



A partial revision of the *Philarius gerlachei* (Nobili, 1905) species complex (Crustacea, Decapoda, Palaemonidae), with description of four new species

IVAN MARIN¹ & ARTHUR ANKER²

¹A. N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia.

E-mail: coralliodecapoda@mail.ru

²Florida Museum of Natural History, University of Florida, Gainesville, FL, USA. E-mail: aanker@flmnh.ufl.edu

Summary

The pontoniine shrimp *Philarius gerlachei* (Nobili, 1905) is revised based on Nobili's type material from the Persian Gulf and specimens recently collected in Madagascar, Australia and French Polynesia. *Philarius gerlachei* is redescribed and four species are described as new: *P. polynescicus* n. sp. from Moorea, French Polynesia; *P. rufus* n. sp. and *P. minor* n. sp., both from Heron Island, Great Barrier Reef, Australia, and *P. albimaculatus* n. sp. from Nosy-Bé, Madagascar. These species differ from *P. gerlachei* and/or from each other by a combination of morphological characters and species-diagnostic colour patterns. All species of *Philarius* appear to be obligate associates of branching corals of the genus *Acropora*.

Key words: Caridea, Palaemonidae, Pontoniinae, shrimp, *Philarius*, new species, Indo-West Pacific, *Acropora*, symbiosis

Introduction

The pontoniine shrimp genus *Philarius* Holthuis, 1952 presently includes three species: *P. lifuensis* (Borradaile, 1898), *P. gerlachei* (Nobili, 1905), and *P. imperialis* (Kubo, 1940) (Bruce, 1994; De Grave *et al.* 2009). In addition, *Periclimenes brevinaris* Nobili, 1906 was referred to *Philarius* by Bruce (1967), but later treated as *incertae sedis* (see Bruce 1994), although it is still listed under *Philarius* in Li's (2000) catalogue of pontoniine shrimps.

Philarius lifuensis is distinguishable from its congeners by the presence of distinct supraorbital teeth (Bruce 1982), whereas *P. imperialis* is the only species of the genus bearing a strong tooth on the carpus of the second pereopods (Kubo 1940; Bruce 1982). All specimens lacking these two features were previously assigned to *P. gerlachei*, the type species of *Philarius*, originally described from the Persian Gulf (Nobili 1905). *Philarius gerlachei* also appears to be the most widespread species in the genus, based on numerous records from throughout the Indo-West Pacific (e.g., Bruce, 1982; Li, 2000). All species of *Philarius* are obligate symbionts of acroporid corals, specifically species of the genus *Acropora* Oken (Bruce, 1982; Bruce & Coombes, 1995; Li 2000).

Recently, several specimens of *Philarius* were collected during large-scale surveys of marine decapod crustaceans at three distant localities in the Indo-West Pacific, viz. Nosy-Bé, Madagascar, in 2008 (Biotas), Moorea, Society Islands, French Polynesia, in 2008 (Biocode Moorea), and Heron Island, Great Barrier Reef, Australia, in 2009 (CReefs). All these specimens are referable to *P. gerlachei* using the key provided by Bruce (1982). However, differences in colour patterns and morphology observed among the specimens from Nosy-Bé, Moorea and Heron Island demanded a more thorough study of this material. This study revealed the presence of four species in our material, one in Nosy-Bé, one in Moorea, and two in Heron Island, distinguishable by subtle characters on the rostrum-orbital region and pereopods, as well as colour patterns. We then examined Nobili's syntypes of *P. gerlachei* from the Persian Gulf, deposited in the collections of the Muséum national d'Histoire naturelle, Paris, France (MNHN), and compared them with the specimens from Nosy-Bé, Moorea, and Heron Island. We found a number of subtle morphological differences between these specimens and *P. gerlachei*. Therefore, *P. gerlachei* is redescribed and refigured below based on Nobili's syntypes from the Persian Gulf, to fix its taxonomic identity. The remaining four species, one from Nosy-Bé, one from Moorea, and two from Heron Island, are described as new in this study. A key to all presently known species of *Philarius* is provided.

The material is deposited in the collections of the Queensland Museum, Brisbane, Australia (QM), and Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (FLMNH UF). Postorbital carapace length (pcl, in mm) is used as standard measurement of size. Other abbreviations used in the text: Abd = abdominal somite; fcn = field collection number; Mxp = maxilliped; P = pereopod.

Family Palaemonidae Rafinesque, 1815

Subfamily Pontoniinae Kingsley, 1878

Genus *Philarius* Holthuis, 1952

Philarius gerlachei (Nobili, 1905)

(Figs. 1–3)

Harpilius gerlachei Nobili, 1905: 160; Nobili, 1906: 45, pl. 4, fig. 10.

Philarius gerlachei—Holthuis, 1952: 152, fig. 69; Bruce, 1982: 169, 170; Bruce, 1994: 116; Li 2000: 251.

Type material. *Periclimenes gerlachei* Nobili: 2 ovigerous females and 4 mature males (MNHN-Na 1899), Persian Gulf, sta, LIII, “parmi les polypiers” = among corals, expedition of J. Bonnier and C. Pérez.

Description. Medium-sized pontoniine shrimp with depressed body. Carapace smooth; antennal tooth strong, sharp. Rostrum long, compressed, slightly descendant or horizontal, with tip not reaching distal margin of scaphocerite blade; dorsal lamina with four large teeth, most-posterior tooth situated anterior to orbit; most-distal portion of rostrum toothless; ventral lamina with single tooth situated slightly anterior to mid-length of rostrum; proximolateral rostral lamina without supraocular lobe. Orbit with inferior orbital angle bluntly produced. Pterygostomial angle bluntly produced anteriorly.

Abdominal somites smooth; pleura of first to fifth abdominal somites (= Abd1–5) rounded. Telson narrow, about 2.6 times as long as proximal width, narrowing distally, with two pairs of dorsal submarginal spines inserted at about 0.6 and 0.8 of telson length, respectively; distal margin armed with three pairs of spines, including one pair of short lateral spines, one pair of longer intermediate spines and one pair of median spines shorter than intermediate spines.

Eyes large, with subovate cornea; eyestalk cylindrical, about as long as wide, with well-marked accessory pigment spot.

Antennule with basal segment about as long as wide, distolateral angle with acute tooth; ventromesial tooth small, acute; proximal fused portion of lateral (= upper) antennular flagellum with at least 25 segments, accessory ramus with three segments. Antenna with basicerite bearing sharp distoventral tooth; scaphocerite about 2.5 times as long as maximal width; blade narrow, strongly convex distally; distolateral tooth strong, acute, reaching slightly beyond distal margin of blade.

Mouthparts not dissected in syntypes, appearing typical for genus in external view (see Fig. 6 illustrating mouthparts of closely related *P. polyneticus* n. sp.). Third maxilliped (= Mxp3) robust, with well-developed exopod; lateral plate of coxa ear-shaped, curved distally; arthrobranch absent.

First pereopod (= P1) relatively slender, moderately setose; coxa with curved distoventral lobe; basis as long as wide; ischium about three times as long as wide, distal margin bluntly projecting over ischio-meral articulation; carpus slender, slightly longer than merus, twice as long as wide, flaring distally, with several stout simple setae at carpo-propodal articulation; palm approximately as long as wide, subcylindrical; fingers, simple, tapering distally, about half as long as palm, about 2.5 times as long as wide, with straight cutting edges; fixed finger with one tuft of stiff plumose setae at mid-length of lateral margin.

Second pereopod (= P2) subsymmetrical in shape, subequal in size, robust; surface of distal segments covered with numerous simple setae; carpus cup-shaped, flaring distally, with two triangular blunt teeth ventrally, distodorsal margin rounded; palm subcylindrical, about three times as long as wide, smooth; fingers robust, about three times as long as wide, more than half-length of palm, with acute, curved tips; cutting edges bearing a few small subtriangular teeth proximally; rounded depression present on ventroproximal portion of dactylus.

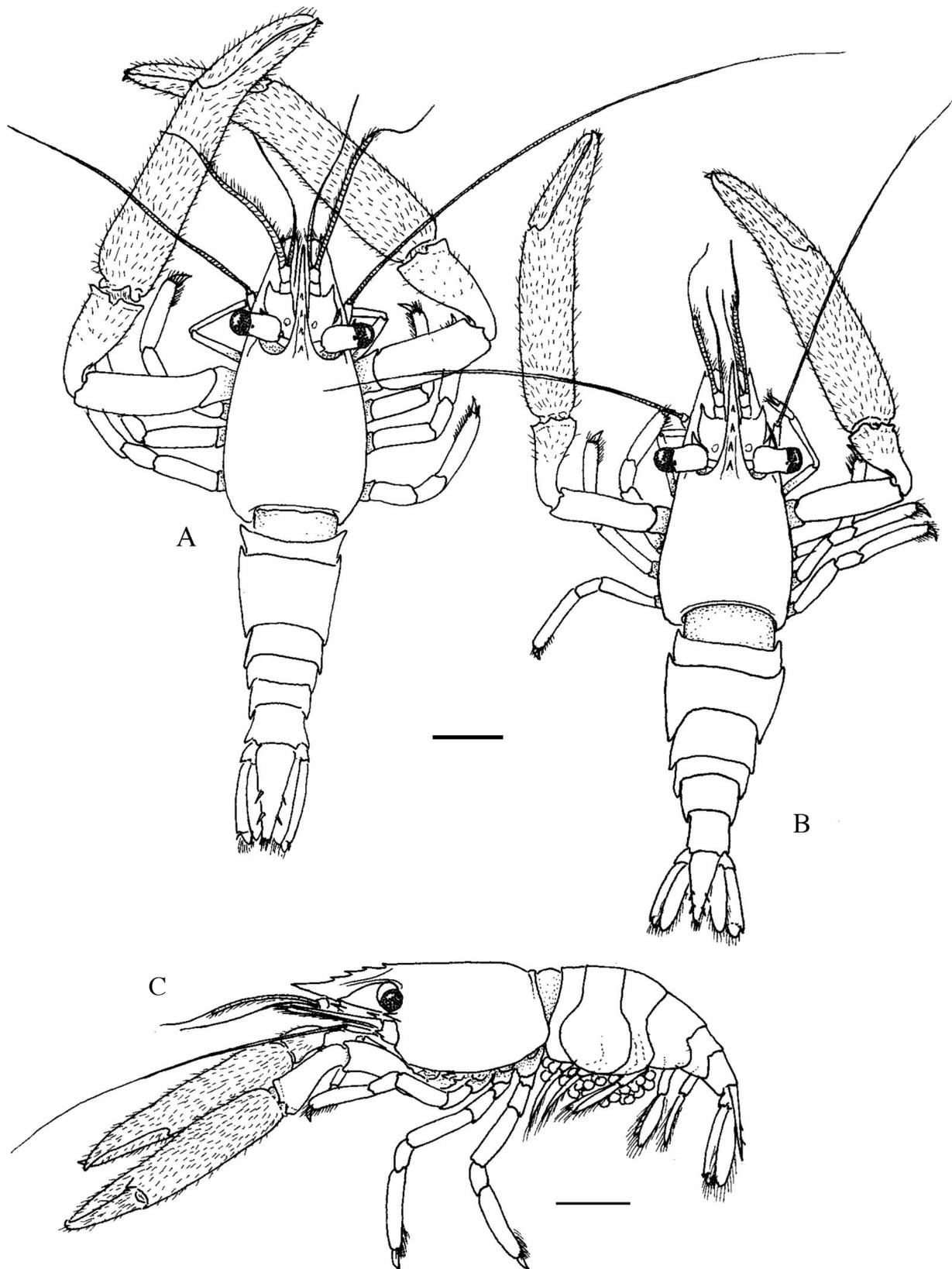


FIGURE 1. *Philarius gerlachei* (Nobili, 1905), syntypes from Persian Gulf (MNHN-Na 1899): A, male, dorsal view; B, oviparous female, dorsal view; C, same as B, lateral view. Scale bars = 2 mm.

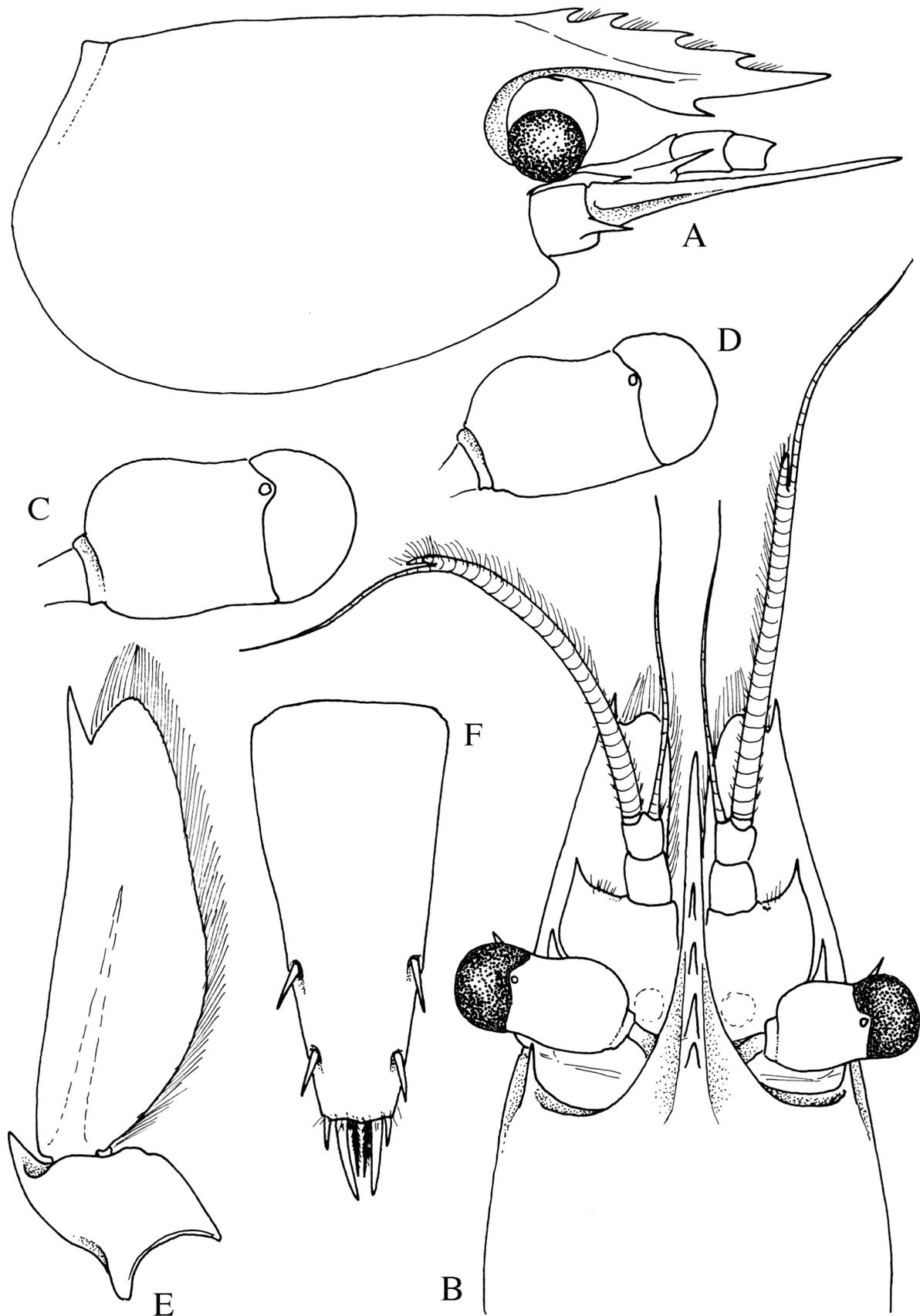


FIGURE 2. *Philarius gerlachei* (Nobili, 1905), female, syntype from Persian Gulf (MNHN-Na 1899): A, carapace and frontal appendages, lateral view; B, frontal region, dorsal view; C, D, eyestalk, dorsal view; E, antennal scaphocerite and basicerite, dorsal view; F, telson, dorsal view.

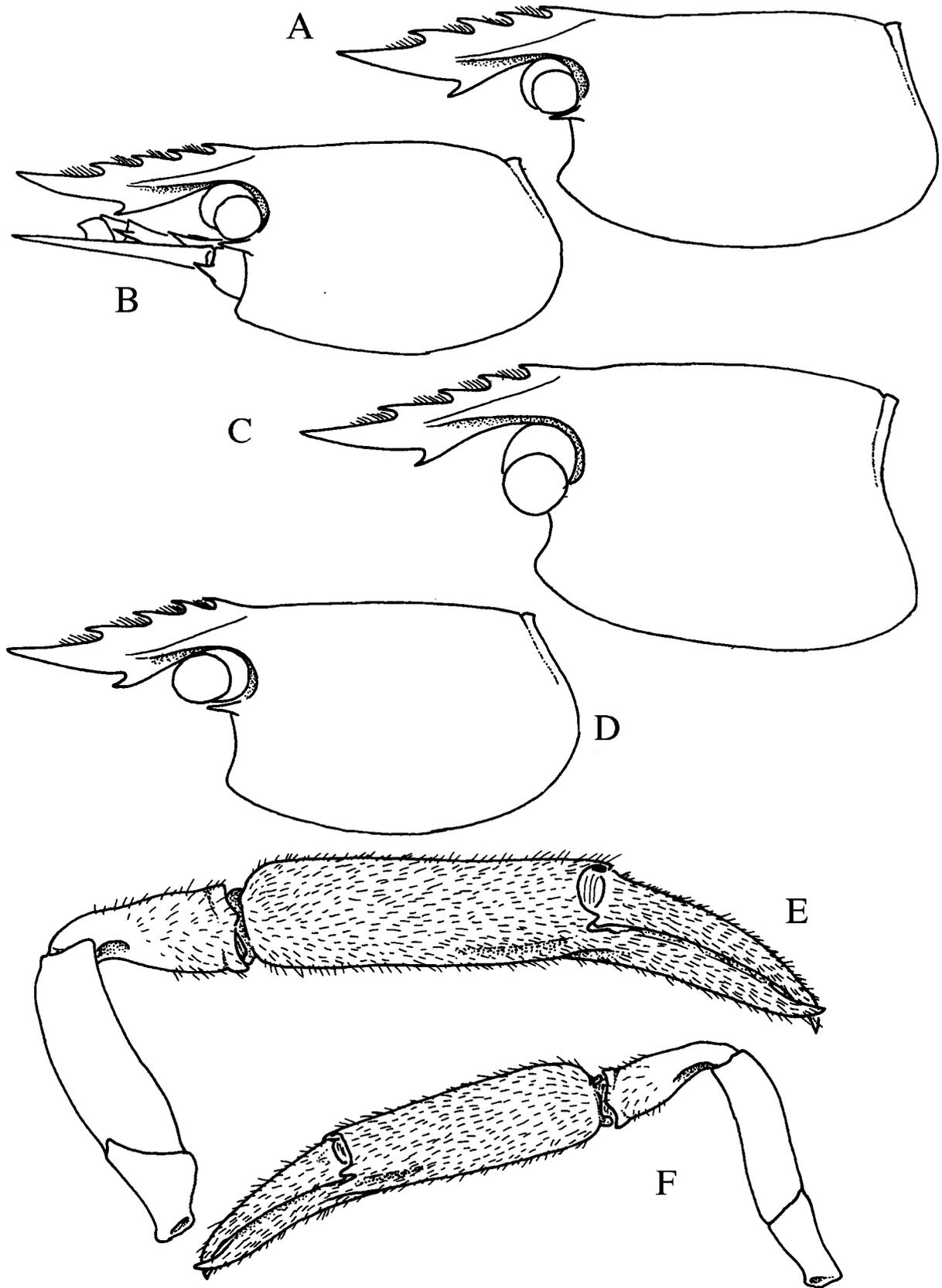


FIGURE 3. *Philarius gerlachei* (Nobili, 1905), syntypes from Persian Gulf (MNHN-Na 1899): A–D, carapace, lateral view; E, male second cheliped, dorsal view; F, female second cheliped, dorsal view.

Third to fifth pereopods (= P3–5) similar in general shape, robust; P3 with ischium, merus and carpus unarmed, covered only with small simple setae; propodus about 3.5 times as long as wide, with straight lateral margins, with three tufts of long simple setae along distoventral margin and one row of simple setae on distal margin; dactylus simple, stout, strongly curved, distally acute.

Uropods relatively slender, slightly exceeding telson; distolateral tooth and spine subequal in length, moderately strong.

Colour pattern. The colour of the type specimens was described as “vert bouteille” = bottle-green (Nobili 1906). To our knowledge, there are no published photographs of *P. gerlachei* from the Indian Ocean. Bruce (1982) provided a black-and-white drawing showing the colour pattern of *P. gerlachei* from the Great Barrier Reef, which, however, is characterised by the presence of large dark dorsolateral spots on the first three abdominal somites.

Ecology. Appears to be associated with a variety of species of the genus *Acropora*, e.g., *A. digitifera* (Dana) (Bruce & Coombes 1995).

Type locality. Persian Gulf.

Distribution. Widely distributed in the Indo-West Pacific, ranging from the Red Sea and East Africa to French Polynesia and Japan (e.g., Bruce 1982; Chace & Bruce 1993; for full list of records see Li 2000); however, at least some of the previous records may refer to one of the below-described new species.

Remarks. Bruce (1982) gave the rostral formula for *P. gerlachei* as 3–5 / 1. Interestingly, in four examined syntype specimens, the rostral formula is 4 / 1, which so appears to be the typical rostral formula for *P. gerlachei* *s. str.* (*sensu* Nobili 1905). The proportions of the carpus and the palm / fingers ratio of P2 also appear to be variable in *P. gerlachei*. Nobili (1906) noted in the text (p. 47) that in some of his specimens, the carpus was proportionally shorter than shown in his figure (Nobili 1906, fig. 10a; see also Fig. 1A, B). Some differences also exist in the armature of the finger cutting edges in P2; for instance, specimens from southern China have only two proximal teeth on the dactylus (Li 2007, fig. 153e).

Philarius gerlachei is closely related to the four species described below, but can be separated from each of them by a combination of subtle morphological characters summarised in Table 1 [see also Remarks under each species below].

***Philarius polynesticus* n. sp.**

(Figs. 4–8, 9A–E)

(?) *Philarius gerlachei* Poupin 1998: 17.

Type material. Holotype: 1 male, pcl 3.2 mm (FLMNH UF Arthropoda 16148), French Polynesia, Society Islands, Moorea, S of Vaiare Pass, 17.5303 S 149.7621 W, outer reef slope, from *Acropora valida*, depth: 5–6 m, coll. C. Meyer, S. McKeon, G. Paulay, J. Moore, processed by A. Anker, 27.X.2008 (fcn BMOO 4574). Paratypes: 1 ovigerous female, pcl 4.5 mm (FLMNH UF Arthropoda 16159), same data as for holotype (fcn BMOO 4588); 1 male, pcl 2.4 mm (FLMNH UF Arthropoda 15924), French Polynesia, Society Islands, Moorea, Haapiti, SE of Matauvau Pass, 17.5779 S 149.8768 W, outer reef slope, from *Acropora valida*, depth: 6–8 m., coll. S. McKeon, J. Moore, G. Paulay, processed by A. Anker, 21.X.2008 (fcn BMOO 3621).

Description. Medium-sized pontonine shrimp with depressed body. Carapace smooth; antennal tooth sharp. Rostrum long, compressed, slightly descendant, with tip not reaching distal margin of scaphocerite blade; dorsal lamina with four to five relatively large dorsal teeth, most-posterior tooth situated anterior to orbit; most-distal portion of rostrum toothless; ventral lamina with single tooth situated at about 0.6 length of rostrum; proximolateral rostral lamina without supraocular lobe. Orbit with inferior orbital angle somewhat bluntly produced. Pterygostomial angle bluntly produced anteriorly.

Pleura of Abd1–5 rounded. Telson broad, about 2.2 times as long as proximal width, narrowing distally, with two pairs of small dorsal submarginal spines at 0.5 and 0.75 of telson length, respectively; distal margin armed with three pairs of spines, including one pair of short lateral spines, one pair of longer intermediate spines and one pair of median spines slightly shorter than intermediate spines.

Eyes as described for *P. gerlachei*.

Antennule with basal segment about as long as wide, distolateral angle with acute tooth; ventromesial tooth small, acute; proximal fused portion of lateral antennular flagellum with about 16 segments, accessory ramus with

three or four segments. Antenna with basicerite bearing sharp distoventral tooth; scaphocerite about 2.5 times as long as maximal width; blade fairly broad, strongly convex distally; distolateral tooth strong, acute, reaching slightly beyond distal margin of blade.

Mouthparts typical for genus. Mandible robust, without palp; incisor process broad, with three large terminal teeth; molar process robust, with stout sharp teeth distally. Maxillule with well-developed palp; dorsal lacinia broad, slightly curved, flaring distally, with stout setae along distal margin; ventral lacinia more slender, tapering distally, with simple setae. Maxilla with well-developed, simple, distally pointed palp, with slender single endite furnished with long simple stiff setae; scaphognathite well developed. First maxilliped (= Mxp1) with completely fused endites, exopod well developed, broad, with feebly developed caridean lobe; epipod ear-shaped. Second maxilliped (= Mxp2) with well-developed, broad exopod; propodus with straight distolateral margin covered with simple setae; dactylus narrow, about four times as long as broad; epipod square-shaped. Third maxilliped (= Mxp3) as described for *P. gerlachei*.

P1 as described for *P. gerlachei*. P2 subsymmetrical in shape, subequal in size, robust; surface of distal segments covered with numerous simple setae; carpus cup-shaped, flaring distally, with two subtriangular blunt teeth ventrally, distodorsal margin rounded; palm subcylindrical, about three times as long as wide, smooth; fingers robust, about three times as long as wide, more than half-length of palm, with acute, curved tips; cutting edges bearing six to eight small triangular teeth along approximately 0.7 of their length; rounded depression present on ventroproximal portion of dactylus.

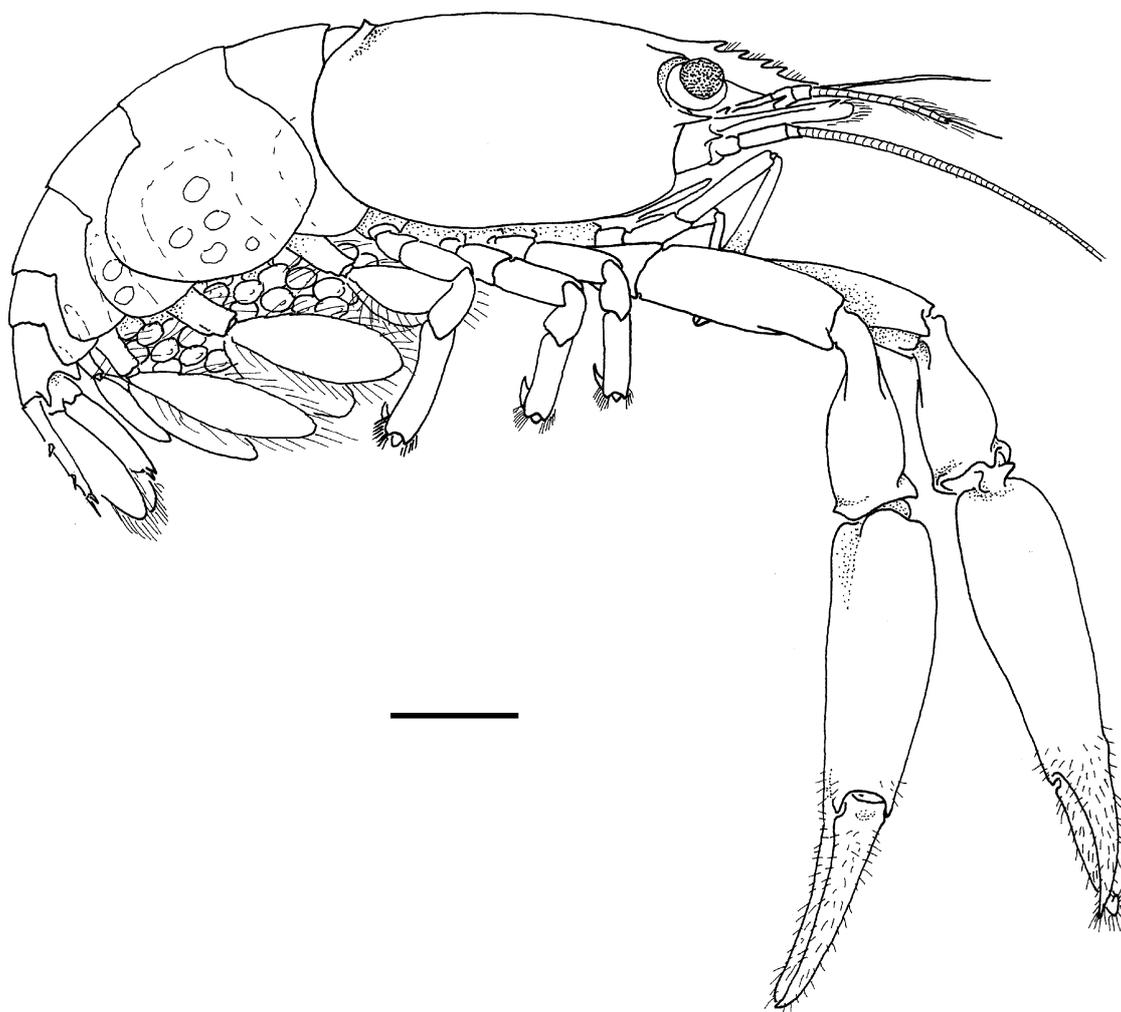


FIGURE 4. *Philarius polyneticus* n. sp., paratype, ovigerous female from Moorea, French Polynesia (FLMNH UF Arthropoda 16159), lateral view. Scale bar = 2 mm.

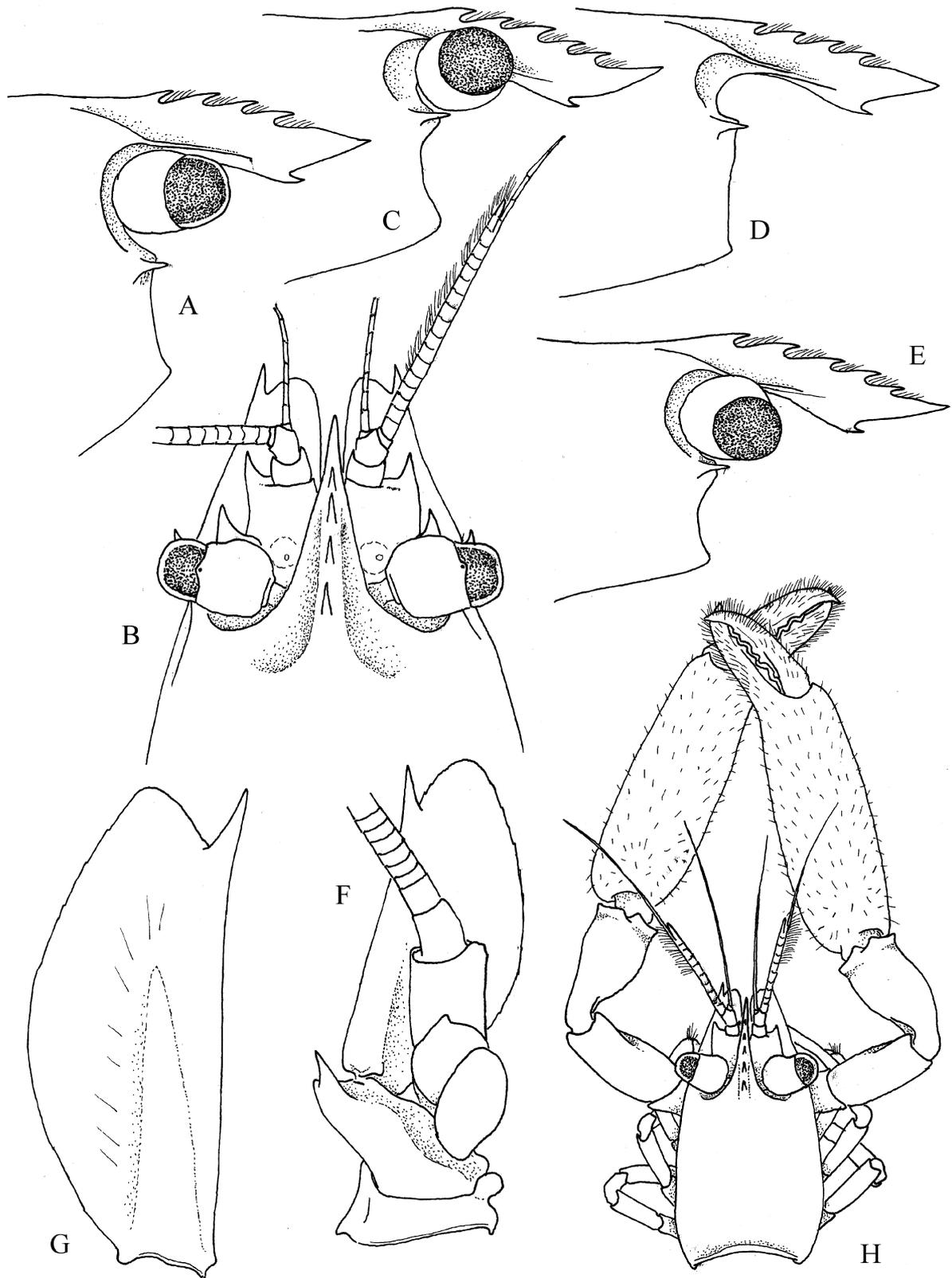


FIGURE 5. *Philarius polyneticus* n. sp., paratype, ovigerous female from Moorea, French Polynesia (FLMNH UF Arthropoda 16159) [A, B, D, F, G]; paratype, male from Moorea (FLMNH UF Arthropoda 15924) [C]; holotype, male from Moorea (FLMNH UF Arthropoda 16148) [E, H]: A, C, D, E, anterior carapace, lateral view (eye detached in D); B, frontal region, dorsal view; F, antenna, ventral view; G, scaphocerite, dorsal view; H, carapace and cephalothoracic appendages, dorsal view.



FIGURE 6. *Philarius polynesianus* n. sp., paratype, ovigerous female from Moorea, French Polynesia (FLMNH UF Arthropoda 16159): A, mandible; B, maxillula; C, maxilla; D, first maxilliped; E, second maxilliped; F, third maxilliped, all in lateral view.

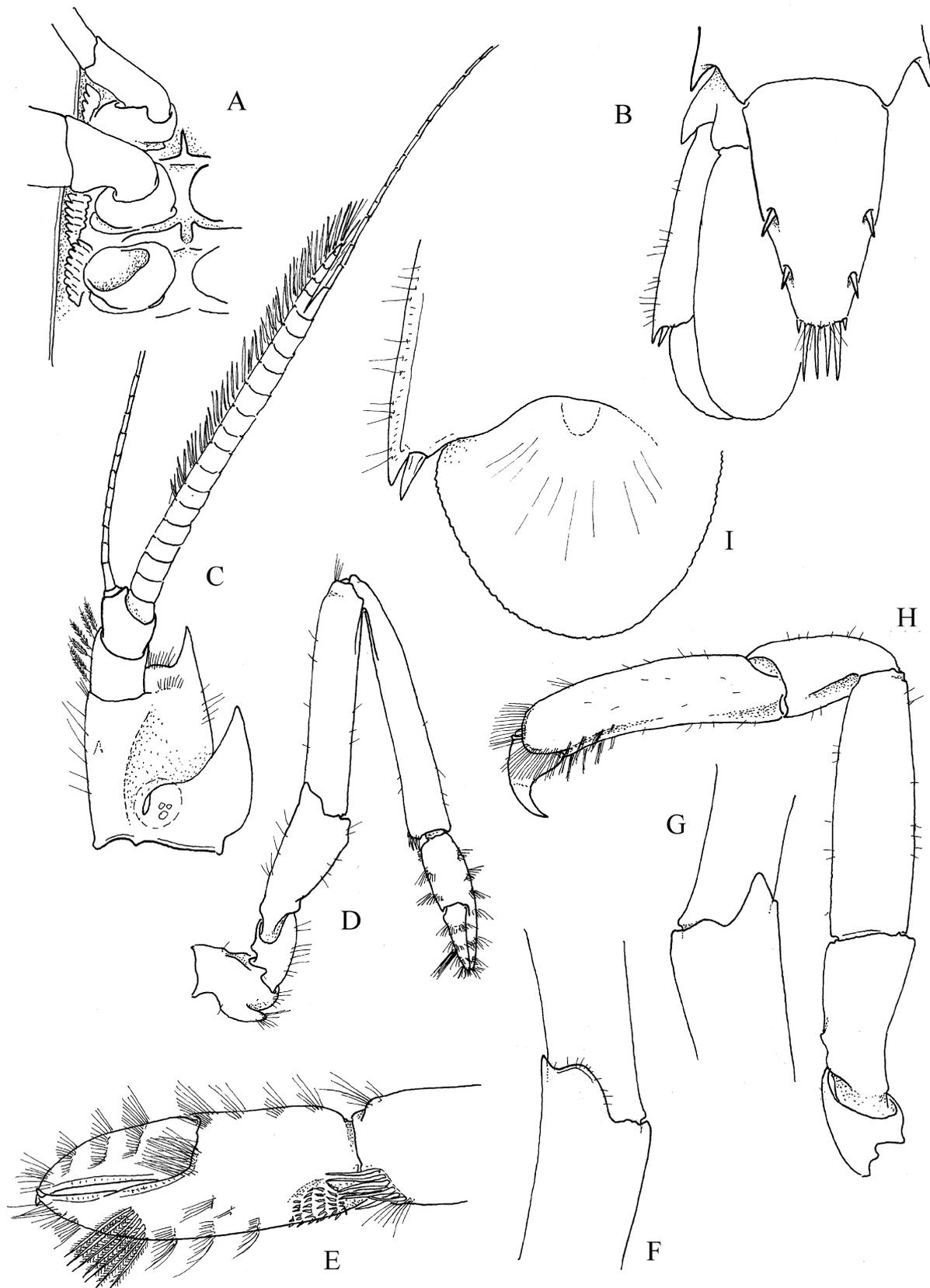


FIGURE 7. *Philarius polynesianus* n. sp. (Nobili, 1905), paratype, ovigerous female from Moorea, French Polynesia (FLMNH UF Arthropoda 16159): A, anterior part of thoracic sternum, ventral view; B, telson and uropods, dorsal view; C, antennule, dorsal view; D, first pereiopod, lateral view; E, same, chela, mesial view; F, G, distal part of ischium, lateral (F) and mesial (G) view; H, third pereiopod, lateral view; I, distal portion of uropodal exopod, dorsal view.

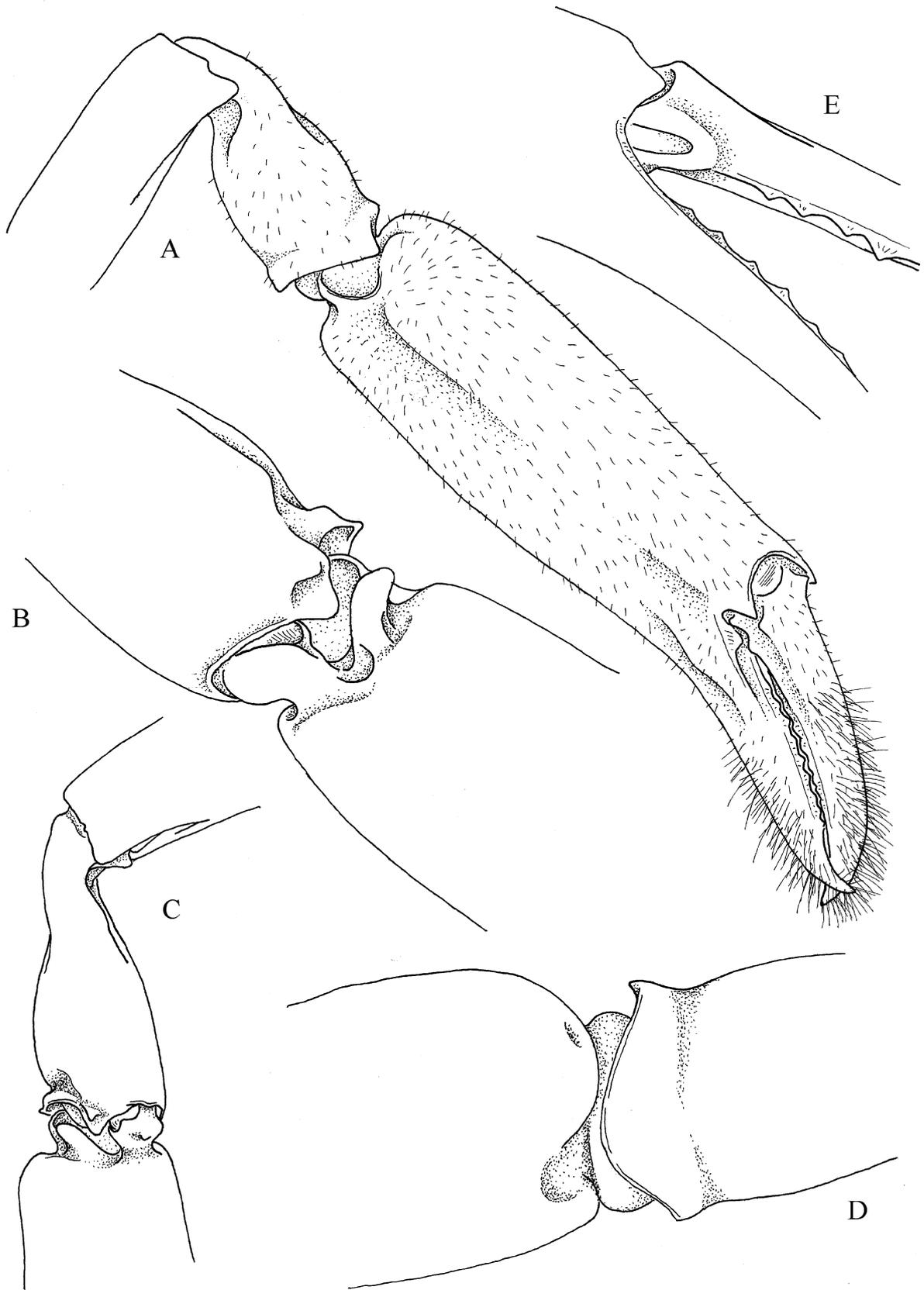


FIGURE 8. *Philarius polyneticus* n. sp., paratype, ovigerous female Moorea, French Polynesia (FLMNH UF Arthropoda 16159): A, second pereiopod, distal merus, carpus and chela, dorsal view; B–D, same, carpo-propodal articulation viewed from different angles; E, same, proximal portion of fingers, mesial view.

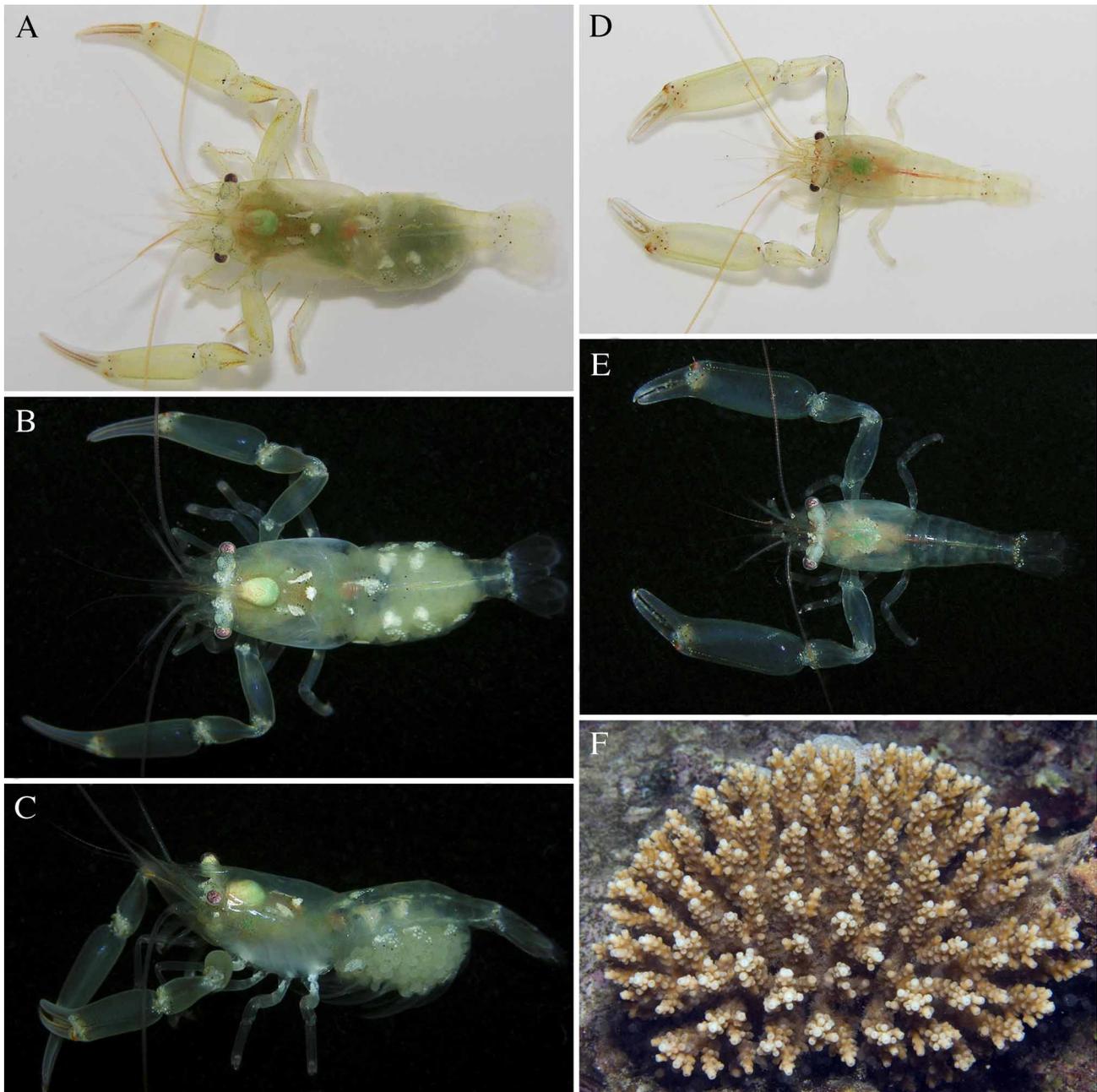


FIGURE 9. *Philarius polyneticus* n. sp., paratype, ovigerous female from Moorea, French Polynesia (FLMNH UF Arthropoda 16159) [A–C]; holotype, male from Moorea (FLMNH UF Arthropoda 16148) [D, E]; colony of *Acropora valida* (Dana), host of *P. polyneticus* n. sp. in Moorea [F]. Photographs: A–E by A. Anker; F by G. Paulay.

P3–5 similar in general shape, robust; P3 with ischium, merus and carpus unarmed, covered with simple setae; propodus about 3.5 times as long as wide, with straight lateral margins, with three tufts of long simple setae along distoventral margin and one long row of simple setae on distal margin; dactylus simple, stout, strongly curved, distally acute.

Uropods fairly slender, slightly exceeding telson; distolateral tooth and spine subequal in length, moderately strong.

Colour pattern. Body semitransparent, pale yellow-greenish or pale yellow, with small dark brown or blackish spots dorsally on carapace, first and sixth abdominal somites, and proximal portion of telson; in females, carapace and first two or three abdominal somites also with whitish patches; P1 and P3–5 uniform pale yellow-greenish, with more or less marked brownish longitudinal line on each article, areas near articulation conspicuously pale-yellow or whitish; P2 pale yellow-greenish, markedly paler near articulations, and with some brown spots on distal

portions of merus and carpus, and most-proximal and most-distal portions of palm; propodo-dactylar articulation more conspicuously orange-brown; finger cutting edges olive-green proximally; antennular and antennal flagella pale orange-yellow; corneas blackish; inner organs partly visible through carapace, greenish and brown (Fig. 9A–E).

Etymology. Referring to French Polynesia, a French overseas territory that includes Moorea, the type locality of this new species; used as adjective.

Ecology. All specimens were extracted from colonies of *Acropora valida* (Dana), collected at a depth range of 5–8 m.

Distribution. Presently known only from the type locality in Moorea, Society Islands, French Polynesia; perhaps also in Mururoa (Poupin 1998, as *P. gerlachei*).

Remarks. *Philarius polynesticus* n. sp. is closely related to *P. gerlachei*, differing from it only by the broader scaphocerite blade (cf. Figs. 2E, 5G); the broader telson, with more anteriorly positioned dorsal spines (cf. Figs. 2F, 7B); the lesser number of segments in the fused portion of the lateral antennular flagellum (around 16 in *P. polynesticus* n. sp. vs. 25 in *P. gerlachei*, cf. Figs. 2B, 7C); and the longer toothless terminal portion of the rostrum (cf. Figs. 3A–D, 5A–E). The new species also lacks dark dorsolateral spots on the abdomen illustrated by Bruce (1982) in a specimen of *P. gerlachei* from the Great Barrier Reef. *Philarius polynesticus* n. sp. can be distinguished from the three below-described species by the same criteria as *P. gerlachei* [see Table 1 and Remarks under species described below].

***Philarius rufus* n. sp.**
(Figs. 10–14, 19A, B)

Type material. Holotype: ovigerous female, pcl 3.7 mm (QM W29052) Australia, Great Barrier Reef off S Queensland, Heron Island, sta. 98, 23.45322 S, 151.90045 E, outer reef, rubble, depth: 24–26 m, coll. S. McKeon, G. Cranich and others, 24.XI.2009 (fcn AUST 6115).

Description. Medium-sized pontonine shrimp with subcylindrical body. Carapace smooth; antennal tooth sharp. Rostrum long, compressed, straight, with slightly ascendant tip overreaching distal margin of scaphocerite blade; dorsal lamina with five large dorsal teeth, four situated anterior to orbit (rostral teeth) and one situated slightly posterior to orbit (= postorbital tooth); most-distal portion of rostrum toothless; ventral margin with single tooth situated at about 0.6 length of rostrum; proximolateral rostral lamina without supraocular lobe. Pterygostomial angle slightly produced anteriorly, rounded.

Pleura of Abd1–5 rounded. Telson about three times as long as proximal width, narrowing distally, with two pairs of small dorsal submarginal spines situated at 0.5 and 0.8 of telson length, respectively; posterior margin armed with three pairs of spines, including one pair of short lateral spines, one pair of longer intermediate spines and one pair of median spines almost equal to intermediate spines.

Eyes as described for *P. gerlachei*.

Antennule with basal segment about 1.5 times as long as wide; distolateral angle with acute tooth; ventromesial tooth small, acute; intermediate and distal segments equal in length, as long as wide; proximal part of lateral antennular flagellum with 11 segments, accessory ramus with at least three visible segments. Antenna with basicerite bearing sharp distoventral tooth; scaphocerite relatively slender, about three times as long as maximal width, overreaching end of antennular peduncle, with well-developed, acute distolateral tooth, latter overreaching distal margin of blade.

Mouthparts typical for genus. Mxp2 with very narrow dactylus. Mxp3 relatively slender, with well-developed, slender exopod; lateral plate of coxa ear-shaped, curved distally; arthrobranch absent.

P1 smooth, relatively slender; ischium about 2.5 times as long as wide, with distally projecting blunt lobe; merus slender, about five times as long as wide; carpus slender, slightly longer than merus, about six times as long as wide, flaring distally, with several stout simple setae at carpo-propodal articulation; palm about 1.5 times as long as wide, subcylindrical; fingers stout, simple, tapering distally, about 2.5 times as long as wide, with straight cutting edges; fixed finger with one tuft of stiff plumose setae at mid-length of lateral margin.

P2 symmetrical in shape, slightly unequal in size, robust; surface of distal segments covered with simple setae; ischium about 2.5 times as long as wide; merus about 3.5 times as long as wide, with straight margins; carpus flar-

ing distally, swollen mesially, with two blunt teeth distoventrally, rounded dorsally; palm subcylindrical, smooth, about three times as long as wide; fingers slender, about 1.5 times shorter than palm, about five times as long as wide; cutting edges with small triangular teeth along almost entire length; finger tips acute, simple, slightly curved.

P3–5 similar in general shape, robust; P3 with ischium, merus and carpus unarmed, covered with simple setae; propodus about five times as long as wide, with smooth margins, without setal tufts on distoventral margin, with one tuft of simple setae on distal margin; dactylus simple, stout, curved, distally acute.

Uropods moderately slender, slightly exceeding telson; distolateral tooth and spine subequal in length, moderately strong.

Colour pattern. Body semitransparent, pale orange-reddish, with minute red and white chromatophores forming bands (some half-moon shaped) on carapace and abdomen; two larger red spots present dorsally on second abdominal somite (within patch of white chromatophores); additional red spots present laterally on second and third pleurae; P1 and P3–5 uniform pale orange, with orange-red longitudinal line on each article; P2 pale orange, with some orange lines on merus and carpus, palm with small but conspicuous red spot proximally; fingers reddish; antennular and antennal flagella pale orange-yellow; corneas reddish (Fig. 19A, B).

Etymology. Name referring to the characteristic reddish colour pattern of the new species (*rufus* = red or reddish-coloured in Latin); used as adjective.

Ecology. The single specimen was found among rubble (which possibly included pieces of *Acropora*), at a depth of 24–26 m.

Distribution. Presently known only from the type locality in Heron Island, Great Barrier Reef off southern Queensland, Australia.

Remarks. *Philarius rufus* n. sp. lacks supraorbital teeth and a well-marked tooth on the P2 carpus, and therefore, appears to be closely related to *P. gerlachei*, *P. polyneticus* n. sp. and the below-described *P. minor* n. sp. and *P. albimaculatus* n. sp. However, *P. rufus* n. sp. can be separated from these four species by the slightly less depressed body and the absence of setal tufts on the distoventral margin of the P3 propodus (present in all other species). *Philarius rufus* n. sp. also differs from *P. gerlachei* and *P. polyneticus* n. sp. by the rostrum distinctly

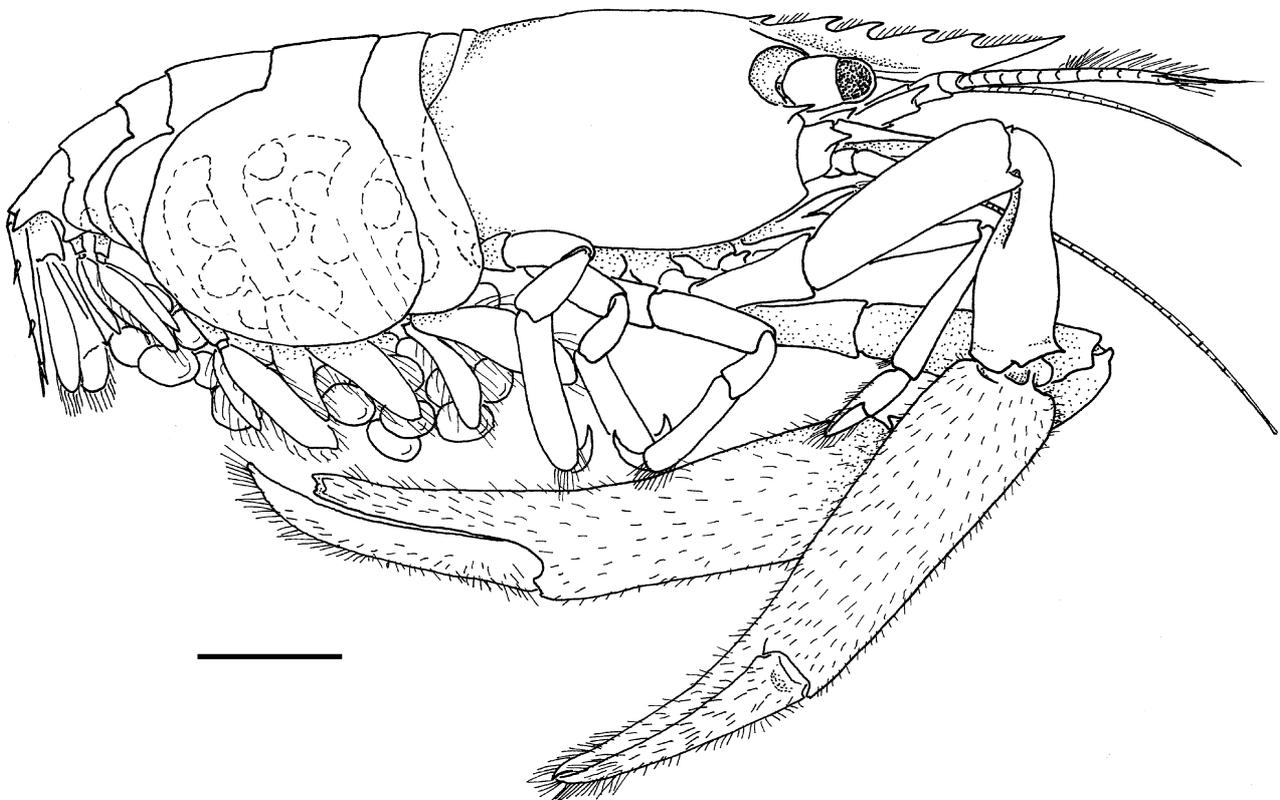


FIGURE 10. *Philarius rufus* n. sp., holotype, ovigerous female from Heron Island, Australia (QM W29052), lateral view. Scale bar = 2 mm.

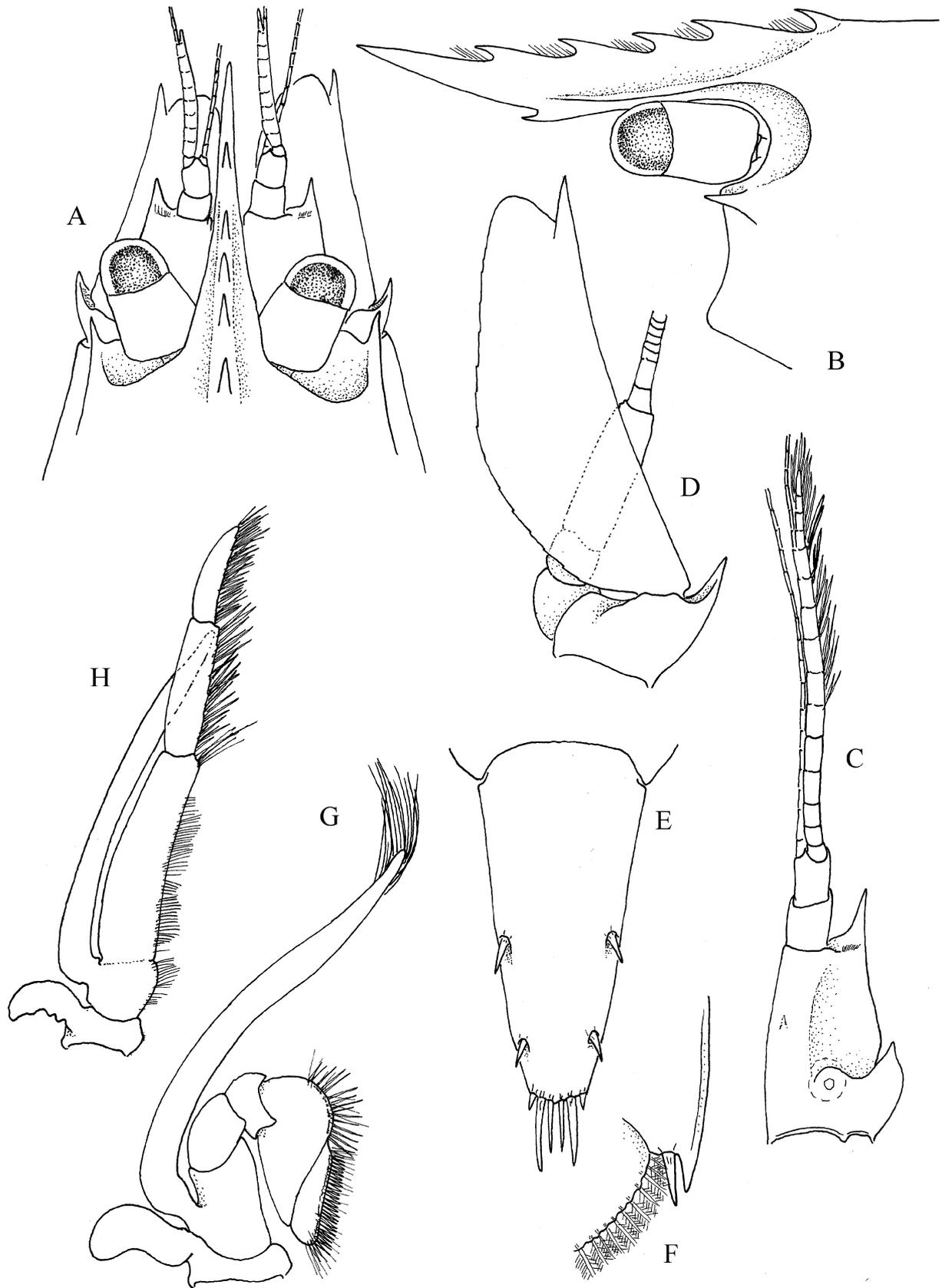


FIGURE 11. *Philarius rufus* n. sp., holotype, ovigerous female from Heron Island, Australia (QM W29052): A, anterior carapace, lateral view; B, frontal region, dorsal view; C, antennule, dorsal view; D, antenna, dorsal view; E, telson, dorsal view; F, distolateral margin of uropodal exopod, dorsal view; G, second maxilliped, lateral view; H, third maxilliped, lateral view.

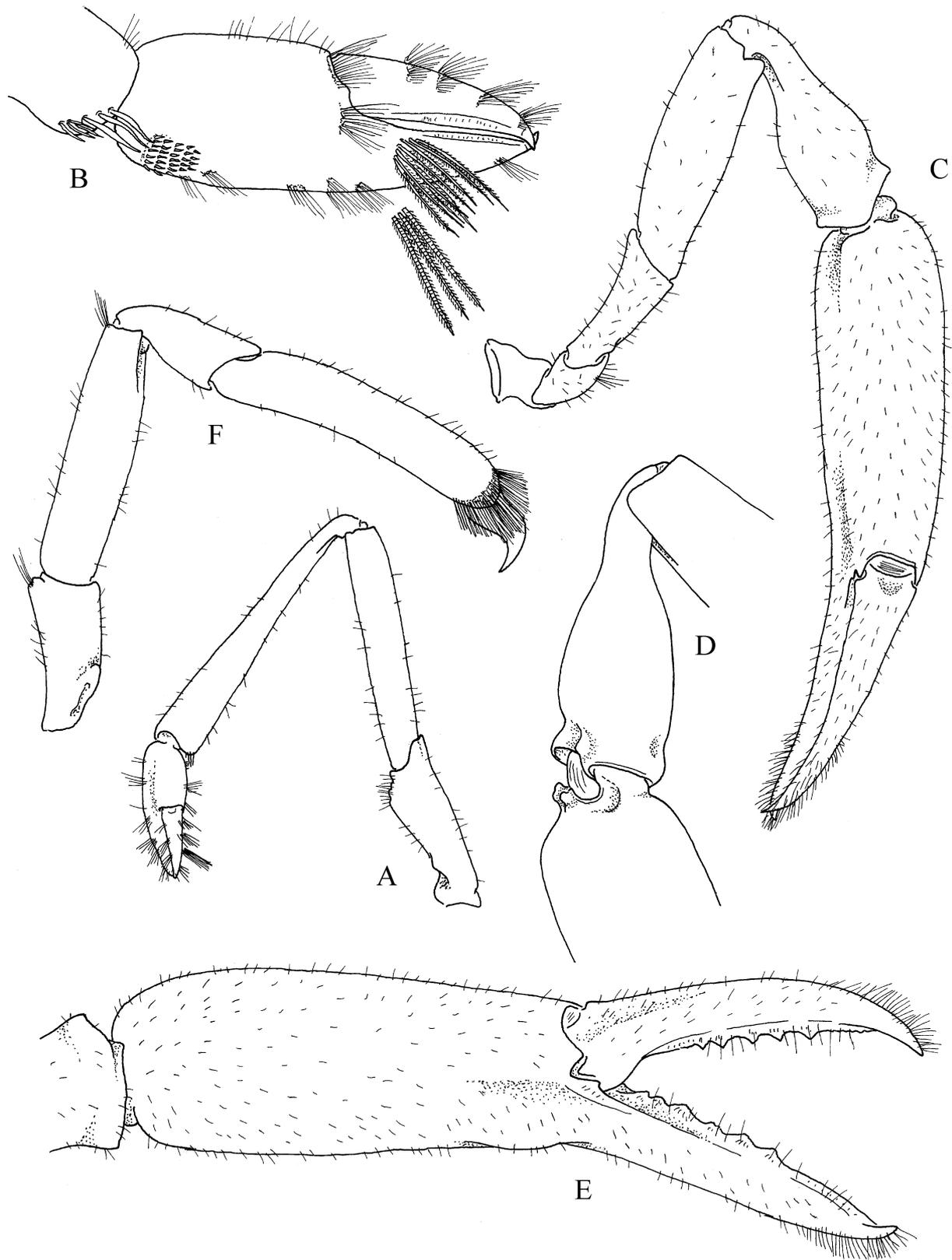


FIGURE 12. *Philarius rufus* n. sp., holotype, ovigerous female from Heron Island, Australia (QM W29052): A, first pereiopod, lateral view, B, same, chela, mesial view; C, second pereiopod, dorsal view; D, same, carpus, lateral view; E, same, chela, mesial view; F, third pereiopod, lateral view.

overreaching the scaphocerite blade and having a longer toothless terminal portion; and from these two species as well as *P. minor* n. sp. by the post-orbital position of the most-posterior tooth on the dorsal lamina (vs. antero-orbital position of the most-posterior tooth in the other three species); and from *P. albimaculatus* n. sp., which is the only other species of the *P. gerlachei* complex with the most-posterior tooth of the dorsal lamina situated posterior to the orbit, by the presence of only four teeth on the rostrum, anterior to the orbit (vs. six in *P. albimaculatus* n. sp.). In life, *P. rufus* n. sp. can be separated from *P. polynesianus* n. sp., *P. minor* n. sp. and *P. albimaculatus* n. sp. by its characteristic reddish colour pattern (Fig. 9A, B); the background colour of other species is either pale greenish (*P. polynesianus* n. sp., *P. minor* n. sp.) or semitransparent with white spots (*P. albimaculatus* n. sp.) [see also Table 1].

***Philarius minor* n. sp.**

(Figs. 13–15, 19C, D)

Type material. Holotype: ovigerous female, pcl 2.6 mm (QM W29050), Australia, Great Barrier Reef off S Queensland, Heron Island, sta. 125, 23.47262 S, 151.95988 E, outer reef, depth 14–16 m, in *Acropora* sp., coll. F. Michonneau, S. McKeon, N. Bruce and others, 28.XI.2009 (fcn AUST 6627). Paratypes: 1 male, pcl 2.2 mm (QM W29051), same collection data as for the holotype (fcn AUST 6626); 1 non-ovigerous female, pcl 2.9 mm (FLMNH UF Arthropoda 24982), Australia, off S Queensland, Great Barrier Reef, Heron Island, Broomfield Reef, sta. 25, 23.26012 S, 151.91692 E, shallow reef, depth: 3–6 m, in *Acropora* sp., coll. S. McKeon, F. Michonneau, G. Cranich and others, 15.XI.2009 (fcn AUST 5136); 1 male, pcl 2.6 mm (FLMNH UF Arthropoda 24983), same collection data as for the previous specimen (fcn AUST 5137).

Description. Small-sized pontoniine shrimp with depressed body. Carapace smooth; antennal tooth sharp. Rostrum long, compressed, more or less straight, with slightly ascendant tip overreaching distal margin of scaphocerite blade; dorsal lamina with four large dorsal teeth all situated anterior to orbit; most-distal portion of rostrum toothless; ventral lamina with one tooth situated slightly anterior to half-length of rostrum; proximolateral rostral lamina well developed, with blunt supraocular lobe adjacent to rostral base. Pterygostomial angle bluntly produced anteriorly.

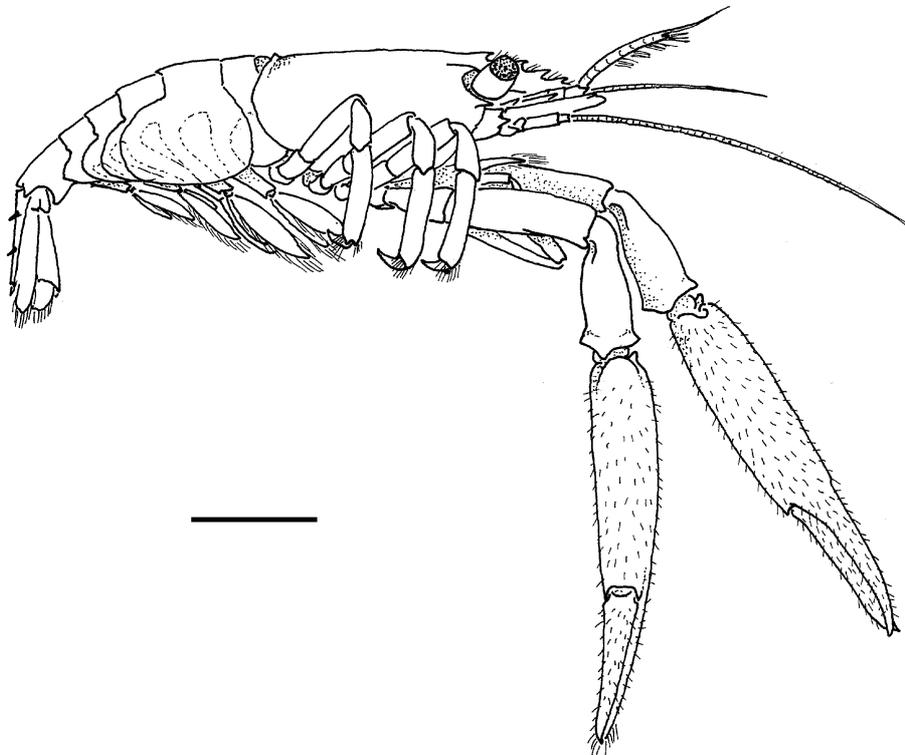


FIGURE 13. *Philarius minor* n. sp., paratype, female from Heron Island, Australia (FLMNH UF Arthropoda 24982), lateral view. Scale bar = 2 mm.

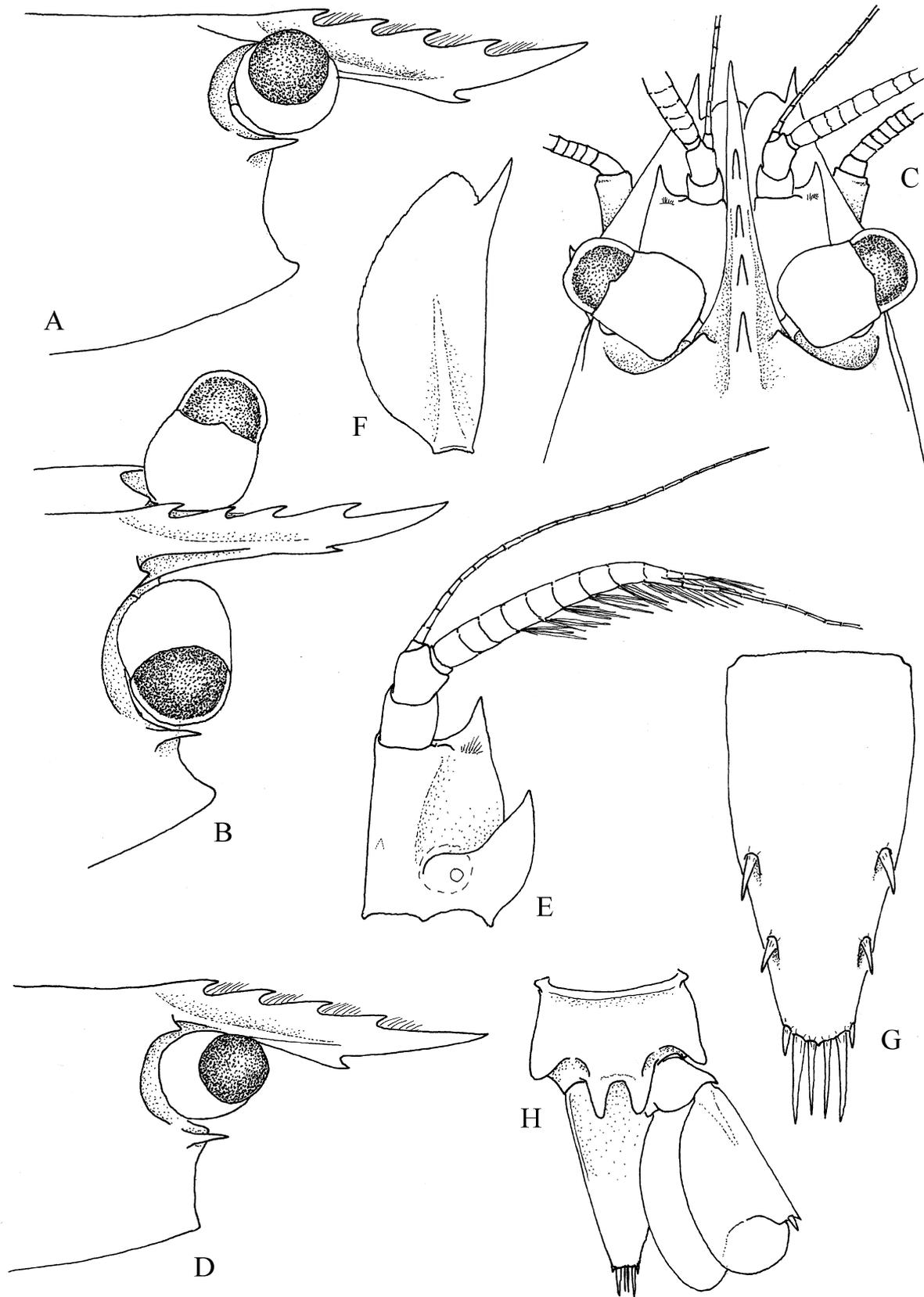


FIGURE 14. *Philarius minor* n. sp., paratypes, ovigerous female from Heron Island, Australia (FLMNH UF Arthropoda 24982) [A-C, E-H]; male from Heron Island, Australia (QM W29051) [D]: A, B, D, anterior carapace, lateral view; C, frontal region, dorsal view; E, antennule, lateral view; F, scaphocerite, dorsal view; G, telson, dorsal view; H, sixth abdominal somite, telson and uropods, ventral view.

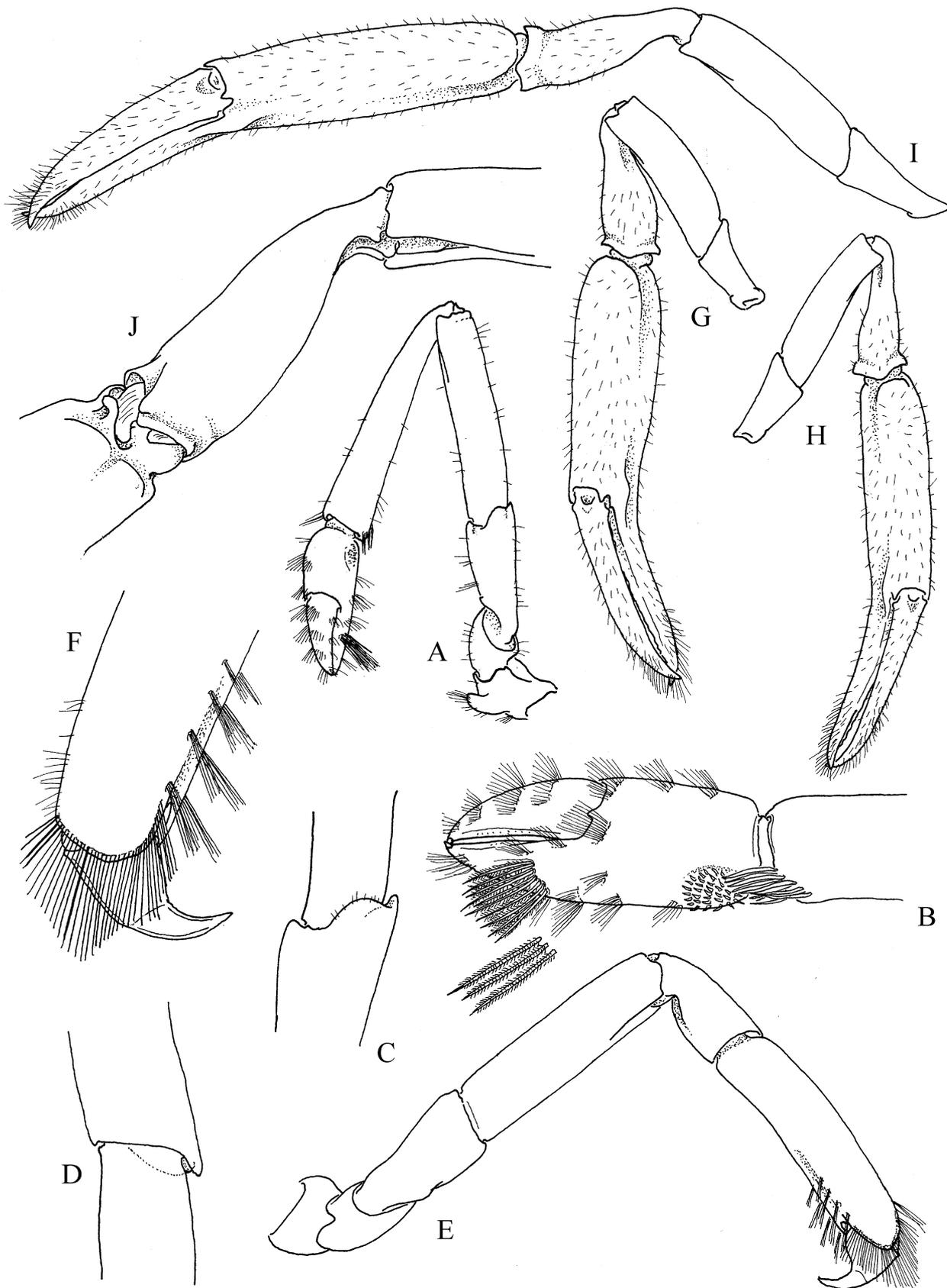


FIGURE 15. *Philarius minor* n. sp., paratypes, ovigerous female from Heron Island, Australia (FLMNH UF Arthropoda 24982) [A-F, I, J]; male from Heron Island, Australia (QM W29051) [G, H]: A, first pereiopod, lateral view; B, same, chela, mesial view; C, D, same, distal margin of ischium, lateral (C) and mesial (D) view; E, third pereiopod, lateral view; F, same, distal propodus and dactylus; G–I, second pereiopod, dorsal view; J, same, carpus.

Pleura of Abd1–5 rounded. Telson about twice as long as proximal width, narrowing distally, with two pairs of dorsal submarginal spines inserted at 0.5 and 0.7 of telson length, respectively; posterior margin with three pairs of spines, including one pair of short stout lateral spines, one pair of long slender intermediate spines and one pair of simple medial spines subequal in length to intermediate spines.

Eyes as described for *P. gerlachei*.

Antennule with basal segment about as long as wide; distolateral angle with acute tooth; ventromesial tooth small, acute; proximal fused portion of lateral antennular flagellum with eight segments, accessory ramus with two segments. Antenna with basicerite bearing sharp distoventral tooth; scaphocerite rather broad, about twice as long as maximal width, overreaching intermediate segment of antennular peduncle; blade strongly convex distally; distolateral tooth strong, acute, reaching well beyond distal margin of blade.

Mouthparts typical for genus. Mxp3 as described for *P. gerlachei*.

P1 smooth, moderately setose; coxa with curved distoventral lobe; basis as long as wide; ischium about 2.5 times as long as wide, with projecting blunt lobe distally; merus slender, about four times as long as wide; carpus slender, slightly longer than merus, about 4.5 times as long as wide, flaring distally, with several stout simple setae at carpo-propodal articulation; palm about 1.5 times as long as wide, subcylindrical; fingers stout, simple, tapering distally, about 2.5 times as long as wide, with straight cutting edges; fixed finger with one tuft of stiff plumose setae at mid-length of lateral margin.

P2 symmetrical in shape, slightly unequal in size, fairly robust, somewhat larger in males than in females; coxa with curved distoventral lobe; ischium about twice as long as wide; merus about three times as long as wide, with straight margins; carpus vase-shaped, flaring distally, swollen mesially; distal margin with two blunt ventral projections, dorsal margin rounded; palm subcylindrical, about four times as long as wide, smooth; fingers slender, about 0.7–0.8 palm length, about four times as long as wide; cutting edges armed with small subtriangular teeth along entire length; finger tips acute, simple, curved.

P3–5 similar in general shape, robust; P3 with ischium, merus and carpus unarmed, sparsely covered with simple setae; propodus about five times as long as wide, with straight, smooth margins, with four to five tufts of long simple setae along distoventral margin and one tuft of simple setae on distal margin; dactylus simple, stout, curved, distally acute.

Uropods slightly exceeding telson; distolateral tooth and spine subequal in length, moderately strong.

Colour pattern. Body semitransparent, pale greenish, with minute, barely noticeable reddish chromatophores on carapace and abdomen; P1 and P3–5 semitransparent, with white patch distally; P2 semitransparent with greenish and blue-purplish tinge, palm with some orange and green iridescence; antennular and antennal flagella purplish blue; corneas pale golden-brownish (Fig. 19C, D).

Etymology. Referring to the relatively small size of this new species (minor = smaller, inferior in Latin), which appears indeed to be one of the smallest species in the genus *Philarius*; used as noun in opposition.

Ecology. All specimens were extracted from colonies of *Acropora* sp., at a depth range of 3–16 m.

Distribution. Presently known only from the type locality in Heron Island, Great Barrier Reef off S Queensland, Australia.

Remarks. *Philarius minor* n. sp. is morphologically very similar to *P. gerlachei*, *P. polynesianus* n. sp., *P. rufus* n. sp. and *P. albimaculatus* n. sp., differing from all of them by the presence of blunt supraocular lobes on each side of the rostral base (Fig. 14B, C). It differs specifically from *P. polynesianus* n. sp. by the more slender rostrum, overreaching the distolateral tooth of the scaphocerite (vs. not reaching it in *P. polynesianus* n. sp.); the shorter antennal scaphocerite; and the more slender P2 chela in both males and females; from *P. rufus* n. sp. by the dorsoventrally flattened body (vs. more laterally compressed in *P. rufus* n. sp.); and from *P. albimaculatus* n. sp. by the absence of a blunt crest on the distodorsal margin of the P2 palm. *Philarius minor* n. sp. also appears to have fewer segments (8) in the fused portion of the lateral antennular flagellum than *P. gerlachei* (~25), *P. polynesianus* n. sp. (~15) and *P. rufus* n. sp. (11), but more than *P. albimaculatus* n. sp. (5). In life, *P. minor* n. sp. may be separated from *P. polynesianus* n. sp., *P. rufus* n. sp., and *P. albimaculatus* n. sp. by the colour pattern, especially the conspicuously purplish-blue coloured antennular and antennal flagella (vs. whitish or pale orange in other species, cf. Figs. 9, 19). In addition, *P. minor* n. sp. appears to be one of the smallest species within the *P. gerlachei* complex, with all available specimens ranging 2.8–3.2 mm cl (although the only available specimen of *P. albimaculatus* n. sp. is even smaller at cl 2.4 mm, see below) [see also Table 1].

TABLE 1. Characters useful for separation of species of the *Philarius gerlachei* complex. Rostral formula given as number of rostral teeth + number of post-orbital teeth.

Species	<i>P. gerlachei</i> Nobili	<i>P. polynesicus</i> n. sp.	<i>P. rufus</i> n. sp.	<i>P. minor</i> n. sp.	<i>P. albimaculatus</i> n. sp.
Characters					
Number of dorsal teeth anterior to orbit (rostral teeth)	4	4-5	4	4	6
Number of dorsal teeth posterior to orbit (post-orbital)	0	0	1	0	1
Rostrum tip	not reaching distal margin of scaphocerite blade	not reaching distal margin of scaphocerite blade	overreaching distal margin of scaphocerite blade	overreaching distal margin of scaphocerite blade	overreaching distal margin of scaphocerite blade
Supraocular lobe	absent	absent	absent	present	absent
Telson, width / length ratio	narrow, ratio ~2.8	broad, ratio ~2.2	narrow, ratio ~2.8	moderately broad, ratio ~2.5	narrow, ratio ~2.8
Telson, position of anterior pair of dorsal spines	0.65 telson length	0.5 telson length	0.55 telson length	0.6 telson length	0.5 telson length
Fused portion of lateral antennular flagellum	~25 segments	~15 segments	~11 segments	~8 segments	5 segments
Scaphocerite blade, width / length ratio	stout	stout	more slender	stout	stout
Mxp3, antepenultimate segment	straight	straight	straight	straight	with blunt crest
P2 distodorsal margin of palm	with 4-5 setal tufts	with 4-5 setal tufts	without setal tufts	with 4-5 setal tufts	with 7 setal tufts
P3 propodus, distoventral margin	“bottle-green” (Nobili 1906)	semitransparent pale greenish / yellowish	semitransparent reddish	semitransparent greenish	semitransparent whitish
Colour pattern (1), background	? (large dark dorsolateral spots on abdomen, see Bruce 1982)	small dark spots on P1, carapace and abdomen	small red spots on P1 and abdomen	no conspicuous spots	large white spots on body, P1-5, antennular peduncles etc.
Colour pattern (2), spots antennular/antennal flagella	?	pale yellow-orange	pale yellow-orange	bluish-purple	whitish, colourless

***Philarius albimaculatus* sp. nov.**

(Figs. 16–18, 19E, F)

Type material. Holotype: male, pcl. 1.9 mm (FLMNH UF Arthropoda 14472), Madagascar, Nosy-Bé. W side of Sakatia, 13.2989° S 48.1472° E, gentle reef slope with rocks, algae and corals, in *Acropora* sp., depth: 3–8 m, coll. G. Bakary, H. Bruggemann, F. Michonneau, G. Paulay, T. Werner, processed by A. Anker, 18.V.2008 (fcn NBE 1817).

Description. Small-sized pontoniine shrimp with depressed body. Carapace smooth; antennal tooth sharp. Rostrum long, compressed, slightly descendant, with tip overreaching distal margin of scaphocerite blade; dorsal lamina with five large teeth and one small subapical tooth, in addition to one tooth in post-orbital position; ventral lamina with one tooth situated at about 0.7 rostrum length; proximolateral rostral lamina without supraocular lobe. Pterygostomial angle bluntly produced anteriorly.

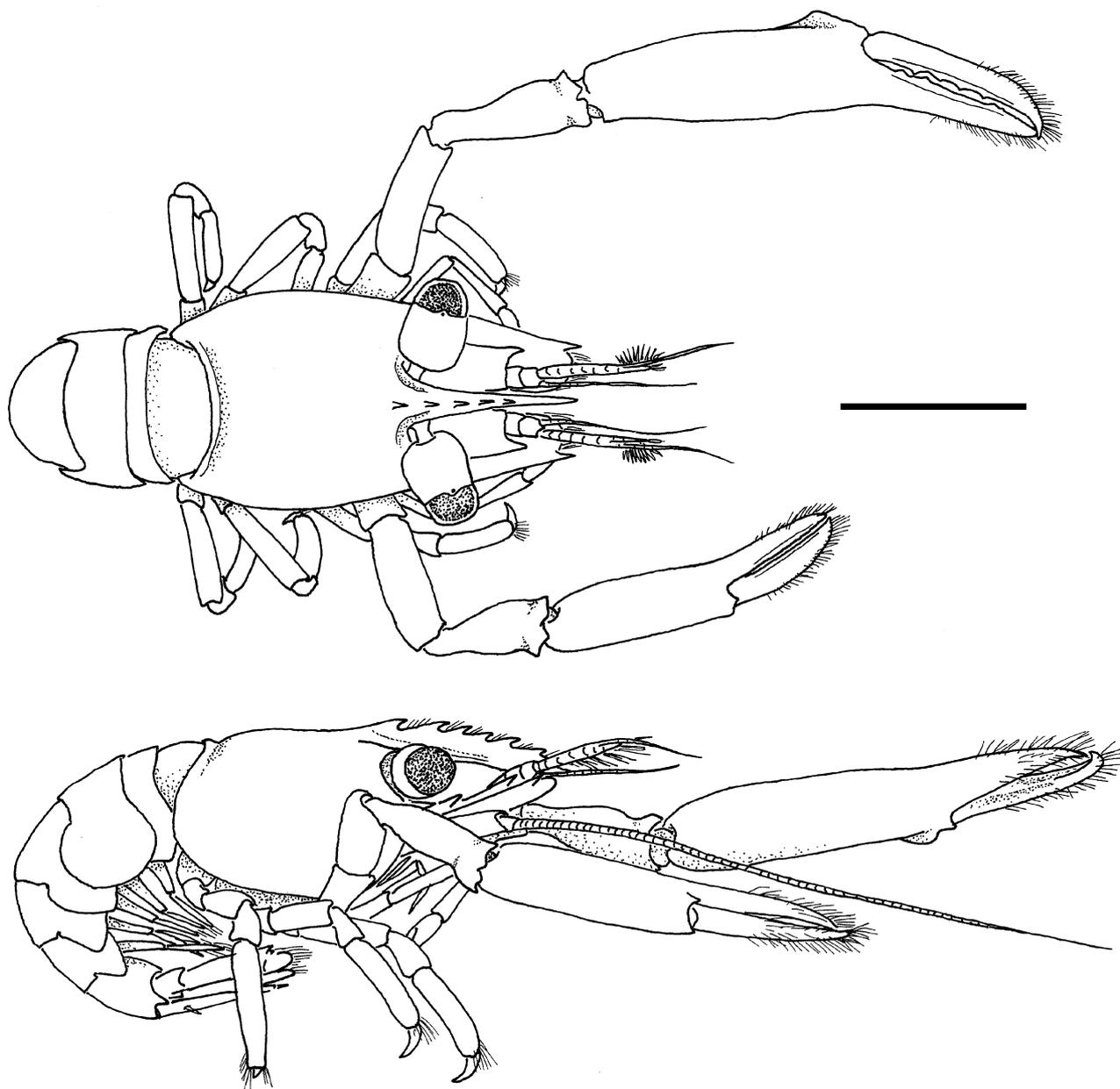


FIGURE 16. *Philarius albimaculatus* n. sp., holotype, male from Nosy-Bé, Madagascar (FLMNH UF Arthropoda 14472), dorsal and lateral views. Scale bar = 2 mm.

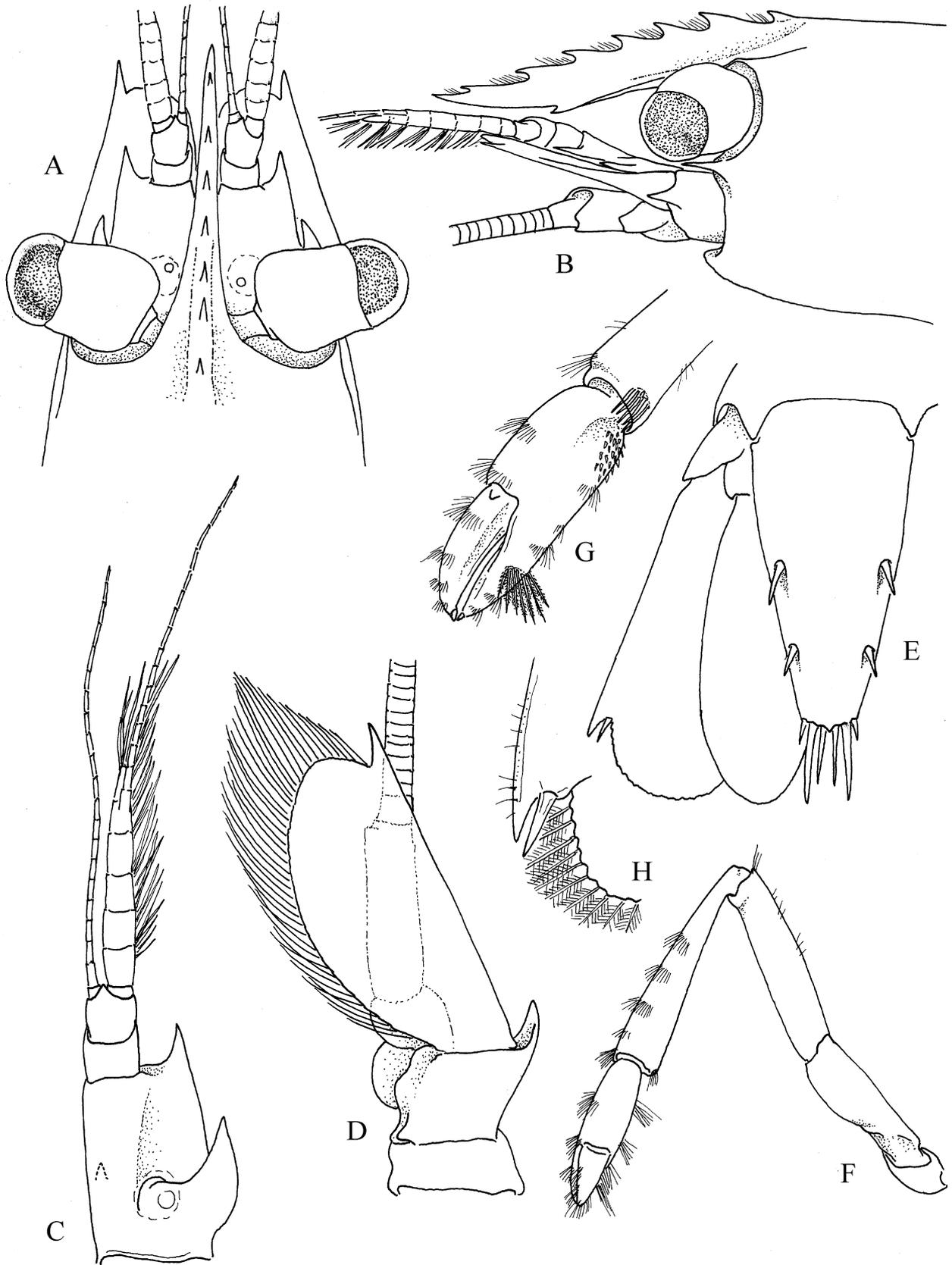


FIGURE 17. *Philarius albimaculatus* n. sp., holotype, male from Nosy-Bé, Madagascar (FLMNH UF Arthropoda 14472): A, frontal region, dorsal view; B, same, lateral view; C, antennule, dorsal view; D, antenna, dorsal view; E, telson and uropods, dorsal view; F, first pereiopod, lateral view; G, same, chela, mesial view; H, distolateral margin of uropodal exopod, dorsal view.

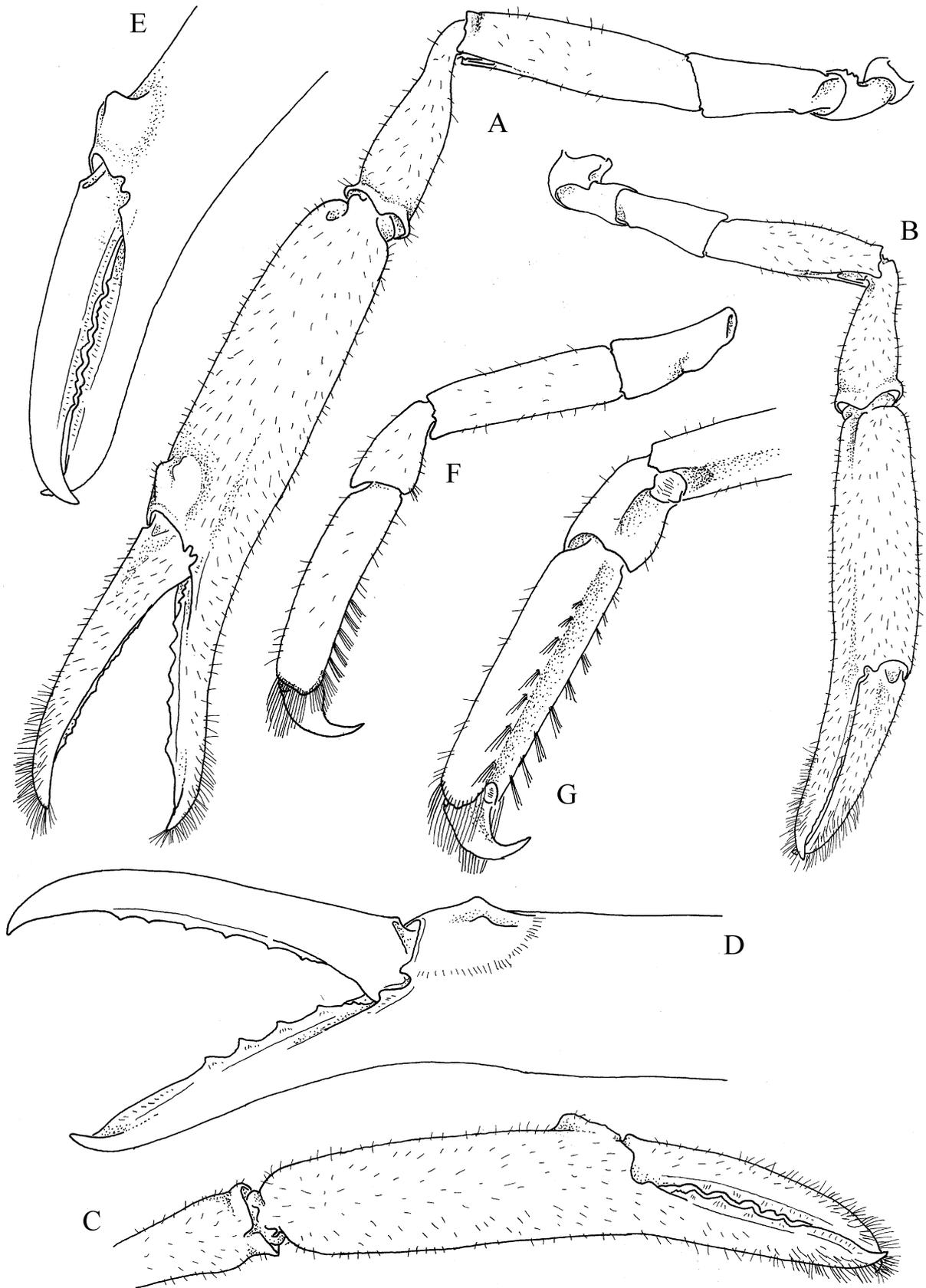


FIGURE 18. *Philarius albimaculatus* n. sp., holotype, male from Nosy-Bé, Madagascar (FLMNH UF Arthropoda 14472): A, right second pereopod, dorsal view; B, left second pereopod, dorsal view; C, chela of right second pereopod, lateral view; D, E, same, distal propodus and fingers, mesial view; F, third pereopod, lateral view; G, same, carpus, propodus and dactylus, ventrolateral view.

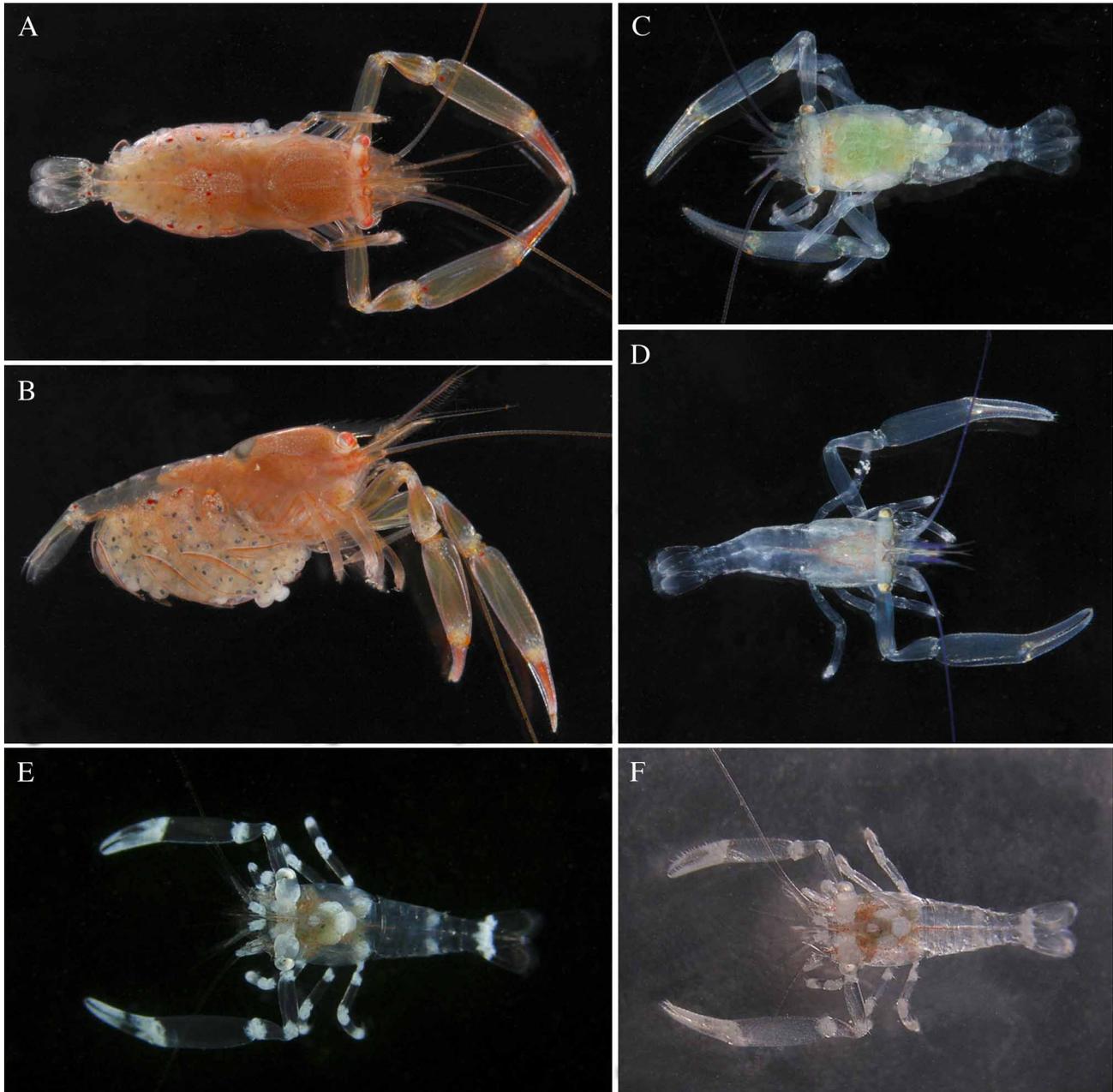


FIGURE 19. Colour patterns of three species of *Philarius*: A, B, *Philarius rufus* n. sp., holotype, ovigerous female from Heron Island, Australia (QM W29052); C, D, *Philarius minor* n. sp., holotype, ovigerous female (C) and paratype male (D) from Heron Island, Australia (QM W29050, W29051); E, F, *Philarius albimaculatus* n. sp., holotype, male from Nosy-Bé, Madagascar (FLMNH UF Arthropoda 14472). Photographs: A-D by F. Michonneau; E, F by A. Anker.

Pleura of Abd1–5 rounded. Telson about twice as long as proximal width, narrowing distally, with two pairs of dorsal submarginal spines inserted at about 0.5 and 0.75 of telson length, respectively; posterior margin with three pairs of spines, including one pair of short lateral spines, one pair of long intermediate spines and one pair of simple medial spines about 0.8 of length of intermediate spines.

Eyes as described for *P. gerlachei*.

Antennule with basal segment about 1.3 times as long as wide; distolateral angle with acute tooth; ventromesial tooth small, acute; proximal fused portion of lateral antennular flagellum with five segments, accessory ramus apparently with only one segment. Antenna with basicerite bearing sharp distoventral tooth; scaphocerite broad, about twice as long as maximal width, overreaching end of antennular peduncle; blade broadly rounded distally; distolateral tooth strong, acute, reaching beyond distal margin of blade.

Mouthparts typical for genus. Mxp3 as described for *P. gerlachei*.

P1 smooth, moderately setose; coxa with well-developed curved distoventral lobe; basis as long as wide; ischium about three times as long as wide, with distally projecting blunt lobe; merus slender, about four times as long as wide; carpus slender, slightly longer than merus, about four times as long as wide, flaring distally, with several stout simple setae at carpo-propodal articulation; palm about as long as wide, subcylindrical; fingers stout, about half as long as palm, simple, tapering distally, about 2.5 times as long as wide, with straight cutting edges; fixed finger with one tuft of stiff plumose setae at mid-length of lateral margin.

P2 subsymmetrical in shape, slightly unequal in size, slender, covered with simple setae distally; ischium about twice as long as wide; merus about three times as long as wide, with straight margins; carpus flaring distally, slightly swollen mesially, with two blunt projections distoventrally and rounded dorsal margin; palm subcylindrical, about 3.5 times as long as wide; distodorsal surface of palm somewhat elevated forming a blunt crest near propodo-dactylar articulation; fingers slender, equal to palm in length, about five times longer than wide; cutting edges armed with minute triangular teeth along entire length; finger tips acute, simple, curved.

P3–5 similar in general shape, robust; P3 with ischium, merus and carpus unarmed, covered with simple setae; propodus about five times as long as wide, with straight, smooth margins, with seven tufts of long simple setae along ventral margin and one tuft of simple setae on distal margin; dactylus simple, strong, curved, distally acute.

Uropods slightly exceeding telson; distolateral tooth and spine subequal in length, moderately strong.

Colour pattern. Body semitransparent; carapace with large white patches dorsally (some of them possibly on internal organs); abdomen mostly transparent, with conspicuous, broad white band on sixth somite, near telson; P3–5 transparent with large white bands near articulations; P2 similar to P3–5, in addition with large white patch on proximal portion of palm; distal portion of palm and fingers also white (Fig. 19E, F).

Etymology. Referring to the species-diagnostic white spots (*albimaculatus* = white-spotted or white-speckled in Latin); used as adjective.

Ecology. The single holotype specimen was found in *Acropora* sp., at a depth of 3–8 m.

Distribution. Presently known only from the type locality in Nosy-Bé, northwestern Madagascar.

Remarks. *Philarius albimaculatus* n. sp. is related to the other four species of the *P. gerlachei* complex, differing from them by the greater number of teeth on the dorsal lamina of the carapace (7 teeth vs. 4–5 teeth in the other species); the very short proximal portion of the lateral antennular flagellum (5 segments vs. 8–25 segments in the other species); the presence of a blunt crest on the distolateral surface of the P2 palm; and the larger number of setal tufts on the ventral margin of the P3 propodus (7 setal tufts vs. 4–5 tufts in the other species). In life, *P. albimaculatus* n. sp. can be easily recognised by its characteristic colour pattern, in particular by the white spots and patches on the body and appendages (Fig. 19E, F) [see also Table 1].

Philarius sp.

(Fig. 20)

Material examined. 1 ovigerous female, pcl 2.3 mm (FLMNH UF Arthropoda 24709), Australia, Great Barrier Reef, Heron Island, First Point, sta. 6, 23.43322 S, 151.93375 E, depth: 1–2 m, rubble and corals with sandy patches, in rubble, coll. CReefs team, 12.XI.2009 (fcn AUST 4684).

Colour pattern. Semitransparent with greenish tinge; antennular and antennal flagella bluish; colour pattern generally similar to that of *P. minor* n. sp. (cf. Fig. 19C, D).

Remarks. Unfortunately, this specimen is too incomplete to be positively identified, missing both P2 and most P3–5. It is generally similar to *P. polynesianus* n. sp. and *P. minor* n. sp., differing from the former by the colour of the antennular and antennal flagella and the fewer segments in the fused portion of the lateral antennular flagellum, and from the latter by the absence of supraocular lobes on the proximolateral rostral lamina and the somewhat stronger dorsal rostral teeth (Fig. 20A). We hope that ongoing DNA analyses of the FLMNH decapod collections will soon elucidate the identity of this specimen.

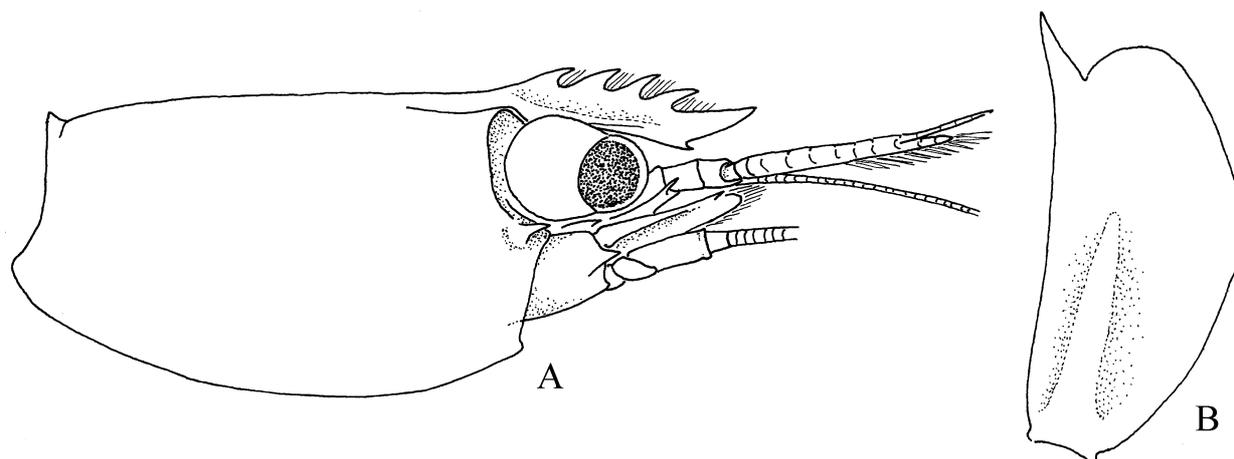


FIGURE 20. *Philarius* sp., ovigerous female (damaged) from Heron Island, Great Barrier Reef, Australia (FLMNH UF Arthropoda 24709): A, carapace and frontal appendages, lateral view; B, antennal scaphocerite, dorsal view.

Key to the presently known species of *Philarius* Holthuis, 1952 based on morphology and colour patterns (where known)

1. Suprarbital teeth conspicuous, acute [rostral formula: 7–10 / 1–2; pereiopods with large white areas adjacent to joints; intensely red spots on eyestalks, at dactylar hinge of P2 chelae, within white patches on pleurae etc.] *P. lifuensis* (Borradaile, 1898)
- . Supraorbital teeth absent (at most small blunt lobes adjacent to rostral base) 2
2. P2 carpus with strong sharp tooth distomesially [rostral formula: 7–9 / 1; dark V-shaped line present dorsally on the carapace] *P. imperialis* (Kubo, 1940)
- . P2 carpus without strong sharp tooth distomesially 3
3. Dorsal lamina of carapace with most-posterior tooth situated posterior to orbit 4
- . Dorsal lamina of carapace with most-posterior tooth situated anterior to orbit 5
4. Body dorsoventrally flattened, depressed; rostrum with 6 teeth (not counting 1 post-orbital tooth); proximal fusion portion of lateral antennular flagellum with ~5 segments; P2 palm with blunt bumps distodorsally [body and appendages transparent, with large white spots and patches] *P. albimaculatus* n. sp.
- . Body somewhat compressed laterally; rostrum with 4 teeth (not counting 1 post-orbital tooth); proximal fusion portion of lateral antennular flagellum with ~11 segments; P2 palm almost straight distodorsally [body and appendages reddish, with small red spots] *P. rufus* n. sp.
5. Supraocular lobes present; proximal fusion portion of lateral antennular flagellum with ~8 segments; rostrum with tip reaching beyond distal margin of scaphocerite blade [antennular and antennal flagella purplish-blue] *P. minor* n. sp.
- . Supracular lobes absent; proximal fusion portion of lateral antennular flagellum with at least 15 segments; rostrum with tip not reaching distal margin of scaphocerite blade [antennular and antennal flagella pale orange or yellowish] 6
6. Proximal fusion portion of lateral antennular flagellum with ~15 segments; scaphocerite with blade broad, ~2.2 times as long as wide; telson relatively broad, with anterior pair of dorsal spines inserted at about half-length of telson [greenish with minute black spots and larger pale or white patches on the abdomen] *P. polynesianus* n. sp.
- . Proximal fusion portion of lateral antennular flagellum with ~25 segments; scaphocerite with blade narrow, ~2.8 times as long as wide; telson relatively narrow, with anterior pair of dorsal spines inserted posterior to half-length of telson [possibly with large dorsolateral spots on the abdomen] *P. gerlachei* (Nobili, 1905)

Acknowledgments

IM would like to thank Gustav Paulay (FLMNH) for the financial support enabling him to study the FLMNH palaemonid shrimp collections. AA is grateful to colleagues and students who helped collecting or processing material, in particular François Michonneau, Jenna Moore and Seabird McKeon (FLMNH). The material reported in this study was collected during the following expeditions: BIOTAS, based at Centre National de Recherche Océanographique (CNRO) in Nosy-Bé, Madagascar (2008), and organised by Henrich Bruggemann (Université de la Réunion, Saint-Denis) and G. Paulay; Biocode Moorea, based at the Richard B. Gump South Pacific Research Station of the University of California in Moorea, French Polynesia (2008), organised by G. Paulay and Chris Meyer

(Smithsonian Institution, National Museum of Natural History, Washington DC), and sponsored through the Gordon and Betty Moore Foundation; and CReefs Australia based at Heron Island Research Station (2009), organised by Julian Caley and Shawn Smith (Australian Institute of Marine Science, Townsville) and funded by BHP-Billiton. Collection permits in Moorea were issued by the Délégation à la Recherche of the Government of French Polynesia. Sammy De Grave (Oxford University Museum of Natural History, Oxford, UK) kindly reviewed the final draft of the manuscript.

References

- Borradaile, L.A. (1898) A revision of the Pontoniinae. *Annals of Magazine of Natural History, series 7*, 2, 376–391.
- Bruce, A.J. (1967) The results of the re-examination of the type specimens of some pontoniid shrimps in the collection of the Muséum National d'Histoire Naturelle, Paris. *Bulletin du Muséum National d'Histoire Naturelle, Paris, 2e série*, 3, 564–572.
- Bruce, A.J. (1982) Notes on some Indo-West Pacific Pontoniinae. XL. The rediscovery of *Periclimenes lifuensis* Borradaile, 1898 (Decapoda, Pontoniine) and the establishment of its systematic position. *Crustaceana*, 42, 158–173.
- Bruce, A.J. (1994) A synopsis of the Indo-West Pacific genera of the Pontoniinae (Crustacea: Decapoda: Palaemonidae). *Theses Zoologicae*, 25, 1–172.
- Bruce, A.J. & Coombes, K.E. (1995) The palaemonoid shrimp fauna (Crustacea: Decapods: Caridea) of the Cobourg Peninsula, Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 12, 101–144.
- Chace, F.A. Jr. & Bruce, A.J. (1993) The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition 1907–1910, Part 6: Superfamily Palaemonoidea. *Smithsonian Contributions to Zoology*, 543, 1–152.
- De Grave, S., Pentcheff, N.D., Ahyong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D. & Wetzer, R. (2009) A classification of living and fossil genera of decapod crustaceans. *The Raffles Bulletin of Zoology*, Supplement 21, 1–109.
- Holthuis, L.B. (1952) The Decapoda of the Siboga Expedition. Part XI. The Palaemonidae collected by the Siboga and Snellius Expeditions with remarks on other species II. Subfamily Pontoniinae. *Siboga Expeditie*, 39-A10, 1–253.
- Kubo, I. (1940) A new shrimp, *Harpilius imperialis*. *Journal of the Imperial Fisheries Institute*, 34, 1–4.
- Li, X. (2000) Catalog of the genera and species of Pontoniinae Kingsley, 1878 (Decapoda, Pontoniinae). Xueyuan Press, Beijing, China. 319 pp.
- Nobili, G. (1905) Décapodes nouveaux des côtes d'Arabie et du Golfe Persique (diagnoses préliminaires). *Bulletin du Muséum National d'Histoire Naturelle*, 11, 158–164.
- Nobili, G. (1906) Mission J. Bonnier et Ch. Pérez (Golfe Persique, 1901). Crustacés décapodes et stomatopodes. *Bulletin Scientifique de la France et de la Belgique*, 90, 13–159, pls. 2–5.
- Poupin, J. (1998) Crustacea Decapoda and Stomatopoda of French Polynesia (Dendrobranchiata, Stenopodidea, Caridea, Thalassinidea, and Stomatopoda, with additions to the Astacidea, Palinuridea, Anomura, and Brachyura). *Atoll Research Bulletin*, 451, 1–62.