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A new species of *Pseudopandarus* Kirtisinghe, 1950 (Copepoda: Siphonostomatoida: Pandaridae) from sharks of the genus *Squalus* L. in New Caledonian waters

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Abstract Both sexes of a new species of pandarid copepod are described from sharks of the genus *Squalus* L. (Squaliformes: Squalidae). Specimens of *Pseudopandarus cairae* n. sp. were collected from *Squalus bucephalus* Last, Séret & Pogonoski and *S. melanurus* Fourmanoir & Rivaton in New Caledonian waters, the first parasitic copepod to be described from either host species. This is the eighth nominal species of *Pseudopandarus* Kirtisinghe, 1950 and the first to be described from a shark of the order Squaliformes. *Pseudopandarus cairae* n. sp. is easily distinguished from *P. australis* Cressey & Simpfendorfer, 1988, *P. longus* (Gnanamuthu, 1951) Cressey, 1967, and *P. pelagicus* Rangnekar, 1977 in having the female genital complex concealed beneath an elongate dorsal genital shield with a trilobed posterior margin. It can be distinguished from *P. gracilis* Kirtisinghe, 1950 and *P. scyllii* Yamaguti & Yamasu, 1959 by the armature of the leg 4 endopod and by the proportions of the dorsal genital shield. The new species is unique among known species of *Pseudopandarus* in its possession of only 1 setal element on the distal endopod segment of leg 4. In addition to describing the new species, the host associations of all species of *Pseudopandarus* are reviewed and observations are made regarding sexual dimorphism and mode of attachment. A key to the species considered valid is provided.

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Introduction

Copepods of the siphonostomatoid family Pandaridae are typically ectoparasites of a variety of elasmobranchs and, less commonly, species of actinopterygian fish. Most species of the copepod genus *Pseudopandarus* Kirtisinghe, 1950 are known from sharks of the order Carcharhiniformes. The present study was prompted by the collection of male and female specimens of a new species of *Pseudopandarus* from the sharks *Squalus bucephalus* Last, Séret & Pogonoski and *Squalus melanurus* Fourmanoir & Rivaton caught in waters off New Caledonia in 2002 and 2008. The material from *S. melanurus* was provisionally identified as *Pseudopandarus gracilis* Kirtisinghe, 1950 and was listed under that name by Boxshall & Huys (2007). This material, the first specimens of *Pseudopandarus* reported from a host belonging to the order Squaliformes, is included in our study. We also provide the first record of a parasite from the recently described shark *S. bucephalus*. Often, only female copepods are found attached to the host at the time of collection, and for many pandarid species the male remains undescribed. Here we describe both sexes, comment on sexual dimorphism and mode of attachment in the new species, review the host associations of all known species of *Pseudopandarus*, and provide a key to the valid species of *Pseudopandarus*.

Materials and methods

One specimen of *Squalus melanurus* was collected off the south coast of New Caledonia in February 2002, and one of *Squalus bucephalus* was collected off Récif Kué, New Caledonia in 2008. In total, ten females and one male of a new species of *Pseudopandarus* were removed from the outer body surface at the time of collection: three females were collected from the *S. melanurus*, and one male and seven females from *S. bucephalus*. The copepods were fixed in seawater-buffered formalin (9:1, seawater:full-strength formalin), and later transferred to 80% industrial methylated ethanol for storage and examination. Prior to examination, copepod specimens were cleared in lactic acid for at least 3 h and observed in glass cavity slides using a Leica dissecting microscope. When necessary, appendages were dissected using tungsten wire needles that had been electrolytically sharpened in aqueous potassium hydroxide following standard protocols.

Observations were made on an Olympus BX51 compound microscope equipped with differential interference contrast (DIC). Formal drawings were made with the aid of a drawing tube using pen and ink and Adobe Photoshop CS4, or with Adobe Illustrator CS4, or a combination of the 3. Caudal ramus measurements were made on the same microscope using an ocular reticule, while body length, width, and cephalothorax measurements were made on a Zeiss AxioZoom v.16 using Zen imaging software (Zeiss). Measurements are given in micrometres and are presented as the range followed in parentheses by the mean, standard deviation, and number of specimens measured. Shark taxonomy follows Fishbase (Froese & Pauly, 2016). Museum specimen abbreviations are as follows: NHMUK, The Natural History Museum, Department of Life Sciences, London, UK; MNHN, Muséum national d'histoire naturelle, Paris, France.

***Pseudopandarus cairae* n. sp.**

Syn. *Pseudopandarus gracilis* Kirtisinghe, 1950 of Boxshall & Huys (2007)

Type-host: *Squalus melanurus* Fourmanoir & Rivaton (Squaliformes: Squalidae).
Other host: *Squalus bucephalus* Last, Séret & Pogonoski (Squaliformes: Squalidae).
Type-locality: Waters off south coast of New Caledonia.
Other localities: Waters off Récif Kué, New Caledonia.
Site on host: Body surface.
Type-material: Holotype female (MNHN-IU-2016-5690) from skin of *Squalus melanurus* Fourmanoir & Rivaton caught off south coast of New Caledonia on 1.ii.2002 (coll. J.-L. Justine). Paratypes: 2 females, from skin of *Squalus melanurus* caught off south coast of New Caledonia on 1.ii.2002 (coll. J.-L. Justine); 1 female in MNHN-IU-2016-5691, 1 female (dissected) in NHMUK 2015.2937. Allotype male (NHMUK 2015.2943, part dissected) and 7 paratype females, from skin of *Squalus bucephalus* Last, Séret & Pogonoski caught off Récif Kué, New Caledonia, on 20.vii.2008 (coll. J.-L. Justine); 2 females in MNHN-IU-2016-5692; 5 females in NHMUK, 2015.2938-2942.
Comparative material: 1 female *Pseudopandarus gracilis* Kirtisinghe, 1950 NHMUK 1984.131 (BL = 5.75 mm), from upper surface of pectoral fin of *Mustelus* sp. caught off Durban, Republic of South Africa, 12.vi.1981 (coll. R.A. Bray).
Etymology: This species is named in honor of Janine Caira in recognition of her support of young investigators studying parasite taxonomy.

Description (Figs. 1–7)

Adult female (Figs. 1–4). Female body dorsoventrally flattened (Fig. 1A); body length 6,288–7,130 (6,669; n = 9), measured from anterior margin of frontal plates to posterior margin of dorsal genital shield; maximum width 1,997–2,165 (2,099; n = 10) at midlevel of cephalothorax. Cephalothorax wider than long, 1,997–2,165 (2,099; n = 10) wide by 1,154–1,916 (1,490; n = 8) long, incorporating first pedigerous somite, with marginal membrane. Nauplius eye visible dorsally through cuticle (Fig. 1A). Second to fourth pedigerous somites free, each bearing dorsal plates.

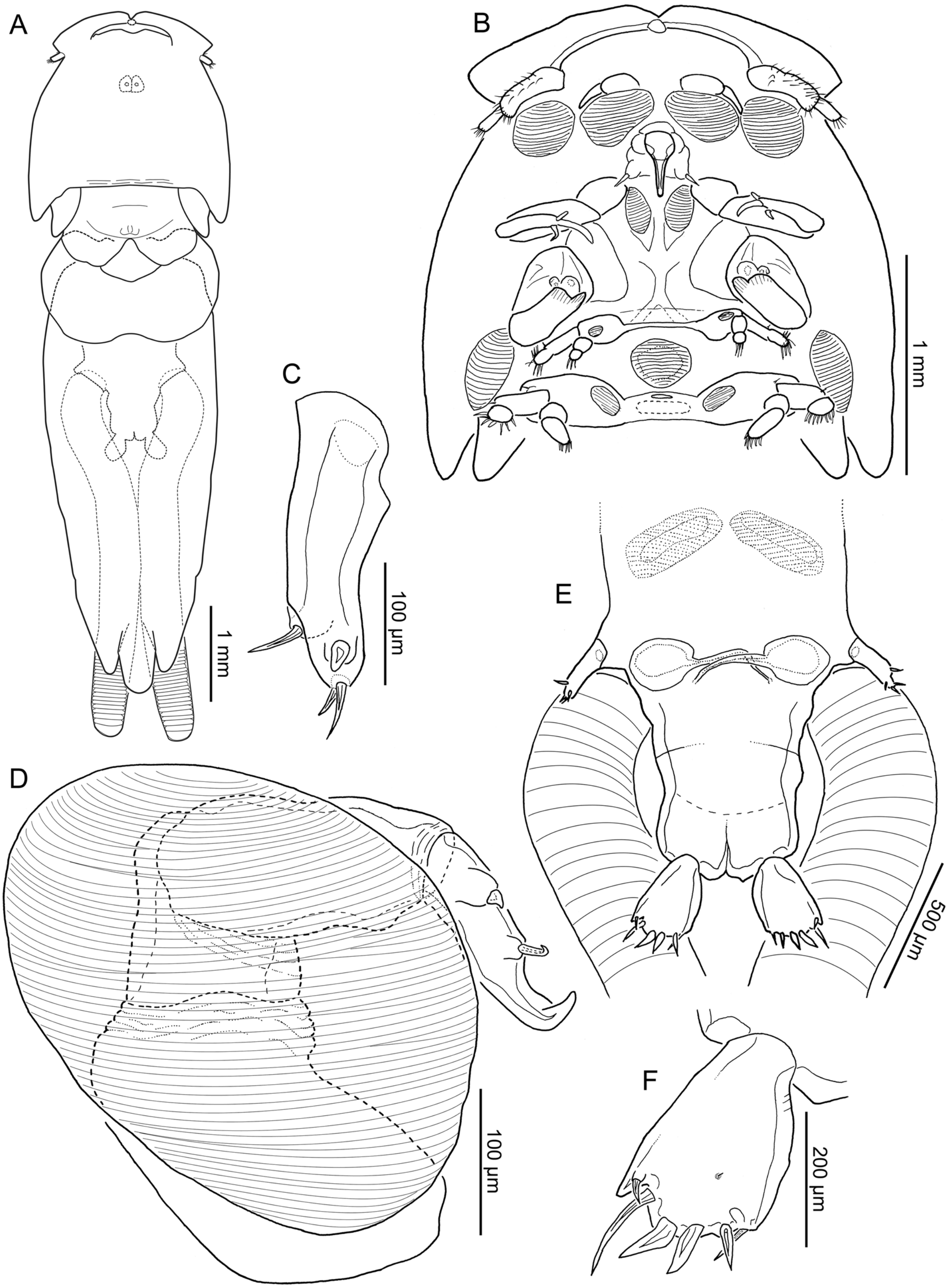

Fig. 1 *Pseudopandarus cairae* n. sp. female A, Habitus, dorsal view; B, Cephalothorax, ventral view: composite of multiple specimens to give ideal view of appendages; C, Leg 5, ventral view; D, Antenna, ventral view; E, Genital complex, ventral view; F, Caudal ramus, ventral view

Second pedigerous somite bearing pair of short, widely-separated, dorsal plates located laterally. Third pedigerous somite bearing bilobed dorsal plate, with free posterior margin indented medially: tips of lobes extending beyond tips of lateral plates on preceding somite. Fourth pedigerous somite with broad dorsal plate weakly indented in mid-posterior margin. Genital complex comprising at least fifth pedigerous somite and genital double-somite; complex completely covered by elongate dorsal genital shield (Fig. 1A) extending well beyond posterior end of body. Genital complex bearing paired oviduct openings laterally, just behind fifth legs, and paired sperm pores ventrally into which spermatophores discharge; 2 inconspicuous adhesive pads present on ventral surface (Fig. 1E). Abdomen 1-segmented, indistinctly separated from genital complex: bearing paired caudal rami on distal margin. Caudal rami 290–334 (309; n = 9) long by 208–232 (221; n = 9) wide, bearing 6 naked setae of varying length (Fig. 1F). Single sensilla present on ventral surface of caudal rami (Fig. 1F). Egg-strings uniseriate, elongate, extending near to or beyond posterior margin of dorsal genital shield.

Antennule 2-segmented, as in male; adhesion pad present (Fig. 5C). Proximal segment bearing 27 irregularly plumose setae. Distal segment narrow at base, bearing 13 setal elements: 2 conspicuously plumose, 2 aesthetascs visible on distal margin, 1 seta on mid-dorsal surface.

Antenna uniramous, 3-segmented, proximal 2 segments largely covered ventrally by ovoid adhesion pad (Fig. 1D). First 2 segments unarmed; distal segment curved anteroventrally forming strong terminal claw, bearing 2 setae each on raised base near anterior margin of segment. Distal seta narrow and elongate, curved anteriorly, on raised base; proximal seta short and robust, curved posteriorly, on large thumb-like base (Fig. 1D).

Oral cone tapering distally with narrow opening (Fig. 1B). Mandible elongate, stylet-like, bearing 12 marginal teeth near apex (Fig. 2A). Maxillule comprising anterior papilla and large posterior process (Fig. 2C). Anterior papilla bearing 3 naked setae; 1 seta conspicuously longer than others. Adhesion pad present posterior to maxillule, near medial margin of maxillary base (Fig. 2C). Adhesion pad with conspicuously jagged transverse ridges (Fig. 2C).

Maxilla 2-segmented, distal segment bearing 3 processes: 1 apical and 2 subapical processes (Fig. 2B); apical process larger than subapical processes; with spinulate margins; distal tip curved dorsally; anterior subapical process short, with smooth unornamented margins, with hollow channel extending from base proximally along length of second maxillary segment (Fig. 2B). Posterior subapical process slightly recurved, with spinose margins. Pore located on ventral surface of posterior margin of base of maxilla (Fig. 2B).

Maxilliped comprising robust proximal segment and broad, swollen distal segment: proximal segment with expanded myxal margin bearing 3 raised, strongly sclerotized lobes (Fig. 2E). Distal segment with conspicuous raised tubercle proximally and terminating in bilobed spatulate plate opposing raised protuberances on myxal margin of proximal segment (Fig. 2E).

Leg 1 biramous, comprising fused coxa and basis, 2-segmented endopod, and partially fused, 2 segmented exopod (Fig. 2D). Basipod with outer spine on anterior ventral surface and inner plumose seta posteriorly on dorsal surface; ornamented with adhesion pad on posterior margin. Exopod segments partially fused; proximal segment rectangular, conspicuously longer than distal, bearing recurved spine; distal segment with raised area on outer lateral margin ornamented with surface spinules (Fig. 2D). Setation formula for distal exopod segment III + I: 3; all but terminal element naked; terminal element with short, brush-like setules on posterior distal margin. Endopod proximal segment unarmed, slightly shorter than distal segment; distal segment armed with 3 naked distomedial setae.

Leg 2 biramous with 2 segmented rami (Fig. 3A). Coxa with medial adhesion pad ornamented with single sensilla, posterior adhesion pad extending dorsally at base of segment, patch of surface ornamentation along anterolateral margin, and small surface spinules on posterior margin (Fig. 3A). Basis with sensilla on ventral surface, outer spine, and rounded tubercle near base of exopod; tubercle with surface ornamentation. Exopod 2-segmented; proximal segment with outer spine and patch of spinulation near base of spine; distal segment with patch of surface spinulation and 9 setal elements; outermost lateral element originating on dorsal surface (Fig. 3A, C). Elements naked or with small hairs along one or both margins (Fig. 3A, C). Fourth element from outer margin particularly robust, conspicuously recurved in

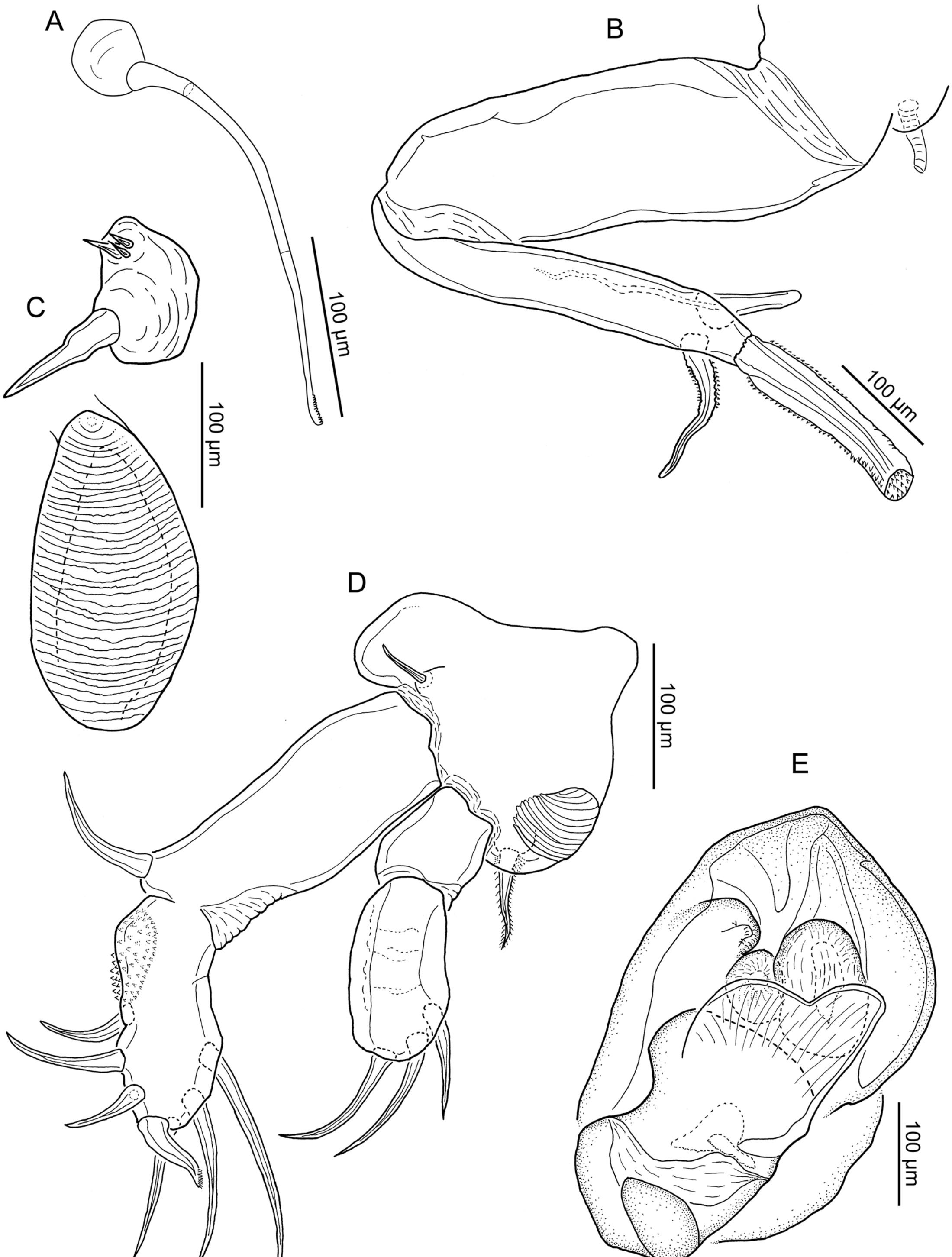

Fig. 2 *Pseudopandarus cairae* n. sp. female A, Mandible, ventral view; B, Maxilla, ventral view; C, Maxillule and associated adhesion pad, ventral view; D, Leg 1, ventral view; E, Maxilliped, ventral view

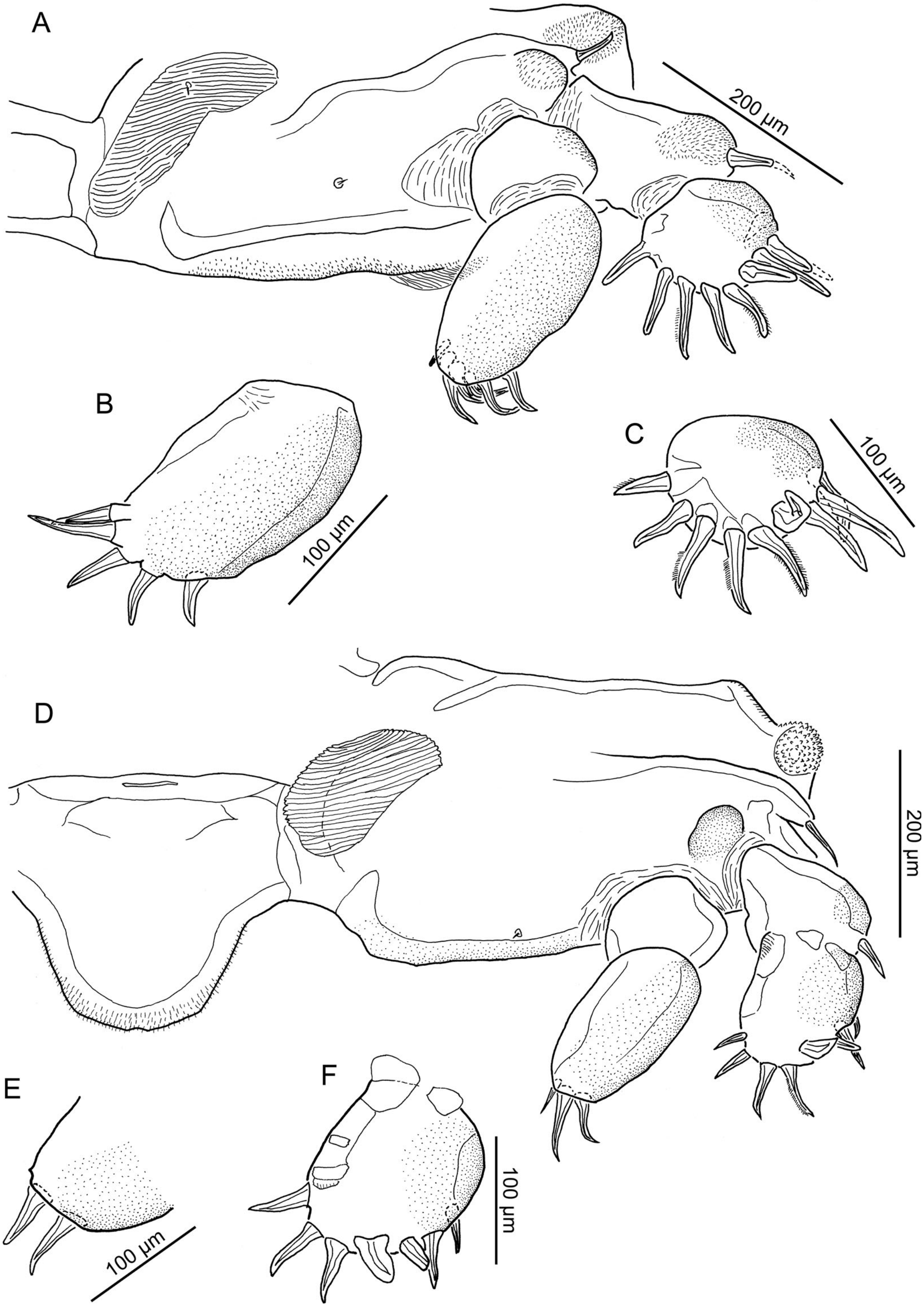

Fig. 3 *Pseudopandarus cairae* n. sp. female A, Leg 2, ventral view; B, Distal endopod segment of specimen with five setal elements, ventral view; C, Distal exopod segment of alternate specimen showing recurved setal element and relative lengths of setal elements, ventral view; D, Leg 3, ventral view; E, Tip of distal endopod segment from specimen with two setal elements, ventral view; F, Distal exopod segment from specimen with seven setal elements, ventral view

some specimens (Fig. 3C). Endopod 2-segmented; proximal segment with patch of surface elements on anterior lateral margin like exopod segment 1; distal segment with 5 or 6 setal elements depending on the specimen (see Table 1; Fig. 3A, B). Patch of small surface spinulation extending over outer margin of distal endopod segment.

Leg 3 biramous with large tongue-shaped extension on interpodal bar connecting coxae of leg pair (Fig. 3D); posterior margin of interpodal bar ornamented with short hair-like setules. Coxa with adhesion pad on anterior surface and, on outer margin, medial raised tubercle covered with spinules. Fine surface spinulation present along posterior margin of basis. Basis with ventral sensilla, raised tubercle with fine surface spinulation; outer spine located on swollen base; spine angled posteriorly. Exopod 2-segmented, segments partially fused; proximal segment with outer spine and small patch of surface spinulation; distal segment with 7 or 8 setal elements depending on specimen, and patch of fine surface spinulation (see Table 1; Figs. 3D, F). Setal elements usually naked, terminal element occasionally with fine setules on inner margin; fourth setal element from outer margin more robust (Fig. 3D, F). Endopod 2-segmented; proximal segment unarmed, surface spinulation not observed; distal segment with patch of fine surface spinules, armed with 2 or 3 setal elements (see Table 1; Figs. 3D, E).

Leg 4 biramous with segments of both rami fused (Fig. 4A). Coxa bearing medial adhesion pad and tubercle on lateral margin; tubercle and lateral margin with fine surface spinulation. Basis with single sensilla, fine surface spinulation along posterior margin, and lateral spine. Raised tubercle with surface spinulation present on basis near origin of exopod. Exopod segments fully fused, with 5 or 6 setal elements (see Table 1; Fig. 4A, B); fourth setal element from outer edge conspicuously robust relative to other elements; two rounded cuticular elements present on inner margin of exopod; two patches of fine surface spinulation present on outer margin of exopod. Endopod segments fused, with single terminal element and 2 patches of fine surface spinulation on outer margin.

Table 1 Setal elements of *Pseudopandarus cairae* n. sp. legs 2–4. Number of elements followed by the number of observations in parentheses

Leg	Distal endopod segment	Distal exopod segment
2	5 (n = 5); 6 (n = 4)	9 (n = 8); 8 (n = 1)
3	2 (n = 4); 3 (n = 6)	7 (n = 4); 8 (n = 6)
4	1 (n = 8)	5 (n = 4); 6 (n = 4)

Fifth legs located posterolaterally on genital complex, each 1-segmented with 4 setal elements (Fig. 1C). Outer setal element on raised base originating ventral to other elements. Sixth leg represented by unarmed plate closing off genital openings.

Adult male (Figs. 5–7). Male body dorsoventrally flattened (Fig. 5A); body length 3,504 measured from anterior margin of frontal plates to posterior margin of caudal rami, excluding caudal setae. Maximum width 1,590 at midlevel of cephalothorax. Cephalothorax longer than wide; 1,798 long by 1,590 wide, incorporating first pedigerous somite; marginal membrane present, extending across frontal plates (Fig. 1B) and along lateral margins of dorsal cephalothoracic shield. Nauplius eye visible dorsally (Fig. 5A). First pedigerous somite incorporated into cephalothorax. Second to fourth pedigerous somites free, each with simple tergite and lacking dorsal plates. Genital complex longer than wide; 827 long by 763 wide; narrower than cephalothorax (Fig. 1A); comprising fifth pedigerous and genital somites, ornamented with paired sensillae on ventral surface lateral to leg 6. Free abdomen 2-segmented: first abdominal somite bearing paired lateral sensillae on ventral surface (Fig. 5D). Anal somite bearing 2 pairs of sensillae on dorsal surface (not shown in figure). Caudal rami 235 long by 200 wide; ornamented with setules along inner margin. Each ramus bearing 6 setae; lateral setae short, ornamentation not observed; medial 4 setae of each ramus elongate and plumose (Fig. 5D).

Most appendages dimorphic relative to female except antennule (Fig. 5C) and mandible. Antennae 3-segmented, with numerous cuticular ridges and folds, lacking adhesion pad (Fig. 5F); second segment curved posteriorly; distal segment recurved forming strong terminal claw armed with 2 setae; distal seta elongate; proximal seta robust.

Oral cone tapering distally with narrow apical opening (Fig. 5B), as in female. Mandible as in female (Fig. 2A). Maxillule comprising anterior papilla with 2 naked setae and large, asymmetrical posterior process (Fig. 6C). Adhesion pad absent.

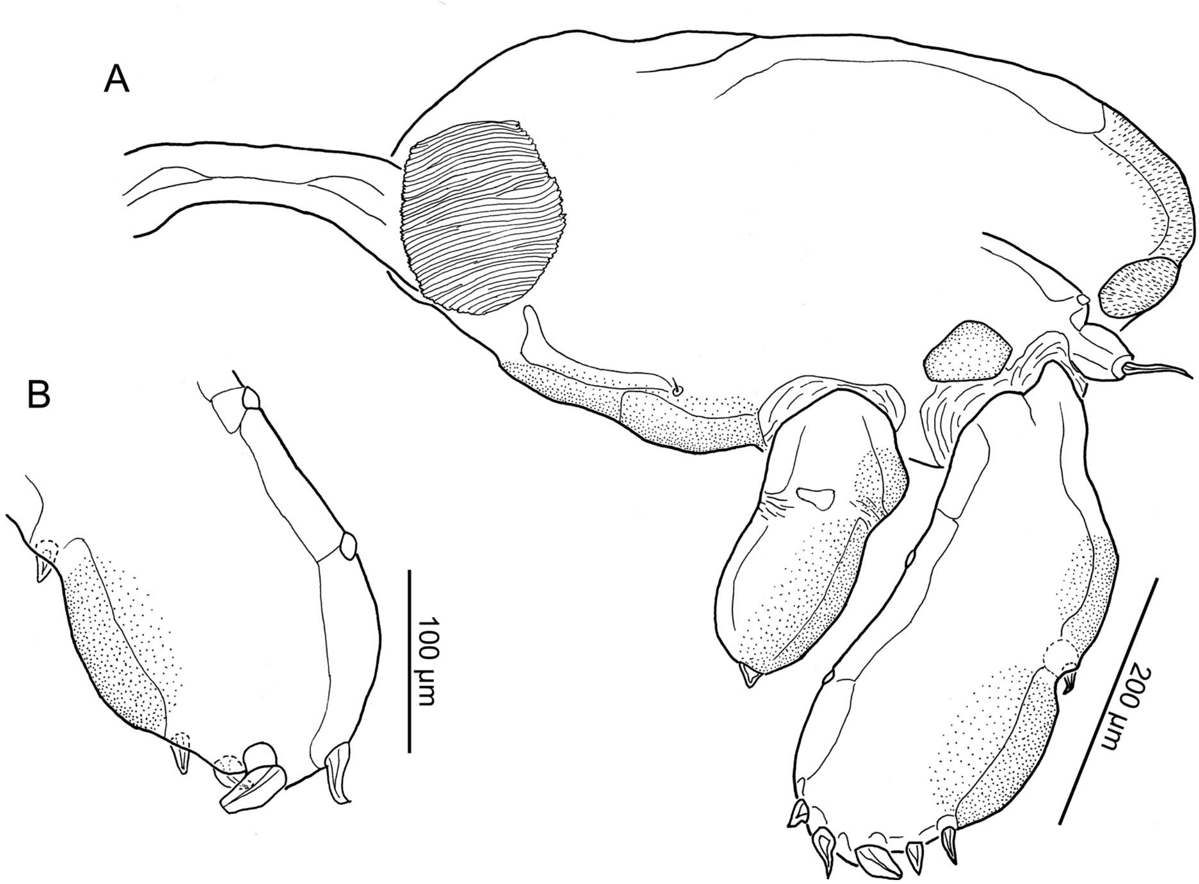

Fig. 4 *Pseudopandarus cairae* n. sp. female A, Leg 4, ventral view; B, Distal exopod with five setal elements, ventral view

Maxilla 2-segmented (Fig. 6A); apical and posterior subapical elements as in female. Anterior subapical element ornamented with stout setules; no channel observed. Pore located on ventral surface of posterior margin of base of maxilla.

Maxilliped 2-segmented; basal segment broad proximally, narrowing in middle but with distal part swollen and bearing 3 adhesion pads on myxal surface; distal subchela with broader base bearing apical claw with flange along inner margin (Fig. 6B). Conspicuous raised tubercle on posterior margin of distal segment as in female.

Leg 1 biramous and armed with elongate plumose setae (Fig. 6D). Exopod 2-segmented, segments distinct unlike female; setules present along inner margin of proximal exopod segment. Distal segment of exopod with spinules proximally on outer margin, 4 naked outer spines, and 3 plumose inner setae. Endopod as in female except setae plumose and setules present along outer margin of distal segment.

Leg 2 biramous, with extensive interpodal bar bearing subtriangular plate-like expansion ornamented with setules along posterior margin (Fig. 7B). Coxa and basis largely fused; coxa with inner plumose seta; basis with single sensilla, outer spine, and fine setules on inner posterior margin. Exopod 2-segmented; first segment bearing outer spine and inner plumose seta; ornamented with spinules on distal outer margin. Second segment with 4 spines and 6 plumose setae; terminal spine setulate along inner margin only. Endopod 2-segmented; proximal segment with plumose inner seta and long setules on outer margin; distal segment bearing 8 plumose setae, ornamented with long setules along outer margin, and short setules along inner.

Leg 3 like leg 2 but with more extensive interpodal bar (Fig. 7D) and differing armature on distal exopod segment; distal exopod segment with spinules and 4 naked spines increasing in size distally (Fig. 7A).

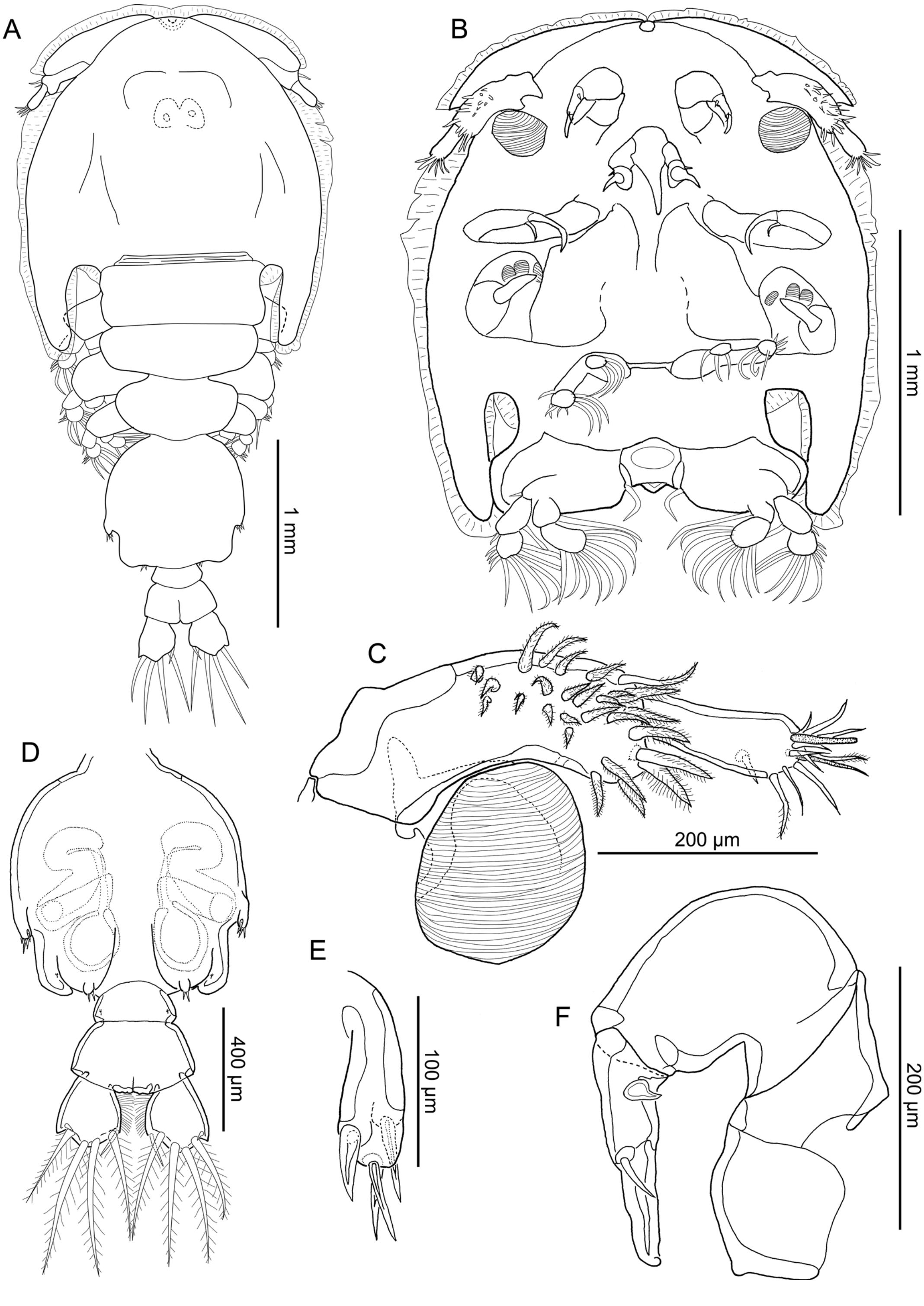

Fig. 5 *Pseudopandarus cairae* n. sp. Allotype male (NHMUK 2015.2943) A, Habitus, dorsal view; B, Cephalothorax, ventral view; C, Antennule, ventral view; D, Genital complex, ventral view; E, Leg 5, ventral view; F, Antenna, ventral view

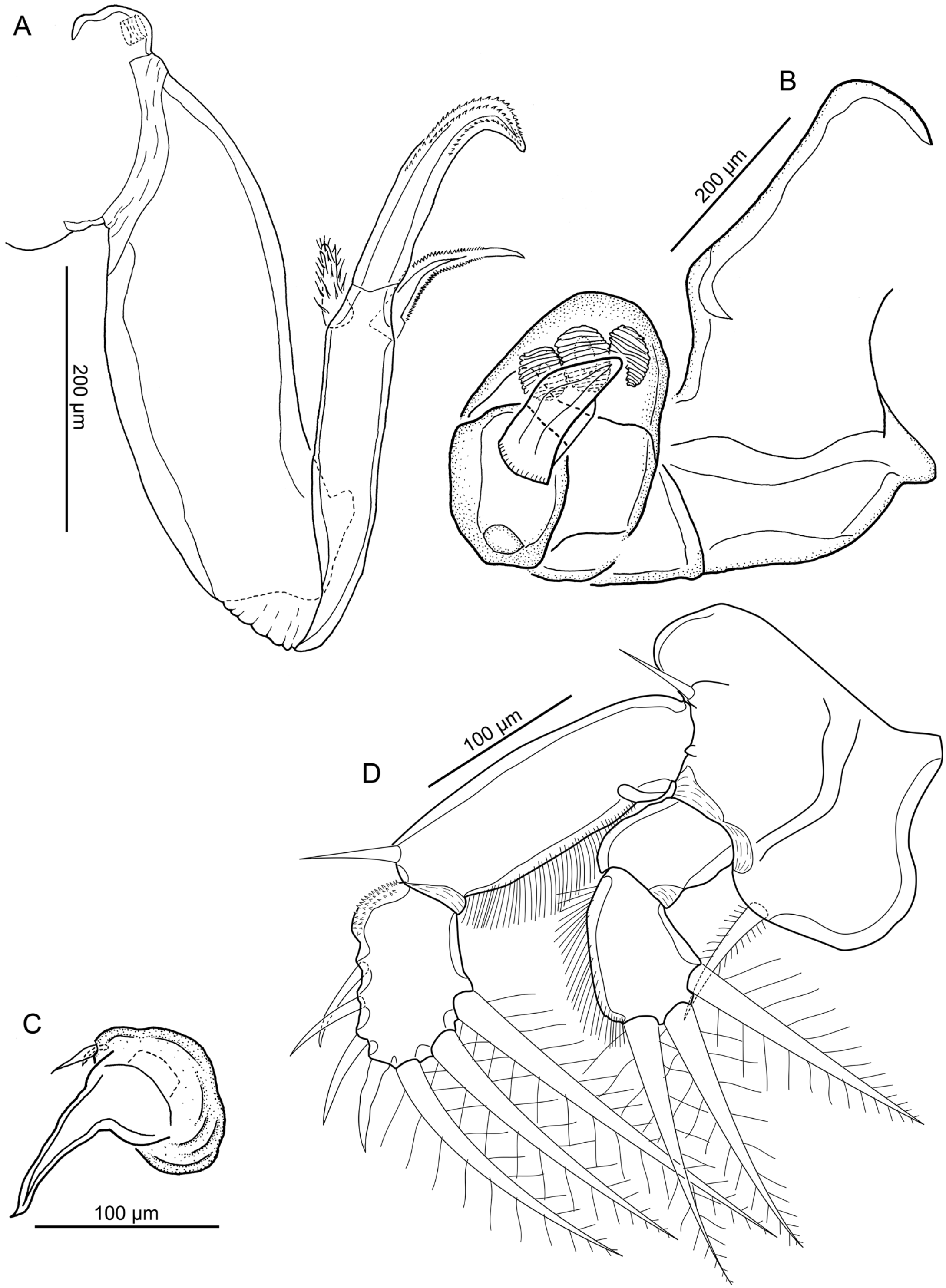

Fig. 6 *Pseudopandarus cairae* n. sp. Allotype male (NHMUK 2015.2943) A, Maxilla, ventral view; B, Maxilliped, ventral view; C, Maxillule, ventral view; D, Leg 1, ventral view

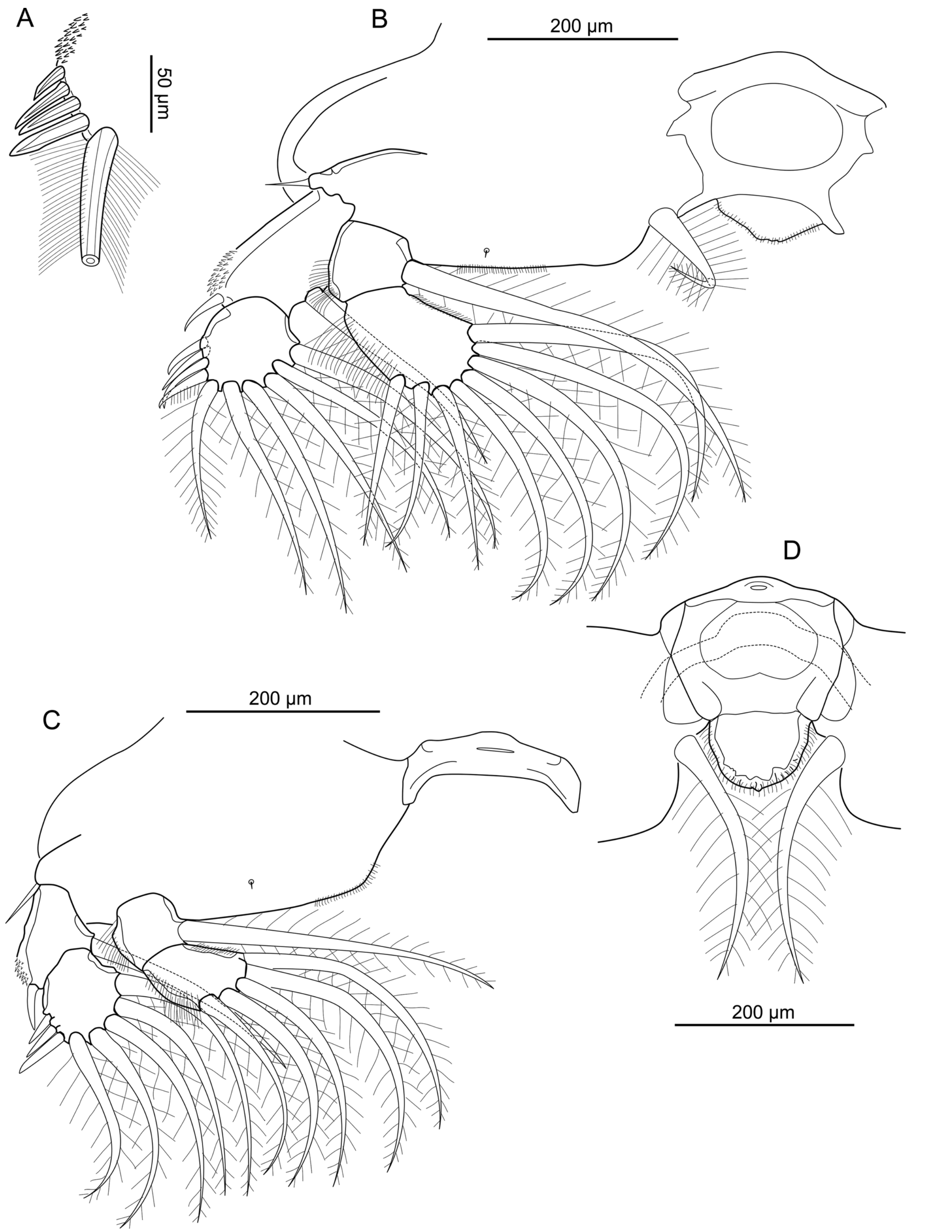

Fig. 7 *Pseudopandarus cairae* n. sp. Allotype male (NHMUK 2015.2943) A, Spines and terminal seta of leg 3 distal exopod segment, ventral view; B, Leg 2, ventral view; C, Leg 4, ventral view; D, Interpodal region of leg 3, ventral view

Leg 4 biramous with less extensive interpodal bar (Fig 7C). Coxa lacking inner seta. Basis with outer spine, sensilla near posterior margin, and setules along part of inner margin. Exopod 2-segmented; first segment with outer spine and inner plumose seta, spinules present along outer distal margin; second segment bearing 3 spines, increasing in length distally, and 5 plumose setae. Endopod 2-segmented; proximal segment with inner plumose seta and long setules along outer margin; distal segment bearing 5 plumose setae, long setules along outer margin, and short setules along inner.

Leg 5 located posterolaterally on genital complex, 1-segmented, armed with 4 setal elements (Fig. 5E). Sixth leg represented by unarmed plate closing off genital openings.

Remarks

There are seven nominal species of *Pseudopandarus*: *P. gracilis* Kirtisinghe, 1950; *P. longus* (Gnanamuthu, 1951) Cressey, 1967; *P. scyllii* Yamaguti & Yamasu, 1959; *P. bombayensis* Rangnekar & Rangnekar, 1972; *P. shiinoi* Rangnekar & Rangnekar, 1972; *P. pelagicus* Rangnekar, 1977; and *P. australis* Cressey & Simpfendorfer, 1988, but only six of these are currently treated as valid. In his revision of the family Pandaridae Milne-Edwards, 1840, Cressey (1967a) redescribed the type-species *P. gracilis* and treated *P. scyllii* as a junior subjective synonym of *P. gracilis*, although he did not examine type-material of *P. scyllii*. Pillai (1985) accepted this synonymy and, in addition, considered both *P. bombayensis* and *P. shiinoi* to be synonyms of *P. longus*. Cressey & Simpfendorfer (1988) made no mention of Pillai's monograph when they described *P. australis*, and included both *P. bombayensis* and *P. shiinoi* in their comparisons, effectively treating them as valid. We do not accept the synonymy of *P. scyllii* and *P. gracilis* and will discuss these species separately here. However, we follow the recommendation of Pillai (1985) to treat *P. bombayensis* and *P. shiinoi* as synonyms of *P. longus*, as there are no substantive differences apparent between these inadequate descriptions. We consider it likely that Pillai's monograph was unavailable to Cressey & Simpfendorfer (1988) at the time.

The new species can be readily distinguished from *P. australis*, *P. longus* and *P. pelagicus* in having an elongate dorsal genital shield with a trilobed posterior margin. In all of these species the caudal rami are visible in dorsal view, whereas the abdomen and caudal rami of the adult female are completely concealed in the new species. *Pseudopandarus cairae* n. sp. resembles *P. scyllii* and *P. gracilis* in this feature, but can be distinguished by other characters.

The new species differs from *P. scyllii* as described by Yamaguti & Yamasu (1959) in possessing a single setal element on the tip of the endopod of leg 4, whereas *P. scyllii* possesses two apical setae on this ramus. We noted variation in setation of both rami of legs 2 and 3, and of the exopod of leg 4 (see Table 1), but the endopod of leg 4 carried a single stumpy conical element on both right and left legs of all four specimens where this leg was intact. There are other subtle differences in gross morphology; for example, the dorsal genital shield is longer relative to the length of the genital complex and abdomen in the new species. In *P. scyllii* the posterior margins of the caudal rami reach over half the distance from the posterior margin of the dorsal plates on the fourth pedigerous somite to the end of the dorsal genital shield, whereas in the new species the posterior margins of the caudal rami extend only about one third of this distance. The dorsal genital shield, measured from the posterior margin of the dorsal plates on the fourth pedigerous somite, is twice as long as wide in the new species but less than 30% longer than wide in *P. scyllii*.

The new species is most similar to *P. gracilis* as redescribed by Cressey (1967a) based on his examination of the Kirtisinghe's paratypes. Indeed, the material from *S. melanurus* was provisionally identified as *P. gracilis* in the list of Boxshall & Huys (2007). However, the new species is unique in the possession of a single stumpy setal element on the endopod of leg 4, rather than the two setae reported by Cressey for *P. gracilis* (see Cressey, 1967a). In addition, the gross morphology of the dorsal genital shield differs in these two species: in *P. gracilis* the trilobed posterior end of the shield begins at the level of the caudal rami (figure 147 in Cressey, 1967a) whereas in *P. cairae* n. sp. the abdomen extends less than half the length of the shield. The new species also differs from *P. gracilis* in its possession of seven setal elements on the distal exopod segment of leg 1, rather than six and in its possession of five or six, rather than seven, setal elements on the distal endopod segment of leg 2. However, interpreting exactly what constitutes a setal element can be problematic in *Pseudopandarus* since elements can be reduced to mere nodules on the margin of the ramus (see Fig. 4A, B).

Pillai (1985) also redescribed female *P. gracilis* based on new material he collected. His description differs slightly from that of Cressey (1967a), which was based on examination of the paratypes from Sri Lanka as well as six females collected from off Madagascar. Pillai illustrates three setae as present on the tip of the endopod of leg 4, rather than the two found by Cressey. The apical element on the maxilla is blunt and recurved in Pillai's material rather than tapering to a point (as in Cressey's). In addition, the median lobe of the dorsal genital shield is shorter than the lateral lobes in Pillai's description but longer in Cressey's, and shield is relatively longer in Pillai's material. These differences suggest that Pillai's (1985) *P. gracilis* might not be attributable to *P. gracilis* as defined by Cressey's (1967a) redescription of the paratypes, but this can only be resolved by the study of additional material from Indian waters.

Key to the valid species of *Pseudopandarus* based on adult females

1a Genital complex of female concealed in dorsal view by elongate, trilobed, dorsal genital shield …………………………………………………. 2

1b Genital complex elongate, with caudal rami clearly visible in dorsal view; dorsal genital shield bearing 2 blunt lateral lobes on posterior margin ..…………………………………….. 4

2a Leg 4 with 2 setal elements on apex of endopod; dorsal genital shield, as measured from the posterior margin of the dorsal plates on the fourth pedigerous somite, less than 30% longer than wide ……………………….…………….... 3

2b Leg 4 with single stout element on apex of endopod; dorsal genital shield about twice as long as wide …………………… *P. cairae* n. sp.

3a Posterior margins of caudal rami reaching about half distance from posterior margin of dorsal plates of fourth pedigerous somite to end of dorsal genital shield …..………………. *P. scyllii*

3b Posterior margins of caudal rami reaching to paired clefts marking subdivisions of trilobed posterior end of dorsal genital shield ..…………………………………… *P. gracilis*

4a Genital complex of female wider than long …………………..…………….…. *P. pelagicus*

4b Genital complex of female longer than wide ………………………………………………. 5

5a Leg 1 endopod with 1 seta on outer margin; paired dorsal plates of fourth pedigerous somite separated by shallow concave indentation ……………………………..….. *P. australis*

5b Leg 1 endopod with 3 setae on inner margin; paired dorsal plates of fourth pedigerous somite separated by V-shaped cleft …………………… ……………………………………… *P. longus*

Host reports of species of *Pseudopandarus*

All known host reports for species of *Pseudopandarus* are listed in Table 2. Host records are based on literature searches and reports gathered from WoRMS (Walter & Boxshall, 2016) and Shark-References Parasite-Host list (Pollerspöck & Straube, 2016). There is uncertainty regarding the identity of some of the hosts recorded for *Pseudopandarus* species. Host records for the type-species, *P. gracilis,* are most problematic as Kirtisinghe only noted in his description that specimens came from "a large dogfish" (Kirtisinghe, 1950: 84). Cressey (1967a) noted that Kirtisinghe loaned him paratypes from *Scoliodon palasorrah*, and Cressey (1967b: 3) added an authority for the host of a *P. gracilis* specimen as "*Scoliodon palasorrah* (Bleeker)". However, Compagno & Niem (1998) considered this combination to be a synonym of *Rhizoprionodon acutus* (Rüppell), *R. oligolinx* Springer and *Scoliodon laticaudus* Müller & Henle. Since all three of these species occur in the waters off Sri Lanka where Kirtisinghe was working, it is unclear which host Kirtisinghe's paratypes came from although Dippenaar (2004) considered the valid host to be *R. acutus*. In addition, as part of this study we examined specimens consistent with Cressey's (1967a) redescription of *P. gracilis* collected from a species of *Mustelus* in waters off South Africa. Because species of *Mustelus* are difficult to identify with confidence (Ebert & Stehmann, 2013) and multiple species are known to occur in waters off South Africa (Froese & Pauly, 2016), we list this host report as *Mustelus* sp. Gnanamuthu (1951: 1236) described *P. longus* from hosts recorded only as "carcharhinid sharks caught near Rameshvaram, India". Cressey (1967a) helped clarify the host records by reporting specimens of *P. longus* collected from *Rhizopriondon acutus* and *Carcharhinus obesus*.

Table 2 *Pseudopandarus* spp. hosts

Valid copepod species	Reported host species	Reference
Pseudopandarus australis	Type-host: *Rhizoprionodon taylori* (Ogilby, 1915)	Cressey & Simpfendorfer (1988)
	Other hosts: *Carcharhinus dussumieri* (Müller & Henle, 1839)	Cressey & Simpfendorfer (1988)
	Hemigaleus microstoma Bleeker, 1852	Cressey & Simpfendorfer (1988)
	Rhizoprionodon acutus (Rüppell, 1837)	Cressey & Simpfendorfer (1988)
	Sphyrna lewini (Griffith & Smith, 1834)	Cressey & Simpfendorfer (1988)
Pseudopandarus cairae n. sp.	Type-host: *Squalus bucephalus* Last, Séret & Pogonoski, 2007	Present study
	Other hosts*: Squalus melanurus* Fourmanoir & Rivaton, 1979	Present study
Pseudopandarus gracilis	Type-host: "large dogfish"	Kirtisinghe (1950)
	Other hosts: *Mustelus mosis* Hemprich & Ehrenberg, 1899	Dippenaar & Jordaan (2007)
	Scoliodon sp.	Cressey (1967b)
	"*Scoliodon palasorrah* Bleeker"[a]	Cressey (1967b)
	Mustelus sp.	Present study
Pseudopandarus longus	Type-host: "carcharinid sharks"	Gnanmuthu (1951)
	Other hosts: *Triaenodon obesus* (Rüppell, 1837) (as *Carcharinus obesus)*	Cressey (1967a)
	Carcharhinus dussumieri (Müller & Henle, 1839)	Dippenaar (2004)
	Carcharhinus obscurus (Lesueur, 1818)	Dippenaar & Jordaan (2007)
	Carcharhinus sealei (Pietschmann, 1913)	Dippenaar & Jordaan (2007)
	Carcharhinus sorrah (Müller & Henle, 1839)	Henderson et al. (2013)
	Carcharhinus tjutjot (Bleeker, 1852)	Cressey (1967b)
	Mustelus mosis Hemprich & Ehrenberg, 1899	Dippenaar & Jordaan (2007)
	Rhizoprionodon acutus (Rüppell, 1837)	Cressey (1967a, b)
	Rhizopriondon sp.	Cressey (1967b)
(as *P. bombayensis*)	Type-host: *Carcharinus limbatus* (Müller & Henle, 1839)	Rangnekar & Rangnekar (1972)
(as *P. shiinoi*)	Type-host: *Tetrodon oblongus* (Bl. & Schn.)[b]	Rangnekar & Rangnekar (1972)
Pseudopandarus pelagicus	Host unknown; collected in plankton	Rangnekar (1977)
Pseudopandarus scyllii	Type-host: *Triakis scyllium* Müller & Henle, 1839	Yamaguti & Yamasu (1959)

[a] Possibly *Rhizopriodon acutus*, *R. oligolinx* Springer, 1964 or *Scoliodon laticaudus* according to Compagno & Niem (1998)

[b] Valid name of this host *Takifugu oblongus* (Bloch, 1786), but see text for comments

However, the latter species was recognized as belonging to the genus *Triaenodon* Müller & Henle by Compagno (1984) and given the new combination *Triaenodon obesus* (Rüppell) Compagno, 1984; this combination has already been treated as the valid host report by Dippenaar (2004).

Rangnekar & Rangnekar (1972) gave the host *of P. shiinoi* as "*Tetrodon oblongus* (Bl. & Schn.)", so this is the only species of the genus reported from a non-elasmobranch. The currently accepted name of this fish is *Takifugu oblongus* (Bloch). Rangnekar & Rangnekar (1972) mentioned that they had examined numerous other pufferfish in an unsuccessful attempt to find additional material. They considered it likely that the parasites had left their usual host after capture. We also consider the presence of *Pseudopandarus* on

Takifugu oblongus to be a likely result of contamination post-capture and in need of confirmation. One species of *Pseudopandarus*, *P. pelagicus*, was found free in the plankton (Rangnekar, 1977) and its host remains unknown.

Discussion

Five of the eight described species of *Pseudopandarus* are known from the Indian Ocean. Outside of the Indian Ocean, *P. scyllii* is known from the coast of Japan, while *P. australis* and *P. cairae* n. sp. are known from the southwestern Pacific. Collectively, existing reports suggest species of *Pseudopandarus* are endemic to the Indian Ocean and western Pacific Ocean, but many potential host species from localities around the globe remain to be examined for species of *Pseudopandarus*, so at this time it is unclear if this is a true distribution or perhaps the result of sampling bias. Nonetheless, current reports indicate a broad host range for species of *Pseudopandarus*. *Pseudopandarus cairae* represents the first report of a *Pseudopandarus* species from a shark of the order Squaliformes. Prior to this study, virtually all reports of *Pseudopandarus* were from sharks of the order Carcharhiniformes, the exception being the description of *P. shiinoi* from a pufferfish. Yet even among carcharhiniform sharks, the host range of *Pseudopandarus* species is quite varied. Most reports have come from members of the Carcharhinidae, but species of *Pseudopandarus* have also been reported from three other families of the Carcharhiniformes: Sphyrnidae, Hemigaleidae, and Triakidae. Individual species are known to parasitize different host families; for instance, *P. australis* has been reported from species of Carcharhinidae, Sphyrnidae, and Hemigaleidae (Cressey & Simpfendorfer, 1988). Despite the substantial phylogenetic range of host taxa, it is noteworthy that many host species exhibit some ecological similarities. For instance, similar to species of *Squalus*, most charcharhiniform sharks from which species of *Pseudopandarus* have been reported are small to medium sized, shallow water, bottom dwelling sharks. In fact, species of *Squalus* are known to sometimes occur in mixed species schools with sharks of the genera *Triakis* Müller & Henle and *Mustelus* Linck (Compagno, 1984), which also host species of *Pseudopandarus*. Overlapping distributions on geographic and local scales are thought to play an important role in host specificity because they increase the encounter rate of a parasite with sympatric taxa that may serve as potential hosts (Poulin et al., 2011). Mixed schooling is an extreme example of habitat overlap, and may facilitate host switching.

There seem to exist two morphotypes within the genus *Pseudopandarus*. In the first morphotype, comprising *P. gracilis*, *P. scyllii*, and *P. cairae* n. sp., females possess an elongate, trilobed, dorsal genital shield that conceals the genital complex in dorsal view. In the second morphotype, exhibited by *P. australis*, *P. longus*, and *P. pelagicus*, the genital complex is more elongate, with caudal rami unconcealed by a dorsal genital shield that bears only two blunt lateral lobes on the posterior margin. Due to the lack of specimens preserved for molecular analyses (i.e. in 95–100% ethanol rather than formalin) we were unable to evaluate these morphotypes using molecular data, but it would be interesting to test the relationship of these morphotypes with morphological and molecular phylogenetic analyses.

Pseudopandarus cairae n. sp. is the first species of the former morphotype for which the male has been described. Like other pandarids, males and females of the new species exhibit a number of sexually dimorphic traits in addition to the typical dimorphic traits of parasitic copepods (i.e. larger body size, relatively larger genital complex in females). For instance, *P. cairae* n. sp. females possess 11 pairs of adhesion pads and a single adhesion pad between leg 1 and 2, while males possess only a single pair at the base of the antennules (Figs. 1B, 5B). Typically, these pads are associated with an appendage, as with those near the antennules, antennae, maxillae and swimming legs; however, an inconspicuous pair of adhesion pads is also present on the female genital complex anterior to leg 5, and 2 pads are present on postero-lateral sides of the cephalothorax. In females, the coxa of leg 2 bears an additional, less conspicuous adhesion pad on its posterior margin (see Fig. 3A). This is particularly interesting in light of the functional morphology of pandarid adhesion pads described by Ingram & Parker (2006), which provided a number of mechanisms through which adhesion pads may increase friction for attachment. Unlike the other pads, the adhesion pad at the posterior margin of leg 2 is not located at a primary contact point between the copepod body and the host's scales (i.e. along the main plane of the ventral surface of the female body) where it would provide the most friction (Ingram & Parker, 2006). At this time, the function of this adhesion pad is unclear, but its peculiar position on leg 2 suggests it may form a clamp with the endopod to grasp a host scale. Because of the important role adhesion pads are suspected to play in this host parasite system, and the fact that the pandarids that attach primarily to gills possess fewer adhesion pads (Cressey, 1967a), we recommend that particular attention be paid to the presence and arrangement of adhesion pads, and drawings be made of the ventral view of the cephalothorax in pandarid descriptions. DIC is particularly useful for observing inconspicuous adhesion pads; this could be why we were the first to note the presence of adhesion pads on the female genital complex and the second pair of adhesion pads on the posterior margin of leg 2 in a species of *Pseudopandarus* (see Figs. 1E, 3A). It would be interesting to examine other species of *Pseudopandarus* for these adhesion pads using DIC microscopy.

In addition to the arrangement of adhesion pads, the maxillipeds and swimming legs exhibit marked sexual dimorphism in *P. cairae* and other pandarids. Benz (1992) and Dippenaar & Jordaan (2006) showed that the female maxillipeds of *Pandarus bicolor* Leach, 1816 and *Nesippus orientalis* Heller, 1868, respectively, acutely grasp individual placoid scales. Interestingly, the male maxilliped differs conspicuously from that of the female, and the nature by which this appendage interdigitates with host scales has not been demonstrated. It is likely that male maxilliped morphology diverges because it must securely grasp not only placoid scales, but also females during fertilization as was observed in *Nesippus orientalis* by Dippenaar & Jordaan (2006). Finally, the swimming legs, and particularly their setae, differ substantially in males and females, suggesting important differences in attachment and motility. While all male swimming legs possess elongate plumose setae, females lack functional swimming setae and possess more robust, claw-like setal elements. We infer from this that adult males retain some ability to swim, possibly between host individuals in search of females, while the lack of plumose setae, the fusion of female leg segments, and the greater number of adhesion pads suggest adult females cannot swim efficiently but are instead more adapted for attachment to their host.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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