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Synalpheus pinkfloydi sp. nov., a new pistol shrimp from the tropical eastern Pacific (Decapoda: Alpheidae)

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Abstract

A new, conspicuously coloured species of the alpheid genus *Synalpheus* Spence Bate, 1888, is described based on material collected on the Pacific coast of Panama. *Synalpheus pinkfloydi* **sp. nov.** is closely related to the western Atlantic *S. antillensis* Coutière, 1909, the two taxa being transisthmian, cryptic sister species. Both species are characterised by the distal areas of their major and minor chelae coloured in an intense, almost glowing pink-red. The morphological differences between *S. pinkfloydi* **sp. nov.** and *S. antillensis* Coutière, 1909 are subtle, being limited to the slightly different proportions of the merus of both chelipeds, distodorsal armature of the major cheliped merus, relative length of the antennal scaphocerite, and body size. However, they are genetically different with a 10.2% sequence divergence in COI. Based on molecular clock estimates, these transisthmian taxa diverged around 6.8–7.8 mya, i.e. well before the final closure of the Isthmus of Panama 2.5–3 mya.

Key words: Malacostraca, Caridea, snapping shrimp, Pacific Ocean, transisthmian taxa

Introduction

The snapping or pistol shrimps of the family Alpheidae are one of the most studied model taxa for marine transisthmian speciation (e.g. Knowlton *et al.* 1993; Williams *et al.* 2001; Morrison *et al.* 2004; Lessios 2008; Hurt *et al.* 2009; Hultgren & Duffy 2011; Hultgren *et al.* 2014). Most of the published studies deal with members of the two largest alpheid genera, *Alpheus* Fabricius, 1798 and *Synalpheus* Spence Bate, 1888.

Despite significant taxonomic effort, which has resulted in the description of numerous new taxa over the last decade (e.g. Anker *et al.* 2007, 2008, 2009; Ríos & Duffy 2007; Anker & Tóth 2008; Hultgren *et al.* 2010; Bracken-Grissom *et al.* 2014), many taxonomic uncertainties still remain, in particular among transithmian species complexes of *Synalpheus*. For instance, in the *S. brevicarpus* (Herrick, 1891)—*S. minus* (Say, 1818) clade, also known as the *S. brevicarpus* species group, the existence of closely related species was already postulated upon by Coutière (1909), who established several "varieties" based on morphological criteria. Coutière's suspicions were recently confirmed by a preliminary molecular assessment of the worldwide diversity of *Synalpheus* (Hultgren *et al.* 2014), which included numerous transisthmian taxa. In their study, Hultgren *et al.* (2014) clearly showed that several members of the *S. brevicarpus* group indeed contained two or more genetically distinct taxa, i.e. putative cryptic species. One of them is *S. antillensis* Coutière, 1909, which itself was revived from the synonymy of *S. minus* only quite recently (Anker *et al.* 2012). The molecular analyses of Hultgren *et al*. (2014) revealed that the western Atlantic specimens of *S. antillensis* were genetically clearly distinct from the eastern Pacific specimens, which therefore were referred to as "*S.* aff. *antillensis*". In the present study, this eastern Pacific taxon, which hitherto remained without a proper scientific name, is described as a new species.

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Material and methods

Type material is deposited in the collection of the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP), and the Zoological Collections of the Oxford University Museum of Natural History, Oxford, United Kingdom (OUMNH.ZC). All comparative material of *S. antillensis* listed below is deposited in the OUMNH.ZC.

All drawings were made using a dissecting stereomicroscope equipped with a camera lucida. Carapace length (cl, in mm) was measured from the tip of the rostrum to the posterior margin of the carapace. The abbreviations "fcn" is used for field collection number, which in most cases also corresponds to a photographic voucher of the specimen.

The mean Kimura 2-parameter distance (K2P) of the COI gene was calculated using MEGA version 6 (Tamura *et al.* 2013). The previously published molecular clock estimates of genetic divergence in the COI sequence, viz. 1.4% divergence/my (Morrison *et al.* 2004) and 1.5% divergence/my (Knowlton 1993; Knowlton & Weigt 1998) and the mean K2P distance (n=6 comparisons) were used to calculate approximate divergence times between the two presumed sister taxa. A more comprehensive molecular analysis of the *S. brevicarpus* group, using Bayesian methodology (as in Hultgren *et al.* 2014), will be published elsewhere.

Comparative material examined. *Synalpheus antillensis* Coutière, 1909: 1 male (cl 3.7 mm), OUMNH.ZC. 2012.07.038, Panama, Isla Grande, western point, depth: less than 2 m, in coral rubble crevices, leg. A. Anker & C. Hurt, 06.x.2005; 1 male (cl 3.8 mm), OUMNH.ZC. 2007.20.058, Honduras, Utila, small shallow bay, 16°05.458'N 086°54.533W, depth: 1 m, in coral rubble crevices, leg. A. Anker & S. De Grave, 03.vii.2007; 1 male (cl 3.8 mm), 1 ov. female (cl 4.5 mm), OUMNH.ZC. 2009.01.079, Belize, Carrie Bow Cay, outer reef, 16°48.138'N 88°04.842'W, intertidal, in coral rubble crevices, leg. D.L. Felder & S. De Grave, 21.ii.2009; 1 male (cl 3.1 mm), OUMNH.ZC. 2012.07.110, Mexico, Gulf of Mexico, Alacranes Reef, St. ALN49, 22°24'14.2"N 89°42'48.8"W, depth: 12 m, in crevices of coral rocks, leg. J. Duarte-Gutiérrez, 14.viii.2009; 1 male (cl 3.4 mm), OUMNH.ZC. 2012.07.144, Brazil, Alagoas, Maceió, Ponta Verde, fossil coral platform partly exposed at low tide, in deep crevices of fossilised corals, leg. A. Anker & P.P.G. Pachelle, 02.viii.2012.

Taxonomy

Family Alpheidae Rafinesque, 1815

Genus *Synalpheus* Spence Bate, 1888

Synalpheus pinkfloydi sp. nov.

(Figs. 1–3)

Synalpheus aff. *antillensis*—Hultgren *et al.* 2014: Suppl. Data 1; Suppl. figs. 2, 3, 5; fig. 3 (cladogram).

Type material. Holotype: male (cl 5.5 mm), MZUSP 33778, Panama, Pacific coast, Las Perlas Archipelago, Isla Bartolomé (near Isla Contadora), intertidal and shallow subtidal rocky bottom, in crevices of rocks and living and dead corals, low tide, leg. A. Anker *et al.*, 18.iv.2015. Paratypes: 1 ovig. female (cl 6.6 mm), MZUSP 34615, same collection data as for holotype; 1 female (cl 5.3 mm), MZUSP 33779, Panama, Pacific coast, Las Perlas Archipelago, Isla Contadora, eastern end of Playa Galeon, in crevices of rocks and coral rubble, low tide, leg. A. Anker *et al.*, 16.iv.2015; 1 female (cl 4.9 mm), OUMNH.ZC. 2013.03.044, Panama, Pacific coast, Las Perlas Archipelago, Isla Saboga, intertidal, in crevices of rock and coral rubble, leg. A. Anker *et al.*, 15.xi.2005 (fcn 05-074).

Additional material examined. 1 ovig. female (cl 4.7 mm), OUMNH.ZC. 2013.03.046, Panama, Pacific coast, Taboga Archipelago, Isla Taboga, channel between Isla Taboga and Isla Taboguilla, rocky intertidal with partly exposed corals, coral rubble and large rocks, leg. A. Anker *et al.*, 21.ii.2007 (fcn 07-066); 1 immature specimen (cl 3.5 mm), OUMNH 2013.03.045, same collection data (fcn 07-061); 1 male (cl 5.2 mm), 1 ovig. female (cl 5.2 mm), OUMNH. 2013.03.047, same collection data (fcn 07-065).

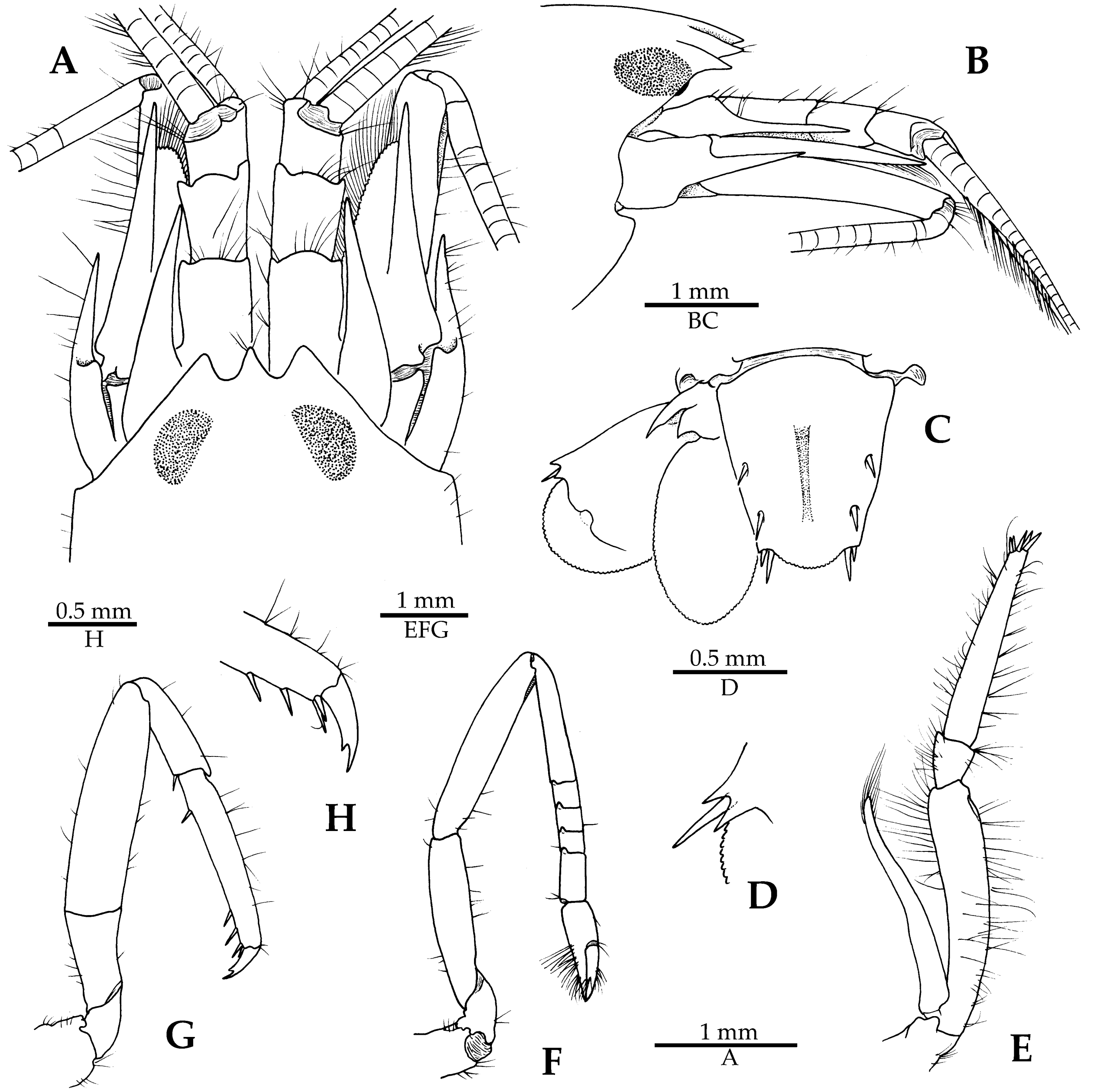

FIGURE 1. *Synalpheus pinkfloydi* **sp. nov.**, holotype male (MZUSP 33778), Las Perlas Archipelago, Panama: A, frontal region, dorsal view; B, same, lateral view; C, telson and left uropod, dorsal view; D, uropod, detail of distolateral area, dorsal view; E, third maxilliped, lateral view (arthrobranch omitted); F, second pereiopod, lateral view; G, third pereiopod, lateral view; H, same detail of distal propodus and dactylus, lateral view.

Description. Small-sized species of *Synalpheus brevicarpus* group (maximum cl 6.6 mm in females), with subcylindrical, non-compressed body. Carapace and abdomen smooth, with few scattered setae. Rostrum subtriangular in dorsal view, rounded or subacute distally, slightly longer than wide, equal in length to orbital teeth, of equal width or slightly narrower than orbital teeth (Fig. 1A), occasionally reduced. Orbital hoods feebly inflated; orbital teeth broadly triangular, as wide as long or slightly wider, blunt distally; margin between rostrum and orbital teeth forming deep rounded V-shaped sinus (Fig. 1A); orbito-rostral process feebly developed. Pterygostomial angle anteriorly produced, blunt (Fig. 1B). Posterior margin of carapace with small cardiac notch.

Males with relatively slender pleon; first pleuron with posteroventral margin produced into triangular, slightly ventrally directed tooth; second to fourth pleura truncate ventrally, with blunt angle posteroventrally; fifth pleuron more rounded posteroventrally. Females with bulkier pleon and all pleura rounded ventrally. Telson broad, gradually and slightly tapering distally, posterior margin about 0.6 length of anterior margin; dorsal surface with slight median longitudinal depression and two pairs of spiniform setae, situated approximately at mid-length and 0.7 length of telson, respectively; posterior margin broadly rounded, with two spiniform setae at each posterolateral corner, mesial distinctly longer than lateral; posterolateral corners slightly projecting (Fig. 1C).

Antennular peduncle with first article by far longest; stylocerite well developed, with sharp tip and slightly convex lateral margin, reaching 0.7 length of second article; second article slightly longer than wide; third article shortest, wider than long; lateral flagellum with distinct accessory branch (Fig. 1A, B). Antenna with basicerite armed with strong, very long distoventral tooth, latter exceeding distal margin of first article of antennular peduncle, but not reaching to stylocerite tip, reaching mid-length of carpocerite; dorsal margin of basicerite bluntly projecting, without acute tooth; scaphocerite with well-developed blade exceeded by strong distolateral tooth, latter not exceeding distal margin of antennular peduncle; carpocerite robust, reaching well beyond end of antennular peduncle (Fig. 1A, B).

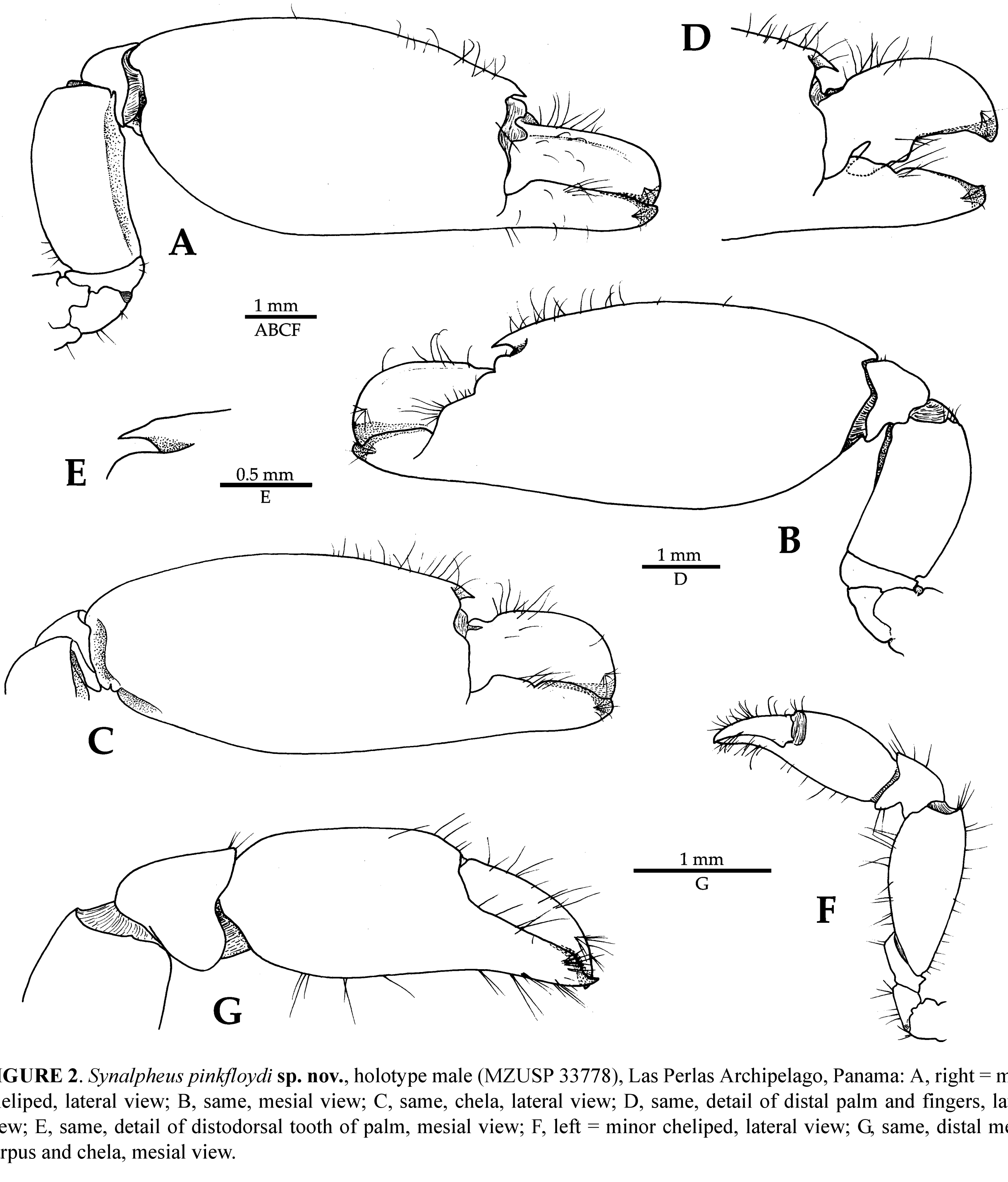

FIGURE 2. *Synalpheus pinkfloydi* **sp. nov.**, holotype male (MZUSP 33778), Las Perlas Archipelago, Panama: A, right = major cheliped, lateral view; B, same, mesial view; C, same, chela, lateral view; D, same, detail of distal palm and fingers, lateral view; E, same, detail of distodorsal tooth of palm, mesial view; F, left = minor cheliped, lateral view; G, same, distal merus, carpus and chela, mesial view.

FIGURE 3. *Synalpheus pinkfloydi* **sp. nov.**, habitus and colour in life: A, holotype male (MZUSP 33778); B, paratype female (MZUSP 34615), Las Perlas Archipelago, Panama. Photographs by A. Anker.

Mouthparts typical for genus. Third maxilliped with coxa bearing small blunt lateral plate; antepenultimate article as long as ultimate, more robust; penultimate article short, widening distally; ultimate article distally tapering, with distal circlet of at least five, relatively slender, spiniform setae; exopod not overreaching distal margin of antepenultimate article (Fig. 1E); arthrobranch well developed (not drawn in Fig. 1E).

Major cheliped with very short ischium; merus robust, about 2.2 times as long as wide, with strongly convex dorsal margin and flattened ventral surface, distodorsal margin unarmed; carpus very short, cup-shaped; chela ovoid, inflated, subcylindrical; palm smooth, with distodorsal protuberance ending in acute tooth, latter directed somewhat ventrally (downwards); fingers slightly less than half-length of palm; pollex subequal to dactylus; dactylus with relatively short, distally truncate plunger (Fig. 2A–E). Minor cheliped with short ischium; merus about 2.5 times as long as maximal width, with convex ventral margin; carpus cup-shaped, constricted ventrally; palm subcylindrical, slightly compressed laterally; fingers shorter than palm; dactylus with setae isolated or organised in tufts, without setal rows; finger tips sharp, simple (Fig. 2F, G).

Second pereiopod (fig. 1F) with ischium slightly shorter than merus; carpus consisting of five articles, latter with ratio more or less equal to 4 : 1 : 1 : 1 : 2; chela simple, longer than distal-most carpal article, with dense groups of setae ventrally and acute finger tips. Third pereiopod relatively stout; ischium widening distally, unarmed; merus about 3.6 times as long as wide, not particularly inflated; carpus distinctly more slender than merus, about 0.4 length of merus, distoventral margin with small spiniform seta; propodus shorter than merus, armed with several (three to five) spiniform setae on ventral margin, in addition to one distal pair of stronger spiniform setae adjacent to dactylus; dactylus biunguiculate, with accessory (flexor) unguis much shorter than terminal (extensor) unguis (Fig. 1G, H). Fourth pereiopod similar to third, more slender. Fifth pereiopod more slender than third and fourth, with much shorter merus; carpus unarmed distoventrally; propodus with four or five small spiniform setae on ventral margin, two spiniform setae adjacent to dactylus and several (at least six) transverse combs of stiff cleaning setae, distolaterally.

Second to fifth pleopods with appendices internae. Uropod reaching far beyond posterior margin of telson; exopod with slender spiniform seta between stout sharp fixed distolateral tooth on exopodal margin and similarly stout lateral tooth of diaeresis, remaining part of diaeresis sinuous; exopod and endopod subequal in length (Figs. 1C, D).

Ovigerous female paratype with 17 eggs (majority of eggs from other ovigerous females were subsampled for DNA analyses): eggs ellipsoid, diameter approximately 1.1 x 0.7 mm.

Colour pattern. Body semitransparent with greenish or yellow-olive tinge; deep-red line present between the eyes (seemingly composed of chromatophores on internal wall of carapace or on eyestalks); third maxilliped pinkish distally; major chela bright pink-red on distal half of palm and fingers (colour usually preserved in alcohol), except for amber-yellow finger tips; distal portion of palm and fingers of minor chela also intensely pink; second pereiopod colourless; third to fifth pereiopods with conspicuous reddish chromatophores on carpus and propodus; tail-fan colourless with slight greenish tinge; eggs or ovaries in females dull-green (Fig. 3).

Etymology. Named after the well-known British rock band Pink Floyd, inspired by the bright pink-red claw of the new species. Suggested vernacular name: Pink Floyd pistol shrimp.

Type locality. Las Perlas Archipelago, Bay of Panama.

Distribution. Presently known only from the type locality on the Pacific side of Panama; likely more widespread in the tropical eastern Pacific, but unlikely to occur on the Dark Side of the Moon due to lack of suitable habitat.

GenBank accession numbers. *Synalpheus pinkfloydi* **sp. nov.**, Panama, Pacific coast (as *S.* aff. *antillensis*): KJ477706, KJ595016, KJ595015 (COI 5’ end); KJ625120 (PEPCK); KJ494388, KJ595167, KJ595166 (16S) [OUMNH.ZC. 2013.03.046, 2013.03.047]. *Synalpheus antillensis*, Tobago: KJ595033 (COI 5’ end), KJ625121 (PEPCK), KJ595175 (16S) [FLMNH UF 10944]; Panama, Caribbean coast: KJ595034 (COI 5’ end), KJ625122 (PEPCK), KJ595176 (16S) [voucher deposited in the crustacean reference collection of the Universidad de Panamá, fcn 07-246, specimen listed in Anker *et al.* 2012].

Remarks. Within the speciose genus *Synalpheus*, *S. pinkfloydi* **sp. nov.** clearly belongs to the *S. brevicarpus* group, as first defined by Coutière (1909) and recently confirmed to be small monophyletic clade restricted to the Americas (Hultgren *et al.* 2014). The *S. brevicarpus* group is mainly characterised by the rostrum and orbital teeth being similar in shape and length, and includes the western Atlantic *S. minus*, *S. brevicarpus* and *S. antillensis*, and the eastern Pacific *S. digueti* Coutière, 1909 and *S. pinkfloydi* **sp. nov.** (= *S.* aff. *antillensis* in Hultgren *et al.* 2014). According to the results of the molecular analyses in Hultgren *et al.* (2014), *S. minus*, *S. brevicarpus* and *S. digueti* are genetically heterogeneous and at least the latter two taxa may represent species complexes, which remain to be resolved. As a result, the taxonomic status of Coutière's (1909) varieties and subspecies currently treated as junior synonyms, such as *S. minus bahiensis* Coutière, 1909, *S. digueti ecuadorensis* Coutière, 1909 and *S. brevicarpus guerini* Coutière, 1909, will need a thorough re-assessment. The clade containing *S. antillensis* and *S. pinkfloydi* **sp. nov.** is genetically more distant from the other members of the *S. brevicarpus* group, forming their sister clade (Hultgren *et al.* 2014). They differ morphologically from *S. minus*, *S. brevicarpus* and *S. digueti* by the noticeably stouter antennular peduncles (see illustrations in Coutière 1909) and also by the uniform intense pink-red colour of the distal half of the major and minor cheliped (Fig. 3; see also Anker *et al.* 2012: fig. 10a–c). In the absence of other species with similar morphology and colour in the region and worldwide, *S. antillensis* and *S. pinkfloydi* **sp. nov.** represent, beyond any shadow of a doubt, a pair of transithmian sister taxa (see also below).

The only noticeable morphological differences between *S. pinkfloydi* **sp. nov.** and *S. antillensis* lie in the relative proportions of the merus of the major and minor chelipeds, the distodorsal armature of the major cheliped merus, and the length of the antennal scaphocerite. In *S. pinkfloydi* **sp. nov.**, the major cheliped merus appears shorter and stouter, its maximal width being only about 0.5 of its length (Fig. 2B), whereas the minor cheliped merus is about 2.2 times as long as wide and with a conspicuously convex ventral margin (Fig. 2F). In *S. antillensis*, the major cheliped merus is relatively more slender, its maximal width being at most 0.4 of its length (Anker *et al.* 2012: fig. 9d), whereas the minor cheliped merus is about 2.5 times as long as wide, its ventral margin being only slightly convex (*ibid.*: fig. 9e). In *S. pinkfloydi* **sp. nov.**, the distodorsal margin of the major cheliped merus is blunt or bears at most a small blunt projection (Fig. 2A, B), although in the majority of specimens the latter is poorly developed to absent. In the majority of specimens of *S. antillensis*, this margin typically bears a small, but relatively well developed, sometimes sharp and curved tooth (Anker et al. 2012: fig. 9d). The scaphocerite of *S. pinkfloydi* **sp. nov.** is slightly shorter than that of *S. antillensis*, with its distolateral tooth reaching, but usually not overreaching the distal margin of the antennular peducle (Fig. 1A). In *S. antillensis*, the distolateral tooth of the scaphocerite distinctly overreaches the distal margin of the antennular peduncle (Anker *et al.* 2012: fig. 9a; see also Coutière 1909: fig. 27a). In addition, *S. pinkfloydi* **sp. nov.** appears to be larger than *S. antillensis*, with four individuals of the material examined exceeding 5.0 mm in cl, in contrast to only a single individual of *S. antillensis* in the comparative material reaching 4.5 mm in cl.

The above-listed morphological differences are rather subtle and may be subject to some variation. For instance, the proportions of the cheliped merus may be difficult to evaluate directly on the specimens, especially in the absence of comparative material, and may be limited to adult males. Therefore, *S. pinkfloydi* **sp. nov.** and *S. antillensis* can be considered as cryptic species with little to almost no morphological differentiation, similar or identical colour patterns, but being geographically clearly separated as well as genetically distinct. Other examples of transisthmian cryptic species pairs include the alpheid shrimps *Alpheus cylindricus* Kingsley, 1878 / *A. vanderbilti* Boone, 1930 (see Anker *et al.* 2008), and the sesarmid mangrove crabs *Aratus pacificus* Thiercelin & Schubart, 2014 / *A. pisonii* (H. Milne Edwards, 1837) (see Thiercelin & Schubart 2014).

The molecular phylogenetic analysis of *Synalpheus*, which included most of the members of the *S. brevicarpus* group clearly corroborate the sister position of *S. pinkfloydi* **sp. nov.** relative to *S. antillensis*, as already indicated by morphology and colouration (Hultgren *et al.* 2014: fig. 3, as *S.* aff. *antillensis*). That is, multiple specimens of *S. pinkfloydi* **sp. nov.** formed a monophyletic clade—sister to a monophyletic clade formed by specimens of *S. antillensis*—using individual gene trees of the mtDNA genes COI and 16S (Hultgren *et al.* 2014, Suppl. fig. 2, 3), as well as in combined phylogenetic analyses of nuclear and mitochondrial data (Hultgren *et al.* 2014: fig. 3). The mean genetic distance between *S. pinkfloydi* **sp. nov**. and its sister *S. antillensis* (COI gene, K2P distance) was 10.2%, which is approximately equal to 10 times the mean intraspecific genetic distance in all studied species of *Synalpheus,* also exceeding the mean divergence between other sister species pairs in this genus (8.1%, Hultgren *et al.* 2014).

Based on genetic data (10.2% K2P COI distance) and calibration methods used herein, these two taxa diverged approximately 6.8–7.8 mya, i.e. well before the final closure of the Isthmus of Panama, which created an impenetrable barrier in the Central American Seaway (Lessios 2008 and references therein). The recently proposed, radically different views of the happening and timing of the closure of the Isthmus of Panama (Bacon *et al.* 2015; Montes *et al.* 2015) would contradict the calculated divergence times and imply that the separation of the two transisthmian sister species happened at least 10 mya (in the case of Bacon *et al.* 2015 already in the Pliocene, i.e. more than 20 mya), which seems rather unlikely given their morphological similarity (see also criticism by O'Dea *et al.* 2016).

Verrill (1922), in his taxonomically problematic and difficult-to-use report on the Decapoda of Bermuda, named an eastern Pacific taxon as *Synalpheus bradleyi* Verrill, 1922, providing only a very short descriptive paragraph in the remarks under *S. minus*, as well as one diagrammatic drawing of the major cheliped (Verrill 1922: pl. XXIV, fig. 1). As it was possible that the herein described new species was S. *bradleyi*, at our request, Eric A. Lazo-Wasem of the Yale Peabody Museum of Natural History, Yale University, New Haven, USA (YPM), provided high-resolution photographs of two specimens labelled "syntype" of *S. bradleyi*, viz. YPM IZ 000742CR (cl 7.9 mm) and YPM IZ 006629CR (cl 5.3 mm). However, only the first specimen was listed in Verrill's original report (Verrill 1922: p. 108). The very distinctive shape of the frontal margin of the carapace of this specimen (YPM IZ 000742CR) indicates that *S. bradleyi* is not closely related to *S. minus* or any other species of the *S. brevicarpus* group, including *S. pinkfloydi* **sp. nov.** and *S. antillensis*. The frontal region of the other specimen labelled as "syntype" (YPM IZ 006629CR) is very different from that of the syntype of *S. bradleyi*, suggesting that it belongs to a different taxon, which is also distant from the *S. brevicarpus* group. Since *S. bradleyi* has absolutely no affinity to *S. pinkfloydi* **sp. nov.**, its taxonomic status will be discussed elsewhere.

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