Proposal of *Fiersiphontina* gen. nov., redescription of *Fiersiphontina sensillata* comb. nov., and new data on the distribution of *Spiniferaphonte* (Copepoda, Harpacticoida, Laophontidae)

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Abstract

The taxonomic position and original description of *Laophontina sensillata* Wells & Rao, 1987 are reviewed based on specimens
collected from the interstitial fauna of littoral coral sands of several islands of the Philippines and New Caledonia,
and the species is designated as the type species of *Fiersiphontina* **gen. nov**. The new genus is proposed based on the total
loss of sexual dimorphism in the P3 and P4 exopods, and the sexual dimorphism in P2 exopod. *Fiersiphontina* is highly
adapted to the littoral interstitial habitat of coral sandy beaches, and is related to *Laophontina* Norman & T. Scott, 1905,
Wellsiphontina Fiers, 1991 and *Spiniferaphonte* Gheerardyn & Fiers, 2007. The shared characteristics that indicate a
strong affinity of *Fiersiphontina* to *Spiniferaphonte* are the robust, dorsally bent, and strongly sclerotised caudal seta V
and the morphology of the genital field. The phylogenetic relationship of *Spiniferaphonte* and *Fiersiphontina* is also suggested
by the analysis of the last ontogenetic phases of the species of the two genera. We re-describe here the adults of
both sexes, describe the last three copepodid stages of *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.**, and
provide notes on the biogeography of the four related genera, and on the ecology of *Fiersiphontina* and
Spiniferaphonte.

Key words: Eastern Pacific, new genus, marine interstitial, coral degradation zone

Introduction

During surveys of the littoral and continental interstitial fauna of several islands in the Philippines and New Caledonia
spanning several years, we collected several specimens which we identified as *Laophontina sensillata* Wells
& Rao, 1987. The genus *Laophontina* Norman & T. Scott, 1905 was revised and redefined by Fiers (1991), who
maintained four species from the Mediterranean and East Atlantic, and allocated other species to the genera *Galapalaophonte*
Mielke, 1981, *Wellsiphontina* Fiers, 1991, *Amerolaophontina* Fiers, 1991 and *Mexicolaophonte* Cottarelli,
1977. Unfortunately, *Laophontina sensillata* was not included in the list of revised taxa. This species was
collected in the Andaman and Nicobar Islands by Wells & Rao (1987), and from Sulawesi by Mielke (1997); the
latter attributed his specimens to *Laophonte sensillata* (meaning *Laophontina sensillata*, *lapsus calami* in Mielke
1997, p. 228) with reservation, without apparently taking into account Fiers's (1991) genus revision. After a comprehensive
examination of the published data and of the specimens of *L. sensillata* in our collection (having been
unable to obtain a loan of the type material), we propose to allocate *Laophontina sensillata* to *Fiersiphontina* **gen. nov.** The new genus is established based on characters proposed and discussed in the revision of the genus *Laophontina*
by Fiers (1991), and on the total loss of sexual dimorphism in P3 and P4 exopods present in *F. sensillata*
(Wells & Rao, 1987) **comb. nov**. (as already reported by Wells & Rao, op. cit. p 191) but not in other species of
Laophontina. The adults of both sexes are re-described based on our specimens from several locations; in addition,
a description of the last three copepodid stages of *F. sensillata* improve our understanding of the ontogenetic development
of the characteristic features of the genus.

We collected one female of *Spiniferaphonte* cf. *ornata* Gheerardyn & Fiers, 2007 (which we briefly describe
and discuss) along the coast of Mindoro Island, Philippines, from the same habitat (i.e., coarse coral gravel in the
tidal and subtidal zone) and similar depth (5 m; in the type locality the species was collected at 2–3 m depth) as the
nominal species. Interestingly, we collected several specimens of *F. sensillata* in the same location and date, but in

the interstitial zone of the corresponding beach. The records discussed in this paper underline once again the rich diversity of Laophontidae T. Scott, 1905 in the various habitats created by coral degradation (Cottarelli & Puccetti 1988; Gheerardyn *et al.* 2006, 2007), which are often characterized by distinct assemblages of species, each with peculiar morphological and, presumably, ecological adaptations.

Material and methods

Specimens were collected on the beach using the Karaman-Chappuis method (Chappuis 1942) and underwater by hand-picking coral sand and fragments, rinsing them several times and filtering the washout. Samples were fixed in

the field in 5% buffered formalin solution, they were sorted in the laboratory and mounted in Faure's medium between two coverslips to allow observation from two sides. Once the Faure's medium was dry, the coverslips were fixed to a microscope slide with pieces of adhesive tape. To avoid deformation of non-dissected specimens, some of them were mounted between two coverslips with fragments of human hair (Karanovic 2005). Drawings were made at different magnifications, to a maximum of 1250 X, using drawing tubes mounted on a Zeiss Axioskop® phase-contrast microscope and a Polyvar Reichert-Jung® interferential- contrast microscope.

The following abbreviations are used throughout the text and figures: enp = endopod; exp = exopod; A1 = antennule; A2 = antenna; ae = aesthetasc; P1-P6 = first to sixth thoracic appendages. The nomenclature and descriptive terminology follows Huys & Boxshall (1991).

Specimens are deposited in the Natural History Museum, London (NHMUK) and Department of Environmental Sciences, Università degli Studi della Tuscia, Viterbo (DSAUT).

Systematics
Family Laophontidae T. Scott, 1905
Subfamily Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000
Fiersiphontina gen. nov.

Diagnosis. Female. Body cylindrical, caudal rami narrowing distally, shorter than anal somite, carrying three distinct

hook-like process anterior to seta VII, one small process anterior to seta I, one process on distal outer corner, two ventral distal processes, and seven setae; seta V robust, dorsally bent, and strongly sclerotised. Genital field with one small seta on each P6 vestige and copulatory pore distinctly posterior to the transverse ridge. Antennule 6-

segmented, first segment with blunt process on outer margin, second segment with large, posteriorly directed hook along outer margin, aesthetasc on fourth and sixth segments. Antennary exopod one-segmented, carrying four subequal

pinnate setae. Exopod P1 one-segmented; endopod P2 represented by one seta and exopod fused to basis carrying one naked seta and one strong bipinnate spiniform seta; endopod P3 and P4 represented by small tubercle carrying one short seta; exopod P3 one-segmented and exopod P4 two-segmented; P5 distinct, with three setae on exopod, basis with one seta on outer peduncle, endopodal lobe with two setae, exopod with three setae.

Male. No sexual dimorphism in P1, P3, P4; sexual dimorphism: antennule seven-segmented, aesthetasc on fifth and seventh segments; exopod P2 vestigial, with one apical strong spiniform seta and two inner sparsely plumose setae; P5 fused, with three long setae on the exopod and very reduced naked endopodal lobe; P6 vestigial, asymmetrical,

right P6 with reduced, non-functional plate, left P6 with large internal plate articulated with the somite, each P6 with a process carrying two setae.

Type and only species. *Fiersiphontina sensillata* (Wells & Rao, 1987) (= *Laophontina sensillata* Wells & Rao, 1987: pp. 184–186, figs 149–150), here designated. The diagnosis of the genus coincides with that of the only known and type species of the genus, and must, therefore, be considered provisional.

Etymology. The generic name is dedicated to Dr. Frank Fiers, Royal Belgian Institute of Natural Sciences, Brussels, Belgium, for his important contribution to the knowledge of Laophontidae. The generic name is a combination

of his name and the suffix –*phontina* commonly used in genus type names of this family. Gender feminine.

Fiersiphontina sensillata (Wells & Rao, 1987) comb. nov.
(Figs 1–7)

Synonymy. *Laophontina sensillata* n. sp.—Wells & Rao, 1987: pp. 184–186, figs 149–150.
Laophontina sensillata Wells & Rao—Mielke, 1997: pp. 227–228, fig. 4; Wells, 2007; pp. 62, 433, 456.
Laophonte sensillata Mielke, 1997: p 228.

Material examined. Ten females (NHMUK 2011.696, 2011.697, 2011.698, DSAUT 101-107), eleven males

(NHMUK 2011.699, 2011.700, DSAUT 108-116), one C3 (DSAUT 117) and one C4 copepodid (DSAUT 118), each mounted on one slide, from the interstitial habitat of a coral sandy beach near Sabang Village, Eastern Mindoro

Province, Philippines, 13° 31' 17" N; 120° 58' 23" E, 20 March 1998.

One male (NHMUK 2011.701) mounted on slide, from the interstitial habitat of a coral sandy beach on the southern shore of North Pandan Island, Western Mindoro Province, Philippines, 12° 51' 24" N; 120° 45' 12" E, 26 January 2006.

Two males (NHMUK 2011.702, DSAUT 119) each mounted on one slide, from the interstitial habitat of a coral sandy beach in Sumilon Island, Visayas Archipelago, Philippines, 13° 33' 22" N; 121° 03' 23" E, 13 January 1985.

One male (DSAUT 120) and two C4 copepodids (DSAUT 121, 122), each mounted on one slide, from the interstitial habitat of a coral sandy beach in Verde Island, Batangas Province, Philippines, 9° 251' 45" N; 123° 23' 35" E, 14 February 2004.

Two males (NHMUK 2011.703, DSAUT 123) and one female (NHMUK 2011.704), each mounted on one slide, from the interstitial habitat of a coral sandy beach in Salag Do-Ong beach, Visayas Archipelago, Siquijor Island, Philippines, 9° 12' 47" N; 123° 40' 59" E, 5 April 1998.

One C5 female copepodid (DSAUT 124), mounted on one slide, from the interstitial habitat of a coral sandy beach in Gaspar Island, Marinduque Island, Philippines, 13° 15' 13" N; 121° 52' 03" E, 24 August 1992.

One C5 male copepodid (DSAUT 125), mounted on one slide, from the interstitial habitat of a coral sandy beach south of Nouméa, New Caledonia, 22° 18' 2" N; 166° 26' 17" E, 20 October 1982.

All material collected by V. Cottarelli.

Description of female. Total body length, measured from anterior margin of rostrum to posterior margin of caudal rami = 405–480 µm (n = 9; mean = 437 µm). Largest width measured at posterior margin of cephalothorax: 92 µm. Body distinctly cylindrical, habitus as in Fig. 1A. Cephalothorax with parallel margins. Free prosomites as wide as cephalothorax. Urosome slightly tapering posteriorly. Second and third urosomites fused only ventrally to form genital double-somite. Integument of cephalothorax densely pitted in the median and anterolateral areas but with symmetrical pattern of smooth areas; in the anterodistal areas pits less dense and progressively substituted by striae intersecting and creating irregular polygons (Fig. 2A). Distal margin of cephalothorax with one band of short,

straight setules (Fig. 2A). Cephalothorax with 31 sensilla, and eight sensilla along distal margin, slightly expanded into several lobes. Distodorsal margins of free somites (Fig. 2B) (except penultimate urosomite) carrying the following

number of small sensilla: first and second prosomites: ten sensilla; third prosomite and first urosomite: eight sensilla; genital double-somite and following urosomite: six sensilla. One pair of sensilla flanking each pair of swimming legs, and one pair of sensilla on distoventral margin of genital double-somite (Figs 1A, 2C). All somites densely hairy on dorsal (Fig. 2B) and ventral surface (Fig. 1A), the latter with less dense hairs; free prosomites and first urosomite hairy also on lateral surface (Fig. 1A). Dorsal and lateral distal margin of cephalothorax

smooth, those of free prosomites and following four urosomites serrate, serration and sensilla present also along the separated portions of genital double-somite. Genital double-somite subdivided dorsally and laterally, ventral suture marked by chitin patches (Fig. 2C), row of spinules only along the midventral distal margin, between

the two medialmost sensilla (Fig. 2C). Fourth and fifth urosomites with row of spinules along the ventral distal margin (Fig. 1A). Genital field with one thin seta on each vestigial P6 and circular copulatory pore forming posterior

margin of an elongated receptaculus seminis, and opening posteriorly to transversal ridge (Fig. 2C). Anal somite with four ventral pores; lateral distal margin from end of operculum to insertion of caudal ramus projecting

and serrate (Fig. 2D). Anal operculum (Figs 2D, 2E) distinctly posteriorly produced, semilunar, flanked by two sensilla, and with strongly incised margin forming ten large, tooth-like processes; a characteristic tuft of long hairlike

setules increasing in length towards middle present below operculum.

Caudal rami (Figs 2D, 2E): conical, shorter than anal somite, slightly wider than long (length measured to insertion of seta V, width measured at ramus insertion); ventral and outer sides hairy. Seven hook-like processes: three anterior to seta VII (the largest one flanking seta VII) (1–3, Figs 2D, 2E), one small process anterior to seta I (4, Figs 2D, 2E), one larger process on distal outer distal corner (5, Figs 2D, 2E), two ventral distal processes (6, 7,

Figs 1A, 2E). Seven setae inserted distally; seta I, II, and III of different lengths: seta III smallest, seta II longest; seta IV plumose; seta V robust, dorsally bent, strongly sclerotised; seta VI short and slender; seta VII as long as seta IV, naked.

Rostrum (Fig. 2F): large and prominent, broadly triangular, not fused to cephalothorax, with pair of sensilla anteriorly, dorsal surface pitted.

Antennule (Fig. 2G): six-segmented; first and second segments wider than following ones; first segment with blunt process on outer margin and longitudinal spinule row along inner margin; second segment with large, posteriorly directed hook along outer margin; fourth segment with distal tubercle carrying very long aesthetasc and two setae of same length; sixth segment with acrothek carrying one short aethetasc and one seta. All setae naked; armature formula: 1-[1], 2-[9], 3-[6], 4-[2 + ae], 5-[1], 6-[8 + acrothek].

Antenna (Fig. 3A): coxa bare; allobasis with pinnate abexopodal seta inserted in distal third. Exopod one-segmented and small, carrying four subequal bipinnate setae. Endopod with two subapical spinules along outer margin; two bipinnate subapical inner spines; apically from inner to outer: one plain spine, one bipinnate spine, one unipinnate spine, three geniculate spines.

Mandible (Fig. 3B): with well-developed, strongly sclerotised gnathobase carrying four blunt teeth and one bipinnate seta. Palp uniramous, with three long setae and a short one (vestige of endopod?).

Maxillule (Fig. 3C): praecoxal arthrite well developed; with transverse row of long spinules on posterior surface; distal margin with four setae of same length and a shorter one, and four strong, curved and unidenticulate spines. Coxal endite with two naked setae of same length. Basal endite with four naked setae, two of which geniculate. Endopod small, partially fused to basis, with three apical and one subapical naked setae; exopod one-segmented, completely fused to basis, with two apical setae.

Maxilla (Fig. 3D): syncoxa with row of long spinules along outer margin, increasing in length towards the middle of row, transverse rows of short spinules on posterior surface, and row of short spinules along inner margin. Two endites, each with one strong unipinnate spine and two slender and long setae. Allobasis drawn out into strong, slightly curved, armed claw carrying two setae. Endopod very reduced, fused to allobasis, carrying two naked setae of same length.

Maxilliped (Fig. 3E): syncoxa elongate with short outer subdistal naked seta. Basis long and slender, slightly enlarged in middle part, naked. Endopod drawn out into long unipinnate claw, as long as basis, with short accessory seta anteriorly.

P1-P4: intercoxal sclerite separated from coxa.

P1 (Fig. 3F): coxa cylindrical with row of long spinules along inner margin and two setae at about 2/3 of same margin. Basis slightly shorter than coxa, with one short distal seta and hair-like setules along inner and outer margins. Exopod one-segmented, hair-like spinules on inner margin, three subequal naked setae along outer margin, one seta on outer distal corner, one normal and one geniculate apical setae of different length. Endopod two-segmented, first segment very long and 3.8 times as long as second segment, bare; second segment apically with armed claw, one minute, naked accessory seta and one smaller spine.

P2 (Fig. 3G): coxa bare, slightly longer than wide. Basis with outer tubercle carrying seta; exopod fused to basis, represented by lobe carrying one inner sparsely plumose seta and one apical strong spiniform bipinnate spine. Endopod represented by one sparsely plumose seta.

P3 (Fig. 4A): coxa and basis completely fused, outer basipodal tubercle carrying one seta. Exopod one-segmented, with one sparsely plumose seta on distal inner corner, one sparsely plumose seta and two strong bipinnate spines apically. Endopod fused to coxobasis represented by one tubercle carrying one sparsely plumose seta.

P4 (Fig. 4B): coxa and basis completely fused, outer basipodal tubercle carrying one seta. Exopod two-segmented, first segment with one strong, long, bipinnate spine on outer distal corner; second segment with two sparsely plumose setae on distal inner corner, one sparsely plumose seta and one strong bipinnate spine apically. Endopod fused to coxobasis represented by tubercle carrying one naked seta.

FIGURE 1. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, female: habitus, ventral view (ornamentation of antennule and some mouthparts schematic); B, male: habitus, ventral view (ornamentation of antennule and some mouthparts schematic). Scale bar: 50 μm.

FIGURE 2. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, female: cephalothorax, dorsal view; B, female: first

free thoracic somite, dorsal view; C, female: genital double somite, genital field, P6, ventral view; D, female: anal somite, anal operculum, caudal ramus, lateral view (setae numbered in Latin numerals, hook-like processes numbered in Arabic numerals); E, female: anal somite, anal operculum, caudal rami, dorsal view; F, female: rostrum; G, female: antennule, ventral view. Scale
bars: 50 µm.

FIGURE 3. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, female: antenna; B, female: mandible; C, female: maxillule; D, female: maxilla; E, female: maxilliped; F, female: P1; G, female: P2. Scale bar: 50 µm.

P5 (Fig. 4C): baseoendopod separate from exopod, with spinules along inner margin and outer basal seta arising from long peduncle. Endopodal lobe carrying two pinnate setae. Exopod rectangular, longer than wide, with spinules along outer and inner margins, carrying three apical pinnate setae, innermost seta longest.
Description of male. Total body length, measured from anterior margin of rostrum to posterior margin of caudal rami = 402–467 µm (n = 10; mean = 429 µm). Largest width measured at posterior margin of cephalothorax: 74 µm. Habitus (Fig. 1B) similar to female, but proportionally thinner, with fully separated second and third urosomites.
Body surface ornamentation as in female, second urosomite ornamented as first one. Caudal rami similar
to those of female in shape and ornamentation, seta I longer (both absolutely and relative to setae II–III), seta II shorter (about as long as seta III), seta V proportionally longer and thinner (Fig. 4D) than in female (Fig 1B). Anal operculum (Fig. 4D), similar to that of female but with 11 tooth-like processes.
A2, mouth parts, P1, P3, P4 (Figs 4F, 4G) similar to those of female except small differences in the length of some setae and spines. Spermatophore as in Fig. 5A.
Antennule (Figs 5D, 5E): seven-segmented; sub-chirocer. First segment as in female but with additional distal row of spinules; setules along outer margin longer, less numerous and with more restricted distribution than in female. Second segment as in female but with transformed seta (asterisked in figure); fifth segment strongly enlarged with distal tubercle carrying very long aesthetasc and two setae of same length, and seven setae, one of which (ventral) is unipinnate; seventh segment with acrothek carrying one thin and long aethetasc, and one seta. Armature formula: 1-[1], 2-[9], 3-[6], 4-[2], 5-[9 + ae], 6-[0], 7-[8+ ae].
P2 (Fig. 4E): similar to that of female but vestigial exopod carrying one additional inner sparsely plumose seta.
P5 (Fig. 5B): baseoendopods fused, very reduced naked endopodal lobe: exopod with three subequal pinnate setae.
P6 (Figs 1B, 5C): vestigial, asymmetrical, right P6 with reduced, non-functional plate, left P6 with large internal plate articulated with the somite, each P6 with a process carrying two setae of different thickness.
Description of third copepodid (C3). Seven somites, habitus as in fig. 6A; length, measured from anterior margin of rostrum to posterior margin of caudal rami, 305 µm. Distal margin of cephalotorax smooth, distal margin
of all somites and of anal operculum denticulate as in the adult. Anal operculum (Fig. 6B) with some denticles (not
present in the adult) transversely aligned dorso-laterally near sensilla.
Caudal rami (Fig. 6B): seta V transformed and fused with the caudal ramus, dorsal process not completely developed. Armature incomplete: two lateral setae (setae I and II) missing.
Antennule four-segmented; first segment similar to that of adult, second segment with a small posteriorly directed hook.
P1 (Fig. 6C): similar to that of adults, all exopodal setae not geniculate.
P2 (Fig. 6D): protopodite still fused to somite; exopod represented by one lobe fused with the protopodite and carrying three setae, one of which enlarged and spiniform. Endopod represented by one seta.
P3 (fig. 6E): protopodite still fused to somite; exopod represented by one lobe fused with the protopodite and carrying two normal setae and one laminate seta with finely extruded apex; endopod represented by one tubercle with one seta.
P4 (Fig. 6F): protopod still fused to somite; exopod represented by one lobe fused with the protopodite and carrying
four setae, one enlarged and spiniform; endopod represented by one tubercle with one seta.
P5 (fig. 6G): two small adjacent tubercles, each with one seta.
P6 (Fig. 6H): one small bare lobe.
Description of fourth copepodid (C4). Eight somites; habitus and ornamentation of cephalotorax and somites as in C3. Total body length, measured from anterior margin of rostrum to posterior margin of caudal rami = 355 µm.
Anal somite (Fig. 6I): dorsolateral row of denticles more marked. Anal operculum (Fig. 6I): distal denticles ornamentation almost identical to that of the adult; the characteristic tuft of long hair-like setules increasing in

length towards the middle is already present below the operculum.

Caudal rami (Fig. 6I): seta IV and V as in the adult, ramus quadrangular in lateral view (not yet conical as it is in the adult) with a strong dorsal hook-like process anteriorly to seta VII, which is strongly similar to that of the copepodid and adult of *Spiniferaphonte* (see Fiers 1991 and Gheerardyn *et al.* 2007).

Antennule (Fig. 6J): four-segmented; first and second segment very similar to those of adult; projection of second segment larger and more pointed than in adult.

FIGURE 4. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, female: P3; B, female: P4; C, female: P5. D, male: anal somite, anal operculum, caudal rami, dorsal view; E, male: P2; F, male: P3; G, male: P4. Scale bars: 50 µm.

FIGURE 5. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, male: spermatophore, B, male: P5; C, male: P6; D, male: antennule (schematic); E, male: antennule (disarticulated); F, male: P4 (variability). Scale bars: 50 µm.

FIGURE 6. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, third stage copepodid: habitus, B, third stage copepodid:
anal somite, anal operculum, caudal rami, dorsal view; C, third stage copepodid: P1; D, third stage copepodid: P2; E, third stage copepodid: P3; F, third stage copepodid: P4; G, third stage copepodid: P5; H, third stage copepodid: P6; I, fourth stage copepodid: anal somite, anal operculum, caudal rami, lateral view; J, fourth stage copepodid: antennule (schematic); K, fourth stage copepodid P2; L, fourth stage copepodid: P3, M, fourth stage copepodid: P4, N, fourth stage copepodid: P5; O, fourth stage copepodid: P6. Scale bars: 50 µm.

FIGURE 7. *Fiersiphontina sensillata* (Wells & Rao, 1987) **comb. nov.** A, C-I, fifth stage copepodid, female: B, J, fifth stage copepodid, male. A, fifth stage copepodid, female: anal somite, anal operculum, caudal rami, dorsal view; B, fifth stage copepodid,
male: anal somite, anal operculum, caudal rami, lateral view; C, fifth stage copepodid, female: antennule (schematic); D, fifth stage copepodid, female: P1; E, fifth stage copepodid, female: P2; F, fifth stage copepodid, female: P3; G, fifth stage copepodid, female: P4; H, fifth stage copepodid, female: P5; I, fifth stage copepodid, female: P6; J, fifth stage copepodid, male:
P5. Scale bars: 50 µm.

P2 (Fig. 6K): protopodite still fused to somite; exopod represented by one lobe fused with the protopodite and carrying two setae, one enlarged and spiniform. Endopod represented by one tubercle with one small seta.

P3 (fig. 6L): protopodite still fused to somite; exopod represented by one lobe fused with the protopodite and carrying yhree setae, two enlarged and spiniform. Endopod represented by one tubercle with one small seta.

P4 (Fig. 6M): exopod one-segmented with five setae (same number as those present in the two-segmented exopod of the adult), three enlarged and spiniform. Endopod represented by one seta.

P5 (fig. 6N): distinct expodal lobe with three setae. Endopodal lobe not recognizable.

P6 (fig. 6O): two small lobes, each one with one seta.

Decription of female fifth copepodid (C5). Nine somites, total body length, measured from anterior margin of rostrum to posterior margin of caudal rami = 450 µm. Anal somite (Fig. 7A): with dorso-lateral row of denticles.

Anal operculum (Fig. 7A): distal denticles ornamentation almost identical to those of adult. Caudal rami (Fig. 7A):
almost completely developed: each carrying six normal and one transformed setae, two dorsal hook-like processes anterior to seta VII still inserted on large protrusion (see figure in lateral view for male C5 as described below). Hooks and protrusion shrunk in the adult to form conical shape of ramus.

A1 as in Fig. 7C.

P1 (Fig. 7D): with one seta at midlength of the inner margin of basis, apical seta of exopod geniculate.

P2-P4 (Figs 7E, 7F, 7G): as in C4, but proportionally larger.

P5 (Fig 7H): exopodal lobe with three setae, endopodal lobe with two small setae.

P6 (Fig. 7I): two adjacent lobes, each one with one seta.

Description of male fifth copepodid (C5). Nine somites, total body length, measured from anterior margin of rostrum to posterior margin of caudal rami = 419 µm. Anal somite (Fig. 7B), anal operculum (Fig. 7B), A1, A2, mouth parts, P1-P4 and P6 as in the female C5. Caudal rami (Fig. 7B) sexually dimorphic: transformed seta V is longer than in female C5.

P5 (Fig. 7J): setae on the exopodal lobe shorter than those of female C5, baseoendopodal lobe bare.

Variability. In adult specimens, the number of tooth-like processes on the anal operculum ranges from 9 to 12 in females, and from 9 to 14 in males. In one male paratype from Siqujior the second segment of exp-P4 is longer than wide (Fig. 5F).

Spiniferaphonte **cf.** *ornata* Gheerardyn & Fiers, 2007
(Fig. 8)

Material examined. One female (DSAUT 126) mounted on one slide, from washout of coral sand and fragments, hand-collected by snorkeling at 5 m depth, in front of beach near Sabang Village where *Fiersiphontina sensillata* **comb. nov.** was collected , Eastern Mindoro Province, Philippines, 13° 31' 17" N; 120° 58' 23" E, 20 March 1998.

Material collected by V. Cottarelli.

Description of female. Total body length, measured from anterior margin of rostrum to posterior margin of caudal rami = 711 µm. Habitus, body ornamentation, rostrum A1 (Fig. 8A), A2, mouth parts, P1, as in *S. ornata*. Anal operculum: with 11 tooth-like processes (Fig. 8B).

Caudal rami (Fig. 8B): armature as in *S. ornata* but seta V proportionally longer and thinner, one tubepore adjacent
to seta VI (arrowed in figure).

P2 (Fig. 8C): exopod one-segmented narrowing at tip, with three apical plumose setae, two innermost shorter and of same length; one strong bipinnate spine on outer distal corner.

P3 (Fig. 8D): basis with one pore; exopod three-segmented, first and second segments with one very strong bipinnate spine on outer distal corner; third segment with three apical and one inner pinnate setae of subequal length, inner seta inserted at midlength of segment.

P4 (Fig. 8E): exopod three-segmented, first segment with very strong bipinnate spine on outer distal corner; second segment with long bipinnate spiniform seta on outer distal corner; third segment with four pinnate setae of different length.

P5 (Fig. 8F): exopod shorther than in *S. ornata*, with similar armature but three subequal distal pinnate setae and one longer and pinnate subapical outer seta. Endopodal lobe with four setae as in *S. ornata*, but less developed.

Remarks. Only the characters which distinguish this specimen from the original description are given above. *Spiniferaphonte* cf. *ornata* differs in body length (711 µm vs 564–610 µm); the morphology and armature of P2-P5
and anal operculum (stronger spines on the P2-P4 exopods, one additional seta on 3-exp P3, a much longer P4 endopod, and an anal operculum with more processes on the distal margin in *Spiniferaphonte* cf. *ornata*). The caudal
rami and P5 have additional differences in setal/spinal length (the caudal rami have an additional secretory tube pore, not recorded in *Spiniferaphonte ornata*). These differences might be large enough to attribute *Spiniferaphonte*
cf. *ornata* to a new species, but the availability of only one specimen does not allow us to evaluate the possible intraspecific variability, or to describe the male morphology. As a consequence, we postpone a more precise definition
of the taxonomic status of this specimen until we are able to collect more material.

FIGURE 8. *Spiniferaphonte cf. ornata* Gheerardyn, Fiers, Vincx & De Troch, 2007. A, female: rostrum and antennule (schematic);
B, female: anal somite, anal operculum, caudal rami, dorsal view; C, female: P2; D, female: P3; E, female: P4, F, female: P5. Scale bars: 50 µm.

FIGURE 9. Distribution (from published records and present study) of the genera *Laophontina* Norman & T. Scott, 1905 (black circles), *Wellsiphontina* Fiers, 1991 (grey triangles), *Spiniferaphonte* Gheerardyn & Fiers, 2007 (black triangles), *Fiersiphontina*
gen. nov. (white circles).

Discussion

In his revision, Fiers (1991) discussed *Laophontina* Norman & T. Scott, 1905 and *Wellsiphontina* Fiers, 1991 as the
two "most closely related" genera, with *Laophontina* probably originating from a *Wellsiphontina*-related group. Gheeradyn *et al.* (2007) described the new genus *Spiniferaphonte* Gheerardyn and Fiers, 2007 as originating "from
the same stock as *Wellsiphontina* and *Laophontina*". Therefore, *Fiersiphontina* **gen. nov.** fits well in this group of phylogenetically related taxa. A list of phylogenetically informative characters which allow us to characterize the position of *Fiersiphontina* within this group of genera is presented in Table 1 and briefly discussed below.

A plesiomorphic character maintained only in *Fiersiphontina*, and not in *Laophontina*, *Wellsiphontina* and *Spiniferaphonte,* is the absence of sexual dimorphism in the P4 exopod and endopod. In *Wellsiphontina* and *Laophontina*
the P4 is typically transformed in the male: it is smaller than in the female, carrying much stronger exopodal spines, and fewer elements on the last segment. In *Spiniferaphonte,* the last segment of P4 in the male has a

reduced armature.

Fiersiphontina, *Laophontina*, *Wellsiphontina* and *Spiniferaphonte*, share the following apomorphies: a denticulate operculum, and absence of sexual dimorphism in the P2 and P3 endopods. *Fiersiphontina*, *Wellsiphontina* and *Laophontina* share the following apomorphies: one-segmented P1 exopod and absence of seta on the endopodal part of the male P5. The presence of the plesiomorphic conditions of these two characters (two-segmented P1 exopod,

and presence of a seta on the endopodal part of the male P5) allowed Gheerardyn *et al.* (2007) to propose a new genus and species, *Spiniferaphonte ornata* Gheerardyn & Fiers, 2007. On the other hand, *Fiersiphontina* shares with *Spiniferaphonte* the important apomorphy represented by the robust, dorsally bent, and strongly sclerotised

caudal seta V. These two genera also share the morphology of the genital field (i.e., position of the gonopore and armature of the P6 vestiges), which was listed as an important diagnostic feature by Fiers (1991), although its phylogenetic value is not clear, being present in two alternative states (one or two setae on P6, gonopore anterior or

posterior) in taxa of the family which are not phylogenetically related. Nonetheless, *Fiersiphontina* and *Spiniferaphonte*

both have a gonopore opening posterior to the transverse ridge, and only one seta on the P6 vestiges. Other

morphological characteristics shared by the two genera which strengthen the hypothesis of their affinity include: the presence of several upwards processes on the caudal rami; similar cephalothoracic ornamentation; strongly incised distal margin of the penultimate somite "forming large tooth-like processes (Gheerardyn *et al.* 2007)" in *Spiniferaphonte ornata* (this same feature is present in *Fiersiphontina*, but less pronounced); and ornamentation of somites and similar number and position of sensilla.

The sexually dimorphic P2 exopod, with one additional, sparsely plumose seta in the male is the most important autapomorphy of *Fiersiphontina*. The presence of a less reduced P2 in the male is a conservative condition which is present in other laophontids: for instance, in *Afrolaophonte brignolii* Cottarelli, 1985 the P2 exopod is not

fused to the basis in the male.

An additional interesting character is the ratio between the lengths of the first and second segment of the antennule

in females which, from the published material and from the analysis of specimens in our collection, differs between the two groups *Laophontina-Wellsiphontina* and *Fiersiphontina-Spiniferaphonte*. In the first group, the first segment is longer then the second (the ratio ranging from 1.3 to 1.7 for *Laophontina*, and 1.2–1.4 for *Wellsiphontina*).

In the second group, the first segment is as long as or slightly longer than the second (ratio is 1 for *Spiniferaphonte*,

and 1.2 for *Fiersiphontina*). A longer antennule would provide a better leverage for movement within the interstitial space (see below).

In conclusion, if we take into account the affinities discussed by Fiers (1991) and Gheerardyn *et al.* (2007) for *Laophontina* and *Spiniferaphonte*, and the affinities of *Fiersiphontina* and *Spiniferaphonte*, we hypothesize that two lineages could have originated from an ancestral taxon strictly related to *Wellsiphontina*. One lineage is represented

by *Laophontina*, the other a common ancestor to *Fiersiphontina* and *Spiniferaphonte*.

The phylogenetic relationship of *Spiniferaphonte* and *Fiersiphontina* is also shown by the analysis of the last ontogenetic phases of the species of the two genera. The fifth male copepodid of a "Laophontidae gen. sp." was described by Fiers (1991) and later defined as "closely related to *Spiniferaphonte ornata*" (Gheerardyn *et al.* 2007).

This copepodid (which will be called herein copepodid of *Spiniferaphonte* sp.), shares numerous characters with the C5 and adult of *F. sensillata* **comb. nov.**, although the differences in armature which distinguish the adults of the two species are already partially present in the C5 (Table 2).

TABLE 2. Main morphological differences among the male and female C5 and adults of *Fierrsiphontina sensillata*, the male C5 of *Spiniferaphonte* sp. (from Fiers, 1991), the male and female adults of *Spiniferaphonte ornata* Gheerardyn & Fiers, 2007.

The only leg which differs between the copepodids of the two species is the P2, which in the C5 and adults of both sexes of *Fiersiphontina sensillata* is represented by one segment, derived by the fusion of basis, exopod and endopod, whereas the C5 of *Spiniferaphonte* sp. has a distinct exopod with four setae, almost identical to those of the adult in *S. ornata*.

The morphological peculiarities of the caudal rami of *Spiniferaphonte ornata* prompted Gheerardyn *et al.*

(2007) to examine other taxa of Laophontidae which have "one or more upwardly directed processes on the dorsal

	F. sensillata: male and female C5	*Spiniferaphonte* sp.: male C5	*F. sensillata*: adult male and female	*S. ornata*: adult male and female
P1 exopod	One-segmented, with six setae	One-segmented, with six setae	One-segmented, with six setae	Two-segmented, with one seta on exp-1, five setae on exp-2
P3 exopod	One-segmented, with two enlarged and one normal setae	One-segmented, with three spiniform and one normal setae	One-segmented, with two enlarged and two normal setae	Three-segmented, with a total of two spiniform and three normal setae
P4 exopod	One-segmented, with two enlarged and three normal setae	One-segmented, with four spiniform and one normal setae	Two-segmented, with a total of two enlarged and three normal setae	Three-segmented, with a total of two spiniform and four normal setae
P5 exopod	Distinct lobe, with three setae	Distinct lobe, with three setae	Distinct segment, with three setae	Distinct segment, with five setae
P5 endopod	Rudimentary lobe, with two small setae in the female, bare in the male	Rudimentary lobe, bare	Endopodal lobe with two setae in the female, bare in the male	Endopodal lobe with four setae in the female, bare in the male

surface of the caudal rami", and they detected two distinct derived conditions for the position and origin of such processes. In the first group (*Indolaophonte* Cottarelli, Saporito & Puccetti, 1986, *Raowellsia* Özdikmen, 2008) there is one spinous process, derived from a posterior outgrowth of the distolateral corner of each caudal ramus; in

the second group (*Amerolaophontina* Fiers, 1991, *Galapalaophonte* Mielke, 1981, *Laophontina, Mexicolaophonte* Cottarelli, 1977, *Pseudolaophonte* A. Scott, 1896, *Spiniferaphonte*, *Wellsiphontina* and *Fiersiphontina*) the spinous

process is developed medially of seta VII, or anteriorly to the same seta. According to the same authors, in certain genera one of the apical caudal setae is modified into a strong, dorsally bent spine to form a functional analogue of the dorsal apical process present in the above-mentioned second group: seta VI (*Pseudolaophonte*) or seta V are thickened proximally, with a thorn-like process dorsally, and continuing as a slender seta (three out the four species

of *Laophontina*, all *Wellsiphontina*, *Amerolaophontina*, *Galapalaophonte*, *Mexicolaophonte*, and *Maiquilaophonte*

Mielke, 1985, and in certain species of *Klieonychocamptoides* Noodt, 1958). Only in *Spiniferaphonte, Laophontina*

noodti Kunz, 1983 and *Fiersiphontina* **gen. nov.** (and in the genus *Oniscopsis* Chappuis, 1954, belonging to Paramesochridae) the caudal seta V is strongly sclerotised and dorsally bent, apparently having lost the slender distal

section. The presence of a "hook" on the caudal rami, represented by a spinous process or a modified seta, is present in numerous non-related taxa of marine interstitial harpacticoids of families other than Laophontidae (e.g., in most species of several genera in the families Leptopontiidae Lang, 1948, and Arenopontiidae Martínez Arbizu & Moura, 1994) indicating that there may be a strong selective pressure in the interstitial habitat favoring the convergent

evolution of an anchoring structure, which would help propelling the body forward. In the case of the modification

of the seta V, Gheerardyn *et al.* (2007) remarked how this structure is present only in interstitial species, where it is often associated with distinct processes on the caudal rami and/or the anal operculum, and with a strong

thorn-like processes on the proximal segments of the antennule, thus providing a possible evolutionary advantage over a simple vermiform body shape. This suite of characters provides a mechanism to anchor the animal to the sediment (the caudal rami) and to propel an individual forward (hooks on the antennule), thus helping the animal to

penetrate and move through the sediment, as already discussed by Kunz (1974) for the Paramesochridae Lang, 1944 *Kliopsyllus furcavaricatus* (Kunz, 1974). *Fiersiphontina* follows this morphological pattern. This taxon is typical of an environment where repeated wave action constantly shifts the unconsolidated sediment.

Biogeographical and ecological notes. In tropical reefs, the area between the reef and the beach (which often corresponds to the intertidal zone) is characterized by the fragments of dead coral, with variable granulometric range (Gheerardyn *et al.* 2008). This "coral degradation zone" (Gheerardyn *et al.* 2007) is the elective habitat of several meiobenthic taxa of the sub family Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000, which represents

almost 95% of all Laophontidae (Gheerardyn *et al.* 2006).

Spiniferaphonte ornata and *Spiniferaphonte* cf. *ornata* were collected from the interstices of coarse gravel in the submersed coral degradation zone, whereas *Fiersiphontina sensillata* was always collected in the interstitial habitat between high and low tide levels by Wells & Rao (1987), Mielke (1997), and by us. In fact, *Fiersiphontina* is morphologically highly adapted to the life and movement in the interstitial spaces (cylindrical body, reduced appendices, and the morphological adaptations discussed above); thus, *Spiniferaphonte* and *Fiersiphontina* could represent two different degrees of adaptations to the process of colonization of littoral interstitial habitat from marine benthic ancestors.

The distribution of the newly erected genus also shows an interesting zoogeographical pattern (Fig. 9): so far, *Fiersiphontina* has been collected in the northwestern Pacific (Philippine Sea), in the southwestern Pacific, and in the Eastern Indian Ocean, whereas *Laophontina* is distributed from the Mediterranean to the Northeast Atlantic. Up

to now, the genus *Spiniferaphonte* was only known from the western Indian Ocean, in one location on the Kenyan coast, with a possible additional record from the Seychelles (Gheerardyn *et al.* 2007). The collection of a new specimen

in the Philippines considerably widens the geographical distribution of *Spiniferaphonte* to the northwestern Pacific. *Wellsiphontina* is present in the western Indian Ocean. Thus, the geographical distributions of *Fiersiphontina*

and *Spiniferaphonte* fit well with the phylogeny of the taxa following vicariance events, as already discussed by Fiers (1991). In fact, *Laophontina* is an ancient taxon which originated from a *Wellsiphontina*-related group after the closure of the Tethyan seaway, which once connected the Atlantic Ocean with the Indo-Pacific via the Mediterranean, in the Late Early to Middle Miocene (Teske *et al.* 2007). The taxon which represents the common

ancestor of *Fiersiphontina* and *Spiniferaphonte* would have originated in the western Indian Ocean and dispersed from there to the eastern Indian Ocean and finally to the western Pacific. The Philippines, where *F. sensillata* is particularly widespread, originated quite recently, during the Pleistocene, and the area named "East Indies Trian-

gle," which extends from north of the Philippines, south-west across the Malayan Peninsula, and eastward beyond New Guinea, there is a powerful center of origin and evolutionary radiation (Briggs 2004), although its importance

as a center of high species diversity for harpacticoid copepods has still not been definitively proven (Chertoprud *et*

al. 2010).

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