A new species of *Pontonia* Latreille, 1829 (Crustacea, Decapoda, Palaemonidae) associated with sea squirts (Tunicata, Ascidiacea) from the Pacific coast of Panama

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ABSTRACT

Pontonia panamica n. sp., is described on the basis of 14 specimens from the Pacific coast of Panama. The new species associates with sea squirts, *Ascidia* cf. *interrupta* Heller, 1878 (Ascidiidae) attaching underneath rocks partly submerged in silty sand in the lower intertidal. *Pontonia panamica* n. sp. is closely related to *P. longispina* Holthuis, 1951 from the Gulf of California, but can be distinguished from the latter species by the absence of a subdistal tooth on the ventral margin of the rostrum; the more developed distolateral tooth on the first antennular segment; the longer proximal segments in the endopod of the second maxilliped; the dactylus of the minor cheliped with one simple triangular tooth on the cutting edge; and the comparatively longer carpi of both minor and major chelipeds. The recently proposed phylogeny of *Pontonia* (Fransen 2002) and the association of *P. panamica* n. sp. with an ascidian host suggest a host switch from Ascidiacea to Mollusca relatively early in the evolutionary history of this genus.

KEY WORDS
Crustacea,
Decapoda,
Caridea,
Palaemonidae,
Pontoniinae,
Pontonia,
eastern Pacific,
Panama,
symbiosis,
ascidians,
host switch,
new species.

RÉSUMÉ

Une nouvelle espèce de Pontonia *Latreille, 1829 (Crustacea, Decapoda, Palaemonidae) associée à des ascidies (Tunicata, Ascidiacea) de la côte Pacifique du Panama.*

Pontonia panamica n. sp. est décrite d'après 14 spécimens récoltés sur la côte Pacifique du Panama. La nouvelle espèce vit en association avec les ascidies, *Ascidia* cf. *interrupta* Heller, 1878 (Ascidiidae), qui s'attachent sur la surface inférieure des roches partiellement enfoncées dans le sable fin dans la partie basse de la zone des balancement des marées. *Pontonia panamica* n. sp. est très proche de *P. longispina* Holthuis, 1951 du Golfe de Californie; cependant, elle peut être séparée de cette dernière espèce par l'absence d'un denticule subdistal sur le bord ventral du rostre; le premier segment antennulaire avec un denticule plus marqué; l'endopodite du deuxième maxillipède avec les segments proximaux plus allongés; le bord coupant du dactyle du deuxième chélipède muni d'une dent triangulaire simple; et les carpes des petit et grand chélipèdes qui sont comparativement plus allongés. Dans le contexte de l'hypothèse phylogénétique du genre *Pontonia* récemment proposée par Fransen (2002), l'association de *P. panamica* n. sp. avec une ascidie pourrait indiquer un changement de groupe d'hôtes, des Ascidiacea vers les Mollusca, assez tôt dans l'histoire évolutive de ce genre.

MOTS CLÉS
Crustacea,
Decapoda,
Caridea,
Palaemonidae,
Pontoniinae,
Pontonia,
Pacifique est,
Panama,
symbiose,
ascidies,
changement d'hôtes,
espèce nouvelle.

INTRODUCTION

The pontoniine shrimp genus *Pontonia* Latreille, 1829, as redefined by Fransen (2002), presently includes 10 species. Five species (*P. margarita* Smith, 1869, *P. pinnae* Lockington, 1878, *P. chimaera* Holthuis, 1951, *P. longispina* Holthuis, 1951 and *P. simplex* Holthuis, 1951) are known exclusively from the eastern Pacific; two species (*P. domestica* Gibbes, 1850 and *P. mexicana* Guérin, 1856) are restricted to the western Atlantic; two species (*P. pinnophylax* (Otto, 1821) and *P. pilosa* Fransen, 2002) are found only in the eastern Atlantic; finally, one species (*P. manningi* Fransen, 2000) occurs on both sides of the Atlantic Ocean (Holthuis 1951, specimens identified as *P. margarita* Smith, 1869; Fransen 2002). Most species live symbiotically inside the mantle cavity of lamellibranch bivalves, mainly fan clams (Pinnidae) and pearl oysters (Pteriidae), although one species, *P. chimaera*, associates with the large gastropod *Strombus galeatus* Swainson, 1823 (Holthuis 1951). The host of *P. longispina*, presently known only from two specimens from the Gulf of California, remains unknown. However, Fransen (2002) noted that *P. longispina* is morphologically intermediate between *Pontonia* and its sister genus, *Ascidonia* Fransen, 2002, which includes species associated with ascidians.

During a survey of intertidal shrimps at Playa Venao, about 10 km west of Panama City on the Pacific coast of Panama, the authors collected numerous specimens of an ascidian-associated species presenting all features of *Pontonia* (*sensu* Fransen 2002). A close inspection revealed that these specimens belong to an undescribed species closely related to *P. longispina*. This species is herein described as new.

Postorbital carapace length (pcl, in mm) and total body length (tbl, in mm) are used as standard measurements. The type material is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Oxford University Museum of Natural History, Oxford (OUMNH); Nationaal Natuurhistorisch Museum, Leiden (RMNH), and Colección de Referencia, Deparamento de Biología Marina, Universidad de Panamá, Panama City (UP).

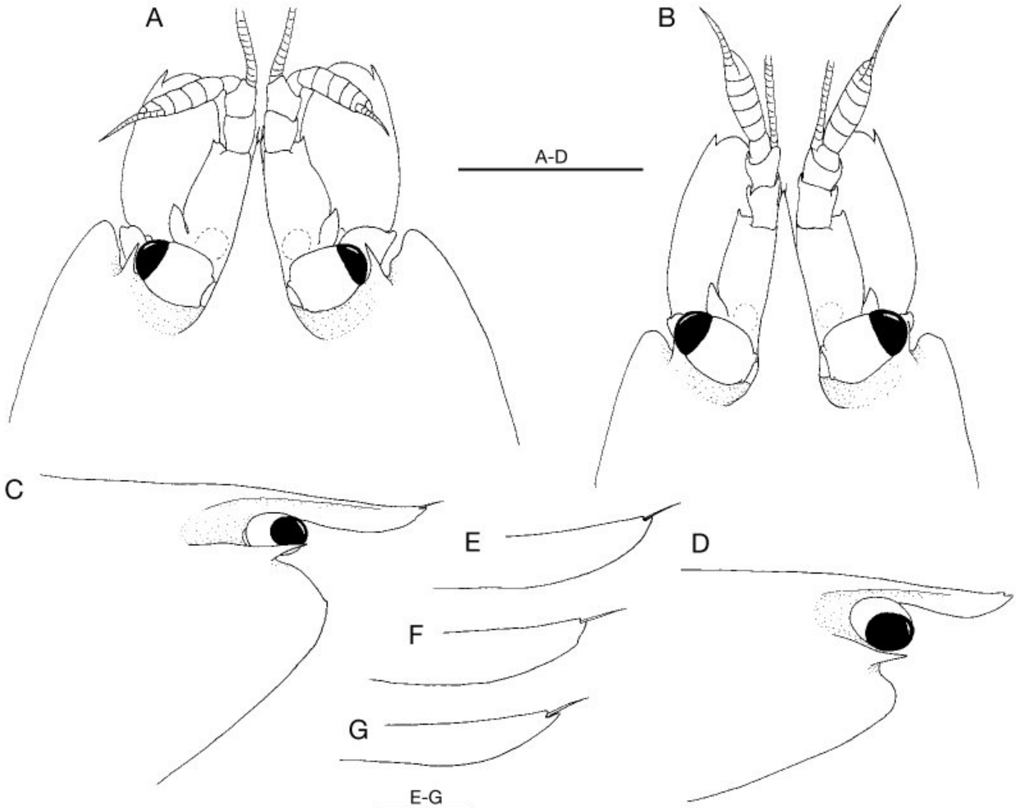

FIG. 1. — *Pontonia panamica* n. sp.: **A**, **B**, anterior part of carapace, dorsal view; **C**, **D**, anterior part of carapace, lateral view; **E**-**G**, distal rostrum; **A**, **E**, ♀ holotype, pcl 7.4 mm (MNHN-Na 16392); **B**, ♂ allotype, pcl 5.5 mm (MNHN-Na 16393); **C**, **F**, ♀ paratype, pcl 6.0 mm (MNHN-Na 16394); **D**, **G**, ♂ paratype, pcl 4.8 mm (MNHN-Na 16394). Scale bars: 1 mm.

SYSTEMATICS

Family PALAEMONIDAE Rafinesque, 1815
Subfamily PONTONIINAE Kingsley, 1878
Genus *Pontonia* Latreille, 1829

Pontonia panamica n. sp.
(Figs 1-7)

TYPE MATERIAL. — Holotype: Panama, Playa Venao, 10 km west of Panama City, lower rocky intertidal, silty sand with large rocks, in ascidian, *Ascidia* cf. *interrupta*, attached under rocks, close to water-line at low tide, coll. I. Marin, 18.IV.2007, 1 ovig. ♀, pcl 5.5 mm (MNHN-Na 16392). Allotype: same data as holotype, 1 ♂, pcl 7.4 mm (MNHN-Na 16393).
Paratypes: Panama, Playa Venao, 10 km west of Panama City, lower rocky intertidal, silty sand with large rocks, in ascidians, *Ascidia* cf. *interrupta*, attached under rocks, close to water-line at low tide, coll. I. Marin and A. Baeza, 20.IV.2007, 1 ovig. ♀, pcl 6.0 mm, 1 ♂, pcl 4.8 mm [dissected] (MNHN-Na 16394); 1 ovig. ♀, pcl 7.5 mm, 1 ♂, pcl 6.0 mm (USNM 1103080); 1 ovig. ♀, pcl 5.2 mm, 1 ♂, pcl 4.9 mm (OUMNH-ZC 2007-13-030); 1 ovig. ♀, pcl 7.6 mm, 1 ♂, pcl 5.4 mm (OUMNH-ZC 2007-13-030); 1 ovig. ♀, pcl 6.7 mm, 1 ♂, pcl 5.4 mm (USNM 1103082); 1 ovig. ♀, pcl 6.5 mm, 1 ♂, pcl 4.2 mm (RMNH D 51824); 1 ovig. ♀, pcl 7.5 mm, 1 ♂, pcl 4.2 mm (RMNH D 51825); 1 ovig. ♀, pcl 7.2 mm, 1 ♂, pcl 4.7 mm (UP).

ETYMOLOGY. — The new species is named after the country of the type locality, Panama.

TYPE LOCALITY. — Playa Venao, Pacific coast of Panama.

DISTRIBUTION. — Presently known only from the type locality on the Pacific coast of Panama.

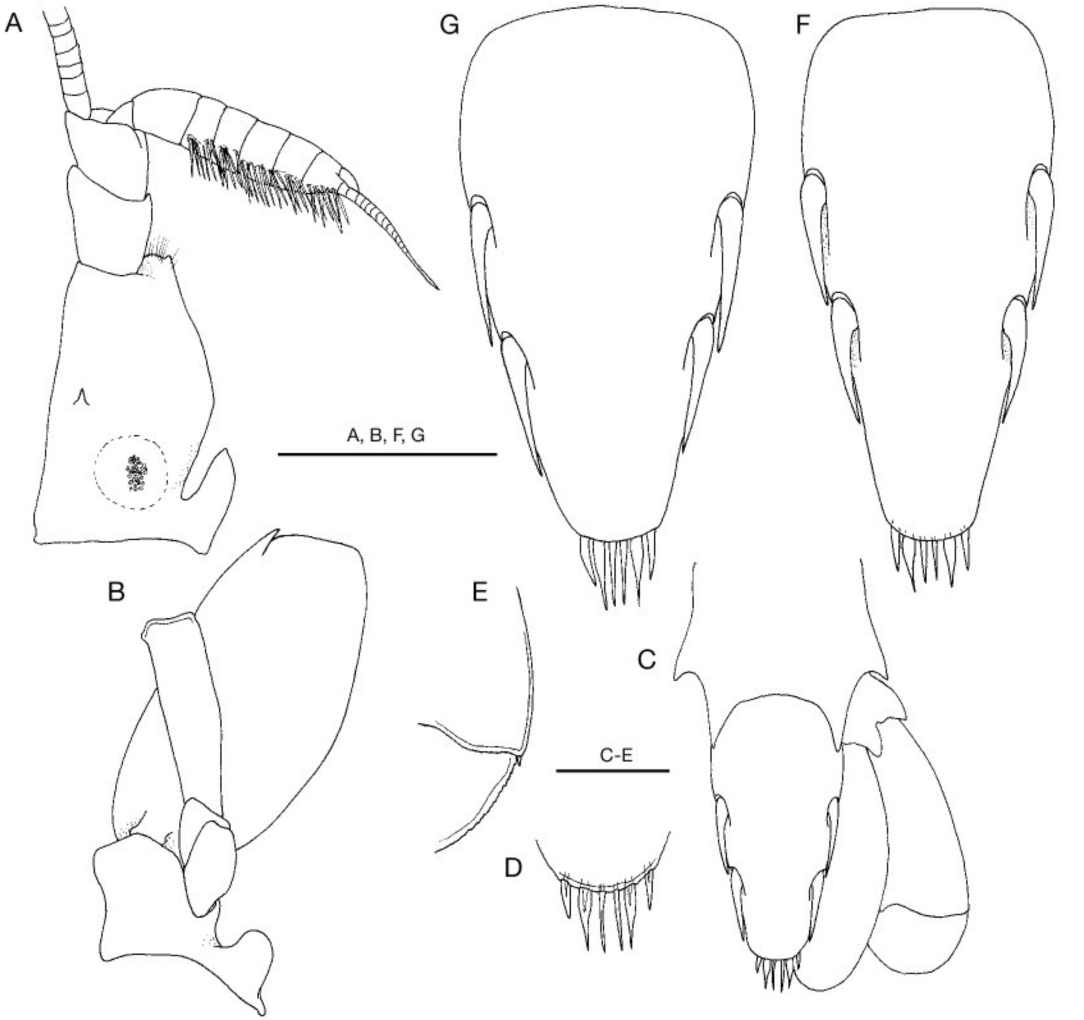

FIG. 2. — *Pontonia panamica* n. sp.: **A**, antennule, ventral view; **B**, antenna, ventral view; **C**, telson and uropods, dorsal view; **D**, posterior margin of telson, dorsal view; **E**, distolateral margin of uropodal exopod, dorsal view; **F**, **G**, telson, dorsal view; **A**-**E**, ♀ paratype, pcl 6.0 mm (MNHN-Na 16394); **F**, ♂ paratype, pcl 4.8 mm (MNHN-Na 16394); **G**, ♀ paratype, pcl 6.0 mm (USNM 1103080). Scale bars: 1 mm.

DESCRIPTION (based on female holotype)
Large-sized pontoniine shrimp with depressed, somewhat expanded body (Fig. 7). Carapace swollen, smooth, with well-developed acute antennal tooth. Rostrum (Fig. 1A-D) long and slender, reaching to midlength of second segment of antennular peduncle, with slightly marked lateral carina and ventral carina distally; tip (Fig. 1E-G) with small subdistal tooth and two long smooth setae dorsally, without distinct subdistal tooth ventrally.

Abdominal somites (pleomeres) smooth; tergites non-carinate, not posteriorly produced; pleura of first to fifth pleomere posteroventrally rounded. Telson (Fig. 2C, G, F) about twice as long as wide proximally, tapering distally, with two pairs of stout dorsal spines, each about 0.3 telson length, inserted at about 0.4 and 0.6 telson length, respectively; pos-

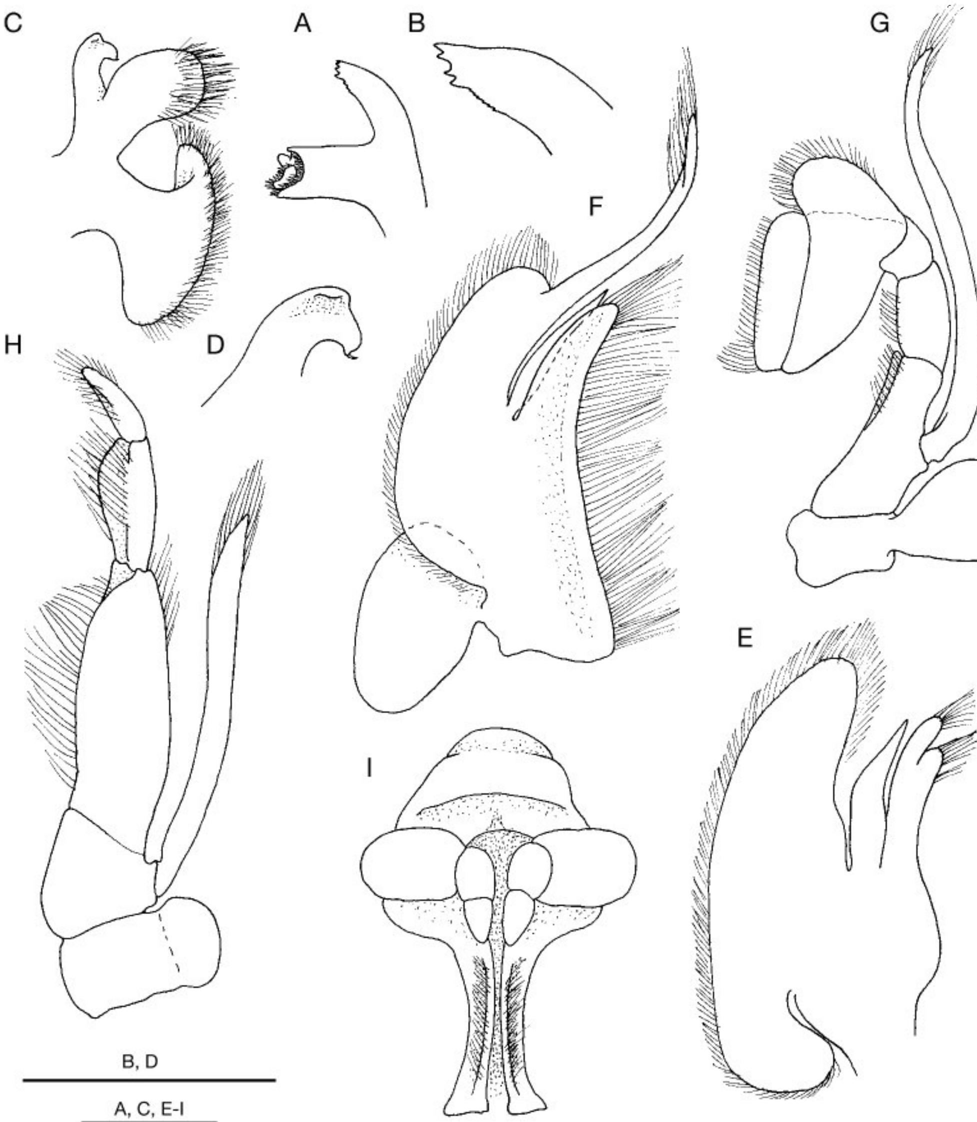

FIG. 3. — *Pontonia panamica* n. sp., ♀ paratype, pcl 6.0 mm (MNHN-Na 16394): **A**-**H**, lateral view; **A**, mandible; **B**, same, distal margin of incisor process; **C**, maxillule; **D**, same, distal margin of palp; **E**, maxilla; **F**, first maxilliped; **G**, second maxilliped; **H**, third maxilliped; **I**, paragnath, ventral view. Scale bars: 1 mm.

terior margin broadly rounded, with three pairs of relatively long, slender spines, intermediate spines longest (Fig. 2D).

Eyes fairly large, with rounded cornea; basal portion of eyestalks exposed.

Antennules (Fig. 2A) with first peduncular segment about twice as long as maximum width, with small ventromesial tooth and well-defined acute distolateral tooth; lateral margin distinctly convex; stylocerite distally acute, reaching to about 0.3 of first segment; second and third segments stout, unarmed, rectangular; lateral flagellum thick, main ramus with six segments, accessory ramus with one segment; mesial flagellum filiform, with more

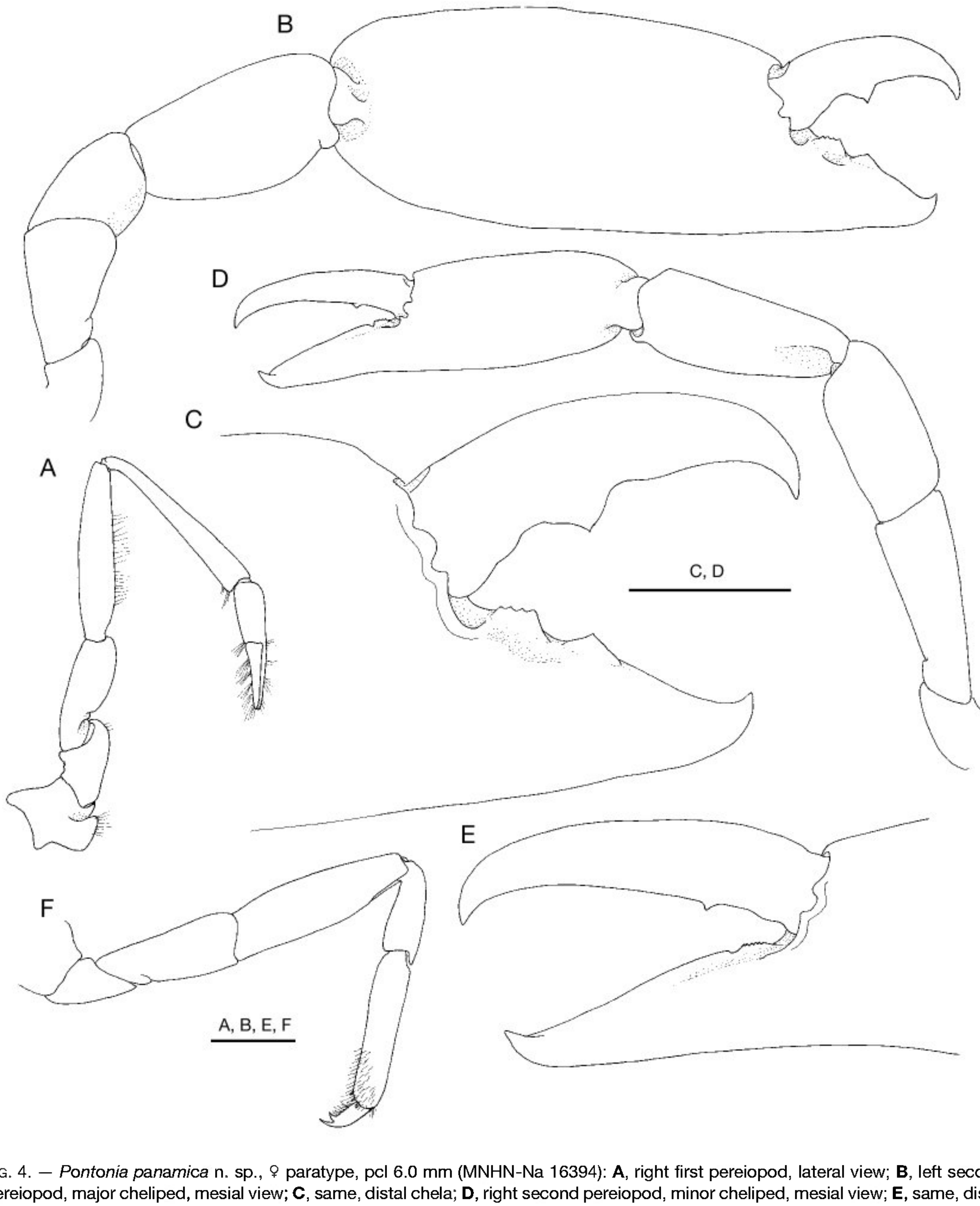

Fig. 4. — *Pontonia panamica* n. sp., ♀ paratype, pcl 6.0 mm (MNHN-Na 16394): **A**, right first pereiopod, lateral view; **B**, left second pereiopod, major cheliped, mesial view; **C**, same, distal chela; **D**, right second pereiopod, minor cheliped, mesial view; **E**, same, distal chela; **G**, left third pereiopod, mesial view. Scale bars: 1 mm.

than 30 segments. Antenna (Fig. 2B) with distolateral margin of basicerite unarmed; scaphocerite subrectangular, slightly exceeding antennular peduncle, twice as long as maximum width; distal margin of blade protruding, forming blunt angle; distolateral tooth well-developed, not exceeding blade; carpocerite reaching about 0.7 length of scaphocerite.

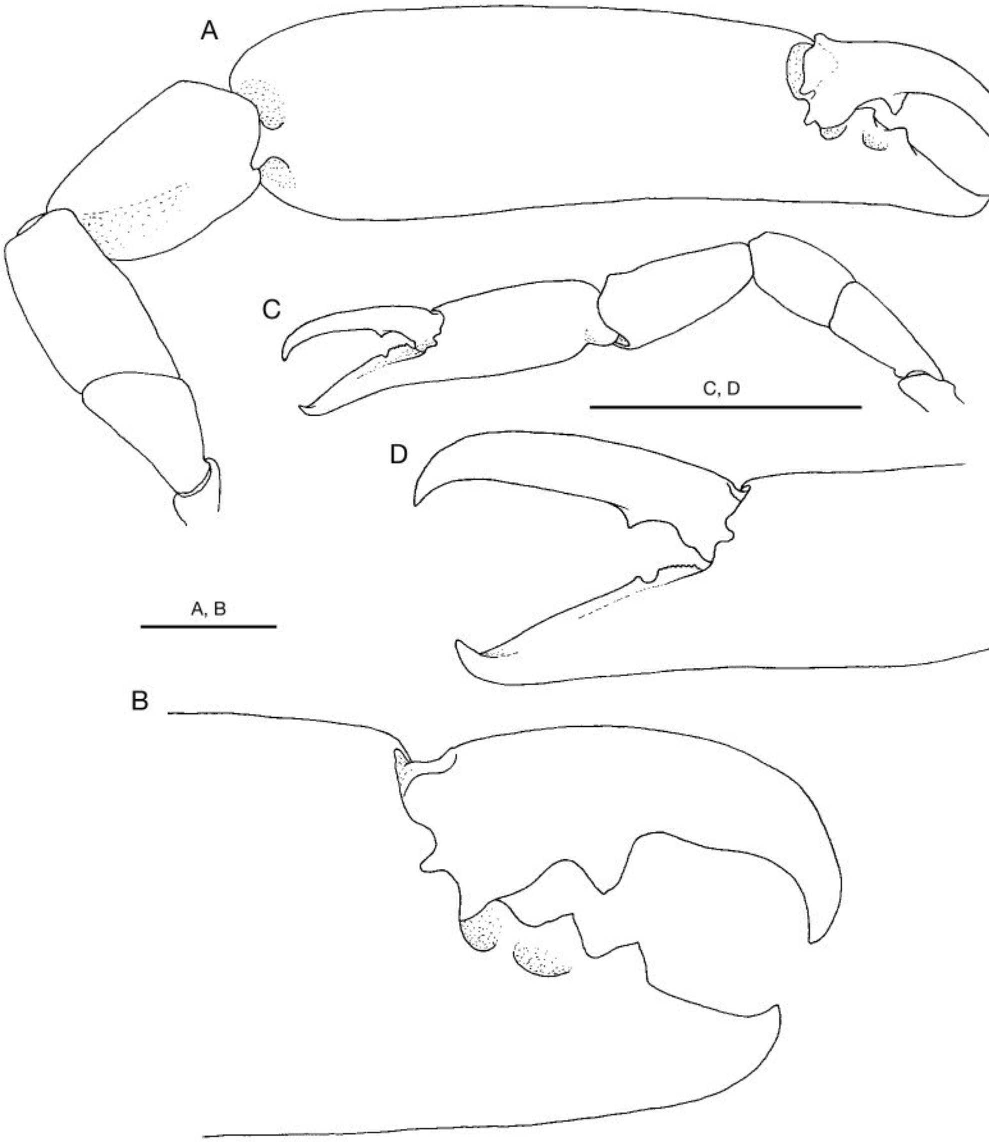

FIG. 5. — *Pontonia panamica* n. sp., ♂ paratype, pcl 4.8 mm (MNHN-Na 16394): **A**, left second pereiopod, major cheliped, mesial view; **B**, same, distal chela; **C**, right second pereiopod, minor cheliped, mesial view; **D**, same, distal chela. Scale bars: 1 mm.

Epistome with blunt medial carina; labrum oval. Paragnath (Fig. 3I) well-developed, alae with large subcircular distal lobes and small ovate ventromedial lobes; corpus with medial groove bordered by parallel submedial setose carina.

Mandible (Fig. 3A) without palp; incisor process slender, not tapering distally, with four large stout subtriangular teeth distally and row of minute teeth along distolateral margin (Fig. 3B); molar process well-developed, stout. Maxillule (Fig. 3C) with well-developed, bilobed palp, dorsal lobe of palp proximally excavated, ventral lobe with short, distally curved seta (Fig. 3D); ventral lacinia significantly larger than dorsal lacinia, broadened, with simple setae distoventrally and marginally; dorsal lacinia broad, distally rounded and with serrulate spines and numerous simple setae. Maxilla (Fig. 3E) with well-developed, distally tapering, simple palp; basal endite simple, distally rounded, furnished with stiff, elongated setae; coxal endite well-developed, distally rounded, furnished with long simple setae; scaphognathite moderately broad. First maxilliped (Fig. 3F) with completely fused basal and coxal endites; palp slender, pointed distally, without distal setae; exopod with expanded caridean lobe; epipod oval. Second maxilliped (Fig. 3G) with slender proximal segments; distolateral margin of propodus broadly rounded, with slender setae; dactylus about three times as long as broad, with numerous spines along distal margin; exopod and epipod well-developed, latter oval-shaped; podobranch absent. Third maxilliped (Fig. 3H) relatively stout; coxa with rounded epipod; antepenultimate segment stout, basis and ischiomerus clearly separated by oblique suture; penultimate segment with convex mesioventral margin, about three times as long as wide; ultimate segment markedly more slender than penultimate segment, about three times as long as wide, tapering distally; exopod reaching almost midlength of penultimate segment; arthrobranch absent.

First pereiopod (Fig. 4A) slender, segments unarmed; basis about 1.5 times as long as wide; ischium about three times as long as wide; merus slender, about four times as long as wide, with simple setae along mesiolateral margin; carpus slender, widening distally, slightly longer than merus, six times as long as distal width; palm about twice as long as wide, subcylindrical in cross-section; fingers subcylindrical, slender, about four times as long as wide proximally, with simple tips and straight cutting edges.

Second pereiopods (chelipeds) unequal in size, subsymmetrical in shape (Fig. 6). Major cheliped (Fig. 4B) with rectangular basis; ischium about twice as long as maximum width; merus stout, about 1.5 times as long as maximum width; carpus about 1.8 times as long as maximum width, rounded distally; palm subcylindrical, about twice as long as maximum width, fingers robust, about 2.5 times length of palm; pollex (Fig. 4C) robust, tapering, about 1.3 times as long as wide, with two large triangular teeth in proximal half; tip acute, curved; dactylus subcylindrical, curved, with well-marked cutting edge bearing large triangular tooth near midlength, tip acute, curved. Minor cheliped (Fig. 4D) with rectangular basis; ischium about three times as long as maximum width; merus stout, about twice as long as maximum width; carpus relatively slender, about 2.5 times as long as maximum width, rounded distally; palm flattened, about twice as long as wide, fingers slender, subequal to palm length; pollex (Fig. 4E) slender, about three times as long as wide, cutting edge well-defined, proximally with finely serrated (distal margin with about seven minute acute denticles) tooth, followed by small rounded hiatus; tip acute, curved; dactylus (Fig. 4E) with well-defined cutting edge bearing one medium-sized, simple tooth at about proximal 0.3 dactylus length.

Third pereiopod (Fig. 4F) relatively stout; basis rectangular; ischium about 2.5 as long as wide; merus about three times as long as wide; carpus about half as long as merus, about three times as long as wide, with slightly projecting distodorsal margin; propodus four times as long as wide, distally with numerous simple setae and three small distoventral spines; dactylus (Fig. 6A) biunguiculate, about three times as long as wide, with numerous simple, proximally curved setae on distal and ventral margins; accessory unguis well-developed, simple, acute; main unguis slender, smooth, acute. Fourth and fifth pereiopods similar to third.

Pleopods without specific features. Uropods (Fig. 2C) exceeding telson; lateral margin of uropodal exopod with small distolateral spine but without distolateral tooth.

Male allotype smaller in size, more slender (Fig. 7), with distinctly longer, more robust, more markedly unequal and asymmetrical chelipeds (Figs 5A, C; 7); major cheliped (Fig. 5A, B) with relatively longer palm, about 3.5 times as long as wide, with fingers about 0.4 times palm length; minor cheliped (Fig. 5C, D) similar to that of female; endopod of first pleopod fringed with setae along margins, including one subdistal seta (Fig. 6D); endopod of second pleopod (Fig. 6B) with well-developed appendix interna and appendix masculina, latter furnished with at least six slender setae distally and one subdistal seta (Fig. 6C).

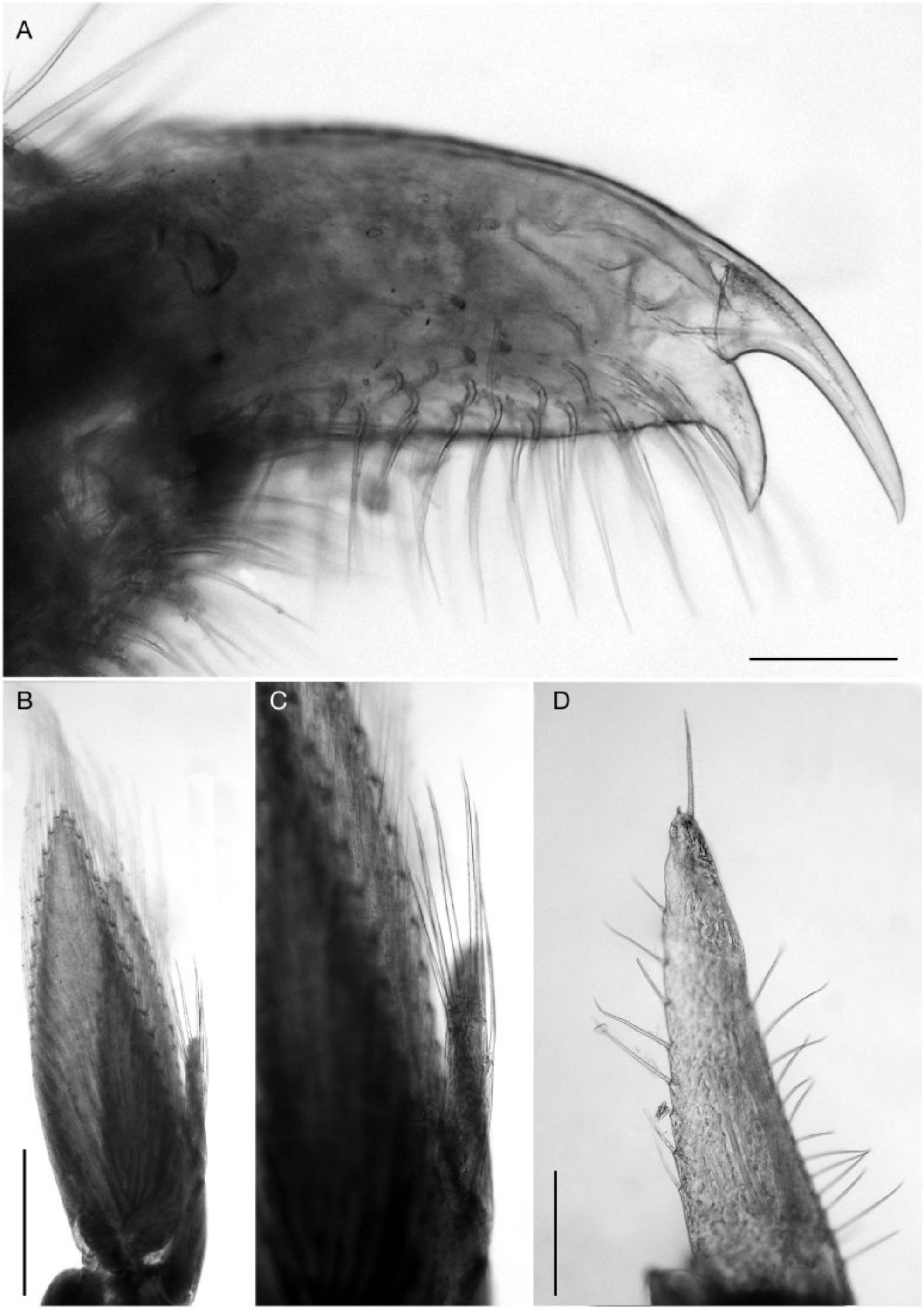

FIG. 6. — *Pontonia panamica* n. sp., ♂ paratype, pcl 4.8 mm (MNHN-Na 16394): **A**, third pereiopod dactylus; **B**, second pleopod, lateral view; **C**, same, detail of appendix masculina; **D**, endopod of first pleopod, mesial view. Scale bars: A, D, 0.1 mm; B, 0.3 mm.

FIG. 7. — *Pontonia panamica* n. sp., general habitus and colour pattern: **A**, ♀ holotype, pcl 7.4 mm (MNHN-Na 16392); **B**, ♂ allotype, pcl 5.5 mm (MNHN-Na 16393).

VARIATION
In one female paratype, the ventral margin of the rostrum presents a minute notch subdistally, however no distinct tooth (Fig. 1F). The typical position of dorsal spines on the telson is illustrated in Figure 2G, F; in one paratype (Fig. 2C), the posterior pair is situated slightly more posteriorly.

COLOUR PATTERN
Semitransparent, with numerous white stripes and patches arranged in complex pattern, latter more defined on abdomen, tail fan, antennules, antennae, walking legs and chelipeds, especially in males; females appearing more yellowish due to brown gonads and/or eggs (Fig. 7).

SIZE
Pcl ranges from 5.2 to 7.6 mm in females, and from 4.2 to 6.0 mm in males. The female holotype and the male allotype are among the largest specimens in the type series, with a tbl of approximately 22 and 18 mm, respectively. The largest female (pcl 7.6 mm, OUMNH)

FIG. 8. — Playa Venao, Pacific coast of Panama, type locality of *Pontonia panamica* n. sp.: **A**, general view of rocky intertidal at extreme low tide (arrow indicating exact location where specimens were collected); **B**, rocks close to water-line, partly immerged in sand-mud, where ascidians hosting shrimps where found; **C**, two solitary ascidians, *Ascidia* cf. *interrupta* Heller, 1878 (white arrows), hosts of *P. panamica* n. sp., attached to the lower surface of an overturned rock.

has approximately 1430 eggs, with an average diameter of 0.5 × 0.4 mm (measured on 10 eggs).

Ecology

Playa Venao, the type locality of *Pontonia panamica* n. sp., is a typical tropical eastern Pacific rocky shore composed of large silt-covered rocks lying densely on silty sand mixed with smaller rocks, mud, shells, etc. The intertidal portion of this rocky shore is exposed for at least 200 m from the beach seawards during extreme low tides (January to April). All shrimps were found in the lower intertidal section, close to the water-line (Fig. 8A). They were dwelling inside colourless or slightly yellowish, leathery ascidians, *Ascidia* cf. *interrupta* Heller, 1878 (Ascidiidae), attached underneath large rocks partly immerged in muddy sand (Fig. 8C). The ascidians were completely submerged in muddy water, with only their long siphons being occasionally visible between rocks. They filter surrounding mud-filled water as their stomachs were filled with muddy substance. Shrimps were always found as heterosexual pairs, and only inside larger hosts, i.e., with body volume more than 45-50 ml.

Host

Ascidia interrupta is currently believed to occur on the coasts of both the eastern Pacific and western Atlantic (F. Monniot pers. comm.). However, in Bocas del Toro, Caribbean coast of Panama, *A. interrupta* appears to occur in aggregations on mangrove roots and has green or greenish-yellow siphons (Collin *et al.* 2005), whereas our individuals from Playa Venao, Pacific coast of Panama (hosts of *P. panamica* n. sp.), occur individually beneath intertidal rocks and have inconspicuously brownish siphons. These differences in colour and ecology may indicate presence of transisthmian cryptic taxa.

DISCUSSION

Pontonia panamica n. sp. is one of three species of *Pontonia* with distinctly elongated dorsal spines on the telson, the other two being the presumably amphi-Atlantic *P. manningi* and the eastern Pacific *P. longispina*. The new species can be easily separated from *P. manningi* by: 1) the more slender dactylus on the third to fifth pereiopods; 2) the less elongated dorsal spines on the telson; 3) the shape of the paragnaths; 4) the presence of a mesial tooth on the first segment of the antennular peduncle (absent in *P. manningi*); and 5) the absence of subdistal tooth on the ventral margin of the rostrum (very distinct and protruding in *P. manningi*).

Pontonia panamica n. sp. is more closely related to *P. longispina*, a species known from only two female specimens from the Gulf of California (Holthuis 1951; Fransen 2002). Since the males of *P. longispina* are unknown, the comparison between the two species is based solely on female features. The females of *P. panamica* n. sp. differ from those of *P. longispina* by: 1) the absence of a ventral subdistal tooth on the rostrum (this tooth is small but distinct in *P. longispina*); 2) the well-marked distolateral and mesioventral teeth on the first segment of the antennular peduncle (both teeth are very small in *P. longispina*); 3) the narrower endopod of the maxilla; 4) the longer proximal segments of the endopod of the second maxilliped; 5) the dactylus of the minor cheliped with a simple tooth (with a tridentate tooth in *P. longispina*); 6) the pollex of the minor cheliped with the shorter proximal tooth, bearing seven denticles distally (with longer tooth, bearing 10 denticles distally in *P. longispina*); and 7) the proportions of the distal articles of the chelipeds, viz. the carpus of major cheliped about 1.5 times as long as wide and about 0.6 times palm length (vs. subrectangular and about 0.33 times palm length in *P. longispina*); the dactylus of the major cheliped about 0.4 times palm length (vs. 0.6 in *P. longispina*); and the carpus of the minor cheliped about 2.5 times as long as wide (vs. 1.8 in *P. longispina*).

Fransen (2002) noted about *P. longispina*: "Of the species retained in *Pontonia*, it is morphologically most closely related to *Ascidonia* gen. nov. with which it forms a monophyletic group." However, in none of Fransen's cladograms, *P. longispina* came out as a monophyletic group together with *Ascidonia*, but instead as a sister clade to all remaining species of *Pontonia*, i.e., it formed the most basal clade within *Pontonia*. Fransen (2002) distinction between *Ascidonia* and *Pontonia* is based on rather subtle characters, one of them with an exception. Below is the corresponding excerpt from Fransen's key to the genera of *Pontonia sensu lato*.

— Rostrum with subdistal ventral tooth; antennal spine distinctly separated from infraorbital margin, acute; scaphocerite with distolateral tooth less than 0.1 of scaphocerite length; submedian carinae of corpus of paragnath parallel, setose; alae of paragnath medially rounded; proximal pair of dorsal spines at 1/3 to 1/2 of telson length; distal pair of dorsal telson spines in distal third of telson .... *Pontonia*

— Rostrum without ventral tooth; antennal spine merged with inferior orbital angle, blunt (acute in *Ascidonia flavomaculata*); scaphocerite with distolateral tooth more than 0.2 of scaphocerite length; submedian carinae of corpus of paragnath oblique, non-setose; alae of paragnath medially bilobed or excavate; proximal pair of dorsal spines at 1/4 of telson length; distal pair of [dorsal] telson spines in proximal third of telson .... *Ascidonia*

We would like to comment on some of these features.

1. Subdistal ventral tooth on the rostrum: since this tooth is absent in *P. panamica* n. sp., a change in the key and a slight emendation of the generic diagnosis is needed (see below).

2. Antennal spine: the distinction between "distinctly separated" and "merged" is somewhat problematic (subjective); however, as correctly pointed out by Fransen (2002), in *Ascidonia*, the antennal spine can be really blunt, as in *A. californiensis* (Rathbun, 1902) or *A. pusilla* (Holthuis, 1951), or strongly acute as in *A. flavomaculata* (Heller, 1864). In both *P. longispina* and *P. panamica* n. sp., this spine is distinctly acute.

3. Distolateral tooth of the scaphocerite: this tooth is indeed stronger, with deeper cleft in *Ascidonia*; and weaker, with smaller cleft in *Pontonia*, including *P. longispina* and *P. panamica* n. sp.

4. Paragnaths: at least the configuration of the submedian carinae of the corpus is a good character to distinguish the two genera; these carinae are oblique, non-setose in *Ascidonia*, and parallel, fringed by a row of setae in *Pontonia*, including *P. longispina* and *P. panamica* n. sp.

5. Dorsal spines of telson: in *Ascidonia*, both pairs of spines are "displaced" to the proximal half of the telson, whereas in *Pontonia*, at least the distal pair is inserted posterior to the telson midlength, sometimes at midlength. The telson dorsal spines in *P. longispina* and *P. panamica* n. sp. are so typical to *Pontonia* in their position; however, in their length and robustness, they are more similar to the spines of most *Ascidonia* species.

Thus, the only feature truly shared by *P. longispina*, *P. panamica* n. sp and species of *Ascidonia* are the stout elongated dorsal spines on the telson. Because of the basal position of *P. longispina* within *Pontonia* (see Fransen 2002) and great morphological similarities between *P. longispina* and *P. panamica* n. sp., suggesting their phylogenetic relatedness, the stout elongated spines is a plesiomorphic state that is retained in basal (i.e., least derived) species of *Pontonia* and in *Ascidonia*, and not a result of a parallel evolution between *Pontonia* and *Ascidonia*. Noteworthy, there is a clear tendency towards reduction of dorsal spines on the telson in more derived species of *Pontonia*; this is especially obvious in *P. domestica* and *P. chimaera*.

The generic diagnosis of *Pontonia* provided by Fransen (2002: 69, 70) needs to be emended at two locations: "ventral margin [of rostrum] usually with, sometimes without subdistal tooth" and "Hosts. — Associated with Mollusca or Ascidiacea." We also propose a slight modification of Fransen's original key as following:

— Rostrum usually with subdistal ventral tooth (rarely without tooth); antennal spine acute; distolateral tooth of scaphocerite small, with minute cleft; submedian carinae of paragnath corpus parallel, setose; dorsal spines of telson minute to moderately long, rarely strong and elongated, at least distal pair inserted in distal half of telson; colour pattern (where known): translucent with white bands ("skeleton pattern"); species usually associated with Mollusca (rarely with Ascidiacea) .... *Pontonia*

— Rostrum without ventral tooth; antennal spine usually blunt (rarely acute); distolateral tooth of scaphocerite strong, with deep cleft; submedian carinae of paragnath corpus oblique, non-setose; dorsal spines of telson always strong, elongated, both pairs inserted in proximal half of telson; colour pattern (where known): translucent with spots (no "skeleton pattern"); species associated with Ascidiacea .... *Ascidonia*

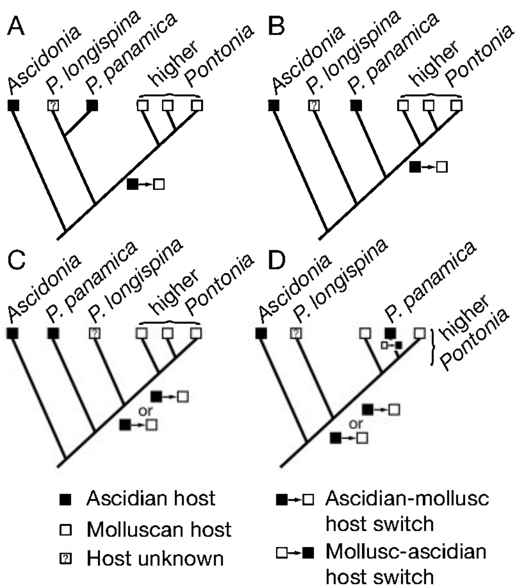

FIG. 9. — Four possible evolutionary scenarios for host group switch within *Pontonia*: **A**-**C** would imply a single host switch from Ascidiacea to Mollusca; **D** would imply an initial host switch from Ascidiacea to Mollusca, followed by a reversal, i.e., a second host switch from Mollusca back to Ascidiacea in *P. panamica* n. sp. (see text for discussion). For full resolution within clade called here "higher *Pontonia*" see Fransen (2002).

The finding of a new *Pontonia* species associated with an ascidian is extremely interesting as it indicates that a host switch occurred within *Pontonia*. As mentioned above, *P. panamica* n. sp. is morphologically very close to *P. longispina*, for which the host is unknown. However, most shared features, such as the strong, elongated dorsal spines of the telson, appear to be plesiomorphic within *Pontonia*. We could not find any distinct and unambigous synapomorphy shared by *P. longispina* and *P. panamica* n. sp. Therefore, the exact position of *P. panamica* n. sp. within *Pontonia* is extremely difficult to ascertain without including this taxon in a proper phylogenetic analysis together with other taxa. Fransen (2002) performed several analyses with different data sets (e.g., ordered vs. unordered characters; omitting certain characters susceptible to reveal as homoplasies) to arrive to his combined consensus tree (Fransen 2002: 43, fig. 24), a procedure that would be relatively complicated and time-consuming to repeat.

All four scenarios are therefore possible: 1) *P. longispina* and *P. panamica* n. sp. may be two eastern Pacific sister species, and form a sister clade to all the remaining *Pontonia* species (Fig. 9A); 2) *P. panamica* n. sp. may represent a separate clade branching off temporarily before *P. longispina* clade, i.e. form a sister clade to the remaining *Pontonia* species all by itself (Fig. 9B); 3) *P. panamica* n. sp. may represent a separate clade branching off temporarily after *P. longispina* clade (Fig. 9C); 4) *P. panamica* n. sp. may be embedded anywhere within the clade of "higher *Pontonia*" (Fig. 9D). This last scenario appears to be the least likely because of several putative plesiomorphies retained by *P. panamica* n. sp. (relatively unspecialized, slender dactylus on the third to fifth pereiopod; telson with stout and elongated dorsal spines, etc.). Furthermore, because of the association of *P. panamica* n. sp. with an ascidian, this scenario would imply a double host group switch within *Pontonia*: Ascidiacea → Mollusca → Ascidiacea (Fig. 9D). On the other hand, the first three scenarios (Fig. 9A-C) all suggest that the common ancestor of all recent *Pontonia* was an ascidian symbiont, and that a single host group switch Ascidiacea → Mollusca occurred relatively early in the evolutionary history of the genus. Among *Pontonia*-allied genera, host group switches Ascidiacea → Mollusca occurred in the clade *Bruceonia* Fransen, 2002, with one species, and in one of six species of the clade *Dactylonia* Fransen, 2002 (see Fransen 2002). Within "higher *Pontonia*", one species (*P. chimaera*) apparently switched the host group from Bivalvia to Gastropoda (*Strombus*). The identification of host for *P. longispina*, the description of male specimens of this species, as well as DNA analyses of all species of *Pontonia* will be crucial in refining the phylogeny of this interesting genus.

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