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A trifecta of Swiftian symbioses: stony corals, gall crabs and their parasites (Scleractinia; Brachyura: Cryptochiridae; Isopoda: Epicaridea and Cirripedia: Rhizocephala)

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Coral reefs harbour an immense diversity of species, many of which live in association with one or more host organisms. Stony corals (Scleractinia) have been documented to host nearly 900 organisms, of which > 310 are decapod crustaceans. This associated fauna is also involuntary host to a diverse parasite fauna. Coral-dwelling gall crabs (Cryptochiridae) are obligate symbionts of scleractinian corals; however, records of their parasites are scarce, with only two named epicaridean isopod species known. Fieldwork focused on cryptochirids in the Indo-West Pacific and Caribbean yielded diverse new collections of both hosts and parasites. This new material was compared with material deposited in museum collections. Both previously described species were encountered in the newly collected material, as well as a new genus and species of bopyrid, a new genus and species of cryptoniscoid, four new species of *Danalia*, and the first record of a rhizocephalan parasitizing a gall crab, which is also described as a new species. Parasitism of gall crabs is more widespread than what could be assumed based on literature records, and all parasite species appear to be specific to hosts in this crab family. This is the first review of hypersymbioses between stony corals, gall crabs and the crabs' parasites and hyperparasites.

ADDITIONAL KEYWORDS: Crustacea – host specificity – hyperparasites – hypersymbioses – museum collections – new species – parasitism.

INTRODUCTION

Coral reefs worldwide have been documented to host > 870 coral-associated invertebrates, of which > 310 are decapod crustaceans (Stella *et al.*, 2011). The majority of these occur in the so-called 'Coral Triangle' in the Indo-West Pacific ecoregion, where the diversity of scleractinian corals is > 600 species. One of the most

understudied groups found on coral reefs are the gall crabs (Cryptochiridae), comprising ~53 described species in 21 genera (Davie & Türkay, 2009). These obligate symbionts inhabit corals (Scleractinia) belonging to ~66 genera (Castro, 2015; S. E. T. van der Meij, unpublished observations). The greatest diversity of gall crabs is found in the Indo-West Pacific, with only six species known from the Atlantic.

Cryptochirid females (and sometimes males) live in galls, tunnels or pits formed in the skeletons of their coral hosts. They are common inhabitants of coral reefs, but are easily overlooked because of their small size and sequestered lifestyle. Generally, ~20% of host corals in an area are inhabited by these crabs (van Tienderen & van der Meij, 2016). Genera of gall crabs used to be

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defined by their host coral specificity (Fize & Serène, 1957). This specificity has been shown to be variable, with some crab genera appearing to be specific to corals at the level of host genus, but others being of a more generalist nature (van der Meij, 2014a; van der Meij *et al.*, 2015). Moreover, the classification of stony corals has seen a major overhaul in recent years based on skeletal microstructures as well as molecular data (e.g. Fukami *et al.*, 2008; Huang *et al.*, 2014; Kitahara *et al.*, 2016), which in turn has changed our understanding of the evolutionary diversification of cryptochirids (van der Meij, 2015a). There is a similar range of host specificity in the bopyrid isopods, where some genera occur on a single host taxon, whereas others occur on a broad range of host species and even genera within a family or, rarely, an even higher taxonomic group (Williams & Boyko, 2012; Boyko *et al.*, 2013).

As is the case with most organisms, gall crabs are host to a diverse parasite fauna. Before the present study, however, only two named parasites, both epicaridean isopods, were known from gall crabs: one bopyrid (*Carcinione platypleura* Bourdon, 1983) and one cryptoniscoid (*Danalia hapalocarcini* Fize, 1955). There were, however, a few reports in the literature of unidentified gall crab parasites (e.g. Utinomi, 1944; Kropp & Manning, 1987). Based on the paucity of these literature records, it could be concluded reasonably that gall crabs were not heavily impacted by parasites.

The obligate nature of the association between parasites and cryptochirids as well as the crabs and their coral hosts prompts questions about possible cospeciation between these levels of association. Multiple cospeciation and duplication events have already been shown between gall crabs found on fungiid hosts (van der Meij *et al.*, 2015), and it would be very interesting to compare these results with an analysis of the relationships between the epicaridean parasites and the gall crabs. Unfortunately, the molecular data for epicarideans are still extremely scanty (Boyko *et al.*, 2013) and, to make matters worse, none of the DNA from samples examined during this study could be amplified successfully.

Recently, the second author conducted extensive fieldwork in both the Indo-West Pacific and Caribbean, collecting, identifying and describing species of gall crabs from a diverse assortment of coral host species (e.g. van der Meij, 2014a, b, 2015b). Based on these new collections, 40 parasitized gall crabs were collected and found to bear 11 species of parasites. These include both of the previously known epicaridean parasites, as well as a new genus and species of bopyrid found parasitizing the abdomen of its host, a new genus and species of cryptoniscoid, and four new species of *Danalia* Giard, 1887. In addition, the first species of rhizocephalan is herein reported and described from five different gall crab species.

MATERIAL AND METHODS

Gall crab parasites were encountered during fieldwork (2007–2012) in Indonesia (Raja Ampat, West Papua; Bunaken, North Sulawesi; Ternate, North Moluccas; Lembah Strait, North Sulawesi) and Malaysia (Semporna, North Borneo), Curaçao (2013), the Maldives (2015) and Okinawa, Japan (2016). An additional parasitized gall crab specimen was collected by F. Benzoni from Kavieng, Papua New Guinea (2014). Surprisingly, during two separate fieldwork trips to the Saudi Arabian part of the Red Sea not a single parasitized gall crab was encountered. Scleractinian corals were searched for galls and pits, photographed and, subsequently, split with hammer and chisel. Gall crab specimens were preserved in 80% ethanol after being photographed with a digital SLR camera equipped with macro lens.

Subsequently, parasitized gall crab specimens were examined from the collections of the Museum National d'Histoire Naturelle (MNHN), Paris, the Naturalis Biodiversity Center, Leiden (formerly Rijksmuseum van Natuurlijke Historie, collection coded as RMNH.Crus.D, for decapod hosts, RMNH.Crus.I, for isopod parasites, and RMNH.Crus.C, for rhizocephalans), the National Museum for Natural History, Smithsonian Institution (USNM), Washington, DC, and Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore. Measurements provided (in millimetres) are given for the length of the isopod, as anterior margin of cephalon to posterior of pleon (excluding pleopods), whereas those for the hosts are given as carapace length × width; total length × width of the externae are given for rhizocephalans. Cryptoniscus larvae are not described because, except in the case of those belonging to a *Cabirops* species (which will be described at a later date), they are not in particularly good condition.

Camera lucida sketches made of specimens were scanned into a Macintosh™ computer. Images were then prepared using the programs Adobe Photoshop™ and Adobe Illustrator™ (Figs. 1–9). Color images of parasitized gall crabs hosts were prepared using Adobe Photoshop™ (Figs. 10–12).

SYSTEMATIC DESCRIPTIONS

ISOPODA LATREILLE, 1817

EPICARIDEA LATREILLE, 1831

BOPYROPIDEA RAFINESQUE, 1815

BOPYRIDAE RAFINESQUE, 1815

PSEUDIONINAE CODREANU, 1967

CARCINIONE BOURDON, 1983

CARCINIONE PLATYPLEURA BOURDON, 1983

(Figs 1, 2, 10)

‘Seventeen specimens of epicarids ... collected from four genera of crabs (including *Pseudohapalocarcinus*)’

- Monod & Serène, 1976: 24 (in part) [ex *Pseudohapalocarcinus ransoni* Fize & Serène, 1956a, Indonesia, examined in this study].
- ? 'bopyrid parasites' Takeda & Tamura, 1980: 54–55 59, pl. 5 [ex *P. ransoni* Fize & Serène, 1956a, Ryukyu Islands, Japan].
- Carcinione platypleura* Bourdon, 1983: 854–855, fig. 6 [ex *P. ransoni* Fize & Serène, 1956a, Banda Neira, Indonesia, examined in the present study]. – van der Meij, 2014: 45 [ex *Opearcinus cathya* van der Meij, 2014, Halmahera, Indonesia, examined in this study]. – van der Meij, 2015: fig. 7B [ex *Fungicola syzygia* van der Meij, 2015, Bunaken Island, Indonesia, examined in the present study]. – van der Meij, Reijnen & Reimer, 2017: fig. 1F [ex *Lithoscaptus* sp., Odo Beach, Okinawa, Japan, examined in the present study].
- 'bopyrid isopod' Kropp, 1994: 534 [ex *P. ransoni* Fize & Serène, 1956a, Banda Neira, Moluccas, examined in the present study].
- 'unidentified bopyrid' Williams & Boyko, 2012: fig. 1G [ex *Lithoscaptus helleri* (Fize & Serène, 1957), Indonesia, examined in the present study].

Type material

Indonesia: Mature female holotype (2.0 mm) [MNHN-IU-2007-3670 (= MNHN-EP336)] and cryptoniscus paratype (0.6 mm) [MNHN-IU-2017-8 (= MNHN-Ep336)], ex female *P. ransoni* Fize & Serène, 1956a (3.3 mm long × 3.4 mm wide) (MNHN-IU-2016–10934), parasites under right branchiostegite, ex *Pavona cactus* (Forskål, 1775) (Agariciidae), Banda Neira, Amboine (= Ambon), 29 January 1975, collected by Rumphius II (R. Serène & T. Monod) [crab and coral originally identified by R. Serène, with the coral only identified to genus; crab identification confirmed and coral identified to species by S. E. T. van der Meij].

Additional material

Indonesia: Immature female (1.5 mm) (MNHN-IU-2017-9), ex right branchiostegite of male *P. ransoni* Fize & Serène, 1956a (2.4 mm long × 2.3 mm wide) (MNHN-IU-2009-5734 [= MNHN-B12674]), ex *Pavona cactus* (Forskål, 1775) (Agariciidae), southwest corner of Naira Island, at southern entrance to channel between Gunung Api Island and Naira Island, coral, Amboine (= Ambon), 29 January 1975, collected by Rumphius II [this specimen is not part of the type series, although it was collected at the same time, in the same place, and from the same host species as the holotype, but it was not mentioned in the original description by Bourdon (1983)]; mature non-ovigerous female (1.8 mm) and mature male (0.5 mm) (RMNH. Crus.I.7719), ex left branchiostegite, mature ovigerous female (1.7 mm), mature male (0.7 mm) (RMNH. Crus.I.7720), ex right branchiostegite, ex juvenile female *Dacryomaia japonica* (Takeda & Tamura, 1981)

(2.7 mm long × 2.0 mm wide) (RMNH.Crus.D.54193), ex *Leptastrea* cf. *transversa* Klunzinger, 1879 (*Scleractinia incertae sedis*), Teluk Makawide Reef, Lembeh Strait, 01°29'05"N, 125°14'26"E, 9 February 2012, coll. S. E. T. van der Meij; mature non-ovigerous female (3.3 mm) and mature male (0.9 mm) (RMNH. Crus.I.7721), ex right branchiostegite of mature non-ovigerous female *F. syzygia* van der Meij, 2015 (5.0 mm long × 4.3 mm wide) (RMNH.Crus.D.53224), ex *Pleuractis granulosa* (Klunzinger, 1879) (Fungiidae), Tanjung Pasir Putih Reef, Ternate, 00°51'50"N, 127°20'37"E, 2 November 2009, coll. S. E. T. van der Meij; mature ovigerous female, non-ovigerous (3.6 mm) and mature male (1.1 mm) (RMNH.Crus.I.7722), ex right branchiostegite, cryptoniscus larva (0.6 mm) (RMNH. Crus.I.7723), ex left branchiostegite, ex mature non-ovigerous female *F. syzygia* van der Meij, 2015 (4.3 mm long × 3.7 mm wide) (RMNH.Crus.D.56481), ex *Pleuractis paumotensis* (Stutchbury, 1833) (Fungiidae), Alung Banua Reef, Bunaken Island, 01°37'07"N, 124°45'30"E, 19 December 2008, coll. S. E. T. van der Meij; mature non-ovigerous female (2.3 mm) (RMNH. Crus.I.7724), ex right branchiostegite of male *F. syzygia* van der Meij, 2015 (3.3 mm long × 3.2 mm wide) (RMNH.Crus.D.56482), ex *Pleuractis paumotensis* (Stutchbury, 1833) (Fungiidae), Siladen I Reef, Siladen Island, 01°37'31"N, 124°47'54"E, 18 December 2008, coll. S. E. T. van der Meij; mature ovigerous female (3.6 mm), mature male (1.3 mm) (RMNH.Crus.I.7725), ex right branchiostegite of male *Lithoscaptus prionotus* Kropp, 1994 (5.3 mm long × 3.5 mm wide) (RMNH. Crus.D.54171), ex *Oulophyllia crispa* (Lamarck, 1816) (Merulinidae), Tanjung Kuning Reef, Lembeh Strait, 01°23'10"N, 125°10'23"E, 11 February 2012, coll. S. E. T. van der Meij; mature ovigerous female (4.3 mm), mature male (1.5 mm) (RMNH.Crus.I.7726), ex left branchiostegite of non-ovigerous female *L. helleri* (Fize & Serène, 1957) (5.7 mm long × 4.2 mm wide) (RMNH. Crus.D.54057), ex *Favites* cf. *complanata* (Ehrenberg, 1834) (Merulinidae), Siladen I Reef, Siladen Island, 01°37'31"N, 124°47'54"E, 18 December 2008, coll. S. E. T. van der Meij; mature ovigerous female (2.5 mm), mature male (1.0 mm), cryptoniscus larva (0.7 mm) (RMNH.Crus.I.7727), ex right branchiostegite of male *L. helleri* (Fize & Serène, 1957) (3.5 mm long × 2.6 mm wide) (RMNH.Crus.D.56121), ex *Favites* cf. *complanata* (Ehrenberg, 1834) (Merulinidae), Lekuan I Reef, Bunaken Island, 01°35'44"N, 124°46'12"E, 11 December 2008, coll. S. E. T. van der Meij; mature ovigerous female (2.2 mm), mature male (0.9 mm) (RMNH.Crus.I.7728), ex right branchiostegite of male *Lithoscaptus* cf. *bani* (Fize & Serène, 1957) (telson abnormally wide) (3.2 mm long × 2.3 mm wide) (RMNH. Crus.D.56121), ex *Goniastrea pectinata* (Ehrenberg, 1834) (Merulinidae), Negiri Reef, Manado Tua Island, 01°36'58"N, 124°41'39"E, 5 December 2008, coll.

- S. E. T. van der Meij; mature ovigerous female (3.3 mm), mature male (0.9 mm) (RMNH.Crus.I.7729), ex right branchiostegite of non-ovigerous female *Lithoscaptus* sp. 1(A) (4.3 mm long × 2.9 mm wide) (RMNH.D.54067), ex *Astrea curta* Dana, 1846 (Merulinidae), Ron's Point, Bunaken Island, 01°36'21"N, 124°44'13"E, 9 December 2008, coll. S. E. T. van der Meij; mature ovigerous female (3.1 mm), mature male (1.3 mm) (RMNH.Crus.I.7730), ex right branchiostegite, mature ovigerous female (3.1 mm), mature male (1.1 mm) (RMNH.Crus.I.7731), ex left branchiostegite of non-ovigerous female *Lithoscaptus* sp. 2(B) (4.0 mm long × 3.3 mm wide) (RMNH.Crus.D.54106), ex *Plesiastrea versipora* (Lamarck, 1816) (Scleractinia *incertae sedis*), Lekuan III, Bunaken Island, 01°36'20"N, 124°46'08"E, 12 December 2008, coll. S. E. T. van der Meij; mature ovigerous female (2.7 mm), mature male (1.0 mm) (RMNH.Crus.I.7732), ex left branchiostegite of juvenile female *Lithoscaptus* sp. 2(B) (4.0 mm long × 2.5 mm wide) (RMNH.Crus.D.54172), ex *P. versipora* (Lamarck, 1816) (Scleractinia *incertae sedis*), Pulau Abadi, Lembah Strait, 01°26'01"N, 125°12'22"E, 10 February 2012, coll. S. E. T. van der Meij; cryptoniscus larvae (0.6 mm) (RMNH.Crus.I.7733), ex dorsal carapace of feminized male *Opecarcinus* sp. 1(F) (3.0 mm long × 2.3 mm wide) (RMNH.Crus.D.53990; host also parasitized by one *Sacculina quadrialata* sp. nov., RMNH.Crus.C.10249), ex *Leptoseris mycetoseroides* Wells, 1954 (Agariciidae), South Pilongga, Tidore, 00°42'44"N, 127°28'47"E, 12 November 2009, coll. S. E. T. van der Meij; mature ovigerous female (4.0 mm), mature male (1.5 mm) (RMNH.Crus.I.7734), ex right branchiostegite of non-ovigerous female *Opecarcinus pholeter* Kropp, 1989 (5.3 mm long × 4.3 mm wide) (RMNH.Crus.D.54000), ex *Pavona explanulata* (Lamarck, 1816) (Agariciidae), Sulamadaha II, Ternate, 00°52'02"N, 127°19'46"E, 6 November 2009, coll. S. E. T. van der Meij; immature female (1.8 mm), mature male (0.8 mm) (RMNH.Crus.I.7735), ex right branchiostegite, immature female (1.5 mm), mature male (0.7 mm) (RMNH.Crus.I.7736), ex left branchiostegite of male *O. pholeter* Kropp, 1989 (3.3 mm long × 2.7 mm wide) (RMNH.Crus.D.54000), ex *P. explanulata* (Lamarck, 1816) (Agariciidae), Sulamadaha II, Ternate, 00°52'02"N, 127°19'46"E, 6 November 2009, coll. S. E. T. van der Meij; mature ovigerous female (2.8 mm), mature male (1.2 mm) (RMNH.Crus.I.7737), ex right branchiostegite of male *Opecarcinus cathyae* van der Meij, 2014 (4.0 mm long × 2.7 mm wide) (RMNH.Crus.D.53923), ex *Pavona clavus* (Dana, 1846) (Agariciidae), South Lela, Gura Ici, 00°01'51"S, 127°15'03"E, 10 November 2009, coll. S. E. T. van der Meij; mature non-ovigerous female (1.5 mm), ex right brachiostegite, mature non-ovigerous female (1.5 mm), ex left brachiostegite, mature male (0.8 mm), ex unknown brachiostegite (RMNH.Crus.I.7738), ex juvenile female *Xynomaia sheni* (Fize & Serène, 1956b) (2.7 mm long × 1.8 mm wide) (RMNH.Crus.D.54115), ex *Mycedium elephantotus* (Pallas, 1766) (Merulinidae), Lobangbatu Besar, Lembah Strait, 01°25'49"N, 125°11'26"E, 7 February 2012, coll. S. E. T. van der Meij; mature ovigerous female (2.4 mm), mature male (1.2 mm) (RMNH.Crus.I.7739), ex right branchiostegite of male *X. sheni* (Fize & Serène, 1956b) (4.0 mm long × 2.7 mm wide) (RMNH.Crus.D.54085), ex *Pectinia* sp. (Merulinidae), Mandolin, Bunaken Island, 01°36'44"N, 124°43'57"E, 9 December 2008, coll. S. E. T. van der Meij.
- Malaysia*: Mature ovigerous female (5.0 mm), mature male (1.5 mm) (RMNH.Crus.I.7740), ex left branchiostegite of non-ovigerous female *L. prionotus* Kropp, 1994 (7.1 mm long × 5.2 mm wide) (RMNH.Crus.D.53719), ex *Oulophyllia crispa* (Lamarck, 1816) (Merulinidae), Erzherzog Reef, Semporna, Malaysia, 04°14'26"N, 118°23'35"E, 1 December 2010, coll. S. E. T. van der Meij.
- Maldives*: Immature female (1.7 mm) ex right branchiostegite, immature female (1.6 mm) ex left branchiostegite (RMNH.Crus.I.7700), ex female *F. syzygia* van der Meij, 2015 (3.3 mm long × 3.1 mm wide) (RMNH.Crus.D.57063), ex *P. granulosa* (Klunzinger, 1879) (Fungiidae), Sunny Reef, Faafu Atoll, 03°08'40"N, 73°00'45"E, 19 February 2015, coll. S. E. T. van der Meij; mature non-ovigerous female (1.5 mm), mature male (0.7 mm) (RMNH.Crus.I.7701), ex left branchiostegite of female *Opecarcinus* sp. (2.0 mm long × 1.7 mm wide) (RMNH.Crus.D.57064), ex *L. mycetoseroides* Wells, 1954 (Agariciidae), Wallino, Faafu Atoll, 03°05'12"N, 72°57'23"E, 21 February 2015, coll. S. E. T. van der Meij; mature female with brood of epicaridean larvae (3.3 mm), mature male (1.1 mm) ex right branchiostegite, mature non-ovigerous female (3.1 mm), mature male (1.2 mm) (RMNH.Crus.I.7704) ex left branchiostegite of female *Lithoscaptus* sp. Z (5.4 mm long × 3.7 mm wide) (RMNH.Crus.D.57066); immature female (1.1 mm), mature male (0.9 mm) (RMNH.Crus.I.7704) ex right branchiostegite of male *Lithoscaptus* sp. Z (RMNH.Crus.D.57066), ex *Dipsastraea cf. vietnamensis* (Veron, 2000) (Merulinidae), Wallino, Faafu Atoll, 03°05'13"N, 72°57'24"E, 26 February 2015, coll. S. E. T. van der Meij; mature ovigerous female (1.5 mm), mature male (0.8 mm) (RMNH.Crus.I.7703), ex left branchiostegite of male *Lithoscaptus* sp. Z (3.6 mm long × 2.3 mm wide) (RMNH.Crus.D.57066), ex *D. cf. vietnamensis* (Veron, 2000) (Merulinidae), Wallino, Faafu Atoll, 03°05'13"N, 72°57'24"E, 26 February 2015, coll. S. E. T. van der Meij; mature ovigerous female (3.3 mm), mature male (1.4 mm) (RMNH.Crus.I.7702), ex left branchiostegite of female *Lithoscaptus* sp. (5.2 mm long × 3.0 mm

wide) (RMNH.Crus.D.57065), ex *Favites* aff. *flexuosa* (Dana, 1846) (Merulinidae), Beyrufushi, Faafu Atoll, 03°06'29"N, 73°01'07"E, 26 February 2015, coll. S. E. T. van der Meij.

Japan: Immature female (1.1 mm) (RMNH.Crus.I.7741), ex right branchial chamber of male *Dacryomaia* sp. (2.3 mm long × 1.5 mm wide) (RMNH.Crus.D.57231), ex *Leptastrea* sp. (*Scleractinia incertae sedis*), Red Beach, Okinawa, 26°26'47"N, 127°54'43"E, 14 April 2016, coll. S. E. T. van der Meij; mature female (3.5 mm) (RMNH.Crus.I.7742) with immature female *Cabirops* (2.1 mm) and cryptoniscus larva (1.3 mm) (RMNH.Crus.I.7743) in marsupium, immature male (1.7 mm), ex right branchial chamber of female *Lithoscaptus* sp. (5.2 mm long × 3.8 mm wide) (RMNH.Crus.D.57232), ex *Coelastrea aspera* (Verrill, 1866) (Merulinidae), Odo Beach, Okinawa, 26°05'22"N, 127°42'33"E, 22 April 2016, coll. S. E. T. van der Meij; ovigerous female (2.6 mm) (RMNH.Crus.I.7744) with three associated *Cabirops* cryptoniscus larvae (1.2, 1.2, 1.3 mm) (RMNH.Crus.I.7745–7746), mature male (1.1 mm), (RMNH.Crus.I.7747), ex right branchial chamber, mature female (2.9 mm) with ovigerous *Cabirops* female (2.9 mm long × 1.5 mm wide) and cryptoniscus larva (1.0 mm) (RMNH.Crus.I.7748) in brood chamber, mature male (1.0 mm), ex left branchial chamber of male *Xynomaia* sp. (4.3 mm long × 3.8 mm wide) (RMNH.Crus.D.57233), ex *Pectinia* sp. (Merulinidae), Blue Tombs, Henza Island, Okinawa, 26°21'46"N, 127°59'50"E, 29 April 2016, coll. S. E. T. van der Meij.

Redescription

Female (Fig. 1): Body length 4.3 mm, maximal width 2.3 mm, head length 0.9 mm, head width 0.9 mm. Pereon nearly straight, head not deflected (Fig. 1A, B). All body regions and pereomeres distinctly segmented.

Head subrectangular, approximately as broad as long, usually overlapping entire first pereomere medially (Fig. 1A), but sometimes only overlapping in part Fig. 1C), with moderately broad frontal lamina (Fig. 1A, C). Eyes minute, distolaterally placed. Antennule of four articles; antenna of two articles (Fig. 1D). First oostegite (Fig. 1E) anterior lobe globular, posterior lobe slightly smaller than anterior lobe, ovate with rounded margins, distal projection lacking but with medially directed smooth lobe, internal ridge thick, smooth. Oostegites completely enclosing the marsupium. Maxilliped (Fig. 1F) with short, rounded fleshy spur; palp lacking, anterior segment triangular, rounded, posterior segment irregularly subquadrate. Barbula smooth (Fig. 1G).

Pereon composed of seven pereomeres (Fig. 1A, C), broadest across pereomeres III–V, only slightly tapering anteriorly and posteriorly; pereomere I posterior

margin usually under head, II anteromedially concave, III weakly anteromedially concave to weakly convex, IV anteromedially straight to weakly convex, V–VII weakly convex. Coxal plates very reduced, largest on pereomeres I, II, large dorsolateral bosses on pereomeres I–IV or I–V (those on V sometimes much smaller than other pairs). Anterior pereopods (Fig. 1H) much smaller than posterior pairs (Fig. 1I), posterior pairs about two times as large.

Five pleomeres plus pleotelson (Fig. 1A, C), lateral plates well developed, edges crenulated, those on pereopods I–III about twice as broad as other pairs (Figs 1A–C, 2A). Pleomere I with biramous pleopods, II–V with uniramous pleopods all subequal in size, uniramous uropods resembling lateral plates, edges crenulated (Fig. 2A).

Male (Fig. 2B): Length 1.5 mm, maximal width 0.5 mm, head length 0.2 mm, head width 0.3 mm, pleon length 0.5 mm.

Head ovate, widest posteriorly, distinct from first segment of pereon (Fig. 2B); eyes present posterolaterally. Antennule of four articles (Fig. 2D), distally setose, not extending beyond margin of head; antenna of three articles, terminal article less than half as large as second segment, distally setose (Fig. 2D).

Pereomere III–V broadest, others gradually tapering anteriorly and posteriorly. All pereomeres slightly concave anteriorly, convex posteriorly, distal margins rounded. All pereopods (Fig. 2C) subequal, all articles distinctly separated.

Pleon with five segments plus pleotelson. All pleomeres directed laterally (Fig. 2B, C), with distolateral margins rounded. Midventral tubercles, pleopods and uropods lacking; small anal cone mediodistally on pleotelson (Fig. 2C).

Remarks

Bourdon (1983) described this species on the basis of the single female mentioned obliquely by Monod & Serène (1976); although he had a cryptoniscus larva, he did not describe it. The male has not been described previously. The characters of the female, particularly the wide anterior lateral plates, made Bourdon (1983) unsure of the subfamily in which to place this species. He indicated that he did not think it belonged to the 'Céponiens' (now Keponinae), but that the female somewhat resembled those of Pseudioninae. Given the lack of female characters that clearly placed this genus in any particular subfamily, Boyko *et al.* (2013) somewhat arbitrarily placed the genus with the other brachy-uran parasites in Keponinae. However, the discovery of the male provides characters that are very similar to those of most males in Pseudioninae and not at all like males belonging to Keponinae. Therefore, *Carcinione* is here placed with confidence in Pseudioninae.

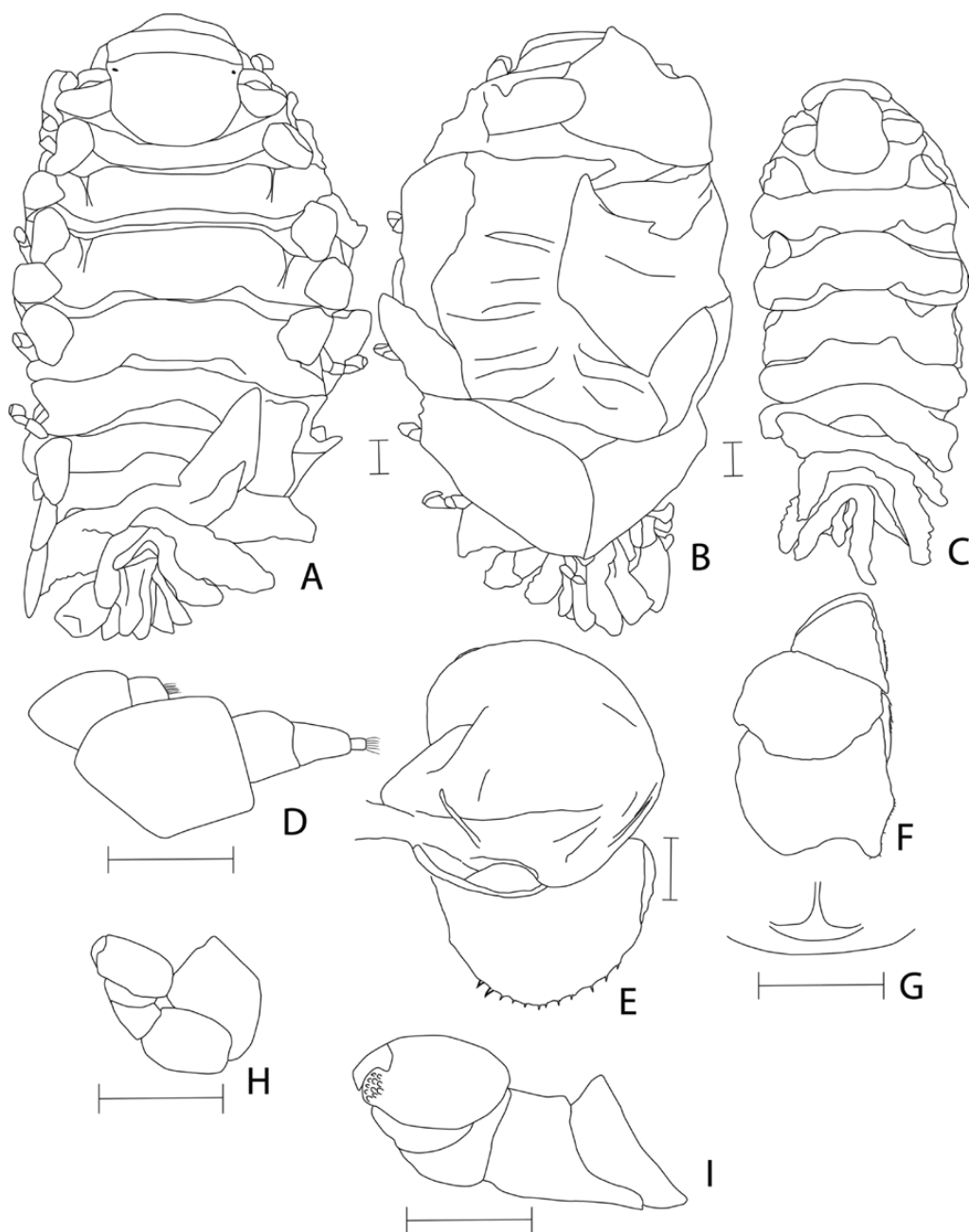


Figure 1. *Carcinione platypleura* Bourdon, 1983. A, B, D–I, female (RMNH.Crus.I.7726 ex RMNH.Crus.D.54057); C, female (RMNH.Crus.I.7721 ex RMNH.Crus.D.53224). A, dorsal view. B, ventral view. C, dorsal view. D, left antennule and antenna. E, left oostegite I, internal view. F, left maxilliped. G, barbula. H, left pereopod I. I, right pereopod 7. Scale bars: 0.25 mm (A–C), 0.1 mm (D–F, H, I) and 0.16 mm (G).

This species appears to be the most common parasite of gall crabs, with a wide distribution in the Indo-West Pacific. The fact that it was described from only a single mature female and a cryptoniscus larva and has subsequently been reported only once before the present study (Sanabe & Tsuchiya, 2005) is explained by limited sampling of hosts rather than genuine scarcity of the parasites. This conclusion is

supported by the data of Sanabe & Tsuchiya (2005), where 10.64% of *P. ransonii* ($N = 357$) collected in the Ryukyus, Japan, were infested with a bopyrid identified as *C. platypleura*. Although we have not seen any of Sanabe & Tsuchiya's specimens, we are confident in their identification of the bopyrid species.

The parasitized *Xynomaia* sp. from Okinawa might well hold the record for the most parasites and

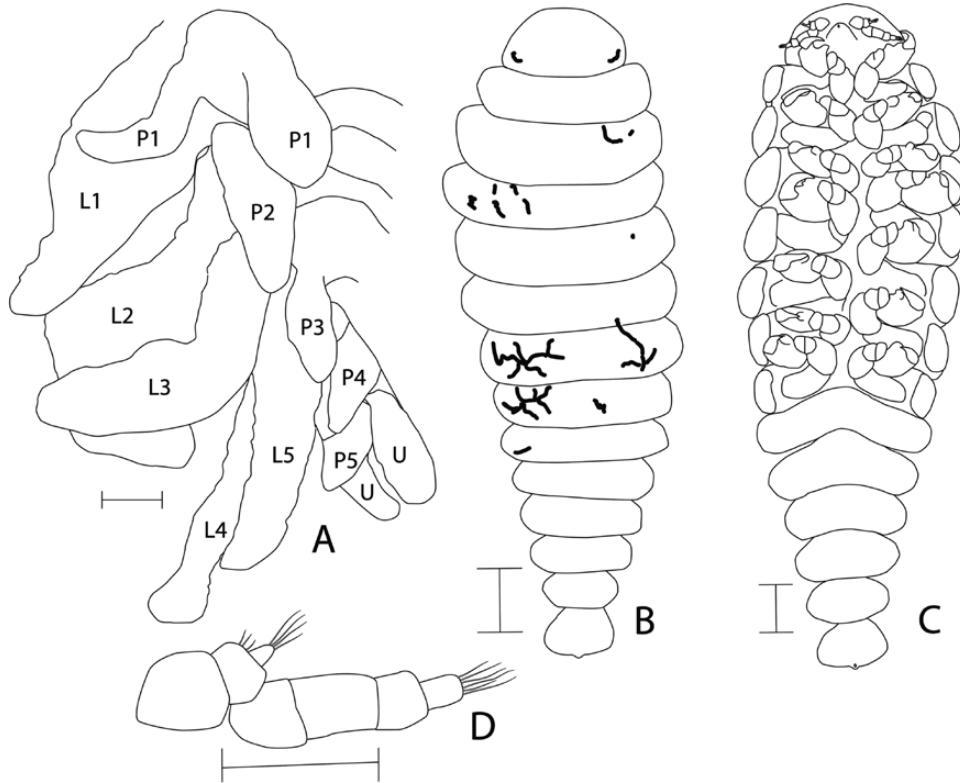


Figure 2. *Carcinione platypleura* Bourdon, 1983. A, female (RMNH.Crus.I.7721 ex RMNH.Crus.D.53224); B–D, male (RMNH.Crus.I.7726 ex RMNH.Crus.D.54057). A, pleon, ventral view. B, dorsal view. C, ventral view. D, left antennule and antenna. L, lateral plate; P, pleopod; U, uropod. Scale bars: 0.1 mm (A, C), 0.16 mm (B) and 0.05 mm (D).

hyperparasites associated with a single host. This male crab has an ovigerous female *C. platypleura* with a mature male in the right branchial chamber and a mature, non-ovigerous *C. platypleura* in the left branchial chamber. The bopyrid in the right chamber, despite being ovigerous, co-occurs with three *Cabirops* cryptoniscus larvae, one of which is in the marsupium amongst the eggs. The bopyrid in the left branchial chamber contains an ovigerous *Cabirops* in the marsupium and a cryptoniscus larva. As if this were not enough energy burden on the host, there is an immature female bopyrid (RMNH.Crus.I.7750) under the abdomen, which belongs to a new bopyrid genus and species described in the next subsection. This single host, therefore, has an astounding five bopyrid parasites, belonging to two species, and five hyperparasitic cryptoniscoids associated with it. The *Cabirops* species, being hyperparasitic and found associated with *C. platypleura* from two hosts in Okinawa, will be described in a future paper.

Known hosts

Dacryomaia japonica (Takeda & Tamura, 1981), *Dacryomaia* sp., *F. syzygia* van der Meij, 2015, *Lithoscaptus* cf. *bani* (Fize & Serène, 1957),

L. helleri (Fize & Serène, 1957), *L. prionotus* Kropp, 1994, *Lithoscaptus* sp., *Lithoscaptus* sp. 1(A), *Lithoscaptus* sp. 2(B), *Lithoscaptus* sp. Z, *Opecarcinus cathyae* van der Meij, 2014, *Opecarcinus pholeter* Kropp, 1989, *Opecarcinus* sp. 1(F), *P. ransoni* Fize & Serène, 1956a, *X. sheni* (Fize & Serène, 1956b), *Xynomaia* sp.

Distribution

Known from localities in Indonesia, Malaysia, Maldives and Japan.

SPATHIONE GEN. NOV.

urn:lsid:zoobank.org:act:B47EFD34-1336-48F2-B0AD-E3C0B6CD0584

Diagnosis

Female: Body compact, little deflected except for head with slight sinistral deflection. Head about as long as wide, overlapping almost entire first pereomere medially, inflated dorsoventrally, small lateral eyes present, frontal lamina present but very thin. Antennule of four segments; antenna of two segments. All pereomeres distinct, body highly vaulted ventrally, coxal plates very small, pronounced tergal projections on pereomeres one to seven,

those on one to four irregular in shape, those on five to seven smooth and rounded at ends (similar to appearance of lateral plates); five pairs of well-developed oostegites on pereomeres I–V, completely closing marsupium. Maxilliped palp lacking. Five pleomeres plus pleotelson, lateral plates well developed, tubular, rounded distally and recurved; biramous tubular pleopods on pleomeres I–IV as ventrally directed extensions of lateral plates; uniramous pleopods on pleomere V, bulbous uniramous uropods.

Male: Longer than broad, all segments clearly separated; abdomen not abruptly narrower than pereon, tapering anteriorly and posteriorly. Head ovate, eyes present. Antennae of four segments; antennules of two segments. Anterior pereomeres straight; posterior pereomeres and pleomeres curved posterolaterally (in dorsal view) and curved ventrally (in lateral view). Dactyli and propodi of all pereopods subequal. Four pleomeres plus pleotelson, distal margins rounded, no midventral tubercles on pleon; pleopods and uropods lacking.

Type and only species

Spathione asprosdovrima sp. nov.

Remarks

The finding of a bopyrid parasite in the marsupium of a gall crab was unexpected, as only species of *Rhopalione* Pérez, 1920 were known to be adapted to this environment, and gall crabs and pinnotherids, although both thoracotreme brachyurans, are not closely related (Wetzer, Martin & Boyce, 2009; van der Meij & Schubart, 2014; Tsang *et al.*, 2014). However, *Spathione* gen. nov. is indeed very closely related to *Rhopalione*, which contains four species (and one *nomen nudum*), all of which are parasitic in the marsupia of pinnotherid crabs. This is not, therefore, a case of convergent evolution of the bopyrids towards marsupial pouch parasitism, but rather a diversification of a prior preference towards marsupium parasitism from the original host to other crabs with similar structures. The only such crabs where females bear enlarged marsupial abdomens are species in the Pinnotheroidea (Aphanodactylidae and Pinnotheridae) and Cryptochiroidea (Cryptochiridae). Which taxon was the original host for the common ancestor of *Rhopalione* and *Spathione* gen. nov. cannot be determined or even suggested, because there is no lengthy fossil record for gall crabs (but see below), and the oldest pinnotherid (a species of *Viapinnixa* Schweitzer & Feldmann, 2001) is only Danian (Paleocene, 61.6–66 Mya; Brösing, 2008) and appears to belong to Pinnothereliinae, species whose females do not have the requisite marsupial pouch needed for *Rhopalione* to be able to occupy it. Schweitzer *et al.* (2010) did later move *Viapinnixa* to Pinnotherinae but without giving any rationale, and it is not clear that this is the proper placement (S. T. Ahyong, personal

communication). Recently, De Angeli & Ceccon (2015) described a putative fossil gall crab, *Montemagrechirus tethysianus*, from Italian Eocene deposits, but this is not a cryptochirid (see Klompmaker & Boxshall, 2015; Klompmaker, Portell & van der Meij, 2016). Currently, gall crabs in the fossil record date back only to the Pleistocene and Pliocene and are known only from their crescentic pits as an ichnotaxon (Klompmaker, Portell & van der Meij, 2016).

Superficially, *Rhopalione* and *Spathione* gen. nov. species appear very similar, but the two genera can be distinguished easily by numerous characters, as follows: female head subquadrate in *Spathione* gen. nov. vs. head rounded in *Rhopalione*; female and male antennae of four articles each, antennules of two articles in *Spathione* gen. nov. vs. five articles and three articles, respectively, in *Rhopalione*; first oostegite with rounded posterior margin in *Spathione* gen. nov. vs. with sharp point in *Rhopalione*; coxal plates small in *Spathione* gen. nov. vs. well developed in *Rhopalione*; female first pereopods approximately half as large as seventh pereopods in *Spathione* gen. nov. vs. pereopods isomorphic in *Rhopalione*; tergal projections of pereomeres IV–VII similar in shape to lateral plates of pleomeres vs. tergal projections of pereomeres IV–VII not extended and not resembling lateral plates of pleomeres in *Rhopalione*; female pleopods biramous as two separate tubular stalk-like rami extending from ventral surface of lateral plate in *Spathione* gen. nov. vs. pleopods as biramous as pair of flattened oval structures arising from common junction at base of ventral lateral plate in *Rhopalione*; males with four pleomeres, lacking pleopods, plus pleotelson in *Spathione* gen. nov. vs. males with five pleomeres, rounded pleopods on each segment, plus pleotelson in *Rhopalione*; and female uropods as short, rounded lateral lobes of pleotelson in *Spathione* gen. nov. vs. posteriorly extended and foliaceous in *Rhopalione*.

Rhopalione has been placed in Ioninae *sensu lato* (= Keponinae Boyko, Moss, Williams & Shields, 2013; e.g. Markham, 1992; Boyko *et al.*, 2013; An *et al.*, 2014), but several characters, particularly the biramous pleopods of the female and lack of midventral tubercles and presence of a non-bifurcated pleotelson of the male, support its transfer herein to Pseudioninae. *Spathione* gen. nov. is likewise placed in Pseudioninae and shows the additional character of the male having fewer than five pleomeres; this character is variable in Pseudioninae, whereas males of species in Keponinae have five pleomeres.

Etymology

The generic name is derived from a combination of the Greek σπάθη (spáthē), meaning saber, because of the extended, non-lamellar, lateral plates on the pleon, and *Ione*, a genus of bopyrid itself and also a common suffix for other bopyrid genera.

SPATHIONE ASPRODOVRIMA SP. NOV.

(FIGS 3–5, 10E)

urn:lsid:zoobank.org:act:94BB49B0-A076-485B-BAA4-9F1E60CB5B77

Type material

Indonesia: Mature non-ovigerous holotype female (3.48 mm), mature allotype male (1.8 mm) (RMNH. Crus.I.7749), ex abdominal marsupium of female *Lithoscaptus tri* (Fize & Serène, 1956b) (4.0 mm long × 2.5 mm wide) (RMNH. Crus.D.54029), ex *Echinopora lamellosa* (Esper, 1795) (Merulinidae), Sulamadaha I Reef, Ternate, 00°52'03"N, 127°19'33"E, 6 November 2009, coll. S. E. T. van der Meij.

Japan: Immature paratype female (2.0 mm) (RMNH. Crus.I.7750), ex abdomen of male *Xynomaia* sp. (4.3 mm long × 3.8 mm wide) (RMNH. Crus.D.57234), ex *Pectinia* sp. (Merulinidae), Blue Tombs, Henza Island, Okinawa, 26°21'46"N, 127°59'50"E, 29 April 2016, coll. S. E. T. van der Meij.

Description

Female (Fig. 3): Body length 3.4 mm, maximal width 2.6 mm, head length 0.71 mm, head width 0.78 mm. Pereon nearly straight, head slightly deflected sinistrally (Fig. 3A, B). All body regions and pereomeres distinctly segmented.

Head subrectangular, approximately as broad as long, overlapping almost entire first pereomere medially, inflated dorsoventrally with very thin frontal lamina (Fig. 3A, C). Eyes minute, lateral. Antennule of four articles; antenna of two articles (Fig. 3D). First oostegite (Fig. 3E) anterior lobe globular, posterior lobe slightly smaller than anterior lobe, ovate with rounded margins, distal projection lacking but with medially directed smooth lobe, internal ridge thick, smooth. Oostegites completely enclosing marsupium. Maxilliped (Fig. 3F) with short subacute fleshy spur; palp lacking, anterior segment rounded, posterior segment triangular. Barbula of three short, rounded fleshy lobes (Fig. 3G).

Pereon composed of seven pereomeres, broadest across pereomere V, gradually tapering anteriorly and posteriorly; pereomere I posterior margin under head, II weakly concave, III–VII medially concave. Coxal plates very small on anterior pereomers, pronounced, separated, tergal projections on pereomeres one to seven, those on one to four irregular in shape, those on five to seven smooth and rounded at ends (similar to appearance of lateral plates). Anteriormost pair of pereopods (Fig. 3H) about half as large as other pairs (Fig. 3I).

Five pleomeres plus pleotelson, lateral plates well developed, tubular, rounded distally and recurved (Fig. 3J). Pleomeres I–IV with biramous, widely spaced, tubular pleopods as ventrally directed extensions of lateral plates; uniramous pleopods on pleomere V, bulbous uniramous uropods.

Male (Fig. 5): Length 1.8 mm, maximal width 0.82 mm, head length 0.23 mm, head width 0.47 mm, pleon length 0.46 mm.

Head ovate, widest medially, distinct from first segment of pereon (Fig. 5A, B); eyes present. Antennule of four articles (Fig. 5C), distally setose, scarcely extending beyond margin of head; antenna of two articles, terminal article stout, distally setose (Fig. 5C).

Pereomere V broadest, others gradually tapering anteriorly and posteriorly. Pereomeres I–V straight, VI and VII posteriorly concave, distal and ventral margins of all pereomeres rounded. All pereopods (Fig. 5B, D, E) subequal; carpus and merus nearly fused, all other articles distinctly separated.

Pleon with four segments plus pleotelson. All pleomeres directed posterolaterally (in dorsal view; Fig. 5A), with distolateral margins rounded; extended ventrally (in lateral view). Midventral tubercles, pleopods and uropods lacking (Fig. 5B).

Etymology

From a combination of the Greek ἀπροσδόκητος (aprosdókēti), meaning unexpected, and εὕρημα (evrima), meaning finding, because of the unexpected finding of a sister taxon to *Rhopalione* on a species of gall crab (Cryptochiridae).

Remarks

See under Remarks for the genus. The juvenile specimen (RMNH. Crus.I.7750; Fig. 4) already shows the overall body shape and pleopod formation seen in the adult female, and little additional modification to the body seems to occur between the immature and mature female forms. The occurrence of the juvenile female on a male host is perplexing, because the holotype female occupies the entirety of the female's marsupium, hence the paratype female appears to have made a poor host choice because the male abdomen will not develop into an appropriate structure to hold the adult female. There is no evidence in the literature that bopyrids can markedly feminize their hosts à la rhizocephalans.

Known hosts

Lithoscaptus tri (Fize & Serène, 1956b), *Xynomaia* sp.

Distribution

Known from Indonesia and Japan.

CRYPTONISCOIDEA KOSSMANN, 1880

CRYPTONISCIDAE KOSSMANN, 1880

DANALIA GIARD, 1887***DANALIA CERVIX SP. NOV.***

(FIGS 6A, 11F)

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'cryptoniscine isopod parasites' Kropp & Manning, 1987: 10, 12 [Belize, examined herein].

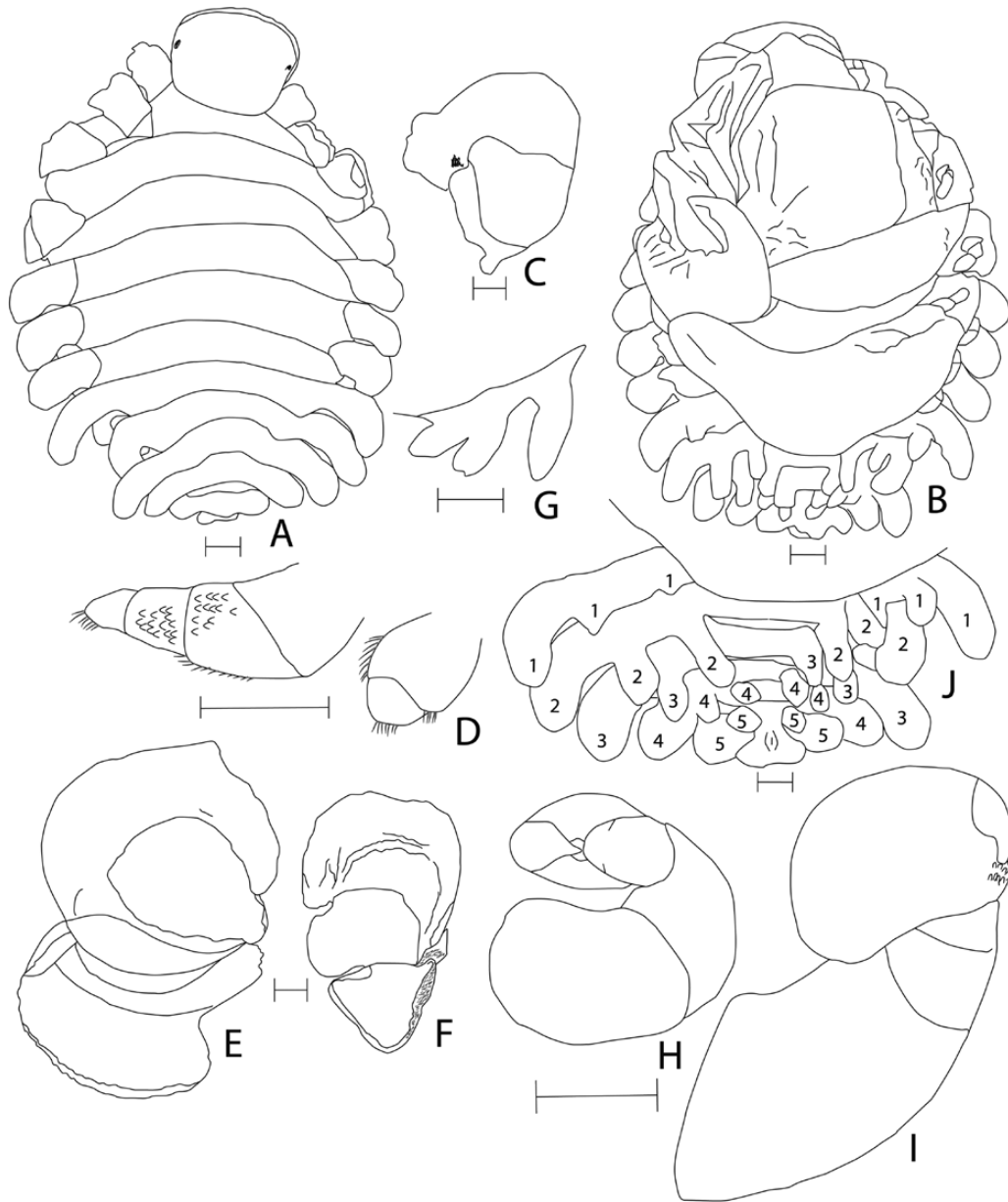


Figure 3. *Spathione asprosdovrima* gen. et sp. nov. Holotype female (RMNH.Crus.I.7749 ex RMNH.Crus.D.54029). A, dorsal view. B, ventral view. C, head, left side lateral. D, left antenule and antennae. E, left oostegite I, external view. F, left maxilliped. G, barbula, left side. H, left pereopod I. I, right pereopod 7. J, pleon, ventral view, with segments numbered. Scale bars: 0.1 mm (D–F, H, I), 0.16 mm (C, G, J) and 0.25 mm (A, B).

Type material

Curaçao: Immature holotype female (9.0 mm), two paratype cryptoniscus larvae (1.05 mm each) (RMNH.Crus.I.7751), ex abdomen of female *Opecarcinus hypostegus* (Shaw & Hopkins, 1977) (5.6 mm long × 4.5 mm wide) (RMNH.D.56099), ex *Agaricia lamarcki* H. Milne Edwards & Haime, 1851 (Agariciidae), Playa Lagun, 12°19'69"N, 69°09'00"W, 35 m depth, 29 October 2013, coll. S. E. T. van der Meij.

Belize: Two immature paratype females (0.6, 0.7 mm) (USNM 1437664), ex abdomen of female *Opecarcinus hypostegus* (Shaw & Hopkins, 1977) (2.0 mm long × 1.5 mm wide) (USNM 231677), ex *Agaricia* sp. (Agariciidae), Carrie Bow Cay, Dangrega District, Belize, 16°48'12"N, 88°04'30"W, 15.2 m depth, 20 April 1981, coll. G. Hendler.

Description

Female (Fig. 6A): 9 mm long; mature female stout, body strongly recurved, proximal end truncate, distal

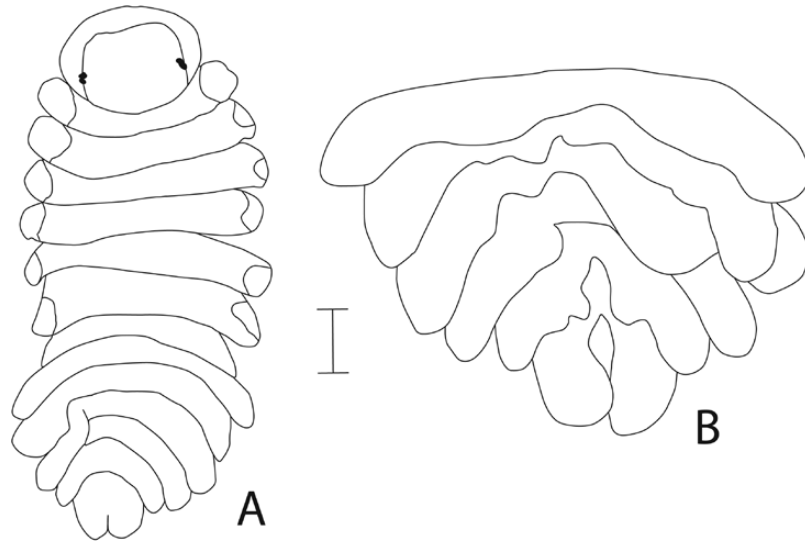


Figure 4. *Spathione asprosdovrima* gen. et sp. nov. Immature paratype female (RMNH.Crus.I.7750 ex RMNH.Crus.D.57234). A, dorsal view. B, ventral view of pleon. Scale bar = 0.125 mm (B), 0.25 mm (A).

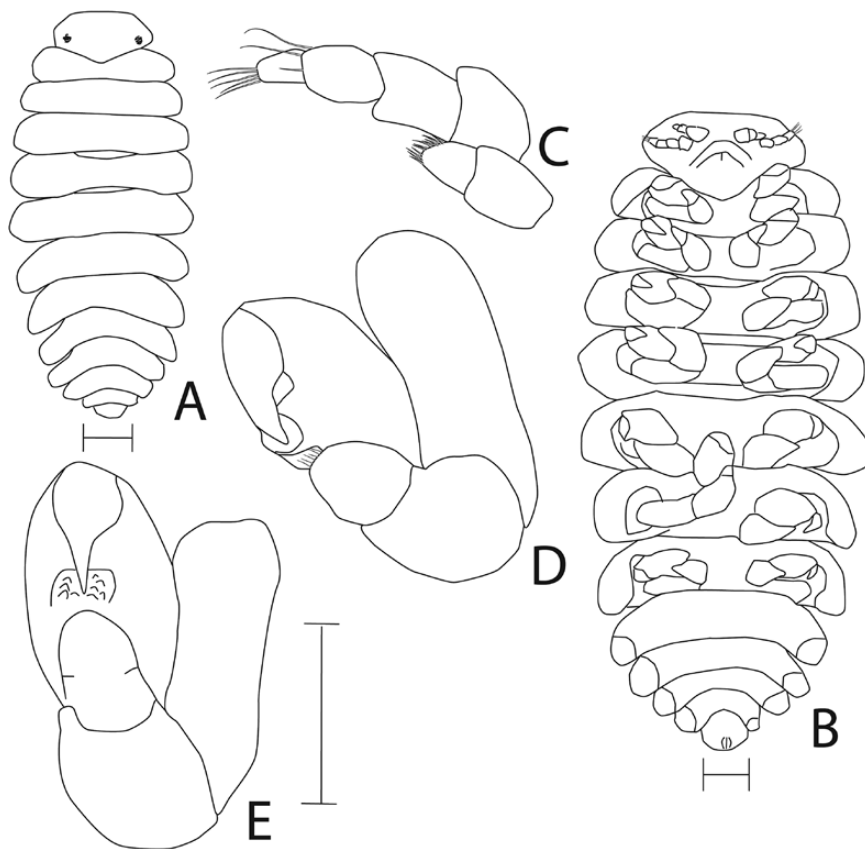


Figure 5. *Spathione asprosdovrima* gen. et sp. nov. Allotype male (RMNH.Crus.I.7749 ex RMNH.Crus.D.54029). A, dorsal view. B, ventral view. C, left antennule and antenna. D, left pereopod I. E, left pereopod 7. Scale bars: 0.1 mm (C–E), 0.16 mm (B) and 0.25 mm (A).

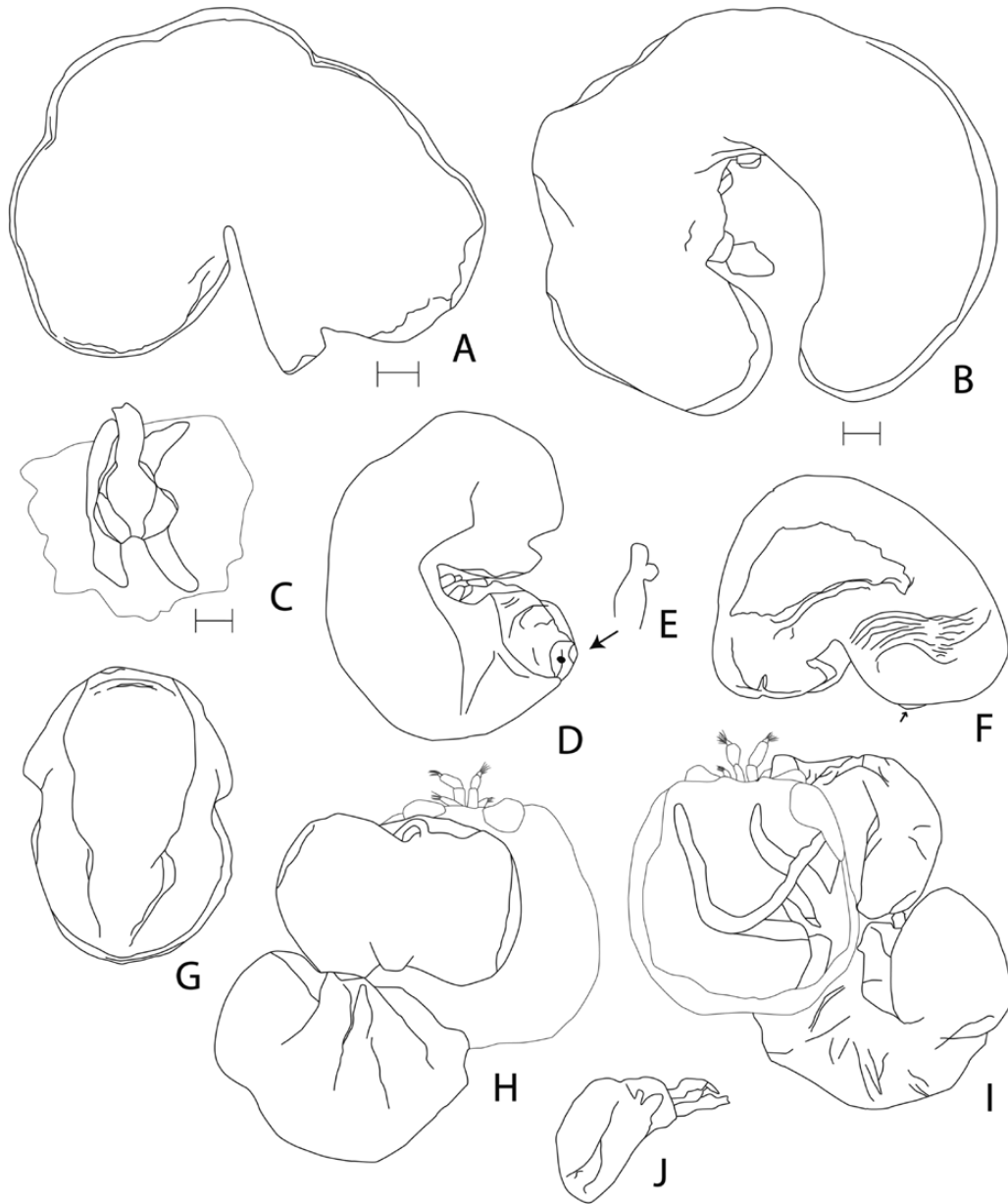


Figure 6. A, *Danalia cervix* sp. nov. (RMNH.Crus.I.7751 ex RMNH.Crus.D.56099); B–E, *Danalia falsicrura* sp. nov. (B, C, USNM 1461192 ex USNM 234257; D, E, RMNH.Crus.I.7752 ex RMNH.Crus.D.54222); F, G, *Danalia galea* sp. nov. (RMNH.Crus.I.7753 ex RMNH.Crus.D.53188); H–J *Danalia hapalocarcini* Fize, 1955 (H, I, RMNH.Crus.I.7754 ex RMNH.Crus.D.53703; J, MNHN-IU-2017-10 ex MNHN-IU-2009-5733). A, lateral view of holotype. B, lateral view of holotype. C, ventral view of attachment process and host cuticle of holotype. D, lateral view; arrow indicates insertion point of attachment process. E, lateral view of attachment process. F, lateral view of holotype. G, dorsal view of holotype. H, dorsal view of host and two *D. hapalocarcini* specimens. I, ventral view of host carapace interior, showing ramification of attachment processes on interior surface of carapace; two *D. hapalocarcini* bodies visible on right. J, immature specimen, lateral view. Scale bars: 0.25 mm (B–E, J) and 0.5 mm (A, F–I).

end rounded, surface smooth but with indentations showing indications of four or five segments dorsally, internal segmentation not visible; anteroventral shield small. Trunk thick and strongly extended,

inserted into body at an angle of $\sim 45^\circ$, extending out from body slightly anterior to midventral indentation, attachment lobes missing (presumed thin and fragile). Directly parasitizing cryptochirid host.

Etymology

The species name is from the Latin *cervix*, meaning nozzle, and refers to the large attachment process trunk that is partly fused with the body. It is used as a noun in apposition.

Remarks

The thick attachment trunk, partly fused with the body and not terminally positioned, is unique to this species. It is therefore difficult to know to which other species of *Danalia* this new species is most closely related. This is the only species of *Danalia* known from the western Atlantic; *Danalia frassei* Nierstrasz & Brender à Brandis, 1925, also from Curaçao, was shown to belong to *Cabirops* by Boyko (2013).

Known host

Opearcinus hypostegus (Shaw & Hopkins, 1977).

Distribution

Known from Curaçao (type locality) and Belize.

DANALIA FALSICRURA SP. NOV.

(FIGS 6B–E, 11C)

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‘three small sac-like parasites’ Utinomi, 1944: 696–697, fig. 4 [ex *Pseudocryptochirus viridis* Hiro, 1938, ex *Turbinaria contorta* Bernard, 1896 [= *T. frondens* (Dana, 1846)] (Dendrophyllidae), Tanabe Bay, Japan]. ‘*Danalia* sp. Utinomi, 1944’ Boyko, 2015: 76.

Type material

Guam: Immature holotype female (6.6 mm) (USNM 1461192), ex abdomen of female *Opearcinus crescentus* (Edmondson, 1925) (2.1 mm long × 1.8 mm wide) (USNM 234257), ex *Pavona duerdeni* Vaughan, 1907 (Agariciidae), main patch reef, double reef, 24 February 1984, coll. R. K. Kropp.

Indonesia: Immature paratype female (4.8 mm) (RMNH.Crus.I.7752), ex abdomen of female *Fungicola utinomi* (Fize & Serène, 1956a) (4.3 mm long × 2.5 mm wide) (RMNH.Crus.D.54222), ex *Lithophyllon repanda* (Dana, 1846) (Fungiidae), North Pulau Dua, Lembah Strait, 01°23′28″N, 125°12′58″E, 13 February 2012, coll. S. E. T. van der Meij.

Description

Female (Fig. 6B–E): 6.6 mm long; mature female cylindrical, body strongly recurved, proximal and distal ends rounded, surface smooth without indications of segments, internal segmentation not visible; anteroventral shield large. Trunk thick but very short, variably inserted into body either subterminally (Fig. 6B) or terminally (Fig. 6D, E), attachment lobes variable (probably owing to development), either from two

short, rounded lobes terminally on stalk (Fig. 6E) or four thin, flat lobes extending from central stalk (Fig. 6C). Directly parasitizing cryptochirid host.

Etymology

The species name is a combination of *falsum* and *crura*, meaning ‘false legs’, which refers to the stump-like processes emanating from the centre of the ventral surface that resemble the prolegs of caterpillars (Lepidoptera). It is used as a noun in apposition.

Remarks

Utinomi (1944) found two female *Pseudocryptochirus viridis* infested with one or two parasites on each of their ventral abdominal surfaces, and his description and drawings leave little doubt that his specimens from Japan are conspecific with *D. falsicrura* sp. nov. The shape of the body is nearly identical, and the presence of four small foot-like ventral projections is unique to this species. Utinomi’s (1944) females all had the attachment process centrally located on the proximal end of each parasite, which is also seen in the specimen from Indonesia. The Guam female, however, has the attachment process set back from the proximal end and positioned more ventrally than in the other specimens. Utinomi’s (1944) fig. 4B appears to show indistinct surface lobes indicating the presence of five segments to the body, but this is not seen in his fig. 1A or in the present specimens.

Known hosts

Fungicola utinomi (Fize & Serène, 1956a), *Opearcinus crescentus* (Edmondson, 1925), *Pseudocryptochirus viridis* Hiro, 1938.

Distribution

Known from Guam (type locality), Indonesia and Japan.

DANALIA GALEA SP. NOV.

(FIGS 6F, G, 11A, B)

urn:lsid:zoobank.org:act:22A465BF-D0C5-4E2A-A8A4-F88C175439D4

Type material

Indonesia: Mature non-ovigerous holotype female (6.3 mm) (RMNH.Crus.I.7753), ex ventral abdomen of female *Lithoscaptus paradoxus* A. Milne-Edwards, 1862 (6.0 mm long × 3.3 mm wide) (RMNH.Crus.D.53188), ex *Platygyra lamellina* (Ehrenberg, 1834) (Merulinidae), Timur I, Bunaken Island, 01°36′38″N, 124°46′59″E, 11 December 2008, coll. S. E. T. van der Meij.

Papua New Guinea: Mature non-ovigerous paratype female (1.7 mm long × 1.0 mm wide) (RMNH.Crus.I.7705), between fourth and fifth pereopod, left side, inserted into fifth pereopod base of female *Dacryomaia* sp. (3.5 mm long × 1.9 mm wide) (RMNH.Crus.D.57067), ex *Psammocora* cf. *digitata* H. Milne Edwards & Haime,

1851 (Psammocoridae), Steffen Channel, Kavieng, 02°43'22"S, 150°34'28"E, 18 August 2014, coll. F. Benzoni.

Description

Female (Fig. 6F, G): 6.3 mm long; mature females very broad in dorsal view, body robust, width nearly two-thirds of length, intersection of proximal and distal portions of body giving a laterally indented appearance in dorsal view, body with slight ventral indentation, proximal and distal ends rounded, surface without lobes but with irregular indentations dorsally, some of surface with areas of cuticular lines, internal segmentation not visible; anteroventral shield very small. Trunk short and barely extending from body, inserted into body subterminally at proximal end, attachment lobes missing (presumed thin and fragile). Directly parasitizing cryptochirid host, either on the ventral surface of the abdomen or on posterior pereopods.

Etymology

The species name is from the Latin *galea*, meaning helmet, for the overall appearance of the female body. It is used as a noun in apposition.

Remarks

The distinctive helmet-like shape is unique to this species and the attachment stalk perhaps the shortest known in species of the genus. The attachment position of the paratypes on posterior pereopods of the host is unusual, but other species in the genus (e.g. *Danalia hapalocarcini*, see next subsection) parasitize locations other than the ventral surface of the abdomen. However, given that this species was found in two locations on hosts, it is unclear whether one is the preferred location or if both are equally suitable to the parasite.

Known hosts

Dacryomaia sp., *L. paradoxus* A. Milne-Edwards, 1862.

Distribution

Indonesia and Papua New Guinea.

DANALIA HAPALOCARCINI FIZE, 1955

(FIGS 6H–J, 11D)

Danalia hapalocarcini Fize, 1955: 2444–2447, figs. 1–4.
– Fize, 1956: 22–28, figs. 15–18. – Altes, 1982: 28–29.
– Grygier, 1993: 189–190. – Boyko, 2015: 76, fig. 2H.

Material examined

Malaysia: Mature non-ovigerous female (3.0 mm), mature female (2.9 mm) (RMNH.Crus.I.7754), on carapace of female *Hapalocarcinus marsupialis* Stimpson, 1859 (2.9 mm long × 2.8 mm wide) (RMNH.Crus.D.53703), ex *Seriatopora* cf. *caliendrum* Ehrenberg, 1834 (Pocilloporidae), Horn Reef, Semporna, 04°14'32"N, 118°26'25"E, 1 December 2010, coll. S. E. T. van der Meij.

Indonesia: Cryptoniscus larva (1.33 mm) (RMNH.Crus.I.7755), on carapace of female *H. marsupialis*

Stimpson, 1859 (2.6 mm long × 2.6 mm wide) (RMNH.Crus.D.53189), ex *Seriatopora* cf. *caliendrum* Ehrenberg, 1834 (Pocilloporidae), Tanjung Sidangolo, Halmahera, 00°53'40"N, 127°29'28"E, 5 November 2009, coll. S. E. T. van der Meij.

New Caledonia: Immature female (0.9 mm) (MNHN-IU-2017-10), on lower left carapace of immature female *H. marsupialis* Stimpson, 1859 (2.5 mm long × 3.0 mm wide) (MNHN-IU-2009-5733), ex *Stylophora* sp. (Pocilloporidae), New Caledonia, Ilot Maître, Lagoon, 5 m depth, 22°19'48"S, 166°25'06"E, 24 April 1995, coll. P. Castro.

Redescription

Female (Fig. 6H–J): 3.0 mm long; mature female very broad in dorsal view, body weakly cuticularized, sac like; body moderately recurved, proximal and distal ends rounded; surface without lobes but with irregular folds dorsally, internal segmentation not visible; anteroventral shield small. Trunk short, inserted into body terminally at proximal end; attachment lobes extremely long and slender, covering large portion of ventral surface of host carapace. Directly parasitizing cryptochirid host on ventral surface of carapace.

Remarks

The new records of this species are the first since the species was described based on specimens from Vietnam. The attachment processes are the most elaborately extended of any species in the genus and reach nearly across the entire ventral surface of the host's carapace, presumably to maximize nutrient absorption. This was the only species of *Danalia* known to parasitize through the dorsal surface of the carapace of its hosts before the discovery of *Danalia vesica* sp. nov. (see next subsection). It can be distinguished from *D. vesica* sp. nov. by the shape of body (sac like but recurved in *D. hapalocarcini* vs. sac like but disc shaped in *D. vesica* sp. nov.) and in the length of the attachment processes (long in *D. hapalocarcini* vs. short in *D. vesica* sp. nov.).

Known host

Hapalocarcinus marsupialis Stimpson, 1859.

Distribution

Vietnam (type locality), Malaysia, Indonesia and New Caledonia.

DANALIA VESICA SP. NOV.

(FIG. 7A, B)

urn:lsid:zoobank.org:act:728A215D-468D-433C-A36E-9380E436C9A8

Type material

Mature non-ovigerous holotype female (3.3 mm long × 2.5 mm wide) (RMNH.Crus.I.1742), on

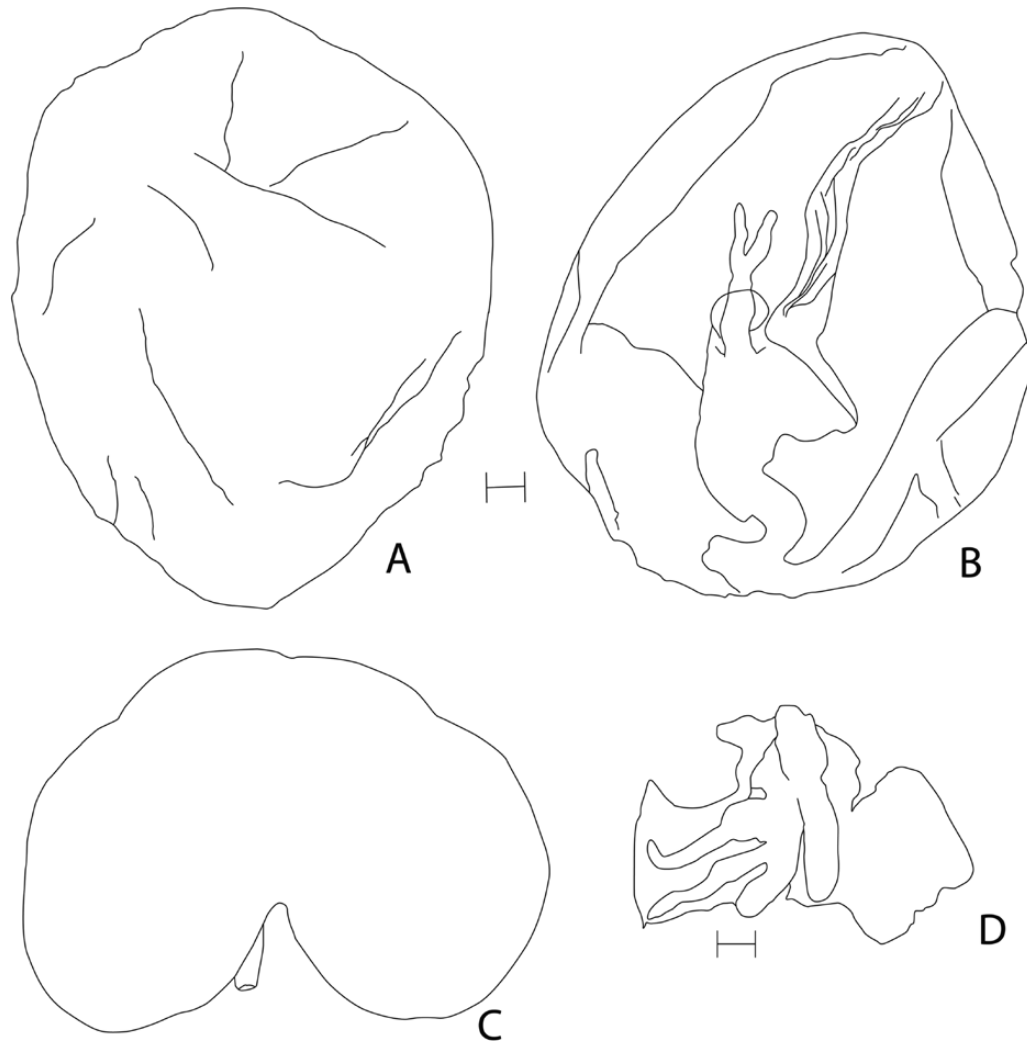


Figure 7. A, B, *Danalia vesica* sp. nov. (RMNH.Crus.I.1742); C, D, *Danalia* sp. (RMNH.Crus.I.7756 ex RMNH. Crus.D.54220). A, dorsal view of holotype. B, ventral view of holotype. C, lateral view. D, ventral view of attachment process and host cuticle. Scale bars: 0.25 mm.

carapace of female *H. marsupialis* Stimpson, 1859 (3.0 mm long × 3.0 mm wide), (RMNH.Crus.D.57235), ex unknown host coral (probably Pocilloporidae, because it is the only known host family for this gall crab species), Mamba Bawi, east coast of Zanzibar, 19 September 1970, coll. A. J. Bruce.

Description

Female (Fig. 7A, B): 3.3 mm long; mature female nearly circular in dorsal view, body weakly cuticularized, sac like; body not recurved; convex dorsally and concave ventrally, conforming to the dorsal surface of the host carapace; surface without lobes but with irregular folds dorsally; internal segmentation not visible; anteroventral shield small. Trunk short, inserted into body near centre of ventral surface; attachment lobes, apparently only two, short and slender, covering small portion of ventral surface of host carapace. Directly parasitizing cryptochirid host on ventral surface of carapace.

Etymology

The species name is derived from the Latin for bladder or balloon, in reference to the female resembling a deflated balloon.

Remarks

This species, known presently only from the female holotype, can be distinguished from its closest relative, *D. hapalocarcini*, by the characters given in the Remarks for that species. The presence of only two attachment processes instead of the usual four is unusual but, because there is only the single specimen known, needs confirmation as a species-specific character through collection and examination of additional specimens.

Known host

Hapalocarcinus marsupialis Stimpson, 1859.

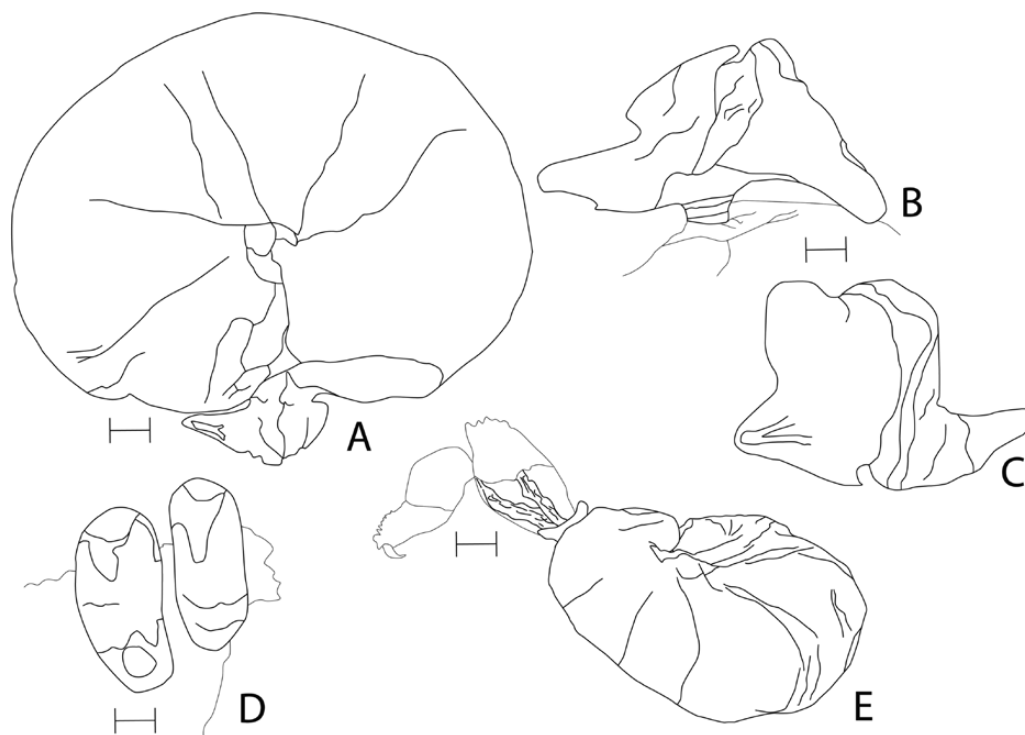


Figure 8. *Cabirnalialia nausicaa* gen. et sp. nov. (A–D, MNHN-IU-2009-5735; E, RMNH.I.7757 ex RMNH.D.53737). A, lateral view of holotype. B, attachment process, lateral view. C, attachment process, frontal view. D, pair of immature specimens and host cuticle. E, lateral view of parasite and host pereopod, with attachment process visible through cuticle of merus. Scale bars: 0.25 mm (B–D) and 0.5 mm (A, E).

Distribution

Known only from Zanzibar.

DANALIA SP.

(FIGS 7C, D, 11E)

Material examined

Indonesia: Immature female (4.3 mm) (RMNH. Crus.I.7756), on abdomen of female *F. syzygia* van der Meij, 2015 (3.2 mm long × 2.7 mm wide) (RMNH.Crus.D.54220), ex *Cycloseris sinensis* H. Milne Edwards & Haime, 1851 (Fungiidae), Teluk Makawide, Lembah Strait, 01°29'05"N, 125°14'26"E, 9 February 2012, coll. S. E. T. van der Meij.

Remarks

This unique specimen most resembles some specimens of *D. curvata* (Fraisie, 1878) in overall shape, but the position of the trunk (offset from the ventral median) differs from that of *D. curvata* (terminal on anterior end). However, *D. curvata* is a Mediterranean species that has been recorded parasitizing the rhizocephalan *Drepanorchis neglecta* (Fraisie, 1878) found on the spider crab *Inachus communissimus* Rizza, 1839, rather than being a direct crab parasite. Given that only a single immature specimen exists, and the shape could be altered

with development (i.e. as occurs with *D. curvata*), it is not advisable to describe the specimen at this time, despite the characters that suggest it represents a new species.

Known host

Fungicola syzygia van der Meij, 2015.

Distribution

Known only from Indonesia.

DANALIA SP. CRYPTONISCUS LARVA

'cryptoniscine isopod' Kropp & Manning, 1987: 7, 8 [Ghana, examined herein].

Material examined

Ghana: Cryptoniscus larva (1.0 mm) (USNM 1461194), on abdomen of female *Detocarcinus balssi* (Monod, 1956) (2.2 mm long × 2.2 mm wide) (USNM 231665), ex *Schizoculina africana* (Thiel, 1928) (Oculinidae), Kpone Bay, 05°44'N, 00°04'W, 10 m depth, 11 March 1970, coll. J. Laborel.

Remarks

The cryptoniscus is not in particularly good condition, but it clearly is that of a *Danalia* species. The seventh pereopod dactyli are nearly identical to those of cryptonisci

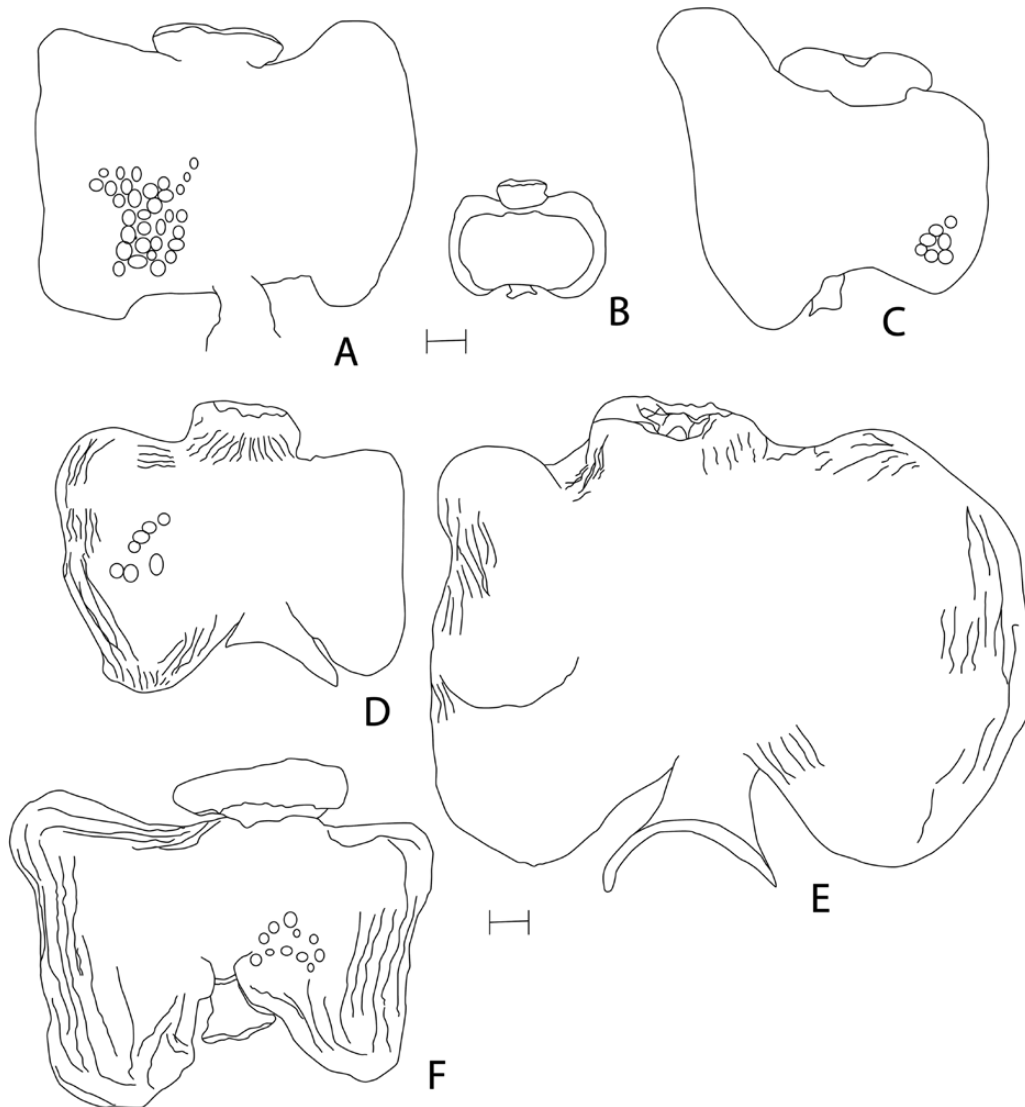


Figure 9. *Sacculina quadrialata* sp. nov. A, ovigerous holotype female (RMNH.Crus.C.10249) ex *Opecarcinus* sp. 1 (RMNH.Crus.D.53990). B, immature female (RMNH.Crus.C.10253) ex *Opecarcinus* aff. *sierra* Kropp, 1989 (RMNH.Crus.D.54208). C, ovigerous female (RMNH.Crus.C.10252) ex *Lithoscaptus* cf. *bani* (Fize & Serène, 1957) (RMNH.Crus.D.53993). D, ovigerous female (RMNH.Crus.C.10251) from double infection ex *Fizeserenia heimi* (Fize & Serène, 1956) (RMNH.Crus.D.54108). E, female (RMNH.Crus.C.10251) from double infection ex *F. heimi* (RMNH.Crus.D.54018). F, ovigerous female (RMNH.Crus.C.10254) ex *Xynomaia sheni* (Fize & Serène, 1956b) (RMNH.Crus.D.54166). Scale bars: 0.25 mm. A subsample of eggs is drawn in ovigerous females to show size; the mantle cavity is completely full of eggs in these individuals.

of other species of *Danalia*, such as *D. curvata* (Fraisie, 1878) (see Boyko, 2015: fig. 1C6) and *D. hapalocarcini* Fize, 1955 (see Fize, 1956: fig. 18F). Based on the locality from which the specimen was collected, it is unlikely to be conspecific with any other species of *Danalia*.

Known host

Detocarcinus balssi (Monod, 1956).

Distribution

Known only from Ghana.

CABIRNALIA GEN. NOV.

urn:lsid:zoobank.org:act:61D0157E-D349-4BC4-B24C-9F4C30AD41CF

Diagnosis

Mature female: strongly recurved, circular in outline. Strongly convex dorsal margin without lobes but with cuticular indentations indicating segmentation; ventral sides meeting medially, with several small, plate-like areas demarcated at midpoint. Attachment trunk

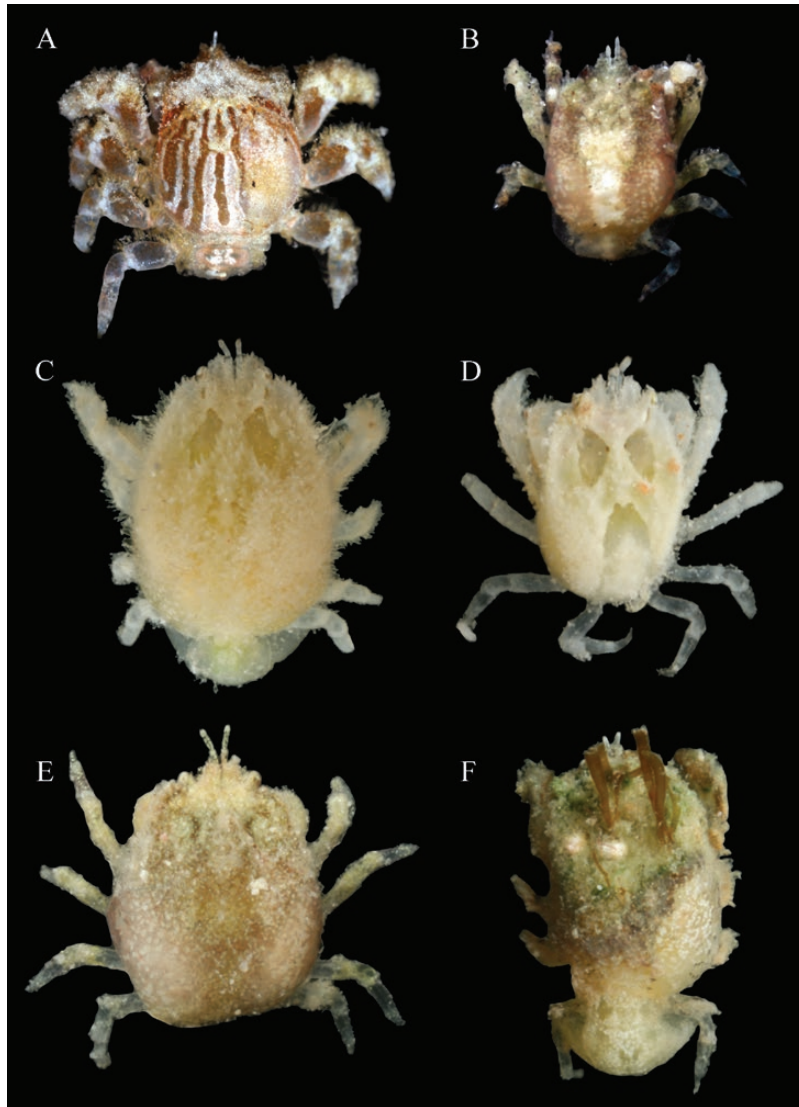


Figure 10. *Carcinione platypleura* Bourdon, 1983 (Bopyridae) parasitizing: A, right branchiostegite of non-ovigerous female *Opecarcinus pholeter* Kropp, 1989 (RMNH.Crus.D.54000); B, left and right branchiostegite of juvenile female *Dacryomaia japonica* (Takeda & Tamura, 1981) (RMNH.Crus.D.54193); C, left and right branchiostegites of female *Lithoscaptus* sp. Z (RMNH.Crus.D.57066); D, left and right branchiostegites of male *Lithoscaptus* sp. Z (RMNH.Crus.D.57066); E, left and right branchiostegites, with *Cabirops* sp. as hyperparasite in left and right branchiostegites and in marsupium; ***Spathione asprosdovrima* gen. et sp. nov.** under abdomen of male *Xynomaia* sp. (RMNH.Crus.D.57234); F, right branchiostegite, with *Cabirops* sp. as hyperparasite in right branchiostegite and marsupium of female *Lithoscaptus* sp. (RMNH.Crus.D.57232). Photographs not to scale; sizes of gall crab hosts can be retrieved from the main text.

short, with single attachment lobe, medially divided and expanded into two broad sections. Parasitic on abdomen or pereopods of crab hosts.

Type species

Cabirnalina nausicaa sp. nov.

Etymology

The generic name is a combination of *Cabirops* and *Danalia*, because the genus has characters found in both genera. The gender is feminine.

Remarks

This genus is most similar to *Danalia* in the overall shape of the mature females and the presence of an attachment trunk. However, the medioventral area of the holotype of the type species shows several small plate-like structures, very similar to those seen on species of *Cabirops* and not found in any species of *Danalia* except *D. caulleryi* Nierstrasz & Brender à Brandis, 1923 (see Boyko, 2015). As *Cabirops* species do not possess any attachment structures and

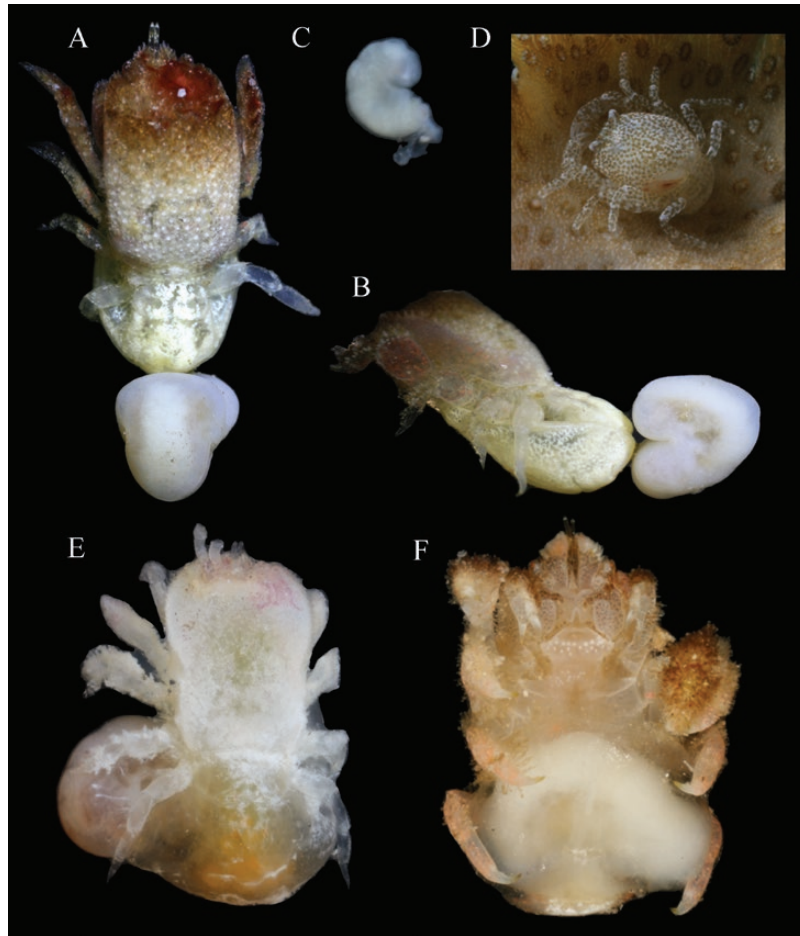


Figure 11. Various *Danalia* species as parasites of gall crab hosts. A, *Danalia galea* sp. nov. attached to abdomen of *Lithoscaptus paradoxus* A. Milne-Edwards, 1862 (RMNH.Crus.D.53188). B, lateral view of same specimen. C, *Danalia falsicrura* sp. nov., separated from host *Fungicola utinomi* (Fize & Serène, 1956a) (RMNH.Crus.D.54222). D, *Danalia hapalocarcini* Fize, 1955 (cryptoniscus male) on *Hapalocarcinus marsupialis* Stimpson, 1859 (RMNH.Crus.D.53189) on its host *Seriatopora* cf. *caliendrum* Ehrenberg, 1834. E, *Danalia* sp. in marsupium of *Fungicola syzygia* van der Meij, 2015 (RMNH.Crus.D.54220). F, *Danalia cervix* sp. nov. in marsupium of *Opecarcinus hypostegus* (Shaw & Hopkins, 1977) (RMNH.Crus.D.56099). Photographs not to scale; sizes of gall crab hosts can be retrieved from the main text.

Danalia species do not possess medioventral plates, this new genus is necessary to accommodate the new species described below. *Danalia caulleryi* is also placed in *Cabirnalina* gen. nov., as *Cabirnalina caulleryi* comb. nov., because the unique holotype has medioventral plates and shows evidence of a now-lost attachment trunk (see Boyko, 2015). Even though the structure of the attachment trunk of *C. caulleryi* comb. nov. is not known, it is not likely to be conspecific with *C. nausicaa* gen. nov., sp. nov. because (1) the cuticular ridges of *C. caulleryi* comb. nov. are much more robust than those found on the type species and (2) the host of *C. caulleryi* comb. nov. is a galatheid, not a gall crab. *Cabirnalina* gen. nov. is therefore unique among cryptoisocoids in containing species found parasitizing both brachyuran and anomuran hosts.

CABIRNALIA NAUSICAA SP. NOV.

(FIGS 8, 12C–F)

urn:lsid:zoobank.org:act:27FFC15A-5D05-41F4-A6B3-B26FCC86DBF0

Type material

New Caledonia: Mature holotype female (14.1 mm) (MNHN-IU-2017-11), two immature paratype females (1.6 mm each) (MNHN-IU-2017-12), ex abdomen of female *H. marsupialis* Stimpson, 1859 (4.0 mm long × 4.0 mm wide) (MNHN-IU-2009-5735), ex *Pocillopora* sp. (Pocilloporidae), New Caledonia, lagoon, Passe de Boulari, 10–20 m depth, 22°29'54"S, 166°26'33"E, 28 April 1995, coll. P. Castro.

Malaysia: Three mature paratype females (5.0, 5.5 and 6.3 mm), paratype cryptoniscus larva (1.3 mm)

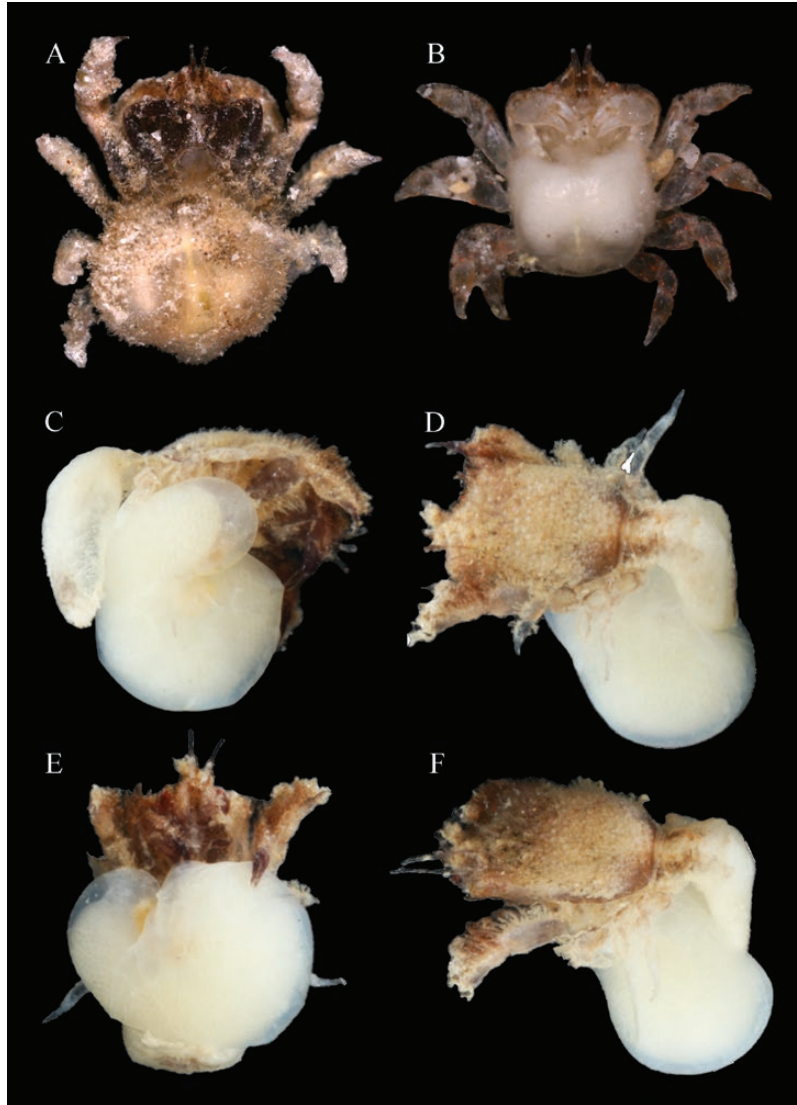


Figure 12. *Sacculina quadrialata* sp. nov. in the marsupium of: A, female *Fizesereneia heimi* (Fize & Serène, 1956a) (RMNH.Crus.D.54018); and B, feminized male *Opecarcinus* sp. F (RMNH.Crus.D.53990). C–F, *Cabirnalina nausi-caa* gen. et sp. nov. parasitizing *Lithoscaptus* sp. 2(B) (RMNH.Crus.D.57236) ventromedially between second and third sternite in various views. Photographs not to scale; sizes of gall crab hosts can be retrieved from the main text.

(RMNH.Crus.I.7757), ex posterior pereopods (females) and abdomen (larva) of female *L. helleri* (Fize & Serène, 1957) (4.2 mm long × 2.7 mm wide) (RMNH.Crus.D.53737), ex *Favites* cf. *halicora* (Ehrenberg, 1834) (Merulinidae), Batura Reef, Semporna, 04°30'49"N, 118°48'31"E, 7 December 2010, coll. S. E. T. van der Meij.

Japan: Mature female (4.8 mm long × 3.5 mm wide) (RMNH.Crus.I.7758), inserted ventromedially between second and third sternites of female *Lithoscaptus* sp. 2(B) (RMNH.Crus.D.57236), ex *P. versipora* (*Scleractinia incertae sedis*), Mizugama, Okinawa, 26°21'35"N, 127°44'18"E, 15 April 2016, coll. S. E. T. van der Meij.

Other material

Thailand: Immature female (2.2 mm), ex third pereopod of male *L. paradoxus* A. Milne-Edwards, 1862, 1862 (2.5 mm long × 1.5 mm wide) (ZRC 2016.0435), ex unknown coral, coral reef, Phuket, December 1998, coll. P. K. L. Ng; immature female (1.6 mm), ex abdomen of female *L. paradoxus* A. Milne-Edwards, 1862 (4.8 mm long × 3.3 mm wide) (ZRC 2016.0443), ex unknown coral, Ao Thang Khen, Phuket, May 2000, coll. P. K. L. Ng & K. L. Yeo.

Description

Mature female (Fig. 8): 4.8–14.1 mm long; strongly recurved, circular in outline (viewed laterally); body robust, strongly convex dorsal margin without lobes

but with cuticular indentations indicating segmentation; body with slight ventral indentation; ventral sides meeting medially, with several small, plate-like areas demarcated at midpoint. Attachment trunk short, with single attachment lobe, medially divided and expanded into two broad sections. Directly parasitizing cryptochirid hosts on ventral surface of abdomen, on posterior pereopods, or on sternites.

Etymology

The species is named after the main character in the film 風の谷のナウシカ (*Nausicaä of the Valley of the Wind*) by Hayao Miyazaki (Toei 1984), because the attachment processes greatly resembles the gas mask worn by Nausicaä when entering the Toxic Jungle.

Remarks

See under Remarks for the genus. Note that this parasite can grow to be larger than its host (e.g. RMNH.Crus.I.7758, from Okinawa), and this would seem to limit the mobility of the host; however, gall crabs, particularly females, probably do not move outside their dwellings. The non-type material is provisionally assigned to this species. The smaller specimen from Thailand is a non-descript sac, with an attachment stalk somewhat resembling that of *D. cervix* sp. nov. from the Atlantic, but the larger specimen, which is still immature, was partly moulted and shows a smooth outer cuticle covering a segmented inner cuticle. This pattern of metamorphosis from smooth to segmented sac is also seen in species of *Cabirops* (see Reverberi & Catalano, 1963), but *Cabirops* species lack attachment stalks.

Known hosts

Hapalocarcinus marsupialis Stimpson, 1859 (type host), *L. helleri* (Fize & Serène, 1957), *Lithoscaptus* sp. 2(B); probably also on *L. paradoxus* A. Milne-Edwards, 1862.

Distribution

Known from New Caledonia (type locality), Malaysia and Japan; probably also from Thailand.

CIRRIPEDIA BURMEISTER, 1834
RHIZOCEPHALA MÜLLER, 1862
SACCULINIDAE LILLJEBORG, 1861
SACCULINA THOMPSON, 1836

SACCULINA QUADRIALATA SP. NOV.

(FIGS 9, 12A, B)

urn:lsid:zoobank.org:act:A646BB1F-4BA5-46EE-96C1-AF7A4BDE1FCB

Type material

Indonesia: mature holotype externa (1.6 mm long × 1.2 mm wide) (RMNH.Crus.C.10250), ex abdomen of feminized male *Opecarcinus* sp. 1(F) (3.0 mm long × 2.3 mm wide)

(RMNH.Crus.D.53990), ex *L. mycetoseroides* Wells, 1954 (Agariciidae), South Pilongga, Tidore, 00°42'44"N, 127°28'47"E, 12 November 2009, coll. S. E. T. van der Meij; two mature paratype externae (2.0 mm long × 3.4 mm wide, 1.4 mm long × 2.0 mm wide) (RMNH.Crus.C.10251), ex abdomen of female *Fizesereneia heimi* (Fize & Serène, 1956a) (5.3 mm long × 4.5 mm wide) (RMNH.Crus.D.54018), ex *Lobophyllia* cf. *radians* (H. Milne Edwards & Haime, 1849) (Lobophylliidae), Tanjung Sidangolo, Halmahera, 00°53'40"N, 127°29'28"E, 5 November 2009, coll. S. E. T. van der Meij; mature paratype externa (1.4 mm long × 1.9 mm wide) (RMNH.Crus.C.10252), ex abdomen of feminized male *Lithoscaptus* cf. *bani* (Fize & Serène, 1957) (3.1 mm long × 2.0 mm wide) (RMNH.Crus.D.53993), ex *Goniastrea edwardsi* Chevalier, 1971 (Merulinidae), West Mansuar, Raja Ampat, 00°30'41"S, 130°33'35"E, 9 December 2007, coll. S. E. T. van der Meij; immature paratype externa (0.7 mm long × 1.0 mm wide) (RMNH.Crus.C.10253), ex abdomen of female *Opecarcinus* cf. *sierra* Kropp, 1989 (1.9 mm long × 1.4 mm wide) (RMNH.Crus.D.54208), ex *Pavona* cf. *varians* Verrill, 1864 (Agariciidae), North Tanjung Pandean, Lembah Strait, 01°24'21"N, 125°10'04"E, 14 February 2012, coll. S. E. T. van der Meij; mature paratype externa (0.8 mm long × 1.1 mm wide) (RMNH.Crus.C.10254), ex abdomen of female *X. sheni* (Fize & Serène, 1956b) (1.9 mm long × 1.3 mm wide) (RMNH.Crus.D.54166), ex *M. elephantotus* (Pallas, 1766) (Merulinidae), Tanjung Labuhankompeni, Lembah Strait, 01°25'55"N, 125°11'10"E, 4 February 2012, coll. S. E. T. van der Meij.

Description

Externa of immature specimens with rounded subequal lateral lobes; mature (ovigerous) externae with lateral lobes produced anteriorly and posteriorly into wing-like extensions, sometimes subequal but often of differing degrees of extension. Mantle opening medio-distally located opposite stalk. Mantle opening ranging from smooth to crenulated, raised off the surface of the externa. Stalk short but externa raised off the surface of the host abdomen. Cuticle with varying degrees of wrinkling, particularly prominent in larger specimens.

Etymology

The species name alludes to the four wing-like lobes (*quadri* + *alata*) of the mature externa.

Remarks

Vervoort (in Martin & Davis, 2001) stated that 'Sacculinidae must be ascribed to Lilljeborg (1860)'. However, nowhere in Martin & Davis (2001) was the actual bibliographic reference to Lilljeborg, '1860' given. After careful analysis of all the publications of Lilljeborg dealing with rhizocephalans, we must conclude that the date was given incorrectly by Vervoort, and is, in fact, Lilljeborg (1861).

Although it would be desirable to perform histology on at least some of these specimens, the hosts were not

preserved with rhizocephalan histology in mind, and it is doubtful that any internal characters can be gleaned from such treatment. Additionally, the utility of many of Boschma's internal characters in terms of showing evolutionary relationships has yet to be demonstrated; some of these characters may be homoplasies, but this remains to be tested. Rybakov & Høeg (2002) showed the utility of studying the retinacula found on the mantle of externae, but there are no such structures in this new species nor are they known in many of the species of *Sacculina*. However, this new species can be described and named because the presence of the four laterally extended wing-like lobes on the mature externae is unlike the externae shapes seen in other species of *Sacculina*. The most similar species to this new species is *S. rugosa* Van Kampen & Boschma, 1925, but the shapes of the externae are only vaguely similar. Additionally, there are no previous records of any rhizocephalans from gall crab hosts.

Known hosts

Opecarcinus sp. 1(F) (type host), *F. heimi* (Fize & Serène, 1956a), *Lithoscaptus* cf. *bani* (Fize & Serène, 1957), *Opecarcinus* cf. *sierra* Kropp, 1989, *X. sheni* (Fize & Serène, 1956b).

Distribution

Known only from Indonesia.

DISCUSSION

Parasites of cryptochirids were encountered at one to eight localities per fieldwork period, each of which encompassed 3–4 weeks of diving and collecting. The newly collected material of cryptochirids contains 40 parasitized specimens, in a total of ~1300 collected lots (most of which contain multiple specimens). At the only Caribbean fieldwork site (Curaçao), only a single parasitized specimen was found, whereas in the Red Sea none of the collected cryptochirids was infested. These low infestation rates seem somewhat to contradict the *C. platypleura* infestation rate of 10.64% in *P. ransonii* reported by Sanabe & Tsuchiya (2005). Typically, infestation rates for bopyrids are low, in the range of 0.1–3.8%; however, higher rates, up to 19.1%, are known (McDermott, Williams & Boyko, 2010). The causal mechanisms of higher rates are unknown.

The data presented here show that parasitism of gall crabs is not, as might be inferred from the infrequent mention in the literature of such parasites, an insignificant energy burden and reproductive issue for some gall crab populations, at least in the Indo-West Pacific region. The bopyrids affect their hosts by taking away energy that could be used for egg development, whereas rhizocephalans completely sterilize their hosts and *de facto* remove any potential contribution of the crabs to the gene pool, except as new sources of rhizocephalan

genes. The newly described parasite species and genera in this manuscript bring the total number of cryptochirid-associated parasites to 11, with at least one undescribed species of *Cabirops* awaiting description.

The nested set of symbiotic interactions, or hypersymbioses, seen here between stony corals, gall crabs, parasites and hyperparasites brings to mind the parasitological verse 'On poetry: a rhapsody (1733)' by Jonathan Swift (1667–1745):

The vermin only teaze and pinch
Their foes superior by an inch.
So nat'ralists observe, a flea
Hath smaller fleas that on him prey,
And these have smaller fleas to bite 'em,
And so proceed *ad infinitum*.

Starr (1975), Williams & McDermott (2004) and McDermott (2009) referred to such nested relationships as 'hypersymbiotic', a term that is useful but lacks specificity in the type(s) of symbiotic associations it encompasses, unlike the term 'hyperparasite', which is very specific. 'Hyper-' literally means 'over' in the sense of exaggeration, but clearly 'hypersymbioses' does not apply to the relationships between an organism and its multiple symbionts within a single host (e.g. an isopod parasite and a nematode parasite both parasitizing the same host, an example of multiparasitism; Starr, 1975); instead, it is used for a nested, or layered, set of symbioses. Alternative terms that can be used are 'secondary' and 'tertiary' symbioses; this follows similar usage by Freeman (2005), who also noted the Swiftian connection, for nested levels of strict parasitism. Applied to the present study, the coral acts as host for the gall crab (primary symbiont), the secondary symbiont is either an epicaridean or a rhizocephalan, and the tertiary symbiont is the cabiropid isopod found parasitizing the bopyrid marsupium. Given the multiple levels of symbioses and their potential direct and indirect effects (e.g. bopyrids may indirectly affect corals by altering the crabs' behaviour and/or fitness, which would affect how the crabs interact with their host corals) encountered in the present study, all the hypersymbionts discussed here can also be considered part of a larger symbiotic web (*sensu* Rees, 1967).

In terms of defining the nature of the symbiosis between cryptochirids and host corals, these crabs are simply referred to as symbionts by most authors. However, there are indications that the influence of the crabs on their host corals can be positive, negative or neutral, depending on the type of interaction (e.g. settlement, feeding, coral growth anomalies; Castro, 2015; van der Meij, 2015b; Terrana *et al.*, 2016). It would be interesting to determine whether parasitism by bopyrids on gall crabs also indirectly had a negative impact on the crabs' hosts, as was found in a recent

study on the negative effects imparted by parasitism of boyrids not only to their pinnotherid hosts, but also on the oysters hosting the pinnotherids (Yasuoka & Yusa, 2017). Pinnotherids, unlike cryptochirids, are generally accepted invariably to have negative effects on mollusc hosts, even when they are not themselves parasitized by boyrids (Bierbaum & Ferson, 1986).

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