the genus *Paralaophonte* since Wells' (2007) checklist: *P. lamellipes* (Nicholls, 1944), comb. n., *P. galapagoensis* Mielke, 1981, grad. n.,

Table 3. Differentiating characters of *Paralaophonte* species [A1 = number of antennular segments in ♀; Pr = protuberance on second antennary segment (– : absent; + : small conical or blunt protuberance; s : straight spinous process; H : prominent, recurved, unguiform process); P1 (exp = number of exopodal segments; sd = number of setae/spines on distal exopodal segment); P3 exp ♂ = armature formula with A indicating precense of apophysis on middle segment; ? = unknown].

	A1	Pr	P1		P2		P3		P4		P5 ♀		P5 ♂		P3 exp ♂
			exp	sd	exp	enp	exp	enp	exp	enp	exp	benp	exp	benp	
<i>Paralaophonte</i> LANG, 1944															
<i>P. brevinotris</i> (Claus, 1863) ^a	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. meineri</i> (Brady, 1899)	7	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. congenera congenens</i> (Sars, 1908b) ^b	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. congenera mediterranea</i> Lang, 1948	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	4	1	0.A.220
<i>P. lacerdai</i> Jakobi, 1953	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	4	1	0.A.220
<i>P. royi</i> (Jakubisiak, 1932)	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. octavia</i> (Monard, 1935) ^c	7	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	?	?	?
<i>P. dieuzeidei</i> (Monard, 1936)	6	H	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. gurneyi</i> (Lang, 1934) ^d	7	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	6	4	5	1	0.A.220
<i>P. majae</i> Petkovski, 1964	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	5	5	1	0.A.220
<i>P. asellopsiformis</i> Lang, 1965	6	H	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. pacifica</i> Lang, 1965	6	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. galapagoensis</i> Mielke, 1981, grad. n.	6	+	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. ornieres</i> Raibaut, 1969	6	–	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	4	4	5	1	0.A.220
<i>P. septemarticulata</i> Chislenko, 1978	7	s	3	4	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	4	4	?	?	?
<i>P. perplexa</i> (T. Scott, 1899)	7	–	2	5	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	0	0.221
<i>P. hyperborea</i> (Sars, 1909) ^e	7	–	2	5	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	5	4	5	0	0.A.220
<i>P. pilosoma</i> Vervoort, 1964 ^f	?	H	2	5	0.1.123	0.220	0.1.223	0.321	0.1.223	0.121	?	?	5	1	0.A.220
<i>P. macera</i> (Sars, 1908b) ^g	7	+	2	5	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	0	0.A.120
<i>P. sculpia</i> Hamond, 1973 ^h	7	–	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	?	?	?
<i>P. problematica</i> Mielke, 1981	6	s	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. echinata</i> Fiers, 1986	6	–	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	1	0.A.220
<i>P. gracilipes</i> (Brady, 1910)	7	–	3	4	0.1.123	0.220	0.1.223	0.221	0.1.223	0.121	5	4	5	1	0.A.220

PARALAPHONTE LANG, 1944	A1	Pr	P1	P2	P3	P4	P5 ♀	P5 ♂	P3 enp ♂
<i>P. imae</i> Chislenko, 1977 ⁱ	7	–	2 5	0.1.123 0.220	0.1.223 0.320	0.1.223 0.121 5	4	5	0 0.320
<i>P. panamensis</i> Mielke, 1982	6	+	2 5	0.1.123 0.220	0.1.223 0.321	0.1.222 0.121 5	4	5	1 0.A.220
<i>P. harpagone</i> Gheerdyn, Fiers, Vincx & De Troch, 2006	6	+	2 4	0.1.123 0.220	0.1.223 0.220	0.1.222 0.120 4	4	5	1 0.220
<i>P. taurina</i> (Monard, 1928)	7	H	3 4	0.1.123 0.220	0.1.223 0.320	0.1.123 0.121 5	5	?	?
<i>P. longipes</i> (T. Scott, 1894b)	7	–	2 5	?	0.1.123 0.321	?	5	?	?
<i>P. karmensis</i> (Sars, 1911) ^j	7	+	2 5	0.1.123 0.220	0.1.123 0.321	0.1.123 0.121 4	4	5	1 0.A.220
<i>P. tenera</i> (Sars, 1920a)	7	+	2 5	0.1.123 0.220	0.1.123 0.321	0.1.123 0.121 5	4	4	1 0.A.120
<i>P. lunata</i> (Willey, 1930)	7	–	2 5	0.1.123 0.220	0.1.123 0.321	0.1.123 0.121 5	4	5	1 0.A.220
<i>P. spitzbergensis</i> Mielke, 1974	7	+	2 5	0.1.123 0.220	0.1.123 0.321	0.1.123 0.121 5	4	5	0 0.A.220
<i>P. zimneri</i> (Douwe, 1929)	6	+	3 4	0.1.123 0.220	0.1.123 0.321	0.1.123 0.121 5	4	5	1 0.A.220
<i>P. obscura</i> Vervoort, 1962	7	+	3 4	0.1.123 0.220	0.1.123 0.221	0.1.123 0.121 5	4	4	1 0.A.220
<i>P. pallaresae</i> , sp. n.	7	–	3 4	0.1.123 0.220	0.1.123 0.221	0.1.123 0.121 5	4	5	1 0.A.220
<i>P. quaterspinata</i> (Brian, 1917) ^k	6-7	–	3 4	0.1.123 0.220	0.1.123 0.221	0.1.123 0.121 5	4	5	1 0.A.220
<i>P. livingstoni</i> Apostolov, 2004	7	+	3 4	0.1.123 0.220	0.1.123 0.220	0.1.123 0.121 5	2	5	1 0.220
<i>P. kolarovi</i> (Apostolov, 2008) comb. n. ^l	?	–	3 4	0.1.123 0.220	0.1.123 0.220	0.1.123 0.120 ?	?	5	1 0.220
<i>P. aenigmaticum</i> Wells, Hicks & Coull, 1982	6	–	2 5	0.1.123 0.220	0.1.123 0.320	0.1.022 0.120 5	3-4	4	1 0.220
<i>P. lamellipes</i> (Nicholls, 1944) ^m	7	–	2 5	0.1.122 0.220	0.1.222 0.220	0.1.222 0.120 5	4	5	0 0.220
LOUREIROPHONTE JAKOBI, 1953									
<i>L. minutum</i> Gómez & Boyko, 2006	?	–	2 5	0.1.023 0.210	0.1.023 0.020	0.1.022 1	?	5	1 0.020
<i>L. isabellensis</i> Mielke, 1981	6	+	2 5	0.1.023 0.210	0.1.023 0.120	0.0.022 110 5	4	5	1 0.120
<i>L. fuscata</i> Fiers, 1993 ⁿ	?	+	2 5	0.1.023 0.210	0.1.023 0.120	0.0.022 110 ?	?	5	1 0.120
<i>L. catharinensis</i> Jakobi, 1953 ^o	6	+	2 5	0.0.023 0.210	0.0.023 0.120	0.0.022 110 5	4	5	1 0.120
<i>L. panamaensis</i> Jakobi, 1953 ^{o,p}	6	+	2 5	0.0.023 0.210	0.0.023 0.120	0.0.022 110 5	4	5	1 ?
<i>L. cesareae</i> (Por, 1964)	6	+	2 5	0.1.023 0.210	0.1.023 0.020	0.0.023 010 5	4	5	1 0.020
<i>L. mediterranea</i> Fiers, 1993 ^q	6	+	2 5	0.1.023 0.210	0.1.023 0.020	0.0.023 010 5	4	5	1 0.020
<i>L. majacola</i> Fiers, 1993	6	+	2 5	0.0.023 0.210	0.0.023 0.020	0.0.023 010 5	3	5	1 0.020

<i>LOUREIROPHONTE</i> JAKOBI, 1953															
<i>L. subterranea</i> (Lang, 1965) ^c	6	–	2	5	0.0.012	0.1(-2)10	0.0.012	0.1(-2)20	0.0.022	020	4	4	5	1	0.120
<i>L. laingensis</i> Fiers, 1993	6	+	2	5	0.0.023	0.210	0.0.023	0.120	0.0.022	110	5	4	5	1	0.120
<i>L. majabudensis</i> Fiers, 1993	6	+	2	5	0.0.023	0.210	0.0.023	0.120	0.0.022	110	5	4	5	1	0.120
<i>L. psammophila</i> Mielke, 2001	6	+	2	5	0.1.022	0.210	0.1.022	0.120	0.0.022	010	5	4	5	1	0.120

^a Wells and Rao (1987) also recorded specimens with a 7-segmented antennule in the female and without a spur on the second segment; Hamond (1972) also observed the 7-segmented condition while Perkowski (1964) recorded a female with a 6-segmented antennule without a spur on the second segment. According to Wells and Rao (1987) the shape and size of the rostrum and the cephalothorax remains as the only reliable criterion to distinguish *P. brevirostris* from *P. congenera*. Pending a re-examination of topotype material, Willey's (1935) variety *fissirostris*, which was upgraded to subspecific level by Lang (1965), is no longer recognized as valid.

^b Sars' (1908b) original description of the male shows 2 setae on the P5 baseoendopod; re-examination of the type material revealed that the short inner element represents a tube-pore. Both Hamond (1972, 1973) and Wells and Rao (1987) pointed out the difficulties in discriminating *P. congenera* and *P. brevirostris*. Hamond's (1969) male shows a spur on the second segment of the antennule [also present in the North Carolina material examined by Hamond (1973)] and a distinctly pitted cephalothorax; Sars (1908b) did not observe these characters in the Norwegian material. Yoo and Lee's (1995) record from the Yellow Sea displaying only 4 setae on P5 exopod ♂, appears to represent a different species; Wells (2007) pointed out that their illustration of the P4 in reality refers to the P2.

^c Monard's (1935) report of an 8-segmented antennule in this species is considered unlikely (cf. Lee and Huys 1999). The species was originally described from Salammbô (Tunisia) and has not been recorded again until recently when Nurul Huda and Zaleha (2005) found it in Peninsular Malaysia; their record (and that of Zaleha et al. 2006) which gives only the armature formula of P2–P4 requires confirmation. Goddard's (2006) claim that his material from Robinson Crusoe Island (Juan Fernández Archipelago, Chile) may be attributed to *P. octavia* cannot be substantiated because it displays only one inner seta on P3–P4 exp-3; the only other known species which displays the same reduced formula is *P. zimmeri* but this species has a 6-segmented antennule in the female and a small spinous process on its second segment [8-segmented (?) and without such process in Goddard's material].

^d Both Gurney (1927) and Sewell (1940) erroneously illustrated the female antennule as 8-segmented (cf. Lee and Huys 1999: 324).

^e Kornev and Chertoprud's (2008) swimming leg armature formula for this species is radically different from that mentioned in previous descriptions (Sars, 1909; Mielke, 1974): P2 (exp: 0.1.1.23; exp: 1.120), P3 (exp: 0.1.223; exp: 0.221), P4 (exp: 0.0.023; exp: 0.121). The reported absence of the spur on the second antennary segment requires confirmation.

- [†]Vervoort (1964) reported a very long inner seta on P3 enp-2 in the male but re-examination of the holotype has proven this to be erroneous (Huys and Lee 2000).
- [‡]Kornev and Chertoprud (2008) confirmed the presence of a small spur on the second antennular segment of the female [overlooked in Sars' (1908b) original description and Chislenko's (1967) redescription]; their swimming leg armature given on p. 311 contradicts the illustrations of P2 and P4.
- ^hAlthough Hamond (1973) showed no hesitation in placing *P. sculpta* in the *gracilipes*-group of *Paralaophonte*, its generic assignment remains doubtful because of the absence of males.
- ⁱChislenko (1977) did not figure the male P3 or P4, suggesting there is no sexual dimorphism in these legs; if this proves to be correct *P. immae* is sufficiently different from *P. perplexa* to warrant distinct species status, however, females of these two species may be extremely difficult to separate.
- ^jChislenko's (1967) specimens from the White Sea differ from Sars' (1911) type population in several aspects and may represent a distinct species: (1) second antennular segment ♀ without a spur; (2) P5 exopod ♀ with 5 elements instead of 4; (3) P2 enp-2 ♂ distinctly longer; (4) P3 exp-1 ♂ outer spine much larger; (5) P3 exp-3 ♂ with only 1 inner seta instead of 2; and (6) P5 exopod ♂ and its middle element distinctly longer. Unfortunately, Kornev and Chertoprud's (2008) report on *P. karmensis* from the White Sea did not resolve the issue but instead added to the confusion surrounding it. They confirmed the presence of the antennular spur but presented a radically divergent armature formula for P1 (exopod 3-segmented), P3 (exp: 0.1.123; enp: 0.121) and P4 (exp: 0.0.123) and considered the number of setae on the P5 exopod ♀ variable (4 or 5).
- ^kThere is considerable confusion over the segmentation pattern of the female antennule. Brian (1921) described it as 5-segmented with segments 1–2 partially fused; Brian (1917) and Pesta (1959) as 6-segmented; and Lang (1948) as indistinctly 7-segmented with segments 5–6 incompletely separated (based on Monard's (1928) redescription).
- ^lApostolov (2008) shows 2 inner and 2 distal setae on P3 enp-2 ♂ (formula 220); the 2-segmented condition and absence of an apophysis suggest that the outer spine is lacking in the female (as in *e.g.* *P. immae*); the number of inner setae expressed in *P. kolarovi* females may be 2 or 3 (in the latter case one seta is typically lost in male *Paralaophonte*).
- ^mNicholls (1944) stated that the P1 exp is 2-segmented, the distal two segments being fused with only 3 terminal setae (in reality the distal segment bears 5 elements); Huys and Lee (2000: 81) confirmed the true nature of the modified male P2 endopod and suggested a relationship with *Paralaophonte*; Wells (2007: 64) placed it as *species incertae sedis* in this genus; it is here formally transferred to *Paralaophonte* as *Paralaophonte lamellipes* (Nicholls, 1944) comb. nov. Lee and Huys (1999: 324) also confirmed that the female antennule is 7-segmented instead of 8-segmented.
- ⁿThe modified inner distal seta resembles more the condition in *Paralaophonte* (Fiers 1993; Fig. 2c).
- ^oSetal formula as reinterpreted by Fiers (1993).
- ^pFiers (1993) doubted the presence of an outer seta on P3 enp-2 and P4 endopod; these "elements" are here reinterpreted as ornamental spinules.
- ^qFiers (1993) also reported specimens with a 2-segmented P4 endopod (formula 0.010).
- ^rThe inner setae of P2 enp-2 are displaced towards the apical margin of the segment creating the impression that there are 1 inner and 2 distal setae instead of 2 inner and 1 distal setae; taking into account the observed variability Lang (1965) erroneously tabulated the setal formula as 0.(0–1)20; Fiers' (1993) formula [0.(1–2)20] is equally incorrect (his Table 1).

P. harpagone Gheerardyn, Fiers, Vincx & De Troch, 2006, *P. kolarovi* (Apostolov, 2008), comb. n. and *P. pallaresae*, sp. n. Although Wells (2007) listed *Laophonte royi* Jakubisiak, 1932 only as a *species incertae sedis* in the Laophontidae it is here included as a valid species of *Paralophonte*, being very closely related to *P. majae* Petkovski, 1964. The 39 species currently recognized as valid in the genus *Paralaophonte* can be identified with the key below.

1. Caudal rami broadly lamellar, close together, with seta V very short **2**
- Caudal rami usually cylindrical, with seta V elongate..... **3**
2. P1 exopod 2-segmented; P3 exp-3 with 1 inner seta; P4 exp-3 with 7 setae/spines; P3 exopod ♂ 2-segmented; P5 exopod ♂ with 4 spines..... ***P. aenigmaticum***
- P1 exopod 3-segmented; P3 exp-3 with 2 inner setae; P4 exp-3 with 4 setae/spines; P3 exopod ♂ 3-segmented; P5 exopod ♂ with 5 setae..... ***P. asellopsiformis***
3. P1 exopod 2-segmented, with 4 setae on exp-2; maxillipeds very large and specialized..... ***P. harpagone***
- P1 exopod 3-segmented with 4 setae on exp-3, or 2-segmented with 5 setae on exp-2 **4**
4. P3 exp-3 with 1 inner seta **5**
- P3 exp-3 with 2 inner setae..... **15**
5. P4 enp-2 with 3 elements (formula 120)..... **6**
- P4 enp-2 with 4 elements (formula 121)..... **7**
6. Caudal ramus about 1.5 times as long as wide ***P. kolarovi***
- Caudal ramus at least twice as long as wide..... ***P. livingstoni***
7. P1 exopod 2-segmented..... **8**
- P1 exopod 3-segmented..... **12**
8. Caudal ramus conical and about 3 times as long as wide; P5 endopodal lobe ♀ with 3 setae..... ***P. longipes***
- Caudal ramus cylindrical and not more than twice as long as wide; P5 endopodal lobe ♀ with 4 setae..... **9**
9. P5 exopod ♀ with 4 setae; P3 exp-3 ♂ with 7 setae/spines..... ***P. karmensis***
- P5 exopod ♀ with 5 setae; P3 exp-3 ♂ with at most 6 setae/spines **10**
10. First and second abdominal somites with dorsal bilobate lappets; second antennular segment ♀ without protuberance; P5 ♂ with 5 setae on exopod and 1 on endopodal lobe ***P. lunata***
- First and second abdominal somites without dorsal bilobate lappets; second antennular segment ♀ with small conical protuberance; P5 ♂ with different armature **11**
11. Caudal ramus 1.5 times as long as wide; P5 ♂ with 5 setae on exopod and none on endopodal lobe ***P. spitzbergensis***
- Caudal ramus twice as long as wide; P5 ♂ with 4 setae on exopod and 1 on endopodal lobe ***P. tenera***
12. Abdominal somites with a middorsal spinous process; P3 enp-2 ♀ with 4 elements; P3 endopod ♂ 2-segmented..... ***P. quaterspinata***

- Abdominal somites without a middorsal spinous process; P3 enp-2 ♀ with 5–6 elements; P3 endopod ♂ 3-segmented with apophysis on enp-2..... **13**
- 13. Antennule ♀ 6-segmented; P3 enp-2 ♀ with 6 elements; P3 enp-2 ♂ apophysis shorter than endopod; longest seta of P5 exopod ♂ about 5 times the length of segment ***P. zimmeri***
- Antennule ♀ 7-segmented; P3 enp-2 ♀ with 5 elements; P3 enp-2 ♂ apophysis as long or longer than endopod; longest seta of P5 exopod ♂ at most 2.5 times the length of segment **14**
- 14. Second antennular segment ♀ without small conical protuberance; P5 exopod ♀ longer than wide, inner distal seta twice the length of proximal inner one; P5 exopod ♂ with 5 elements ***P. pallaresae*, sp. n.**
- Second antennular segment ♀ with small conical protuberance; P5 exopod ♀ semicircular, inner distal seta only slightly longer than proximal inner one; P5 exopod ♂ with 4 elements ***P. obscura***
- 15. P2–P3 exp-3 with 2 outer spines; caudal ramus about 6 times as long as wide..... ***P. lamellipes***
- P2–P3 exp-3 with 3 outer spines; caudal ramus distinctly shorter **16**
- 16. P4 exp-3 with 2 outer spines..... ***P. panamensis***
- P4 exp-3 with 3 outer spines..... **17**
- 17. P4 exp-3 with 1 inner seta ***P. taurina***
- P4 exp-3 with 2 inner setae..... **18**
- 18. P1 exopod 2-segmented..... **19**
- P1 exopod 3-segmented..... **22**
- 19. Second antennular segment with distinct recurved hook-like process; P5 baseoendopod ♂ with 1 seta ***P. pilosoma***
- Second antennular segment with at most a small conical protuberance; P5 baseoendopod ♂ without setae **20**
- 20. Caudal ramus about 3.5 times as long as wide; P3 enp-2 ♀ with 2 inner setae; P3 endopod ♂ 2-segmented with 3 setae on enp-2 ***P. macera***
- Caudal ramus at most 2.5 times as long as wide; P3 enp-2 ♀ with 3 inner setae; P3 endopod ♂ 2-segmented with 5 setae on enp-2 or 3-segmented with 4 setae on enp-3..... **21**
- 21. Caudal ramus about 2.5 times as long as wide; P3 enp-2 ♀ with 6 elements; P3 endopod ♂ 3-segmented ***P. hyperborea***
- Caudal ramus about twice as long as wide; P3 enp-2 ♀ with 5 elements; P2 enp-1 ♂ as long as enp-2; P3 endopod ♂ 2-segmented..... ***P. innae***
- Caudal ramus about 1.5 times as long as wide; P3 enp-2 ♀ with 6 elements; P2 enp-1 ♂ distinctly longer than enp-2; P3 endopod ♂ 2-segmented. ***P. perplexa***
- 22. Caudal ramus at least 3 times as long as wide **23**
- Caudal ramus at most 2.5 times as long as wide..... **26**
- 23. Cephalothorax with distinct integumental pits; P3 endopod ♀ with 5 elements..... ***P. sculpta***

- Cephalothorax without distinct integumental pits; P3 endopod ♀ with 6 elements.....**24**
- 24. Antennule ♀ 7-segmented, without protuberance on second segment; caudal ramus at most 3 times as long as wide..... ***P. octavia***
- Antennule ♀ 6-segmented, with protuberance on second segment; caudal ramus more than 3 times as long as wide; associated with *Maja squinado*.....
..... **25**
- 25. P5 baseoendopod ♀ with 4 setae; caudal ramus 4 times as long as wide.....
..... ***P. royi***
- P5 baseoendopod ♀ with 5 setae; caudal ramus 3.5 times as long as wide
..... ***P. majae***
- 26. Second antennular segment with prominent recurved unguiform process...
..... ***P. dieuzeidei***
- Second antennular segment with straight conical or spinous projection, or without any protuberance**27**
- 27. Caudal ramus at most 1.2 times as long as maximum width**28**
- Caudal ramus distinctly longer**29**
- 28. Antennule ♀ 6-segmented; P1 enp-1 1.7 times the length of exopod; P5 exopod ♀ with 5 elements ***P. pacifica***
- Antennule ♀ 7-segmented; P1 enp-1 twice the length of exopod; P5 exopod ♀ with 4 elements..... ***P. septemarticulata***
- 29. Second antennular process with distinct straight spinous projection.....**30**
- Second antennular process with or without small protuberance**31**
- 30. Antennule ♀ 7-segmented; P3 enp-2 ♀ with 6 elements; P5 exopod ♀ with 5 elements; innermost element of P5 exopod ♂ setiform; caudal ramus 1.5 times as long as wide..... ***P. meinerti***
- Antennule ♀ 7-segmented; P3 enp-2 ♀ with 6 elements; P5 exopod ♀ with 6 elements; innermost element of P5 exopod ♂ setiform; caudal ramus more than twice as long as wide
..... ***P. gurneyi***
- Antennule ♀ 6-segmented; P3 enp-2 ♀ with 5 elements; P5 exopod ♀ with 5 elements; innermost element of P5 exopod ♂ an enlarged plumose spine; caudal ramus 1.5 times as long as wide ***P. problematica***
- 31. Antennule ♀ 7-segmented; P5 exopod ♂ with 4 elements; caudal ramus at least twice as long as wide**32**
- These characters not combined**33**
- 32. Caudal ramus 2.5 times as long as wide; P5 endopodal lobe ♀ with both inner setae equal in length P5; endopodal side P5 ♂ with conical projection ...
..... ***P. congenera mediterranea***
- Caudal ramus twice as long as wide; P5 endopodal lobe ♀ with proximal inner seta distinctly longer than distal inner one; endopodal side P5 ♂ without conical projection ***P. lacerdai***

33. Caudal ramus 2.5 times as long as wide; P5 exopod ♀ with 4 elements *P. ormieresi*
 – Caudal ramus at most twice as long as wide; P5 exopod ♀ with 5 elements ..34
34. P3 enp-2 ♀ with 5 elements35
 – P3 enp-2 ♀ with 6 elements36
35. Antennule ♀ 6-segmented; P1 enp-2 about 4.5 times as long as maximum width; P3 exopod ♂ strongly modified *P. echinata*
 – Antennule ♀ 7-segmented; P1 enp-2 about 7 times as long as maximum width; P3 exopod ♂ not modified *P. gracilipes*
36. Antennule ♀ 6-segmented, with blunt protuberance on segment 2; P4 enp-2 about 1.5 times as long as maximum width; P3 exp-3 ♂ distal outer spine much shorter than middle outer one..... *P. galapagoensis*
 – Antennule ♀ typically 7-segmented and without protuberance on segment 2; P4 enp-2 about 2.8 times as long as maximum width; P3 exp-3 ♂ distal outer spine about as long as middle outer one..... *P. congenera congenera*
 – Antennule ♀ typically 6-segmented and with small pointed process on segment 2; P4 enp-2 about 3 times as long as maximum width; P3 exp-3 ♂ distal outer spine about twice as long as middle outer one *P. brevirostris*

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A new genus and species of Grapholitini (Lepidoptera, Tortricidae) from Florida, U.S.A.

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Abstract

Riculatorampha ancyloides Rota & Brown, **gen. n.**, **sp. n.** from Florida, is described and illustrated. The type series was reared from the fruit of redbay, *Persea borbonia* (Lauraceae). The new genus is assigned provisionally to the *Dichrorampha*-group of genera (Grapholitini) on the basis of the following characters: forewing termen with a row of black dots, forewing fringe with a shallow subapical notch, hindwing veins R_5 and M_1 separate and parallel or subparallel, female frenulum with two bristles, and corpus bursae with a single signum. The last character is shared with *Dichrorampha* Guenée, *Ricula* Heinrich, *Riculoides* Passtrana, and *Goditha* Heinrich.

Keywords

Dichrorampha-group, fruit-borer, genitalia, morphology, Lauraceae, *Persea*, *Riculatorampha ancyloides*, wing venation

Introduction

The tortricid tribe Grapholitini includes about 898 species assigned to 62 genera, with about 89 described species still lacking convincing generic assignments (Brown 2005). The tribe occurs worldwide but is particularly species-rich in the

Holarctic. The Neotropical and Afrotropical faunas are probably the least known, with more undescribed than described species represented in major collections worldwide (Brown pers. obs.). Grapholitines are among the most notorious lepidopterous pests of fruit, with species such as codling moth (*Cydia pomonella* (L.)), Oriental fruit moth (*Grapholita molesta* Busck), and false codling moth (*Thaumatotibia leucotreta* (Meyrick)) causing millions of dollars in damage annually. In contrast, one species of *Dichrorampha* Guenée from Jamaica has been released for biological control of a siam weed (*Chromolaena odorata* (L.) King & H.E. Robins; Asteraceae) in South Africa (Brown and Zachariades 2007). Larval biologies are diverse throughout the tribe, including gall-inducers (e.g., species of *Cydia* Hübner, *Grapholita* Treitschke, *Ecdytolopha* Zeller, *Riculoides* Pastrana) (Miller 2005), seed feeders (e.g., species of *Cydia*, *Matsumuraeses* Issiki, *Grapholita*), and fruit-feeders (e.g., species of *Gymnandrosoma* Dyar, *Cryptophlebia* Walsingham, *Thaumatotibia* Zacher). A few species are inquilines in galls of cynipid wasps (e.g., species of *Andrioplecta* Obratzsov and *Cydia latiferreana* Walsingham) (Komai 1999, Brown et al. 2008).

While a broad picture of the diversity and phylogeny of Grapholitini is beginning to emerge (e.g., Komai 1999, Horak 2006), there are still many genera and species awaiting description, and our understanding of relationships within the tribe remains preliminary. The purpose of this contribution is to describe a new genus and species of Grapholitini from southern Florida that has been reared from the fruit of redbay, *Persea borbonia* (Lauraceae) and may have been introduced from the Neotropics. We also discuss characters that may help define, or possibly broaden, the concept of the *Dichrorampha*-group of genera.

Methods

Dissection methods follow those presented in J. Brown and Powell (1991) for genitalia and Zimmerman (1978) for wings. Forewing length is measured on a straight line from the base of the costa to the apex including the fringe. Whole specimens and genitalic slides were examined using a Leica MZ12 stereo dissecting scope under 6.5× to 40× power. Finer details of the morphology of the genitalia were examined using a Leitz Labrolux S compound microscope. Terminology follows Horak (1984) for features of the wing venation, R. Brown and Powell (1991) for elements of the forewing pattern, and Gilligan et al. (2008) for genitalic structures. Images of adults and genitalia were captured using a Visionary Digital© imaging system and enhanced using Adobe Photoshop CS© software. The holotype and three paratypes are deposited in the Florida State Collection of Arthropods (FSCA), Gainesville, FL. A male and female paratype are deposited in the collection of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Systematics

Riculorampha, gen. n.

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Type species: *Riculorampha ancylroides*, sp. n.; designated by monotypy
Figs 1–6

Riculorampha is provisionally assigned to the *Dichrorampha*-group of genera on the basis of the following putative synapomorphies: forewing termen with a row of black dots, forewing termen with a shallow subapical notch, hindwing veins R_s and M_1 separate and parallel or subparallel, female frenulum with two bristles, and corpus bursae with a single signum. The significance of these characters is discussed below.

Diagnosis. Superficially, *Riculorampha* is similar to nearly all other genera in the *Dichrorampha*-group, with a subapically “notched” termen of the forewing, a row of black dots along the forewing termen, and a two-bristled frenulum in the female. It shares with *Dichrorampha*, *Goditha* Heinrich, *Ricula* Heinrich, and *Riculoides* the loss of one of the two signa in the corpus bursae in the female genitalia. The male genitalia of *Riculorampha* can be separated from those of *Ricula* and *Riculoides* by the reduction of socii (long and extremely slender in *Ricula* and *Riculoides*), the broad, rounded dorsum of the tegumen (narrow and attenuate dorsally in *Ricula* and *Riculoides*), and the large, triangular sacculus (smooth and rounded in *Ricula* and *Riculoides*). The last character also serves to distinguish *Riculorampha* from *Goditha* and *Dichrorampha* and all other members of the *Dichrorampha*-group.

Description. *Head*: Vertex with large scale patches overlapping mediodorsally (Fig. 2); upper frons with overhanging tuft of relatively smooth scales; lower frons sparsely covered with appressed scales; ocellus relatively large, ca. $0.2\times$ diameter of compound eye. Antenna slightly shorter than 0.5 length of forewing costa, somewhat thickened, with fine, short, dense sensory setae in both sexes. Length of labial palpus subequal to diameter of compound eye, upcurved, smooth scaled. Maxillary palpus rudimentary. *Thorax*: Dorsum smooth scaled, without posterior tuft. Legs unmodified in male. Forewing length (Fig. 1) ca. $2.0\times$ width, forewing termen broadly bilobed, notched at vein M_1 ; row of black dots along termen; discal cell length ca. $0.6\times$ wing length; all veins present and separate (Fig. 3); chorda present, weakly defined basally. M vein well developed throughout discal cell. M_2 , M_3 , and CuA_1 parallel beyond discal cell and remote at termen. CuA_2 originating from ca. $0.66\times$ length of discal cell. Hindwing length ca. $1.75\times$ width; cubital pecten absent in both sexes; female frenulum with two bristles; R_s and M_1 separate, but relatively close together and parallel in basal 0.25 ; M_3 and CuA_1 connate. *Abdomen*: Male with internal glands on segment three; sternite of segment eight with Y-shaped sclerotization medially. Male genitalia (Fig. 4) with tegumen nearly parallel-sided, ca. $0.6\times$ length of valve, rounded dorsally, expanded medially into triangular flap; no trace of uncus; socius present as short, subtriangular, hairless pad (in slide-mounted preparation of holotype, one socius hidden beneath

triangular flap of tegumen); valva elongate, upcurved, constricted at neck, narrowed apically, rounded at apex, with dense setae and spines on cucullus; basal cavity large, extending distally to neck; sacculus strongly produced apically, triangular, smooth with exception of scattered setae; microtrichiae present on outer surface of valva. Phallus curved at 0.2 from base, then straight and weakly attenuate in distal 0.8; vesica with ca. 5 slender, elongate spindle-shaped cornuti. Female genitalia (Fig. 6) with papilla analis unmodified; apophysis anterioris and posterioris subequal in length and slender, anterioris extending slightly anterad of ostium; sternite of segment eight wrinkled anterad of ostium; ductus bursae ca. $2.0\times$ as long as abdominal segment eight, with posterior 0.5 strongly sclerotized, slightly narrowed from ostium to end of sclerotization, with rough surface texture; ductus seminalis originating at about 0.5 length of ductus bursae; ductus bursae about $1.5\times$ wider at ostium than at junction with corpus, at junction with corpus ca. $0.25\times$ width of corpus. Corpus bursae almost round, with rough surface texture and a single spine-shaped signum [assumed to be unmated].

Pupa (Based on 3 exuvia). Typically olethreutine (Fig. 5); head without apical projection; thorax and abdomen without conspicuous sculpturing; abdomen with row of small spines dorsally near middle of segments A2–A6, extending over nearly entire dorsum; slightly shorter row of larger spines near anterior edge of segments A3–A8; cremaster absent; 4 pairs of long hook-tipped setae at posterior end; pair of spines absent from anal rise.

Etymology. The name is a combination of *Ricula* and *Dichrorampha*, to which the genus appears to be related; it is interpreted as feminine in gender.

Riculatorampha ancyloides, sp. n.

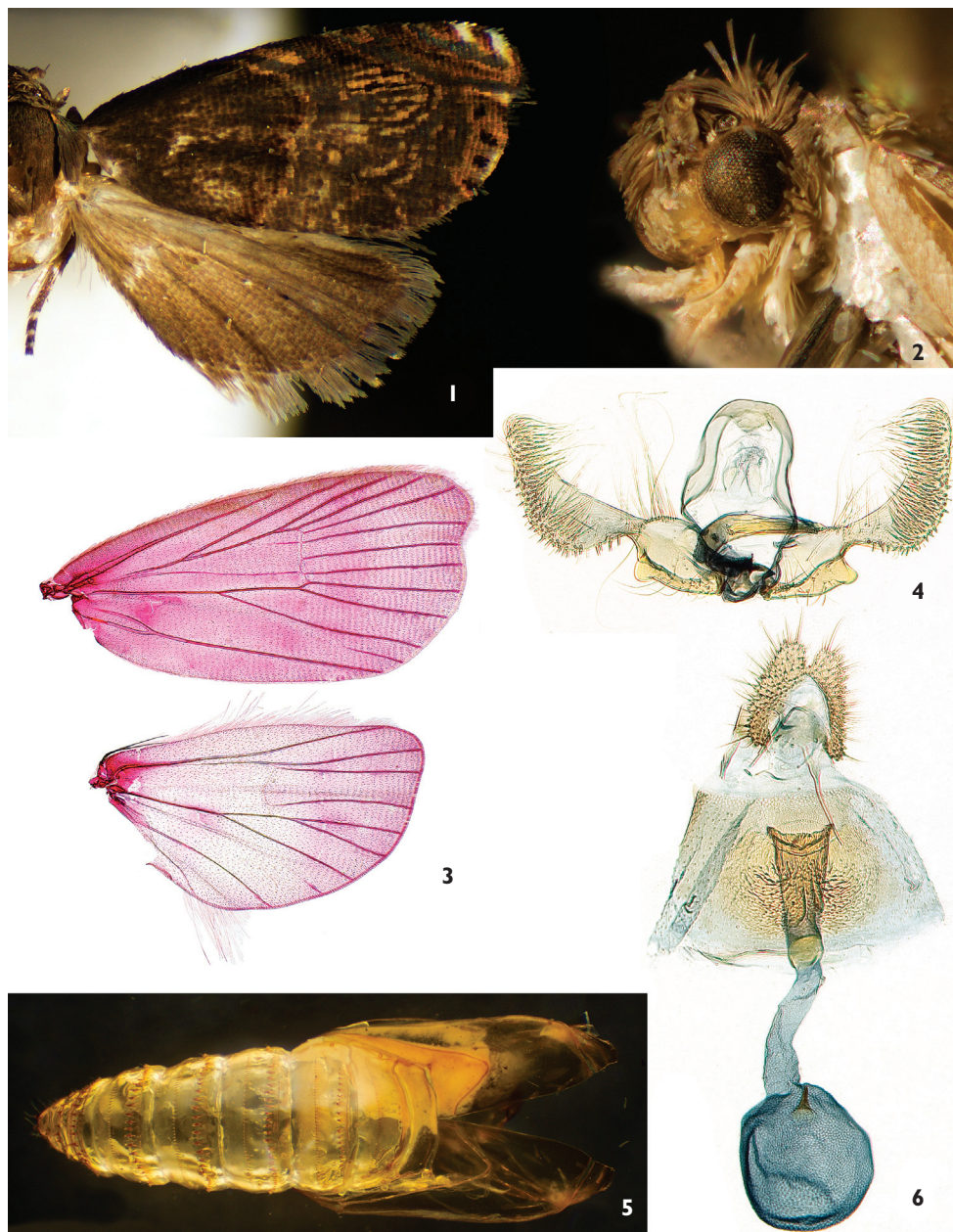
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Figs 1–6

Diagnosis. *Riculatorampha* is monotypic, with the single species *R. ancyloides*. The species can be distinguished from all other Grapholitini by its large, triangular sacculus in the male genitalia, reminiscent of that of many species of *Ancylis* Hübner (*Enarmo-niini*).

Description. *Head:* Lower frons with light brown scales, upper frons with brown, somewhat iridescent scales; vertex brown. Labial palpus (Fig. 2) pale beige, distal end of segment three dark brown. *Thorax:* Dark brown dorsally, off white and shiny ventrally. Forewing length 3.5–4.5 mm (mean=4.0; $n=3$) in males, 4.0–5.0 mm (mean=4.7; $n=3$) in females. Upper side with basal ca. 0.5 dark brown, distal ca. 0.5 gray-brown, basal and distal areas separated by thin orange line (Fig. 1); an oblique violet-leadened metallic streak from mid-costa towards termen bordered by orange; two oblique blue-leadened metallic streaks from apical third of costa to termen; costal strigulae weakly developed except for pair 9 before apex and pair 10 at apex; short longitudinal black and orange striations just beyond discal cell; four black dots along termen within contiguous orange patch; apical notch at M_1 ca. 0.25 from apex on termen denoted by a strigula of orange and white scales; fringe pale brown. Underside pale brown with me-

tallic sheen, two oblique white marks on costa before apex representing strigulae 9 and 10, strigula of yellow scales at apical notch. Hindwing length 3.0 mm in males (n=3), 3.5 mm in females (n=2); upper side pale gray brown basally, darker towards apex; fringe with brown basal portion and beige distal portion; fringe along anal edge 2–3× longer than along remainder of wing, scales extremely slender in basal 0.5, somewhat



Figures 1–6. *Riculorampha ancylroides*. 1 Adult female 2 Lateral view of head 3 Wing venation 4 Male genitalia 5 Pupal exuvium 6 Female genitalia.

oar-shaped in distal 0.5. Underside pale brown. *Abdomen*: Brown. Male genitalia (Fig. 4) as described for genus. Female genitalia (Fig. 6) as described for genus.

Holotype. ♂, USA, FLORIDA, Dade Co., Homestead, 16 Sept 1993, ex: *Persea borbonia* fruit, W. Jackson, genitalia slide USNM 119089 (FSCA).

Paratypes. USA, FLORIDA, Dade Co., Homestead, ex: *Persea borbonia* fruit, 28 Jul 1993 (1♂), J. Peña (FSCA); 29 Jun 1993 (1♂) (USNM), 13 Aug 1993 (1♀), R. E. Duncan and Z. Alegria (USNM); 16 Sept 1993 (1♀), W. Jackson (FSCA); 3 Sept 1993 (1♀), R. E. Duncan and Z. Alegria (FSCA).

Distribution and biology. *Riculorampha ancyloides* is known only from southern Florida. However, its host plant, redbay (*Persea borbonia*; Lauraceae), occurs throughout much of the southeastern U.S. and the Caribbean (USDA Plants Database 2009). It is possible that adults of this species are not attracted to light, as may be the case for other Grapholitini (e.g., *Talponia* Heinrich), and rearing infested fruits of redbay may be the best way to collect adults. Alternatively, pheromone lures could be employed, such as those for codling moth or Oriental fruit moth, which often cross-attract males of related genera. The type series of *R. ancyloides* was obtained through rearings (J. Peña, pers. comm.).

Etymology. The species is named for the similarity of its saccular process of the male genitalia to that of *Ancylys*; the species epithet is an adjective in nominative singular.

Remarks. We examined one male from Venezuela (Aragua, Rancho Grande, 1–3 Apr 1978, J. B. Heppner, USNM) that may be conspecific with *R. ancyloides* based on its genitalia. Consequently, it is possible that *Riculorampha* has been introduced into Florida from the Neotropics.

Discussion

Although the monophyly of Grapholitini was questioned by Horak and Brown (1991), who suggested that the tribe may represented a para- or polyphyletic assemblage of genera with similarly reduced male genitalia (e.g., uncus and socii reduced or lost), Komai (1999) presented putative synapomorphies that may define the tribe and generic groups within it. Based on the Palearctic fauna, Komai (1999) divided the tribe into three groups, the *Dichrorampha*-group, the *Cydia*-group, and the *Grapholita*-group, each defined by one or more putative synapomorphies. Horak (2006) followed Komai's (1999) assessment, adding a fourth group – the *Loranthacydia*-group.

As circumscribed by Komai (1999) and followed by Horak (2006), the *Dichrorampha*-group consists of *Dichrorampha* and *Pammenemima* Diakonoff and can be defined by the following features: hindwing veins R_s and M_1 separate and parallel or subparallel; forewing with a row of dots along the termen; and sterigma, seventh sternite, and sclerotized part of ductus bursae completely fused. While Komai (1999) was unable to assign several New World genera (e.g., *Satronia* Heinrich, *Ethelgoda* Heinrich, *Talponia*, *Ricula*, *Riculoides*) to any of the three groups, some evidence suggests that these

genera may be referable to the *Dichrorampha*-group. Each possesses one or more of the synapomorphies identified by Komai, but none possesses all of them. Additional features shared by many of these genera include the forewing having a small subapical notch between R_5 and M_1 , female frenulum with two bristles, and corpus bursae with a single signum. While the subapical notch of the forewing and two-bristled female frenulum are found in one or more species in genera not included in the *Dichrorampha*-group (e.g., 11 of 81 species examined of *Cydia* have a predominantly two-bristled frenulum; 35 of 41 species of *Grapholita*; Rota et al. (in press)), loss of one of the signa may represent a synapomorphy for at least five genera provisionally assigned to the *Dichrorampha*-group (i.e., *Dichrorampha*, *Ricula*, *Riculoides*, *Goditha*, and *Riculorampha*). *Goditha*, *Ricula*, *Riculoides*, and *Riculorampha* also share the presence of large cornuti on the vesica and the absence of the cubital pecten. Features that are inconsistent with this assignment include presence of male paired hairpencils on segment eight in *Ricula* and *Riculoides*, which are absent in *Dichrorampha*, *Goditha*, and *Riculomorphia*; presence of a Y- or T-shaped sclerotization on the sternite of the abdominal segment eight in *Riculoides* and *Riculorampha*, that is absent in *Dichrorampha*, *Goditha*, and *Ricula*; and the shape of the tegumen, which is broad in *Dichrorampha*, *Ricula*, and *Riculomorphia*, and attenuate dorsally in *Goditha* and *Riculoides*.

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Revision of the bee genus *Chlerogella* (Hymenoptera, Halictidae), Part I: Central American species

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Abstract

The Central American species of the rare bee genus *Chlerogella* Michener (Halictinae: Augochlorini) are revised. Aside from the previously described *Chlerogella elongaticeps* Michener and *C. clidemiae* Engel, five new species are added to the fauna and figured as *C. prolixa* **sp. n.**, *C. fortunaensis* **sp. n.**, *C. kelliiae* **sp. n.**, *C. anthonoma* **sp. n.**, and *C. pinocchio* **sp. n.** These species include the first records from Costa Rica (*C. kelliiae*, *C. anthonoma*, and *C. pinocchio*) and the first description of the male for *C. elongaticeps*. A dichotomous key to the species is provided.

Keywords

Apoidea, Anthophila, Halictinae, Augochlorini, *Chlerogella*, taxonomy, new species, identification key, Panamá, Costa Rica

Introduction

The bee genus *Chlerogella* Michener is a rarely encountered representative of the halictid tribe Augochlorini. Originally described on the basis of a single female from central Panamá (Michener 1954), further information on the genus was not forthcom-

ing until Moure and Hurd (1987) recognized that two earlier species described from Peru by Vachal (1901) and Enderlein (1903) also belonged therein. However, like the type species *Chlerogella elongaticeps* Michener, both *C. buyssoni* (Vachal) and *C. nasus* (Enderlein) were known only from their female holotypes. The same was true for the two most recently described species, *C. clidemiae* Engel (2003a) from Panamá and *C. mourella* Engel (2003b) from Ecuador, although the former was captured at flowers of *Clidemia crenulata* Gleason (Melastomataceae), representing the first such record for the genus. Today the genus remains one of the more rare among the Augochlorini and although there are numerous species (Engel, in prep.), only a few are known from significant series of individuals.

Herein I provide a review of those species in Central America, expanding the formerly documented diversity of two species to seven and expanding the generic range into Costa Rica. The extensive South American fauna and a revised concept for the genus will be provided in the second part of this work (Engel, in prep.). Given the rarity with which individuals have been collected and the large regions of suitable habitat between collection localities (Maps 1, 2) further species will undoubtedly be discovered. Most specimens of the genus have been captured in traps and even then only infrequently. It is unclear why individuals should be so seemingly rare and perhaps the eventual elucidation of *Chlerogella* biology will provide answers to this mystery. In the interim it is hoped that these works will bring the genus to the attention of a wider range of melittologists and to highlight what glimpses into its diversity are presently available.

Material and Methods

Material for this first portion of the study consisted of 14 specimens (6♀♀, 8♂♂, despite 15 years of looking for *Chlerogella* in museums) from the following collections:

- AEI** American Entomological Institute, Gainesville, Florida, USA.
- AMNH** Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York, New York, USA.
- INBio** Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
- SEMC** Division of Entomology (Snow Entomological Collection), University of Kansas Natural History Museum, Lawrence, Kansas, USA.

Morphological terminology for this study follows that of Michener (1944, 2007) and Engel (2000, 2001) except that the elongate “teeth” of the metatibial spurs are here referred to as “branches” as this term more accurately reflects their shape and the main body of the spur from which the branches arise is termed the “rachis”. The abbreviations S and T are used in place of metasomal sternum and tergum, respectively. The format for the descriptions is generally taken from that used elsewhere in Augochlorini (e.g., Engel 2007). Measurements were prepared using an ocular micrometer on an

Olympus SZX-12 stereomicroscope. Head length was calculated by measuring from the vertex to the apex of the clypeus, head width from the maximum outer borders of the compound eyes, intertegular distance from the inner borders of the tegulae, and total body length by measuring the individual lengths of the head, mesosoma, and metasoma and summing the values. A comparison of some measurements of the head and antennae for Central American *Chlerogella* is provided in Table 1. The surface sculpturing was studied through diffused light to minimize metallic reflectance and permit the details to be discerned.

Systematics

Genus *Chlerogella* Michener
Chlerogella elongaticeps Michener
Figs 1–6, 20, 21; Map 1

Chlerogella elongaticeps Michener, 1954: 75. Eickwort, 1969: 444–445; Moure and Hurd, 1987: 218; Engel, 2003a: 1–2; Moure et al., 2007: 794.

Holotype. ♀; PANAMÁ: Coclé [Province], El Valle de Antón, 1 April 1945, C.D. Michener (AMNH).

Additional material. PANAMÁ: 1♂, Panamá [Province], Cerro Campana, 800–860m, 17 July 1978, E.M. Fisher (SEMC).

Table 1. Comparison of head metrics across Central American species of *Chlerogella*; values in millimeters where appropriate; ML vs. MB is the malar length as a function of the number of times the basal mandibular width; the abbreviation F is used for flagellomere and FII vs. FI is the length of the second flagellomere as a function of the number of times the length of the first flagellomere (only meaningful in males where there is significant variation).

Species	Head length	Head width	Malar length	Eye length	Malar-Eye %	ML vs. MB	FII vs. FI
Females (♀)							
<i>C. elongaticeps</i> Michener	2.40	1.50	0.36	1.46	25%	2.0×	n.a.
<i>C. clidemiae</i> Engel	3.04	1.58	1.04	1.52	68%	5.4×	n.a.
<i>C. prolixa</i> , sp. n.	2.93	1.87	0.73	1.63	45%	3.1×	n.a.
<i>C. kelliæ</i> , sp. n.	2.83	1.60	0.73	1.60	46%	3.1×	n.a.
Males (♂)							
<i>C. elongaticeps</i> Michener	2.47	1.67	0.33	1.57	21%	1.7×	—
<i>C. prolixa</i> , sp. n.	2.93	1.80	0.73	1.60	46%	3.7×	4.0×
<i>C. fortunaensis</i> , sp. n.	2.76	1.62	0.78	1.40	56%	3.9×	—
<i>C. kelliæ</i> , sp. n.	2.80	1.67	0.73	1.52	48%	3.7×	3.2×
<i>C. anthonoma</i> , sp. n.	2.80	1.53	0.83	1.43	58%	4.2×	3.0×
<i>C. pinocchio</i> , sp. n.	2.57	1.40	0.70	1.33	53%	3.5×	2.8×

Diagnosis. *Chlerogella elongaticeps* is a distinctive species in that it has an elongate upper surface to the pronotum (medial length nearly two times an ocellar diameter), a relatively short malar space (only 21–25% of the compound eye length: cf. values in table 1) (Figs 2, 3, 5, 6), the form of the male SIV (Fig. 20), and the male genitalia (Fig. 21). The amber mesosoma with a darkened mesoscutum bearing metallic reflections



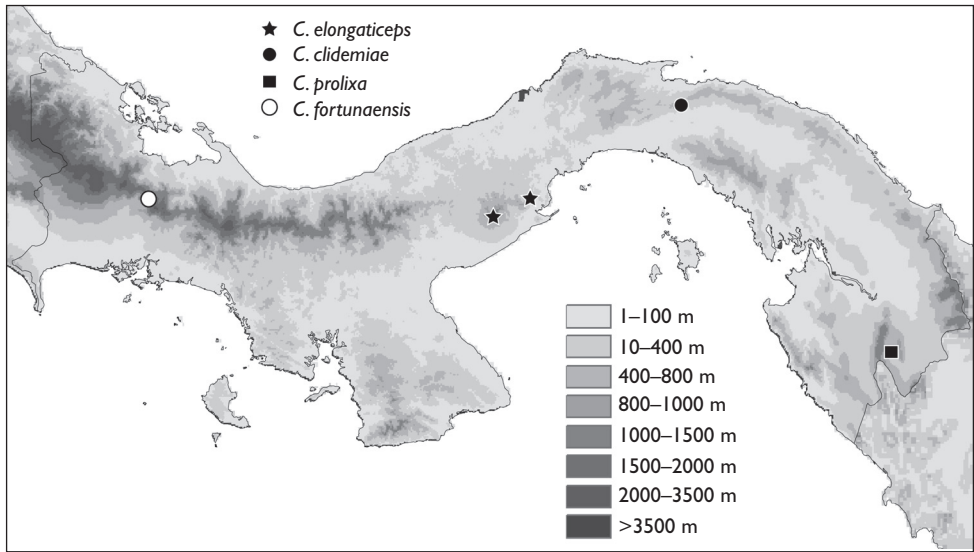
Figures 1–3. Holotype female of *Chlerogella elongaticeps* Michener. **1** Lateral habitus and view of separately mounted metasoma **2** Lateral aspect of head **3** Facial aspect.

(Figs 1, 4) is similar among Central American species to the female of *C. clidemiae* and the male of *C. anthonoma*.

Description. *Female*: Total body length 8.95 mm [Michener's (1954) value of 7.50 mm was made with the head in repose rather than considering it stretched forward as in the calculation provided here]; forewing length 5.52 mm. Head length 2.40 mm, width 1.50 mm. Base of clypeus at lower tangent of compound eyes. Malar space 25% of compound eye length (malar length 0.36 mm; compound eye length 1.46 mm).



Figures 4–6. Male of *Chlerogella elongaticeps* Michener. **4** Lateral habitus **5** Facial aspect **6** Lateral aspect of head.



Map I. Collection localities for Panamanian *Chlerogella*.

Upper interorbital distance 0.72 mm; lower interorbital distance 0.54 mm. Upper portion of pronotum elongate, medially about two times ocellar diameter in length; ventral portion of preëpisternal sulcus not broad, similar to scrobal sulcus and upper portion of preëpisternal sulcus; intertegular distance 1.26 mm; mesoscutellum weakly convex, not bigibbous. Basal vein distad cu-a by three times vein width; 1rs-m distad 1m-cu by five times vein width; 2rs-m distad 2m-cu by seven times vein width, 2rs-m gently arcuate; first submarginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell slightly narrowed anteriorly, anterior border of second submarginal cell along Rs about as long as that of third submarginal cell; posterior border of third submarginal cell nearly three times as long as anterior border. Distal hamuli arranged 2-1-2. Inner metatibial spur with three branches (not including apical portion of rachis).

Clypeus and supraclypeal area smooth with weak punctures separated by 1–3 times a puncture width, punctures weaker and sparser medially. Upper half of face with small punctures separated by a puncture width or less, otherwise faintly imbricate; lower half of face sculptured as on supraclypeal area except punctures separated by a puncture width; malar space largely impunctate and smooth; punctures on vertex minute and separated by 1.5–3 times a puncture width; gena smooth, with scattered faint, minute punctures; postgena strongly imbricate and impunctate. Pronotum faintly imbricate; mesoscutum smooth to faintly imbricate with punctures separated by a puncture width except punctures smaller and weaker anteriorly; mesoscutellum sculptured as on mesoscutum although punctures a bit more separated; metanotum faintly imbricate to smooth. Preëpisternum and hypoepimeral area smooth; mesepisternum smooth with minute punctures separated by five or more times a puncture width; metepisternum weakly imbricate. Propodeum weakly imbricate except posterior surface smooth. Metasoma weakly imbricate.

Mandible amber, with reddish apex; labrum and clypeus amber, remainder of head reddish brown with strong copper and weaker metallic green highlights; scape and pedicel amber, remainder of antenna brown. Mesosoma amber except mesoscutum dark reddish brown with metallic green-copper highlights and metanotum and basal margin of basal area (dorsal-facing surface) of propodeum light brown with faint highlights; tegula amber. Wing membranes hyaline; veins amber except pterostigma and Sc+R brown. Legs amber. Metasomal TI–II amber-yellow, with light reddish brown apically, TIII basally amber, apical half reddish brown; TIV–VI dark brown; SI–II amber; SIII–VI brown.

Pubescence golden and generally scattered; laterally on propodeum setae elongate with a few, short, apical branches; scopa composed of moderately-dense elongate plumose setae on metafemur and moderate-length dense palmate setae on metatibia.

Male: As for female with the following modifications: Total body length 9.00 mm; forewing length 5.54 mm. Head length 2.47 mm, width 1.67 mm. Malar space 21% of compound eye length (malar length 0.33 mm; compound eye length 1.57 mm). Upper interorbital distance 0.77 mm, lower interorbital distance 0.43 mm. Intertegular distance 1.17 mm; mesoscutellum very weakly bigibbous. Apical margin of metasomal SIII entire; SIV deeply concave and slightly scalloped, with apicolateral, incurved, thumb-like processes with two, thick, spike-like setae at apex; another weak point one-quarter width bearing a single, thick seta; a very weak point at about one-third width bearing a short peg (Fig. 20); SV entire; SVI emarginate; hidden and fused sterna unknown [specimen had been previously dissected and the sterna were not present in the capsule]; genital capsule as in figure 21.

Amber in malar space near base of mandible (Fig. 6); face above antennae dark brown with metallic copper-green highlights; supraclypeal area, face below antennae, and remainder of malar space reddish brown with metallic copper highlights. Mesoscutum dark brown to dark reddish brown with metallic copper-green highlights; metanotum and basal area of propodeum light brown with metallic copper highlights; metasomal terga amber with light brown near apical margins; sterna amber.

Typical gender pilosity except inner surface of metafemur with several long, apically-branched setae. Metasomal SIII with diffuse, apicolateral areas of long, apically-branched, erect setae; discs of SIV–VI without setal modifications (marginal setal modifications of SIV described above).

Comments. The holotype of *C. elongaticeps* is in moderately good condition (Fig. 1), although the metasoma became detached at some time in the past and an unknown individual glued it to the label, wisely choosing to mount it on its side so that the sterna are easily visible. Areas of the integument have apparently faded over time as the colors have paled by comparison to Michener's description (e.g., he noted "head dull metallic green" and "mesoscutum, which is black with a dark green tint"). The dark metallic green of the head has now largely faded to a deep reddish brown as has the mesoscutum, although areas of the metallic coloration can still be discerned (Fig. 3). It is not uncommon for coloration resulting multilayer reflectors to change when subjected to extreme environmental stress such as long-term UV exposure (Seago et al.

2009). Given that this specimen apparently had most of its original color in the late 1960s when examined by Eickwort (1969: p. 446 he notes the green tints and does not indicate any significant differences from Michener's original account) and has otherwise resided in a darkened museum drawer it is not clear why it should have become so faded. Unfortunately, newer material of *C. elongaticeps* has not appeared aside from a male in relatively poor condition. The male, presumably long-stored in alcohol, has the setae largely matted and the wings crumpled, with the antennae largely missing except for the left scape, pedicel, and first flagellomere (Figs 4–6).

***Chlerogella clidemiae* Engel**

Figs 7–9; Map 1

Chlerogella clidemiae Engel, 2003a: 2. Moure et al., 2007: 794.

Holotype. ♀, PANAMÁ: San Blas, 19km N of El Llano [El Llano is in Panamá Province with the collection locality 19km North and just across the border into San Blas Province], 350m, 31 January 1985, G. de Nevers, on flowers of *Clidemia crenulata* (SEMC).

Diagnosis. *Chlerogella clidemiae* is most similar to *C. elongaticeps* in that both species are largely amber-yellow (Fig. 7). The former differs from the latter most noticeably by the combination of a more elongate head [malar space 68% of compound eye length vs. 25% in *C. elongaticeps*; malar space 5.4 times longer than basal mandibular width vs. twice as long in *C. elongaticeps* (cf. figures 8, 9 vs. 2, 3)], the clypeus below the lower tangent of the compound eyes (Fig. 9), the shorter pronotal upper surface (medially about ocellar diameter in length vs. medially about two ocellar diameters in length in *C. elongaticeps*) the more widely spaced mesoscutal punctation, the light reddish brown coloration with faint coppery highlights on the head and mesoscutum, and the larger number of branches to the metatibial spur (five vs. three in *C. elongaticeps*).

Description. The description of this species was published only recently and given that no further material has become available I have chosen not to repeat that text here. Refer to Engel (2003a) for a complete description of the holotype.

***Chlerogella prolixa* Engel, sp. n.**

urn:lsid:zoobank.org:act:7606FD3D-FA41-4203-AF31-467FBE1C2910

Figs 10–16, 22, 23; Map 1

Holotype. ♀, PANAMÁ: Darien, Cana Biological Station, Serrania de Pirre, 1250m, 7°45'18"N, 77°41'6"W, 7 June 1996, J. Ashe, ex: flight intercept trap (SEMC).

Paratypes. PANAMÁ: 1♀, 2♂♂, Darien, Cana Biological Station, Serrania de Pirre, 1250m, 7°45'18"N, 77°41'6"W, 4 June 1996, J. Ashe, R. Brooks, ex: flight intercept trap (SEMC); 1♂, Darien, Cana Biological Station, Serrania de Pirre,

1380m, 7°45'18"N, 77°41'6"W, 4–7 June 1996, J. Ashe, R. Brooks, ex: flight intercept trap (SEMC).

Diagnosis. Among Central American species *C. prolixa* is noteworthy for the dull, blue-black integument (Figs 10–15) of the head and mesosoma, the widened ventral portion of the preëpisternal sulcus, the off-white clypeal apex in males (Fig. 14), yellow ventrolaterally on the scape in males (Fig. 15), the structure of the male SIV (Fig. 16), and



Figures 7–9. Holotype female of *Chlerogella clidemiae* Engel. **7** Lateral habitus **8** Lateral aspect of head **9** Facial aspect.

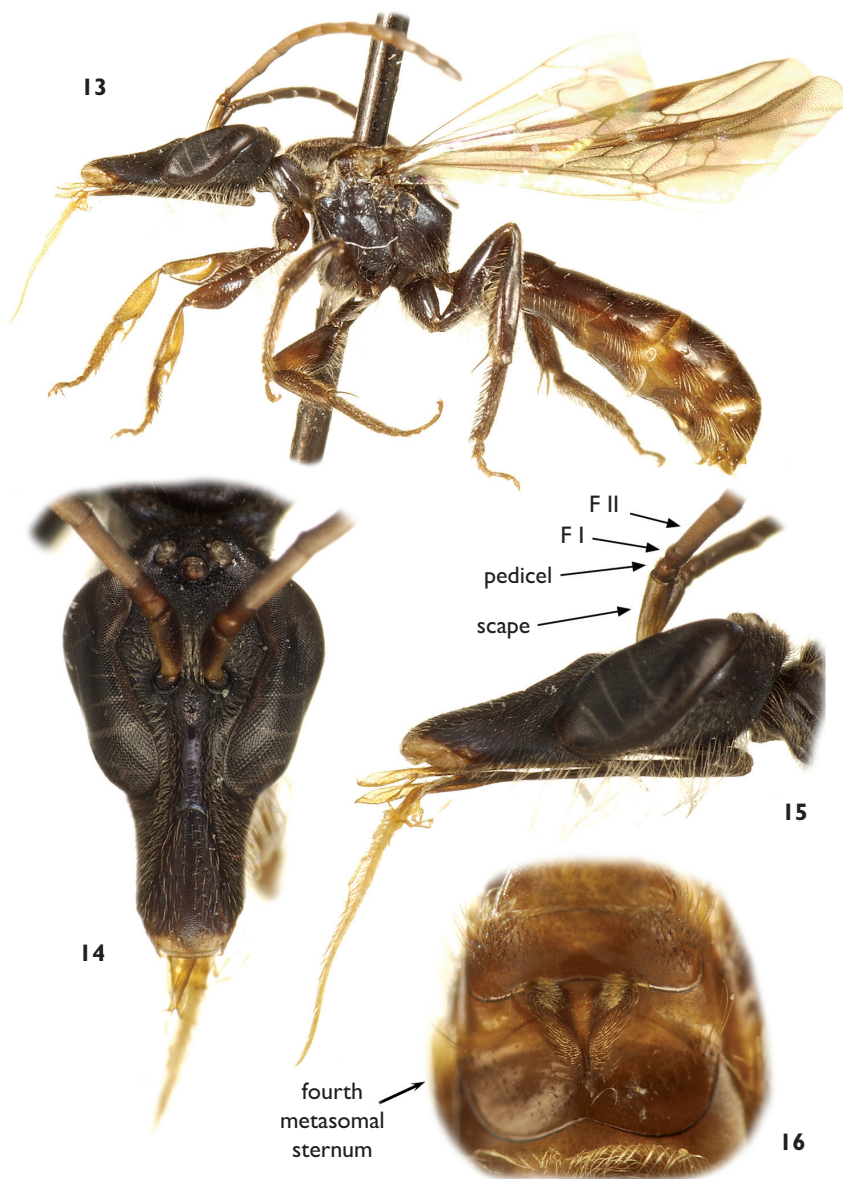
the male terminalia (Figs 22, 23). The male is most similar to *C. fortunaensis* but differs by the off-white mandible, labrum, and clypeal apex, largely off-white scape, the presence of an apical fringe on SIII, the structure of SIV (Fig. 16), and the genitalia (Fig. 23).

Description. *Female*: Total body length 9.40 mm; forewing length 6.48 mm. Head length 2.93 mm, width 1.87 mm. Clypeus beginning below lower tangent of compound eyes. Malar space 45% compound eye length (malar length 0.73 mm; compound eye length 1.63 mm). Upper interorbital distance 0.87 mm; lower interorbital distance



Figures 10–12. Holotype female of *Chlerogella prolixa*, sp. n. **10** Lateral habitus **11** Facial aspect **12** Lateral aspect of head.

0.63 mm. Upper portion of pronotum medially depressed, not elongate, medially less than 0.25 times ocellar diameter in length; ventral portion of preëpisternal sulcus distinctly broad dorsally at junction of scrobal sulcus and upper portion of preëpisternal sulcus; intertegular distance 1.60 mm; mesoscutellum weakly convex, not bigibbous. Basal vein distad cu-a by three times vein width; 1rs-m distad 1m-cu by twice vein width; 2rs-m distad 2m-cu by seven times vein width, 2rs-m straight; first submar-



Figures 13–16. Paratype male of *Chlerogella prolixa*, sp. n. **13** Lateral habitus **14** Facial aspect **15** Lateral aspect of head **16** Detail of modifications on metasomal sternum IV.

ginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell not narrowed anteriorly, anterior border of second submarginal cell along Rs slightly longer than that of third submarginal cell; posterior border of third submarginal cell nearly three times longer than anterior border. Distal hamuli arranged 2-1-2. Inner metatibial spur with six branches (not including apical portion of rachis).

Clypeus and supraclypeal area imbricate with weak punctures separated by 1–3 times a puncture width; face with small, contiguous punctures, more widely spaced in malar space; ocellocular area and vertex faintly imbricate with minute punctures separated by 1–5 times a puncture width; gena smooth with minute punctures separated by 1–6 times a puncture width; postgena imbricate and impunctate. Pronotum smooth with minute punctures separated by 1–2 times a puncture width; mesoscutum smooth with minute punctures separated by 1–3 times a puncture width on lateral thirds and along posterior border, medially punctures giving way to imbricate integument; mesoscutellum smooth with minute punctures separated by 1–3 times a puncture width; metanotum smooth with minute punctures separated by a puncture width. Preëpisternum smooth to faintly imbricate with minute punctures separated by 2–3 times a puncture width; mesepisternum imbricate with minute punctures separated by 4–5 times a puncture width, punctures weak; metepisternum faintly imbricate. Propodeum strongly imbricate. Metasoma weakly imbricate.

Mandible dark brown except reddish at apex; labrum black; clypeal apex black, remainder blue-black; remainder of head blue-black. Antenna dark brown except ventral surfaces of flagellomeres III–X brown. Mesosoma blue-black, blue faint in most areas; tegula dark brown; propodeum dark metallic blue dorsally, blue-black laterally. Wing membranes weakly infumate; veins dark brown. Legs dark brown. Metasoma dark brown.

Pubescence gold to off-white except fuscous on mesoscutum, mesoscutellum, metanotum, outer surfaces of protibia and protarsus, outer surfaces of mesotibia and mesotarsus, inner surface of metatibia, metasomal T5–6, and S5–6; black on inner surfaces of tarsi and tibiae.

Male: As described for the female except as follows: Total body length 10.49 mm; forewing length 6.61 mm. Head length 2.93 mm, width 1.80 mm. Malar space 46% compound eye length (malar length 0.73 mm; compound eye length 1.60 mm). Upper interorbital distance 0.76 mm; lower interorbital distance 0.47 mm. First flagellomere about as long as pedicel, about as long as wide; second flagellomere four times length of first flagellomere (Fig. 15); ventral surfaces of second through eleventh flagellomeres densely covered in placoid sensilla, placoid fields disrupted by narrow mediolongitudinal line of fine, minute trichoid sensilla for lengths of flagellomeres V–VIII, at base and apex of flagellomere IV and basal half of flagellomere IX. Intertegular distance 1.37 mm; mesoscutellum bigibbous. Inner metatibial spur serrate. Apical margin of metasomal SIII entire; apical margin of SIV medioapically produced, with concave emargination between setose lobes (Fig. 16), with narrow medio-longitudinal furrow in apical half of disc (Fig. 16), furrow widening apically, basally bordered by short carinae; apical margin of SV minutely emarginate; apical margin of SVI emarginate; terminalia as depicted in figures 22 and 23.

Mandible, labrum, and clypeal apex off-white; small, faint off-white patch on malar space near mandible base. Ventral surface and base of scape pale yellow. Inner surface of protibia, profemur, and inner apex of mesofemur yellow.

Typical gender pilosity except postgena with numerous elongate, sinuate setae, such setae with short apical branches; inner surfaces of trochanters, mesofemur, metacoxa, metatrochanter, and metafemur with elongate, apically-plumose setae, similar setae on inner surface of metatibia except largely simple. Apical margin of metasomal SIII with fringe of moderate-length golden setae; SIV with medioapical pads of short golden setae bordering medial furrow (Fig. 16); SV laterally with diffuse pads of elongate, inwardly-curved setae (Fig. 16).

Etymology. The specific epithet is based on the Latin term *prolixus*, meaning “stretched out long”.

***Chlerogella fortunaensis* Engel, sp. n.**

urn:lsid:zoobank.org:act:92FA9B32-B9DA-49D4-87CA-76F801781154

Figs 17–19; Map 1

Holotype. ♂, PANAMÁ: Fortuna, Chiriquí, 1050m, 8°44'N, 82°15'W, 10–16. VIII.1977 [10–16 August 1977], H. Wolda, at light (SEMC).

Diagnosis. Among the darker Central American species *C. fortunaensis* can be recognized by the combination of metallic blue integument on the head and mesosoma (Figs 17–19), unmodified sterna III–V, brown clypeal apex and pedicel, and largely brown scape.

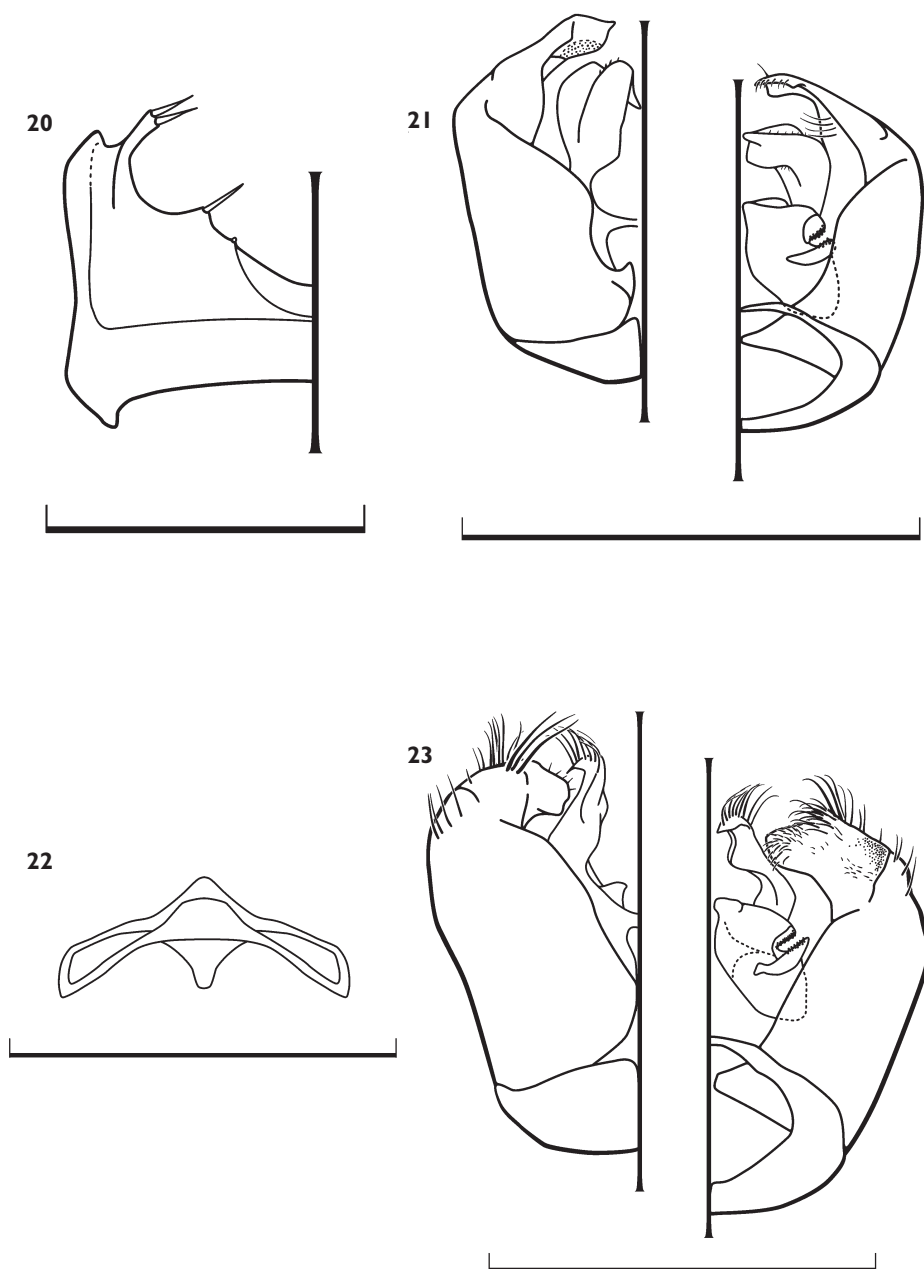
Description. *Male:* Total body length 9.36 mm; forewing length 6.0 mm. Head length 2.76 mm, width 1.62 mm. Base of clypeus below lower tangent of compound eyes. Malar space 56% compound eye length (malar length 0.78 mm; compound eye length 1.4 mm). Upper interorbital distance 0.8 mm; lower interorbital distance 0.42 mm. First flagellomere about as long as pedicel, about as long as wide. Intertegular distance 1.28 mm; mesoscutellum bigibbous. Basal vein distad cu-a by three times vein width; 1rs-m distad 1m-cu by three times vein width; 2rs-m distad 2m-cu by seven times vein width, 2rs-m straight; first submarginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell not narrowed anteriorly, anterior border of second submarginal cell along Rs slightly shorter than that of third submarginal cell; posterior border of third submarginal cell approximately twice as long as anterior border. Distal hamuli arranged 2-1-2. Inner metatibial spur serrate. Exposed portion of genitalia (gonostyli and apical halves of penis valves) similar to *C. anthonoma* except apex of valves densely covered with moderate-length thick setae, those more apical slightly longer, dorsally with two thick moderate-length setae reaching over apex.

Clypeus and supraclypeal area faintly imbricate with weak punctures separated by 1–2 times a puncture width; face smooth with minute punctures separated by 1–2 times a puncture width, punctures becoming more widely spaced in ocellocular area and on vertex and gena, separated by 2–5 times a puncture width; postgena imbricate and impunctate. Pronotum smooth; mesoscutum smooth with minute punctures separated by

2–3 times a puncture width except around median line punctures more coarse and separated by 1–2 times a puncture width; mesoscutellum smooth with punctures separated by 1–2 times a puncture width; metanotum smooth with scattered minute punctures;



Figures 17–19. Holotype male of *Chlerogella fortunaensis*, sp. n. **17** Lateral habitus as preserved **18** Facial aspect **19** Lateral aspect of head.



Figures 20–23. Male terminalia for Panamanian *Chlerogella* species (excluding *C. fortunaensis*, sp. n. which was not dissected owing to condition of the holotype and the unknown male for *C. clidemiae* Engel) **20** *Chlerogella elongaticeps* Michener, sternum IV **21** *C. elongaticeps*, genital capsule (left is dorsal aspect, right is ventral aspect) **22** *C. prolixa*, sp. n., hidden and fused sterna VII and VIII **23** *C. prolixa*, sp. n., genital capsule (left is dorsal aspect, right is ventral aspect). All scale bars = 1.0 mm.

pleura smooth with minute punctures separated by 3–5 times a puncture width except metepisternum impunctate. Propodeum imbricate. Metasoma weakly imbricate.

Mandible amber with reddish apex; labrum amber; clypeal apex brown, remainder of clypeus and head brilliant metallic blue with a few metallic purple highlights; base of scape amber, remainder of scape and pedicel brown, first flagellomere dark brown (remainder of antenna not preserved). Mesosoma brilliant metallic blue with a few metallic purple highlights; tegula brown with a few metallic blue highlights anteriorly. Wing membranes hyaline; veins dark brown. Legs brown to dark brown with metallic blue highlights on coxae, metatrochanter, and metafemur. Metasoma dark brown.

Pubescence generally white except fuscous on metatarsus. Typical pilosity for gender except postgena with scattered elongate, sinuate setae, a few with minute apical branches; ventral surfaces of metafemur and metatibia with widely scattered elongate, sinuate, largely simple setae. Metasoma SIII without apical setal fringe and SIV without medioapical setal pads.

Female: Unknown.

Etymology. The specific epithet is based on the type locality, Fortuna, Panamá.

Comments. This species is based on a poorly-preserved male captured in a trap sampling insects in Chiriquí. The head became detached at some time in the past and was mounted on the block beneath the body. The head is missing the antennae except for the scape, pedicel, and first flagellomere of the left antenna. The body is somewhat covered in fine debris and scales and the apex of the metasoma opened with the apex of the genitalia exposed. Given the fragility of the specimen it was not dissected further but fortunately the male genitalia are sufficiently visible to further confirm the distinctness of the species.

***Chlerogella kellieae* Engel, sp. n.**

urn:lsid:zoobank.org:act:65F1860A-3A61-40C5-93DA-91BF08881783

Figs 24–29, 36, 37; Map 2

Holotype. ♂, COSTA RICA: Guanacaste, Cacao Biological Station, 1050m, 10°55'38"N, 85°27'7"W, 10–11 July 2000, J. Ashe, R. Brooks, Z. Falin, ex: flight intercept trap (SEMC).

Paratypes. COSTA RICA: 1♀, Est. Carrillo, 700m, P.N. Braulio Carrillo, Prov. S. José, 15–17 February 1993 (INBio); 1♀, Río San Lorenzo, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste, 1050m, November 1992, G. Rodríguez (INBio).

Diagnosis. *Chlerogella kellieae* can be distinguished by the metallic green color of the head and mesosoma (Figs 24–29), the metasoma that is extensively marked with yellow in the male (Fig. 24) and amber in the female (Fig. 27), the malar space that is slightly less than one-half the compound eye length (table 1), and the structure of the male terminalia (Figs 36, 37).

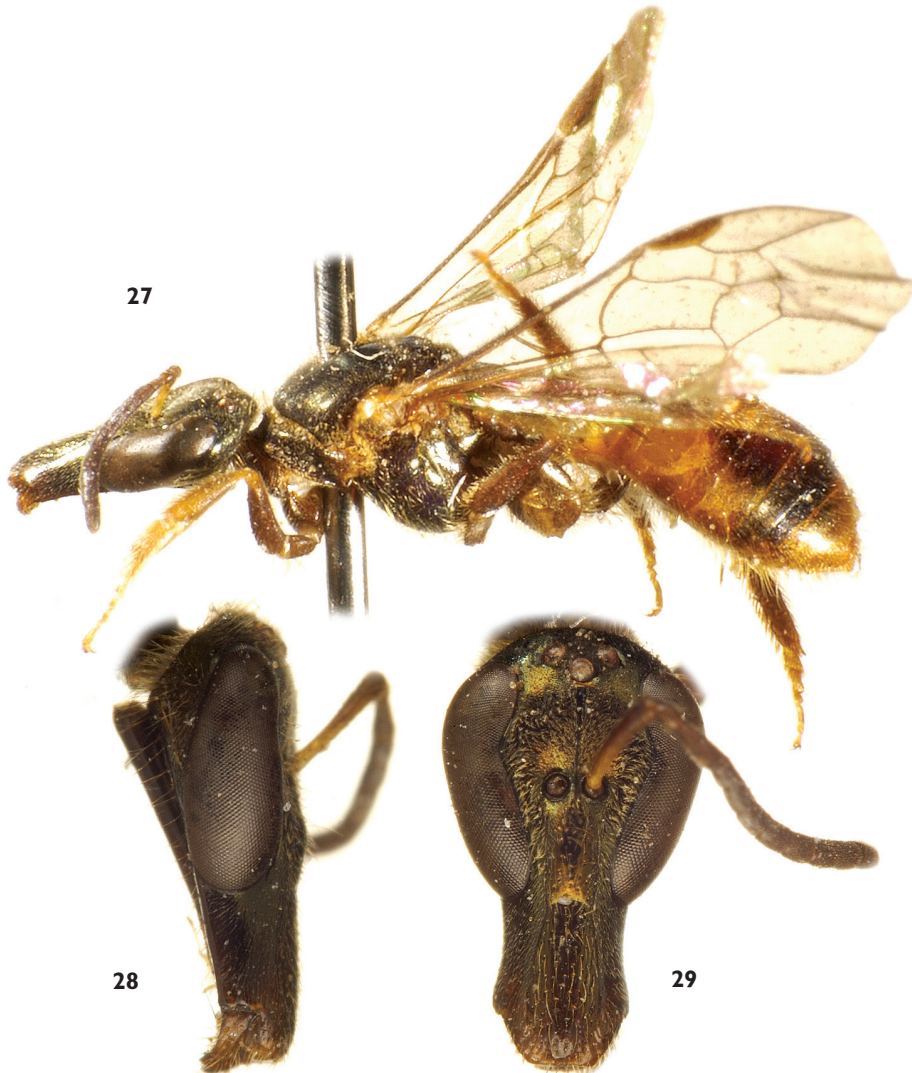
Description. *Male*: Total body length 8.93 mm; forewing length 6.40 mm. Head length 2.80 mm, width 1.67 mm. Base of clypeus at lower tangent of compound eyes.

Malar space 48% of compound eye length (malar length 0.73 mm; compound eye length 1.52 mm). Upper interorbital distance 0.76 mm; lower interorbital distance 0.40 mm. First flagellomere about as long as pedicel, about as long as wide; second flagellomere 3.2 times length of first flagellomere; ventral surfaces of second through eleventh flagellomeres densely covered in placoid sensilla, placoid fields disrupted by narrow



Figures 24–26. Holotype male of *Chlerogella kelliiae*, sp. n. **24** Lateral habitus **25** Facial aspect **26** Lateral aspect of head.

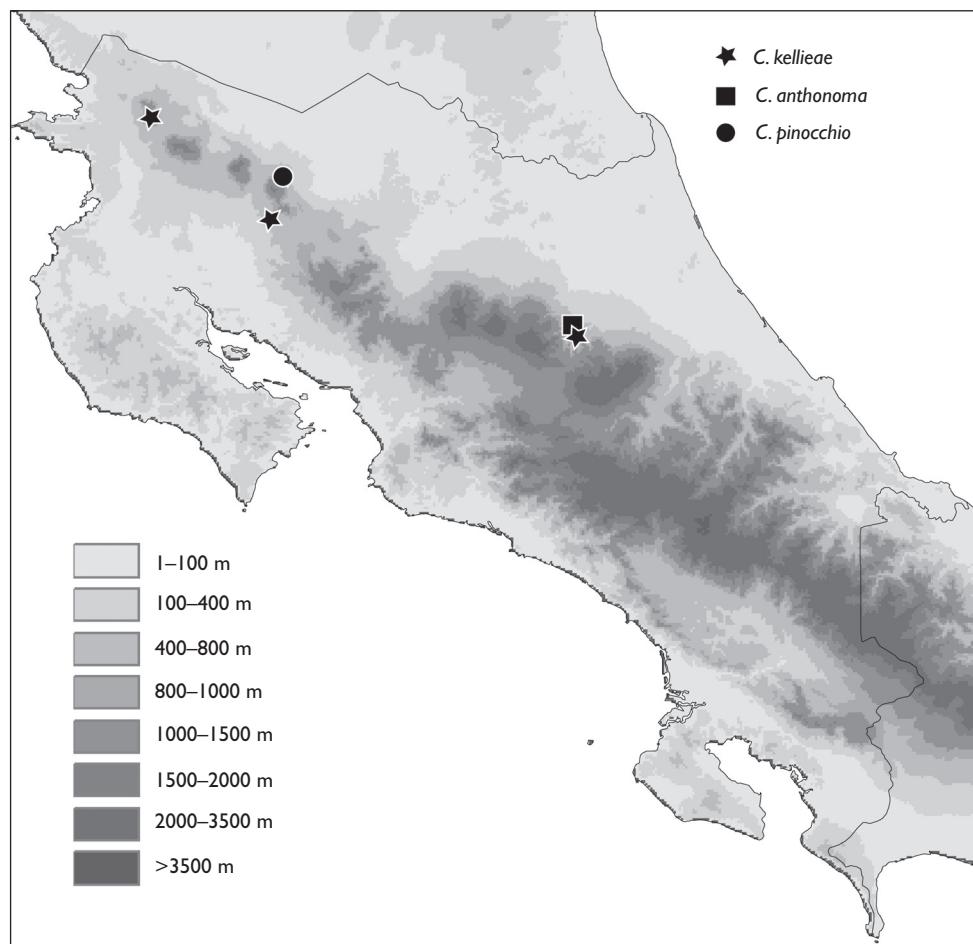
mediolongitudinal line of fine, minute trichoid sensilla for lengths of flagellomeres V–VIII, at base and apex of flagellomere IV and basal half of flagellomere IX. Intertegular distance 1.29 mm; mesoscutellum bigibbous. Basal vein distad cu-a by two times vein width; 1rs-m distad 1m-cu by two times veins width; 2rs-m distad 2m-cu by five times vein width, 2rs-m relatively straight; first submarginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell not narrowed anteriorly, anterior border of second submarginal cell along border with Rs about as long as that of third submarginal cell; posterior border of third submarginal cell about twice as long



Figures 27–29. Paratype female of *Chlerogella kelliæ*, sp. n. **27** Lateral habitus (note that apparently darker areas on the metasoma are due to discoloration of shriveled internal tissues visible through the somewhat translucent terga, the metasomal coloration is otherwise amber) **28** Lateral aspect of head **29** Facial aspect.

as anterior border. Distal hamuli arranged 2-1-2. Inner metatibial spur serrate. Metasomal sterna III–IV unmodified, with apical margins straight except for a minute median emargination on SIV; apical margin SVI emarginate; terminalia as in figures 36 and 37.

Clypeus and supraclypeal area weakly imbricate, with weak punctures separated by 1–3 times a puncture width. Head above level of antennae smooth with small punctures separated by a puncture width or less, below level of antennae and in malar space with minute punctures separated by 1–3 times a puncture width, integument faintly imbricate; punctures of face becoming more minute and separated by 2–5 times a puncture width in ocellocular area, on vertex and gena; postgena strongly imbricate and impunctate. Pronotum smooth to faintly imbricate. Mesoscutum smooth, with small punctures separated by 1–2.5 times a puncture width, anteriorly punctures become weaker and integument weakly imbricate; mesoscutellum sculptured as on mesoscutum; metanotum smooth with minute punctures separated by 2–3 times a puncture width. Preëpisternum and mesepisternum smooth with minute punctures separated by 5 times a puncture



Map 2. Collection localities for Costa Rican *Chlerogella*.

width or more; metepisternum smooth with minute punctures separated by 3 times a puncture width or more. Propodeum imbricate. Metasoma weakly imbricate.

Mandible, labrum, clypeal apex, and area in malar space bordering mandible yellow; remainder of clypeus dark brown with strong metallic green highlights; remainder of head metallic green with copper highlights. Scape and pedicel yellow, remainder of antenna dark brown. Mesosoma metallic green with copper highlights except pronotal lobe yellow and small amber-brown patch posteriorly on mesepisternum; tegula translucent yellow. Wing membranes lightly infumate; veins brown except Sc+R dark brown. Legs largely yellow with extensive brown on hind legs except metatarsus beyond the metabasitarsus and on outer surfaces of pro- and mesotibiae. Metasoma largely brown with yellow markings laterally and basally and as a thin transverse band on TII–V and laterally and mediodorsally on TI; TVI largely yellow-brown; sterna largely yellow except brown markings apically on SIII–V, faint medially on SI.

Pubescence generally golden except darkly fuscous on inner surface of metabasitarsus; typical gender pilosity except inner surface of metafemur with several long, apically-branched setae; metasomal SIV with diffuse apicolateral areas of appressed, short, inwardly-directed setae, intermingled with longer erect to suberect, simple setae; SV with diffuse apicolateral lines of short, erect to suberect, largely simple setae.

Female: As described for the male except as follows: Total body length 8.89 mm; forewing length 6.33 mm. Head length 2.83 mm, width 1.60 mm. Base of clypeus at lower tangent of compound eyes. Malar space 46% of compound eye length (malar length 0.73 mm; compound eye length 1.60 mm). Upper interorbital distance 0.80 mm; lower interorbital distance 0.53 mm. Antenna not so modified as in male, as in figure 29. Upper portion of pronotum not elongate, medially less than 0.25 times ocellar diameter in length; ventral portion of preepisternal sulcus not broad, similar to scrobal sulcus and upper portion of preepisternal sulcus; intertegular distance 1.40 mm; mesoscutellum weakly convex, not bigibbous. Distal hamuli arranged 2-1-2. Inner metatibial spur pectinate, with four or five branches (not including apical portion of rachis).

Mandible brown, with reddish apex; labrum brown; clypeal apex brown, remainder of clypeus brown with strong metallic green-copper highlights; remainder of head dark metallic green with copper highlights. Scape ventrally yellow, dorsally brown, pedicel yellow-brown, remainder of antenna dark brown. Legs largely brown with amber around podite articulations and on tarsi except metabasitarsus. Metasoma amber to reddish amber (note that apparently darker areas in figure 27 are due to discoloration of shriveled internal tissues visible through the somewhat translucent terga).

Etymology. The specific epithet is a matronym honoring my loving and supporting wife, Mrs. Kellie K. Magill Engel.

Comments. One of the females attributed to this species was captured near the type locality for *C. anthonoma* (*vide infra*) and at some distance from the Guanacaste records for the holotype and other female paratype. Nonetheless, the San José Province female has the same proportions as the Guanacaste female, same sculpturing, same coloration, and similar wing venation as to the holotype and other paratype. They are clearly conspecific and I feel confident that the San José specimen is not the unknown

female for *C. anthonoma* which is clearly a separate species as evidenced by its wing venation, head proportions, and male terminalia.

***Chlerogella anthonoma* Engel, sp. n.**

urn:lsid:zoobank.org:act:783629FA-13EA-475A-80D2-E8DFD90375C9

Figs 30–32, 38, 39; Map 2

Holotype. ♂, COSTA RICA: San José, Braulia Carville [sic] N.P., 400m, 10–11 April 1983, H. Goulet, tropical rainforest (AEI).

Diagnosis. This species is related apparently to *C. kelliæ* described above (*vide supra*) as evidenced by the similar overall structure, body proportions, and genitalia. *Chlerogella anthonoma* can be distinguished by the combination of an amber mesosoma with only the mesoscutum dark metallic green (resembling in this respect *C. elongaticeps*) (Fig. 30), the clypeus more extensively marked with amber (cf. Figs 25 vs. 31), the slightly more elongate head (Figs 31, 32), the entirely golden setae of the inner surface of the metabasitarsus, the entirely amber metasoma, the greatly reduced second submarginal cell, and the structure of the terminalia (Figs 38, 39).

Description. *Male:* Total body length 8.36 mm; forewing length 5.68 mm. Head length 2.80 mm, width 1.53 mm. Base of clypeus at lower tangent of compound eyes. Malar space 58% of compound eye length (malar length 0.83 mm; compound eye length 1.43 mm). Upper interorbital distance 0.73 mm; lower interorbital distance 0.30 mm. First flagellomere about as long as pedicel, about as long as wide; second flagellomere three times length of first flagellomere; ventral surfaces of second through eleventh flagellomeres densely covered in placoid sensilla, placoid fields disrupted by mediolongitudinal line of fine, minute trichoid sensilla for lengths of flagellomeres V–VIII, those on flagellomeres V and VI medially constricted, and at base and apex of flagellomere IV. Intertegular distance 1.17 mm; mesoscutellum weakly bigibbous. Basal vein distad cu-a by two times vein width; 1rs-m distad 1m-cu by two times veins width; 2rs-m distad 2m-cu by seven times vein width, 2rs-m relatively straight; first submarginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell narrowed anteriorly, anterior border of second submarginal cell along border with Rs about one-quarter that of third submarginal cell; posterior border of third submarginal cell about 1.3 times as long as anterior border. Distal hamuli arranged 2-1-2. Inner metatibial spur serrate. Metasomal sterna III–IV unmodified, with apical margins straight; apical margin SVI emarginate; terminalia as in figures 38 and 39.

Clypeus and supraclypeal area faintly imbricate, with weak punctures separated by 1–3 times a puncture width, more sparse medially. Head above level of antennae smooth with small punctures separated by a puncture width or less, below level of antennae and in malar space with minute punctures separated by 1–3 times a puncture width, integument faintly imbricate; punctures of face becoming more minute and separated by 1–3 times a puncture width in ocellocular area, on vertex and gena; post-gena strongly imbricate and impunctate. Pronotum smooth to faintly imbricate. Mes-

oscutum smooth, with minute punctures separated by 2–4 times a puncture width, anteriorly punctures become weaker and integument weakly imbricate; mesoscutellum sculptured as on mesoscutum; metanotum smooth with minute punctures separated by 2–5 times a puncture width. Pleura smooth with minute punctures separated by five times a puncture width or more. Propodeum imbricate. Metasoma weakly imbricate.

Mandible, labrum, clypeal apex, and area in malar space bordering mandible amber; apical third of clypeus amber, remainder dark brown with strong metallic green highlights; remainder of head metallic green with copper highlights, blending to a bluish cast on vertex. Scape and pedicel yellow, remainder of antenna dark brown. Mesosoma amber except mesoscutum metallic green with copper highlights. Wing



Figures 30–32. Holotype male of *Chlerogella anthonoma*, sp. n. **30** Lateral habitus **31** Facial aspect **32** Lateral aspect of head.

membranes lightly infumate; veins brown except Sc+R dark brown. Legs amber. Metasoma amber, with thin transverse brands of amber-brown apically on TI–III.

Pubescence golden; typical gender pilosity except postgena with numerous elongate setae, such setae with a few short apical branches; inner surface of metafemur with several long, apically-branched setae, similar setae on inner surface of metatibia except largely simple; metasomal sterna with scattered, short, suberect to erect, simple setae, setae more numerous apicolaterally on SIV and SV.

Female: Unknown.

Etymology. The specific epithet is the Greek term *anthonomos*, meaning “feeding on flowers”.

***Chlerogella pinocchio* Engel, sp. n.**

urn:lsid:zoobank.org:act:97D3CBB5-A234-4A98-892C-11A24912CB70

Figs 33–35, 40, 41; Map 2

Holotype. ♂, COSTA RICA: Prov. Alajuela, Est. Pílon [Estación Biológica El Pílon], 700m, 16 July 2004, J. Azofeifa, Ip. Luz Mercurio, Zuampo (INBio).

Diagnosis. Among darker species from Central America, *C. pinocchio* can be distinguished by the metallic dark hunter green integument of the head and mesosoma (Figs 33–35) and the combination of unmodified metasomal sterna III–V with an entirely yellow scape and pedicel, pale yellow clypeal apex, and yellow protibia and tarsi (except metabasitarsus largely brown).

Description. *Male*: Total body length 8.37 mm; forewing length 5.24 mm. Head length 2.57 mm, width 1.40 mm. Base of clypeus below lower tangent of compound eyes. Malar space 53% compound eye length (malar length 0.70 mm; compound eye length 1.33 mm). Upper interorbital distance 0.70 mm; lower interorbital distance 0.33 mm. First flagellomere about as long as pedicel, about as long as wide; second flagellomere 2.8 times length of first flagellomere; ventral surfaces of second through eleventh flagellomeres densely covered in placoid sensilla, placoid fields disrupted by relatively broad mediolongitudinal line of fine, minute trichoid sensilla for lengths of flagellomeres V–IX, at base and apex of flagellomere IV and basal half of flagellomere X. Interregula distance 1.0 mm; mesoscutellum bigibbous. Basal vein distad cu-a by three times vein width; 1rs-m distad 1m-cu by four times vein width; 2rs-m distad 2m-cu by six times vein width, 2rs-m weakly and gently arcuate; first submarginal cell longer than combined lengths of second and third submarginal cells; second submarginal cell not narrowed anteriorly, anterior border of second submarginal cell along Rs slightly longer than that of third submarginal cell; posterior border of third submarginal cell about 2.5 times longer than anterior border. Distal hamuli arranged 2-1-2. Inner metatibial spur serrate. Apical margins of metasomal SIII–V entire; apical margin of SVI emarginate; terminalia as depicted in figures 40 and 41.

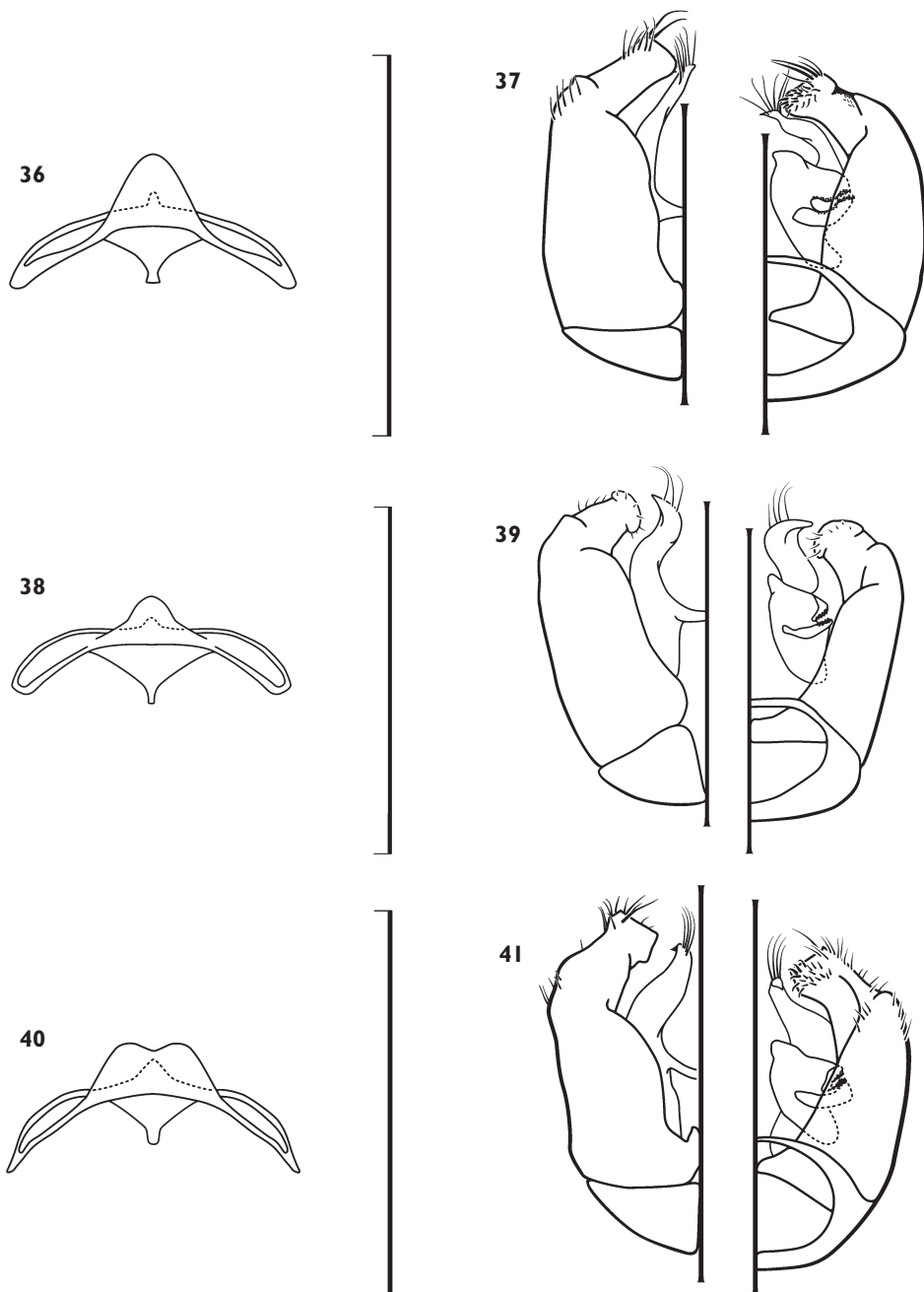
Clypeus and supraclypeal area weakly imbricate with weak punctures separated by 1–3.5 times a puncture width; face smooth with small punctures separated by a puncture width, such punctures more widely spaced in malar space, approximately

1–2.5 times a puncture width, integument between faintly imbricate; ocellocular area and vertex smooth with even more minute punctures separated by 2–5 times a puncture width; gena smooth with minute punctures separated by 2–6 times a puncture width; postgena imbricate and impunctate. Pronotum smooth with minute punctures separated by 2–5 times a puncture width; mesoscutum smooth with minute punctures separated by 2–5 times a puncture width; mesoscutellum and metanotum sculptured as on mesoscutum. Preëpisternum and mesepisternum smooth with minute punctures separated by 3–6 times a puncture width; metepisternum faintly imbricate. Propodeum strongly imbricate. Metasoma weakly imbricate.

Mandible, labrum, and clypeal apex pale yellow; remainder of clypeus dark brown with metallic green highlights; remainder of head metallic green, turning slightly blu-



Figures 33–35. Holotype male of *Chlerogella pinocchio*, sp. n. **33** Lateral habitus **34** Facial aspect **35** Lateral aspect of head.



Figures 36–41. Male terminalia for Costa Rican *Chlerogella* species **36** *Chlerogella kelliiae*, sp. n., hidden and fused sterna VII and VIII **37** *C. kelliiae*, sp. n., genital capsule (left is dorsal aspect, right is ventral aspect) **38** *C. anthonoma*, sp. n., hidden and fused sterna VII and VIII **39** *C. anthonoma*, sp. n., genital capsule (left is dorsal aspect, right is ventral aspect) **40** *C. pinocchio*, sp. n., hidden and fused sterna VII and VIII **41** *C. pinocchio*, sp. n., genital capsule (left is dorsal aspect, right is ventral aspect). All scale bars = 1.0 mm.

ish on vertex and gena; scape and pedicel yellow, flagellum dark brown. Mesosoma dark metallic hunter green; tegula translucent light brown. Wing membranes hyaline; veins brown except Sc+R darker. Legs brown to dark brown except protibia and tarsi (excluding large basal portion of metabasitarsus) yellow, with light brown to yellowish brown areas around podite articulations. Metasoma brown, blending gradually to dark brown by apex; metasomal T1 with small medial yellowish brown spot.

Pubescence generally golden; typical gender pilosity except postgena with numerous elongate setae, such setae with a few short apical branches; inner surfaces of trochanters, mesofemur, metacoxa, metatrochanter, and metafemur with elongate setae, such setae apically with a few short branches; similar setae on inner surface of metatibia except largely simple and of moderate-length. Metasomal sternal discs with sparsely scattered, short, simple, erect setae; apical margin of metasomal SIII with diffuse line of moderate-length, apically-curved setae, such setae slightly more numerous and longer laterally; SIV with apicolateral areas of diffuse short, appressed, inward-directed setae; SV without setal modifications.

Female: Unknown.

Etymology. The specific epithet is a noun in apposition and refers to the fictional wooden doll, Pinocchio, famed for his inveracity and impudence and whose nose grew with each falsehood (Collodi 1883). The name alludes to the elongate rostrum that is shared between this species and its namesake.

Comments. The head of the holotype, and only known specimen, is detached and was mounted by someone in the past on a small point beneath the body. Otherwise the specimen is in excellent condition.

Key to Central American species of *Chlerogella*

Males remain unknown for *C. clidemiae* and females for *C. fortunaensis*, *C. anthonoma*, and *C. pinocchio*.

1. Females 2
- Males 5
- 2(1). Metasoma with at least TI–II amber-yellow (Figs 1, 7, 27); ventral portion of preëpisternal sulcus as wide as scrobal sulcus and upper portion of preëpisternal sulcus 3
- Metasoma with all terga dark brown (Fig. 10); ventral portion of preëpisternal sulcus distinctly broad dorsally at junction of scrobal sulcus and upper portion of preëpisternal sulcus (Panamá) *C. prolixa*, sp. n.
- 3(2). Pleura and legs amber-yellow (Figs 1, 7); clypeus largely light reddish brown or extensively marked with amber-yellow (Figs 3, 9) 4
- Pleura and legs largely brown with strong metallic copper highlights (Fig. 27); clypeus dark brown with strong metallic copper highlights, exceedingly narrow transverse band of lighter integument at extreme apex (Fig. 29) (Costa Rica) *C. kellieae*, sp. n.

- 4(3). Malar space 25% of compound eye length, length about twice basal mandibular width (Figs 2, 3); clypeus at lower tangent of compound eyes; mesoscutum dark brown with strong metallic green-copper highlights; inner metatibial spur with three branches, excluding apical portion of rachis; mesoscutum with punctures separated by a puncture width or frequently less; upper pronotal surface expanded, about two ocellar diameters in medial length (Panamá) ***C. elongaticeps* Michener**
- Malar space 68% of compound eye length, length more than five times basal mandibular width (Figs 8, 9); clypeus below lower tangent of compound eyes; mesoscutum light reddish brown with faint copper highlights; inner metatibial spur with five branches, excluding apical portion of rachis; mesoscutum with punctures separated by 1–2 times a puncture width; pronotal postero-dorsal surface not expanded, at most a single ocellar diameter in medial length (Panamá) ***C. clidemiae* Engel**
- 5(1). Metasoma entirely dark brown, without amber coloration (Figs 13, 17, 33) **6**
- Metasoma marked with amber-yellow or entirely amber (Figs 4, 24, 30) **8**
- 6(5). Metasomal SIV unmodified, apical margin straight, medial furrow and setal pads absent; integument of head and mesosoma dark metallic blue or green **7**
- Metasomal SIV medioapically produced and emarginate, with medial longitudinal furrow bordered by inward-directed setal pads (Fig. 16); integument of head (Fig. 14) and mesosoma blue-black (Panamá) ***C. prolixa*, sp. n.**
- 7(6). Integument of head and mesosoma metallic green (Figs 33, 34); scape and pedicel entirely yellow; clypeal apex pale yellow (Fig. 34); legs brown to dark brown (except protibia and tarsi, excluding large portion of metabasitarsus, yellow) with light brown to yellowish brown areas around podite articulations (Costa Rica) ***C. pinocchio*, sp. n.**
- Integument of head and mesosoma dark metallic blue with purple highlights (Figs 17, 18); scape and pedicel brown except extreme proximal end of scape a little yellow; clypeal apex brown (Fig. 18); legs entirely brown to dark brown (Panamá) ***C. fortunaensis*, sp. n.**
- 8(5). Malar space more than 50% of compound eye length (Figs 25, 26, 31, 32) **9**
- Malar space less than 25% of compound eye length (Figs 5, 6) (Panamá)
..... ***C. elongaticeps* Michener**
- 9(8). Metasoma entirely amber (Fig. 30); pleura largely amber; setae on inner surface of metabasitarsus golden; second submarginal cell very narrow, anterior border along Rs less than one-third length of anterior border of third submarginal cell along Rs (Costa Rica) ***C. anthonoma*, sp. n.**
- Metasomal terga largely brown, marked with yellow on TI and laterally-basally on terga, sterna almost entirely yellow (Fig. 24); pleura metallic copper-green; setae on inner surface of metabasitarsus dark fuscous; second submarginal cell normally rectangular, anterior border along Rs approximately equal in length to anterior border of third submarginal cell along Rs (Costa Rica)
..... ***C. kelliiae*, sp. n.**

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