A new genus, a new species, and a new record of the family Darcythompsoniidae Lang, 1936 (Copepoda, Harpacticoida) from the Gulf of California, Mexico

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A new genus and new species of the family Darcythompsoniidae Lang (1936), and a new record of *Darcythompsonia fairliensis* (T. Scott, 1899), from a coastal lagoon in the south-eastern Gulf of California (Mexico), are reported and fully described and illustrated. ***Pabellonia olganoguerae* gen. nov., sp.nov.** shares features with *Darcythompsonia* T. Scott, 1906, such as the presence of a dimorphic second endopodal segment of the male second swimming leg, and with *Kristensenia* Por, 1983, the lack of sexual dimorphism in the caudal rami, anal operculum and urosomites. Thus it is considered closely related to these genera, and to represent a third component of this lineage. Some notes on the biogeography of *Darcythompsonia* T. Scott, 1906, are also presented.

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ADDITIONAL KEYWORDS:—Darcythompsoniidae – taxonomy – Mexico.

CONTENTS

INTRODUCTION

At the time Lang (1944) published his 'Monographie der Harpacticiden (vorläufige Mitteilung)', three genera were recognized within the family Darcythompsoniidae:

Leptocaris T. Scott, 1899, *Horsiella* Gurney, 1920, and *Darcythompsonia* T. Scott, 1906. During the early 1960s, based on descriptions of several species regarded as transitions between *Leptocaris* and *Horsiella*, Kunz (1961: 276) and Lang (1965: 95), considered these two genera as synonyms, and united their species within the genus *Leptocaris*.

The family Darcythompsoniidae presently comprises four genera: *Leptocaris*, *Darcythompsonia*, *Kristensenia* Por, 1983, and *Falcocaris* Fiers. Fiers (in Litt) also proposed to Kunz to accommodate *Leptocaris mangalis* Por, 1983, within *Falcocaris* (Kunz 1994: 51), but this genus has not been diagnosed so far. The four genera have been defined by a set of characters and character states such as (1) absence or presence of well developed or rudimentary maxillipeds, (2) P1 END 1 with or without an anteriorly directed inner seta with comb tip, (3) presence or absence and armature of the mandibular palp, (4) shape of anal operculum and caudal rami, (5) presence or absence of sexual dimorphic structures on the second and third male urosomite, and (6) presence or absence of sexual dimorphism in the male P2 END 2, anal operculum and caudal rami.

During a short-term study on the distribution and abundance of meiofauna in a coastal lagoon in the south-eastern Gulf of California, specimens of a taxon clearly related to the globally distributed *Darcythompsonia-Kristensenia* lineage, were collected from sediment samples from a site in Ensenada del Pabellon lagoon (Mexico) that is characterized by moderate levels of organic matter, deteriorated water and soil quality, presence of muddy sediments and well developed mangrove trees (Gómez-Noguera & Hendrickx, 1997), conditions that normally exclude the colonization by most other harpacticoids (Fiers, 1986a; but see also Por, 1983).

MATERIAL AND METHODS

Triplicate sediment samples were taken during a short-term study on the abundance and distribution of meiofauna from Ensenada del Pabellon lagoon (Sinaloa, north-western Mexico). Meiobenthic organisms were retrieved using a 63 μm sieve. Harpacticoids were picked out under a dissecting microscope, counted and stored in 70% ethanol. Dissected parts of the harpacticoids were mounted in glycerin with sealed coverglasses. Observations and drawings were made at 1250 × on a Leitz Periplan phase contrast light microscope equipped with a drawing tube. Terminology and abbreviations utilized follow Lang's (1948) system. Abbreviations used in the text and tables: P1–P6, first to sixth leg; EXO, exopodite; END, endopodite.

TAXONOMICAL ACCOUNT

Pabellonia gen. nov

Diagnosis. Darcythompsoniidae Lang, 1936. Habitus and mouth parts as in *Darcythompsonia* and *Kristensenia*. Anal operculum with serrate and upwardly directed caudal fold. Caudal rami with inner distal corner protruded into an upwardly directed extension. Female antennule seven-segmented. Male antennule six-segmented, subchirocer. Basis of male P1 with dimorphic inner spine and small outer element. First endopodal segment of male P2 comparatively larger than in female, second

segment modified; inner spine of P3 END 1 and outer spine of P3 END 2, outer spine of P3 EXO 2, and inner spine of P4 END 1 comparatively smaller than in female; P3 EXO 3 with proximal hyaline spine. P5 and P6 absent in both sexes.

Type species. Pabellonia olganoguerae gen.nov., sp.nov: by monotypy.

Etymology. The generic name alludes to Ensenada del Pabellón lagoon, the type locality. The specific name in honour to Mrs Olga Noguera-Farfán for her 26th anniversary as biology teacher at the National Autonomous University of Mexico.

Material examined. Found in station 10 (muddy bottom) (see Gómez-Noguera & Hendrickx, 1997), at a depth of 0–3 cm in the sediment. Taken with a 3 cm i.d. plastic corer. 30 April and 23 June 1991. One alcohol preserved female holotype (EMUCOP-230691-01), one dissected male allotype (EMUCOP-300491-06) and two dissected female paratypes (EMUCOP-230691-20, EMUCOP-230691-21) have been deposited in the invertebrate collection of the 'Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología'; one female (2000.1779) and one male (2000.1780) paratype have been deposited in the collection of the Natural History Museum (London).

Type locality. Ensenada del Pabellon lagoon, Sinaloa, Mexico (24°19′–24°35′N, 107°28′–107°45′W) (for more details see Gómez-Noguera & Hendrickx, 1997).

Pabellonia olganoguerae sp. nov.

(Figs 1–6)

Female. Habitus (Fig. 1A) as in *D. fairliensis*; length including rostrum and caudal rami, from 0.9 to 1.13 mm (length of holotype 1.01 mm). Anal somite (Fig. 1A, B, D) with bilobed caudal margin; rounded operculum with serrated and upwardly directed caudal fold. Caudal rami (Fig. 1A–D) with a length about twice the width, with inner margin convex and outer edge slightly concave; inner distal corner protruded into an extension upwardly directed; with five setae. Copulatory pore as in Figure 1E.

Antennule (Fig. 2A), seven-segmented, with aesthetasc on fourth component; all setae smooth.

Antenna (Fig. 2B, C): allobasis with a length about twice the width, ornamented with row of small proximal spinules on inner edge and with one small seta on proximal third. One-segmented exopodite arising in proximal third, with one seta. Endopodal segment ornamented with proximal and median set of spinules, with two strong spines and one seta, and five distal elements.

Mandible (Fig. 2D, E): sclerotized gnathobase furnished with two rows of small spinules; division between coxa-basis and endopodite not evident; coxa-basis with 1, endopodite with 1 lateral and 3 apical setae.

Maxillule (Fig. 2F), with massive arthrite bearing six small apical elements; with 1 subdistal thickened spine, 1 lateral thickened seta, and 2 surface elements. Division between basis, endo- and expodite not clear; basis with 3, endo- and exopodite with 2 setae each.

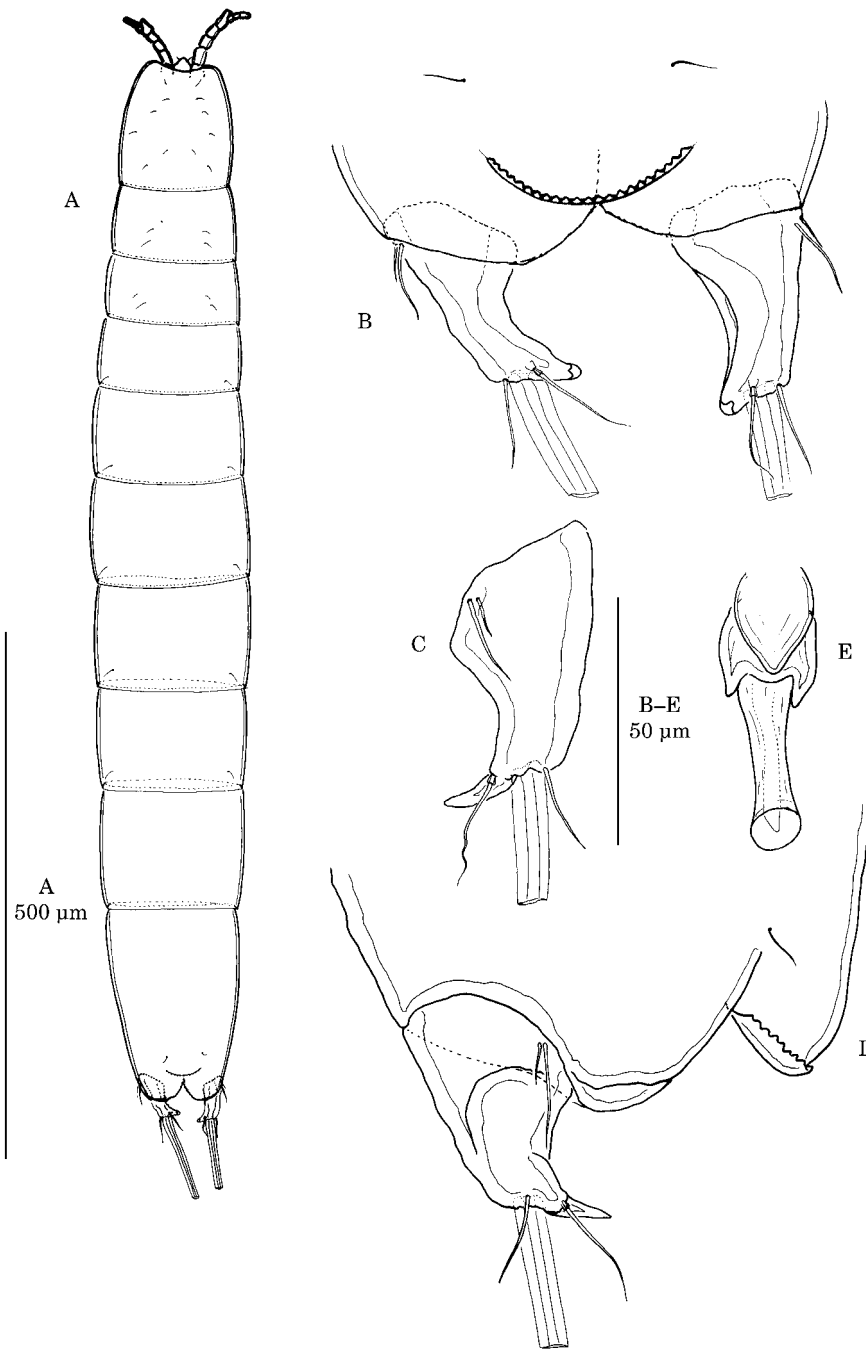Maxilla (Fig. 2G, H): syncoxa furnished with some small spinules; with 1 endite

Figure 1. **Pabellonia olganoguerae sp.nov.**, female. A, habitus, dorsal; B, anal somite and caudal rami, dorsal; C, right caudal ramus, lateral; D, anal somite and left caudal ramus, lateral; E, genital pore.
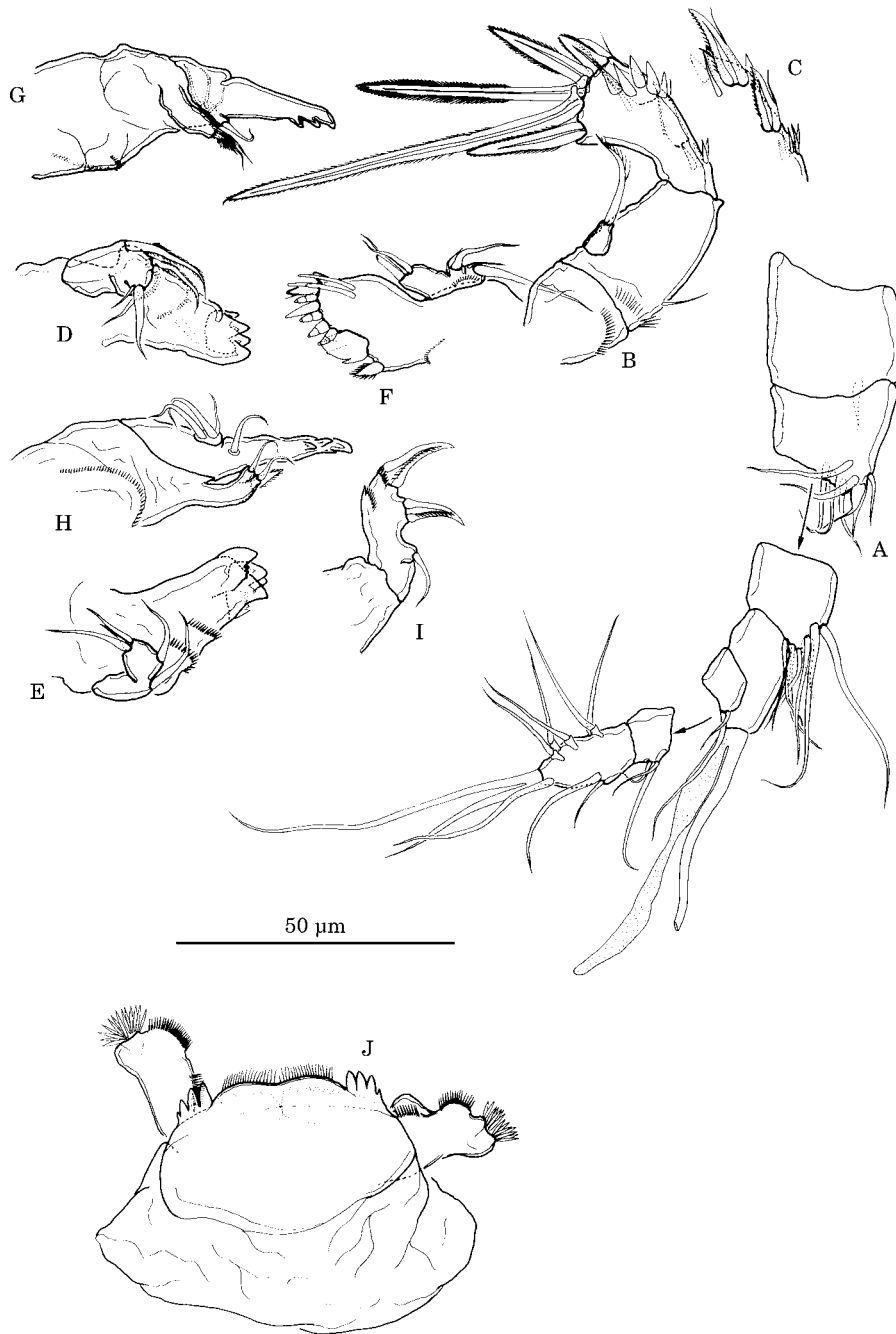
Figure 2. **Pabellonia olganoguerae sp. nov.**, female. A, antennule, exploded; B, antenna; C, ultimate antennal segment, another view; D & E, mandible; F, maxillule; G & H, maxilla; I, maxilliped; J, labrum and paragnaths.
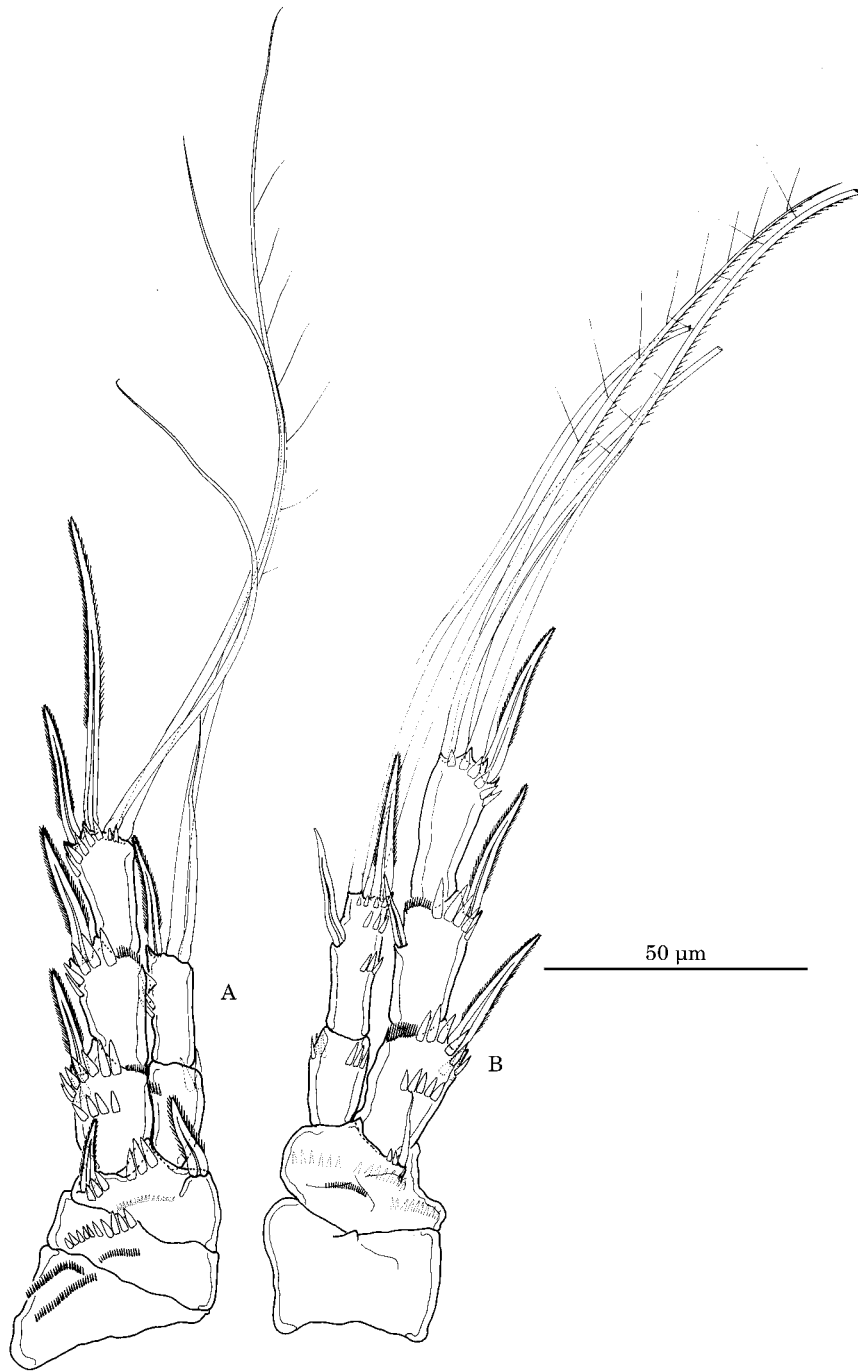
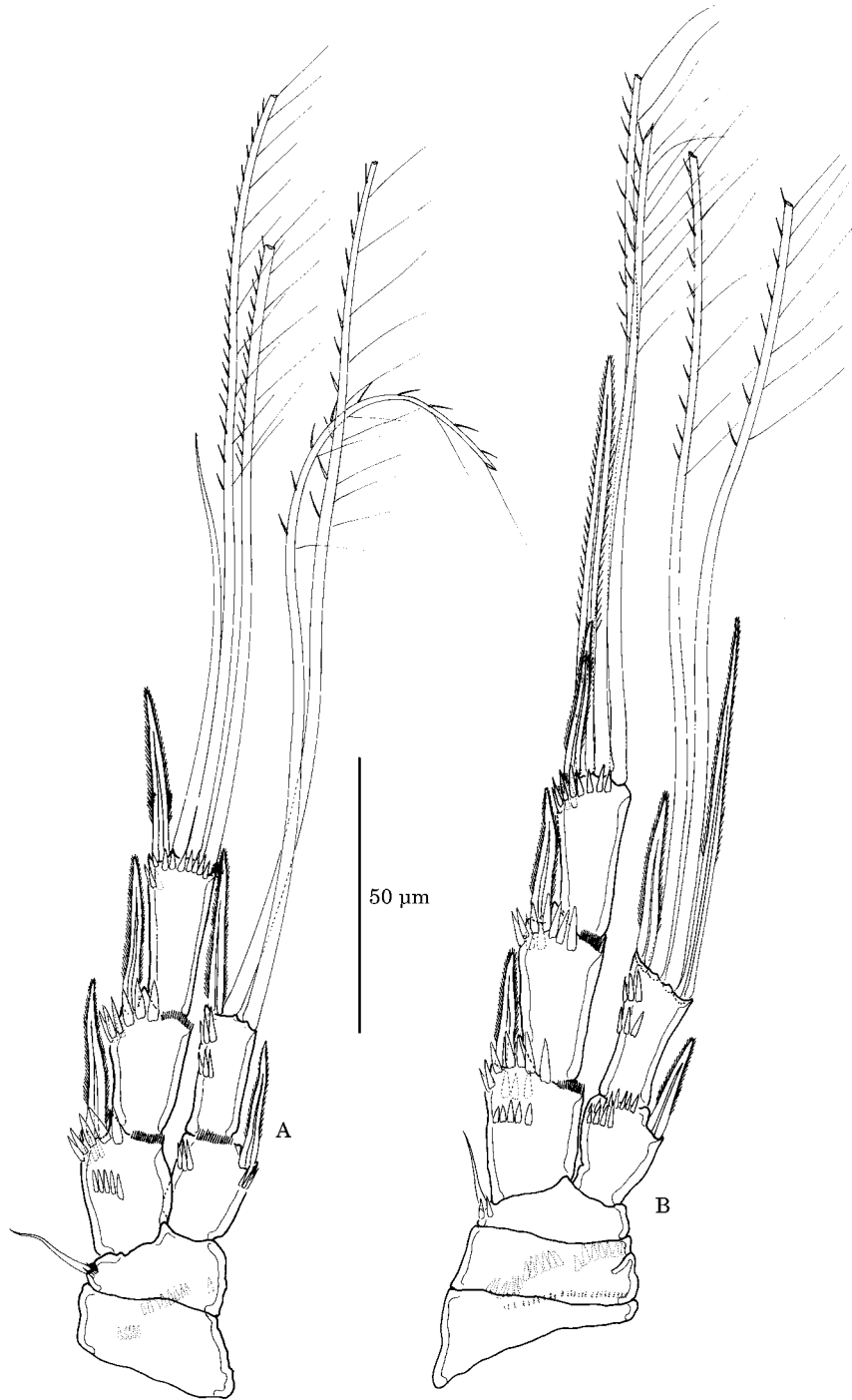Figure 3. **Pabellonia olganoguerae sp. nov.**, female. A, P1; B, P2.

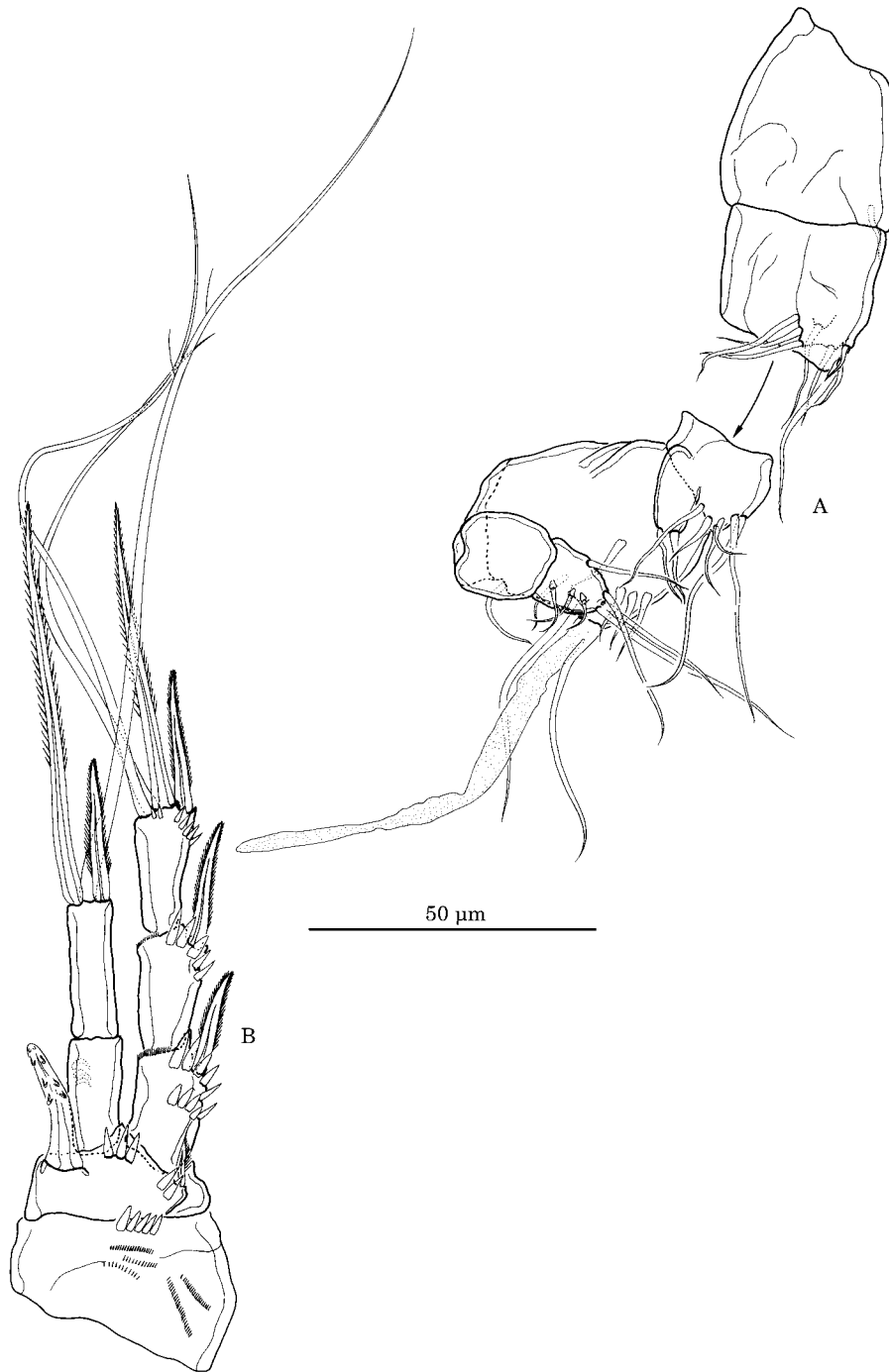Figure 4. *Pabellonia olganoguerae* **sp. nov.**, female. A, P3; B, P4.

50 µm

Figure 5. *Pabellonia olganoguerae* **sp. nov.**, male. A, antennule, exploded; B, P1.
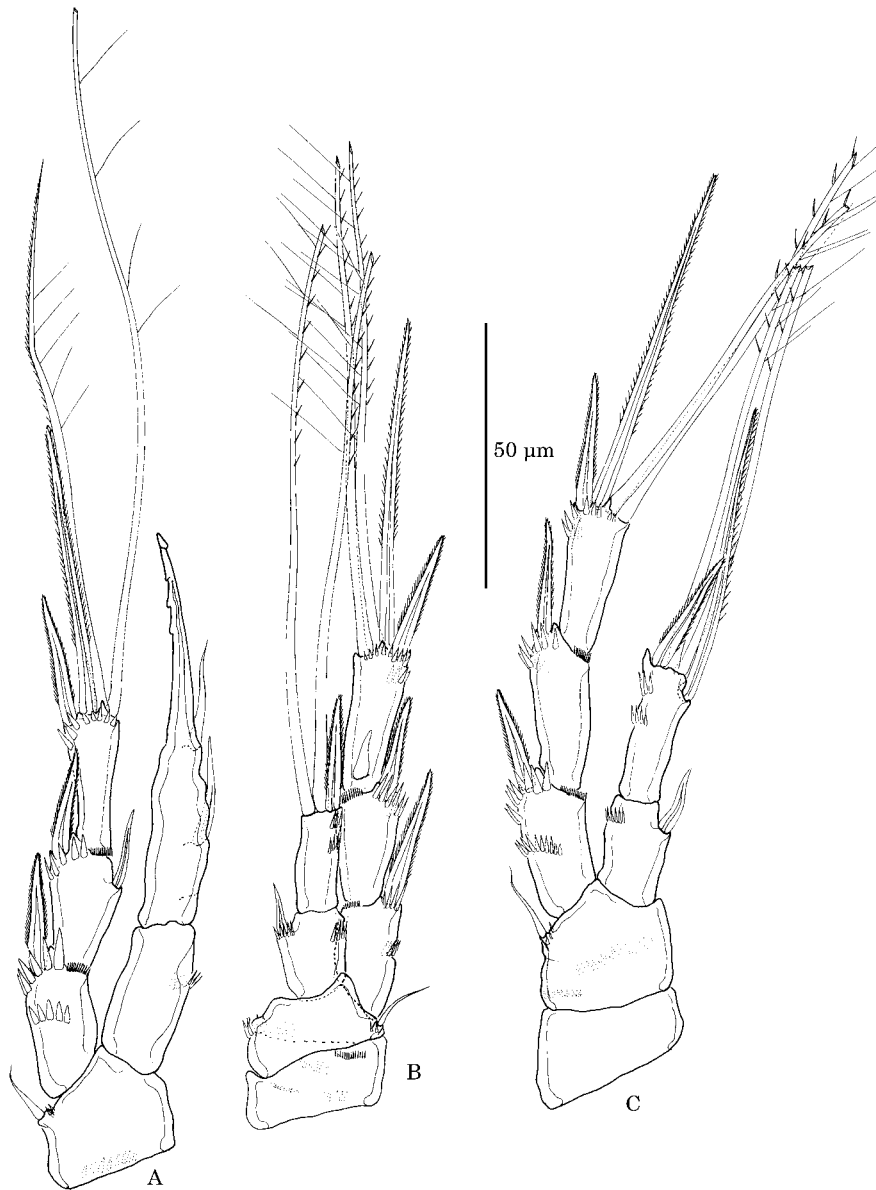
Figure 6. *Pabellonia olganoguerae* **sp. nov.**, male. A, P2; B, P3; C, P4.

bearing 2 slender and 1 plumose setae; basis as illustrated, with one seta. Endopodite represented by three setae.

Maxilliped (Fig. 2I): endopodal segment with 1 median seta, 1 subapical and 1 distal claw; furnished with 1 median and 1 apical row of spinules on outer edge.

Labrum and paragnaths as in Fig. 2J.

P1 (Fig. 3A): praecoxa furnished with two rows of small spinules close to outer distal corner; coxa ornamented with transverse row of small spinules and strong elements; basis with row of small spinules on posterior face, with strong spinules at

TABLE 1. Chaetotaxy of the female of **Pabellonia olganoguerae gen.nov., sp.nov.**

	P1	P2	P3	P4
EXO	0.0.121	0.1.121	0.0.121	0.0.121
END	0.111	0.121	1.111	1.121

base of outer spine and at base of exopodite anteriorly. Exopodite three-, endopodite two-segmented, with the latter reaching the joint between second and third exopodal segment. Chaetotaxy as in Table 1.

P2–P4 (Figs 3B, 4A, B): coxa of P2 massive and larger than in P3 and P4, not ornamented on anterior face; basis of P2 ornamented with small spinules in the middle and with a few anterior strong elements at base of exopodite, with two posterior transverse rows of spinules; basis of P3 and P4 barely ornamented with some spinules at base of outer seta. Exopodite three-, endopodite two-segmented, the latter reaching tip of second exopodal segment; first endopodal segment barely reaching tip of first exopodal component. Chaetotaxy as in Table 1.
P5 absent.

Male. Habitus and mouth parts (not illustrated) as in female.
Antennule (Fig. 5A), six-segmented, subchirocer.
P1 (Fig. 5B): protopodal components as in female, except for dimorphic inner spine and smaller outer element of basis. General structure of rami as in female, except for endopodite reaching proximal fourth of third exopodal segment.
P2 (Fig. 6A): protopodal components and exopodite as in female. Endopodite two-segmented; first endopodal segment reaching proximal third of second exopodal component; second segment as long as entire exopodite, terminating in acute dentate process, with 1 inner and 1 sub-apical seta.
P3 (Fig. 6B), as in female, except for relatively smaller inner and outer spine of first and second endopodal segment, and outer spine of second exopodal component; with hyaline proximal spine on third exopodal segment.
P4 (Fig. 6C), as in female, except for relatively smaller inner spine of first endopodal segment.
P5 and P6 absent.

Darcythompsonia, T. Scott, 1906

Darcythompsonia fairliensis (T. Scott, 1899)

(Figs 7–12)

Original description. Cylindropsyllus fairliensis T. Scott (1899: 258, figs 1–4, 11–14).

Synonyms. Darcythompsonia scotti Gurney, 1920 (Huys, Moore & Hamond, 1996: 210).

Distribution. Western coast of Norway (Sars, 1909); Scotland: Fifth of Clyde (Scott, 1899): Shetland Islands (Scott, 1906); Galapagos Islands (Mielke, 1982); Ireland (Roe, 1958); Italy: Venice (Kunz, 1960), 'Valli di Comacchio' (Ceccherelli & Rossin, 1979); Mexico: southeastern Gulf of California (present study).
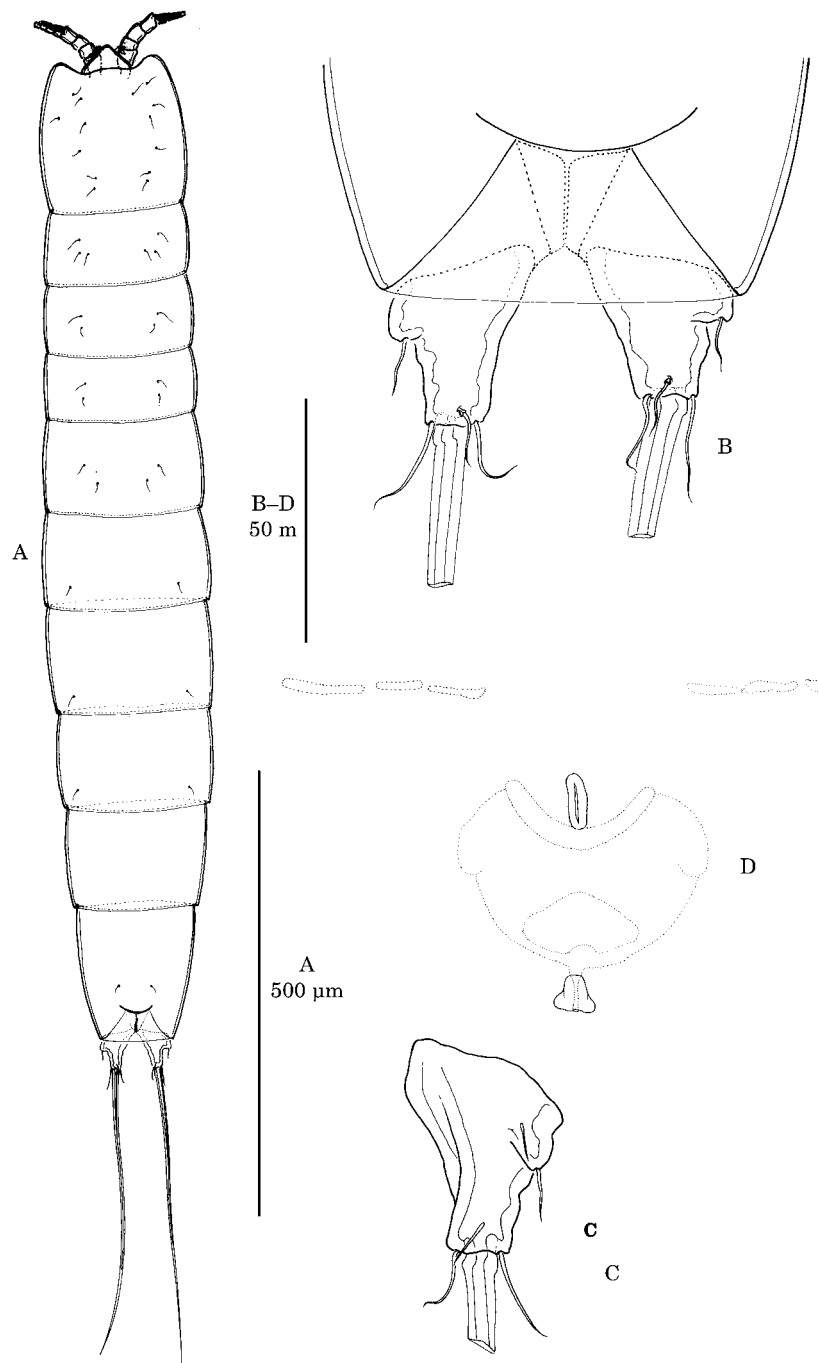
Figure 7. *Darcythompsonia fairliensis* T. Scott, 1899, female. A, habitus, dorsal; B, anal somite and caudal rami, dorsal; C, right caudal ramus, dorsal; D, genital field.
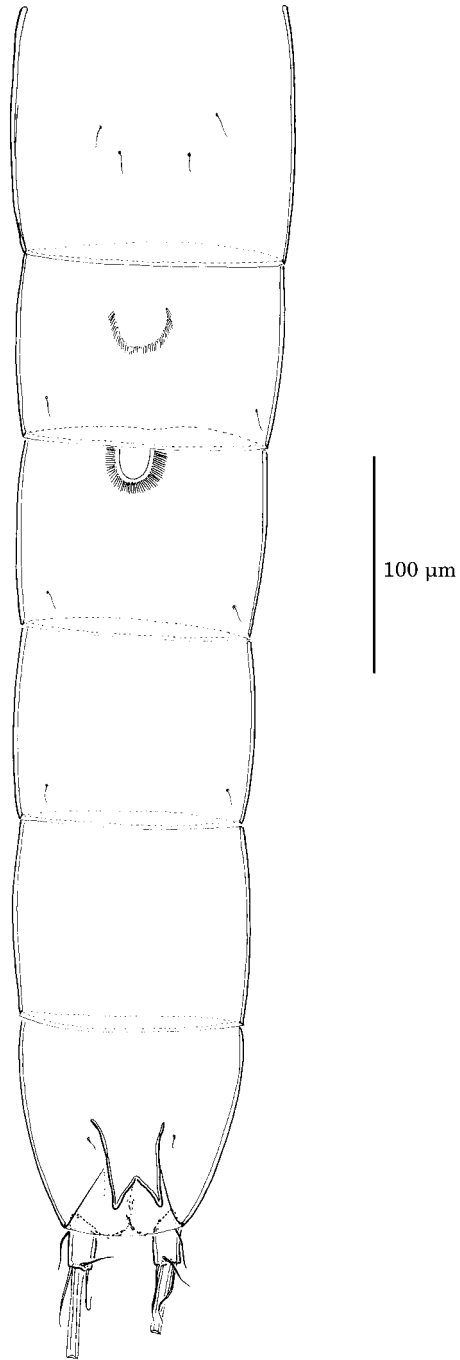
Figure 8. *Darcythompsonia fairliensis* T. Scott, 1899, male. Urosome, dorsal.
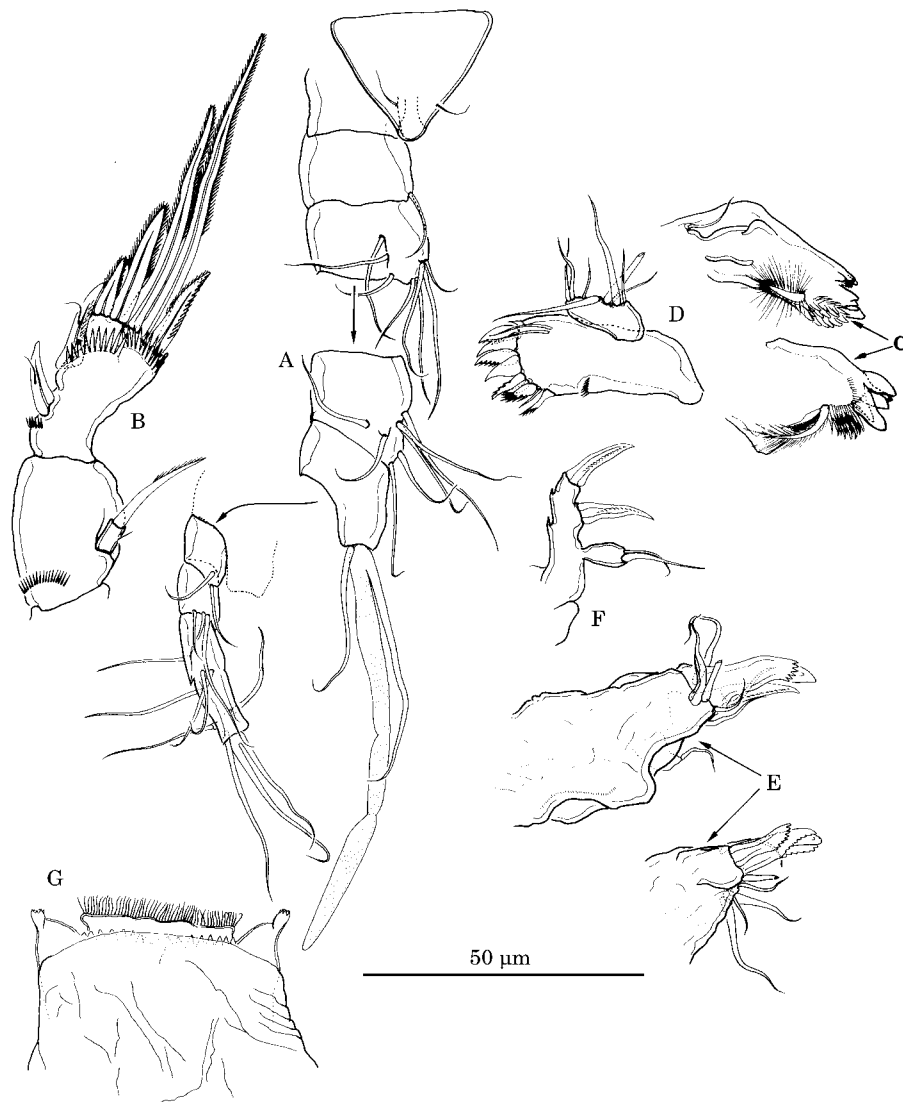
Figure 9. *Darcythompsonia fairliensis* T. Scott, 1899, female. A, rostrum and antennule, the latter exploded; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped; G, labrum.

Material examined. Found in station 6 (fine sand) and 10 (muddy bottom) (see Gómez-Noguera & Hendrickx, 1997), at 0–3 and 3–6 cm depth into the sediment, respectively. Taken with a 3 cm i. d. plastic corer, 22 and 23 June 1991. Eight dissected (EMUCOP-220691-02, EMUCOP-230691-004 to 09 and EMUCOP-230691-12) and 17 alcohol preserved females (EMUCOP-230691-02), two dissected (EMUCOP-230691-10, EMUCOP-230691-11) and five alcohol preserved males (EMUCOP-230691-03).

Discussion. Lang (1944), in his 'Monographie der Harpacticiden (vorläufige Mitteilung)', recognized three genera within Darcythompsoniidae: *Leptocaris, Horsiella,*
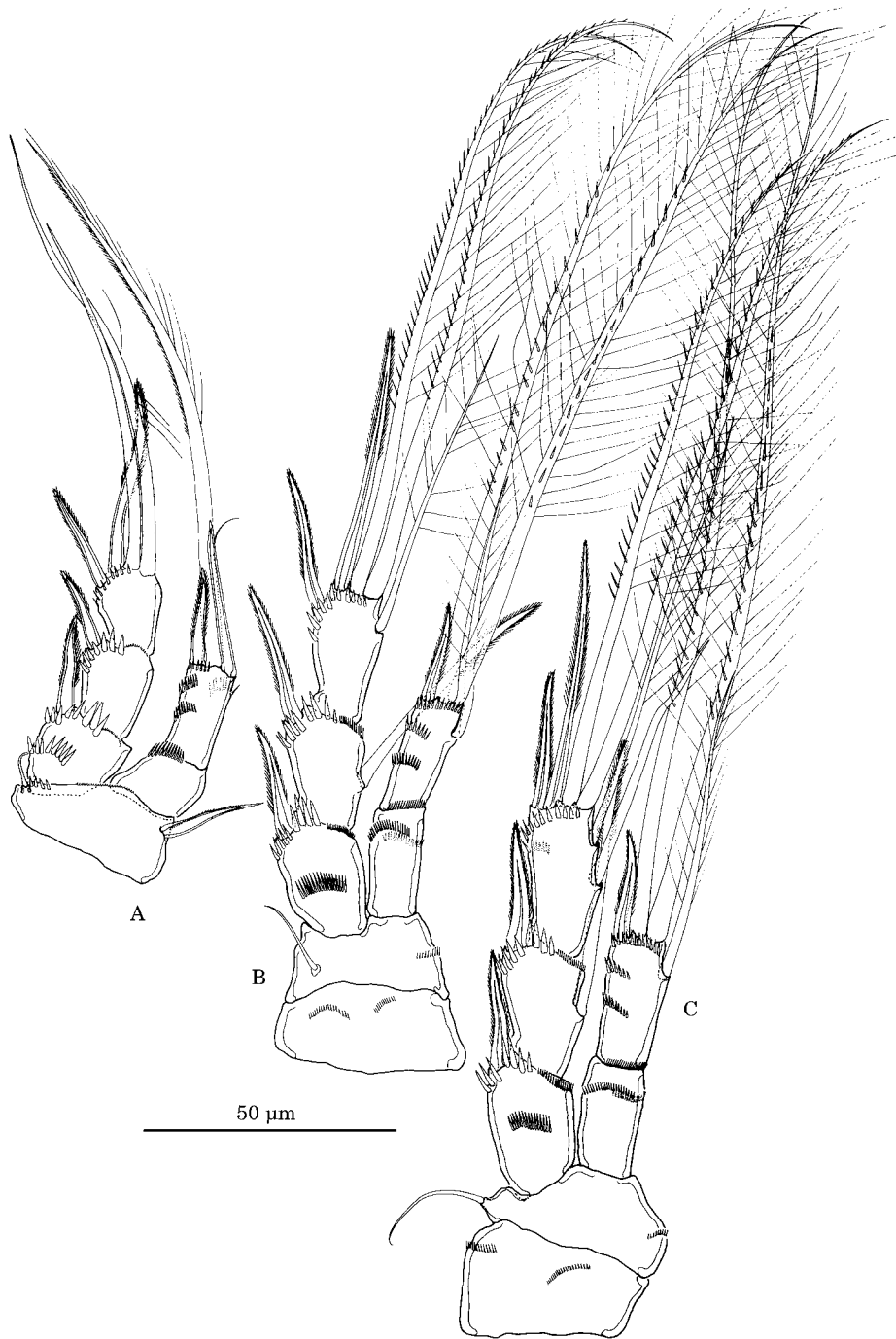
50 μm

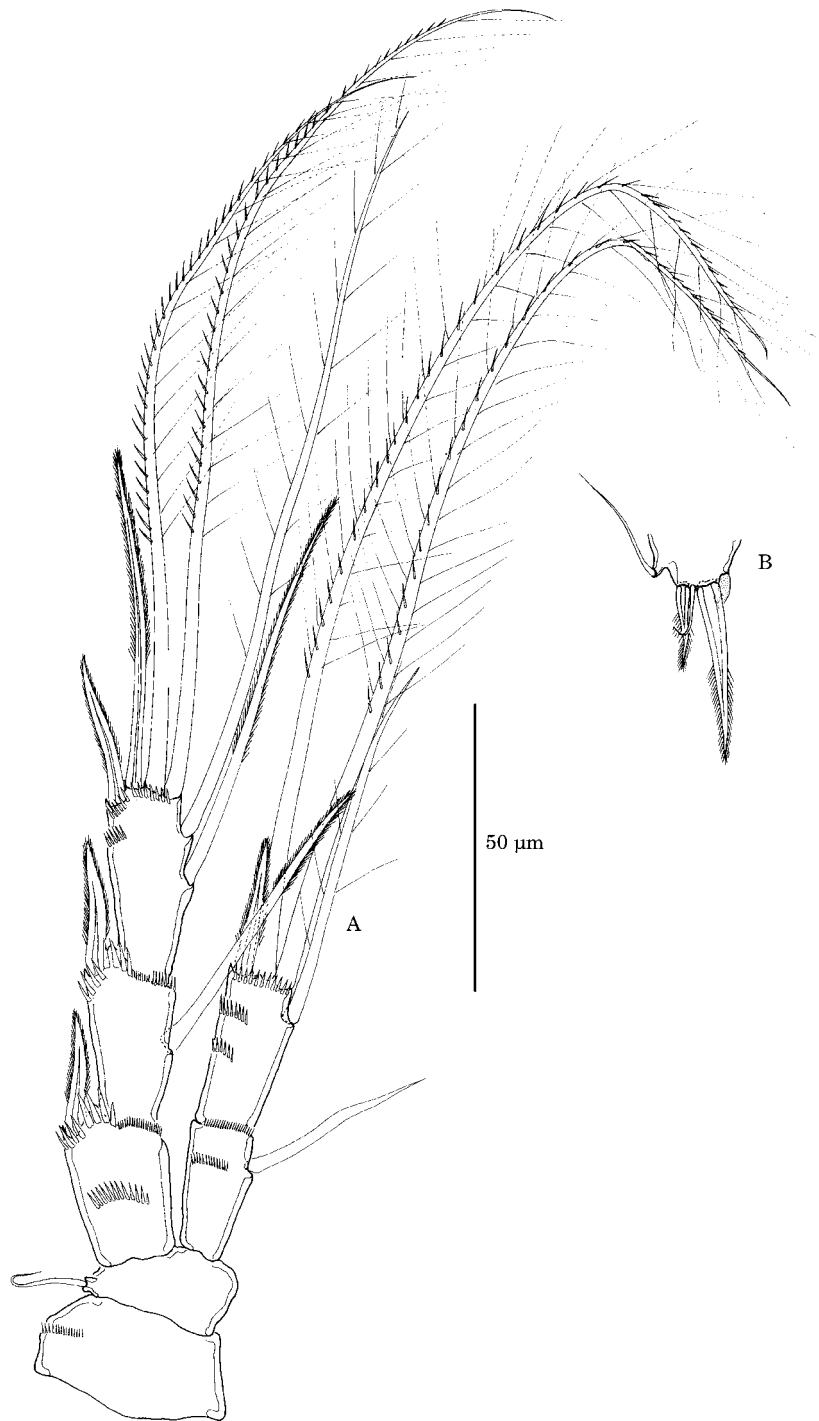Figure 10. *Darcythompsonia fairliensis* T. Scott, 1899, female. A, P1; B, P2; C, P3.

Figure 11. *Darcythompsonia fairliensis* T. Scott, 1899, female. A, P4; B, P5.
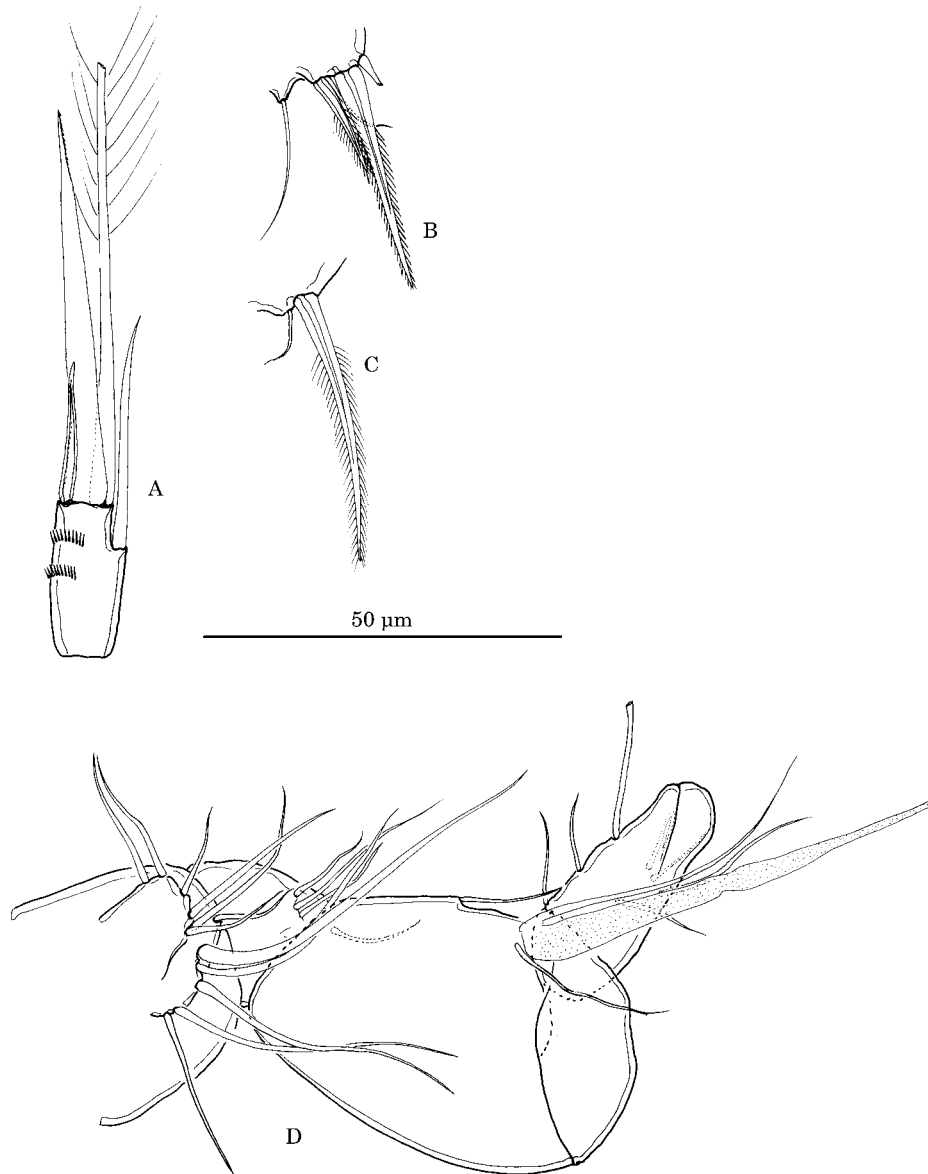
Figure 12. *Darcythompsonia fairliensis* T. Scott, 1899, male. A, P2 END 2; B, P5; C, P6; D, antennule.

and *Darcythompsonia*. Later, and based on the description of a number of species considered as transitions between *Leptocaris* and *Horsiella*, Kunz (1961) and Lang (1965) united the species of these two genera within *Leptocaris*. Presently, the family Darcythompsoniidae is composed of four genera: *Leptocaris, Darcythompsonia, Kristensenia* and *Falcocaris* (though the latter has not been diagnosed so far).

The genus *Leptocaris* has been distinguished principally by a lack of maxilliped (or if present, by it being reduced to a small triangular lobe), presence of an anteriorly directed inner seta with comb tip in the first endopodal segment of P1, mandible

without palp (or represented by a single seta), semi-circular anal operculum and cylindrical caudal rami in both sexes, and lack of any dimorphic features on second and third male urosomites.

On the other hand, the genus *Darcythompsonia* exhibits a moderately well developed maxilliped, lacks inner seta on the first endopodal segment of P1, exhibits a relatively well developed mandibular palp, and displays a series of sexually dimorphic features in (1) male second endopodal segment of P2, (2) anal operculum (semi-circular in female, markedly bifid in male), (3) caudal rami (expanded laterally in proximal half in female; cylindrical in male), and (4) second and third male urosomites with a fanshaped dorsal organ.

Por (1983) defined the so far monospecific genus *Kristensenia*. Although this genus (with *K. pallida* Por, 1983, as its only species) lacks some features usually associated with *Darcythompsonia* (dimorphic male second endopodal segment of P2, the dimorphic caudal rami, anal operculum and the fan-shaped dorsal organ on the second and third male urosomites), these two genera showed to be closely related as they share some other features such as shape of the body, antennal exopodite, maxillula, labrum, paragnaths and the reduced P5 (Por, 1983: 145).

Pabellonia olganoguerae gen.nov., sp.nov.

The new Mexican genus and species clearly belongs to the *Darcythompsonia–Kristensenia* clade as shown by the presence of a number of characters such as the shape of the maxilliped and mandibular palp, and the lack of inner element on the first endopodal segment of P1. *Pabellonia olganoguerae* gen.nov., sp.nov. shares the presence of a dimorphic male P2 END 2 with *Darcythompsonia* (though this dimorphism is different for each genus), whereas, as in *Kristensenia*, the Mexican representatives lack any dimorphic feature in the caudal rami, anal operculum and urosomites. On the other hand, *P. olganoguerae* gen.nov. sp.nov. is unique among the species within the *Darcythompsonia–Kristensenia–Pabellonia* clade by the absence of P5 and P6 in both male and female.

Darcythompsonia fairliensis T. Scott

Darcythompsonia fairliensis has been reported in disparate and, to some extent, isolated localities such as the Adriatic coast of Italy (Kunz, 1960; Ceccherelli & Rossin, 1979), north-eastern Atlantic (Scott, 1899, 1906; Sars, 1909; Roe, 1958), the Galapagos (Mielke, 1982) and the north-western Pacific coast of Mexico (present contribution) (see Fig. 13). The main differences among all the available descriptions (except for Roe [1958] where no comment was made on the armature of the swimming legs, and Kunz [1960] which included only a poor description of the male P5), involve the armature of the mandibular palp, caudal rami and P3 END 1. The Mexican specimens proved identical to previous descriptions except for the number of setae on the mandibular palp (one in the Mexican examples, two in Sars' [1911, fig. 217]), and setal armature of caudal rami (with lateral seta in the Mexican specimens, and without such seta in Sars' [1911, fig. 217] and Ceccherelli & Rossin's [1979: 100, fig. I.4]).

On the other hand, the Mexican specimens and those described by Sars (1909, 1911), Ceccherelli & Rossin (1979) and Mielke (1982), do not exhibit the inner seta on P3 END 1 as recorded by Lang (1948: 270, table 4). In fact, the Mexican specimens proved identical to those described in the Galapagos by Mielke (1982),
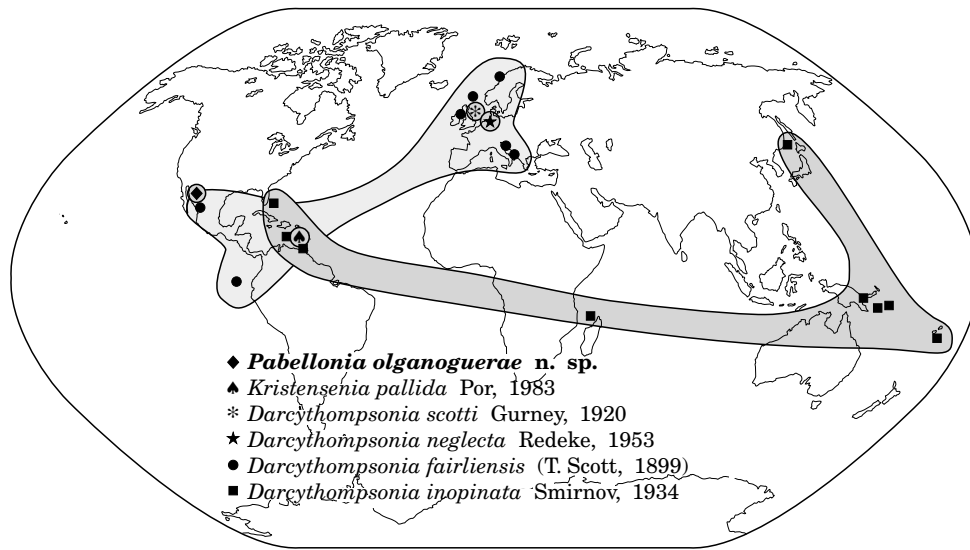
Figure 13. Range of *Darcythompsonia inopinata* Smirnov (after Smirnov, 1934; Fiers, 1986a, b; Yeatman, 1983; Por, 1983), *D. fairliensis* T. Scott (after Sars, 1909; T. Scott, 1899, 1906; Roe, 1958; Kunz, 1960; Ceccherelli & Rossin, 1979; Mielke, 1982; this paper), *D. neglecta* Redeke (after Redeke, 1953), *D. scotti* Gurney (after Gurney, 1920), *Kristensenia pallida* Por (after Por, 1983), and **Pabellonia olganoguerae sp. nov**. Notes: *D. scotti* has been considered as synonym of *D. fairliensis* (after Huys *et al.*, 1996); *D. radans* Por, 1983, has been considered as synonym of *D. inopinata* (after Fiers, 1986a).

especially when comparing the armature and structure of male and female P5, male P2 END 2, and armature of the mandibular palp (Mielke 1982: 470, fig. 3; 472, fig. 4, mixed the figures of P3 and P4).

REMARKS ON THE BIOGEOGRAPHY OF *DARCYTHOMPSONIA* T. SCOTT, 1906

There are four valid species within *Darcythompsonia* (*D. inopinata*, *D. neglecta* Redeke, 1953, *D. fairliensis*, and *D. scotti* Gurney, 1920). *D. inopinata* and *D. fairliensis* have been reported repeatedly (see Fig. 13), whereas *D. scotti* and *D. neglecta* have been reported only once (*D. scotti* has been considered as synonym of *D. fairliensis*, after Huys *et al.*, 1996; *D. radans* Por, 1983, has been considered as synonym of *D. inopinata* Smirnov, 1934, after Fiers, 1986a).

It seems reasonable to assume that the ancestral stock of *Darcythompsonia* could have originated in the equatorial Tethys Sea at sometime during the Late Triassic-Early Jurassic period (about 160 Myr BP). That this taxon has not been reported in the South Atlantic coasts of America and Africa supports the assumption that *Darcythompsonia* did not originate during the Late Jurassic-Cretaceous period, when the Southern Atlantic and the Tethys were connected by the continental drift of Africa and South America (see also Wing & Sues, 1992). It is plausible that, during the Late Jurassic period (about 135 Myr BP), the ancestral stock of *D. fairliensis* and *D. inopinata* were distributed along only a part of the Tethys shores, i.e. those corresponding to the north-eastern coast of South America, the Caribbean Sea, the

ancestral Mediterranean and the eastern North Atlantic, when these regions were much closer to each other (see Monge-Nájera, 1996: 163, fig. 3; Wing & Sues, 1992, fig. 6.3).

As pointed out by Fiers (1986a, b), and as Figure 13 shows, the present-day *D. inopinata* is distributed along the coasts of the Western Pacific and the Indian Ocean, but has been found also in the Bahamas, Netherlands Antilles and Venezuela. A similar distribution has been observed for the *chilensis*-group of the genus *Afrolaophonte* Chappuis, 1960 (Fiers, 1990), the genus *Sunaristes* Hesse, 1867 (Ho, 1988), some species of Scottolana Por, 1967 (pers. obs.), and some parabathynellids (Schminke, 1974). The biogeographical models used by the above mentioned authors to explain the distribution of these taxa, are also useful to understand and explain the present-day distribution of *D. inopinata*.

As stated above, the ancestral stock of *D. inopinata* was distributed along the Tethys shores corresponding to the north-east coast of South America, the Caribbean Sea, the ancestral Mediterranean and the eastern North Atlantic. Probably, the populations inhabiting the proto-Mediterranean dispersed through the Indo-Pacific during the Mid Cretaceous-Early Tertiary and reached the north-western coast of Madagascar (the present-day Grand Comores Archipelago) and the ancestral Malaysian Peninsula. The present Indonesian Arc originated from the disruption of the ancestral Malaysian Peninsula that could have worked as a land bridge for further colonization of the Sea of Japan on the one hand and Papua New Guinea, Samoa, the Solomon Islands and the Fiji Islands on the other hand, probably during the Mid Tertiary period (Monge-Nájera, 1996).

The historical biogeography of *D. fairliensis* is similar to that observed for some other harpacticoid taxa such as some species of *Leptastacus* T. Scott, 1906 (Huys, 1992), and *Longipedia* Claus, 1863 (pers. obs.) and follows a track, to some extent, similar to Rosen's (1975) Eastern Atlantic (West African)-Caribbean track and Stock's (1993: 808, fig. 4) Amphi-Atlantic/eastern Pacific track. As suggested above for *D. inopinata*, the ancestral *Darcythompsonia fairliensis* was probably distributed along only a part of the Tethys shores during the Late Jurassic-Early Cretaceous period (about 135 Myr BP), well before the opening of the Atlantic Ocean. In this area we can find also *D. neglecta* and *D. scotti* (the latter is a synonym of *D. fairliensis*, after Huys *et al.*, 1996). Nevertheless it is still unknown why these populations did not migrate through the Indo-Pacific region. On the other hand, the absence of this species in the Indo-Pacific region could be due to lack of work in that area. Whatever the case might be, it is reasonable to assume that *D. fairliensis* reached the north-western coast of South America (along-shore dispersal is presumed) well before the consolidation of the Central American Isthmus sometime during the Early Tertiary period (about 65 Myr BP) (see Malfait & Dinkelman, 1972; Rosen, 1975). Once in the north-western coast of South America, about 40 Myr BP (Early Oligocene), when the ancestral Galapagos originated as a series of islands, *D. fairliensis* would have had "little difficulty negotiating the short span of water to a new volcanic island as an older extinct volcanic island drifted eastward and subsided beneath the sea" (Holden & Dietz, 1972). Alongshore dispersal would also explain the presence of this species in the mouth of the Gulf of California.

During the early 1970s and early 1980s, McKenna, (1972), (Strauch 1970, 1983) and Friedrich & Simonarson (1981) presented evidence on the existence of a land-bridge (Thule-Land bridge) that might have connected Europe and North America during the Eocene or even during the transition Pliocene-Pleistocene period, through

Scotland, the Faroes, Iceland and Greenland. Huys (1992) used this evidence to explain the presence of the *spatuliseta*-group of the genus *Leptastacus* (Harpacticoida, Leptastacidae) in the North Sea coast of The Netherlands (*L. pygmaeus* Huys), along the coast of Massachusetts and South Carolina (Atlantic coast of North America) (*L. coulli* Huys) and of the Galapagos (*L. spatuliseta* Mielke). However, there is no evidence on the existence of this species-group in Iceland or Greenland to support this model. Besides, it "does not explain how the oceanic gap between the Galapagos and Central America could have been bridged" (Huys, 1992). The scenario presented to explain the present distribution of *D. fairliensis* seems to be more parsimonious in explaining the distribution of this species and of the *spatuliseta*-group as defined by Huys, (1992). The models presented herein are based on Sterrer's (1973) hypothesis. As such, these models would suggest very slow speciation that can be best explained by low numbers of progeny in harpacticoids and the absence of adaptive speciation (continental drift does not produce a sharp change in the type of habitat) (see Sterrer, 1973: 214–215).

ACKNOWLEDGEMENTS

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