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A collection of crabs (Crustacea, Brachyura) from the southwestern coast of India, with a discussion of the systematic position of *Nectopanope* Wood-Mason in Wood-Mason & Alcock, 1891 (Euryplacidae)

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Abstract

A report on the brachyuran crabs collected from the southwestern coast of India by the Indian research vessel FORV *Sagar Sampada* is presented. The material consists of 13 species from three genera and five families, of which four are new records for India: *Heteroplax maldivensis* (Rathbun, 1902) (Euryplacidae), *Cryptopodia collifer* Flipse, 1930 (Parthenopidae), *Thalamita macrodonta* Borradaile, 1903 (Portunidae), and *Paraxanthodes cumatodes* (MacGilchrist, 1905) (Xanthidae). The cruise also obtained the first known male of *Nectopanope rhodobaphes* Wood-Mason in Wood-Mason & Alcock, 1891 (type species of *Nectopanope* Wood-Mason in Wood-Mason & Alcock, 1891), and its characters show that it is in fact a member of the Euryplacidae Stimpson, 1871. The genus had previously been incorrectly classified in the Xanthidae MacLeay, 1838.

Keywords

Brachyura, Euryplacidae, Indian Ocean, new records, rare species, revised taxonomy, systematics

Introduction

We here report on a small but noteworthy collection of brachyuran crabs obtained by a fishery research vessel off the southwestern coast of India in 2017. While consisting of only 13 species from three genera and five families, the material obtained includes several rare species, including one which has not been seen since 1891.

The discovery of a male of *Nectopanope rhodobaphes* Wood-Mason in Wood-Mason & Alcock, 1891, is significant as the family position of the genus *Nectopanope* Wood-Mason in Wood-Mason & Alcock, 1891, has been uncertain, because it was previously known only from the type female. The male characters show that *Nectopanope* is a member of Euryplacidae Stimpson, 1871, and close to *Psopheticoides* Sakai, 1969, from the western Pacific. *Nectopanope* is rediagnosed, while *Nectopanope rhodobaphes* is redescribed and figured. A male of the rarely reported parthenopid *Cryptopodia collifer* Flipse, 1930, not previously known from India, is figured. The euryplacid *Heteroplax maldivensis* (Rathbun, 1902), the rarely reported portunid *Thalamita macrodonta* Borradaile, 1903, and the xanthid *Paraxanthodes cumatodes* (MacGilchrist, 1905), are also recorded from India for the first time.

Materials and methods

All specimens were collected during an exploratory survey (cruise 360) of FORV *Sagar Sampada* belonging to the Center for Marine Living Resources & Ecology (CMLRE) under the Ministry of Earth Sciences, India, in May 2017, conducted along the southwestern coast of India. Specimens were collected using grabs and dredged from depths ranging from 50–200 m. The material studied is in the museum collections of the Department of Aquatic Biology and Fisheries, University of Kerala (DABFUK).

Measurements provided are of the maximum carapace width and length, respectively. The classification and terminology used follows Ng et al. (2008) and Davie et al. (2015a, b). Complete synonymies are only provided for species which are treated at length.

Systematics

Family Raninidae De Haan, 1839
Notosceles Bourne, 1922

Notosceles serratifrons (Henderson, 1893)

Fig. 1A

Material examined. 2 males (9.1 × 17.6 mm, 9.0 × 17.5 mm), 8°19.972'N, 76°35.897'E, 100 m.

Remarks. Henderson (1893) described this species from Sri Lanka. It has since been found in India (Alcock 1896; Dev Roy 2013; Trivedi et al. 2018) as well as Australia, Japan, mainland China and Taiwan (Sakai 1976; Chen and Sun 2002; Ahyong et al. 2009).

Family Leucosiidae Samouelle, 1819

Nursilia Bell, 1855

Nursilia tonsor Alcock, 1896

Fig. 1B

Material examined. 1 young female (6.0 × 5.3 mm), 8°22.727'N, 76°43.545'E, 50 m.

Remarks. The species was first described from the Andaman Sea (Alcock 1896) and has since been reported from other parts of India, Southeast Asia, China, and Japan (Sakai 1976; Serène and Soh 1976; Tan 1996; Chen and Sun 2002; Dev Roy and Nandi 2012).

Arcania Leach, 1817

Arcania gracilis Henderson, 1893

Fig. 1C

Material examined. 1 juvenile male (7.7 × 5.5 mm), 7°16.713'N, 77°37.582'E, 200 m.

Remarks. The genus was revised by Galil (2001) who confirmed that the two Indian Ocean species, *Arcania quinquespinosa* Alcock & Anderson, 1894, and *A. gracilis* Henderson, 1893, are subjective synonyms. The species has a wide distribution in India and the Indo-West Pacific (see Galil 2001; Trivedi et al. 2018).

Coleusia Galil, 2006

Coleusia urania (Herbst, 1801)

Fig. 1D

Material examined. 1 juvenile female (10.1 × 12.0 mm), 7°27.978'N, 77°32.297'E, 100 m.

Remarks. The identity of this species and the confused status of the types were resolved by Ng et al. (2014). The species has a wide range in the Indo-West Pacific (see also Ng et al. 2014; Promdam et al. 2014).

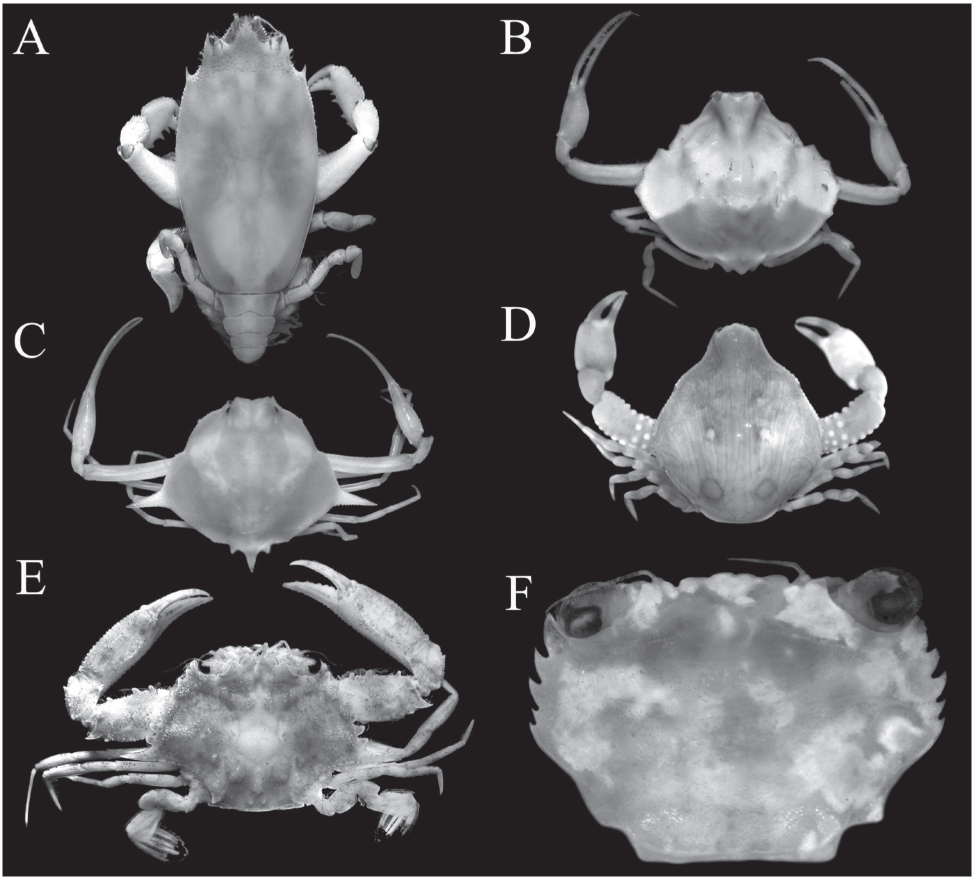

Figure 1. Overall dorsal habitus. **A** *Notosceles serratifrons* (Henderson, 1893), male (9.1 × 17.6 mm) **B** *Nursilia tonsor* Alcock, 1896, female (6.0 × 5.3 mm) **C** *Arcania gracilis* Henderson, 1893, male (7.7 × 5.5 mm) **D** *Coleusia urania* (Herbst, 1801), female (10.1 × 12.0 mm) **E** *Xiphonectes tuberculosus* (A. Milne-Edwards, 1861), male (21.1 × 12.4 mm) **F** *Thalamita macrodonta* Borradaile, 1902, female (8.4 × 5.8 mm).

Family Portunidae Rafinesque, 1815
Xiphonectes A. Milne-Edwards, 1873

Xiphonectes tuberculosus (A. Milne-Edwards, 1861)
Fig. 1E

Material examined. 1 male (21.1 × 12.4 mm), 1 female (18.6 × 10.1 mm), 7°27.978'N, 77°32.297'E, 200 m.

Remarks. This species was described from Hawaii but has since been reported from all across the Indo-West Pacific to Madagascar (A. Milne-Edwards 1861; Stephenson 1972a; Davie 1987). In India, it has previously been reported from Tamil Nadu and the Andaman Sea (Alcock 1894, 1899b; Dev Roy 2015; Dev Roy and Nandi 2007, 2012).

Monomia Gistel, 1848

Monomia argentata argentata (A. Milne-Edwards, 1861)

Material examined. 1 young male (18.2 × 10.2 mm), 8°58.270'N, 76°17.365'E, 50 m.

Remarks. This is a well-known and widely distributed species in the Indo-West Pacific (Stephenson 1972b; Apel and Spiridonov 1998); and is found in most states in India (Trivedi et al. 2018).

Thalamita Latreille, 1829

Thalamita macrodonta Borradaile, 1902

Fig. 1F

Material examined. 1 young female (8.4 × 5.8 mm), 8°22.727'N, 76°43.545'E, 50 m.

Remarks. Borradaile (1902) described *Thalamita exetastica macrodonta* from two specimens from two islands in the Maldives, Kolumadulu and Suvadiva. Crosnier (1975) examined the syntypes and commented that the two specimens are not conspecific. He noted that the specimen from Kolumadulu Island was almost certainly *T. sexlobata* Miers, 1886, while the other from Suvadiva Island is the actual *T. macrodonta* which he treated as a distinct species. Apel and Spiridonov (1998) re-examined the type material and selected the second syntype from Suvadiva as the lectotype of *T. macrodonta* s. str.

The present specimen from India is incomplete and not in good condition, but agrees with the description and figures of *T. macrodonta* by Crosnier (1975: fig. 4c, d) and Apel and Spiridonov (1998: fig. 59).

Family Euryplacidae Stimpson, 1871

Nectopanope Wood-Mason in Wood-Mason & Alcock, 1891

Nectopanope Anonymous, 1891: 56 (nomen nudum).
Nectopanope Wood-Mason in Wood in Wood-Mason & Alcock, 1891: 261.

Diagnosis. Carapace (Fig. 3A, B) subhexagonal, wider than long, dorsal surface smooth, regions poorly indicated; front (Fig. 3C–E) wide, straight with small median notch, with transverse sulcus along margin. Anterolateral borders (Fig. 3A, B) convex; with two low teeth posterior to broadly triangular outer orbital angle, first tooth wider than acute second tooth. Orbits (Fig. 3C–E) wide, spherical, deep; supraorbital margin with submedian notch, small acute lobe before notch with front; low suborbital tooth on broad, suborbital border; eye peduncles short, stout, with large subreniform (dorsoventrally flattened) cornea (Fig. 3D, E). Basal antennal article mobile, completely closing orbital hiatus (Fig. 3D). Ischium of third maxilliped (Fig. 3B) elongate; anteroexternal margin of merus auriculiform. Cheliped fingers (Figs 3A, G, 4E, F) stout, as long as propodus, not pigmented; carpus with small, sharp spine on inner margin, merus with acute anterodorsal tooth. Dorsal margins of ambulatory legs (P2–P5) (Figs 3A, 4G–J) meri, carpi, propodi unarmed, dactyli slender, smooth, setose; P5 propodus, dactylus proportionally short, flattened, fringed with many short setae. Thoracic sternum (Fig. 4A, D) relatively wide; sternites 1, 2 completely fused; suture 2/3 complete, gently convex towards buccal cavity; sternites 3, 4 medially fused, with shallow median groove, almost indiscernible with only lateral notch distinct; sutures 4/5, 6/7, 7/8 medially interrupted, 5/6 complete; median groove on thoracic sternites 7, 8. Male sternopleonal cavity (Fig. 4A, D) deep, reaching median part of sternite 4, just before sternite 3. Press-button of male pleonal-locking mechanism (Fig. 4D) present as low tubercle on sternite 5, near thoracic suture 4/5. Male pleon (Fig. 4A–C) narrow, slender, T-shaped, lateral margins of somites 4–6 abruptly narrowing from somite 3 to transversely narrow, acutely triangular telson (Fig. 4B); somite 3 wide, reaching inner margins of P5 coxae; no part of thoracic sternite 8 exposed by closed pleon, somite 2 transversely shorter than somite 3, somite 1 (Fig. 4C) conspicuous, narrow. G1 (Fig. 7A–D) long, slender, almost straight; distal quarter distinctly chitinised; apex sharp, distal third with numerous sharp denticles. G2 (Fig. 7E) less than one-third G1 length, relatively straight, apex spatuliform. Male genital opening (gonopore) coxal; penis long. Female characters not known.

Remarks. The type species of *Nectopanope* has been somewhat confused. Only one species, *Nectopanope longipes*, was recognised in Anonymous (1891: 56) but both these names are nomina nuda. Wood-Mason (in Wood-Mason and Alcock 1891: 261, 262) provided valid descriptions for the genus and species, and included *N. rhodobaphes* as a second species. Ng et al. (2008: 80) noted that the type species of *Nectopanope* was *N. rhodobaphes* by monotypy, but this is not correct. Although Wood-Mason (in Wood-Mason and Alcock 1891) did not explicitly state which was the type species for *Nectopanope* Wood-Mason in Wood-Mason & Alcock, 1891, they wrote "*Nectopanope rhodobaphes*, gen. et sp. n., Wood-Mason" (Wood-Mason in Wood-Mason and Alcock 1891: 261). Under Article 68.2.1 of the Code (ICZN 1999), this is sufficient to recognise it as the type species of the genus (see Huys et al. 2014: 27). Alcock (1898: 213) later commented that *Nectopanope* should be restricted to *N. rhodobaphes* and that "*Nectopanope longipes*, which was provisionally referred to this genus by Wood-Mason, who had insufficient material for examination, turns out, now that numerous good specimens have been dredged by the 'Investigator,' to be a Catometope belonging to the genus *Carcinoplax*." Alcock (1899a: 64) repeated the same comments in his treatment of the deep-sea Crustacea of the Indian Seas. *Nectopanope longipes* Wood-Mason in Wood-Mason & Alcock, 1891, is now generally regarded as a valid species in *Carcinoplax* H. Milne Edwards, 1853 (Goneplacidae MacLeay, 1838) (see Castro 2007).

Nectopanope Wood-Mason in Wood-Mason & Alcock, 1891, was originally placed in Cancridae Latreille, 1802, by Wood-Mason (in Wood-Mason and Alcock 1891) with Alcock (1898, 1899a) later transferring the genus to Xanthidae s. lato. Alcock (1898) recognized a new group in his xanthid subfamily Pilumninae, Heteropanopioida

Alcock, 1898, in which he included *Heteropanope* Stimpson, 1858, *Eurycarcinus* A. Milne-Edwards, 1867, and *Nectopanope*. Ng et al. (2008: 204) transferred *Nectopanope* to Xanthinae (Xanthidae) without explanation. This was necessary as *Heteropanope* and *Eurycarcinus* had already been moved to the Pilumnidae (present Pilumnoidea) by then (see Ng et al. 2018).

The family position of *Nectopanope* is difficult because its only species, *N. rhodobaphes*, has previously only been known from one female specimen. Wood-Mason (in Wood-Mason and Alcock 1891: 262) noted that he had "one specimen obtained at Station 96, 98 to 102 fathoms; the length of its carapace is 21.4 millim., and the greatest breadth between the points of the third teeth 29 millim." Station 96 was in the Bay of Bengal, 18°30'N, 84°46'E, substrate is sand at a depth of 98–102 fathoms, and dated 4 March 1890 (Anonymous 1914). The sex of the specimen was not stated. Alcock (1899a: pl. 38 fig. 6) figured the specimen but it is not clear what its sex was (Fig. 2). Alcock (1898: 213; 1899a: 65) noted that they only had one female collected from the Godávari coast (in the Bay of Bengal) from 98–102 fathoms, that is the type. A search in the Zoological Survey of India in Calcutta for this specimen was not successful and it could not be located (S. Mitra, personal communication).

The study of the present male specimen resolves the systematic position of *Nectopanope*. The structures of the male pleon and gonopods leave no doubt that *Nectopanope* is in fact a member of Euryplacidae Stimpson, 1871. *Nectopanope* is only superficially resembles *Eurycarcinus* (and the Pilumnidae) due to similar carapace features. Their male pleons and gonopods, however, are completely different (cf. Ng et al. 2018).

In Euryplacidae, the general shape and structure of the carapace as well as smoothness of the surfaces of *Nectopanope* most closely resembles *Psopheticoides* Sakai, 1969 (with only one species, *P. sanguineus* Sakai, 1969), from the western Pacific. They also share a similar eye morphology. The eye of *Psopheticoides* is large and is distinctly flattened dorsoventrally, with the structure appearing reniform (Castro and Ng 2010: fig. 36B). The eye of *Nectopanope* is relatively less distinctly flattened dorsoventrally and only weakly reniform in shape (Fig. 3D, E). No other euryplacids, however, have such a distinct eye structure which has been reported in other deep-sea brachyurans (e.g., *Hexaplax* Doflein, 1904, Hexapodidae; cf. Rahayu and Ng 2014).

The carapace anterolateral margin of *Nectopanope* has three distinct teeth (Figs 2, 3A, C) (with only two teeth in *Psopheticoides*, with the external orbital tooth very broad; Sakai 1969: text-fig. 16b; Sakai 1976: pl. 192, fig. 3). The external orbital tooth of *Psopheticoides*, however, is usually partially medially indented, and although the cleft is not deep, it gives the appearance of having three teeth on the anterolateral margin (cf. Sakai 1969: text-figs 16b, 18b; Sakai 1976: text-fig. 282a; Castro and Ng 2010: fig. 36A). The frontal margin in *Nectopanope* is medially indented (Figs 2, 3A, C) (margin entire in *Psopheticoides*; cf. Castro and Ng 2010: fig. 36A); the ischium of the third maxilliped is proportionately longer with the auriculiform anteroexternal angle of the merus more developed (Fig. 3B) (ischium of third maxilliped relatively shorter and the anterexternal angle of the merus less produced in *Psopheticoides*; cf. Castro and Ng 2010: fig. 36C); the cornea is weakly reniform (Fig. 3D, E) (cornea prominently reniform in *Psopheticoides*;

cf. Castro and Ng 2010: fig. 36B); the male telson is proportionately shorter (Fig. 4A) (elongated and linguiform in *Psopheticoides*; cf. Castro and Ng 2010: fig. 36E); and the G1 is relatively straighter with the tip tapered to a tip (Fig. 7A–D) (G1 slightly sinuous with the tip arrow-shaped in *Psopheticoides*; cf. Castro and Ng 2010: fig. 38D, E).

Nectopanope rhodobaphes **Wood-Mason in Wood-Mason & Alcock, 1891**

Figs 2–4, 7A–E

Nectopanope rhodobaphes Wood-Mason in Wood-Mason & Alcock, 1891: 261; Alcock 1899a: pl. 38 fig. 6; Ng et al. 2008: 204 (list); Huys et al. 2014: 15, 27 (discussion).

Material examined. 1 male (18.4 × 14.7 mm), 7°27.978'N, 77°32.297'E, 200 m.

Diagnosis. As for genus.

Description. Carapace (Figs 2, 3A, C) transversely subhexagonal, 1.25 times wider than long; dorsal surface distinctly convex, smooth, without setae or granules; regions poorly defined, epigastric region not indicated, gastro-cardiac groove shallow. Front (Fig. 3A, C) lamellar, almost straight, smooth, with shallow median notch; postorbital region smooth, without trace of crest; front separated from supraorbital margin by small but distinct right-angled notch; lateral lobe triangular, small. Anterolateral margin (Fig. 3A, C) convex with three teeth including external orbital angle; external orbital angle broadly triangular, subtruncate; first lateral tooth triangular, tip directed anteriorly, separated from other teeth by deep-V-shaped notch, margin gently convex and entire to uneven; second lateral tooth acutely triangular, directed obliquely laterally. Posterolateral margin (Fig. 3A, C) gently convex, converging gradually towards gently convex posterior carapace margin. Suborbital, subhepatic, anterior half of pterygostomial regions (Fig. 3D) smooth. Orbits (Fig. 3D, E) wide, spherical, deep; supraorbital margin concave, smooth with distinct submedian fissure, gradually merging with external orbital tooth; suborbital tooth lined with small granules, with broad low tooth on inner edge, adjacent to antenna. Eye peduncles short, stout, with large subreniform (dorsoventrally flattened) cornea (Fig. 3D, E). Basal antennal article (articles 2 and 3) (Fig. 3D, G) rectangular, longer than broad, mobile, completely closing orbital hiatus. Basal antennular article subrectangular; flagellum long, folding transversely. Epistome (Fig. 3D, F) longitudinally narrow; posterior margin of epistome with prominent subtruncate median projection, with distinct longitudinal fissure; lateral margin almost straight, separated from median part by fissure. Endostomial ridge distinct, long.

Third maxillipeds (Fig. 3B) almost completely closing buccal cavern when closed; merus subquadrate, anteroexternal margin strongly auriculiform; ischium subrectangular, elongated, with submedian oblique sulcus, inner margin serrated, lined with dense stiff setae; exopod stout with prominent subdistal triangular tooth on inner margin, flagellum long, extending past width of merus.

Chelipeds (P1) (Figs 3A, G, 4E, F) unequal, right chela slightly larger; fingers slender, as long as palm; dorsal margin of palm rounded; distal half of chela with ventral margin

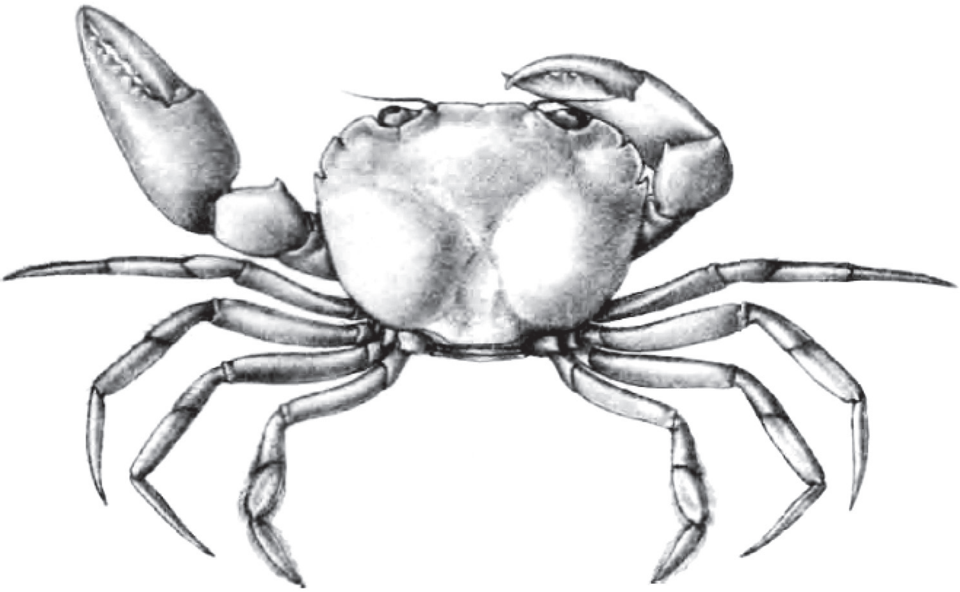

Figure 2. *Nectopanope rhodobaphes* Wood-Mason in Wood-Mason & Alcock, 1891 (after Alcock 1899a: pl. 38 fig. 6).

(including entire pollex) possessing distinct subventral longitudinal sulcus, forming subcristiform ventral margin; outer surface of palm smooth; inner surface smooth with gently convex median part, ventro-proximal part with low lobiform rounded projection; cutting edge of pollex of major chela with prominent large triangular teeth; dactylus gently curved with 2 shallow longitudinal median sulci on outer margin (upper one deeper), cutting edge with large triangular teeth; fingers of minor chela similar to those on major chela.

Ambulatory legs (P2–P5) (Figs 3A, 4G–J) moderately long, slender; P3 longest; P2–P5 merus subcylindrical, slightly flattened laterally, outer surface smooth, glabrous, ventral margin smooth, dorsal margin almost entire; P5 merus gently upcurved; P2–P5 carpus short, outer surface glabrous, dorsal margin smooth; P2–P4 propodus of long, laterally flattened, with distinct shallow longitudinal median sulcus, lateral margins of distal third almost completely glabrous; P5 propodus ovate, laterally flattened, with distinct setae lining margins which partially obscure margin; P2–P4 dactylus elongated, falciform, smooth; P5 shortest, subspatuliform, margins lined with short setae; dactylo-propodal lock not distinct.

Thoracic sternum (Figs 4A, D) relatively wide, surface relatively smooth but with shallow uneven pits; sternites 1, 2 completely fused, distinctly triangular, lateral margins gently concave, separated from sternite 3 by distinct gently convex suture (towards buccal cavity); sternites 3, 4 fused with only lateral part of suture clearly visible, median part indicated by barely discernible shallow broad groove; sutures 4/5, 5/6, 7/8 medially interrupted, suture 6/7 almost complete, separated by very narrow gap; distinct median longitudinal groove extending across sternites 7, 8. Posterior edge of episternite 7 par-

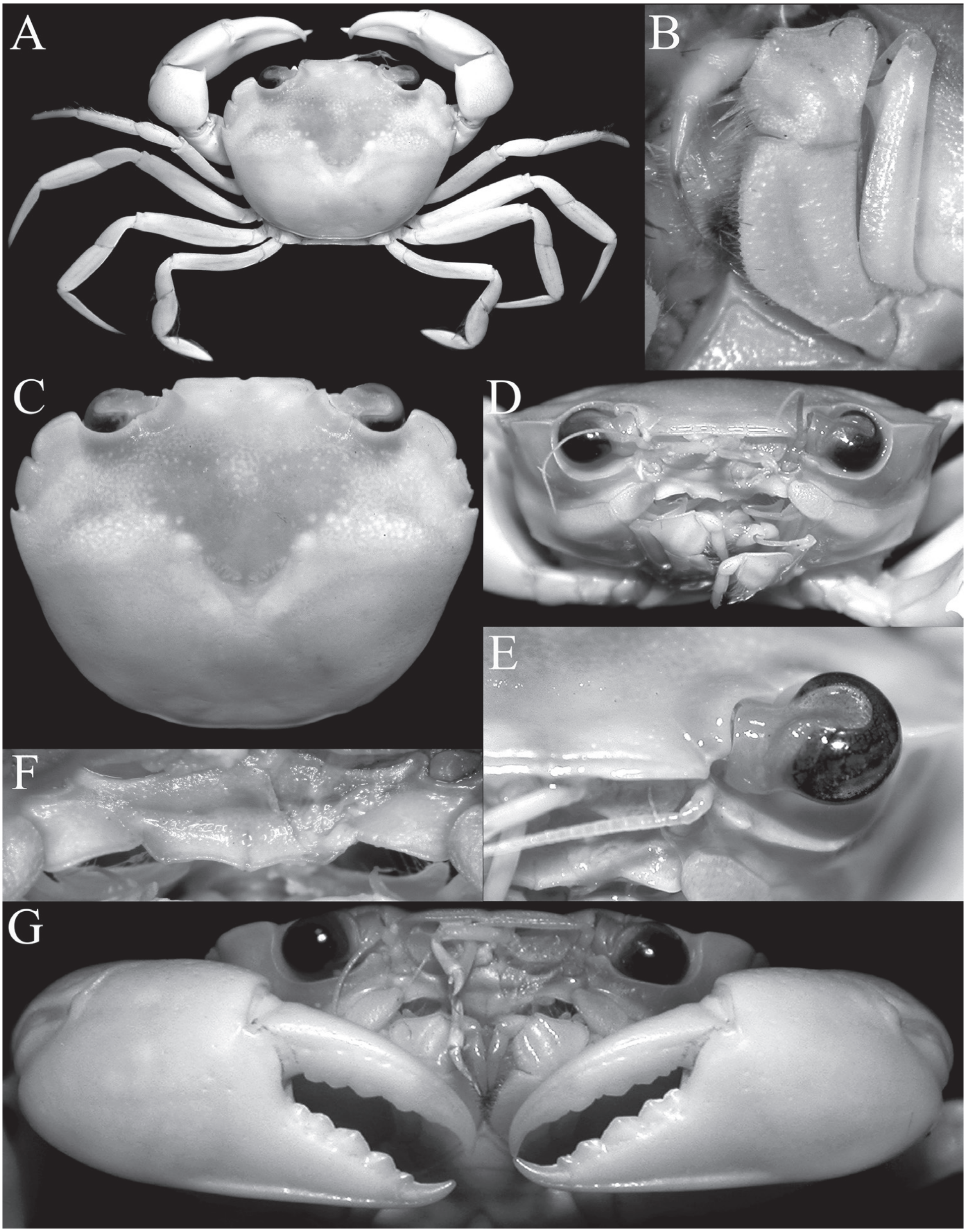

Figure 3. *Nectopanope rhodobaphes* Wood-Mason in Wood-Mason & Alcock, 1891, male (18.4 × 14.7 mm), India. **A** overall dorsal habitus **B** left third maxilliped **C** dorsal view of carapace **D** frontal view of cephalothorax **E** closeup of eye **F** epistome **G** outer view of chelae.

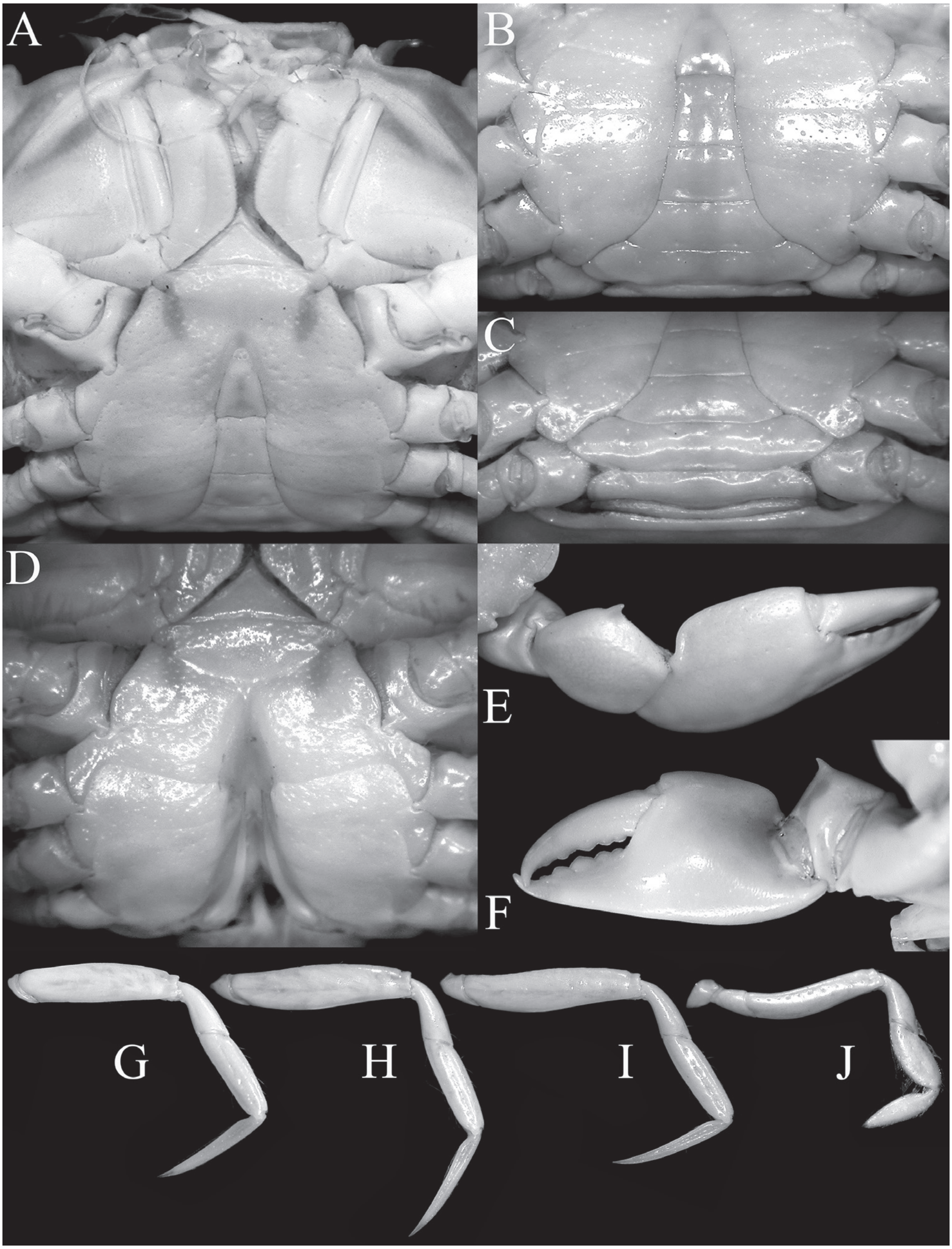

Figure 4. *Nectopanope rhodobaphes* Wood-Mason in Wood-Mason & Alcock, 1891, male (18.4 × 14.7 mm), India. **A** anterior thoracic sternum, pleon, buccal cavity and third maxillipeds **B** thoracic sternum and pleon **C** posterior thoracic sternum and pleon **D** anterior thoracic sternum and sternopleonal cavity **E** subdorsal view of right cheliped **F** inner view of right cheliped **G–J** second to fourth ambulatory legs, respectively (all to same scale).

tially overlapping anterior part of P5 coxa and partially covering anterolateral part of pleonal somite 3 when closed. Sternopleonal cavity (Fig. 4A, D) deep, reaching nearly to anterior edge of sternite 4, just before sternite 3, defined by imaginary line connecting midpoint of coxae of chelipeds; pleon (Fig. 4C) completely covering sternite 8 when closed. Press-button of male pleonal locking mechanism (Fig. 4D) present as short spur-like structure on anterior quarter of sternite 5, just adjacent to sternite 4. Opening for penis coxal, penis relatively short, tubular, exiting at anterior edge of condyle of P5 coxa.

Pleon (Fig. 4A–C) narrow, slender, distinctly T-shaped; somites 3–6 trapezoidal, abruptly narrowing from somite 3–6; telson acutely triangular with convex lateral margins; somite 3 wide, reaching inner margins of P5 coxae; no part of thoracic sternite 8 exposed by closed pleon; somite 2 transversely shorter than somite 3 but reaching P5; somite 1 conspicuous, narrow, almost as wide as somite 2.

G1 (Fig. 7A–D) long, slender, almost straight; distal quarter distinctly chitinised, stiff; apex sharp, distal third with numerous sharp denticles, longer in some specimens than in others. G2 (Fig. 7E) less than one-third G1 length, relatively straight, apex spatuliform.

Remarks. The colour of the fresh type specimen was described as “a beautiful deep-sea pink, with a dotted, V-shaped, white mark between the gastric and branchial regions.” (Wood-Mason in Wood-Mason and Alcock 1891: 262). The present preserved specimen, although faded, retains enough colour to suggest that in life, it had the colour and pattern described in the original description. This colour is somewhat similar to that known for *Psopheticoides sanguineus* which is red to pinkish-red all over but with a white ring on the median dorsal surface (Sakai 1976: pl. 192, fig. 3; Castro and Ng 2010: fig. 39C).

The type female (Fig. 2) shows the branchial regions distinctly swollen but this is probably due to parasites, although the specimen was not dissected. This has precedence in the Australian euryplacid *Eucrate sexdentata* Haswell, 1882, in which one specimen has both sides of the branchial regions swollen and infected by bopyrids (cf. Castro and Ng 2010: fig. 10E).

***Henicoplax* Castro & Ng, 2010**

***Henicoplax maldivensis* (Rathbun, 1902)**

Figs 5, 7F–H

Goneplax maldivensis Rathbun, 1902: 124, figs 3–5; Guinot 1969: 518; Castro 2007: 686, 687 [list].
“?[*Goneplax*] *maldivensis*”: Guinot 1971: 1081 [list].
Otmaroplax maldivensis: Števčić 2005: 134 [genus name nomen nudum]
“*Heteroplax*” *maldivensis*: Ng et al. 2008: 78, 79 [in list].
Henicoplax maldivensis: Castro and Ng 2010: 61, figs 22A–E, 24D–F.

Material examined. 1 male (9.9 × 6.3 mm), 7°27.978'N, 77°32.297'E, 100 m.

Remarks. *Henicoplax* Castro & Ng, 2010, was established for Indo-West Pacific species that had been previously classified in *Goneplax* Leach, 1814, or *Heteroplax*

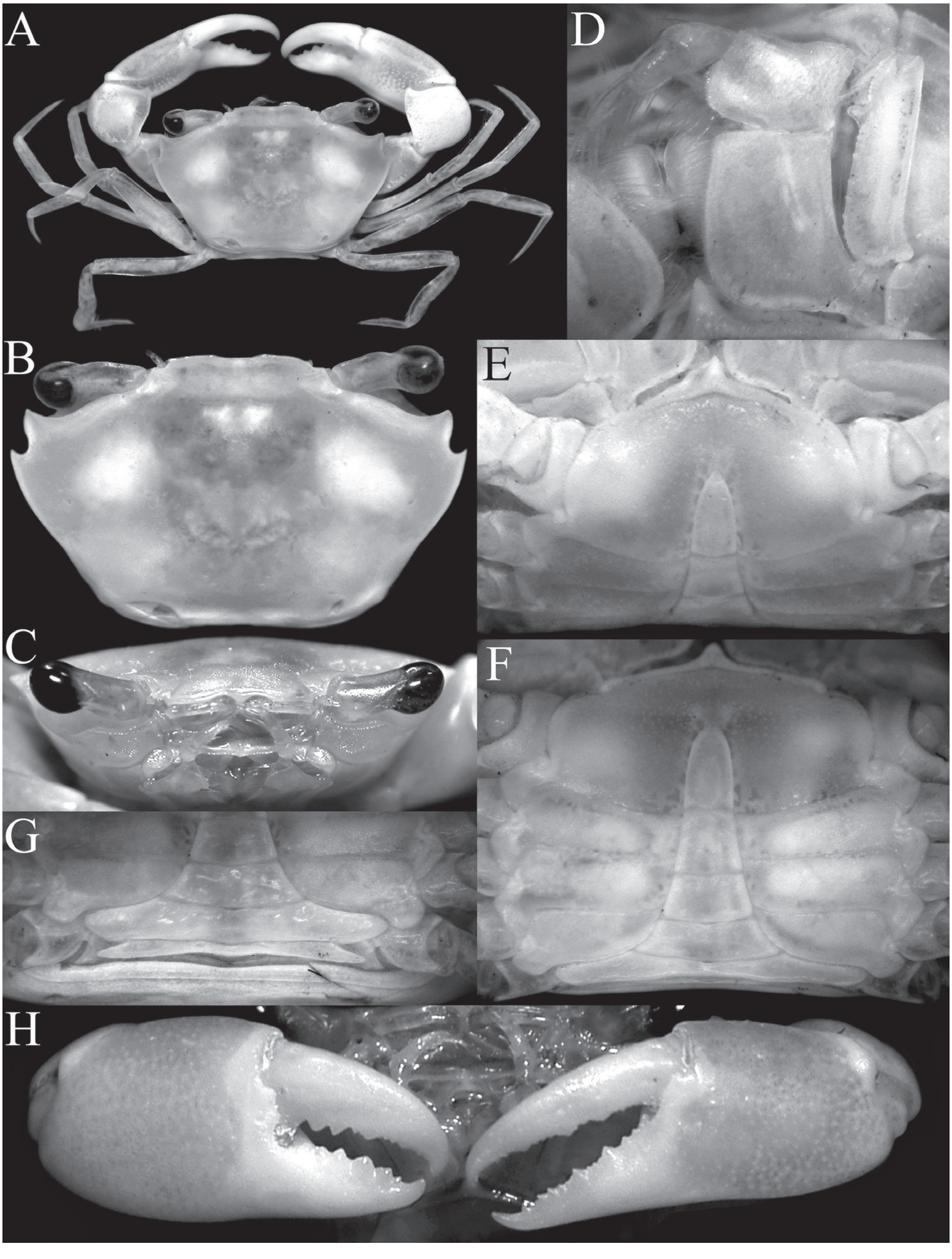

Figure 5. *Henicoplax maldivensis* (Rathbun, 1902), male (9.9 × 6.3 mm), India. **A** overall dorsal habitus **B** dorsal view of carapace **C** frontal view of cephalothorax **D** left third maxilliped **E** anterior thoracic sternum and pleon **F** thoracic sternum and pleon **G** posterior thoracic sternum and pleon **H** outer view of chelae.

Stimpson, 1858. Five species are currently recognised: *H. eriochir* Castro & Ng, 2010, *H. maldivensis* (Rathbun, 1902) [type species], *H. nitida* (Miers, 1879a), *H. pilimeles* Castro & Ng, 2010, and *H. trachydactylus* Castro & Ng, 2010.

The present specimen is clearly *H. maldivensis* as redescribed and figured at length by Castro and Ng (2010: 61). The species was previously known only from the holotype male (7.4 × 4.8 mm) obtained from Gan Island in Addu Atoll in the Maldives. The present male differs from the type male in having the frontal margin slightly more sinuous and the cleft between the external orbital tooth and the anterolateral tooth is more U-shaped (Fig. 5A, B) (versus frontal margin almost straight and the lateral carapace cleft being V-shaped in the holotype; cf. Castro and Ng 2010: fig. 22A); and while the G1 shape is similar, the distal spination is relatively less pronounced and the tip is sharply tapering (Fig. 7F, G) (versus distal half with relatively more spines and the tip is subtruncate in the holotype; cf. Castro and Ng 2010: fig. 24D, E). The differences are not substantial and can easily be explained by variation and size, the present male (9.9 × 6.3 mm) being larger than the type (7.4 × 4.8 mm).

Castro and Ng (2010) showed that records of "*H. nitida*" from the Andaman Sea should be referred to a new species, *H. pilimenes*; and indicated that true *H. nitida* should be restricted to East Asia. The records of "*H. nitida*" from the Gulf of Martaban (south of Myanmar) and off Madras in India by Henderson (1893: 379) are almost certainly not this species. The Myanmar material is probably *H. pilimenes*, while that from India may be this species or even *H. maldivensis* instead. Specimens will need to be re-examined to be certain.

Heteroplax maldivensis is thus far known for certain only from the Maldives (Rathbun 1902; Castro and Ng 2010) and the present specimen represents the first confirmed presence of this species in India.

Family Parthenopidae Macleay, 1838

Pseudolambrus Paulson, 1875

Pseudolambrus beaumonti (Alcock, 1895)

Fig. 6A

Material examined. 1 female (9.4 × 8.8 mm), 7°48.004'N, 77°27.754'E, 50 m.

Remarks. This species was described from off Sri Lanka and Andamans by Alcock (1895) and has since been reported from Mauritius and Japan (Flipse 1930; Michel 1964; Sakai 1976). Ng and Rahayu (2010) figured the syntypes of the species.

Rhinolambrus A. Milne-Edwards, 1878

Rhinolambrus contrarius (Herbst, 1804)

Fig. 6B

Material examined. 1 young female (10.5 × 10.0 mm), 3 juveniles (largest 6.8 × 6.8 mm), 7°48.004'N, 77°27.754'E, 50 m.

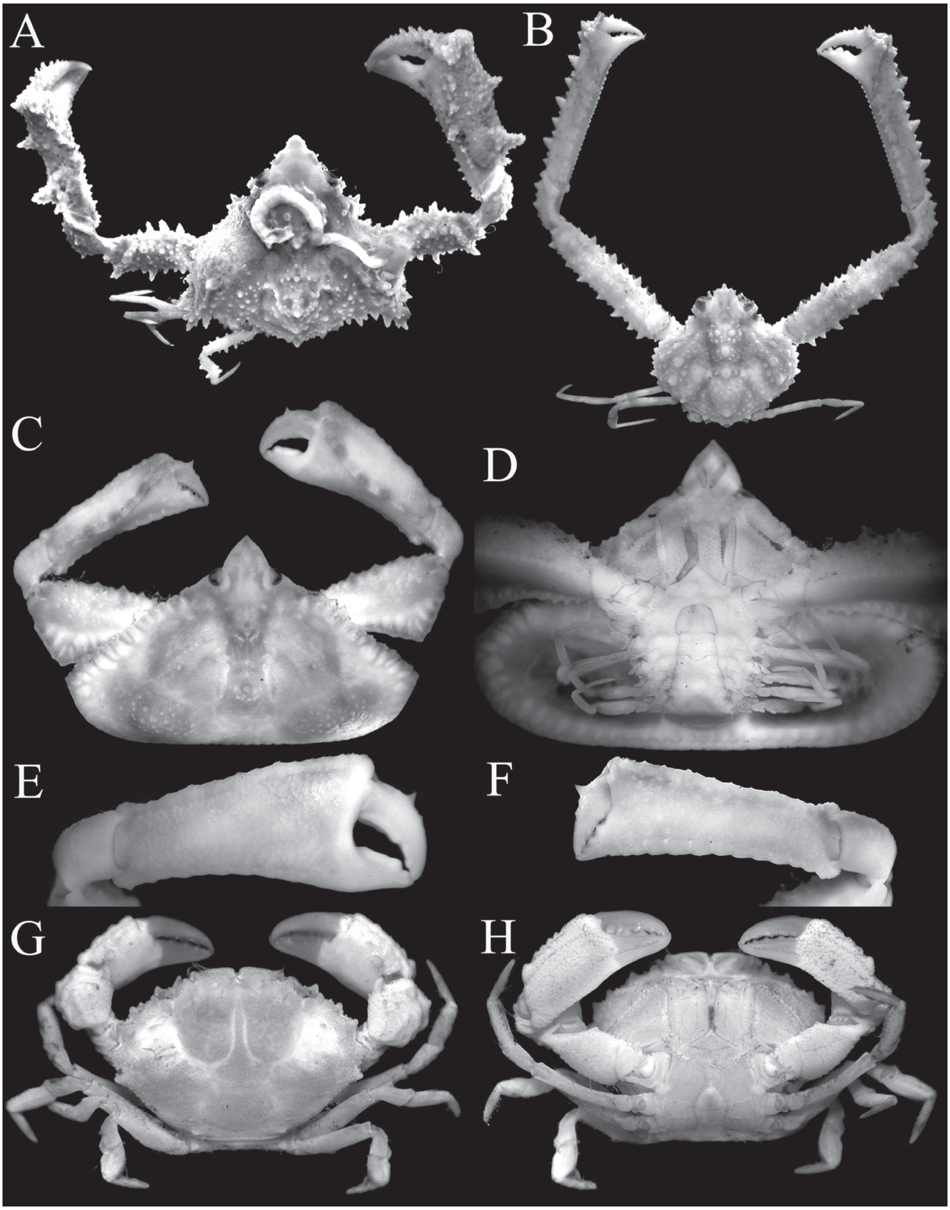

Figure 6. A *Pseudolambrus beaumonti* (Alcock, 1895), female (9.4 × 8.8 mm) **B** *Rhinolambrus contrarius* (Herbst, 1804), female (10.5 × 10.0 mm) **C–F** *Cryptopodia collifer* Flipse, 1930, male (17.5 × 10.6 mm) **G, H** *Paraxanthodes cumatodes* (MacGilchrist, 1905), male (8.3 × 5.5 mm). **A, B, C, G, H** overall dorsal habitus **D** ventral view of cephalothorax **E, F** outer view of chelae.

Remarks. Herbst (1804: 9) described this species from material from somewhere in the "East Indies" and as far as is known, the type is lost (Sakai 1999). This is the type species of *Rhinolambrus* A. Milne-Edwards, 1878. The species has a wide

Indo-West Pacific distribution (see Flipse 1930; Sakai 1976); and in India has been reported from various parts of Tamil Nadu and Andamans (Henderson 1893; Jeyabaskaran et al. 2000; Kathirvel and Gokul 2010; Dev Roy and Nandi 2012; Vidhya et al. 2017).

The present materials are all juveniles, with none of the gonopod structures of the males developed even though the chelipeds are elongated. The pronounced "neck-like" constriction in adults of this species has still not developed (Fig. 6B).

Cryptopodia H. Milne Edwards, 1834

Cryptopodia collifer Flipse, 1930

Figs 6D–F, 7I–M

Cryptopodia collifer Flipse, 1930: 66, fig. 41; Serène 1968: 62 (list); Shen et al. 1982: 144, pl. 1 fig. 8; Dai et al. 1986: 160, pl. 21 fig. 8, text-fig. 91; Dai and Yang 1991: 176, pl. 21 fig. 8, text-fig. 91; Cai et al. 1994: 584 (list); Chiong and Ng 1998: 189, fig. 22; Davie et al. 2002: 322 (list); Ng and Davie 2002: 372 (list); Ng et al. 2008: 130 (list).

Material examined. 1 male (17.5 × 10.6 mm), 7°27.978'N, 77°32.297'E, 100 m.

Remarks. Five species of *Cryptopodia* H. Milne Edwards, 1834, are known from India (Trivedi et al. 2018): *C. angulata* H. Milne Edwards & Lucas, 1841, *C. echinosa* Chiong & Ng, 1998, *C. fornicata* (Fabricius, 1787), *C. patula* Chiong & Ng, 1998, and *C. spatulifrons* Miers, 1879b. The addition of *C. collifer* Flipse, 1930, not previously known from the Indian Ocean, is notable. *Cryptopodia collifer* Flipse, 1930, was described from a single female specimen from eastern Indonesia and has since been reported from China (Shen et al. 1982). In an unpublished study, S.H. Tan and the first author examined specimen of this species from off Phuket, Philippines and Fiji, including males, and they agree well with the specimen obtained here from India, and as figured by Chiong and Ng (1998: fig. 22).

The lateral margins of the rostrum are straight in the holotype of *C. collifer* (cf. Chiong and Ng 1998: fig. 22A) but are gently convex in the present male (Fig. 6C), as was figured by Shen et al. (1982: pl. 1 fig. 8) for the Chinese specimen. The male telson of *C. collifer* is semi-circular in shape (Fig. 6D), and is distinct from the more triangular shapes of other *Cryptopodia* species (see Chiong and Ng 1998). The G1 structure of *C. collifer* is most similar to that of *C. pan* Laurie, 1906, from the Indo-West Pacific (cf. Chiong and Ng 1998: fig. 24A, B, D–K), but the latter species is easily distinguished by its third maxilliped being distinctly swollen (Chiong and Ng 1998: fig. 23C). The third maxilliped of *C. collifer*, like those of other congeners, is quadrate and not inflated (Fig. 6D).

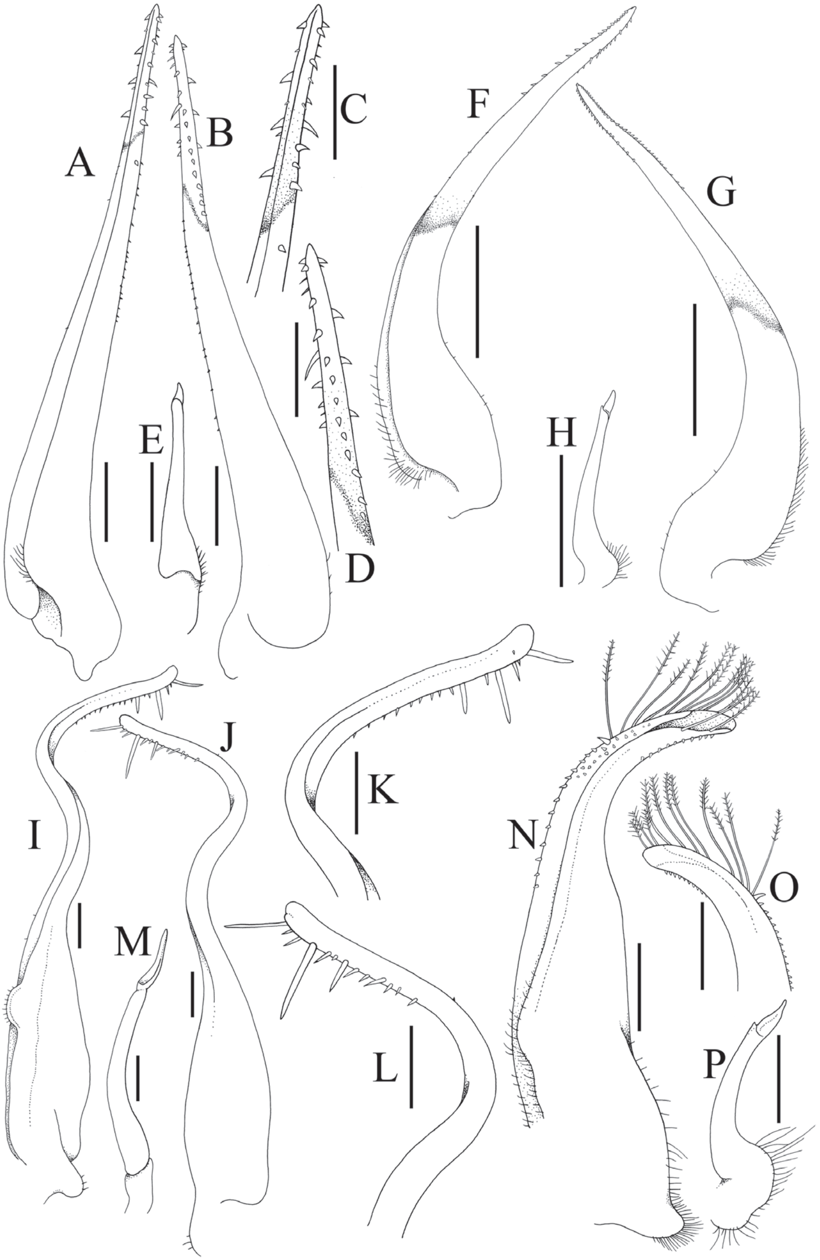

Figure 7. Gonopods. **A–E** *Nectopanope rhodobaphes* Wood-Mason in Wood-Mason & Alcock, 1891, male (18.4 × 14.7 mm) **F–H** *Henicoplax maldivensis* (Rathbun, 1902), male (9.9 × 6.3 mm) **I–M** *Cryptopodia collifer* Flipse, 1930, male (17.5 × 10.6 mm) **N–P** *Paraxanthodes cumatodes* (MacGilchrist, 1905), male (8.3 × 5.5 mm). **A, F** left G1 (ventral view) **B, G** left G1 (dorsal view) **C** distal part of left G1 (ventral view) **D** distal part of left G1 (dorsal view); left G2. Scales bars: 0.5 mm (**A, B, E–H–P**); 0.25 mm (**C, D**).

Family Xanthidae Macleay, 1838

Paraxanthodes Guinot, 1968

Paraxanthodes cumatodes (MacGilchrist, 1905)

Figs 6G, H, 7N–P

Xanthodes cumatodes MacGilchrist, 1905: 205; Alcock et al. 1907: pl. 79 fig. 1, 1A.
Xanthias cumatodes: Balss 1929: 24; Stephensen 1946: 148.
Paraxanthodes cumatodes: Guinot 1968: 723, fig. 60; Guinot 1971: 1069; Serène 1968: 77; Serène 1984: 209, pl. 30 fig. C; Ng et al. 2008: 204 (list); Mendoza et al. 2012: 3, fig. 1D–F, 2E–I.

Material examined. 1 male (8.3 × 5.5 mm), 8°58.270'N, 76°17.365'E, 50 m.

Remarks. The taxonomic problems associated with *Paraxanthodes* Guinot, 1968, and the allied genera *Monodaeus* Guinot, 1967, and *Medaeops* Guinot, 1967, and *Takedax* Mendoza & Ng, 2012, as well the generic affinities of species previously classified in these taxa have been discussed at length by Lai et al. (2011) and Mendoza and Ng (2012). While the genera are distinct at the genetic level, the available morphological characters are not always reliable; and work is still ongoing to clarify their affinities. Mendoza et al. (2012) discussed the generic position of *P. cumatodes*, and suggested that it may not be congeneric with *P. obtusidens* (Sakai, 1965), the type species of *Paraxanthodes*.

We refer the present specimen to *P. cumatodes*, described from the western Indian Ocean by MacGilchrist (1905), with doubt because of its relatively small size. It differs from typical *P. cumatodes* (see Alcock et al. 1907: pl. 79, fig. 1, 1A; Guinot 1968: fig. 60; Serène 1984: pl. 30C; Mendoza et al. 2012: fig. 1D–F) in having the carapace proportionately less broad, the grooves and ridges on the dorsal carapace surface less prominent and the grooves on the thoracic sternum relatively shallower (Fig. 6G, H). The G1 of the present specimen is developed and its structure agrees relatively well with that figured by Mendoza et al. (2012: fig. 2E, G–I) for *P. cumatodes*, except that the distal half is more gently curved and the distal setae less dense (Fig. 7N, O).

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References

Ahyong ST, Naruse T, Tan SH, Ng PKL (2009) Part II. Infraorder Brachyura: Sections Dromiacea, Raninoida, Cyclodorippoida. In: Chan T-Y, Ng PKL, Ahyong ST, Tan SH (Eds) Crustacean Fauna of Taiwan: Brachyuran Crabs, Vol. 1, 27–180.

Alcock A (1894) Natural history notes from H.M. Indian Marine Survey Steamer *Investigator*, Commander RF Hoskyn, RN, commanding. Series. II. No. 1. On the result of the deep-sea dredging during the season 1890–91. Annals and Magazine of Natural History (6)13: 225–245, 321–334, 400–411. https://doi.org/10.1080/00222939408677694

Alcock A (1895) Materials for a carcinological fauna of India. No. 1. The Brachyura Oxyrhyncha. Journal of the Asiatic Society of Bengal 64, part 2(2): 157–291.

Alcock A (1896) Materials for a carcinological fauna of India. No. 2. The Brachyura Oxystoma. Journal of the Asiatic Society of Bengal 65: 134–296.

Alcock A (1899a) Illustrations of the zoology of the Royal Indian Marine survey ship investigator, under the command of commander T.H. Heming, R.N. Fishes. Part VI, Plates XXV. Crustacea.-Part VII, Plates 36–45. Published under the Authority of Captain W. S. Goodridge, R.N., Director of the Royal Indian Marine. Calcutta: Office of the Superintendent of Government Printing, India. [For authorships and publication dates see Clark and Crosnier 1992]

Alcock A (1899b) Materials for a carcinological fauna of India. No. 4. The Brachyura Cyclometopa. Part II. A revision of the Cyclometopa with an account of the families Portunidae, Cancridae and Corystidae. Journal of the Asiatic Society of Bengal, Calcutta 68: 1–104.

Alcock A, Annandale N, MacGilchrist AC (1907) Illustrations of the Zoology of the Royal Indian Marine Survey Ship Investigator, under the command of Captain T.H. Heming, R.N. (Retired). Crustacea (Malacostraca) – Pt. XII, Plates 77–79. Crustacea (Entomostraca) – Pt. I, Plates 1–11. Mollusca – Pt. IV, Plates 14–18. Published under the Authority of Captain GH Hewett, R.N., Director of the Royal Indian Marine. Calcutta: Office of the Superintendent of Government Printing, India. [For authorships and publication dates see Clark and Crosnier 1992]

Anonymous (1891) Appendix No. XIII. Administration Report of the Indian Marine for the Official Year 1890–91. The Government Central Press, Bombay, 52–57.

Anonymous (1914) Biological collections of the R.I.M.S. “Investigator.” List of stations. 1884–1913. Trustees of the Indian Museum, Bapist Mission Press, Calcutta 2: 35 pp.

Apel M, Spiridonov VA (1998) Taxonomy and zoogeography of the portunid crabs (Crustacea: Decapoda: Brachyura: Portunidae) of the Arabian Gulf and adjacent waters. Fauna of Arabia 17: 159–331.

Balss H (1929) Decapoden des Roten Meeres. IV. Die Oxyrhynchen und Schlussbetrachtungen. In: Expedition S.M. Schiff Pola in das Rote Meer, nördliche und südliche Hälfte 1895/96–1897/98. Zoologische Ergebnisse XXXVI. Denkschriften Akademie Wissenschaften in Wien 102: 1–30. [pl. 1]

Borradaile LA (1902) Marine Crustaceans. I. On Varieties. II. Portunidae. In: Gardiner JS (Ed.) The Fauna and Geography of the Maldive and Laccadive Archipelagoes: Being the Account of the Work carried on and of the Collections made by an Expedition during the years 1899 and 1900, 1(2): 191–208. [figs 35–38]

Cai E-X, Huang Z-G, Dai A-Y, Chen H-L, Yang S-L (1994) Brachyura. In: Huang Z-G (Ed.) Marine species and their distributions in China's Seas, Department of Ocean Management and Monitoring State Oceanic Administration. China Ocean Press, Beijing, 576–600.

Castro P (2007) A reappraisal of the family Goneplacidae MacLeay, 1838 (Crustacea, Decapoda, Brachyura) and revision of the subfamily Goneplacinae, with the description of ten new genera and eighteen new species. Zoosystema 29(4): 609–773.

Castro P, Ng PKL (2010) Revision of the family Euryplacidae Stimpson, 1871 (Crustacea: Decapoda: Brachyura: Goneplacoidea). Zootaxa 2375: 1–130. https://doi.org/10.11646/zootaxa.2375.1.1

Chen H, Sun H (2002) Arthropoda Crustacea. Brachyura. Marine primitive crabs. Fauna Sinica. Invertebrata, 30, Science Press, Beijing, 597 pp. [colour pls 1–4, pls 1–16]

Chiong WL, Ng PKL (1998) A revision of the buckler crabs of the genus *Cryptopodia* H. Milne Edwards, 1834 (Crustacea: Decapoda: Brachyura: Parthenopidae). Raffles Bulletin of Zoology 46(1): 157–216.

Clark PF, Crosnier C (1992) Illustrations of the Zoology of the R.I.M.S. *Investigator*: authors, dates, issues, plates and titles. Archives of Natural History 19(3): 365–374. https://doi.org/10.3366/anh.1992.19.3.365

Crosnier A (1975) Sur quelques Portunidae, Grapsidae et Ocypodidae (Crustacea Decapoda Brachyura) de Madagascar ou des îles avoisinantes, nouveaux, rares ou non encore signalés. Bulletin du Muséum national d'Histoire naturelle, Section A (Zoology), série 3, 214(304): 711–741.

Dai A-Y, Yang S-L (1991) Crabs of the China Seas. China Ocean Press, Beijing and Springer-Verlag, Berlin, 608 pp. [figs 1–295, pls 1–74]

Dai A-Y, Yang S-L, Song Y-Z, Chen G-X (1986) Crabs of the China Seas. China Ocean Press, Beijing, Vol. 11, 642 pp. [In Chinese]

Davie PJF (1987) A new species and new records of *Portunus* (Decapoda: Portunidae) from Northern Australia. Memoirs of the Queensland Museum 25(1): 227–231.

Davie PJF, Guinot D, Ng PKL (2015a) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (Eds), Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Volume 9C–I. Decapoda: Brachyura (1): 11–163. https://doi.org/10.1163/9789004190832_004

Davie PJF, Guinot D, Ng PKL (2015b) Classification and Systematics and classification of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (Eds), Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Volume 9C-II. Decapoda: Brachyura (Part 2), 1049–1130.

Davie PJF, Ng PKL, Kaenphet A, Aungtonya C (2002) Annotated checklist of Brachyura (Crustacea: Decapoda) principally obtained during the BIOSHELF survey off western Thailand from 1996–1998. In: Bruce NL, Berggren M, Bussawarit S (Eds) Biodiversity of Crustacea of the Andaman Sea, Proceedings of the International Workshop on the Biodiversity of Crustacea in the Andaman Sea. Phuket Marine Biological Center, 29 November to 20 December 1998. Phuket Marine Biological Center Special Publication 23(2): 313–339.

Dev Roy MK (2013) Diversity and distribution of marine brachyuran crab communities inhabiting West Coast of India. In: Venkataraman C, Sivaperuman, Raghunathan C (Eds)

Ecology and Conservation of Tropical Marine Faunal Communities Part 1. Springer, Berlin/Heidelberg, 147–169. https://doi.org/10.1007/978-3-642-38200-0_10

Dev Roy MK (2015) Conservation concerns on crustacean fauna of India. Journal of Environment and Sociobiology 12(1): 77–98.

Dev Roy MK, Nandi, NC (2007) Brachyuran diversity in coastal ecosystems of Tamil Nadu. Journal of Environment and Sociobiology 4(2): 169–192.

Dev Roy MK, Nandi NC (2012) Brachyuran crabs (Crustacea). In: Director ZSI, Kolkata (Ed.) Fauna of Andaman and Nicobar islands, State Fauna Series, Zoological Survey of India, Kolkata 19(1): 185–236.

Flipse HJ (1930) Die Decapoda Brachyura der Siboga-Expedition. VI. Oxyrhyncha: Parthenopidae. Siboga Expéditie 39c^2: 1–96.

Galil BS (2001) A revision of the genus *Arcania* Leach, 1817 (Crustacea: Decapoda: Leucosioidea). Zoologische Mededelingen 75(11): 169–205.

Guinot D (1968) Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures. IV. Observations sur quelques genres de Xanthidae. Bulletin du Muséum national d'Histoire naturelle, série 2, 39(4), 1967(1968): 695–727.

Guinot D (1969) Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures, VII. Les Goneplacidae (suite). Bulletin du Muséum national d'Histoire naturelle, série 2, 41(2): 507–528. [pl. 2]

Guinot D (1971) Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures, VIII. Synthèse et bibliographie. Bulletin du Muséum national d'Histoire naturelle, série 2, 42(5) [1970]: 1063–1090.

Henderson JR (1893) A contribution to Indian carcinology. Transactions of the Linnaean Society of London Zoology, series 2, 5: 325–458. https://doi.org/10.1111/j.1096-3642.1893.tb00653.x

Herbst JFW (1782–1804) Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschieden Arten. Gottlieb August Lange, Berlin & Stralsund. Volumes 1–3: 1–274 + 1–226 +1–66 + 1–46, 1–54 + 1–49. [Vol. 1, Part 1 (pp 1–86, pl 1): 1782; Vol. 1, Parts 2–5 (pp 87–182, pls 2–9): 1783; Vol. 1, Part 6 (pp 183–206, pls 10–13): 1785; Vol. 1, Part 7 (pp 207–238, pls 14–17): 1788; Vol. 1, Part 8 (pp 239–274, pls 18–21): 1790; Vol. 2, Part 1 (pp 1–48, pls 22–25): 1791; Vol. 2, Part 2 (pp 49–78, pls 26–29): 1792; Vol. 2, Part 3 (pp 79–98, pls 30–33): 1793; Vol. 2, Part 4 (pp 99–146, pls 34–36): 1793; Vol. 2, Part 5 (pp 147–162, pls 37–40): 1794; Vol. 2, Parts 6–end (pp 163–226, pls 41–46): 1796; Vol. 3, Part 1 (pp 1–66, pls 47–50): 1799; Vol. 3, Part 2 (pp 1–46, pls 51–54): 1801; Vol. 3, Part 3 (pp 1–54, pls 55–58): 1803; Vol. 3, Part 4 (pp 1–49, pls 59–62): 1804.]

Huys R, Low MEY, De Grave S, Ng PKL, Clark PF (2014) On two reports associated with James Wood-Mason and Alfred William Alcock published by the Indian Museum and the Indian Marine Survey between 1890 and 1891: implications for malacostracan nomenclature. Zootaxa 3757(1): 1–78. https://doi.org/10.11646/zootaxa.3757.1.1

ICZN (1999) International Code of Zoological Nomenclature. International Commission of Zoological Nomenclature. Fourth Edition. Adopted by the XXI General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature, in association with the British Museum (Natural History), London, 338 pp.

Jeyabaskaran R, Khan AS, Ramaiyan V (2000) Biodiversity project on Gulf of Mannar biosphere reserve. Parangipettai, India. Centre of Advanced Study in Marine Biology, Annamalai University, 177 pp.

Kathirvel M, Gokul A (2010) Checklist of brachyuran crabs from the Gulf of Mannar marine biosphere reserve. Technical Bulletin 4. The Fisheries Technocrats Forum, Chennai, 45 pp.

Lai JCY, Mendoza JCE, Guinot D, Clark PF, Ng PKL (2011) Xanthidae Macleay, 1838 (Decapoda: Brachyura: Xanthoidea) systematics: a multi-gene approach with support from adult and zoeal morphology. Zoologischer Anzeiger 250: 407–448. https://doi.org/10.1016/j.jcz.2011.07.002

MacGilchrist AC (1905) Natural History Notes from the R.I.M.S. 'Investigator', Capt. T. H.Heming, R.N. (retired), commanding. Series III, No. 6. An account of the new and some of the rarer Decapod Crustacea obtained during the Surveying Seasons 1901–1904. Annals and Magazine of Natural History, Series 3, 7(87): 233–268. https://doi.org/10.1080/03745480509443038

Mendoza JCE, Kazmi QB, Moassam M (2012) First report of two rare xanthid crabs (Crustacea: Decapoda: Brachyura: Xanthidae) from Pakistan. Marine Biodiversity Records 5, e51: 1–5. https://doi.org/10.1017/S1755267211001084

Mendoza JCE, Ng PKL (2012) A new genus and species of deep-water xanthid crab (Decapoda, Brachyura, Xanthidae) from the Philippines. In: Komatsu H, Okuno J, Fukuoka K (Eds) Studies on Eumalacostraca: a homage to Masatsune Takeda. Crustaceana Monographs 17: 197–210.

Michel C (1964) Check List of the Crustacea Brachyura (Crabs) recorded from Mauritius. Mauritius Institute Bulletin 6(1): 1–48.

Milne-Edwards A (1861) Études zoologiques sur les Crustacés récents de la famille des Portuniens. Archives du Muséum d'Histoire naturelle 10: 309–428. [pls 28–38] https://doi.org/10.5962/bhl.title.10629

Ng PKL, Abdelsalam KM, Mona MH, Nour Eldeen MF (2018) A synopsis of the genus *Eurycarcinus* A. Milne-Edwards, 1867 (Decapoda, Brachyura, Pilumnidae). Crustaceana 91(4): 471–487. https://doi.org/10.1163/15685403-00003775

Ng PKL, Davie PJF (2002) A checklist of the brachyuran crabs of Phuket and western Thailand. In: Bruce NL, Berggren M, Bussawarit S (Eds) Biodiversity of Crustacea of the Andaman Sea, Proceedings of the International Workshop on the Biodiversity of Crustacea in the Andaman Sea. Phuket Marine Biological Center, 29 November to 20 December 1998. Phuket Marine Biological Center Special Publication 23(2): 369–384.

Ng PKL, Guinot D, Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement 17: 1–286.

Ng PKL, Rahayu DL (2000) On a small collection of Parthenopidae from Indonesia, with description of a new species of *Pseudolambrus* (Crustacea: Decapoda: Brachyura). Proceedings of the Biological Society of Washington 113(3): 782–791.

Ng PKL, Türkay M, Galil BS (2014) On the identity of *Cancer urania* Herbst, 1801 (Crustacea: Decapoda: Brachyura: Leucosiidae). Zootaxa 3786(2): 124–134. https://doi.org/10.11646/zootaxa.3786.2.2

Promdam R, Nabhitabhata J, Galil BS (2014) A new species of *Coleusia* Galil, 2006 (Decapoda: Brachyura: Leucosiidae) from southern Asia. Zootaxa 3786(2): 135–140. https://doi.org/10.11646/zootaxa.3786.2.3

Rahayu DL, Ng PKL (2014) New genera and new species of Hexapodidae (Crustacea, Brachyura) from the Indo-West Pacific and east Atlantic. Raffles Bulletin of Zoology 62: 396–483.

Rathbun MJ (1902) Crabs from the Maldive Islands. Bulletin of the Museum of Comparative Zoology, Harvard College 39(5): 123–138. [pl. 1]

Sakai K (1999) JFW Herbst-collection of decapod Crustacea of the Berlin Zoological Museum, with remarks on certain species. Naturalists, Publications of Tokushima Biological Laboratory, Shikoku University 4: 1–45. [pls 1–21]

Sakai T (1964) On two new genera and five new species of xanthoid crabs from the collection of His Majesty the Emperor of Japan made in Sagami Bay. Crustaceana 8(1): 97–106. https://doi.org/10.1163/156854065X00596

Sakai T (1969) Two new genera and twenty-two new species of crabs from Japan. Proceedings of the Biological Society of Washington 82: 243–280.

Sakai T (1976) Crabs of Japan and the Adjacent Seas. 3 Vols. Kodansha Ltd., Tokyo (29): 773 pp. [English text], 461 pp. [Japanese text]. [251 pls]

Serène R (1968) The Brachyura of the Indo Pacific Region. Prodromus for a Check List of the Non-planctonic Marine Fauna of South East Asia. Special Publication of the Singapore National Academy of Science, No. 1: 33–120.

Serène R (1984) Crustacés Décapodes Brachyoures de l'Océan Indien Occidental et de la Mer Rouge, Xanthoidea: Xanthidae et Trapeziidae. Avec un addendum par Crosnier A: Carpiliidae et Menippidae. Faune Tropicale 24: 1–400. [figs A–C, 1–243, pls 1–48]

Serène R, Soh CL (1970) New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea). Treubia 27(4): 387–416. [pls 1–8]

Shen C-J, Dai A-Y, Chen H-L (1982) New and rare species of Parthenopidae (Crustacea: Brachyura) from China Seas. Acta Zootaxonomica Sinica 7(2): 139–149. [pls 1, 2]

Stephensen K (1946) The Brachyura of the Iranian Gulf. With an appendix: The male pleopoda of the Brachyura. In: Jessen K, Spärck R (Eds) Danish Scientific Investigations in Iran, Part 4 [1945], 1–237.

Stephenson W (1972a) Portunid crabs from the Indo-West Pacific and Western America in the Zoological Museum, Copenhagen (Decapoda, Brachyura, Portunidae). Steenstrupia 2(9): 127–156.

Stephenson W (1972b) An annotated check list and key to the Indo-West Pacific swimming crabs (Crustacea: Decapoda: Portunidae). Bulletin of the Royal Society of New Zealand 10: 1–64.

Stevčić Z (2005) The reclassification of Brachyuran Crabs (Crustacea: Decapoda: Brachyura). Natura Croatica (Fauna Croatica) 14(1): 1–159.

Tan CGS (1996) Leucosiidae of the Albatross expedition to the Philippines, 1907–1910 (Crustacea: Brachyura: Decapoda). Journal of Natural History 30(7): 1021–1058. https://doi.org/10.1080/00222939600770551

Trivedi JN, Trivedi DJ, Vachhrajani KD, Ng PKL (2018) An annotated checklist of marine brachyuran crabs (Crustacea: Decapoda: Brachyura) of India. Zootaxa 4502(1): 1–83.

Wood-Mason J, Alcock A (1891) Natural History Notes from H.M. Indian Marine Survey Steamer "Investigator", Commander R.F. Hoskyn, R.N., commanding. No. 21. On the Results of the last Season's Deep-sea Dredging. Annals and Magazine of Natural History, March 1891 (6)7(39): 258–272.

Vidhya V, Jawahar P, Karuppasamy K (2017) Annotated check list of the brachyuran crabs (Crustacea: Decapoda) from Gulf of Mannar region, south east coast of India. Journal of Entomology and Zoology Studies 5(6): 2331–2336.

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RESEARCH ARTICLE

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A new species of *Polyonyx* (Crustacea, Anomura, Porcellanidae) inhabiting polychaete-worm tubes (Annelida, Chaetopteridae) in the Indo-West Pacific

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Abstract

Polyonyx socialis **sp. n.** from the South China Sea of Vietnam is described. The new species was collected in a previous study that compared the vertebrate and invertebrate symbiont communities living in the tubes of two syntopic species of the polychaete genus *Chaetopterus*. *Polyonyx socialis* **sp. n.** inhabits the tubes of the smaller polychaete species as a heterosexual pair, and frequently shares the cavity of the host's tube with a larger porcellanid, *P. heok*, also present as a male-female pair, and with a species of trinchesiid nudibranch. Less frequently, the new species shares its host with a heterosexual pair of a larger species of pinnotherid crab. *Polyonyx socialis* **sp. n.** belongs to the *P. sinensis* group, a world-wide distributed morphological line within the heterogeneous genus *Polyonyx*. Most species in this group are obligate commensals of chaetopterid polychaetes. The crabs have a transversally cylindrical habitus, which enables them to move laterally along the worm tubes with ease. *Polyonyx socialis* **sp. n.** is a relatively small species that lives attached to the inner walls of the polychaete tube. The small size and flattened chelipeds and walking legs of the new species confers it an advantage to cohabiting the same worm tube with larger decapod species occupying most of the tube's cavity.

Keywords

adaptation, *Chaetopterus*, commensalism, polychaete-inhabiting

Introduction

The porcellanid genus *Polyonyx* Stimpson is a diverse and heterogeneous taxon containing more than 30 species worldwide, most of which distributed in the Indo-West Pacific (IWP) (Johnson 1958; Haig 1960; Werding 2001; Osawa 2007; Osawa and McLaughlin 2010; Osawa and Ng 2016; Osawa et al. 2018; this study). Many species of this genus are known to live commensally with polychaete worms (Haig 1960, 1979; Ng and Sasekumar 1993; Werding 2001; Osawa et al. 2018; own observations). Johnson (1958) arranged the IWP species into three morphological groups, designated as *Polyonyx biunguiculatus* (Dana 1852), *P. denticulatus* Paul'son, 1875, and *P. sinensis* Stimpson, 1858. Nakasone and Miyake (1969) considered the *P. denticulatus* group as the new genus *Aliaporcellana*, which was later redefined by Haig (1978).

The largest of Johnson's (1958) assemblages is the *Polyonyx sinensis* group, which is worldwide distributed, though most of the species in this group have an Indo-West Pacific (IWP) distribution. According to this author this group contains species with a "pronounced tendency towards commensalism". Indeed, most species in this morphological line are commensal (Haig 1964), and have been reported to inhabit the tubes of tube-dwelling polychaetes, mainly of the family Chaetopteridae Audouin and Milne-Edwards, as heterosexual pairs (Pope 1946; Gray 1961; Haig 1965; Ng and Sasekumar 1993; Osawa 2001, 2007; Sanford 2006; Osawa and Poupin 2013; Britayev et al. 2017). In some cases commensalism seems to be facultative, as free-living individuals have been sporadically found in shallow waters under stones or in sand (Haig 1956, 1964; Werding 2001).

The *Polyonyx biunguiculatus* group contains six species, four distributed in the Central Pacific (Osawa 2015) and two in the Indian Ocean. The Central Pacific species, *Polyonyx biunguiculatus*, *P. obesulus* Miers 1884, *P. similis* Osawa 2015, and *P. triunguiculatus* Zehntner 1894, do not seem to have commensal relationships with other invertebrates, although they seem to prefer habitats characterized by corals and sponges (Haig 1964, 1979; Osawa 2007, 2015). The two Indian Ocean species, *P. hendersoni* Southwell 1909, and *P. splendidus* Sankolli 1963, have been rarely found, probably because they inhabit the ducts of sponges. Such life habit is reflected in the distinctive morphology of these two species (see Hiller et al. 2010), which made Werding (2001) consider them as conspecifics of a new genus. However, unpublished molecular data indicate that these species are aberrant forms of the *P. biunguiculatus* group.

In a recent study of symbionts of two syntopic species of chaetopterid polychaetes in the South China Sea of Vietnam, Britayev et al. (2017) found heterosexual pairs of a small porcellanid inhabiting one of this chaetopterid species. This porcellanid is an undescribed species of the *Polyonyx sinensis* group, which we here describe as *Polyonyx socialis* sp. n. The new species was reported by Britayev et al. (2017) to share its host either with *P. heok* Osawa & Ng, 2016, a rather large porcellanid, and a nudibranch species of the genus *Phestilla* Bergh, or with a male-female pair of a pinnotherid crab of the genus *Tetrias* Rathbun.

Materials and methods

Material of *Polyonyx socialis* sp. n. was provided by T Britayev (Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russian Federation) and D Martin (Department of Marine Ecology, Centre d'Estudis Avançats de Blanes, Blanes, Catalunya, Spain), and has been deposited in the Naturmuseum Senckenberg (SMF), Frankfurt a.M., Germany. Colour photographs were provided by T Britayev, and are included in the description. Measurements of carapace length and width (in mm) of type individuals follow collection information.

Systematics

Family Porcellanidae

Polyonyx socialis sp. n.

http://zoobank.org/C8712225-9D4B-40AA-87CA-0B6FCDB3174A
Figs 1, 2a–g, 3

Material. Holotype: female, SMF 52400, South China Sea, south coast of Vietnam, Nhatrang Bay, Tre Island, Dam Bay, 6–8 m, silty sand, hand collection from tube of *Chaetopterus* sp. No 66, cohabiting with a pair of pinnotherid *Tetrias* sp., coll. Britayev and Martin, 15.04. 2016; 4.0 mm x 4.3 mm (Fig. 1). **Paratypes**: male-female pair cohabiting with a pair of *Polyonyx heok*, SMF -52401, South China Sea, south coast of Vietnam, Nhatrang Bay, Mun Island, 16–20 m, silty sand, hand collection from tube of *Chaetopterus* sp. No 4, coll. Britayev and Martin, 04. 2016; male 4.6 mm x 5.7 mm (Fig. 2), female (ov) 5.1 mm x 5.6 mm (Fig. 3), both with bopyrid infestation and therefore, largely deformed.

Description. Carapace (Fig. 1) round to subovate, 1.1 to 1.2 times wider than long, broadest at epibranchial level, moderately convex, surface smooth, shining, covered with distant, shallow transversal striae. Regions scarcely demarcated. Hepatic margin roundly produced, crested. Branchial margins evenly rounded, crested. Rostrum broad, transverse (holotype) or weakly trilobate (paratypes), median lobe forwardly directed, lateral lobes rounded. Orbits shallow, outer orbital angles rounded. Side walls entire, not visible from above.

Third thoracic sternite (Fig. 2a) broad, anterior margin rounded, lateral lobes broad, forwardly directed.

Telson composed of seven plates (Fig. 2b).

Basal article of antennular peduncle unarmed. First antennal article broadly in contact with lower orbital margin, movable articles smooth, second elongate; flagellum long, reaching to tip of chelae.

Third maxilliped (Fig. 2c) with broad ischium and rounded inner projection; merus with subrectangular rounded inner lobe. Exopod long, slender, overreaching middle of merus.

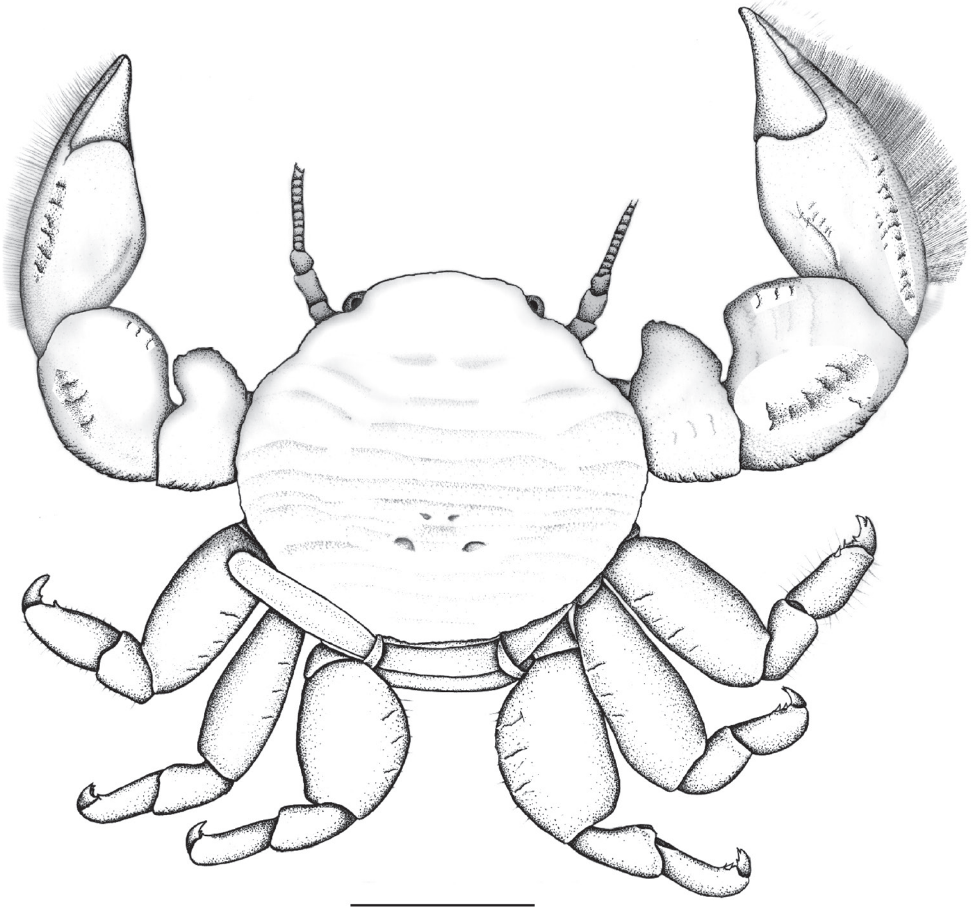

Figure 1. *Polyonyx socialis* sp. n., female holotype, dorsal view, SMF 52400, South China Sea, south coast of Vietnam, Nhatrang Bay, Tre Island, Dam Bay, dorsal view. Scale bar: 2.0 mm.

Chelipeds (Figs 1, 2d) similar in both sexes, heterochaely not very pronounced. Merus with some transverse rugae on upper surface, with large, laminate, forwardly projected lobe; carpus swollen, with similar lobe that makes carpus appear nearly as broad as long; upper surface with some transversal rugae, proximal border concave, outer border with faint, scale-like rugae, and scattered, short setae; distal portion with tuft of simple setae. Manus compact, swollen above, outer border evenly curved outside. Fingers short, approximately 1/3 of total length of manus. Outer border with narrow fringe of densely set, very fine, simple setae. Fingers closing on entire length, movable finger with upper border of cutting edge with fringe of upwardly standing simple setae.

Walking legs (Figs 2e–f) relatively short, merus flattened, ovate from above, 1.4 to 1.5 times longer than wide, surface with scattered, transversal ridges and scattered setae. Carpus and propodus elongate, of similar length, with scattered simple setae, propodus spineless except for terminal triplet. Dactylus elongate, terminating

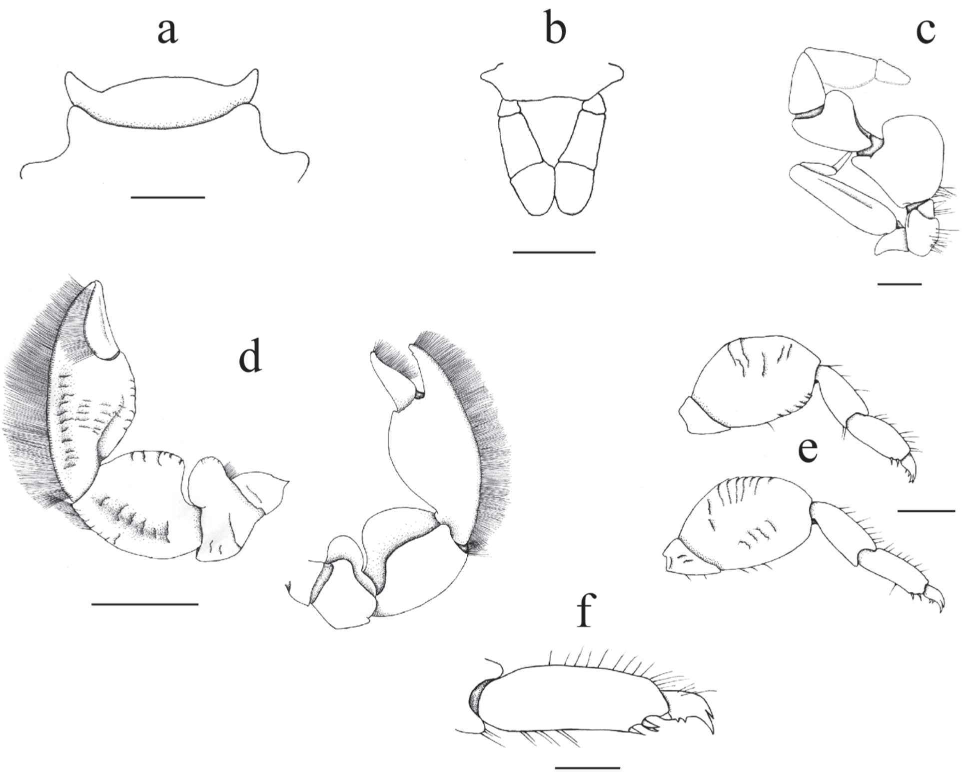

Figure 2. *Polyonyx socialis* sp. n., male paratype, SMF 52401, South China Sea, south coast of Vietnam, Nhatrang Bay, Mun Island. **a** Third thoracic sternite **b** Telson **c** Right third maxilliped, dorsal view (setae omitted) **d** Left (larger) cheliped, dorsal and ventral views **e** First and second right walking legs, dorsal view **f** Detail of dorsal view of propodus and dactylus of right third walking leg. Scale bars: 0.5 mm (**a–c, f**), 2.0 mm (**d**), 1 mm (**e**).

in curved, bifurcate claws, the upper one being smaller, inner margin with two or sometimes three smaller spines.

Males with pair of pleopods on second abdominal segment.

The overall coloration of *Polyonyx socialis* sp. n. (Fig. 3) is light brown with a symmetric pattern of white marks on the carapace. The chelipeds have whitish marks upon the articulation between merus and carpus, and at the level of the articulation with the dactylus. The walking legs have white areas on the proximal part of the merus, and around the articulations.

Ecology. *Polyonyx socialis* sp. n. inhabits the tubes of a *Chaetopterus* sp. worm as heterosexual pairs, and shares its host with other symbionts, either a male-female pair of the porcellanid *P. heok* and the aeolid nudibranch *Phestilla* sp., or a male-female pair of the pinnotherid crab *Tetrias* sp. The hosts were collected between 6 and 20 m depth.

Etymology. The specific name *socialis*, from the Latin, meaning social, refers to the sociable behaviour of the new species, as it tolerates and is tolerated by other symbionts inhabiting the same polychaete host.

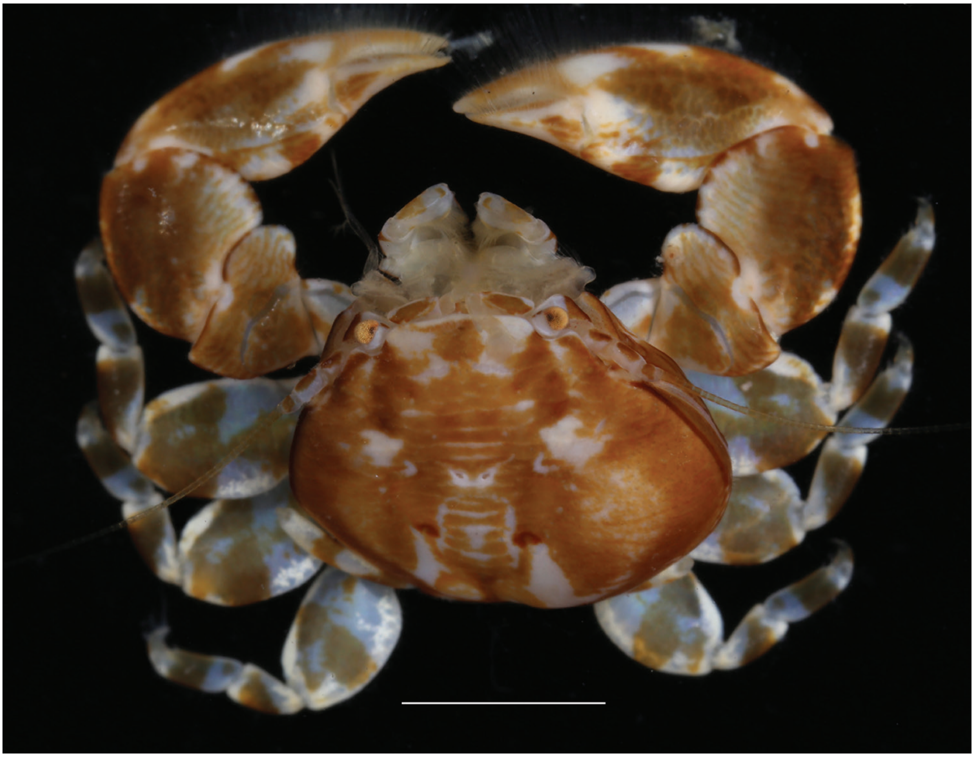

Figure 3. *Polyonyx socialis* sp. n., female paratype, SMF 52401, South China Sea, south coast of Vietnam, Nhatrang Bay, Mun Island. Right side of carapace deformed by parasitic isopods (Bopyridae). Scale bar: 3.0 mm.

Remarks. The new species is morphologically similar and probably systematically close to *P. utinomii* Miyake, 1943 and *P. boucheti* Osawa, 2007, both of which also live in *Chaetopterus* tubes (Osawa 2001). The new species is distinguished from *P. utinomii* and *P. boucheti* by 1) the narrower carapace, with the rostrum being less transverse, 2) the extremely extended and forwardly directed lobes on merus and carpus of the chelipeds, 3) the wide and flattened merus of the walking legs, and 4) the extremely fine and transparent fringes of setae on the chelipeds.

Distribution. Currently known only from the Vietnamese coast of the South China Sea.

Discussion

Polyonyx socialis sp. n. inhabits as a heterosexual pair the tubes of one of two syntopic species of *Chaetopterus*, which according to Britayev et al. (2017), may be a new undescribed species of polychaete from the Vietnamese South China Sea. These authors reported the new porcellanid frequently sharing the polychaete tube with a heterosexual pair of the significantly larger porcellanid *P. heok* and of the tergipedid nudibranch *Phestilla* sp. In one case *Polyonyx socialis* sp. n. shared its host with a male-female pair of the pinnotherid crab *Tetrias* sp. Interestingly, *P. socialis* sp. n. was not found in the tubes of the larger polychaete *Chaetopterus* cf. *appendiculatus* Grube, 1874, which is ecologically close to the porcellanid's host. The inhabitants of the larger polychaete were either the porcellanid *Eulenaios cometes* (Walker, 1887) and the polynoid polychaete *Ophthalmonoe pettiboneae* Petersen & Britayev, 1997, or the carapid fish *Onuxodon fowleri* (Smith 1955). The presence of *P. socialis* sp. n. in the smaller and not the larger polychaete species may be explained by the crab's host specificity, or by a lower tolerance of *Chaetopterus* cf. *appendiculatus* and its commensal inhabitants to sharing the space inside the tube.

The extremely broadened chelipeds and walking legs of *P. socialis* sp. n. are distinctive characters within *Polyonyx*, even when comparing the species with the morphologically closest *P. boucheti* and *P. utinomii*, and to all other tube-dwelling species of the genus. These characters are most likely adaptations to living tightly attached to the walls of the worm tube without being perceived as an obstacle for the larger crabs inhabiting the same tube. The new species is therefore morphologically adapted to cohabiting with a heterosexual pair of a congeneric larger crab, what is quite exceptional. The West Atlantic representative of the *P. sinensis* group, *P. gibbesi* Haig, 1956 inhabits the polychaete host *Chaetopterus variopedatus* (Renier 1804) as a male-female pair (Gray 1961), and very rarely shares its host with the pinnotherid crab *Pinnixa chaetopterana* Stimpson, 1860, which also inhabits the polychaete tube as a heterosexual pair (Grove and Woodin 1996). Studies in North Carolina and in the northern Gulf of Mexico (Pearse 1913, Gray 1961, Williams 1984, McDermott 2005) revealed that these two crab species do not coexist in one worm tube. In seldom cases, only juveniles of the two species were found in one tube. Apparently, the first to colonize the tube impedes the arrival of the other species. Once a heterosexual pair of either crab species has been established in the tube, it transitionally tolerates or completely rejects adults of the other species, which suggests that occupancy of the host by adult crabs involves intra- and interspecific competition (Sanford 2006). The cases where only one crab individual is present in the worm tube are probably transitional situations towards forming a male-female pair.

Polyonyx socialis sp. n. and *P. heok* comprise the first pair of porcellanid crabs observed to share the same host.

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References

Britayev TA, Mekhova E, Deart Y, Martin D (2017) Do syntopic host species harbour similar symbiotic communities? The case of *Chaetopterus* spp. (Annelida: Chaetopteridae). PeerJ 5: e2930. https://doi.org/10.7717/peerj.2930

Dana JD (1852) Crustacea. Part I. United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N. 13. C Sherman, Philadelphia, 685 pp.

Gray IE (1961) Changes in abundance of the commensal crabs of *Chaetopterus*. The Biological Bulletin 120: 353–359. https://doi.org/10.2307/1539537

Grove MW, Woodin SA (1996) Conspecific recognition and host choice in a pea crab, *Pinnixa chaetopterana* (Brachyura: Pinnotheridae). Biological Bulletin 190: 359–366. https://doi.org/10.2307/1543028

Grube E (1874) Descriptiones Annulatorum novornm mare Ceylonicum habitantium ab honoratissimo Holdsworth collectorum. Proceedings of the Zoological Society of London 42: 325–329. https://doi.org/10.1111/j.1096-3642.1874.tb02492.x

Haig J (1956) The Galatheidea (Crustacea Anomura) of the Allan Hancock Atlantic Expedition with a review of the Porcellanidae of the western North Atlantic. Allan Hancock Atlantic Expedition Report 8: 1–44.

Haig J (1960) The Porcellanidae (Crustacea Anomura) of the eastern Pacific. Allan Hancock Pacific Expeditions 24: 1–440.

Haig J (1964) Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. 81. Porcellanid crabs from the Indo-west Pacific, Part I. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn 126: 355–386.

Haig J (1965) The Porcellanidae (Crustacea, Anomura) of Western Australia, with descriptions of four new Australian species. Journal of The Royal Society of Western Australia 48: 97–118.

Haig J (1978) Contribution toward a revision of the porcellanid genus *Porcellana* (Crustacea: Decapoda: Anomura). Proceedings of the Biological Society of Washington 91: 706–714.

Haig J (1979) Expédition Rumphius II (1975) Crustacés parasites, commensaux, etc. Th. Monod et R. Sèrene, éd. V. Porcellanidae (Crustacea, Decapoda, Anomura). Bulletin du Muséum national d'Histoire naturelle, Section A, Zoologie, Biologie et Ecologie Animales, Paris, 4e série 1: 119–136.

Hiller A, Harkantra S, Werding B (2010) Porcellanid crabs from Goa, Eastern Arabian Sea (Crustacea: Decapoda: Porcellanidae). Journal of the Bombay Natural History Society 107: 201–212.

Johnson DS (1958) The Indo-West Pacific species of the genus *Polyonyx* (Crustacea, Decapoda, Porcellanidae). Annals of Zoology (Agra) 2: 95–118.

McDermott JJ (2005) Biology of the brachyuran crab *Pinnixa chaetopterana* Stimpson (Decapoda: Pinnotheridae) symbiotic with tubicolous polychaetes along the Atlantic coast of the United States, with additional notes on other polychaete associations. Proceedings of the Biological Society of Washington 118: 742–764. https://doi.org/10.2988/0006-324X(2005)118[742:BOTBCP]2.0.CO;2

Miers EJ (1884) Crustacea. Report of the Zoological Collections made in the Indo-Pacific Ocean during the voyage of HMS 'Alert', 1881–1882: 178–331, Part 2: 513–575.

Miyake S (1943) Studies on the crab-shaped Anomura of Nippon and adjacent waters. Journal of the Department of Agriculture, Kyūsyū Imperial University 7: 49–158.

Nakasone Y, Miyake (1969) A new porcellanid crab (Anomura: Porcellanidae) from Japan (*Aliaporcellana kikuchii* gen. et sp. nov.), with description of two species of the new genus. Publications from the Amakusa Marine Biological Laboratory, Kyushu University: 17–32.

Ng PKL, Sasekumar A (1993) A new species of *Polyonyx* Stimpson, 1858, of the *P. sinensis* group (Crustacea: Decapoda: Anomura: Porcellanidae) commensal with a chaetopterid worm from Peninsular Malaysia. Zoologische Mededelingen, Leiden 67: 467–472.

Osawa M (2001) *Heteropolyonyx biforma* new genus and species, from Japan, and redescription of *Polyonyx utinomii* (Decapoda: Porcellanidae). Journal of Crustacean Biology 21: 506–520. https://doi.org/10.1163/20021975-99990152

Osawa M (2007) Porcellanidae (Crustacea: Decapoda: Anomura) from New Caledonia and the Loyalty Islands. Zootaxa 1548: 1–49.

Osawa M (2015) A new species of *Polyonyx* Stimpson, 1858 (Crustacea: Decapoda: Anomura: Porcellanidae) from the PANGLAO 2004 Marine Biodiversity Project in the Philippines. The Raffles Bulletin of Zoology 63: 536–545.

Osawa M, McLaughlin PA (2010) Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part II – Porcellanidae. The Raffles Bulletin of Zoology 23 (Supplement): 109–129.

Osawa M, Poupin J (2013) First record of the porcellanid crab, *Polyonyx boucheti* (Crustacea: Decapoda: Anomura) from the Indian Ocean. Marine Biodiversity Records 6: 1–5. https://doi.org/10.1017/S1755267213000493

Osawa M, Ng PKL (2016) Revision of *Polyonyx pedalis* Nobili, 1906 (Crustacea: Decapoda: Anomura: Porcellanidae), with descriptions of three new species. Raffles Bulletin of Zoology 34 (Supplement): 499–518.

Osawa M, Naruse T, Ng PKL (2018) New records of species of the *Polyonyx sinensis* group (Crustacea: Decapoda: Anomura: Porcellanidae) from Japan, the Philippines, Singapore, and Malaysia, with descriptions of two new species. Zootaxa 4429: 303–323. https://doi.org/10.11646/zootaxa.4429.2.6

Paul'son O (1875) Studies on Crustacea of the Red Sea with notes regarding other seas. Part I. Podophthalmata and Edriophthalmata (Cumacea). SV Kul'zhenko, Kiev 14: 92–96. [In Russian, English translation by the Israel Program for Scientific Translations, Jerusalem, 1961]

Pearse AS (1913) On the habits of the crustaceans found in *Chaetopterus* tubes at Woods Hole, Massachusetts. The Biological Bulletin 24: 102–114. https://doi.org/10.1086/BBLv24n2p102

Petersen ME, Britayev TA (1997) A new genus and species of polynoid scaleworm commensal with *Chaetopterus appendiculatus* Grube from the Banda Sea (Annelida: Polychaeta), with a review of commensals of Chaetopteridae. Bulletin of Marine Science 60: 261–276.

Pope EC (1946) *Chaetopterus*, a strange and beautiful worm. Australian Museum Magazine 9: 87–92.

Renier SA (1804) Prospetto della Classe dei Vermi, nominati el ordinati secondo il Sistemo de Bosc. Padua 38: 15–27.

Sanford F (2006) *Polyonyx gibbesi* (Decapoda: Anomura: Porcellanidae) and *Pinnixa chaetopterana* (Decapoda: Brachyura: Pinnotheridae), two crab commensals in tubes of the polychaete worm *Chaetopterus* sp., in the northern Gulf of Mexico. Crustacean Research 6: 23–31. https://doi.org/10.18353/crustacea.Special2006.6_23

Sankolli KN (1963) On a new species of porcellanid crab (Decapoda, Anomura) from India. Journal of the Marine Biological Association of India 5: 280–283.

Smith JLB (1955) The fishes of the family Carapidae in the Western Indian Ocean. Annals and Magazine of Natural History 12: 401–416. https://doi.org/10.1080/00222935508656068

Southwell T (1909) Report on the Anomura collected by Mr. James Hornell at Okhamandal in Kattiawar in 1905-6. Okhamandal Marine Zoology Report, 105–123.

Stimpson W (1858) Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VII, Crustacea Anomura. Proceedings of the Academy of Natural Sciences of Philadelphia 10: 225–252.

Stimpson W (1860) Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VIII, Crustacea Macrura. Proceedings of the Academy of Natural Sciences of Philadelphia 12: 22–47.

Walker AO (1887) Notes on a collection of Crustacea from Singapore. Journal of the Linnean Society of London (Zoology) 20: 107–117. https://doi.org/10.1111/j.1096-3642.1887.tb01440.x

Werding B (2001) Description of two new species of *Polyonyx* Stimpson, 1858 from the Indo-West Pacific, with a key to the species of the *Polyonyx siensis* group (Crustacea: Decapoda: Porcellanidae). Proceedings of the Biological Society of Washington 114: 109–119.

Williams AB (1984) Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press. Washington, DC, 550 pp.

Zehntner L (1894) Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais. Crustacés de l'Archipel Malais. Revue Suisse de Zoologie et Annales du Musée d'Histoire Naturelle de Genève 2: 135–214.

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Gonatopus jaliscanus sp. n., a new Pincer wasp from Jalisco, Mexico (Hymenoptera, Dryinidae)

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Abstract

A new species of *Gonatopus* Ljungh, 1810, *G. jaliscanus* **sp. n.**, from Jalisco, Mexico, is described and illustrated. In the Neotropical region, *G. jaliscanus* is similar to *G. forestalis* Olmi, 1998, but it is distinguished by the black mesosoma (except prothorax, mesoscutum, and mesoscutellum that are yellow), and the metapostnotum being granulated and not rugose; in *G. forestalis* the mesosoma is completely black and the metapostnotum is granulated and strongly rugose. In the Nearctic region, the new species is morphologically similar to *G. curriei* Krombein, 1962, but it is distinguished by the dull and granulated metapostonotum; in *G. curriei* the metapostnotum is shiny and unsculptured. The new species belongs to *Gonatopus* group 7. The keys to the females of the Nearctic and Neotropical species of this group are modified to include the new taxon.

Keywords

Chrysidoidea, Gonatopodinae, keys, taxonomy

Introduction

Dryinidae (Hymenoptera: Chrysidoidea) are parasitoids and often also predators of leafhoppers, planthoppers and treehoppers (Hemiptera, Auchenorrhyncha) (Guglielmino et al. 2013). They comprise 16 subfamilies, 50 genera and more than 1800 species worldwide (Olmi and Xu 2015, Tribull 2015).

Jalisco is a state of Mexico situated in a transition area between the Nearctic and Neotropical regions. Species of Dryinidae collected in this state can belong to either region, so for the identification, researchers have to check the keys of both zoogeographical regions. Dryinidae of the Nearctic and Neotropical regions were studied mainly respectively by Olmi (1984) and Olmi and Virla (2014).

In the Nearctic and Neotropical regions respectively, the genus *Gonatopus* Ljungh, includes 51 (Olmi 1984, 1987, 1992, 1993, 1995, 2003, 2010, Olmi and Guglielmino 2013) and 127 species (Martins and Domahovski 2017a, b, Martins et al. 2015a, b, Martins and Krinski 2016, Olmi and Guglielmino 2016, Olmi and Virla 2014). For its part, Mexico is inhabited by 135 species of Dryinidae and 25 of *Gonatopus* (Moya-Raygoza and Olmi 2010, Becerra-Chiron et al. 2017). In 2017 the authors examined a species of *Gonatopus* collected in Jalisco, Mexico, which is described as new below.

Materials and methods

The description follows the terminology used by Guglielmino et al. (2016, 2018a, b) and Olmi and Virla (2014). The measurements reported are relative, except for the total length (head to abdominal tip, without the antennae), which is expressed in millimetres. In the descriptions POL is the distance between the inner edges of the lateral ocelli; OL is the distance between the inner edges of a lateral ocellus and the median ocellus; OOL is the distance from the outer edge of a lateral ocellus to the compound eye.

The term "metapectal-propodeal complex" is here used in the sense of Kawada et al. (2015). It corresponds to the term "metathorax + propodeum" sensu Olmi (1984) and Olmi and Virla (2014). In apterous Gonatopodinae the terms "anterior surface of metathorax + propodeum" and "posterior surface of metathorax + propodeum", sensu Olmi (1984, 1994), Olmi and Virla (2014), Olmi and Xu (2015) and Xu et al. (2013), correspond here respectively to "metapostonotum" and "first abdominal tergum", sensu Kawada et al. (2015).

The types of all Nearctic and Neotropical species of *Gonatopus* were examined. The material studied in this paper will be deposited in the National Museum of Natural History, Washington, DC, USA (**USNM**).

The description of the new species is based on the study of only a single specimen. The authors are aware that descriptions of new taxa should normally be based on more individuals. However, Dryinidae are so rare that it is uncommon to collect more than one specimen of each species. In addition, on the basis of the experience and knowledge of the authors, the new species is sufficiently delimited by unique characters to justify its description.

Results

Genus *Gonatopus* Ljungh, 1810

Gonatopus Ljungh, 1810: 161. Type species: *Gonatopus formicarius* Ljungh, 1810, by monotypy.

Diagnosis of the genus. Female: Apterous or less frequently macropterous; palpal formula 3/2, 4/2, 4/3, 5/2, 5/3, or 6/3; pronotum crossed or not by transverse furrow; enlarged claw with distal apex pointed and with one large or small subapical tooth (occasionally subapical tooth absent, then enlarged claw with distal group of lamellae); in fully winged forms, segment 5 of protarsus with more than 20 lamellae; tibial spurs 1/0/1. Male: Macropterous; occipital carina absent or incomplete (in this last case, present behind and shortly on sides of posterior ocelli); occiput concave; temple present; palpal formula 3/2, 4/2, 4/3, 5/2, 5/3, or 6/3; tibial spurs 1/1/2.

Gonatopus jaliscanus sp. n.

http://zoobank.org/FEDDFE9E-CD12-4AB7-BC5E-7393473EA1A0
Figs 1, 2

Diagnosis. Female apterous, with mesosoma black, except prothorax, mesoscutum and mesoscutellum yellow; palpal formula 6/3; pronotum crossed by strong transverse furrow (Fig. 1B); stalk between pronotum and metapectal-propodeal complex about as long as disc of pronotum; mesoscutum laterally with two pointed apophyses (Fig. 1A); meso-metapleural suture obsolete; mesopleuron and metapleuron granulated, not transversely striate; metapostnotum granulated; first abdominal tergum transversely striate; protarsomere 1 shorter than 4; enlarged claw with one small subapical tooth (Fig. 2).

Description. Female. Apterous (Fig. 1). Length 3.4 mm. Head, prothorax, mesoscutum, mesoscutellum, metasoma and legs testaceous. Antenna testaceous, except antennomeres 8–10 brown. Metanotum, metapectal-propodeal complex, mesopleuron, metapleuron and petiole black. Antenna clavate. Antennomeres in following proportions: 8:6:21:12:10:8:7:5:5:6. Head excavated, shiny, very weakly granulated. Frontal line complete. Occipital carina absent. POL = 2; OL = 2; OOL = 8. Greatest breadth of lateral ocelli shorter than POL (1:2). Palpal formula 6/3. Pronotum shiny, unsculptured, crossed by strong transverse furrow (Fig. 1B). Mesoscutum laterally with two pointed apophyses (Fig. 1A). Metanotum inclined, not transversely striate, not hollow behind mesoscutellum (Fig. 1B). Metapectal-propodeal complex with metapostnotum dull, granulated. First abdominal tergum granulated and transversely striated. Mesopleuron and metapleuron dull, granulated, not transversely striated. Meso-metapleural suture obsolete. Protarsomeres in following proportions: 13:3:5:20:30. Protarsomeres 2 and 3 produced into hooks. Enlarged claw (Fig. 2) with one small subapical tooth and eleven peg-like hairs, in addition to one bristle. Protarsomere 5 (Fig. 2) with two rows of 16 + 5 lamellae extending beyond 0.5 length of protarsomere and distal apex provided with about 17 lamellae. Tibial spurs 1/0/1.

Male. Unknown.

Material examined. Holotype: female, MEXICO: Jalisco, 8.3 mi. S Autlan, Hwy 80, 5000’, 8/vii/1984, on Oaks, Oak Forest, JB Woolley (TAMU (to be deposited in USNM)).

Hosts. Unknown.

Distribution. Mexico (Jalisco).

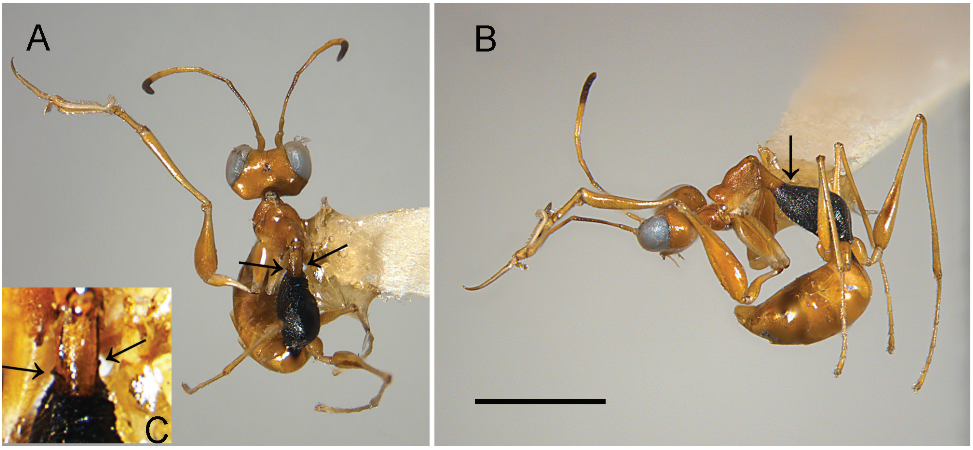

Figure 1. *Gonatopus jaliscanus* sp. n., female holotype: **A** habitus in dorsal view **B** habitus in lateral view **C** magnification of mesoscutum. Arrows indicate lateral apophyses of mesoscutum (**A, C**), and metanotum (**B**). Scale bars: 1.4 mm (**A, B**); 0.6 mm (**C**).

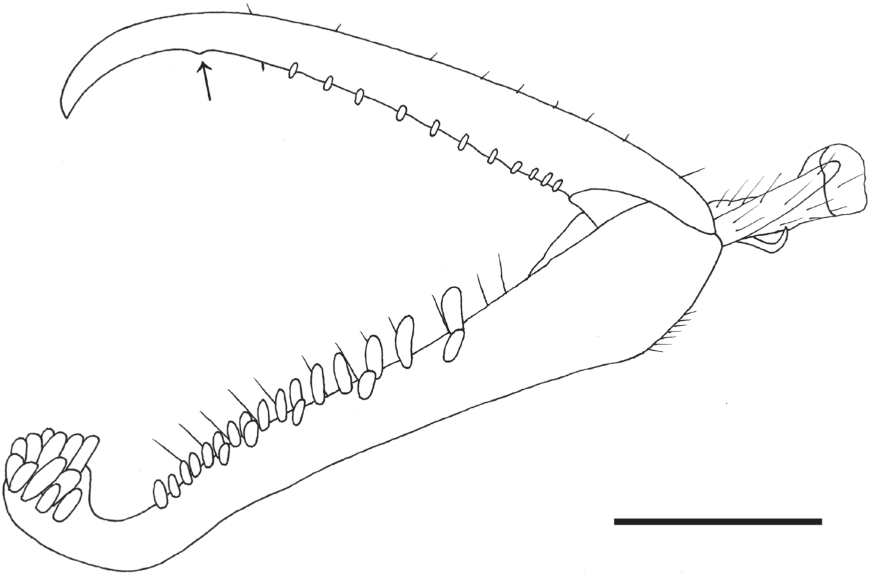

Figure 2. *Gonatopus jaliscanus* sp. n., female holotype: chela. Arrow indicates the enlarged claw subapical tooth. Scale bar 0.19 mm.

Etymology. The species is named after the state of Jalisco, where the holotype was collected.

Remarks. The female of the new species is apterous, with pronotum crossed by a strong transverse furrow (Fig. 1B), the enlarged claw provided of one small subapical tooth (Fig. 2) and the palpal formula 6/3. Because of these characters, *G. jaliscanus* belongs to group 7 of *Gonatopus*, according to the systematics proposed by Olmi and Virla (2014). In this species, the head is excavated, the labial palpus is 3-segmented, the mesoscutum has two lateral pointed apophyses situated in the stalk between pronotum and metapectal-propodeal complex (Fig. 1A), the metanotum is sloping anteriorly (Fig. 1B), the meso-metapleural suture is obsolete, the first abdominal tergum is completely transversely striate, the protarsomere 1 is shorter than protarsomere 4 (Fig. 1A). In the Nearctic region, there is only one species of *Gonatopus* group 7 with the above characters: *G. curriei* Krombein, 1962. The new species can be included in the key to the females of the Nearctic species of *Gonatopus* group 7 presented by Olmi (1984) by replacing couplet 30 as follows:

30 Protarsomere 4 slightly shorter than 1........................***G. argyrias* (Perkins)**
– Protarsomere 4 longer than 1 ....**30’**
30’ Metapostnotum shiny, unsculptured.......................... ***G. curriei* Krombein**
– Metapostnotum dull, granulated.................................... ***G. jaliscanus* sp. n.**

In the Neotropical region, *G. jaliscanus* is similar to *G. forestalis* Olmi, 1998. The new species can be included in the key to the females of the Neotropical species of *Gonatopus* group 7 presented by Olmi and Virla (2014) by replacing couplet 51 as follows:

51 Mesoscutum laterally with two strong pointed apophyses (Fig. 1A) ....**51’**
– Mesoscutum laterally without pointed apophyses **52**
51’ Mesosoma totally black; metapostnotum granulated and strongly rugose...... .... ***G. forestalis* Olmi**
– Mesosoma black, except yellow prothorax, mesoscutum and mesoscutellum (Fig. 1); metapostnotum granulated but not rugose....... ***G. jaliscanus* sp. n.**

Conclusions

Species of *Gonatopus* from Mexico are known mainly through the monographs on Dryinidae of the Nearctic (Olmi 1984) and Neotropical regions (Olmi and Virla 2014), the checklist of Moya-Raygoza and Olmi (2010) and the paper of Becerra-Chiron et al. (2017) totalling 25 species of *Gonatopus* from the country. Following the above description of *G. jaliscanus*, the *Gonatopus* species known from Mexico now number 26.

In Brazil, there are 31 described *Gonatopus* species (Olmi and Virla 2014, Martins et al. 2015a, b, Martins and Krinski 2016, Martins and Domahovski 2017a, b); in Costa Rica 22 (Olmi and Virla 2014); and in Argentina 47 (Olmi and Virla 2014). The higher numbers of *Gonatopus* species from Brazil and Argentina suggest that the true number of species in Mexico will ultimately be much higher. Further research, also on the hosts, will be needed to better characterise this fauna. In fact, hosts are known only for 12 of the 26 *Gonatopus* species recorded from Mexico (Becerra-Chiron et al. 2017, Guglielmino et al. 2013): another gap to be bridged, in spite of the contributions of Prof Moya-Raygoza and his research group (Moya-Raygoza and Olmi 2010, Becerra-Chiron et al. 2017). Among these 12 hosts, leafhopper pests of maize in the Neotropical region are economically important (Guglielmino et al. 2006).

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References

Becerra-Chiron IM, Moya-Raygoza G, Muñoz-Urias A (2017) Host-Dryinidae (Hymenoptera) interactions on edge grasses of maize agroecosystem throughout winter in Mexico. Journal of Hymenoptera Research 57: 155–166. https://doi.org/10.3897/jhr.57.12990

Guglielmino A, Bückle C, Moya-Raygoza G (2006) Description of the larval instars of *Gonatopus bartletti* Olmi, 1984 (Hymenoptera: Dryinidae). Zootaxa 1226: 51–60.

Guglielmino A, Olmi M, Bückle C (2013) An updated host-parasite catalogue of world Dryinidae (Hymenoptera: Chrysidoidea). Zootaxa 3740: 1–113. https://doi.org/10.11646/zootaxa.3740.1.1

Guglielmino A, Olmi M, Marletta A, Speranza S (2018a) A new species of the genus *Gonatopus* Ljungh from the USA (Hymenoptera, Dryinidae). ZooKeys 747: 63–69. https://doi.org/10.3897/zookeys.747.24399

Guglielmino A, Olmi M, Speranza S (2016) Description of *Gonatopus sandovalae* (Hymenoptera Dryinidae), a New Species from Ecuador. Florida Entomologist 99:437–439. https://doi.org/10.1653/024.099.0314

Guglielmino A, Olmi M, Speranza S (2018b) Description of *Gonatopus xui* sp. n. from India (Hymenoptera Dryinidae). Redia 101: 31–33. https://doi.org/10.19263/REDIA-101.18.05

Kawada R, Lanes GO, Azevedo CO (2015) Evolution of metapostnotum in flat wasps (Hymenoptera, Bethylidae): implications for homology assessments in Chrysidoidea. PLoS ONE 10(10): e0140051. https://doi.org/10.1371/journal.pone.0140051.

Ljungh SJ (1810) *Gonatopus*, novum insectorum genus. Beiträge zur Naturkunde 2: 161–163.

Krombein KV (1962) Natural History of Plummers Island, Maryland, XIII. Descriptions of new wasps from Plummers Island, Maryland (Hymenoptera: Aculeata). Proceedings of the Biological Society of Washington 75: 1–18.

Martins AL, Domahovski AC (2017a) New record of *Gonatopus flavoniger* Olmi, 1991 (Hymenoptera: Dryinidae), from Paraná, Brazil, with notes on some aspects of its biology and morphology. Check List 13: 95–99. https://doi.org/10.15560/13.4.95

Martins AL, Domahovski AC (2017b) Redescription and biology of *Gonatopus amazonicus* Olmi (Hymenoptera, Dryinidae) from Southern Brazil. Zootaxa 4324: 592–596. https://doi.org/10.11646/zootaxa.4324.3.12

Martins AL, Krinski D (2016) First record of the parasitoid *Gonatopus flavipes* Olmi, 1984 (Hymenoptera, Dryinidae) in Brazil's Amazon forest. Journal of Hymenoptera Research 50: 191–196. https://doi.org/10.3897/JHR.50.8897

Martins AL, Lara RIR, Perioto NW (2015a) New records of Dryinidae (Hymenoptera: Chrysidoidea) from the Atlantic Rainforest of São Paulo, Brazil. Pan-Pacific Entomologist 91: 196–199. https://doi.org/10.3956/2015-91.2.196

Martins AL, Lara RIR, Perioto NW, Olmi M (2015b) Two new species of Dryinidae (Hymenoptera: Chrysidoidea) from areas of Atlantic Rainforest at São Paulo State, Brazil. Brazilian Journal of Biology 75: 455–459. https://doi.org/10.1590/1519-6984.19613

Moya-Raygoza G, Olmi M (2010) A catalogue of Dryinidae of Mexico, with descriptions of the opposite sexes of some species (Hymenoptera Chrysidoidea). Frustula entomologica (2008)(NS) 31: 77–112.

Olmi M (1984) A revision of the Dryinidae (Hymenoptera). Memoirs of the American Entomological Institute 37: 1–12, 1–1913.

Olmi M (1987) New species of Dryinidae (Hymenoptera, Chrysidoidea). Fragmenta Entomologica 19: 371–456.

Olmi M (1992) Contribution to the knowledge of the Gonatopodinae (Hymenoptera Dryinidae). Bollettino dell'Istituto di Entomologia dell'Università di Bologna 46: 109–122.

Olmi M (1993) A new generic classification for Thaumatodryininae, Dryininae and Gonatopodinae, with descriptions of new species (Hymenoptera Dryinidae). Bollettino di Zoologia Agraria e Bachicoltura (Ser. II) 25: 57–89.

Olmi M (1994) The Dryinidae and Embolemidae (Hymenoptera: Chrysidoidea) of Fennoscandia and Denmark (Fauna Entomologica Scandinavica 30). EJ Brill, Leiden, Netherlands, 100 pp.

Olmi M (1995) Contribution to the knowledge of the world Dryinidae (Hymenoptera Chrysidoidea). Phytophaga 6: 3–54.

Olmi M (1998) New Embolemidae and Dryinidae (Hymenoptera Chrysidoidea). Frustula entomologica [1997](NS) 20: 30–118.

Olmi M (2003) A contribution to the knowledge of Dryinidae (Hymenoptera Chrysidoidea). Frustula entomologica [2001](NS) 24: 21–49.

Olmi M (2010) A contribution to the knowledge of Dryinidae from the Oriental, Nearctic, Neotropical and Australian regions (Hymenoptera Chrysidoidea). Frustula entomologica [2008](NS) 31: 11–34.

Olmi M, Guglielmino A (2013) Description of *Gonatopus rileyi* sp. nov. from Arkansas (Hymenoptera: Dryinidae). Pan-Pacific Entomologist 89: 79–83. https://doi.org/10.3956/2012-60.1

Olmi M, Guglielmino A (2016) Two new species of *Gonatopus* Ljungh from Ecuador (Hymenoptera: Dryinidae). Euroasian Entomological Journal 15(Suppl. 1): 108–112.

Olmi M, Virla EG (2014) Dryinidae of the Neotropical Region (Hymenoptera: Chrysidoidea). Zootaxa 3792: 1–534. https://doi.org/10.11646/zootaxa.3792.2.1

Olmi M, Xu Z (2015) Dryinidae of the Eastern Palaearctic region (Hymenoptera: Chrysidoidea). Zootaxa 3996: 1–253. https://doi.org/10.11646/zootaxa.3996.1.1

Tribull CM (2015) Phylogenetic relationships among the subfamilies of Dryinidae (Hymenoptera, Chrysidoidea) as reconstructed by molecular sequencing. Journal of Hymenoptera Research 45: 15–29. https://doi.org/10.3897/JHR.45.5010

Xu Z, Olmi M, He J (2013) Dryinidae of the Oriental region (Hymenoptera: Chrysidoidea). Zootaxa 3614: 1–460. https://doi.org/10.11646/zootaxa.3614.1.1

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RESEARCH ARTICLE

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A revision of *Lachnodius* Maskell (Hemiptera, Coccomorpha, Eriococcidae)

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Abstract

Lachnodius Maskell is a genus of three named species that are part of an Australian radiation of felt scale insects that induce galls on *Eucalyptus* and *Corymbia* (Myrtaceae). A female's gall usually consists of an open-top pit in swollen plant tissue. Depending on the species, galls can occur on a host's leaves, buds, stems, or trunk. Here, we redescribe the named species: *L. eucalypti* (Maskell), *L. hirsutus* (Froggatt) and *L. lectularius* (Maskell), and describe seven new species: *L. brimblecombei* Beardsley, Gullan & Hardy, **sp. n.**, *L. froggatti* Beardsley, Gullan & Hardy, **sp. n.**, *L. maculosus* Beardsley, Gullan & Hardy, **sp. n.**, *L. melliodorae* Beardsley, Gullan & Hardy, **sp. n.**, *L. newi* Beardsley, Gullan & Hardy, **sp. n.**, *L. parathrix* Beardsley, Gullan & Hardy, **sp. n.**, *L. sealakeensis* Gullan & Hardy, **sp. n.** Descriptions are based primarily on adult females, but for some species short diagnoses of nymphal stages also are provided. The taxonomic history of *Lachnodius* is reviewed, with notes on their biology and ecology. A key to species based on the morphology of adult females is provided, and lectotypes are designated for *Dactylopius eucalypti* Maskell and *Lachnodius lectularius* Maskell.

Keywords

Australian endemics, gall-inducer, taxonomy

Introduction

In Australia, species of *Eucalyptus* and the closely related genus *Corymbia* are host to many species of gall-inducing felt scale insects (Gullan et al. 2005; García Morales et al. 2016). Most belong to one of two major radiations: the genus *Apiomorpha* Rübsaamen and a distantly related clade of Myrtaceae-feeding species (Cook and Gullan 2004). *Lachnodius* Maskell is one of at least eight genera belonging to the latter clade. Our aim here is to revise *Lachnodius*, with re-descriptions of the three currently recognized species and descriptions of seven new species.

Taxonomic history and phylogenetic relationships of *Lachnodius*

Maskell (1896) erected the genus *Lachnodius* for *Dactylopius eucalypti* Maskell, which he had described in 1892, and two other species, *L. hirtus* Maskell and *L. lectularius* Maskell, which he described as new. Fernald (1903) designated *L. eucalypti* as the type species. Beardsley (1982) synonymized the monotypic genus *Pseudopsylla* Froggatt with *Lachnodius* after study of the type specimens of the type species *P. hirsutus* Froggatt. This brought the number of described species of *Lachnodius* to four. Hardy et al. (2011) then transferred *L. hirtus* to their genus *Lobimargo* Hardy & Gullan, and the tally of *Lachnodius* species went back to three. Adult females of *Lachnodius* can be distinguished from other genera of felt scales found on *Eucalyptus* based on the morphological features in the keys of Hardy and Gullan (2007) or Hardy et al. (2011).

In Maskell's brief definition of *Lachnodius*, he did not speculate on how it was related to other scale insects. Fernald (1903) placed *Lachnodius* in her Dactylopiinae, which included the presently recognized families Asterolecaniidae, Eriococcidae, Kermesidae and Pseudococcidae. Froggatt (1921) and Morrison and Morrison (1922) followed the classification of Fernald. The Morrisons also proposed a close relationship between *Lachnodius* and *Sphaerococcopsis* Cockerell. Ferris (1955) was puzzled by *Lachnodius*; he considered erecting an entirely new family for it, before opting to place it awkwardly in Pseudococcidae. Incidentally, the form that Ferris illustrated under the name *Lachnodius eucalypti* is certainly not that species, but may be *L. lectularius*. Hoy (1963) assigned both *Lachnodius* and *Sphaerococcopsis* to the Eriococcidae, a family to which he applied broad limits. Beardsley was of the opinion that *Lachnodius* and *Sphaerococcopsis* could not be placed easily into either Eriococcidae or Pseudococcidae (Beardsley 1972, 1974). He agreed with Ferris, that these genera constituted a previously unrecognized family-level taxon, but one that was more closely related to the Eriococcidae than the Pseudococcidae. Koteja (1974) followed suite, and held *Lachnodius* to be a distinct family-level taxon, tentatively placed in his asterolecaniid group of families, on the basis of comparative studies of the labium, salivary pump and clypeolabral shield of adult females. In sum, the phylogenetic relationships of *Lachnodius* and *Sphaerococcopsis* were an enigma.

In the first scale insect phylogeny inferred from DNA sequence data, Cook et al. (2002) found support for a monophyletic group comprised of an unidentified *Lachnodius* species, *Tanyscelis mammularis* (Froggatt) and *Ascelis praemollis* Schrader (both of the latter being members of Eriococcidae in its current form); all three species induce galls on myrtaceous hosts. Then, in a more comprehensive estimate of the phylogeny of eriococcids, Cook and Gullan (2004) found these same three taxa inside a clade of Myrtaceae-feeding species that formed part of a larger clade of species from the Southern Hemisphere. They also found that the Eriococcidae is not monophyletic, as per previous suggestions based on morphological studies (Cox and Williams 1987; Hodgson 2002). The classification of scale insects has yet to be reconciled with this finding, but the most likely resolution will entail the recognition of the Myrtaceae-feeding (MF) clade of Cook and Gullan (2004) as a formal family-level taxon. This group would include many other mostly gall-inducing genera in addition to *Lachnodius* and *Sphaerococopsis*. Thus, it seems that Ferris, Beardsley, and Koteja were correct: *Lachnodius* and *Sphaerococcopsis* are not a natural fit in any of the existing scale insect families.

Undescribed species diversity of Myrtaceae-feeding clade

The MF clade is species rich and divided into subradiations, each of which is largely restricted to a subclade of Myrtaceae (Cook and Gullan 2004; Gullan et al. 2005). The species diversity of radiations on *Leptospermum* and *Melaleuca* is almost entirely undescribed (LG Cook pers. comm.). More progress has been made in documenting the species that feed on *Eucalyptus* and *Corymbia*. In fact, over the last decade we (e.g., Hardy and Gullan 2007, 2010; Hardy et al. 2011; Semple et al. 2015) have approached complete coverage of the known diversity (which, of course, says nothing about the unknown diversity). Here, we make another step in that direction by describing seven new species and redescribing the three already named species of *Lachnodius*.

Materials and methods

Adult females and immature specimens from recent collections and from dry museum material were slide-mounted in Canada balsam, mainly using a method similar to that described in Gullan (1984b). The morphological terms mainly follow Williams (1985), Miller and McKenzie (1967) and Hardy and Gullan (2007). The adult females of a few species have tiny dorsal sclerotic pits or depressions that are referred to herein as urns or varioles, depending on their shape. Measurements were made using an ocular micrometer attached to a compound microscope. All are given as a range and based on maximum dimensions (e.g., the body width of a slide mounted specimen was measured across the widest transverse section, the location of which varies among specimens, and leg segment lengths were measured along the longest axis). Tarsal length excludes the claw. Spiracle length includes the muscle plate (apodeme). Setal lengths exclude the setal base. All illustrations of the insects were prepared by NBH and photographs of the live insects and galls were taken by PJG.

Depositories are abbreviated as follows:

ANIC	Australian National Insect Collection, CSIRO, Canberra, ACT, Australia;
ASCU	Agricultural Scientific Collections Unit, New South Wales Department of Primary Industries, Orange Agricultural Institute, Orange, New South Wales, Australia;
NHMUK	The Natural History Museum, London;
BPBM	Bernice P Bishop Museum, Honolulu, Hawaii, USA;
NMV	Museum of Victoria, Melbourne, Australia;
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand;
QDPC	Department of Primary Industries Insect Collection, Brisbane, Queensland, Australia;
QM	Queensland Museum, Brisbane, Queensland, Australia;
WAM	Western Australian Museum, Perth, Western Australia, Australia;
USNM	the United States National Collection of Coccoidea of the National Museum of Natural History, Smithsonian Institution, housed at the United States Department of Agriculture, Beltsville, Maryland, USA.

The NZAC houses original slides and dry material of species described by WM Maskell and follows the principle that primary type material should reside in the country of origin of the species, if suitable repositories exist (Deitz and Tocker 1980); thus when lectotypes are designated for Maskell specimens collected in Australia, these specimens can be deposited in the ANIC, as we do here.

Beardsley examined Maskell material at NZAC in 1972 and borrowed and slide-mounted specimens from the pill boxes containing Maskell dry material of *Lachnodius*; unfortunately, the original boxes that Beardsley borrowed appear to have been lost after his death as they were not returned to NZAC (RC Henderson, pers. comm.). The late Helen Brookes (formerly at the Waite Agricultural Research Institute, University of Adelaide, South Australia) acquired and curated a large collection of Coccoidea (including *Lachnodius*) during her career and, following her retirement in 1982, deposited this collection and associated notes and photographs in the Australian National Insect Collection (Upton 1997; Taylor and Keller 2008); she also recorded biological and other information on cards (Gullan and Williams 2010) filed by a Specimen Index Number that consisted of a number for the collection and an abbreviation of the year, for example, 31/67 was her 31st collection for 1967. We have included some of her information on the biology and appearance of *Lachnodius*. Some slide-mounted specimens are DNA vouchers of LG Cook and/or NBH and have voucher codes (e.g., LGC01374, NH150); all are deposited in ANIC. Collector and author names are abbreviated as follows: JWB, JW Beardsley; HMB, HM Brookes, NBH, NB Hardy; PJG, PJ Gullan.

The International Commission on Zoological Nomenclature (1999) requires lectotypes designated after 1999 to "contain an express statement of deliberate designation" (amended Article 74.7.3). We use the statement "here designated" to fulfil this requirement. We have registered each of the new names published in this paper with the Official Registry of Zoological Nomenclature (ZooBank) and cite the Life Science Identifiers (LSIDs) after the heading for each new name. Each LSID is a globally unique identifier for the nomenclatural act of naming a new taxon.

JWB is the coauthor of six new names for *Lachnodius* because he recognized these species in his unpublished work. We provide a short synopsis of his work in the Discussion. A large portion of this study was based upon JWB's collection, which is housed in the BPBM. The BPBM has allowed the holotype of any new Australian species from the JWB collection to be deposited in the ANIC (in correspondence of PJG in 1996).

Notes on parasitoids and the effects of parasitization

Slide-mounted adult female and second-instar specimens of *Lachnodius* frequently show evidence of attack by internal parasitoids. We have noted the chorion of parasitoid eggs and developing parasitoid larvae, sometimes evident only by their mandibles. In the field, JWB occasionally found obviously parasitized adult females of both *L. eucalypti* and *L. lectularius* within their galls on host trees. As the parasitoids matured, the parasitized host became a hard, brown husk from which the adult wasps eventually emerged. Several parasitoids can develop in one host, with as many as 20 adults emerging from a single adult female of *L. lectularius*. JWB determined that the wasps were a kind of Encyrtidae, possibly species of *Metaphycus* or related genera. There are no previously published records of parasitoids attacking *Lachnodius*.

It appears that parasitization affects the development of structures in the host's integument, in particular the macrotubular ducts, making identification of parasitized specimens potentially problematic. Compared to unparasitized individuals, parasitized female specimens identified as *L. lectularius* often have fewer or smaller macrotubular ducts. Normally, the dorsal macrotubular ducts are numerous and large (ca. 6–8 µm rim diameter). In some parasitized specimens the ducts are few, whereas in others they are abundant but small (ca. 2–3 µm in diameter and without well-defined rims).

Taxonomy

Lachnodius Maskell, 1896

Lachnodius Maskell, 1896: 400. Type species: *Dactylopius eucalypti* Maskell. Subsequently designated by Fernald 1903.

Pseudopsylla: Froggatt 1921: 6. Type species: *Pseudopsylla hirsutus* Froggatt, by monotypy and original designation. Synonymy by Beardsley 1982: 31.

Biological notes. The females of all species of *Lachnodius* induce galls of varying complexity on the leaves, buds, stems, or main trunk of species of *Eucalyptus* or *Corymbia* (Myrtaceae) (Figs 1, 2). Galls consist of a pit in swollen plant tissue with insect's

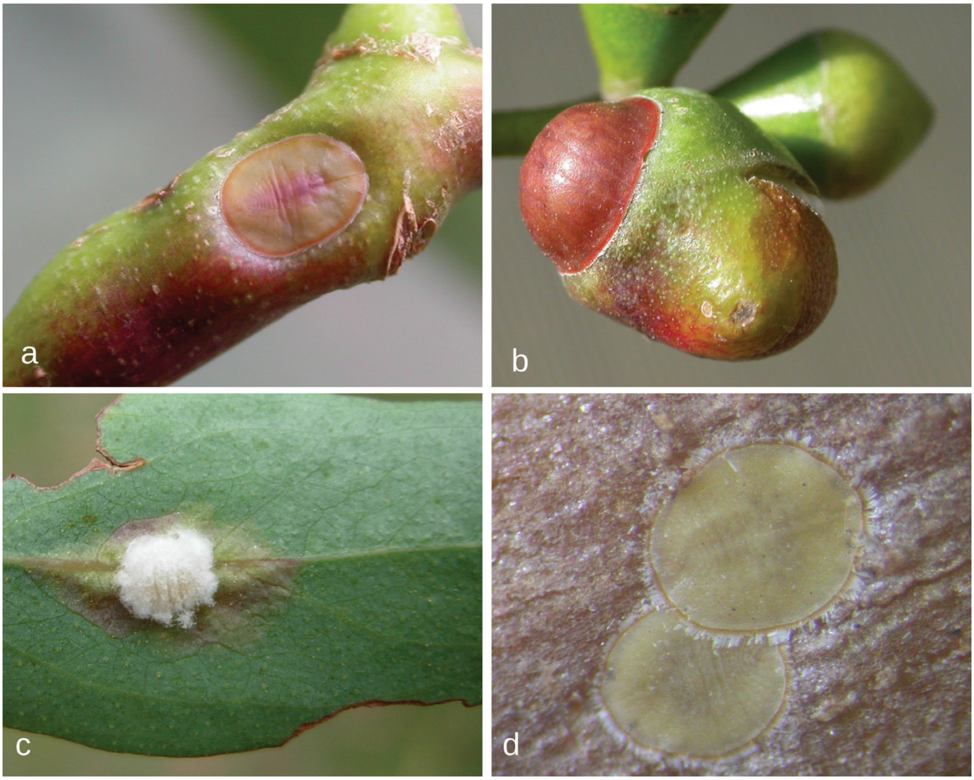

Figure 1. Species of *Lachnodius* in life: **a** gall of *L. brimblecombei* on stem of *Eucalyptus baxteri*, Grampians, Victoria **b** leaf discoloration surrounding pit galls induced by *L. eucalypti* on *E. blakelyi*, near Forbes, New South Wales **c** mature adult females and ovisacs of *L. eucalypti* on trunk of *E. mannifera*, Canberra, A.C.T. **d** adult female of *L. froggatti* in pit gall on leaf of *E. baueriana*, near Narooma, N.S.W. **e** same female of *L. froggatti* removed from its pit gall **f** gall of *L. hirtus* on *Corymbia nesophila*, Gunn Point, Northern Territory.

dorsum either exposed or partially concealed. Females remain in their gall after their imaginal molt, and then at maturity, depending on species, either desert their gall and move elsewhere for oviposition, or remain in their gall for reproduction. Males, in the few species for which they are known, induce galls as first-instar nymphs but then, near the end of their second instar, vacate the gall and move to another site to form cocoons in which they complete their development.

Diagnosis of adult females of the genus *Lachnodius*. Body outline circular to oval. In most species eyes on margin (on venter in *L. froggatti*, and absent in *L. sealakeensis*). Antennae six to seven-segmented. Pair of broad, blister-like frontal lobes between antennae; a series of elongate setae along posterior margin of lobes. Tentorial box usually with anterior aliform extensions. Labium either one-segmented, or composed of two fused segments; proximal segment indicated by a pair of setae on ventral surface; distal segment with one pair of ventral seta, one pair of fleshy apical setae, and one pair of dorsal setae. Legs well developed. Anus ventral, with sclerotic rim having fewer

Figure 2. Species of *Lachnodius* in life. **a** adult female of *L. lectularius* in pit gall on stem of *Eucalyptus viminalis*, Cranbourne, Victoria **b** adult female of *L. lectularius* in pit gall on bud of *E. viminalis*, Tyabb, Victoria **c** adult female of *L. parathrix* in pit gall on mid-vein of *E. elata*, near Narooma, New South Wales **d** two adult females of *L. sealakeensis* in pits on trunk of *E. ?oleosa*, near Sea Lake, Victoria.

than ten setae (except in *L. hirsutus*), base of each seta surrounded by ring of minute pores. Anal lobes absent.

Dorsum. Setae short to minute, ≤ 10 µm long (except up to 25 µm long on *L. hirsutus*). Microtubular ducts and one or two size classes of macrotubular ducts present;

larger macrotubular ducts sometimes with one seta touching rim of dermal orifice; duct shaft of uniform width or constricted near vestibule; macrotubular ducts with vestibule weakly sclerotic and compressed, i.e., not cup-shaped. Derm membranous, sometimes with enlarged microtrichia, sometimes with concave sclerotic granules. Multilocular pores absent. Dorsum delimited by a marginal with fringe of setae, differentiated from other body setae, with shape flagellate, conical or sagittate; marginal fringe either complete around margin, or with break between thorax and abdomen, or with break between thorax and abdomen + break between meso- and metathorax.

Venter. Sometimes larger than dorsum. Setae flagellate, in transverse rows across each abdominal segment, scattered along submargin, in clusters anterior to each coxa. Microtubular ducts usually absent (*L. eucalypti* with scattered microtubular ducts on head); macrotubular ducts similar to those on dorsum. Quinquelocular pores dense around vulva, clusters around each spiracle, scattered along submargin and across each body segment.

Etymology. Although Maskell (1896) did not explicitly state the meaning of the genus name that he coined, his description included a statement that the female insects were either naked or covered in cottony or mealy or waxy secretion. The name *Lachnodius* thus must be derived from the masculine Greek noun *lachno*, meaning woolly hair or down.

Key to species of *Lachnodius* based on adult females

1 Anal ring set at base of sclerotic invagination **2**

– Anal ring flush with body surface, or if recessed not at base of sclerotic invagination **6**

2 Marginal setae fine, strongly recurved **3**

– Marginal setae stout, conical **4**

3 Dorsum beset with minute, urn-shaped sclerites; some dorsal macrotubular ducts with base of a seta touching rim of dermal orifice .... ***Lachnodius melliodorae* sp. n.**

– Dorsum beset with enlarged, sclerotic microtrichia; no dorsal macrotubular ducts with base of a seta touching rim of dermal orifice .... ***Lachnodius newi* sp n.**

4 Eyes absent; dorsum with small concave sclerites, each bearing a tubular duct .... ***Lachnodius sealakeensis* sp. n.**

– Eyes on margin; dorsum with or without small concave sclerites, if with, then each lacking a tubular duct **5**

5 Dorsum beset with minute, concave sclerites .... ***Lachnodius maculosus* sp. n.**

– Dorsum without minute, concave sclerites .... ***Lachnodius parathrix* sp. n.**

6 Eyes on ventral surface of head; some dorsal macrotubular ducts with base of a seta touching rim of dermal orifice .... ***Lachnodius froggatti* sp. n.**

– Eyes on margin; no dorsal macrotubular ducts with base of a seta touching rim of dermal orifice **7**

7 Marginal fringe of alternating sagittate and slender conical setae, both types of setae short (up to 20 μm long); labium one-segmented; microtubular ducts present on ventral surface of head .... ***Lachnodius eucalypti*** **(Maskell)**

– Marginal fringe setae conical, or flagellate, long (38–455 μm long); labium two-segmented, basal segment indicated by pair of setae on ventral surface; microtubular ducts absent from ventral surface of head **8**

8 Anal ring with ≤ 6 setae; quinquelocular pores absent from venter; antennae six-segmented; venter extremely hirsute ...... ***Lachnodius hirsutus*** **(Froggatt)**

– Anal ring with > 10 setae; quinquelocular pores present on venter; antennae seven-segmented; venter not extremely hirsute **9**

9 Venter with dense submarginal band of quinquelocular pores; marginal setae longer than anal ring setae .... ***Lachnodius brimblecombei*** **sp. n.**

– Venter without dense submarginal band of quinquelocular pores; marginal setae shorter than anal ring setae .... ***Lachnodius lectularius*** **Maskell**

Lachnodius brimblecombei **Beardsley, Gullan & Hardy, sp. n.**

http://zoobank.org/5A129F1F-3598-461D-9E50-50D4F8D3715D

Figs 1a, 3

Diagnosis. Gall of adult female covers portion of dorsum; adult female with marginal fringe of close-set setae, each longer than anal ring setae; one size class of dorsal macrotubular ducts.

Description. Adult female (n = 10). Body outline circular to oval; length 2.6–7.3 mm (4.9 mm for holotype), greatest width 2.3–4.9 mm (3.8 mm for holotype). Eyes 43–58 μm wide, on margin. Antennae seven-segmented; length 980–1380 μm; with 4–5 hair-like setae on segment I, 9–11 hair-like seta on segment II, 6–8 hair-like seta on segment III, 2–3 hair-like seta on segment IV, zero or one hair-like + one fleshy seta on segment V, two hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment VII. Frontal lobes 250–300 μm long, 65–165 μm wide. Tentorial box 375–510 μm long, 200–280 μm wide, with anterior extension of the dorsal arms. Labium two-segmented, 160–210 μm long, 170–215 μm wide. Spiracles 190–240 μm long, 140–215 μm wide across atrium. Legs increasing in size caudad, fore leg: trochanter + femur 710–1060 μm, tibia 590–900 μm, tarsus 225–320 μm; mid leg: trochanter + femur 770–1150 μm, tibia 610–900 μm, tarsus 240–325 μm; hind leg: trochanter + femur 810–1260 μm, tibia 650–1040 μm, tarsus 260–400 μm; claw 63–90 μm; fore coxa with 6–8 setae, mid and hind coxae each with 5–7 setae, trochanter with 6–8 setae, femur with 15–31 setae, tibia with 19–38 setae, tarsus with 10–16 setae; tarsal digitules 83–100 μm long, claw digitules 50–73 μm long; translucent pores on all segments of hind leg. Anal ring 80–108 μm wide, with 12–16 setae; ring setae 70–115 μm long. Pair of elongate caudal setae absent.

Dorsum. Derm membranous. Dorsal setae 8–10 μm long, each parallel-sided, with acute apex, scattered over dorsum. Macrotubular ducts with rim of dermal orifice 5 μm in

Figure 3. Adult female of *Lachnodius brimblecombei* sp. n.

diameter, duct shaft 8–10 µm long, scattered over dorsum. Microtubular ducts ca. 5 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of setae, each 70–118 µm long, ca. 200 setae in total on each side of body.

Venter. Larger than dorsum. Ventral setae 40–180 µm long; elongate setae medial of each coxa 150–225 µm long; longest setae on head 205–350 µm long. Macrotubular ducts similar to those on dorsum; in transverse band across each abdominal segment, scattered throughout submargin, medial of meso- and metacoxa. Quinquelocular pores 5 µm in diameter, found wherever setae occur, in transverse band across each segment, in a dense band along submargin, dense on posterior abdominal segments and around each spiracle.

Second-instar female (n = 9). Shape of slide-mounted specimen moderately elongate oval to broadly oval; length 1.9–3.0 mm, width 0.8–1.1 mm. Antennae six-segmented, short (230 µm total length), basally broad, becoming narrower toward apex, segment III ca. 60 µm wide. Legs short, broad, all segments present but tibiae and tarsi partially fused; tarsal claws incompletely developed. Anal ring ca. 30 µm wide, with ca. 10 setae, each of 25 µm maximum length. Dorsum with sparse, scattered setae, very small (mostly 4–5 µm long), acute or with blunt apices, and sparsely scattered, very small, tubular ducts ca. 2–3 µm in orifice diameter. Marginal fringe a moderately sparse series of 85–90 conical setae on each side of body, each seta ca. 35–50 µm long; antepenultimate seta of fringe on each side longer, ca. 80–90 µm long; fringe setae within a narrow marginal band of quinquelocular pores ca. 4–6 pores wide, extending around body; a small number of trilocular and quadrilocular pores scattered among quinquelocular pores. Venter with a few quinquelocular pores near each spiracle. Ventral setae flagellate, ranging from 10–65 µm long on thorax and abdomen, as long as 115 µm on head.

Second-instar male (n = 3). Shape of slide-mounted specimens moderately elongate-oval; length 1.2–1.5 mm. Antennae 7-segmented, ca. 280 µm long, slender, segment III 30–40 µm wide. Legs normal, slender, all segments present with tibiae 1.7–1.9 times length of tarsi; tarsal claws normally developed. Anal lobes narrowly separated by shallow anal cleft. Anal ring ca. 40 µm wide, with approximately 10 setae, 45 µm maximum length. Dorsum with derm finely spiculate. Dorsal setae sparse, scattered, short (ca. 4 µm long), acute, borne on papillae with narrow sclerotized rims. Dorsum with numerous (ca. 80) moderately large (ca. 8 µm rim and 6 µm orifice diameter) macrotubular ducts arranged in segmental rows. Marginal fringe of ca. 85 setae on each side, each seta moderately long (ca. 28–45 µm), conical with more or less filamentous apex; antepenultimate seta on each side much longer, to 105 µm; three most posterior setae on each side (including elongate antepenultimate) borne on a small, sclerotized anal lobe. Venter with a marginal line of quinquelocular pores just mesad of marginal fringe, around entire body, approximately as numerous as fringe setae; pores very sparsely scattered elsewhere on venter. Ventral tubular ducts absent. Ventral setae flagellate, ranging from 15–50 µm on thorax and abdomen, as long as ca. 125 µm on head.

Notes. The slide-mounted adult female of *L. brimblecombei* is most similar to that of *L. lectularius*. Each has a marginal fringe of close-set setae, and the dorsum densely beset with macrotubular ducts of a single type, none of which have a seta touching the dermal orifice. In life the two are easy to distinguish. The adult female of *L. brimble-*

combei induces a deep stem or bud gall with considerable swelling of the surrounding tissue that covers a portion of the female's dorsum (Fig. 1a). If the gall occurs on the stem, it causes the stem to bend (Fig. 1a), often sharply. The adult female of *L. lectularius* also induces a gall on the stem or bud of the host, but the gall does not cover any portion of the female's dorsum (Fig. 2a, b), and if on a stem does not make it crooked. Slide-mounted specimens of *L. brimblecombei* can be distinguished from those of *L. lectularius* by having (1) a dense marginal band of quinquelocular pores on the venter (absent in *L. lectularius*) and (2) the marginal setae longer than the anal ring setae (marginal setae shorter than anal ring setae in *L. lectularius*).

The habitat of the Victorian specimens of *L. brimblecombei*, which develop in galls formed on flower buds, is different from that of the type specimens from Queensland (with galls as in Fig. 2a). But we found no significant morphological differences among specimens from the different states, except for slightly smaller fringe setae and possibly fewer quinquelocular pores in the Victorian specimens. In case further study reveals that the Victoria specimens are different, we have restricted the type series to specimens collected by AR Brimblecombe in Queensland and three adult females from New South Wales, one of which is a DNA voucher.

At Wilson's Promontory in Victoria, galling caused by *L. brimblecombei* on *E. baxteri* reduces bud survival and flowering (Andersen 1989). Monitoring of tagged eucalypt shoots showed that, although less than 12% of buds were galled by *L. brimblecombei* (misidentified as *Opisthoscelis* sp.), the presence of galled buds often caused the abscission of nearby non-galled buds and galling on flowering stems often resulted in the loss of entire inflorescences, but these losses may be exacerbated by low water availability. On heavily galled shoots, the proportion of flowers producing mature fruit was correlated negatively with degree of galling, indicating that there was no compensatory increase in the success of the non-galled buds. Thus *L. brimblecombei* may decrease the fitness of its host, especially during periods of low rainfall.

A live adult female from Wild Cattle Creek State Forest in New South Wales was covered in white powdery wax and had a marginal fringe of white wax filaments ca. 0.2 mm long. Evidence of attack by parasitoid wasps was seen in several of the specimens studied. Two females from Redland Bay, Queensland, contained mandibles of parasitoid larvae, and the specimen from Mittagong, NSW also was parasitized.

We also examined one large (ca. 10 mm long) adult female that may be a developmentally abnormal specimen of *L. brimblecombei* or it might be a new species. It was collected from a stem pit on *E. fasciculosa* at Belair in South Australia (ANIC). It differs from typical adult females of *L. brimblecombei* in having reduced and distorted legs and antennae, many more dorsal fringe setae and in lacking the narrow marginal band of disc pores.

Etymology. Pioneering Australian coccidologist AR Brimblecombe recognized this species and used the manuscript name '*Lachnodius geniculatus*' to refer to it in his dissertation [citation of this name here is NOT intended to be for nomenclatural purposes; the name is not valid]. This species is named in Brimblecombe's honor. The species epithet is a noun in the genitive singular.

Material examined. ***Holotype***: **Queensland**: adult female, on slide: ex pit gall in young twig of *Eucalyptus micrantha*, Redland Bay, 2 Aug 1937, AR Brimblecombe, No. SC 147 (QM). ***Paratypes***: **Queensland**: 15 second-instar females (on three slides, including two on same slide as holotype), five second-instar males (on two slides with second-instar females): same data as holotype (QDPC, QM) [The slide of another adult female from the type series could not be located at QDPC.]; two adult females: *Eucalyptus* sp., Glasshouse Mts., Queensland, 20 Dec 1935, AR Brimblecombe (QDPC). **New South Wales**: one adult female: ex deep pocket gall in twig of *Eucalyptus* sp., Mittagong, 24 Nov 1899, WW Froggatt, #305 (ASCU); one adult female: ex stem depression, *Eucalyptus* sp., west side of Mt Jerrabomberra, 35.35S, 149.23E, 2 May 1993, LG Cook (ANIC); one adult female: ex stem gall, *Eucalyptus* sp. sapling, Wild Cattle Creek State Forest, above Platypus Flat, 30.18S, 152.70E, 11 Oct 1996, PJG, Lach4 of LGC (ANIC). ***Additional material***: **Victoria**: two adult females, four second-instar females: ex deep cavity galls in deformed flower buds, *E. baxteri*, Wilson's Promontory, 8 Feb 1972, JWB (BPBM); one adult female, one second-instar female: ex deep galls in aborted flower buds, *E. baxteri*, Wilson's Promontory, Squeaky Beach, 24 Feb 1972, A Yen (BPBM); two second-instar females, one second-instar male, three first-instar nymphs: ex bud galls, *E. baxteri*, Wilson's Promontory, Tidal Overlook, 23 Sep 1982, AN Anderson (ANIC); eight adult females: same data as previous except 12 Nov 1982 (ANIC); one parasitized second-instar female (probably *L. brimblecombei*), ex pit in swollen stem, *E. baxteri*, Grampians, Wartook Valley, Emu Holiday Park, 37.06S, 142.33E, 10 Jan 2011, PJG (ANIC).

Lachnodius eucalypti (Maskell, 1892)

Figs 1b, c, 4

Dactylopius eucalypti Maskell, 1892: 35; 1893: 233.
Lachnodius eucalypti: Maskell 1896: 400; Morrison and Morrison 1922: 44–48.

Diagnosis. Loose marginal fringe with minute sagittate setae; microtubular ducts on venter of head; macrotubular ducts with distal attenuation.

Description. Adult female (n = ca. 100). Body outline circular to oval; length 2.9–5.5 mm (3.5 mm for lectotype), greatest width 2.7–4.5 mm (3.0 mm for lectotype). Eyes 40–56 µm wide, on margin. Antennae seven-segmented; length 450–740 µm; with 2–3 hair-like setae on segment I, 4–10 hair-like seta on segment II, 2–6 hair-like seta on segment III, 4–7 hair-like seta on segment IV, 2–4 hair-like + one fleshy seta on segment V, 3–5 hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment VII. Frontal lobes 210–300 µm long, 85–200 µm wide. Tentorial box 205–360 µm long, 175–265 µm wide, with anterior extension of the dorsal arms. Labium 90–125 µm long, 110–135 µm wide, one-segmented, proximal segment setae absent. Spiracles 110–175 µm long, 60–115 µm wide across atrium. Legs: trochanter + femur 400–660 µm, tibia 260–450 µm, tarsus 110–150 µm; claw

38–53 µm; fore coxa with six setae, mid and hind coxae each with five setae, trochanter with 4–8 setae, femur with 6–18 setae, tibia with 12–19 setae, tarsus with 4–9 setae; tarsal digitules 63–90 µm long, claw digitules 48–65 µm long; translucent pores on all segments of hind leg. Anal ring 78–115 µm wide, with 18–30 setae; ring setae 60–155 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm membranous. Dorsal setae each parallel-sided, with acute apex, 5–7 µm long, scattered over dorsum. Macrotubular ducts with rim of dermal orifice 5 µm in diameter, duct shaft 13–20 µm long, distal portion (subtending vestibule) constricted, scattered over dorsum. Microtubular ducts ca. 5 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of alternating minute sagittate setae, each 6–18 µm long, and slightly larger setae, 10–20 µm long, ca. 150 setae in total on each side of body.

Venter. Ventral setae 10–75 µm long; elongate setae medial of each coxa 40–115 µm long; longest setae on head 120–150 µm long. Macrotubular ducts similar to those on dorsum; in transverse band across each abdominal segment, scattered throughout submargin. Quinquelocular pores 5 µm in diameter, clustered around vulva and each spiracle, present wherever setae found. Microtubular ducts on head.

First-instar nymph (n = 14 from Bundoora, Victoria). This instar was redescribed and figured well by Morrison and Morrison (1922, figure 14) and only some additional information is provided here. Newly hatched individuals ca. 380–400 µm long; feeding first-instar nymphs removed from leaf galls 550–600 µm long, broadly oval in outline, with venter expanded, balloon-like, to fill gall cavity, dorsum flat. Slide-mounted specimens with medial to submedial dorsal derm bearing small sclerotic spots, mostly 1–2 µm in greatest dimension; marginal setae mostly falcate (incorrectly described as 'flabellate' by Morrison & Morrison) except posterior three pairs lanceolate but often with apex jagged or notched, each marginal seta 15–30 µm long. Pair of elongate caudal setae ca. 65 µm long.

Notes. The adult female of *L. eucalypti* could be confused most easily with that of *L. froggatti* sp. n. Each induces pit galls on leaves and may be covered by waxy secretions. The adult female of *L. eucalypti* differs from that of *L. froggatti* by having (1) a marginal fringe of alternating sagittate and conical setae (marginal setae of *L. froggatti* hair-like to capitate); (2) eyes on margin (eyes on venter of *L. froggatti*); (3) no dorsal macrotubular ducts with setae touching rim of dermal orifice (dorsum of *L. froggatti* having some macrotubular ducts with a seta touching dermal orifice); and (4) microtubular ducts on ventral surface of head (absent in *L. froggatti*). Also, in life the secretions covering an adult female of *L. froggatti* are woolly, in contrast to the clumpy, powdery secretions that cover an adult female of *L. eucalypti*. Populations of *L. eucalypti* are known from all eight Australian states and territories. Specimens of *L. eucalypti* have been collected most commonly from *E. camaldulensis*, which is the most widely distributed species of *Eucalyptus* in Australia (Brooker 2002), but they also have been taken from a number of additional species of *Eucalyptus* in three sections (*Adnataria*, *Exsertaria*, and *Maidenaria*) of the subgenus *Symphyomyrtus*. Two populations of adult females probably both from *E. camaldulensis* (Windjana Gorge in northern Western

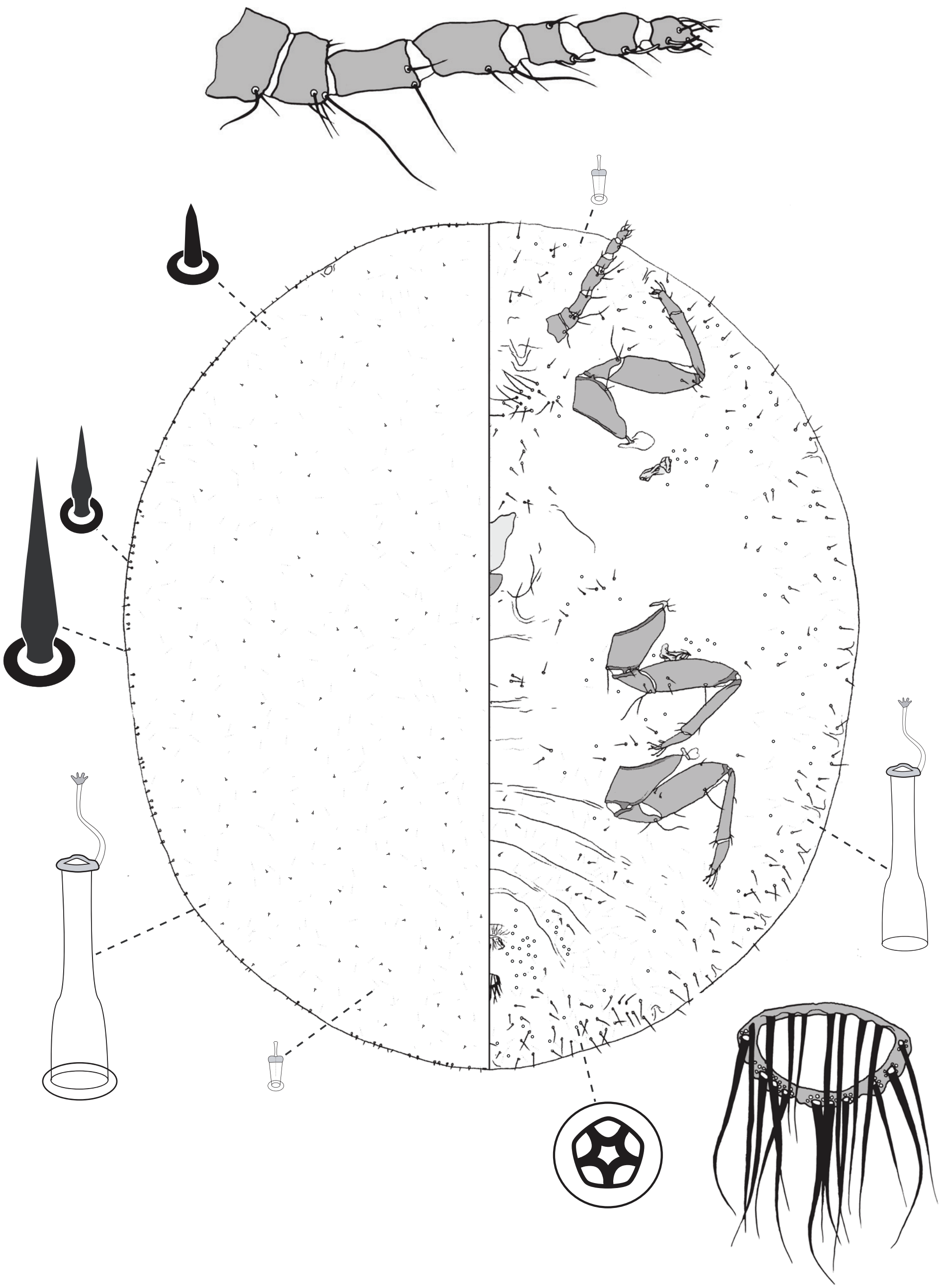

Figure 4. Adult female of *Lachnodius eucalypti* (Maskell).

Australia and near Alice Springs in the Northern Territory) have the sagittate setae of the marginal fringe of more uniform length and larger (15–20 µm long) compared with populations from the eastern and southern states in which the sagittate setae vary in size from 6–18 (mostly < 15) µm long on individual specimens. Due to this difference, we have excluded the females collected in the Northern Territory and Western Australia from the description above. Freshly collected specimens suitable for DNA sequencing might allow a decision on the species status of this morphological variation.

Life history data for *L. eucalypti* were obtained by JWB from a population that infested mature trees of *E. camaldulensis* on the campus of La Trobe University, Bundoora, Victoria, during the spring, summer, and fall of 1971–72. Beginning on 29 September 1971, adult females of *L. eucalypti* were collected while ovipositing on the bark of trunks and major branches of host trees. Oviposition was intermittent between then and mid-February 1972. Individual females appeared to complete oviposition within a short period of two or three days. The eggs were pink and laid in a single layer that formed a long, flat ribbon, 4–6 eggs wide, the top and sides of which were enclosed by a waxy secretion (Fig. 1c). Individual ovisacs were sometimes more than 5 cm long, straight or curved, and contained on the order of several hundred eggs (although no counts were made). A shrivelled, moribund female was often found at the end of an ovisac.

In the laboratory, eggs hatched 7–10 days after deposition. On host trees, the newly-eclosed first-instar nymphs migrated from the oviposition sites to the foliage, where they settled on the upper surfaces of young leaves. Feeding by each nymph resulted in a shallow pit gall on the leaf surface, which enclosed the nymph and grew along with it. The dorsal surface of settled first-instar and second-instar nymphs was nearly flat, smooth, and shiny, without evident waxy secretions. The ventral part of the nymph's body filled the cavity of the pit gall, while the dorsal margin overlapped and sealed the edge of the gall cavity.

In second-instar females the legs are poorly developed and apparently non-functional. Male nymphs, which can be distinguished from females in the second instar by the presence of fully developed legs, developed in leaf galls similar to those of females. Second-instar males eventually abandoned their galls and migrated to the bark of trunks and branches of host trees where they formed ovoid cocoons in protected situations. In the laboratory, males formed cocoons under paper lining the bottom of the petri dishes in which they were held. Cocoons were formed of whitish filaments, which issued from the dorsal tubular ducts.

Females remained in their galls after molting to the third (adult) instar, and continued to feed for an undetermined period, until fully developed. They then abandoned their galls and migrated to the bark to oviposit. When and where mating took place was not determined. At La Trobe University, the population of *L. eucalypti* did not appear to reproduce synchronously. Although ovipositing females were observed only during the spring and summer months (September to February), individuals of all stages were found on the trees during late January.

Maskell (1892) described this species based on adult females, pupal and adult males, and first-instar nymphs, collected from a tree referred to as *E. amygdalina*. The following year, Maskell (1893) indicated that his type material of *Dactylopius eucalypti* was from South Australia, and that the specimens were collected under bark. It appears that Maskell received the type material from the South Australian collections accumulated by Frazer S Crawford of Adelaide, an economic entomologist with an interest in Coccoidea. However, the identification of the host tree as *E. amygdalina* is problematic if the insects came from South Australia, because this eucalypt is endemic to Tasmania. Specimens of a second collection, which Maskell received from WW Froggatt in Sydney, were in pit galls in the leaves of *E. robusta*. This difference in the site of collection on the host trees apparently gave Maskell the impression that the species developed both in leaf galls and under bark, and presumably he was unaware that adult females migrate from leaf galls to bark prior to oviposition.

The Maskell collection in the NZAC contains six slides of *L. eucalypti*, four of which we consider to be type material. The four slides with type specimens are labeled "*Dactylopius eucalypti*" with the word "*Dactylopius*" crossed out and "*Lachnodius*" written above it. These labels also have the locality as "Australia" and the date as "1886." The slides bear (1) an adult female, (2) an adult male, (3) three first-instar nymphs, and (4) adult male parts (part of the thorax, two antennae, and two legs). The other two Maskell slides of this species in the NZAC contain (1) an adult female and (2) eight first-instar nymphs and bear later collection data (1893 and 1894) and therefore could not have been part of the material on which Maskell based his description. Beardsley had intended to designate the 1886 slide bearing the adult female as the lectotype of *Dactylopius eucalypti* Maskell, and labelled it as such in 1972 but this action was not published until now.

Note that there are also two slides of first-instar nymphs from the Maskell collection in the USNM, apparently from the type lot. Morrison and Morrison (1922: 44, 46) referred to one collection as "… a very small amount of material in position on the host, under Maskell No. 206" and listed the other slide as "Cotype. – Cat. No. 24762, U.S.N.M.". We examined both slides and list them below as paralectotypes.

Material examined. ***Lectotype*** (here designated): adult female: on slide labelled: "*Lachnodius* / *Dactylopius* / *eucalypti* / adult female / Australia / 1886 W.M.M." (ANIC). ***Paralectotypes***: one adult male (one slide), antenna and feet of adult male (one slide), three first-instar nymphs (one slide, labelled "Larvae"), same data as lectotype (NZAC); 12 first-instar nymphs: on slide labelled: "*Lachnodius* / eucalypti (Mask.) / Australia / Mask. Coll. N. 82 / Type" and envelope also with "Cotype Cat. No. 24962 / U. S. National Museum" (USNM); two first-instar nymphs: on slide labelled: "*Lachnodius* / *eucalypti* (Mask.) / Australia / Mask. Coll. 206 (USNM). ***Additional material***: **Unspecified locality in Australia**: one adult female: same label data as lectotype except "1893" and "not type, described 1892 / L. L. Deitz 1978" [JWB erroneously added a paralectotype label] (NZAC); eight first-instar nymphs: same label data as lectotype except "1894" and "not type, described 1892" (NZAC); one adult female: ex *Eucalyptus camaldulensis*, quarantine intercept in Cambridge, UK, 1 Nov 1993, Newman, 93-1216 (ANIC). **Australian Capital Territory**: three adult females, 14 first-instar nymphs on three slides: ex trunk, *E. mannifera*, Charnwood (suburb), Canberra, 18 Nov 2015, PJG (ANIC); one adult female (parasitized), 65 first-instar nymphs on eight slides: ex pit gall on leaf, *E. bridgesiana*, Tidbinbilla Nature Reserve, 35.48S, 148.89E, 1

Mar 1992, PJG (ANIC). **New South Wales**: 15 adult females: ex pits in leaves, *E. blakelyi*, 6.5 km SE of Forbes, 28 Nov 1984, PJG (ANIC); one adult female (parasitized): under bark, *E. viminalis*, Bago State Forest, 10 km ESE of Batlow, 14 Jan 1979, PJG (ANIC); three adult females: ex foliage, *Eucalyptus* sp. (ironbark), nr Coonabarabran, Warrumbungle Nat. Park, Camp Pincham, 22 Nov 1985, CAM Reid (ANIC); one adult female: ex pit gall on leaf, *E. saligna*, S. Brooman, "Strathclyde" (property), bank of Clyde River, 35.52S, 150.22E, 10 Jan 1996, PJG (ANIC); one adult female: Dubbo, no date, Froggatt #1049 [JWB must have misread the Froggatt number as this collection matches #1079 for *L. eucalypti*: "WWF 20.11.1921 / Dubbo / Eucalyptus"] (ASCU); partial specimens of adult and second-instar females: ex pit galls, E. *botryoides* leaves, Kurnell, 26 Aug 1915, WW Froggatt, #621 (ASCU); one adult female: ex leaf pit, ?*E. tereticornis* or *E. seeana* , South West Rocks, 30.90S, 153.02E, 30 Dec 2009, LG Cook, LGC01374 (ANIC); one adult female: in leaf pit gall, *E. tereticornis*, Wagga Wagga, 6 Nov 1899, WW Froggatt, # 297 (ASCU). **Northern Territory**: three adult females: *Eucalyptus* sp., N of Alice Springs, near Todd River, 19 Nov 1978, M Kotzman (ANIC). **Queensland**: six adult females: ex *E. propinqua*, Imbil, Oct 1936, AR Brimblecombe, No. D2264-6 (QDPC); three adult females, three second-instar males, five second-instar females: ex foliage, *Eucalyptus* sp., N side of Tamborine Mt, nr Sandy Creek, 26 Sep 1989, PJG (ANIC). **South Australia**: 15 adult females, two adult males, many first-instar nymphs, 14 second-instar males, six pupal males: *E. camaldulensis*, Adelaide, Glen Osmond, Waite Agric. Res. Instit., Dec 1952, HM Brookes, HMB Specimen Index No. 77/54 (ANIC); five adult females, one second-instar female: ex pits in leaves, *E. camaldulensis*, Glen Osmond, 27 Jul 1965, HMB, HMB Specimen Index No. 21/65 (ANIC); six adult females: on *E. camaldulensis*, 1 mile [1.6 km] N of Greenock, 19 Dec 1960, HM Brookes, HMB Specimen Index No. 109/60 (ANIC); 28 adult females: on bark of *E. ?camaldulensis*, Hazelwood Park, 14 Nov 1966, RS Bungey, HMB Specimen Index No. 46/66 (ANIC); four adult females: ex pits in leaves of *E. camaldulensis*, Mt Crawford Forest Reserve, Jan 1982, HM Brookes, HMB Specimen Index No. 1/82 (ANIC); two adult females, four second-instar females: *E. microtheca*, nr Murnpeowie (homestead), 16 Aug 1968, FD Morgan (ANIC); one adult female: under bark, *E. camaldulensis*, nr Mt Barker township, 15 Dec 1985, CAM Reid (ANIC); one adult female, six adult males: under bark, *E. camaldulensis*, Sampson Flat, 7 Sep 1965, DC Purdie (ANIC). **Tasmania**: two adult females: *E. globulus*, Hobart, Sandy Bay, 21 Aug 1965, HMB (ANIC). **Victoria**: one adult female, six second-instar females, one second-instar male, six first-instar nymphs: ex pit galls on young leaves, *E. camaldulensis*, Bundoora, La Trobe University, 24 Jan 1972, JWB (BPBM); one adult female (parasitized mummy): ex pit gall on twig, same data as previous except 5 Jan 1971 JWB (BPBM); two adult females, eight first-instar nymphs: on bark, same data as previous except 29 Sep 1971, V-87 (BPBM except one slide with three nymphs in ANIC); 16 adult females: same data as previous except 10 Dec 1971, V-243 (BPBM); one adult female, two adult males: same data as previous except Oct 1971 (BPBM); three adult females, four second-instar males: on bark, *E. goniocalyx*, Melbourne, Lower Plenty, 11 Sep 1971 or 23 Sep 1971, JWB (BPBM); one adult female: on stem, *E.*

camaldulensis, W of Benalla, 36.48S, 145.95E, 26 Nov 2006, PJG, NH150 (ANIC); five adult females, two second-instar females: on *E. nitens*, Errinundra Plateau, Orbost Forestry District, 21 Oct 1974, FG Neumann and GC Marks, HMB Specimen Index No. 14/74 (ANIC). **Western Australia**: 21 adult females, one second-instar female with pharate adult: ex gall, *E. camaldulensis*, Windjana Gorge Nat. Park, bank of Lennard River, 17.42S, 124.95E, 29 Apr 1992, PJG (ANIC except eight slides in WAM).

Lachnodius froggatti Beardsley, Gullan & Hardy, sp. n.

http://zoobank.org/2869D8E4-DDEE-4563-99C0-09F8A867FDFD

Figs 1 d, e, 5

Diagnosis. Eyes on venter; dorsal derm membranous; two size classes of dorsal marotubular ducts, some larger ducts with seta touching rim.

Description. Adult female (n = 30). Body outline circular to oval; length 2.3–8.9 mm (5.5 mm for holotype), greatest width 1.8–5.8 mm (4.3 mm for holotype). Eyes 47–75 µm wide, on venter between margin and scape. Antennae seven-segmented; length 760–1580 µm; with 6–9 hair-like setae on segment I, 8–21 hair-like seta on segment II, 20–28 hair-like seta on segment III, 10–18 hair-like seta on segment IV, 3–9 hair-like + one fleshy seta on segment V, 4–7 hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment VII. Frontal lobes 150–340 µm long, 75–190 µm wide. Tentorial box 270–480 µm long, 200–330 µm wide, with anterior extension of the dorsal arms. Labium 110–155 µm long, 135–230 µm wide. Spiracles 140–305 µm long, 75–190 µm wide across atrium. Legs: trochanter + femur 545–1080 µm, tibia 420–940 µm, tarsus 150–270 µm; claw 43–70 µm; fore coxa with six setae, mid and hind coxae each with five setae, trochanter with 5–9 setae, femur with 20–40 setae, tibia with 18–51 setae, tarsus with 7–15 setae; tarsal digitules 63–98 µm long, claw digitules 45–68 µm long; translucent pores on all segments of hind leg. Anal ring 83–148 µm wide, with 18–29 setae; ring setae 100–225 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm membranous. Dorsal setae 5–10 µm long, each parallel-side, with acute apex, scattered over dorsum. Macrotubular ducts of two size classes: (1) large ducts with rim of dermal orifice 8–10 µm in diameter, sometimes with seta touching rim, duct shaft 20–30 µm long, scattered over dorsum; (2) smaller ducts, rim of dermal orifice 5–6 µm in diameter, duct shaft 10–20 µm long, scattered over dorsum. Microtubular ducts ca. 5 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of setae, each 18–53 µm long, ca. 200 setae in total on each side of body.

Venter. Ventral setae 18–183 µm long; elongate setae medial of each coxa 120–340 µm long; longest setae on head 185–365 µm long. Macrotubular ducts similar to those on dorsum; found wherever setae occur, in transverse band across each segment, scattered throughout submargin. Quinquelocular pores 5 µm in diameter, sparse, distributed as for macrotubular ducts, with cluster near each spiracle and caudad of vulva.

Second-instar female (n = 5). Broadly oval to nearly circular in outline; length 1.7–3.2 mm. Eyes ca. about one eye diameter removed from fringe line on venter. Antenna six-segmented, ca. 190 µm long, strongly tapered base to apex, segments except apical broader than long. Legs short and broad, all segments differentiated, claws vestigial. Anal ring ca. 35 µm wide, with ca. eight setae to ca. 36 µm long. Dorsum with small setae (4–8 mu long), sparse, spiniform. Dorsal macrotubular ducts, ca. 5 µm orifice diameter, 8 µm rim diameter, ca. 18–20 µm long, some with a satellite seta, sparsely scattered in submarginal band around periphery of body; minute tubular ducts (ca. 2 µm orifice diameter) interspersed among larger ducts. Marginal fringe a moderately sparse series of moderately slender conical setae, 18–28 µm long, with apices blunt or very slightly expanded; ca. 90 setae on each side. Antepenultimate setae slightly longer (30–40 µm long). Venter with very sparse setae, mostly 20–30 µm long, 40–50 µm between legs, to 75 µm on head. Ventral macrotubular ducts absent. Ventral quinquelocular pores sparsely scattered in submarginal peripheral band, plus slight concentrations near spiracles.

Notes. The adult female of *L. froggatti* is most similar to that of *L. eucalypti.* See notes for *L. eucalypti* for a comparison. Populations of *L. froggatti* have been sampled from New South Wales, Victoria, and South Australia. It is known to feed on hosts in the subgenera *Eucalyptus* (section *Eucalyptus*) and *Symphyomytrus* (sections *Adnataria* and *Maidenaria*). The live adult female is white to pale cream or yellow in life, and mature females produce copious dorsal glassy wax filaments and white powdery wax (Fig. 1d, e). The females have been found only on the leaves and the pit below the female's body may be up to 1.5 mm deep (Fig. 1e). The leaf area around the feeding insect is often depressed and discolored or necrotic, and the opposite surface of the leaf has a bulge; on very young foliage, the female causes leaf curling.

Froggatt's first accession notebook (Gullan 1984a) has an entry for the specimen that we have designated as holotype, as follows: "(303) *Dactylopius eucalypti* ?Large funnel leaf Penrith (No 1) (Berlese No 233)". The words "?Large funnel leaf" are written in different handwriting and inserted in the original entry. The mention of a Berlese number refers to part of this collection being sent to Berlese (presumably the Italian coccidologist Antonio Berlese) as a previous entry says "(Sent to Berlese No 230)". It seems that Froggatt confused *L. froggatti* with *L. eucalypti*, as shown by his identification of our holotype of *L. froggatti* (discussed above) as *L. eucalypti*, and also the following record. Two paratype females listed below have a Froggatt number of 27, which Froggatt's first accession notebook records as from Wallsend, which is one of the localities listed by Froggatt (1917, 1921) for *L. eucalypti*. We have restricted the type series of *L. froggatti* to specimens from New South Wales. All specimens in the Froggatt collection are from this state.

Etymology. This species is named in honor of the collector of the type material, the late WW Froggatt, an Australian entomologist employed by the New South Wales Department of Agriculture during the early decades of the 20th century. Froggatt was the first to seriously attempt a systematic treatment of the scale insect fauna of Australia. The species epithet is a noun in the genitive singular.

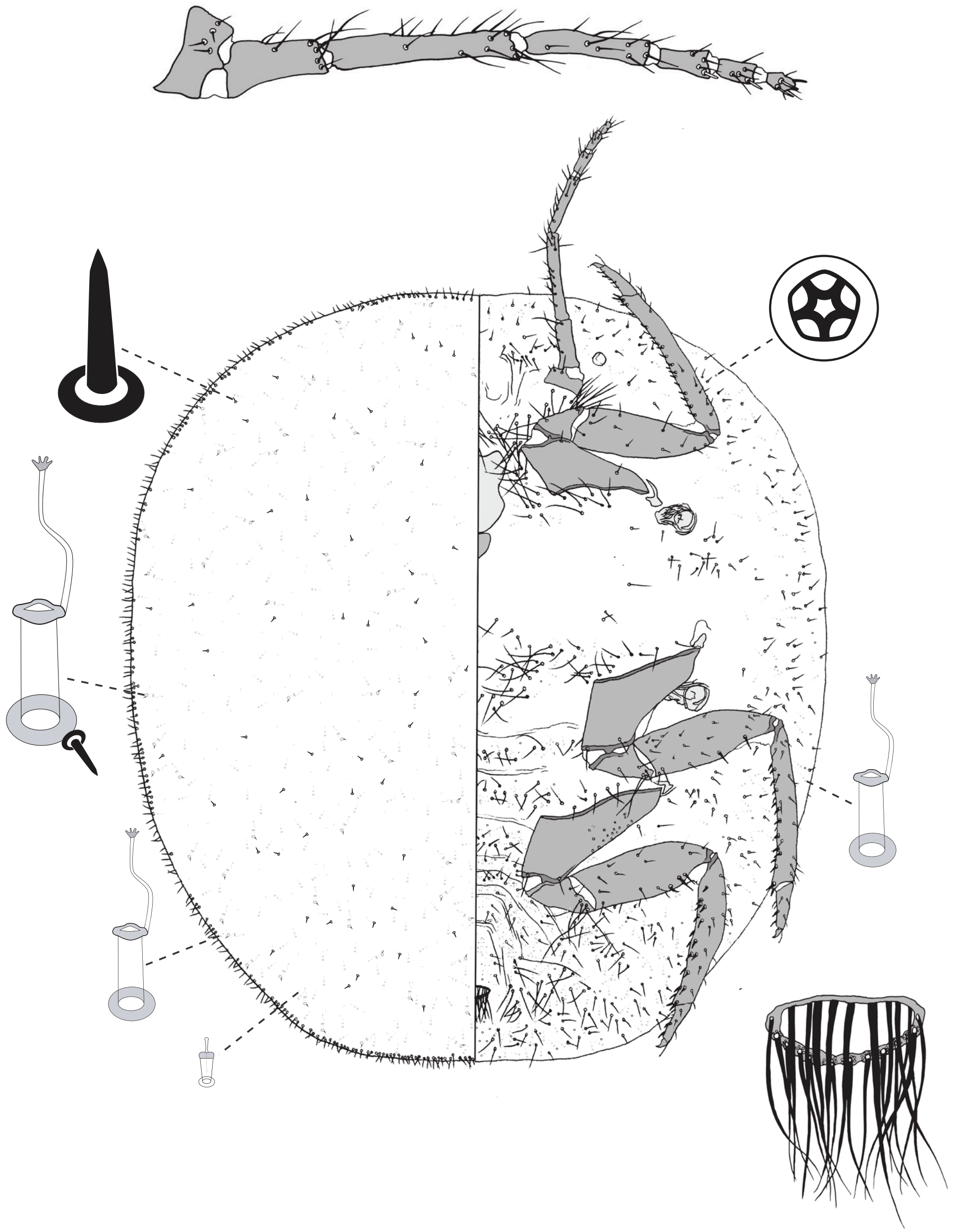

Figure 5. Adult female of *Lachnodius froggatti* sp. n.

Material examined. ***Holotype***: **New South Wales**: adult female, on slide: ex open top pit gall on leaf, *Eucalyptus* sp., Penrith, 24 Nov 1899, W. W. Froggatt collection # 303 (ASCU); this specimen was removed from a dry gall and slide-mounted by JWB in April 1972. ***Paratypes***: **New South Wales**: two adult females: ex leaf pit galls, *Eucalyp-*

tus sp., WW Froggatt number 27 [from Wallsend, see note above], ASCTHE101355, ASCTHE101356 (ASCU); one adult female, three second-instar females: ex pits on leaves, *Eucalyptus* sp., 10 km S of Coonabarabran, roadside verge, 29 Nov 1984, PJG (ANIC); one second-instar female, ex pit in leaf of *E. baueriana*, ca. 6 km WSW of Narooma, Wagonga Scenic Drive, 36.24S, 150.97E, 31 Dec 2008, PJG (ANIC); two adult females, one second-instar female with pharate adult: ex pits in leaves, *E. ?melliodora*, Oallen, 1760 Oallen Ford Road, Windellama, 35.13S, 150.02E, 10 Jan 2018, PJG (ANIC). ***Additional material*: South Australia**: ten adult females, eleven first-instar nymphs: ex pits on leaves, *E. viminalis*, Adelaide, Glen Osmond, Waite Agric. Res. Institute, 3 Oct 1967, NC Stewart, HMB Specimen Index No. 31/67 (ANIC); two adult females, one adult male: ex pits on leaves, *E. fasciculosa*, Belair, National Park, 1 Nov 1963, TCR. White, HMB Specimen Index No. 48/63 (ANIC); three adult females: ex pits in leaves, *Eucalyptus* sp., Mannum, Jan 1971, P Allen (ANIC); one adult female: ex pit on leaf, *E. obliqua*, Netherby, 4 Jan 1964, PG Martin, 2/64 (ANIC); two adult females: ex pits on leaves, *E. obliqua*, Netherby, 28 Nov 1963, SW Brown, HMB Specimen Index No. 70/63 (ANIC). **Victoria**: one adult female: ex pit in leaf, *E.?microcarpa*, 10 km S of Nagambie, on road to Avenel, 36.38S, 145.17E, 7 Feb 2004, PJG, LGC00107 (ANIC); one adult female: ex pit in leaf, *E. microcarpa*, 10 km S of Nagambie, on road to Avenel, 36.38S, 145.17E, 30 Jan 2005, PJG, NH118 (ANIC); four adult females: ex pits on leaves, *E. melliodora*, 9 km N of Nagambie, Weir Road, 500 m W of Hwy M39, 36.70S, 145.17E, 2 Jan 2003, PJG, NH156 (ANIC); ten first-instar nymphs (no associated adult females but of same morphology as nymphs from Adelaide listed above): ex pits on leaves, *Eucalyptus* sp. (mallee), Hattah Lakes Nat. Park, 30 Apr 1972, JWB (BPBM except one slide with four nymphs in ANIC); three adult females: ex leaf pits in leaf curls, *E. largiflorens*, Mildura, River Road, Apex Park, near Murray River, 34.16S, 142.16E, 4 Feb 2005, NBH and PJG, NH39, NH116, NH149 (ANIC).

Lachnodius hirsutus (Froggatt, 1921)

Figs 1f, 6

Pseudopsylla hirsutus Froggatt, 1921: 6.
Lachnodius hirsutus Beardsley, 1982: 31–35.

Diagnosis. Gall of adult female covers portion of dorsum; venter hirsute; anal ring with few setae and pores; microtubular ducts absent.

Description. Adult female (n = 6). Body outline circular to oval; length 3.2–6.8 mm (3.2 mm for lectotype), greatest width 3.1–6.1 mm (3.1 mm for lectotype). Eyes 75–105 µm wide, on margin. Antennae six-segmented; length 850–1320 µm; with 3–4 hair-like setae on segment I, 8–18 hair-like seta on segment II, 8–11 hair-like seta on segment III, 9–15 hair-like seta on segment IV, 5–6 hair-like + one fleshy seta on segment V, and six hair-like setae + three fleshy seta on segment VI. Frontal lobes 275–750 µm long, 200–400 µm wide. Tentorial box 600–950 µm long, 200–450 µm wide, with anterior extension of the dorsal arms. Labium 200–270 µm long,

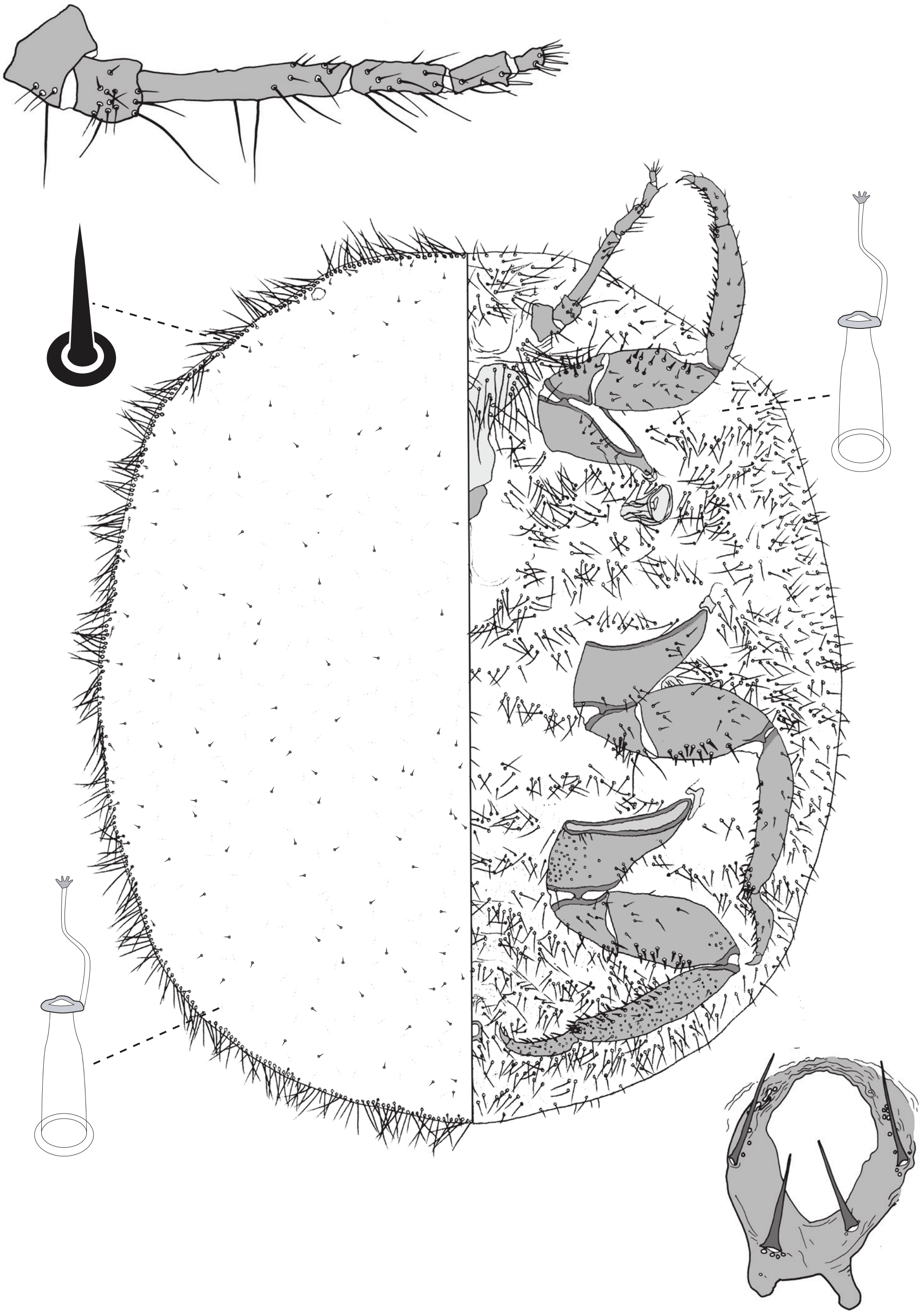

Figure 6. Adult female of *Lachnodius hirsutus* (Froggatt).

210–290 µm wide. Spiracles 250–360 µm long, 190–300 µm wide across atrium. Legs robust, increasing in size caudad, fore leg: trochanter + femur 940–1440 µm, tibia 810–1260 µm, tarsus 350–500 µm; mid leg: trochanter + femur 1020–1460 µm, tibia

890–1280 µm, tarsus 370–520 µm; hind leg: trochanter + femur 1280–1620 µm, tibia 1100–1380 µm, tarsus 500–560 µm; claw 110–160 µm; coxa with 20–44 setae, trochanter with 20–31 setae, femur with 30–70 setae, tibia with 37–75 setae, tarsus with 20–30 setae; tarsal digitules 80–95 µm long, claw digitules 68–85 µm long; translucent pores on all segments of hind leg. Anal ring 130–140 µm wide, ring thickening caudad, with 5–7 setae; ring setae 50–80 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm membranous, nodulose. Dorsal setae 13–25 µm long, each tapering evenly from base to apex, scattered over dorsum. Macrotubular ducts with rim of dermal orifice 5–6 µm in diameter, duct shaft 15–18 µm long, distal (near vestibule) end constricted, ducts scattered over dorsum. Microtubular ducts absent. Dorsum delimited by dense fringe of elongate setae, each 200–455 µm long, ca. 250 setae in total on each side of body.

Venter. Ventral setae 75–210 µm long, distributed densely; elongate setae medial of each coxa 170–305 µm long; longest setae on head 260–360 µm long. Macrotubular ducts similar to those on dorsum, found wherever setae occur, in transverse band across each segment, and along submargin. Quinquelocular pores absent.

Notes. The adult female of *L. hirsutus* can be distinguished from all other species by the combination of 6-segmented antennae, extremely long marginal setae (350–450 µm long), and the scarcity of quinquelocular pores, which occur only near the spiracular openings. The anal ring of *L. hirsutus* is also unique among *Lachnodius* species; it has six or fewer ring setae present, with only a few minute pores near the base of each seta.

In his redescription of this species, Beardsley (1982) omitted the length of the fourth segment from the antennal formula. The correct segment lengths (µm), from the base to the apex, are: 150, 120, 400, 200, 130, and 50. Froggatt (1921: 6) stated "The female coccids produce solid woody galls on the branchlets of eucalypts with an irregular opening on the upper surface (Fig. 1f). At female maturity, the gall of *L. hirsutus* probably splits open at the apex to reveal the female, because enclosed globular twig galls of nymphs have been collected in association with galls resembling those of *L. hirsutus* (Gullan et al. 2005). It is not clear whether the host genus of Froggatt's type material was *Corymbia* or *Eucalyptus*, since the original description simply says "an undetermined species of eucalyptus [sic]". The bloodwood eucalypts were not recognized as a genus (*Corymbia*) separate from *Eucalyptus* until more recently (Hill and Johnson 1995).

Material examined. ***Lectotype*** [designated by Beardsley (1982)]: **Northern Territory**: adult female, on slide: ex open top twig gall, *Eucalyptus* sp., Port Darwin, G. F. Hill, Froggatt # 629, ASCTHE101343 (ASCU); this specimen was remounted from an original Froggatt slide by JWB in April 1972. ***Paralectotype***: **Northern Territory**: one adult female: same data as lectotype, ASCTHE101342 (ASCU). ***Additional material***: **Northern Territory**: three adult females: ex galls on stems, *Corymbia nesophila*, Gunn Point, 9 July 1987, LR Miller (ANIC); Queensland: one adult female: ex gall on stem, *E. tetradonta*, Iron Range Nat. Park, 4.2 km E of Cooks Hut campground, on road to Portland Roads, 79 m, 12.71S, 143.32E, 21 Sep 2006, LG Cook, LGC00642 (body with 2 intact legs), NH122, NH151, NH159 (NH numbers are for individual DNA-extracted legs) (ANIC).

Lachnodius lectularius Maskell, 1896

Figs 2a, b, 7

Lachnodius lectularius Maskell, 1896: 400–402.

Diagnosis. Gall of adult female does not cover any of dorsum; adult female with marginal fringe of close-set setae; one size class of dorsal macrotubular ducts.

Description. Adult female (n > 10). Body outline circular to oval; length 2.1–9.3 mm (4.0 mm for lectotype), greatest width 1.9–7.4 mm (3.0 mm for lectotype). Eyes 25–50 µm wide, on margin. Antennae seven-segmented; length 620–1440 µm; with 3–6 hair-like setae on segment I, 5–13 hair-like seta on segment II, 3–5 hair-like seta on segment III, 2–6 hair-like seta on segment IV, 2–3 hair-like + one fleshy seta on segment V, 2–4 hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment VII. Frontal lobes 155–440 µm long, 88–175 µm wide. Tentorial box 330–500 µm long, 180–270 µm wide, with anterior extension of the dorsal arms. Labium 140–250 µm long, 120–190 µm wide. Spiracles 140–290 µm long, 100–285 µm wide across atrium. Legs: trochanter + femur 500–1340 µm, tibia 370–1150, tarsus 150–300 µm; claw 53–120 µm; coxa with 5–10 setae, trochanter with 6–14 setae, femur with 13–35 setae, tibia with 19–41 setae, tarsus with 11–21 setae; tarsal digitules 70–125 µm long, claw digitules 50–70 µm long; translucent pores on all segments of hind leg. Anal ring 73–185 µm wide, with 15–24 setae; ring setae 43–210 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm membranous. Dorsal setae 5–8 µm long, each with constriction near base and apex acute, scattered over dorsum. Macrotubular ducts with rim of dermal orifice 5 µm in diameter, duct shaft 10–14 µm long, scattered over dorsum. Microtubular ducts ca. 5 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of setae, each 38–90 µm long, ca. 300 setae in total on each side of body.

Venter. Ventral setae 15–210 µm long; elongate setae medial of each coxa 60–190 µm long; longest setae on head 165–300 µm long. Macrotubular ducts similar to those on dorsum; found wherever setae occur, in transverse band across each segment, scattered throughout submargin. Quinquelocular pores 5 µm in diameter, distributed as macrotubular ducts, with cluster near each spiracle, dense on median of posterior abdominal segments, near vulva.

Notes. Adult females feed in a pit in a swollen stem or bud of the host eucalypt (Fig. 2a, b). The body color is variable; it is green with a red longitudinal stripe on the dorsum of younger females and fully orange or red to brown in older females. In life, females can lift up their abdomen and expose their venter. Each seta forming the marginal fringe surrounding the dorsum is covered in a glassy secretion. The life history of *L. lectularius* is similar to that of *L. eucalypti*. For details see Notes under *L. eucalypti*. One exception is that the galls of developing young females of *L. lectularius* are located on succulent young twigs and buds rather than on leaves. Mature females of *L. lectularius* were collected by JWB from *Eucalyptus camaldulensis* at La Trobe, and on other hosts and localities in Victoria during a relatively short period (February 14 to 20, 1972). This suggests that *L. lectularius* may reproduce with more synchrony than *L. eucalypti*. Eggs from females of *L. lectularius* held in the laboratory by JWB began to hatch approximately two weeks after oviposition.

In an unpublished manuscript, JWB treated as a separate species some of the larger specimens of what we consider to be *L. lectularius*. He noted that these specimens closely resemble the type material of *L. lectularius* and that the first-instar nymphs were identical, but pointed out several differences: specifically, the larger females have longer setae, more tubular ducts, a larger anus, more expanded tibial apices, and more translucent pores on the hind legs. Each of these traits appears to be correlated with body size across *Lachnodius* species. Therefore, we have opted to interpret this as part of the phenotypic variation found within *L. lectularius*.

Maskell (1896) described the adult female, the second-instar female, and the first-instar nymph of this species. Apparently, his description was based on material sent to him from Victoria by Mr C French. Type material of this species consists of specimens on 6 unstained slides prepared by Maskell, one adult female in the USNM and eleven adult females mounted by JWB from specimens from two boxes of dried material in NZAC. The original Maskell slides are labelled "*Dactylopius lectularius*" with "*Dactylopius*" crossed out and "*Lachnodius*" written above it, and "1895 – W. M. M." There are no locality or collector data on these slides. The dry material was labelled only "*Dactylopius lectularius* – Australia" but the boxes were lost (see explanation in Materials and Methods). Only one of the original Maskell slides contains an entire adult female. JWB labelled that specimen as the lectotype in 1972 but this action was not published until now (see below). Of the remaining slides (paralectotypes), one contains female mouthparts, one the posterior body and antenna of an adult female, one a second-instar female, and two contain first-instar nymphs. When JWB slide-mounted specimens from Maskell's dry material in 1972, he labelled the slides with the collection data from the original description (but with the wrong collector name), rather than what was written on the box.

Concerning the type material of *L. lectularius*, Maskell (1896: 401) only stated that "Mr. French has sent me a number of specimens and says, 'It does great damage to young trees at Mooroopna, Goulburn River, Victoria'." Therefore, we assume that all of his material was from this one source. Specimens in the dry material are mostly parasitized mummies, and JWB only obtained two satisfactory slide preparations. Both of these adult females show evidence of having been parasitized, containing parasitoid mandibles, encyrtiform eggshells, and small sclerotized first-stage parasitoid larvae. Maskell (1896: 401) recorded the habitat from which the type material was derived as "In Australia, on *Eucalyptus rostrata*." *Eucalyptus rostrata* is a junior synonym of *E. camaldulensis*, the "river red gum," a common species throughout southeastern Australia (Chippendale 1988).

The adult female specimens of *L. lectularius* in the Maskell collection do not agree in all details with his published description and figures. We consider that the discrepancies are errors in Maskell's interpretation. Morrison and Morrison (1922) noted

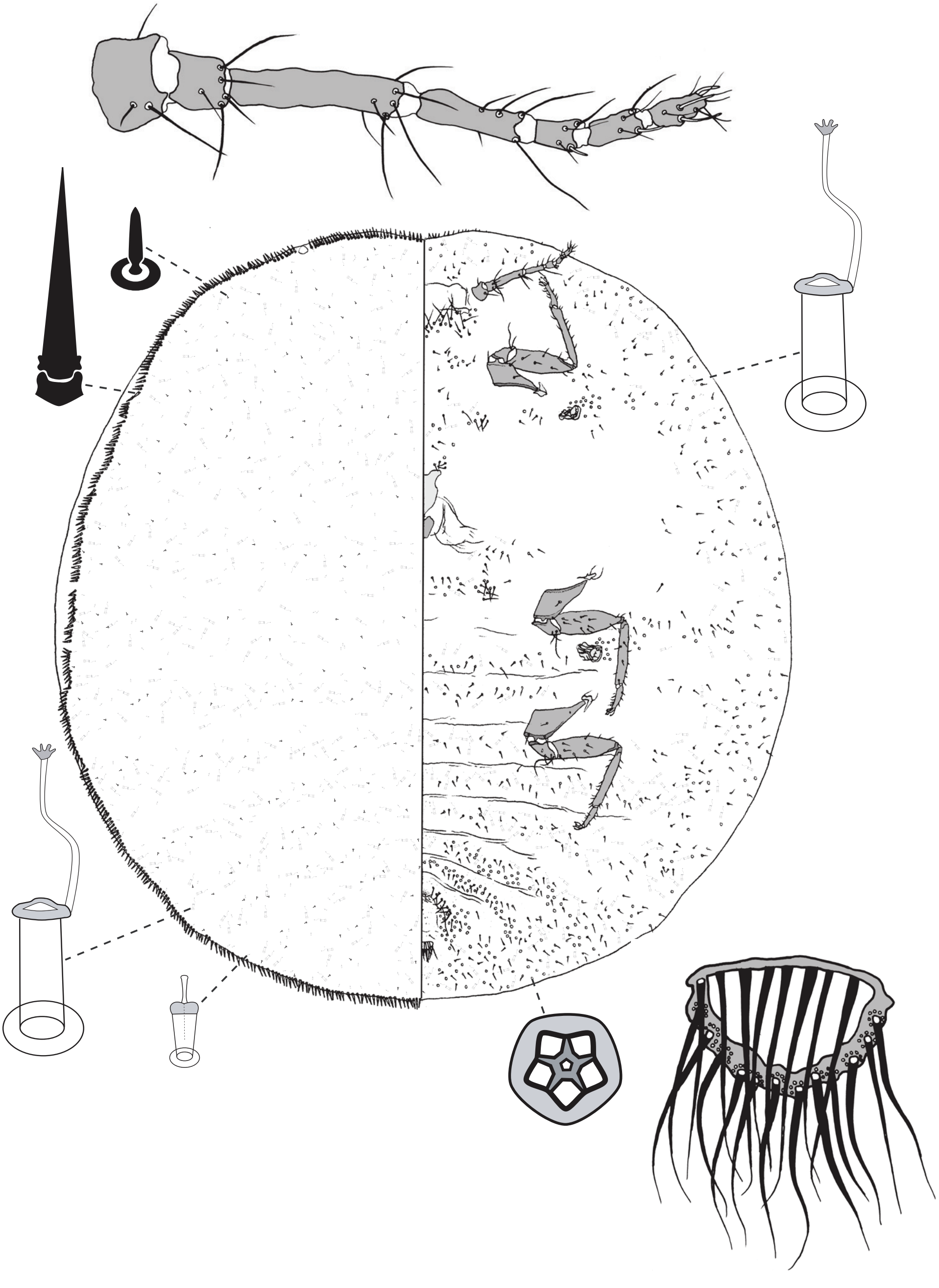

Figure 7. Adult female of *Lachnodius lectularius* Maskell.

that Maskell's descriptions often were inaccurate. Here we point out the mismatches between his description and specimens. In his 1896 description, Maskell stated that the adult female has an "Epidermis bearing many short fine hairs, and near the cephalic and abdominal extremities are two curved series of stronger spiny hairs, about sixty in each." His figure of the female abdomen (Maskell 1896: Plate XXI, fig. 16) shows a series of spine-like setae in the area behind the anal ring. In the drawing these are thicker and more conical in form than the fringe setae, which are depicted (Plate XXI, fig. 17) as being nearly digitiform. By contrast, the Maskell specimens do not have conical or spiniform setae posterior to the anal area, although many of the setae appear to have been broken off and look somewhat like stiff bristles. On the other hand, in fresh preparations, the ventral setae in this region are quite elongate. Thus, we think that he simply confused body surfaces. Maskell also refers to a pair of "strong short conical spines" set close together between the antennae in some specimens, but not in all. In this position in the lectotype, we found a pair of parasitoid mandibles, which he must have mistaken for spines. Likewise, he mistook several pairs of parasitoid mandibles for spines in his description of the second-instar female. Maskell counted 24 of these structures, which is consistent with JWB's observation that the encyrtids that attack *Lachnodius* species can be highly gregarious.

In his notes, JWB recorded having studied two specimens that were not seen by PJG or NBH: Queensland: two adult females: *Eucalyptus* sp., gall no. 9, Acacia Ridge, Brisbane, 10 Jan1968, EC Dahms (these probably are housed in the Queensland Museum in Brisbane).

Material examined. ***Lectotype*** (here designated): **Victoria**: adult female: on slide labelled: "*Lachnodius* / ~~*Dactylopius*~~ / *lectularius* / adult female / 1895 W.M.M." (ANIC). ***Paralectotypes***: **Victoria**: five slides: adult female mouth parts, adult female posterior body and antennae, one second-instar female, and two first-instar nymphs: same label data as lectotype (NZAC); eleven adult females, on six slides prepared and labelled by JW Beardsley from Maskell dry material: "VICTORIA / Mooroopna / Goulburn Riv. / ?1896 / W. W. Froggatt [SIC] / *Eucalyptus* / *rostrata* in / twig depression" (NZAC); one adult female, on slide labelled: "*Lachnodius* / *lectularius* / Mask. / Australia / Mask. Coll. No. 453" (USNM). Note that JWB made an error in writing the collector as "W.W. Froggatt", as the original specimens were collected by C. French. Also, the dry material that JWB mounted did not bear the collection data that he put on his slide labels, but was added by JWB based on the data cited in Froggatt's original description. ***Additional material***: **Australian Capital Territory**: one adult female, ex pit in swollen woody stems, *Eucalyptus* sp., Canberra, Black Mountain, Coll. 6 Dec 1996, JH Martin 6845 (ANIC). **New South Wales**: three adult females: *Eucalyptus* sp. (bloodwood), 5 km W of Bogangar, 23 Nov 1986, S Bhatti, PJG, and C Reid (ANIC); two adult females: ex pits in swollen stems, *E. dives*, 2 km S of Captain's Flat, 35.58S, 149.47E, 4 Jan 2009, PJG (ANIC); one adult female: ex pit gall, *Eucalyptus* sp., Congo, 35.95S, 150.15E, 6 Jan 1992, PJG (ANIC); one adult female: ex swollen stem, *Eucalyptus* sp., 22 km NE of Griffith, Whitton Stock Route, 34.15S, 146.20E, 30 Oct 1993, PJG (ANIC); one adult female: *Eucalyptus* sp., E of Walcha, Oxley Highway, 31.21S, 151.90E, 1130 m, 25 May 2005, LG Cook, LGC00345, NH87 (ANIC); two adult females: ex depressions in swollen fruit, *Eucalyptus* sp., N. Sydney, Beacon Hill, Peninsula Views Estate, 18 Sep 1993, LG Cook, LachB (ANIC). **Queensland**: four adult females (all parasitized): *Eucalyptus drepanophylla,* R-8 Doongul, 27 Sep 1939, AR Brimblecombe (QDPC); one adult female, three second-instar nymphs, 14 first-instar nymphs: *E. crebra*, Moggill, 20 Nov 1953, AR Brimblecombe (QDPC) (these three slides could not be located at QDPC). **South Australia**: eleven adult females, three second-instar females, one first-instar nymph: ex swellings on twigs or stems, *E. camaldulensis*, Glen Osmond, 6 Oct 1982, GS Taylor, HMB Specimen Index No. 20/82 (ANIC). **Victoria**: five adult females, seven first-instar nymphs: ex pits in twigs, *Eucalyptus radiata*, 20 miles [32 km] W of Drouin, 20 Feb 1972, JWB (BPBM except one slide of nymphs in ANIC); 14 first-instar nymphs: ex ovisac on bark, *E. camaldulensis*, Bundoora, La Trobe University, Coll. 21 Feb 1972, JWB (BPBM); three adult female: ex pits in twigs, *E. camaldulensis*, Bundoora, La Trobe University, Coll. 14 Feb 1972, JWB (BPBM); two adult females, one second-instar male: under bark, *E. camaldulensis*, Bundoora, La Trobe University, Wildlife Reserves, Ring Road, 37.72S, 145.05E, 14 Feb 2005, NBH and PJG, NH41, NH154, NH161 (ANIC); two adult females: ex pits in swollen stems, *E. viminalis*, Cranbourne, Royal Botanic Gardens Cranbourne, Possum Gully Track, 38.13S, 145.28E, 9 Feb 2005, PJG, NH40, NH115 (ANIC); one adult female: ex pit in swollen stem, *E. aromaphloia*, Grampians Nat. Park, Victoria Valley, Glenelg River Road, 37.23S, 142.41E, 6 Feb 2005, NBH and PJG, NH119 (ANIC); one adult female: ex pit in swollen stem, *E. ?polyanthemos*, Melbourne, North Warrandyte, corner of Overbank Road and Glynns Road, 37.73S, 145.20E, 14 Feb 2005, NBH and PJG, NH46 (ANIC); one second-instar female: ex pit in twig, *E. radiata*, Mt Eliza, 22 Feb 1972, JWB (BPBM); one adult female: in depression on swollen stem, *Eucalyptus* sp., near Hattah, Nov 1993, LG Cook (ANIC); five adult females, one second-instar female: ex pits in twigs, *E. viminalis*, Tooborac, 24 Feb 1972, JWB (BPBM); two adult females: ex pits in flower buds, *E. viminalis*, Tyabb, junction of Tooradin-Tyabb Road and Callanans Lane, 38.21S, 145.25E, 13 Feb 2005, NBH and PJG (NMV).

Lachnodius maculosus Beardsley, Gullan & Hardy, sp. n.

http://zoobank.org/182CD8B3-7EC4-45C5-9A27-9F61F902C4BB
Fig. 8

Diagnosis. Dorsum with numerous sclerotic invaginations; marginal fringe of conical setae; some dorsal macrotubular ducts with seta touching rim; anal ring invaginated.

Description. Adult female (n = 3). Body outline circular; length 3.45–4.84 mm (4.36 mm for holotype), greatest width 3.30–3.94 mm (3.94 mm for holotype). Eyes dorsal, very weakly developed, ca. 35 µm wide. Antennae seven-segmented; length 680–690 µm; with two hair-like setae on segment I, ca. three hair-like setae on segment II, two or three hair-like setae on segment III, three hair-like seta on segment IV, one fleshy seta on segment V, two hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment V. Tentorial box with anterior extension of the dorsal arms, 285–335 µm long, 245–265 µm wide. Labium 125 µm long, 190–195 µm wide. Spiracles 130–155 µm long, 65–85 µm wide across atrium. Legs increasing in size caudad; fore legs: trochanter + femur 500 µm, tibia 425–460, tarsus 170–210 µm; mid legs: trochanter + femur 510–520 µm, tibia 445–480 µm, tarsus 170–210 µm; hind legs: trochanter + femur 555–560 µm, tibia 495–520 µm, tarsus 200–218 µm; claw 50–56 µm; fore coxa with 6 setae, mid and hind coxae each with 5 setae, trochanter with 5–7 setae, femur with 12–19 setae, tibia with 20–27 setae, tarsus with 6–15 setae; tarsal digitules 68–74 µm long, claw digitules 43–50 µm long; translucent pores on all segments of hind leg, ca. 60 pores on dorsal surface and ca. 30 pores on ventral surface. Anal ring invaginated, cuticle surrounding ring sclerotic, 68–78 µm wide, with 10–12 setae; ring setae 60–140 µm long. Pair of elongate caudal setae ca. 45 µm long.

Dorsum. Derm beset with sclerotic spicules (i.e., well-developed microtrichia), in addition to sclerotic varioles 8–12 µm wide. Dorsal setae lanceolate, 5–8 µm long, scattered over dorsum. Macrotubular ducts of two size-classes: (i) larger ducts ca. 20 µm long, with rim of dermal orifice ca. 10 µm wide; (ii) smaller ducts ca. 10 µm long, with rim of dermal orifice ca. 7 µm in diameter; many of larger ducts with one seta affixed to rim of dermal orifice. Microtubular ducts each ca. 7 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of ca. 275 setae on each side of body; each seta with acute apex, length of setae 18–33 µm; marginal fringe interrupted between thorax and abdomen.

Venter. Ventral setae 22–60 µm long; elongate setae medial of each coxa decreasing in size caudad: ca. 100 µm long near fore coxa, ca. 55 µm long near hind coxa; longest setae on head 120–140 µm long. Macrotubular ducts of two types: (i) larger ducts with shaft subtending vestibule constricted, each ca. 22 µm long, with rim of dermal orifice ca. 6 µm wide, found along posterior margin and in transverse band across abdominal segment IV; (ii) smaller ducts with uniform shaft diameter ca. 15 µm long, with rim of dermal orifice ca. 4 µm wide, along margin anterior of larger ducts, in transverse rows across abdominal segments, amongst clusters of setae medial of each coxa. Quinquelocular pores of two distinct size-classes: (i) larger pores 5–6 µm in diameter, found on posterior abdominal segments; and (ii) smaller pores 3–4 µm in diameter, near spiracles and along margin.

Etymology. The species name is taken from the Latin noun *macula* meaning spot, referring to the shallow, sclerotic pits on the dorsal body surface, combined with the Latin suffix *-osus* to give the meaning abundance of spots or spotted. The species epithet is a Latin masculine adjective.

Notes. Adult females of *L. maculosus* are most similar those of *L. melliodorae* and *L. parathrix*. See notes under *L. melliodorae* for a comparison. Adult females of *L. maculosus* can be distinguished by having (i) two size classes of macrotubular duct on both the dorsal and ventral body surfaces (*L. melliodorae* and *L. parathrix* have only one size class per body surface); and (ii) numerous minute sclerotic invaginations on the dorsum, each with interior margin sinusoidal (*L. parathrix* without minute sclerotic invaginations, *L. melliodorae* with minute sclerotic invaginations urn-shaped, interior margin convex).

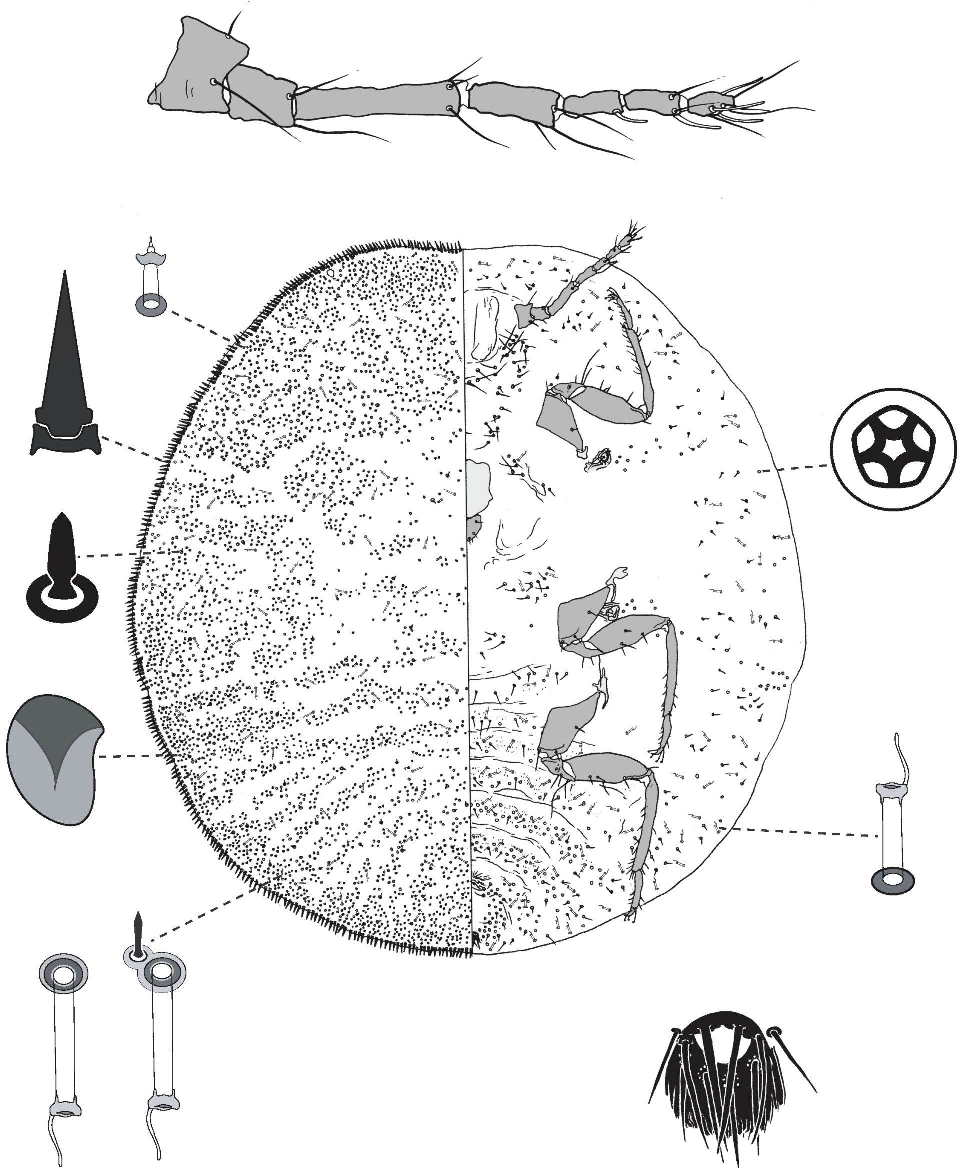

Figure 8. Adult female of *Lachnodius maculosus* sp. n.

HMB's Specimen Index card for collection 161/54 notes that the adult females were laying eggs in large numbers under the bark.

Material examined. ***Holotype***: **South Australia**: adult female, on slide: under bark of *Eucalyptus* sp., National Park, Belair, 5 Dec 1954, DC Swan, HMB Specimen Index No. 161/54 (ANIC). ***Paratypes***: **South Australia**: two adult females, same data as holotype (ANIC).

Lachnodius melliodorae Beardsley, Gullan & Hardy, sp. n.

http://zoobank.org/E160E86A-DB9D-494E-A1B9-A2B019F16EC7
Fig. 9

Diagnosis. Dorsum with numerous urn-shaped sclerotic invaginations; marginal fringe of curved setae; some dorsal macrotubular ducts with seta touching rim; anal ring invaginated.

Description. Adult female (n = 15). Body outline circular to ovate; length 1.96–5.74 mm (4.02 mm for holotype), greatest width 1.53–3.90 mm (3.64 mm for holotype). Eyes dorsal, 38–45 µm wide. Antennae seven-segmented; length 680–882 µm; with 4–11 hair-like setae on segment I, 6–9 hair-like setae on segment II, 8–11 hair-like setae on segment III, 7–8 hair-like seta on segment IV, 3–5 hair-like setae + one fleshy seta on segment V, 5–6 hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment V. Tentorial box with anterior extension of the dorsal arms, 350–475 µm long, 135–165 µm wide. Labium 135–165 µm long, 165–200 µm wide. Spiracles 140–225 µm long, 80–135 µm wide across atrium. Legs increasing in size caudad; fore legs: trochanter + femur 505–690 µm, tibia 410–560 µm, tarsus 183–250 µm; mid legs: trochanter + femur 548–750 µm, tibia 410–570 µm, tarsus 195–265 µm; hind legs: trochanter + femur 540–790 µm, tibia 490–590 µm, tarsus 200–263 µm; claw 45–63 µm; fore coxa with six setae, mid and hind coxae each with five setae, trochanter with 8–15 setae, femur with 20–37 setae, tibia with 28–50 setae, tarsus with 11–21 setae; tarsal digitules 73–93 µm long, claw digitules 45–68 µm long; translucent pores on all segments of hind leg, ca. 150 pores on dorsal surface and ca. 90 pores on ventral surface. Anal ring invaginated, cuticle surrounding ring sclerotic, 58–108 µm wide, with 10–15 setae; ring setae 45–108 µm long. Pair of elongate caudal setae usually absent, present in one specimen, ca. 28 µm long.

Dorsum. Derm beset with sclerotic spicules (i.e., well-developed microtrichia), in addition to sclerotic urns, each 4–6 µm wide. Dorsal setae lanceolate, 5–6 µm long, scattered over dorsum. Macrotubular ducts 15–20 µm long, with rim of dermal orifice 3–7 µm wide, ducts diminishing in size cephalad, many ducts with one seta affixed to rim of dermal orifice. Microtubular ducts ca. 5 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of ca. 225 setae on each side of body; each seta slender and recurved, 15–23 µm long; marginal fringe interrupted by U-shaped sclerite between thorax and abdomen.

Venter. Ventral setae 20–50 µm long; elongate setae medial of each coxa decreasing in size caudad: 125–165 µm long near fore coxa, 50–95 µm long near hind coxa; longest setae on head 153–200 µm long. Macrotubular ducts each ca. 15 µm long, with rim of dermal orifice ca. 6 µm wide, found along margin and in a transverse row across each abdominal segment. Quinquelocular pores of two distinct size-classes: (i) larger pores ca. 5.5 µm in diameter, found on posterior abdominal segments; and (ii) smaller pores ca. 4 µm in diameter, near spiracles and along margin.

Notes. Adult females of *L. melliodorae* are most similar those of *L. parathrix* and *L. maculosus*. These three species share (i) a marginal fringe composed of close-set setae inter-

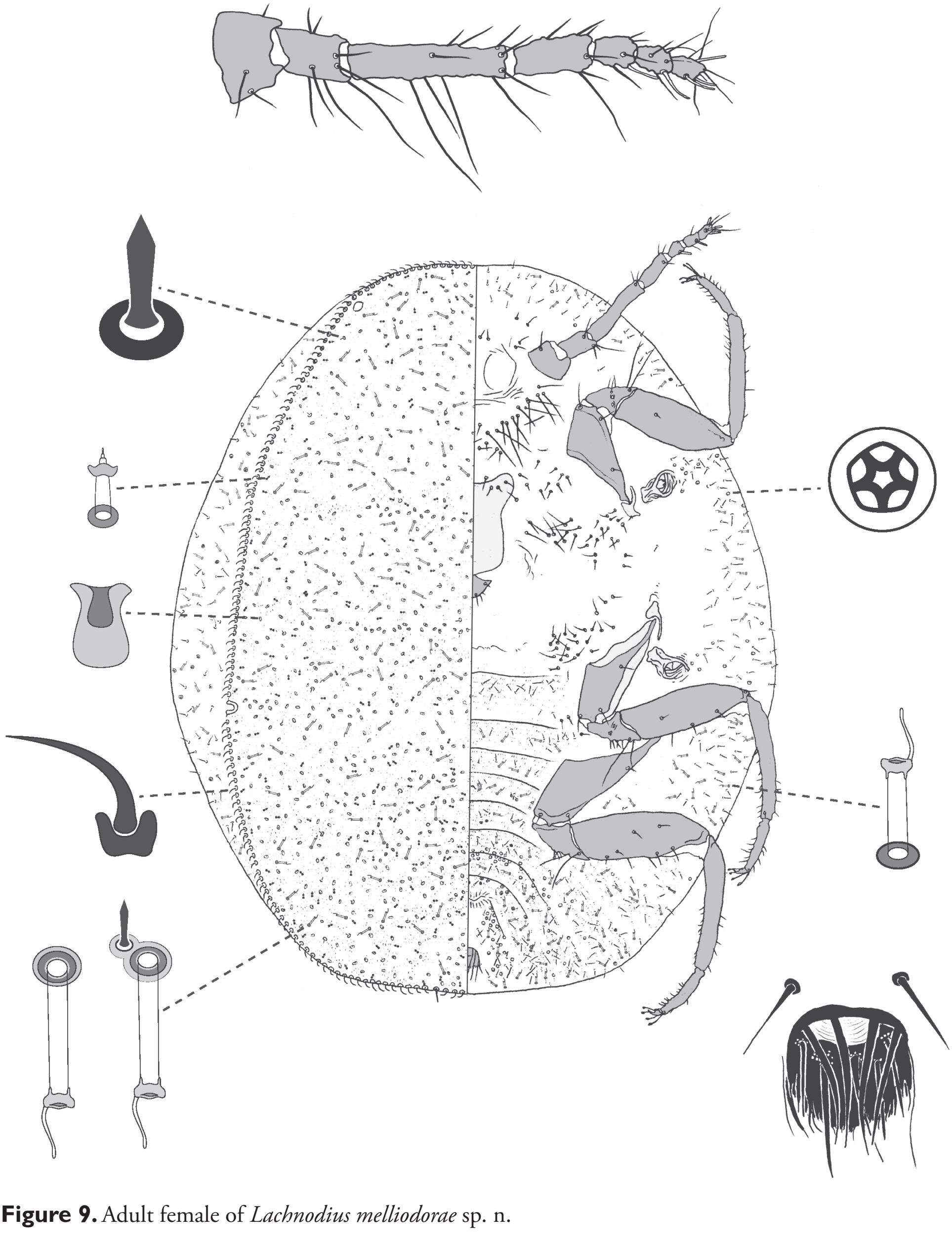

Figure 9. Adult female of *Lachnodius melliodorae* sp. n.

rupted between the thorax and abdomen; (ii) two distinct size classes of quinquelocular pores on the venter; and (iii) several dorsal macrotubular ducts with a seta affixed to the dermal orifice. Adult females of *L. melliodorae* can be distinguished from those of *L. parathrix* and *L. maculosus* by having (i) recurved marginal setae (marginal setae straight in *L. parathrix* and *L. maculosus*) and (ii) an U-shaped sclerite between the thorax and abdomen on the margin on each side of the body (sclerite absent in *L. parathrix* and *L. maculosus*).

Young adult females collected near Benalla, Victoria, by PJG in 1996 and 1997 were pale yellow in life with dorsomedial longitudinal stripe of red-wine color; the anterior spiracular furrow was visible as a pale line on each side of the body. The dorsum was naked (no secretion), but each seta in the marginal fringe was covered in a glassy secretion. The second-instar female had a salmon-colored dorsum.

The type series is restricted to specimens collected at Lower Plenty in Victoria, where JWB made several collections of all instars of this species.

First-instar nymph (n = 8). Body outline ovate; length 280–360 µm, greatest width 215–290 µm. Eyes 12–15 µm wide. Antennae six-segmented but appearing 5-segmented due to partial fusion of segments III and IV; length 65–91 µm; with three hair-like setae on segment I, two hair-like setae on segment II, two hair-like setae on segment III, one fleshy seta on segment IV, one fleshy seta + two hair-like setae on segment V, three fleshy setae + six hair-like setae on segment VI. Tentorial box 63–68 µm long, 50–58 µm wide. Labium 20–25 µm long, 30–33 µm wide. Spiracles ca. 15 µm long, ca. 7 µm wide across atrium. Legs: trochanter + femur 68–75 µm, tibia 30–40 µm, tarsus 43–53 µm; claw 12–14 µm; coxa with ca. six setae, trochanter with four setae, femur with five setae, tibia with four setae, tarsus with five or six setae; tarsal digitules unequal, large proximal digitule 25–32 µm long, small distal digitule ca. 20 µm long, claw digitules 13–15 µm long. Anal ring 17 µm wide, with six setae, each seta ca. 20 µm long. Pair of elongate caudal setae 143–163 µm long.

Dorsum. Derm beset with weakly sclerotic spots, each 2–5 µm in greatest dimension. Dorsal setae ca. 5 µm long; two longitudinal rows on each side of body, medial row with two setae on prothorax, and one seta on each segment from mesothorax to abdominal segment VII, submedial row with three setae on prothorax and one seta on each segment from mesothorax to abdominal segment I. Microtubular ducts each ca. 5 µm long, with rim of dermal orifice subelliptical, ca. 2 µm wide and 3 µm long, two longitudinal rows on each side of body, medial row with one duct on each segment from head to metathorax + abdominal segment VIII, and submarginal row with two ducts on prothorax, one duct on each thoracic segment and abdominal segments I and V (Note: it was an arbitrary decision to include the ducts on each side of head and abdominal segment VIII in the “medial” row). Dorsum delimited by fringe of 31–34 setae on each side of body (excluding caudal setae), each seta 9–15 µm long and 7–9 µm width at base above socket, deltate, with anterolateral margin sinusoidal and posteromedial margin straight; weakly sclerotic cuticle surrounding each setal socket, these sclerotic areas coalescing around the three most posterior fringe setae and the caudal seta, forming broad caudal sclerotization.

Venter. Ventral setae 2–5 µm long, in three longitudinal rows on abdomen; one elongate (ca. 18 µm long) seta medial of each coxa, three elongate setae (18–27 µm long) in longitudinal row on each side of head. Multilocular pores trilocular, 5 µm in diameter; one near each spiracle. Ventral lobe seta absent.

Notes. The first-instar nymphs of *L. melliodorae* are most similar to those of *L. froggatti* and *L. lectularius*, which also have (i) dorsal sclerotic spots (poorly developed in *L. froggatti*); (ii) stout marginal setae subtended by patches of sclerotic cuticle; and (iii) broad caudal sclerotizations (but in *L. lectularius*, only the caudal seta and 1 enlarged fringe seta are part of the sclerotization). The first-instar nymphs of *L. eucalypti* lack both the sclerotized area surrounding the socket of each marginal seta and the broad caudal sclerotizations, but have dorsal sclerotic spots. The nymphs of all four species have a similar arrangement of ducts, pores and setae. The first-instar nymphs of *L. melliodorae* can be distinguished from those of *L. eucalypti*, *L. froggatti* and *L. lectularius* by the distinctive shape of the marginal setae: deltate, with anterolateral margin sinusoidal and posteromedial margin straight, and base broad (marginal setae of *L. eucalypti* mostly falcate, with setal base constricted; of *L. froggatti* falcate but shorter than those of *L. eucalypti*; of *L. lectularius* more elongate, conical, with both margins straight).

Etymology. The species name refers to the name of the host from which the type material was collected. The species epithet is in the genitive singular.

Material examined. ***Holotype***: **Victoria**: adult female, on slide: ex open pit gall on twig, *Eucalyptus melliodora*, Lower Plenty, 19 Dec 1971, JWB (ANIC). ***Paratypes***: **Victoria**: two adult females, same data as holotype (ANIC); four adult females, three second-instar females, same data as holotype, except V-241, 12 Dec 1971 (BPBM); one parasitized second-instar female, same data as holotype, except 16 Oct 1971; four adult females, one second-instar female and eight first-instar nymphs, same data as holotype except 1 Jan 1972 (first-instar nymphs reared in lab from ovisac) (BPBM except one slide of nymphs in ANIC).

Additional material: two adult females, two second-instar females with pharate adults: ex pits on stems, *Eucalyptus* sp. sapling, 10 km NNW of Benalla, roadside, 36.48S 145.95E, 22 Jun 1996 and 25 Apr 1997, PJG (ANIC). **New South Wales**: one adult female: ex open pit twig gall, *Eucalyptus* sp., 15 miles [24 km] S of Kempsey, Pacific Highway, 26 Mar 1972, JWB (BPBM). **South Australia**: one adult female: under bark of *E. viminalis*, 5 km S of Mylor, Mt Lofty Ranges, 18 Nov 1979 MS Harvey and D Cukier (ANIC).

Lachnodius newi Beardsley, Gullan & Hardy, sp. n.

http://zoobank.org/83A4BFEC-226E-4382-8989-F674F704A2B3
Fig. 10

Diagnosis. Dorsum without sclerotic invaginations; marginal fringe of curved setae; anal ring invaginated.

Description. Adult female (n = 1). Body outline of holotype slightly oblong; length 1.98 mm, greatest width 1.35 mm. Eyes 33 µm wide. Antennae seven-segmented; length 490 µm; with seven hair-like setae on segment I, ca. four hair-like setae on segment II, ten hair-like setae on segment III, four hair-like seta on segment IV, two hair-like setae + one fleshy seta on segment V, three hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment V. Tentorial box with anterior extension of the dorsal arms, 245 µm long, 168 µm wide. Labium 98 µm long, 123 µm wide. Spiracles 115–130 µm long, 75–82 µm wide across atrium. Legs

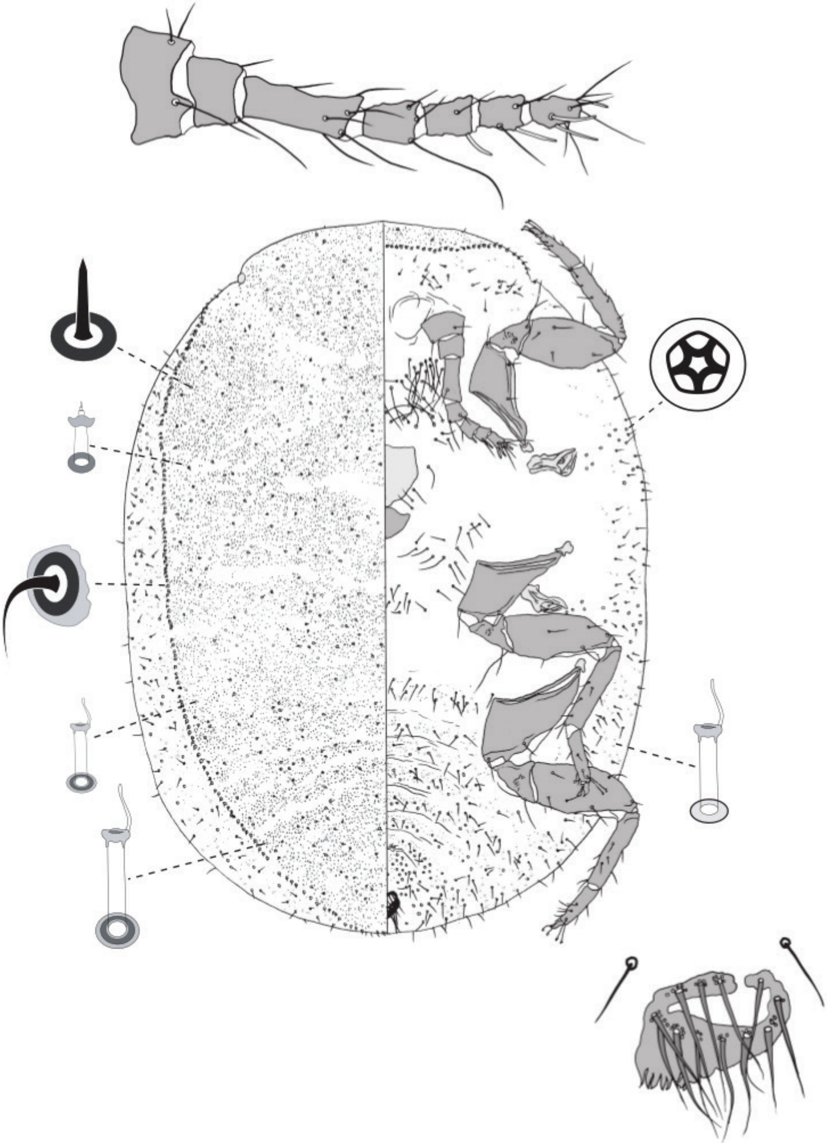

Figure 10. Adult female of *Lachnodius newi* sp. n.

increasing in size caudad; fore legs: trochanter + femur 360 µm, tibia 340 µm, tarsus 130 µm; mid legs: trochanter + femur 385 µm, tibia 350 µm, tarsus 140 µm; hind legs: trochanter + femur 390 µm, tibia 335 µm, tarsus 133 µm; claw 38–40 µm; fore coxa with six setae, mid and hind coxae each with five setae, trochanter with four setae, femur with ca. 12 setae, tibia with 14–16 setae, tarsus with ten or eleven setae; tarsal digitules 63–70 µm long, claw digitules 48 µm long; translucent pores on all segments of hind leg. Anal ring invaginated, cuticle surrounding ring sclerotic, 78 µm wide, with 12 setae; ring setae 63–75 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm densely covered with sclerotic spicules (i.e., well-developed microtrichia). Sclerotic urns and varioles absent. Dorsal setae ca. 3 µm long, scattered over dorsum. Macrotubular ducts ca. 10 µm long, with rim of dermal orifice ca. 5 µm wide. Microtubular ducts ca. 5 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of ca. 180 setae on each side of body; each seta slender and recurved, length of setae ca. 13 µm, each setal socket surrounded by irregular patch of sclerotic cuticle.

Venter. Ventral setae 10–40 µm long; elongate setae medial of each coxa decreasing in size caudad: ca. 68 µm long near fore coxa, ca. 45 µm long near hind coxa; longest setae on head ca. 105 µm long. Macrotubular ducts each ca. 15 µm long, with rim of dermal orifice ca. 5 µm wide, found along margin and in transverse band across each abdominal segment. Quinquelocular pores 5 µm in diameter, dense on posterior abdominal segments, clustered around spiracles.

Etymology. This species is dedicated to Dr TR New, of the former Department of Zoology (now Ecology, Environment and Evolution), La Trobe University, who accompanied JWB during many collecting trips made in Victoria during 1971–72, and who guided JWB to the spot where this species was discovered. The species epithet is a noun in the genitive singular.

Notes. The holotype is the only specimen known for this species, but it is distinctive. The specimen is relatively small and probably not fully expanded. However, the modest size of the antennae and legs, in comparison with other twig gall-inhabiting species (e.g., *L. lectularius*) suggests that even fully expanded adults of *L. newi* would not measure much more than 4 mm long. The adult female of *L. newi* would be confused most easily with those of *L. melliodorae*, as both species have strongly recurved marginal setae. The adult female of *L. newi* can be distinguished from those of *L. melliodorae* by lacking urn-shaped sclerotic structures on the dorsum (present in *L. melliodorae*). In their place are heavily sclerotized microtrichia. The adult female of *L. newi* can be further differentiated from those of *L. melliodorae* by having no dorsal macrotubular ducts with a seta touching the rim of the dermal orifice (some present in *L. melliodorae*) and by lacking long setae at the middle of the posterolateral edge of antennal segment III.

Material examined. ***Holotype***: **Victoria**: adult female, on slide: ex shallow pit gall in twig, *Eucalyptus viminalis*, Otway Ranges, Parker Road, heath area, 27 Oct 1971 JWB, V-168 (ANIC).

Lachnodius parathrix Beardsley, Gullan & Hardy, sp. n.

http://zoobank.org/D3B700AC-23F7-47EF-9C94-DCF5F4C27538

Figs 2c, 11

Diagnosis. Dorsum without sclerotic invaginations; marginal fringe of conical setae; some dorsal macrotubular ducts with seta touching rim; anal ring invaginated.

Description. Adult female (n = 3). Body outline circular; length 1.60–2.70 mm (2.70 mm for holotype), greatest width 1.50–2.22 mm (2.08 mm for holotype). Eyes 25–40 µm wide. Antennae seven-segmented; length 405–700 µm; with six hair-like setae on segment I, six hair-like setae on segment II, 3–6 hair-like setae on segment III, four hair-like seta on segment IV, one fleshy seta on segment V, two hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment V. Tentorial box with anterior extension of the dorsal arms, 150–210 µm long, 125–170 µm wide. Labium 90–110 µm long, 75–110 µm wide. Spiracles 88–110 µm long, 45–70 µm wide across atrium. Legs increasing in size caudad; fore legs: trochanter + femur 280–540 µm, tibia 210–420 µm, tarsus 120–170 µm; mid legs: trochanter + femur 290–560 µm, tibia 210–420 µm, tarsus 120–180 µm; hind legs: trochanter + femur 320–610 µm, tibia 245–470 µm, tarsus 125–180 µm; claw 30–45 µm; coxa with six setae, trochanter with 5–7 setae, femur with 10–16 setae, tibia with 18–26 setae, tarsus with 9–12 setae; tarsal digitules 50–70 µm long, claw digitules 30–50 µm long; translucent pores on all segments of hind leg (except coxae of one female), ca. 80 pores on dorsal surface and ca. 50 pores on ventral surface. Anal ring invaginated, cuticle surrounding ring sclerotic, 63–77 µm wide, with 12–16 setae; ring setae 35–90 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm beset with sclerotic spicules (i.e., well-developed microtrichia). Sclerotic urns and varioles absent. Dorsal setae lanceolate, 3–5 µm long, sparsely scattered over dorsum. Macrotubular ducts 10–12 µm long, with rim of dermal orifice ca. 5 µm wide; many of larger ducts with one seta affixed to rim of dermal orifice. Microtubular ducts ca. 4 µm long, with rim of dermal orifice ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of 210–250 setae on each side of body; each seta with acute apex, length of setae 20–35 µm; marginal fringe interrupted between thorax and abdomen.

Venter. Ventral setae 10–35 µm long; elongate setae medial of each coxa (50–110 µm long), and in a transverse band posterior of frontal lobes (longest seta 105–135 µm long). Macrotubular ducts each 10–15 µm long, with rim of dermal orifice 3–4 µm wide, found along margin and in transverse band across each abdominal segment. Quinquelocular pores of two distinct size-classes: (i) larger pores 5–6 µm in diameter, found on posterior abdominal segments; and (ii) smaller pores ca. 3 µm in diameter, near spiracles and along margin.

Second-instar female (n = 1). Broadly oval, length 2.0 mm. Antennae 6-segmented, short (160–190 µm total length), tapering base to apex, apical segment longest. Legs short, broad, tibiae and tarsi fused, claws weakly developed. Anal ring ca. 40 µm wide, with 10 setae each ca. 25 µm maximum length; a pair of setae, 27–30 µm long, just anterior to anal ring. Dorsum with sparse, small, peg-like setae ca. 4–8 µm long; tubular ducts apparently absent. Marginal fringe with ca. 140 conical setae, each 35–45 µm long, on each side of body. Ventral setae very sparse, filiform, up to 15 µm long; tubular ducts absent; with a widely spaces series of quinquelocular pores, each 3–4 µm in diameter, just inside the marginal fringe and a very few on thorax between margin and spiracles.

Etymology. The species name is based on the Greek words *para*, meaning near or beside, and *thrix*, meaning hair, referring to the close-set setae forming the marginal fringe. It is a noun in apposition.

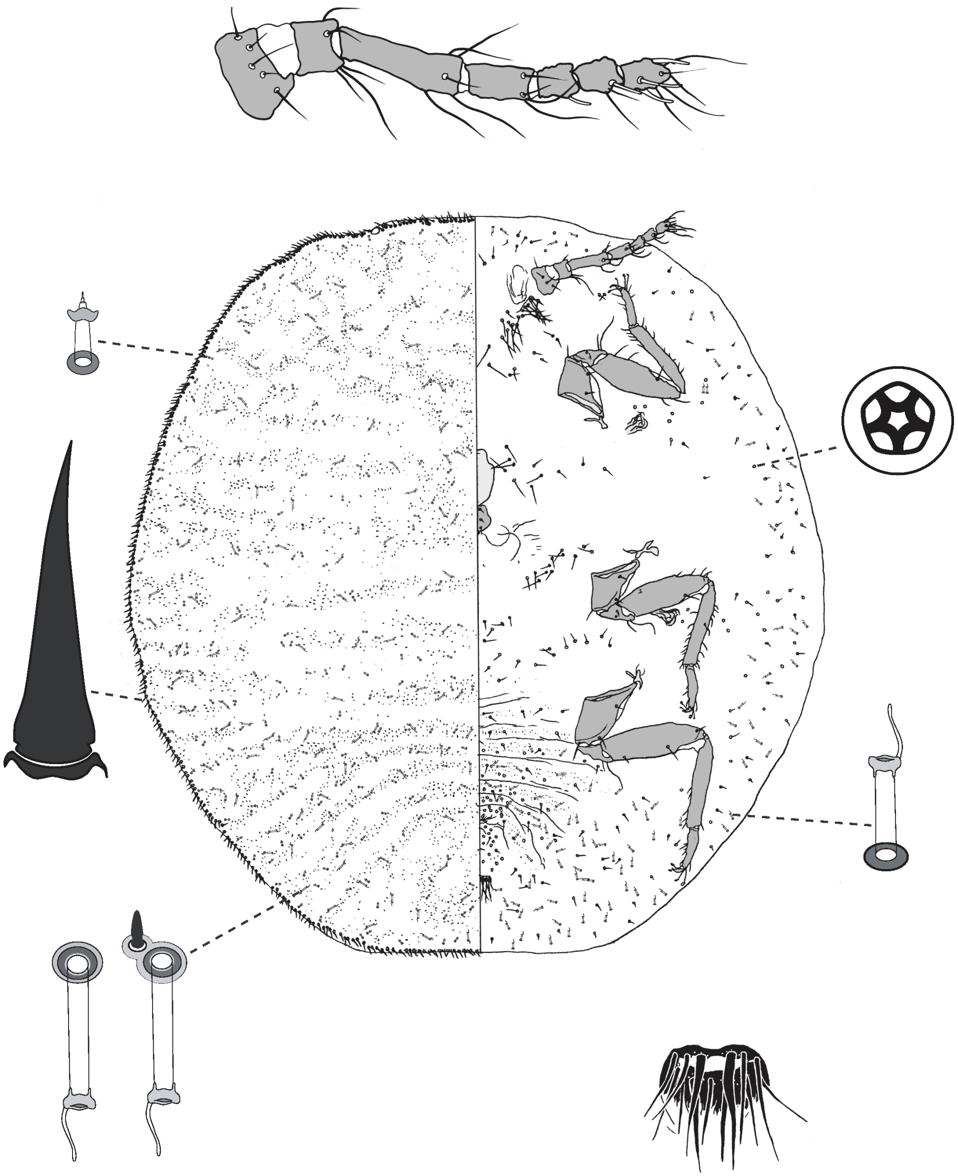

Figure 11. Adult female of *Lachnodius parathrix* sp. n.

Notes. The description of the adult female is based on specimens from both Victoria and New South Wales because they agree in all diagnostic features. The adult female from near Narooma has longer antennae and leg segments and appears to have no translucent pores on the hind coxae, compared with the two Victoria females, but this variation may be due to differences in nutrition or developmental temperatures. Adult females of *L. parathrix* are most similar those of *L. melliodorae* and *L. maculosus*, but can be easily distinguished by lacking the peculiar dorsal urns and varioles present in those species. The two known host species of *L. parathrix* belong to *Eucalyptus* series *Radiatae* and are characterized by the juvenile leaves having numerous oil glands (Brooker 2000).

Material examined. ***Holotype***: **Victoria**: adult female, on slide: ex open pit gall on young twig, *Eucalyptus radiata*, 15 miles [24 km] W of Drouin, Princess Highway, 23 Jan 1972, JWB (ANIC). ***Paratypes***: **Victoria**: one adult female, same data as holotype (BPBM); one pre-adult female exuviae, same data as holotype except: 20 miles [32 km] W of Drouin, 30 Jan 1972 (BPBM). **New South Wales**: one adult female: ex pit on midrib of leaf, *E. elata*, ca. 8 km WNW of Narooma, Wagonga Scenic Drive, 36.20S, 150.05E, 31 Dec 2008, PJG (ANIC).

Lachnodius sealakeensis Gullan & Hardy, sp. n.

http://zoobank.org/2FCC872E-35E0-4BCF-88F1-FC47316422B5
Figs 2d, 12

Diagnosis. Dorsum with dermal orifice of each microtubular duct surrounded by sclerosis; marginal fringe of truncate setae; dorsal setae capitate; anal ring invaginated.

Description. Adult female (n = 16). Body outline oval; length 0.84–1.45 mm (1.18 mm for holotype), greatest width 0.70–1.28 mm (0.90 mm for holotype). Eyes not apparent. Antennae seven-segmented; length 230–355 µm; with two hair-like setae on segment I, one hair-like seta on segment II, one hair-like seta on segment III, two hair-like seta on segment IV, one fleshy seta on segment V, two hair-like setae + one fleshy seta on segment VI and six hair-like setae + three fleshy setae on segment V. Tentorial box with anterior extension of the dorsal arms, 138–190 µm long, 123–155 µm wide. Labium 60–75 µm long, 60–100 µm wide. Spiracles 45–68 µm long, 25–35 µm wide across atrium. Legs increasing in size caudad; fore legs: trochanter + femur 165–250 µm, tibia 105–175, tarsus 80–125 µm; mid legs: trochanter + femur 165–263 µm, tibia 105–165 µm, tarsus 90–125 µm; hind legs: trochanter + femur 190–275 µm, tibia 110–175, tarsus 85–125 µm; claw 28–38 µm; fore coxa with six setae, mid and hind coxae each with five setae, trochanter with four setae, femur with 6–8 setae, tibia with 6–8 setae, tarsus with 7–9 setae; tarsal digitules 45–60 µm long, claw digitules 25–40 µm long; translucent pores on all segments of hind leg. Anal ring invaginated, cuticle surrounding ring sclerotic, 38–75 µm wide, with 10–12 setae; ring setae 40–73 µm long. Pair of elongate caudal setae absent.

Dorsum. Derm covered with sclerotic spicules (i.e., well-developed acanthae or microtrichia). Sclerotic urns and varioles absent but dermal orifice of each microtubular duct surrounded by sclerotic region. Dorsal setae capitate 5–7 µm long, scattered over dorsum. Macrotubular ducts absent. Microtubular ducts ca. 5 µm long, with oral rim ca. 2 µm wide, scattered over dorsum. Dorsum delimited by fringe of 110–150 setae on each side of body, each seta subconical, most setae with truncate, serrated apices, a few setae with acute apices, length of setae 25–45 µm.

Venter. Ventral setae 10–30 (mostly 20–25) µm long; elongate setae medial of each coxa decreasing in size caudad: 50–80 µm long near fore coxa, 25–30 µm long

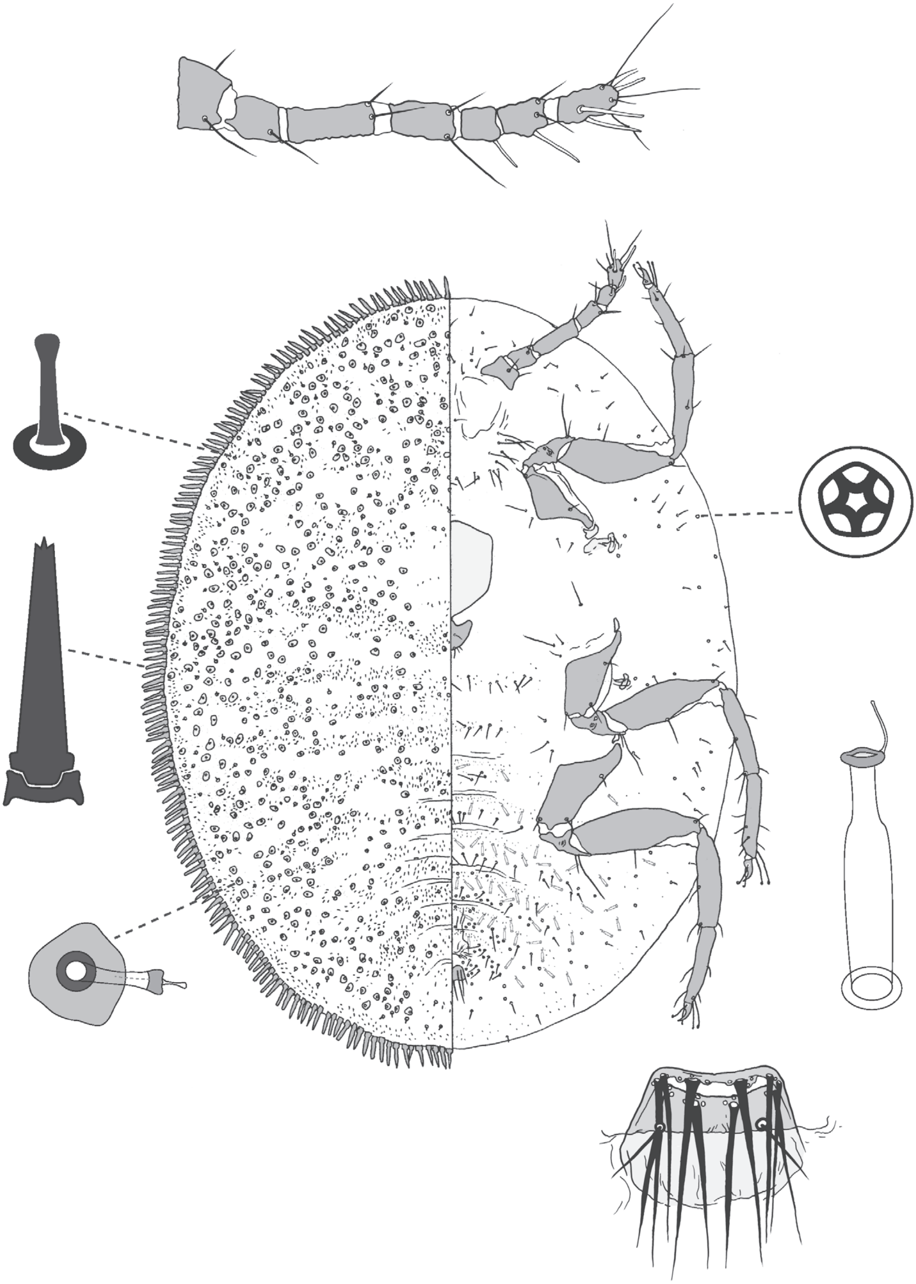

Figure 12. Adult female of *Lachnodius sealakeensis* sp. n.

near hind coxa; longest setae on head 63–123 µm long. Macrotubular ducts each ca. 15 µm long, with oral rim ca. 5 µm wide, duct shaft subtending vestibule constricted; in transverse band across each abdominal segment. Quinquelocular pores of one size-classes: 4–5 µm in diameter, on posterior abdominal segments and around margin, small clusters around spiracles.

Etymology. The species name refers to the type locality, Sea Lake, Victoria. The name is an adjective with the suffix derived from the Latin *-ensis*, denoting place or locality.

Notes. Adult females of *L. sealakeensis* are most superficially similar to those of *L. maculosus*; both species occur under bark, have an invaginated anus, and relatively robust, subconical marginal setae. Adult females of *L. sealakeensis* can be readily distinguished from those of *L. maculosus* by (i) the lack of dorsal macrotubular ducts (two size-classes present in *L. maculosus*); (ii) dorsal microtubular ducts with sclerotic surrounds (these are unique among *Sphaerococcopsis* and *Lachnodius* spp.); (iii) capitate dorsal setae (lanceolate in *L. maculosus*); and (iv) the ventral surface of abdomen with macrotubular ducts with the shaft constricted distally (not constricted distally in *L. maculosus*). Capitate dorsal setae like those of *L. sealakeensis* are also present on adult female of *Sphaerococcopsis platynotum* Beardsley and *S. umbilicus* Beardsley. These differ from *L. sealakeensis* in having (i) 6-segmented antennae (7-segmented in *L. sealakeensis*); (ii) hind legs much larger than fore and mid legs (all legs subequal in *L. sealakeensis*); and (iii) venter much larger than dorsum (venter and dorsum subequal in *L. sealakeensi*).

This is the only species treated here that was not part of JWB's view of *Lachnodius* since the only known specimens were not collected until after his death. NBH and PJG share authorship of its name.

Material examined. ***Holotype***: **Victoria**: adult female, on slide: ex pit under loose bark of *Eucalyptus oleosa*, ca. 6 km N of Sea Lake, intersection of Lake Tyrell Road and Calder Highway, 35.45S, 142.83E, NBH and PJG, 5 Feb 2005 (ANIC). ***Paratypes***: **Victoria**: 17 adult females (all on separate slides), same data as holotype, one female is DNA voucher NH47 (ANIC except 2 slides in NMV; also 2 slides deposited in QDPC in 2009 but could not be located in 2018).

Discussion

This taxonomic work was begun in 1971 by the late Dr JW Beardsley, while he was a visiting Fulbright Research Scholar in the then Zoology Department, La Trobe University, Bundoora, Victoria. During that period, Beardsley encountered a number of undescribed taxa that he felt were new species of *Lachnodius* Maskell. Subsequently, he borrowed specimens of *Lachnodius* from Australian collections, especially those made by the late Ms HM Brookes (formerly of the Waite Agricultural Research Institute of the University of Adelaide) and PJG. He also visited the New Zealand Arthropod Collection in Auckland to examine Maskell's type material. The demands of other work, including ten years as the Chair of the Department of Entomology at the University of Hawaii, delayed progress on his *Lachnodius* revision. That delay ended with his retirement, and by 1993, he had completed written descriptions for several species. However, arthritis in his hands kept him from being able to illustrate them and, when Beardsley died suddenly on 5 February 2001 (Anwar 2001), his work on *Lachnodius* was still unpublished. At that point, PJG acquired Beardsley's notes and slides, with the intention of completing his work, an effort that NBH joined.

When PJG and NBH took over, they modified Beardsley's taxonomic concepts. Specifically, of the species he included in his unpublished revision of *Lachnodius*, they described one as a species of *Opisthoscelis* (Hardy and Gullan 2010), one as the sole member of the genus *Heathcotia* Hardy & Beardsley (Hardy et al. 2011), and six as species of *Lobimargo* Hardy & Gullan (Hardy et al. 2011). This paper treats what is left of Beardsley's concept of *Lachnodius*, and completes his revisionary work. Nevertheless, the monophyly of what we have left of Beardsley's concept of *Lachnodius* is uncertain. These species clearly are closely related to *Sphaerococcopsis*, as well as to *Opisthoscelis* Schrader and *Tanyscelis* Hardy & Gullan. It could be that some are more closely related to these other genera than to some of the other species of *Lachnodius*. More phylogenetic work is required to resolve these relationships.

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References

Andersen AN (1989) Impact of insect predation on ovule survivorship in *Eucalyptus baxteri*. Journal of Ecology 77: 62–69. https://doi.org/10.2307/2260916

Anwar Y (2001) John 'Jack' Beardsley Jr., Isle expert on insects, dead at 74. HonoluluAdvertiser.com, Wednesday, February 14, 2001. http://the.honoluluadvertiser.com/2001/Feb/14/214localnews26.html [accessed 17 July 2017]

Beardsley JW (1972) Systematics of Australian coccid genera *Lachnodius* Maskell and *Sphaerococcopsis* Cockerell (Homoptera). 14th International Congress of Entomology Abstracts, 144.

Beardsley JW (1974) A review of the genus *Sphaerococcopsis* Cockerell, with descriptions of two new species (Homoptera: Coccoidea). Proceedings of the Hawaiian Entomological Society 21: 329–342.

Beardsley JW (1982) On the taxonomy of the genus *Pseudopsylla* Froggatt, with a redescription of the type species (Homoptera: Coccoidea). Proceedings of the Hawaiian Entomological Society 24: 31–35.

Brooker MIH (2000) A new classification of the genus *Eucalyptus* L'Hér. (Myrtaceae) Australian Systematic Botany 13: 79–148. https://doi.org/10.1071/SB98008

Brooker I (2002) Botany of the eucalypts. In: Coppen JJW (Ed.) Eucalyptus: The genus *Eucalyptus*. CRC Press, London, 464 pp. https://doi.org/10.4324/9780203219430_chapter_1

Chippendale GM (1988) *Eucalyptus*, *Angophora* (Myrtaceae). In: George AS (Ed.) Flora of Australia 19. Australian Government Publishing Service, Canberra, 540 pp.

Cook LG, Gullan PJ (2004) The gall-inducing habit has evolved multiple times among the eriococcid scale insects (Sternorrhyncha: Coccoidea: Eriococcidae). Biological Journal of the Linnean Society 83: 441–452. https://doi.org/10.1111/j.1095-8312.2004.00396.x

Cox JM, Williams DJ (1987) Do the Eriococcidae form a monophyletic group? Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri' 43: 13–17.

Deitz LL, Tocker MF (1980) W. M. Maskell's Homoptera: Species-group names and type material. New Zealand Department of Scientific and Industrial Research, Information Series 146: 1–76.

Fernald ME (1903) A catalogue of the Coccidae of the world. Bulletin of the Hatch Experiment Station of the Massachusetts Agricultural College 88: 1–360.

Ferris GF (1955) Some miscellaneous Coccoidea (Insecta: Homoptera). (Contribution No. 91). Microentomology 20: 22–29.

Froggatt WW (1917) A descriptive catalogue of the scale insects ("Coccidae") of Australia. (Part II). Agricultural Gazette of New South Wales 28: 134–140.

Froggatt WW (1921) A descriptive catalogue of the scale insects ('Coccidae') of Australia. Part III. Department of Agriculture, New South Wales Science Bulletin 19: 1–43.

García Morales M, Denno BD, Miller DR, Miller GL, Ben-Dov Y, Hardy NB (2016) ScaleNet: a literature-based model of scale insect biology and systematics. Database. https://doi.org/10.1093/database/bav118 http://scalenet.info [accessed 10 September 2018]

Gullan PJ (1984a) Froggatt's accession notebooks. Australian Entomological Magazine 10: 91–92.

Gullan PJ (1984b) A revision of the gall-forming coccoid genus *Apiomorpha* Rübsaamen (Homoptera: Eriococcidae: Apiomorphinae). Australian Journal of Zoology Supplementary Series, No. 99, 203 pp.

Gullan PJ, Miller, DR, Cook LG (2005) Gall-inducing scale insects (Hemiptera: Sternorrhyncha: Coccoidea). In: Raman A, Schaefer CW, Withers TM (Eds) Biology, Ecology, and Evolution of Gall-Inducing Arthropods. Science Publishers, Enfield (USA) & Plymouth (UK), 159–229.

Gullan PJ, Williams DJ (2010) Helen May Brookes (3.11.1917–1.1.2008): her life and contributions to coccidology. Entomologia Hellenica 19: 170–172. https://doi.org/10.12681/eh.11587

Hardy NB, Gullan PJ (2007) A new genus and four new species of felt scales on *Eucalyptus* (Hemiptera: Coccoidea: Eriococcidae) in south-eastern Australia. Austral Entomology 46: 106–120. https://doi.org/10.1111/j.1440-6055.2007.00576.x

Hardy NB, Gullan PJ (2010) Australian gall-inducing scale insects on *Eucalyptus*: revision of *Opisthoscelis* Schrader (Coccoidea, Eriococcidae) and descriptions of a new genus and nine new species. ZooKeys 58: 1–74. https://doi.org/10.3897/zookeys.58.507

Hardy NB, Beardsley JW, Gullan PJ (2011) Uncovering diversity of Australian *Eucalyptus*-constrained felt scales (Hemiptera: Coccoidea: Eriococcidae). Systematic Entomology 36: 497–528. https://doi.org/10.1111/j.1365-3113.2011.00577.x

Hill KD, Johnson LAS (1995) Systematic studies in the eucalypts. 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). Telopea 6(2–3): 185–504. https://doi.org/10.7751/telopea19953017

Hodgson CJ (2002) Preliminary phylogeny of some non-margarodid Coccoidea (Hemiptera) based on adult male characters. Bollettino di Zoologia Agraria e di Bachicoltura (Milano) 33(3): 129–137.

Hoy JM (1963) A catalogue of the Eriococcidae (Homoptera: Coccoidea) of the world. New Zealand Department of Scientific and Industrial Research Bulletin 150: 1–260.

International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature, 4th ed (with amendments). The International Trust for Zoological Nomenclature, The Natural History Museum, London, 306 pp. http://www.iczn.org/code [accessed 10 September 2018]

Koteja J (1974) On the phylogeny and classification of the scale insects (Homoptera, Coccinea) (discussion based on the morphology of the mouthparts). Acta Zoologica Cracoviensia 19: 267–325.

Maskell WM (1892) Further coccid notes: with descriptions of new species, and remarks on coccids from New Zealand, Australia and elsewhere. Transactions and Proceedings of the New Zealand Institute 24(1891): 1–64.

Maskell WM (1893) Further coccid notes: with descriptions of new species from Australia, India, Sandwich Islands, Demerara, and South Pacific. Transactions and Proceedings of the New Zealand Institute 25(1892): 201–252.

Maskell WM (1896) Further coccid notes, with descriptions of new species and discussions of questions of interest. Transactions and Proceedings of the New Zealand Institute 28: 380-411.

Morrison H, Morrison ER (1922) A redescription of the type species of the genera of Coccidae based on species originally described by Maskell. Proceedings of the United States National Museum (Washington) 60: 1–120. https://doi.org/10.5479/si.00963801.60-2407.1

Semple TL, Gullan PJ, Hodgson CJ, Hardy NB, Cook LG (2015) Systematic review of the Australian 'bush coconut' genus *Cystococcus* (Hemiptera: Eriococcidae) uncovers a new species from Queensland. Invertebrate Systematics 29: 287–312. https://doi.org/10.1071/IS14061

Taylor G, Keller M (2008) Obituary. Helen May Brookes: entomologist and botanical artist. Myrmecia 44(2): 26–28.

Upton MS (1997) A Rich and Diverse Fauna: The History of the Australian National Insect Collection 1926-1991. CSIRO Publishing, Collingwood, Victoria, 386 pp.

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RESEARCH ARTICLE

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The extraordinary genus *Myja* is not a tergipedid, but related to the Facelinidae s. str. with the addition of two new species from Japan (Mollusca, Nudibranchia)

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Abstract

Morphological and molecular data are presented for the first time in an integrative way for the genus *Myja* Bergh, 1896. In accordance with the new molecular phylogenies, the traditional Facelinidae is paraphyletic. Herein is presented the phylogenetic placement of true Facelinidae s. str., including the first molecular data for *F. auriculata* (Müller, 1776), type species of the genus *Facelina* Alder & Hancock, 1855. The taxonomic history of *F. auriculata* is reviewed. The genus *Myja* is related to the clade Facelinidae s. str., but shows disparate morphological traits. Two new species of the genus *Myja*, *M. karin* **sp. n.**, and *M. hyotan* **sp. n.**, are described from the Pacific waters of Japan (middle Honshu), and *M.* cf. *longicornis* Bergh, 1896 is investigated from Thailand. According to molecular analysis and review of available morphological information, the genus *Myja* contains more hidden diversity. The family-level relationship within aeolidacean nudibranchs with emphasis on the family Facelinidae is outlined. The problem of the relationship between Facelinidae Bergh, 1889 and Glaucidae Gray, 1827 is discussed. The family Glaucidae has precedence over Facelinidae and is phylogenetically related to the core group of Facelinidae s. str., but has a profoundly modified aberrant external morphology, thus making a purely molecular-based approach to the taxonomy an unsatisfactory solution. To accommodate recently discovered hidden diversity within glaucids, the genus *Glaucilla* Bergh, 1861 is restored. The family Facelinidae s. str. is separate from, and not closely related to, a clade containing the genera *Dondice* Marcus, 1958, *Godiva* MacNae 1954, *Hermissenda* Bergh, 1879, and *Phyllodesmium* Ehrenberg, 1831 (= *Myrrhine* Bergh, 1905). The oldest valid available name for the separate ex-facelinid paraphyletic clade that contains several facelinid genera is Myrrhinidae Bergh, 1905, and resurrection of this family name under provision of the ICZN article 40.1 can preliminarily solve the problem of paraphyly of the traditional Facelinidae. "Facelinidae" s. l. needs to be further divided into several separate families, pending further study.

Keywords
Facelinidae, morphological data, molecular phylogeny, *Myja*, new species, Nudibranchia, taxonomy, West Pacific Ocean

Introduction

The genus *Myja* Bergh, 1896 was described more than one century ago (Bergh 1896) and since then has never been re-described, nor phylogenetically assessed. It was originally referred to the family Tergipedidae by Bergh (1896), most likely due to some external similarities to the genus *Tergipes*. The morphological characters of the genus *Myja*, an acleioproctic anus in combination with club-shaped cerata that mimic its prey and a diminutive uniserial radula, make taxonomic assessment of this extraordinary-looking genus difficult. In the present study, we obtained recently collected specimens from the Indo-West Pacific tropics (Thailand) for the first time. These are very similar by general external and internal patterns to the type species of the genus *Myja*, *M. longicornis* Bergh, 1896 that was described from the Indo-West Pacific island of Ambon, but also show some fine-scale differences which prevent us from concluding that the Thai specimens belong to the type species of the genus. However, the unique morphological similarity between type species of the genus *M. longicornis* and our material unambiguously allows it to be included in the genus *Myja* and thus reveals the molecular phylogeny of one of the most enigmatic nudibranchs. Additionally, specimens were obtained that are externally and internally similar to the genus *Myja*, from the Pacific coast of the main Japanese island Honshu. The *Myja* from Thailand is shown to be morphologically and genetically distinct from the Japanese and all three species are described here. Furthermore, our molecular phylogenetic analysis shows that the genus *Myja* is unrelated to the family Tergipedidae, contrary to the opinion of Bergh (1896), but instead it is part of the traditional Facelinidae family. Because the family Facelinidae is composed of a large morphological and molecular assemblage (e.g., Miller 1974; Millen and Hermosillo 2012; Korshunova et al. 2017a) the phylogenetic position of the family is also tested after inclusion of the novel molecular data on *Myja*. Previously it has been shown that the traditional Facelinidae is paraphyletic (e.g., Goodheart et al. 2017, 2018) but in the absence of molecular data on the type species of the genus *Facelina* Alder & Hancock, 1855, the position of Facelinidae s. str. was uncertain. In this study we present the first molecular data for *F. auriculata* (Müller, 1776), the type species of the genus *Facelina*, and therefore we are able to identify the group of taxa that relates to Facelinidae s. str. The present analysis is corroborated by previous results (Goodheart et al. 2017, 2018), and confirms that the family Facelinidae is paraphyletic and needs to be separated into several smaller families.

Materials and methods

Collecting data

Three specimens of two new Japanese species were collected by SCUBA diving in the Pacific coast of Japan (Honshu, Osezaki) by Tatiana Korshunova, Alexander Martynov, and Hiroshi Takashige. Three specimens of *Myja* cf. *longicornis* were collected by SCUBA diving in Thailand waters by Rahul Mehrotra and Suchana Chavanich. Additional facelinid specimens were collected in UK, Norway, Sweden, and at the Sea of Japan. All specimens were preserved in 80–95% EtOH.

Morphological analysis

All specimens were examined with a stereomicroscope (MBS-9) and photographed using Nikon D-90 and D-810 digital cameras with a set of extension rings. The pharynxes were removed and processed with a weak solution of domestic bleach (NaClO). The jaws were examined using a stereomicroscope and digital cameras. The jaws and radulae were examined under a scanning electron microscope (JSM and CamScan Series II) (Figs 1–4).

Molecular analysis (Fig. 5)

Specimens of *Myja* from Japan and Thailand were sequenced for the mitochondrial genes cytochrome c oxidase subunit I (COI) and 16S rRNA, and the nuclear gene Histone 3 (H3). Additionally, one specimen of *Facelina auriculata* from the UK was sequenced. DNA extraction procedure, PCR amplification options, and sequence obtainment have been previously described in detail (Korshunova et al. 2017a, b; 2018a). Protein-coding sequences were translated into amino acids for confirmation of the alignment. All new sequences were deposited in GenBank (Table 1, highlighted in bold). Publicly available sequences of representatives of the suborder Aeolidacea, plus several outgroup taxa (*Tritonia*, *Dendronotus*, *Bonisa,* and *Janolus*) were also included in the molecular analysis. Sequences were aligned with the MAFFT algorithm (Katoh et al. 2002). Separate analyses were conducted for COI (657 bp), 16S (471 bp), H3 (327 bp), and concatenated data (1455 bp). Evolutionary models were selected using MrModelTest 2.3 (Nylander et al. 2004). Two different phylogenetic methods, Bayesian inference (BI) and Maximum Likelihood (ML), were used to infer evolutionary relationships.

Table 1. List of samples, localities, and voucher references. The species in bold font are those sequenced in this study.

Species	Voucher, Locality	COI	16S	H3
Aeolidia campbellii (Cunningham, 1871)	ZSM 20020700 Chile	KF317849	KF317837	KF317859
Aeolidia filomenae Kienberger, Carmona, Pola, Padula, Gosliner & Cervera, 2016	MNCN:15.05/74477 France	KU160588	KU160562	KU160606
Aeolidia loui Kienberger, Carmona, Pola, Padula, Gosliner & Cervera, 2016	MNCN:15.05/74483 Oregon, USA	KU160591	KU160565	KU160607
Aeolidia papillosa (Linnaeus, 1761)	ZMMU:Op-559 Russia	KX758257	KX758252	KX758261
Aeolidiella glauca (Alder & Hancock, 1845)	ZMMU Op-560 Norway	KX758255	KX758254	KX758259
Anteaeolidiella cacaotica (Stimpson, 1855)	CASIZ174212 Line Islands	JQ997030	JQ996825	JQ996926
Aeolidiella sanguinea (Norman, 1877)	MNCN/ADN51933 France	JX087537	JX087465	JX087599
Amphorina odhneri (Derjugin & Gurjanova, 1926)	ZMMU:Op-484 Russia	MF523318	MF523396	MF523244
Amphorina pallida (Alder & Hancock, 1842)	GNM9094 Scotland	KY129030	KY128821	KY128616
Bohuslania matsmichaeli Korshunova, Lundin, Malmberg, Picton & Martynov, 2018	ZMMU:Op-600 Sweden	MG323542	MG323548	MG323563
Borealea nobilis (A. E. Verrill, 1880)	ZMMU:Op-510 Russia	MF523347	MF523411	MF523271
Bulbaeolidia japonica (Eliot, 1913)	CASIZ184527 Japan	JQ997033	JQ996828	JQ996929
Bonisa nakaza Gosliner, 1981	CASIZ176146 South Africa	HM162746	HM162670	HM162579
Calma glaucoides (Alder & Hancock, 1854)	ZMMU:Op-603 Norway	MG323544	MG323550	MG323565
Catriona aurantia (Alder & Hancock, 1842)	ZMMU:Op-545 Norway	KY985467	MF523458	MG386404
Cerberilla bernadettae Tardy (1965)	MNCN/ADN51957 Spain	JX087555	JX087489	JX087625
Coryphella verrucosa (Sars M., 1829)	ZMMU:Op-521 Russia	MF523375	MF523421	MF523300
Cratena minor Padula, Araújo, Matthews-Cascon & Schrödl, 2014	ZSM:Mol:20110345 Brazil	KJ940476	–	KM079346
Cratena minor Padula, Araújo, Matthews-Cascon & Schrödl, 2014	ZSM Mol 20110338a Brazil	KJ940477	–	KM079341
Cratena minor Padula, Araújo, Matthews-Cascon & Schrödl, 2014	ZSM Mol 20110338b Brazil	KJ940478	–	KM079342
Cratena peregrina (Gmelin, 1791)	ZSM Mol 20020957 France	KJ940481	–	KM079349
Cratena peregrina (Gmelin, 1791)	ZSM Mol 20100125 Croatia	KJ940480	–	KM079347
Cratena peregrina (Gmelin, 1791)	MNCN15.05/53691 Senegal	HQ616752	HQ616715	–
Cuthona nana (Alder & Hancock, 1842)	ZMMU:Op-522 Russia	MF523376	MF523397	MF523301
Cuthonella soboli Martynov, 1992	ZMMU:Op-524 Russia	MF523378	MF523457	MF523303
Diaphoreolis viridis (Forbes, 1840)	ZMMU:Op-537 Russia	MG266028	MG266026	MG266029
Dendronotus dalli Bergh, 1879	ZMMU:Op-295 Russia	KM397001	KM397083	KM397094
Dendronotus lacteus (W Thompson, 1840)	ZMMU:Op-286 Russia	KC660034	KC611290	KC660050
Dendronotus robustus AE Verrill, 1870	ZMMU:Op-391 Russia	KM396970	KM397053	KM397120
Dondice occidentalis (Engel, 1925)	LACM2003-41.5	JQ699570	JQ699482	JQ699394
Eubranchus tricolor Forbes, 1838	ZMMU:Op-525 Norway	MF523379	MF523399	MF523304
***Facelina auriculata* (Müller, 1776)**	**ZMMU:Op-669 UK**	**MK320904**	**MK320915**	–
Facelina bostoniensis (Couthouy, 1838)	CAS184184 New Hampshire	KY129046	KY128837	KY128632
Facelina vicina (Bergh, 1882)	GNM Gastropoda 9310 Croatia	KY513634	KY513630	–
Facelinidae sp. 2	CASIZ186258 Philippines	JQ997075	JQ996879	JQ996984
Favorinus branchialis (Rathke, 1806)	MNCN15.05/53695 Spain	HQ616761	HQ616724	HQ616790
Favorinus elenalexiae Garcia & Troncoso, 2001	CASIZ178875 Costa Rica	HM162755	HM162679	HM162588

Species	**Voucher, Locality**	**COI**	**16S**	**H3**
Favorinus tsuruganus Baba & Abe, 1964	CASIZ 186044 Philippines	JX220450	JX220482	JX220418
Fiona pinnata (Eschscholtz, 1831)	CASIZ 088586 USA	KU757491	KU757615	KU757600
Fjordia lineata (Lovén, 1846)	ZMMU:Op-508 Norway	MF523345	MF523404	MF523269
Janolus longidentatus Gosliner, 1981	CASIZ176320 South Africa	HM162749	HM162673	HM162582
Glaucus atlanticus Forster, 1777	NM:W7469 Indian	JQ699603	JQ699517	JQ699429
Glaucus atlanticus Forster, 1777	UMMZ302975 North Atlantic	JQ699574	JQ699488	JQ699400
Glaucilla marginata Reinhardt & Bergh, 1864	CASIZ176985 Indian	JQ699604	JQ699518	JQ699430
Glaucilla marginata Reinhardt & Bergh, 1864	CASIZ176985 Indian	JQ699605	JQ699519	JQ699431
Godiva quadricolor (Barnard, 1927)	CASIZ176385 South Africa	HM162756	HM162680	HM162589
Gulenia monicae Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017	ZMMU:Op-408 Norway	MF523373	MF523441	MF523297
Hermissenda crassicornis (Eschscholtz, 1831)	CPIC01115 Canada	KU950178	KU950121	KU950212
Hermissenda opalescens (J. G. Cooper, 1863)	CPIC00565 USA, California	KU950191	KU950126	KU950220
Himatina trophina (Bergh, 1890)	ZMMU:Op-532 Russia	MF523389	MF523460	MF523314
Itaxia falklandica (Eliot, 1907)	ZSM Mol-20070592 Chile	MF523334	MF523467	MF523258
Luisella babai (Schmekel, 1972)	MNCN15.05/53698 Spain	HQ616783	HQ616754	HQ616717
Microchlamylla gracilis (Alder & Hancock, 1844)	ZMMU:Op-503 Norway	MF523338	MF523444	MF523262
Murmania antiqua Martynov, 2006	ZMMU:Op-399 Russia	MF523390	MF523394	MF523315
***Myja karin* sp. n.**	**ZMMU:Op-610 Japan**	**MK320900**	**MK320910**	**MK320905**
***Myja karin* sp. n.**	**ZMMU:Op-611 Japan**	**MK320901**	**MK320911**	**MK320906**
***Myja hyotan* sp. n.**	**ZMMU:Op-612 Japan**	–	**MK320912**	**MK320907**
***Myja* cf. *longicornis* Bergh, 1896**	**ZMMU:Op-667 Thailand**	**MK320902**	**MK320913**	**MK320908**
***Myja* cf. *longicornis* Bergh, 1896**	**ZMMU:Op-668 Thailand**	**MK320903**	**MK320914**	**MK320909**
Occidenthella athadona (Bergh, 1875)	ZMMU:Op-498 Russia	MF523332	MF523414	MF523256
Orienthella trilineata (O'Donoghue, 1921)	CAS179466 California	KY129064	KY128855	KY128649
Phyllodesmium tuberculatum Moore & Gosliner, 2009	CASIZ 177520 Philippines	HQ010490	HQ010525	HQ010457
Phyllodesmium jakobsenae Burghardt & Wägele, 2004	CASIZ 177576 Philippines	HQ010489	HQ010524	HQ010456
Sakuraeolis japonica (Baba, 1937)	MABIK MO0015762 Korea	KX610997	KX610997	–
Sakuraeolis enosimensis (Baba, 1930)	CASIZ178876 USA, California	HM162758	HM162682	HM162591
Samla takashigei Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017	ZMMU:Op-530 Japan	MF523384	MF523463	MF523309
Tenellia adspersa (Nordmann, 1845)	CAS184191 New Hampshire	KY129085	KY128876	KY128668
Tergipes tergipes (Forsskål in Niebuhr, 1775)	WS3463 Barents Sea	KY129090	KY128881	–
Trinchesia caerulea (Montagu, 1804)	ZMMU:Op-622 Norway	MG266024	MG266022	MG266025
Tritonia nilsodhneri Marcus Ev., 1983	CASIZ176219 South Africa	HM162716	HM162641	HM162548
Tritonia plebeia Johnston, 1828	ZMMU:Op-572 Norway	KX788134	KX788122	–
Zelentia ninel Korshunova, Martynov & Picton, 2017	ZMMU:Op-509 Russia	KY952178	MF523400	MF523242
Zeusia hyperborea Korshunova, Zimina & Martynov, 2017	ZMMU:Op-557 Russia	KX758256	KX758251	KX758260

Bayesian estimation of posterior probability was performed in MrBayes 3.2 (Ronquist et al. 2012). Four Markov chains were sampled at intervals of 500 generations. Analysis was started with random starting trees and 10^7 generations. Maximum likelihood-based phylogeny inference was performed in RAxML 7.2.8 (Stamatakis et al. 2008) with bootstrap in 1000 pseudo-replications. Final phylogenetic tree images were rendered in FigTree 1.4.2 (http://tree.bio.ed.ac.uk). Alignment from the 16S of *Myja* specimens was processed in Automatic Barcode Gap Discovery (ABGD, available at http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) with the following settings: a prior for the maximum value of intraspecific divergence between 0.001 and 0.1, 10 recursive steps within the primary partitions defined by the first estimated gap, and a gap width of 0.8. 16S alignment was analysed separately using both proposed models Jukes-Cantor (JC69) and Kimura (K80). The program Mega7 (Kumar et al. 2016) was used to calculate the uncorrected p-distances.

Results

Taxonomy and molecular analysis

The molecular analysis revealed and confirmed the position of the genus *Myja* as not related to the family Tergipedidae, but instead belonging to the Facelinidae s. str. "superclade" (Fig. 5). The part of the traditional "Facelinidae" including genera *Dondice*, *Godiva*, *Hermissenda*, and *Phyllodesmium* in turn show strong paraphyly and are distantly related to the Facelinidae s. str. (Fig. 5). Phylogenetic analysis was performed using five specimens of the genus *Myja*, sixty-one representatives of the suborder Aeolidacea, and seven outgroup specimens. The GTR model was chosen for the combined dataset for the mitochondrial COI and 16S and the nuclear H3. Bayesian Inference (BI) and Maximum Likelihood (ML) analyses based on the combined dataset yielded similar results (Fig. 5).

Molecular phylogenetic analyses among other important results also revealed phylogenetic positions of the type taxon *Facelina auriculata*, and the taxa *Glaucus* and *Glaucilla* within the proper Facelinidae s. str. "superclade" (Fig. 5) (see the Discussion for details).

Family Facelinidae s. str.

Myja Bergh, 1896

Type species. *Myja longicornis* Bergh, 1896.

Diagnosis. One pair of anterior rows of cerata, posterior cerata in rows, few (1–3) peculiar club-shaped cerata per row, anus acleioproctic, rhinophores smooth, oral tentacles present, no anterior foot corners, cnidosacs present, pharynx moderately broad, jaws with wing-shaped anterior expansion, smooth masticatory edges, radula very small, uniserial, radular teeth very narrow, triangular with strong cusp, lateral denticles small, penis unarmed, supplementary glands absent.

Species included. *Myja* cf. *longicornis* (Thailand), *Myja karin* sp. n. (Japan), *Myja hyotan* sp. n. (Japan).

Remarks. All *Myja* specimens studied here clustered together (PP = 1, BS = 100) in a maximum-supported clade. This agrees well with the results of the morphological analysis. Inside the *Myja* clade clustered maximum-supported (PP = 1, BS = 100) *Myja* cf. *longicornis* and *M. karin* sp. n. clades and *M. hyotan* sp. n. clade. The ABGD analysis of the 16S data set run with two different models revealed three potential species: *Myja* cf. *longicornis*, *M. karin* sp. n., and *M. hyotan* sp. n. Additionally, molecular phylogenetic analysis revealed that *Cratena peregrina* (Gmelin, 1791) and *Cratena minor* Padula, Araújo, Matthews-Cascon & Schrödl, 2014 specimens clustered together on two maximum-supported (PP = 1, BS = 100) clades, which are not sister to each other. Furthermore, the *Cratena minor* clade is sister to the *Myja* clade but without high node support (PP = 1, BS = 68). It is assumed that further analysis with the addition of a larger number of species and genes will clarify the phylogenetic relationship in *Cratena* species and may reveal hidden paraphyly of the genus *Cratena*. It is important to note that in Padula et al. (2014), it is shown that the *Sakuraeolis enosimensis* clade was wedged between the *C. minor* and *C. peregrina* clades in the Maximum Likelihood phylogenetic tree based on H3 sequences. The morphological and molecular differences for the known *Myja* species are included below.

Myja cf. *longicornis* Bergh, 1896

Figs 1, 4

Material. 1 specimen, ZMMU Op-667, 6 mm long (fixed), Thailand, Koh Samaesan, 21 June 2018, depth 8 –16 m, soft sediment habitats, hydroids, collectors Rahul Mehrotra, Suchana Chavanich. 2 specimens, ZMMU Op-668, ca. 3 and 2 mm (fixed) same locality and collectors.

Locality. Thailand, Chonburi, Koh Samaesan.

Diagnosis. Up to eight ceratal rows, ground colour translucent greyish, ceratal cores light to dark greyish, ceratal tops dull reddish, apices with white spot, anterior cerata with prominent reddish basal spot (distributed over the whole surface in some cerata), white gonad spherules moderately dense, sparse white spots in the first half of the dorsal part, cerata moderately widened at top without smaller separate cupola-shaped tip, central tooth with sharp to pitted top and numerous lateral denticles, up to 23 small denticles, irregular in size, no distinct furrows and ridges on the teeth surfaces, no accessory penial gland, penis unarmed.

Description. Body very elongate, up to 6 mm in preserved length (up to 10 mm alive) (Fig. 1A, B). Rhinophores similar in size to oral tentacles, smooth. Dorsal papillae cylindrical, forming eight ceratal rows along dorsal edges. Apices of papillae moderately to slightly widened, without cupola-shaped appendage (Fig. 1C). Notal edge absent. Anal opening acleioproctic on right side before first posterior ceratal rows. Reproductive openings lateral, below first anterior and second posterior rows of cerata. Ground colour translucent greyish. Oral tentacles and rhinophores with scattered opaque white dots. Digestive gland in the cerata (ceratal cores) light to dark greyish, digestive gland in upper part of cerata with reddish internal spot, apices with white spot. Anterior cerata with prominent reddish basal spot in some cerata distributed over its whole surface. Central branches of digestive gland visible through dorsal part of body greyish. Numerous small, moderately dense white gonads appear as white spherules that shine through dorsal surface. Jaws broadly triangular with prominent anterior wings, masticatory borders smooth (Fig. 1D). Radula uniserial, very small compared to pharynx internal volume (Fig. 1E, indicated by an arrow). Radular formula 13 × 0.1.0. Central tooth narrowly triangular, with sharp to pitted top (Fig. 1F, G, H) and up to 23 denticles that are small and irregular in size, without distinct dorsal denticle furrows, only sometimes with fine rib-like structures (Fig. 1H).

Reproductive system diaulic (Fig. 4A). Ampulla moderate in size (Fig. 4A, am). Vas deferens short, without distinct prostatic portion (Fig. 4A, vd), penial sheath widened (Fig. 4A, psh), penis unarmed, with elevations (Fig. 4A, p). Single proximal receptaculum seminis very large, oval (Fig. 4A, rsp).

Biology. Subtidal, highly cryptic on *Pennaria disticha* hydroids in soft sediment habitats beyond the coral reef or on the same hydroids at the reef edge (Fig. 1A, B). Egg mass is a long narrow ribbon, white, laid directly onto host hydroids (Fig. 1B).

Distribution. Presently found only at Koh Samaesan, Thailand, but expected to be found in neighbouring regions of the Indo-West Pacific.

Remarks. Thai specimens show closeness to the type species of the genus *Myja longicornis* from Ambon (Indonesia) in such features as the apically widened cerata, only a single pair of anterior cerata, acleioproctic anus, winged jaws, and small uniserial radula. Therefore, studying these specimens allows us to reveal the phylogenetic and taxonomic position of the genus *Myja* via both morphological and molecular means. However, while *M.* cf. *longicornis* from Thailand is similar to the type species of the genus *Myja*, *M. longicornis* from the type locality in Ambon as described in the original description by Bergh (1896), there are differences in several external and internal characters which do not allow us to identify the Thai material as *M. longicornis* and Bergh's figures are reproduced here (Fig. 1I, H). We therefore record here the specimens from Thailand as *M.* cf. *longicornis*. The distinguishing features of *M.* cf. *longicornis* are predominantly greyish without the green digestive gland branches both in the body and in the cerata, as was clearly indicated for *M. longicornis* in the original description (Bergh, 1896: 389, 390). It has a reddish and not brown-chocolate basal spot at anterior pair of cerata, and similar reddish (and not brown) pigment at ceratal apices. Furthermore, the radula of *M. longicornis* as depicted in Bergh (1896; reproduced here Fig. 1J) has more distinct lateral denticles, which are lower in number (10), compared to *M.* cf. *longicornis* (at least 23) (see Fig. 1H). We suspect that there is hidden species diversity in the genus *Myja* of the Indo-West Pacific. Specimens collected in 2016 reveal the presence of at least two more species of the genus *Myja*, which dif-

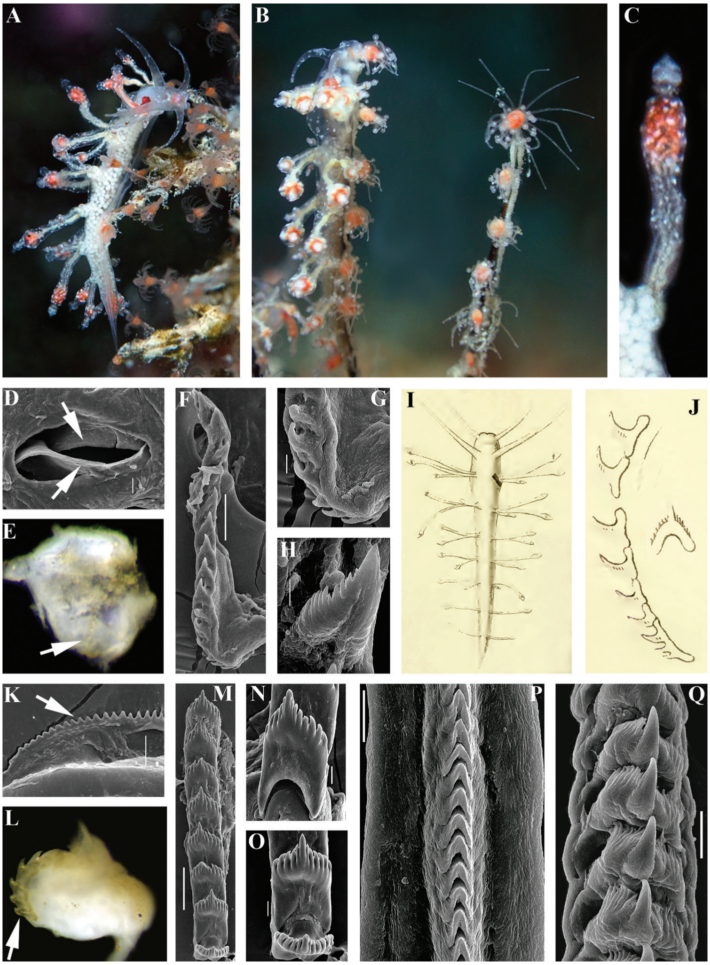

Figure 1. Comparison of *Myja longicornis* Bergh, 1896 with other aeolidacean taxa that have been proposed to have relationships with it (*Calma*, *Tergipes*) and which are covered by present analysis [type species of the genus *Facelina*, *F. auriculata* (Müller, 1776)]. **A–H** *Myja* cf. *longicornis* from Thailand, living animal ca. 10 mm in length **A** dorsal view of hydroids in situ **B** lateral view of hydroids in situ (left), egg mass on the hydroid (right) **C** details of cerata **D** smooth masticatory processes of jaws (indicated by arrows), SEM **E** pharynx, dissected dorsally to show very narrow radula (indicated by an arrow), LM **F** whole radula, SEM **G** anteriormost part of radula to show sacoglossan-like small knife-shaped teeth, SEM **H** teeth from the middle part of radula, SEM; **I, J** *Myja longicornis* Bergh, 1896 external view and radula (anterior part), reproduced from the first description by Bergh (1896); **K–O** *Facelina auriculata* jaws and radula of a specimen from UK, collected together with neotype **K** masticatory process (well-defined denticles indicated by arrow), SEM **L** radula (arrow) on odontophore, to show that anteriormost teeth are not reduced, LM **M** anterior part of radula to show that teeth are not reduced **N** anteriormost tooth of radula **O** two anterior teeth of radula **P** radula (middle part) of *Calma glaucoides* (Alder & Hancock, 1854) from Norway **Q** radula (middle part) *Tergipes tergipes* (Forsskål in Niebuhr, 1775). Scale bars: 20 µm (**D, N, O, Q**); 50 µm (**F, K**); 10 µm (**G, P**); 5 µm (**H**); 100 µm (**M**). Photographs of living specimens by Chanon Ngernthongdee and Siwat Worachananant, SEM images by AV Martynov. Figures I and J are reproduced from Bergh (1896), the publication not currently under copyright.

fer from *M.* cf. *longicornis* based on morphological and molecular data and from *M. longicornis* according to the morphological data, are described as new to science, *Myja karin* sp. n. (see Fig. 2) and *Myja hyotan* sp. n. (see Fig. 3). Minimum uncorrected p-distances of the COI marker which separate *M.* cf. *longicornis* from *M. karin* sp. n. are 11.9%. Minimum uncorrected p-distances of the 16S marker which separate *M.* cf. *longicornis* from *M. karin* sp. n. are 3.71% and from *M. hyotan* sp. n. are 2.55%. Minimum uncorrected p-distances of the H3 marker which separate *M.* cf. *longicornis* from *M. karin* sp. n. are 4.28% and from *M. hyotan* sp. n. are 3.36%, whereas p-distances between the two specimens of *M.* cf. *longicornis* for COI, 16S, and H3 markers are 0.2%, 0%, and 0% respectively.

***Myja karin* sp. n.**

http://zoobank.org/789A7CE3-31D2-457A-9DE0-9D1C4878C9F4
Figs 2, 4B, 5

Type material. Holotype, ZMMU Op-610, ca. 12 mm long (alive), Japan, Osezaki, 10 Sept 2016, depth 7–15 m, stones, rocks, hydroids, collector Tatiana Korshunova, Alexander Martynov. Paratype, ZMMU Op-611, Japan, Uchiura, 09 Sept 2016 depth 20 m, collector Hiroshi Takashige.

Type locality. Japan.

Etymology. In honour of Karin Fletcher (Port Orchard, Washington), who has made considerable recent efforts in uncovering hidden diversity and understanding of the nudibranch fauna of the NE Pacific.

Diagnosis. Up to ten ceratal rows, ground colour translucent greyish, ceratal cores light to dark greyish, ceratal tops dull reddish, apices with white spot, anterior cerata with brownish basal spot, no sparse white spots in the first half of the dorsal part, white gonad spherules moderately dense, cerata moderately widened at top without smaller separate cupola-shaped tip, central tooth narrowly triangular with very sharp non-pitted top and numerous lateral denticles, up to 20–30 small irregular in size denticles, very distinct ridges and furrows on the teeth surface, no accessory penial gland, penis unarmed.

Description. Body very elongate, holotype ca. 12 mm alive (Fig. 2 A–D). Rhinophores ca. 1.5 times longer than oral tentacles, smooth. Dorsal papillae cylindrical to spindle-shaped, forming nine or ten ceratal rows along dorsal edges. Apices of papillae form moderate oval swellings, without cupola-shaped appendage (Fig. 2E). Notal edge absent. Anal opening acleioproctic on right side before first posterior ceratal rows. Reproductive openings lateral, below first anterior and second posterior rows of cerata. Ground colour translucent greyish. Oral tentacles and rhinophores with scattered opaque white dots. On head after oral tentacles shines a small pinkish area, lateral sides of head with thin streaks of brown-orange pigment. Opaque white spots in anterior part of the body behind rhinophores absent. Between rhinophores shines a large brownish area. Digestive gland in the cerata (ceratal cores) whitish to light creamy and light greyish (basal parts can be very pale greenish), digestive gland in upper part of cerata with dull pinkish-brownish internal spot, apices mostly translucent

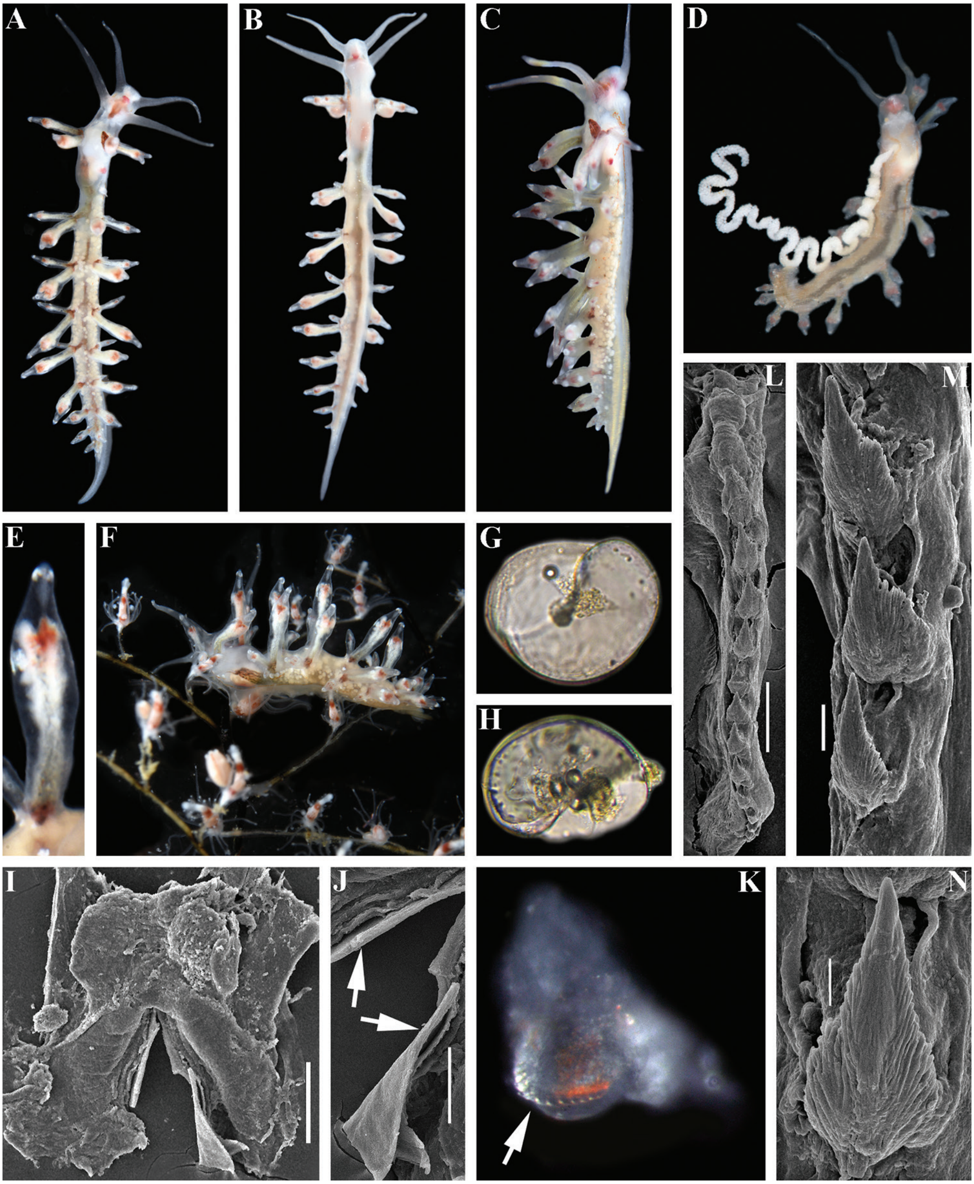

Figure 2. *Myja karin* sp. n. **A–D** holotype **A** dorsal view **B** ventral view **C** lateral view **D** animal with egg mass **E** details of cerata **F** lateral view on hydroids in situ **G, H** veligers; **I–N** paratype **I** jaws **J** smooth masticatory processes of jaws (inidicated by arrows), SEM **K** radula on odontophore, to show narrow teeth and reduced anteriormost teeth (arrow), LM **L** whole radula, SEM **M** teeth from the middle part of radula **N** anterior teeth. Scale bars: 100 µm (**I**); 50 µm (**J, L**); 10 µm (**M**); 5 µm (**N**). Photographs of living specimens by TA Korshunova and AV Martynov, SEM images by AV Martynov.

with small white band at very tip. Anterior cerata with prominent brownish basal spot. A spot similar in colour, but duller brownish and smaller in size, may occur at basal part of other cerata. Central branches of digestive gland shine through dorsal part of body and are brownish with few greyish parts. Numerous, moderately dense, small, white gonads appeared as white spherules that shine through dorsal surface. Jaws broadly triangular with prominent anterior wings, masticatory borders smooth (Fig. 2I, J). Radula uniserial, very small compared to the pharynx internal volume (Fig. 2K). Radular formula 17 × 0.1.0. Central tooth narrowly triangular with very sharp top and up to ca. 20–30 (and probably more) small denticles, irregular in size (Fig. 2L–N), often hard to delineate with very distinct dorsal denticle furrows and fine rib-like structures (Fig. 2M, N).

Reproductive system diaulic (Fig. 4B). Ampulla moderate in size, slightly widened in the middle (Fig. 4B, am). Vas deferens short, without distinct prostatic portion (Fig. 4B, vd), penial sheath widened (Fig. 4B, psh), penis unarmed, with at least two unequal elevations (Fig. 4B, p). Single proximal receptaculum seminis very large, elongated (Fig. 4B, rsp).

Biology. Subtidal, on stony and rocky area with the hydroids *Pennaria* sp. (Fig. 2F). Egg mass is a long, convoluted ribbon (Fig. 2D). Veligers are planktonic, with turbospiral shell (Fig. 2G, H).

Distribution. Central parts of the Pacific coast of the main Japanese island of Honshu; potentially can occur at least at the southern parts of Honshu and Kyushu.

Remarks. The type species of the genus *Myja*, *M. longicornis*, is similar externally to *Myja karin* sp. n. by presence of brown anterior basal ceratal spots, bur readily distinguished by predominantly brownish-pinkish, and not green, main branches of digestive gland, and also by white to greyish rather than green ceratal cores (Fig. 2). Bergh (1896; see Fig. 1) also reported seven pairs of cerata for three large specimens (up to 15 mm alive, 9.5–10 mm fixed), whereas *M. karin* sp. n. of ca. 12 mm length alive has up to ten cerata (Fig. 2A–C). Furthermore the radula of *M. longicornis* as depicted in Bergh (1896) has a sharp apical part (Fig. 1J), somewhat like in *M. karin* sp. n., but there are considerably fewer lateral denticles [6–7 on the figure in Bergh (1896), up to ten in the description in Bergh (1896)], compared to *M. karin* sp. n. with up to 20–30 lateral denticles at least (Fig. 2M, N). *Myja* cf. *longicornis* from Thailand differs from *Myja karin* sp. n. by its reddish and not brownish basal anterior ceratal spots and very considerably by the morphology of its radula (compare Fig. 1F–H with Fig. 2L–N). One more new species of the genus *Myja*, *Myja hyotan* sp. n. described below from Japanese waters, differs from *Myja karin* sp. n. by details of body colour, radular characteristics (see detailed remarks below and Table 2 for details), and according to molecular phylogenetic data (Fig. 5). Minimum uncorrected p-distances of the COI marker which separate *M. karin* sp. n. from *M.* cf. *longicornis* are 11.9%. Minimum uncorrected p-distances of the 16S marker which separate the *M. karin* sp. n. from *M.* cf. *longicornis* are 3.71% and from *M. hyotan* sp. n. are 4.41%. Minimum uncorrected p-distances of the H3 marker which separate *M. karin* sp. n. from *M.* cf. *longicornis* is 4.28% and from *M. hyotan* sp. n. is 3.98%. P-distances between the two specimens of *M. karin* sp. n. for the COI, 16S, and H3 markers are 0.5%, 0.7%, and 0% respectively.

Table 2. Morphological comparison of the species belonging to the genus *Myja*.

	Maximum length alive	**Colour of central branches of digestive gland**	**Colour of digestive branches in cerata**	**Colour of internal spot of digestive gland in upper part of cerata**	**Colour of large spot of digestive glad at the base of right anterior cerata**	**Radula teeth**
M. cf. *longicornis*	10 mm	Greyish	Greyish	Reddish	Reddish	With sharp to pitted central cusp and numerous indistinct, irregularly placed lateral denticles (up to at least 23), no furrows and ribs
M. karin sp. n.	12 mm	Brownish, few pieces greyish	Greyish to whitish	Pinkish-brownish	Brownish	With very sharp central cusp and up to ca. 20–30 of small irregular in size denticles, often hard to delineate, with deep furrows and fine rib-like structures
M. hyotan sp. n.	20 mm	Dark brownish	Whitish to light cream	Dark brownish	Dark brownish	With sharp, largely non-pitted cusp and up to ca. 10 (often no more than 5 denticles) relatively distinct small denticles in anterior part of radula to completely smooth or with very indistinct denticles in posterior part of radula
M. longicornis Bergh, 1896	15 mm	Green	Green	Brown	"Brown-chocolate"	With sharp pointed central cusp and 6–10 distinct regularly placed lateral denticles

Myja hyotan sp. n.

http://zoobank.org/995BFF5F-198C-4C1E-97CB-A018B51B8876
Figs 3, 4C, 5

Eubranchus sp. 7 Nakano, 2004: 244.

Type material. Holotype, ZMMU Op-612, ca. 20 mm long alive, Japan, Osezaki, 10 Sept 2016, depth 7–15 m, stones, rocks, hydroids, collector Tatiana Korshunova, Alexander Martynov.

Type locality. Japan, Osezaki.

Etymology. After the Japanese name hyōtan (瓢箪, ヒョウタン) for the calabash *Lagenaria siceraria*, the fruits of which are very similar in shape to the peculiar cupola-shaped tip of cerata of this new *Myja* species.

Diagnosis. Up to eight ceratal rows, ground colour translucent greyish, ceratal cores white to dark greyish, ceratal tops dull reddish, no apical white spot, anterior cerata with prominent dark brownish basal spot, sparse white spots in the first half of the dorsal part, white gonad spherules very dense, cerata considerably widened at top with smaller separate cupola-shaped tip, central tooth narrowly triangular with largely non-pitted top and only few denticles, up to ten small denticles, irregular in size; no accessory penial gland, penis unarmed.

Description. Body very elongate, holotype ca. 20 mm (alive, Fig. 3A–C). Rhinophores up to ca. two times longer than oral tentacles, smooth. Dorsal papillae cylindrical and then rapidly widened at the top, forming up to eight ceratal rows along dorsal edges. Apices of papillae considerably widened with smaller separate cupola-shaped tip appendage (Fig. 3D). Notal edge absent. Anal opening acleioproctic on right side before first posterior ceratal rows. Reproductive openings lateral, below first anterior and second posterior rows of cerata. Ground colour translucent greyish, but because of presence of numerous, very densely placed gonad spherules, appears as rather opaque white. Oral tentacles and rhinophores with few scattered opaque white dots. On head after oral tentacles to in between of rhinophores shines a pinkish area, lateral sides of head without thin streaks of brown-orange pigment. Opaque white in anterior part of the body after rhinophores. Between rhinophores shines a large brownish area. Digestive gland in the cerata (ceratal cores) whitish to light creamy, digestive gland in upper part of cerata with dark brownish internal spot, apices mostly translucent, without small white band at very tip. Anterior cerata with prominent dark brownish basal spot. A spot similar in colour, but duller brown and smaller in size, may occur at basal part of other cerata. Central branches of digestive gland shining through dorsal part of body are dark brownish. Numerous, very dense small white gonads appear as white spherules that shine through dorsal surface and create a rather opaque white dorsal appearance. Jaws broadly triangular with prominent anterior wings, masticatory borders smooth (Fig. 3F, G). Radula uniserial, very small compared to internal volume of the pharynx (Fig. 3H). Radular formula 15 × 0.1.0. Central tooth narrowly triangular with sharp or rarely pitted top and up to ca. ten (often no more than five) relatively distinct small denticles in anterior part of radula (Fig. 3I–K) to

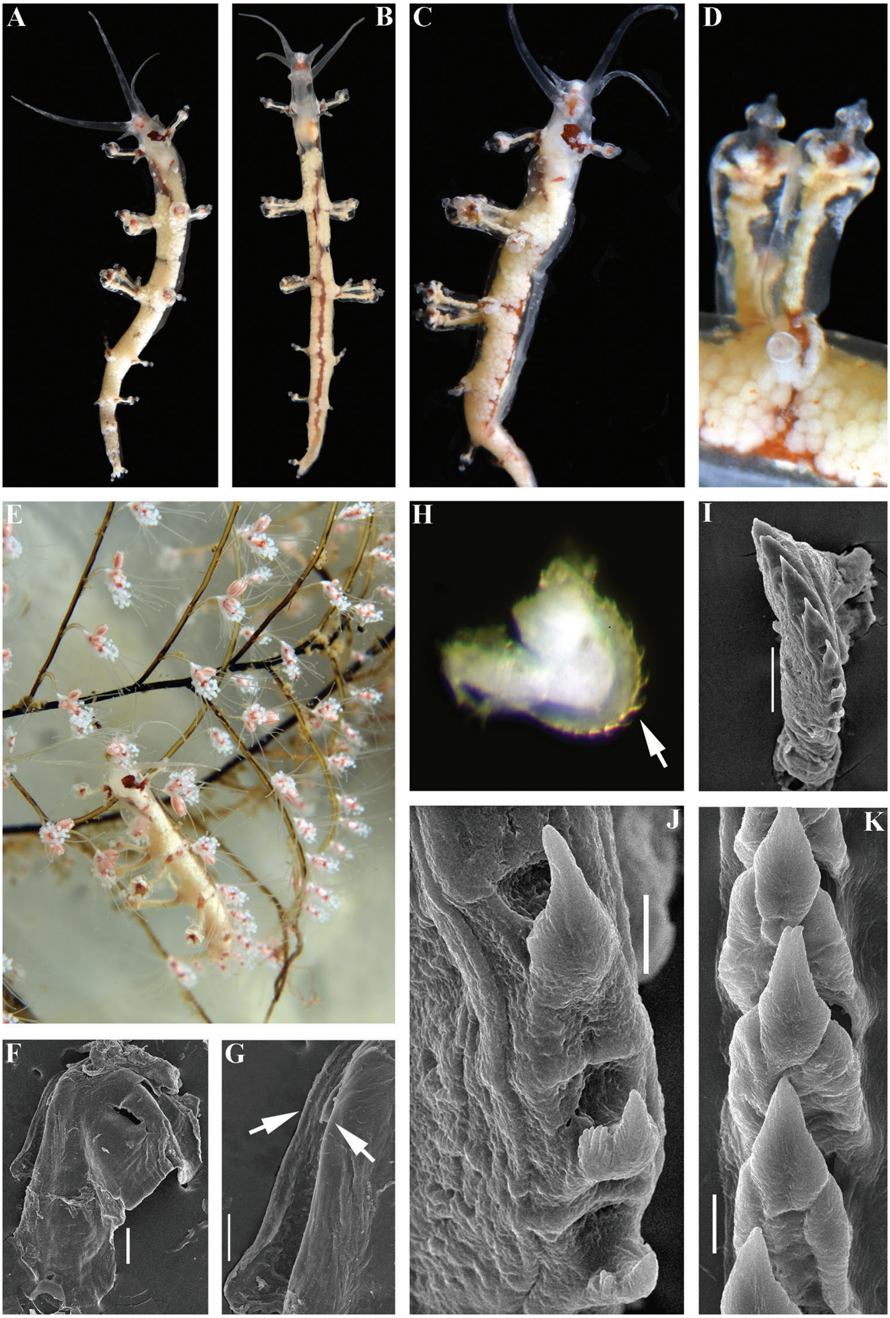

Figure 3. *Myja hyotan* sp. n., holotype. **A** dorsal view **B** ventral view **C** lateral view **D** details of cerata **E** dorsal view on hydroids in situ **F** jaw **G** smooth masticatory processes of jaws (indicated by arrows), SEM **H** radula on odontophore, to show reduced anteriormost teeth (arrow), LM **I** anterior teeth with strongly reduced anteriormost teeth, SEM **J** teeth from the middle part of radula **K** posterior part of radula to show smooth teeth. Scale bars: 100 µm (**F**); 50 µm (**G, I**); 10 µm (**J, K**). Photographs of living specimens by TA Korshunova and AV Martynov, SEM images by AV Martynov.

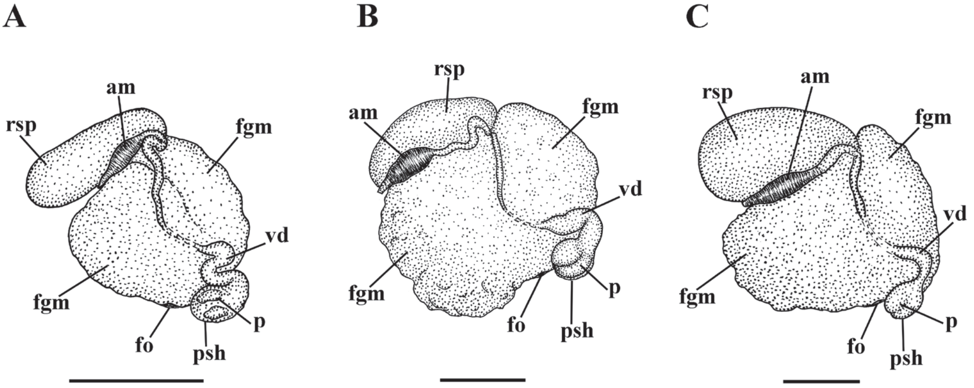

Figure 4. Reproductive systems of new species of the genus *Myja*. **A** *Myja* cf. *longicornis* **B** *Myja karin* sp. n. **C** *Myja hyotan* sp. n. Abbreviations: am – ampulla; fgm – female gland mass; fo – female opening; p – penis; psh – penial sheath; rsp – proximal receptaculum seminis; vd – vas deferens.

completely smooth or with very indistinct denticles in posterior part of radula (Fig. 3K). Few teeth in posterior part of radula may have pitted top (Fig. 3K)

Reproductive system diaulic (Fig. 4C). Ampulla moderate in size, slightly widened in the middle (Fig. 4C, am). Vas deferens short, without distinct prostatic portion (Fig. 4C, vd), penial sheath widened (Fig. 4C, psh), penis unarmed, with elevations (Fig. 4C, p). Single proximal receptaculum seminis very large, pyriform (Fig. 4C, rsp).

Biology. Subtidal, on stony and rocky area with hydroids *Pennaria* sp. (Fig. 3E). No data on egg mass so far.

Distribution. Central parts of the Pacific coast of main Japanese island Honshu; potentially can occur at the southern parts of Honshu and Kyushu.

Remarks. The type species of the genus *Myja*, *M. longicornis* is somewhat similar externally to *Myja hyotan* sp. n. by presence of brown anterior basal ceratal spot, but it is readily distinguished by dark brown and not green main branches of digestive gland, and also by the white rather than green ceratal cores. Another notable difference between the type species and all other species described here from *M. hyotan* sp. n. is the very densely placed white spherules of the gonad that shine through the dorsal body and appear as opaque white in *M. hyotan*. The shape of the cerata in *M. hyotan* sp. n. also readily differentiates it from *M. longicornis*, *M.* cf. *longicornis,* and *M. karin* sp. n. with the presence of an additional, separate, cupola-shaped top chamber in the ceratal apices (Fig. 3D). Furthermore, the radula of *M. longicornis* as depicted in Bergh (1896; reproduced here Fig. 1J) has a sharp apical part, somewhat similar to that of *M. hyotan* sp. n., but the denticles in *M. longicornis* are much more distinct, compared to *M. hyotan* sp. n., in which in most of the radula (except few anterior most teeth) has lateral denticles either absent or very indistinct (Fig. 3I, K). *Myja* cf. *longicornis* differs from *M. hyotan* sp. n. by the reddish and not brownish basal anterior ceratal spot and very considerably by the morphology of radula (compare Fig. 1F–H and Fig. 3I–K). *Myja hyotan* sp. n. differs from the other new species of the genus *Myja* from Japan,

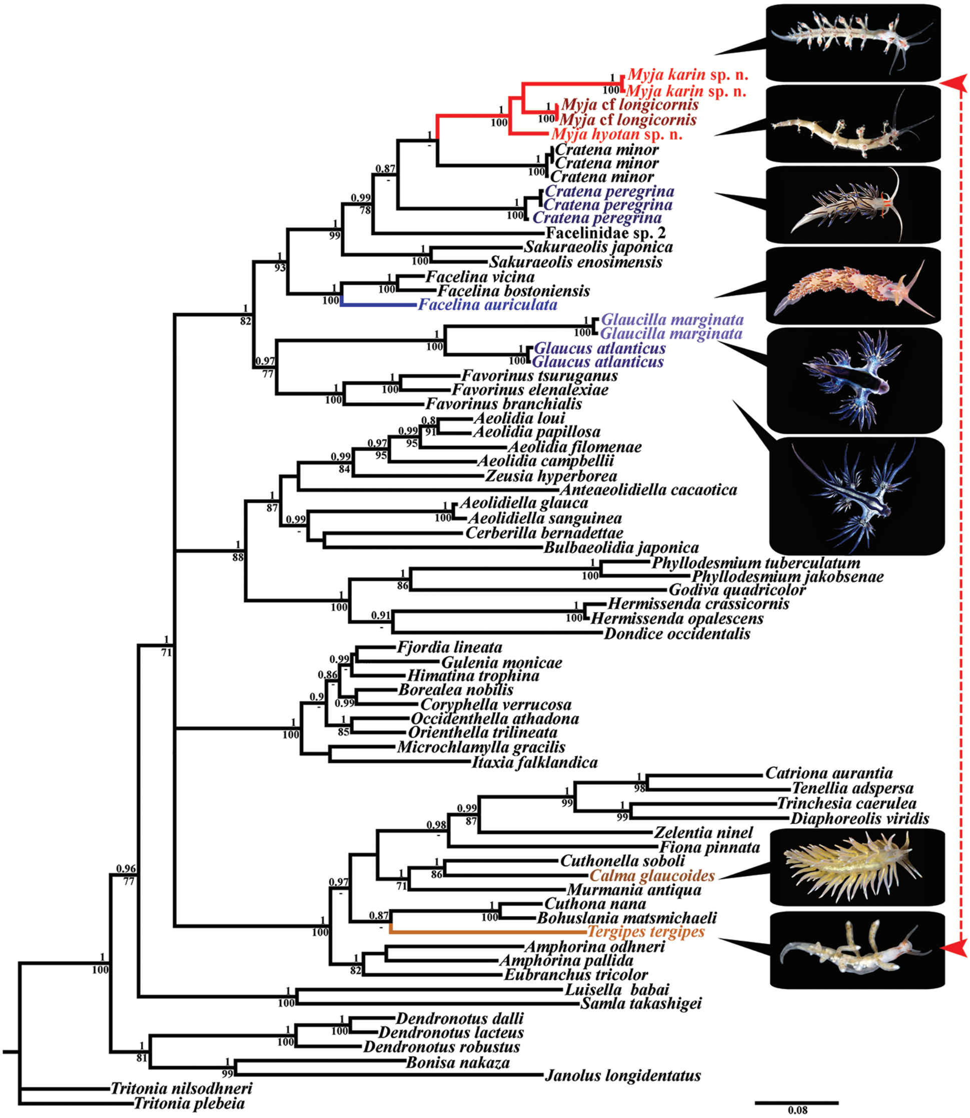

Figure 5. Phylogenetic tree of aeolidacean nudibranchs based on concatenated molecular data (COI + 16S + H3) represented by Bayesian Inference (BI). Numbers above branches represent posterior probabilities from Bayesian Inference. Numbers below branches indicate bootstrap values for Maximum Likelihood. The key clades and illustrated taxa are highlighted in colour. Two taxa with highly convergent external morphology but very distantly related according to the molecular analysis, the Tergipedidae and the genus *Myja*, are connected by a dotted red line. Neotype ZMMU Op-669 of *Facelina auriculata* (Müller, 1776) is illustrated on the tree (photograph BE Picton).

M. karin sp. n., by the shape of the cerata (including cupola-shaped separate tip), very dense white spherules of gonads, presence of white spots on the dorsal part behind the rhinophores, by radular characteristics (*M. hyotan* sp. n. fully devoid of peculiar furrows and ridges on the teeth as present in *M. karin* sp. n., and many teeth of *M. hyotan* sp. n. almost smooth, without denticles) (see Table 2 for details) and according to the molecular phylogenetic data (Fig. 5). Minimum uncorrected p-distances of the 16S marker which separate the *M. hyotan* sp. n. from *M.* cf. *longicornis* is 2.55% and from *M. karin* sp. n. is 4.41%. Minimum uncorrected p-distances of the H3 marker which separate *M. hyotan* sp. n. from *M.* cf. *longicornis* is 3.36% and from *M. karin* sp. n. is 3.98%.

Discussion

The phylogeny and taxonomy of the Aeolidacea have been the subject of numerous recent studies (e.g., Millen and Hermosillo 2012; Carmona et al. 2013; Padula et al. 2014; Kienberger et al. 2016; Korshunova et al. 2017a; Goodheart et al. 2018). The genus *Myja* is unique among both traditional Facelinidae and all known Aeolidacea families by having a combination of tergipedid- or eubranchid-like external appearance with just a single row per side of anterior cerata (with functional cnidosacs) and an acleioproctic anus, facelinid-like winged jaws, the absence of a supplementary gland in the reproductive system, and a unique very small radula. Initially, Bergh (1896) placed the genus *Myja* in the family Tergipedidae probably because of the presence of an acleioproctic anus in combination with few cerata per row and the uniserial radula, despite the absence of the supplementary gland in the reproductive system and shape of the jaws considerably differing from tergipedids and indicating placement within the Facelinidae. Furthermore, together with the first description of the genus *Myja*, Bergh (1896) described a new genus and species *Ennoia briareus* Bergh, 1896 (also within the family Tergipedidae) which was later transferred to the traditional facelinid genus *Phyllodesmium* using only morphological data (Rudman 1991). Thus, in 1896, it was potentially possible to suggest facelinid affinity of the genus *Myja* using available morphological characters. Despite this, during the past century the genus *Myja* and the sole species *M. longicornis* has been included into a few classification reviews (e.g., Thiele 1931; Parker 1982; Vaught 1989) and colour guides and other publications (e.g., Marcus 1965; Cobb and Willan 2006; Coleman 2008) within the family Tergipedidae only. Recently Gosliner et al. (2015: 336) placed *Myja* as an "undetermined family", but no trees or molecular analyses have been presented since that publication. In the recent edition of the colour guide on the Japanese sea slugs *Myja* was also placed in an undetermined family (Nakano 2018). We have conducted this study since 2016 (TK and AM collected *Myja* specimens during research trip to Osezaki, Japan) and while our study was at a final stage, an abstract of a conference mentioning the genus *Myja* has appeared (Ekimova et. al. 2018). Thus, the taxonomic position of the genus *Myja* until recently was not evaluated or challenged in a journal or book publication since Bergh's (1896) first description.

Our present molecular data and morphological analysis of the genus *Myja* clearly shows that previous morphological assessment was incorrect. Our new data places the genus *Myja* as phylogenetically related not just to the Facelinidae s. l., but to the group of Facelinidae s. str. close to the type species of the genus *Facelina* (see below for details). However, in strong contrast to molecular data, the external morphological characters of the species of the genus *Myja* are highly unusual and resemble those of members of the family Eubranchidae, and those of the Tergipedidae (genus *Tergipes*), but are drastically different from any described genera of the family Facelinidae. For example, the external similarity the species described here *Myja hyotan* sp. n. to some members of the family Eubranchidae is so striking that it was previously identified as *Eubranchus* sp. 7 (see Nakano 2004: 244). Furthermore, Bergh (1896) has compared the radula of the genus *Myja* with that of the genus *Calma* (known at that time under the name *Forestia* Trinchese, 1881). While particular radular teeth of the highly unusual partially fused radula of the genus *Calma* have showed some superficial similarities (Fig. 1P) to some of the species of the genus *Myja*, e.g., to the newly described *M. hyotan* (see Fig. 3K), it is not similar either to the type species of *Myja* as described in Bergh (1896) (see Fig. 1J) or to *M. karin* sp. n., described above (Fig. 2M, N). According to the recent molecular phylogenetic data (Korshunova et al. 2018a), the genus *Calma* and family Calmidae are not related to *Myja*.

The long taxonomic problem of the classification of the aeolidacean nudibranch family Facelinidae (e.g., Risso-Dominguez 1962, 1964; Schmekel 1966, 1967; Edmunds 1970; Miller 1974; Picton 1979; Rudman 1980, 1991; Gosliner and Behrens 1986; Hirano 1999; Millen and Hermosillo 2012; Churchill et al. 2014; Goodheart et al. 2017; and others) is one of the best cases to demonstrate the failure of a purely molecular phylogenetic approach (e.g., Carmona et al. 2013) to build a classification. The oldest name for the assemblage of facelinid families is Glaucidae Gray, 1827 and Facelinidae itself was proposed by Bergh much later in 1889 (MolluscaBase 2018a, b), but all facelinid diversity had been suggested to be merged under the name Glaucidae (Miller, 1974). Recently Goodheart et al. (2017: 10) indicated that because of paraphyly of traditional Facelinidae "…until a member of the genus *Facelina* (the type genus for this family) is included in the analyses (ideally the type taxon *Facelina auriculata*), it is impossible to say which clade should receive the Facelinidae designation." In the present study we fully meet these requirements. Obtained here for the first time is molecular data for *Facelina auriculata* (Müller, 1776) (= *Facelina coronata* (Forbes & Goodsir, 1839)) and this is included with data from other *Facelina* species in the molecular phylogenetic analysis (Fig. 5). The analysis has placed at least four species of the genus *Facelina* into a well-supported clade together with the type species *F. auriculata* (Fig. 5).

Originally, the type species of the genus *Facelina* is *F. coronata* (see Alder and Hancock 1845–1855: xxii). The older name *F. auriculata* was restored for this species by Odhner (1939), though he mistakenly synonymised *Eolis drummondi* Thompson, 1844, and hence *Eolis curta* Alder & Hancock, 1843 (currently both are junior synonyms of *F. bostoniensis* (Couthouy, 1838), see Thompson and Brown 1984)) with *F. auriculata*. Thompson (1976) used the name *F. auriculata* in the subspecies combination *F. auriculata coronata*, but later he declined to apply the name *F. auriculata* as senior synonym of *F. coronata* (Thompson & Brown, 1984) because of putatively uncertain separation from *F. bostoniensis*. However, the figure of "*Doris*" *auriculata* as depicted in Müller et al. (1806) clearly shows separated clusters of short cerata and thus cannot be referred to *F. bostoniensis* (including *F. curta*) with overlapping rows of long cerata. The work of Müller et al. (1806) is an integral part of the original "Zoologiae Danicae…" (Müller 1776) and has continuing volume numeration with the latter. Therefore, figure 1 on the plate CXXXVIII of "*Doris*" *auriculata* in Müller et al. (1806) belongs to the original description of *F. auriculata*. Odhner (1939) also mentioned the similarity of Müller's figure of "*Doris*" *auriculata* to *F. coronata*. Importantly, both Müller (1776: 229) and Müller et al. (1806: 21) gave reference to an older work by Hans Ström as "A. Havn., 10. p.16. t. 5. fig. 6" as a basis for their descriptions while describing "*Doris*" *auriculata*. According to Müller (1776: X) "A. Havn." is an acronym for the journal "Det Kiobenhavnske Selskabs Skrifter" (= Skrifter som udi det Kiøbenhavnske Selskab) which in Latin is "Actis Societatis Historiae Naturalis Havniensis". We have thus explored the work by Ström (1765–1769: 16) and found a fairly detailed description (including a figure) under the non-binomial name "Thetys auriculis duabus, pilis dorsi mollibus, fasciculatis, erectis" in Latin. Among other characters Ström mentioned "… the whole body colour is white and glossy (blank), the tassel-shaped lungs [= cerata] purple-red with white tips...." ("at hele Kroppens Farve er hvid og blank, men de Qvast- [= modern Danish "kvast"] dannede Lunger Purpur-røde med hvide Spidser...)" (Ström 1765–1769: 16). This colour description almost perfectly fits the colour pattern of the species that we currently accept under the name *F. auriculata*. Furthermore, in figure 6 in Ström (1765–1769: tab. V) there are clear ceratal clusters, oral tentacles longer than the rhinophores (which are likely perfoliated), and anterior foot corners. Thus, both colour and external characters of Ström's description of "Thetys auriculis duabus…", that becomes the basis for Müller's (1776: 229) description of "*D.*" *auriculata*, agree very well with the characters of the currently recognized *Facelina auriculata*. Apparently Thompson did not check the original description of Hans Ström, because the doubts about synonymy of *F. coronata* with *F. auriculata* as expressed in the work of Thompson and Brown (1984: 150-1) would have been unnecessary. According to ICZN (1999) articles 11.4 and 11.5 Müller (1776: 229) thus made the non-binomial name of Ström the fully valid and available binomial name "*D.*" *auriculata* and provided the bibliographic reference to Ström's (1765–1769) work. Picton and Morrow (1994) started the current usage of the name *F. auriculata* and Picton (2001) published the original figure of "*Doris*" *auriculata* from Müller et al. (1806) and further provided arguments for the validity of *F. auriculata*. Here we present for the first time the pre-binomial history of that species and confirm that Ström's and Müller's descriptions of "*D.*" *auriculata* are fully concordant with the current understanding of *F. auriculata*. However, to avoid potential taxonomic problems caused by hitherto unrecognized hidden diversity within *Facelina* s. str. and taking into consideration the complex taxonomic history of the species *F. auriculata* (e.g., Odhner 1939; Lemche 1964; Thompson, 1976; Thompson and Brown 1984; Picton and Morrow 1994; present study) we designate here a neotype for *F. auriculata* (ZMMU Op-669), for which molecular data have been obtained for the first time.

The photograph of *Facelina auriculata* on the tree (Fig. 5) is precisely the neotype designated here. The SEM of jaws and radula for *F. auriculata* are presented in this study (Fig. 1K, M–O) from another specimen of *F. auriculata* which is externally very similar to the neotype and was collected together with the neotype at the same locality and date. In another recently published paper in which the COI, 16S, and 18S genes were applied, the paraphyly of traditional Facelinidae was again shown (Goodheart et al. 2018). The paraphyletic Facelinidae clades were designated as "Facelinidae 1" and "Facelinidae 2" respectively (Goodheart et al. 2018: 12). Because in the present study we demonstrated that the type species of the genus *Facelina* is nested precisely within "Facelinidae 1" we can confidently confirm here that this group is the true Facelinidae s. str., whereas for the "Facelinidae 2", a separate family name is necessary. The clade which contains the true *Facelina* s. str. is related to the families Favorinidae, Glaucidae s. str., and the genus *Myja*, but not to the clade of paraphyletic Facelinidae which is related to the families Aeolidiidae and Babakinidae (Fig. 5). By this, it is possible to confirm the phylogenetic placement of Facelinidae s. str. (including the type species *F. auriculata*), and state that the genus *Myja* is not related to a clade which contains genera *Dondice*, *Godiva*, *Hermissenda*, *Phyllodesmium*, and others (see Fig. 5).

While Glaucidae is phylogenetically (Fig. 5) related to the core group of Facelinidae s. str., it has a profoundly modified aberrant external morphology that has adapted it to an exclusively pelagic lifestyle compared to the exclusively benthic facelinid family group. Internally however, the Glaucidae appear to conform to the traditional Facelinidae (Miller 1974). According to the molecular data, the genus *Myja* is closest to the Facelinidae s. str., and particularly to the putatively paraphyletic genus *Cratena* (Fig. 5). However, morphologically (and hence, ontogenetically and epigenetically, see Korshunova et al. 2017c) the genus *Myja* differs from the Facelinidae s. str., thus suggesting potential separation of the genus *Myja* into a new family. Despite the proposal to merge the morphologically modified Glaucidae with the phylogenetically related facelinids (Miller 1974; Rudman 1980), this was not applied consistently (e.g., Gosliner et al. 2015). This is against the priority principle as described by the ICZN (1999, article 23.1) because Facelinidae Bergh, 1889 s. str. should be considered a junior synonym of Glaucidae Gray, 1827. This fact is of crucial importance, since many researchers previously were able to recognize a small, morphologically and molecularly distinct taxonomic unit comprising the family Glaucidae, having unique morphological features despite its close relatedness to the facelinids. This challenges the still dominant perception that molecularly related but morphologically different taxa should be merged under the same taxon. Most recently, the family Favorinidae has been suggested to be restored (Goodheart et al. 2017, 2018), despite previously being almost universally considered as a synonym of the Facelinidae and that the Favorinidae is much more complicated to delineate morphologically from Facelinidae s. str. than the Glaucidae.

The family Glaucidae was not included in the analysis in Goodheart et al. (2017: 10), but the same name "Facelinidae" was instead applied for several clades, including those strongly paraphyletic ones. Recently the genus *Glaucus* was included in an analysis by Goodheart et al. (2018) and was shown as closely related to the Facelinidae s. str., thus fully corroborating our results (Fig. 5). Therefore, should these families be explicitly synonymised, as for example was done by Miller (1974), the oldest name

Glaucidae (with Facelinidae s. str. at least as their junior synonym) should be utilised. That the inconsistent usage of the family name Glaucidae has also continued in recent papers, for example in Churchill et al. (2013: 2), the subfamily Glaucinae in a very narrow sense was discussed as "Glaucinae contains a single genus, *Glaucus*…" and thus the facelinid problem was not discussed, despite the mention that *Glaucus* is placed in the clade with such traditionally facelinid genera as *Favorinus* Gray, 1850, *Learchis* Bergh, 1896 and *Hermosita* Gosliner & Behrens, 1986 (Churchill et al. 2013: 4). Churchill et al. (2014: 175) later stated of the family Glaucidae "*Glaucus* is the type genus (and *G. atlanticus* the type species) of the large family Glaucidae Gray, 1827" implying that Facelinidae is included in Glaucidae as a synonym, but this was not discussed. This results in a contrast with previous morphological conclusions that Glaucidae "could be closely related to *Cuthona* (Family Tergipedidae) rather than to *Facelina* and other related groups" (Valdés and Campillo 2004: 381) but in agreement with morphological conclusions of other authors, that Glaucidae is in the same group as Facelinidae (e.g., Miller 1974; Rudman 1980). Valdés and Campillo (2004: 382) further argued that "unless the Glaucinae is, in the future, found to be much more diverse than is currently recognized, the maintenance of a single genus is sufficient to express the diversification that has taken place in this group." The implication is that if more hidden diversity would be discovered, then the generic classification of Glaucidae should be reconsidered. Ten years later it was revealed that hidden diversity within the "*Glaucus marginatus* group" does exist (Churchill et al. 2014). Due to the high concordance of the distinct molecular clades and morphological data, we here restore within glaucids the genus *Glaucilla* Bergh, 1861, stat. n. which clearly differs from the genus *Glaucus* by the different arrangement of the cerata in multiseriate groups, the short posterior end of the body, the different position of the nephroproct, and by the unarmed penis (Bergh 1861; Miller 1974; Valdés and Campillo 2004). Three further described species within the genus *Glaucus* s. l. (Churchill et al. 2014) are fully consistent with these differences and therefore are transferred here to the genus *Glaucilla* as follows: *Glaucilla bennettae* (Churchill, Valdés, Foighil, 2014), comb. n., *Glaucilla mcfarlanei* (Churchill, Valdés, Foighil, 2014), comb. n., and *Glaucilla thompsoni* (Churchill, Valdés, Foighil, 2014), comb. n. The type species of genus *Glaucilla*, *Glaucilla marginata* Reinhardt in Bergh, 1864, stat. n. is therefore returned to its original combination in this work.

The present study confirms that Glaucidae and Facelinidae s. str. are closely related according to the molecular data (Fig. 5). This implies that it is understood that the current classification poorly integrates morphological and molecular information but because of the dominant taxonomic framework, a major reassessment has still not been performed. Under a lumping approach, the genus *Myja* can be included within the family Facelinidae s. str., despite considerable morphological disparity, but then it can be proposed that the family Facelinidae Bergh, 1889 should be synonymised with the family Glaucidae Gray, 1827 as the latter is phylogenetically closely related to Facelinidae and glaucids do not differ fundamentally (morphologically) from facelinids. This approach then would also make the recently restored Favorinidae (Goodheart et al. 2017) redundant. However, as has already been shown (Korshunova et al. 2017a), such a broad approach as the synonymy of Glaucidae with Facelinidae would only be the beginning of an avalanche-like potential synonymisation process of the families within the suborder Aeolidacea. For example, Babakinidae is phylogenetically related to both Aeolidiidae and Facelinidae but has a radula that is similar to Facelinidae but not to Aeolidiidae (Roller 1972, 1973; Carmona et al. 2011; Korshunova et al 2017a). The family Apataidae in turn is not related closely to the Flabellinidae, but to the superfamily Fionoidea; however, it has a triserial radula and a reproductive system that does not differ fundamentally from the family Flabellinidae. Furthermore, the family Eubranchidae has a triserial radula and a trinchesiid-like reproductive system and is phylogenetically related to both the family Apataidae and the superfamily Fionoidea. Finally, the genus *Fiona* is a complete analogue of Glaucidae as the latter has peculiar morphological adaptations to the neustonic environment and is morphologically very different from the majority of the Fionoidea by the presence of a distinct notal edge and the absence of the supplementary penial gland. It is also, however, phylogenetically closely related to the morphologically disparate Tergipedidae and Trinchesiidae (Korshunova et al. 2017b, 2018a, b). Thus, the internal groups within the suborder Aeolidacea form a very complicated morphological and molecular mosaic and under a super-lumping approach it would be unavoidable to unite all aeolidacean families into a single one. Such a decision would further raise the question of the delineation of the suborder Aeolidacea from other major nudibranch subgroups. Although the Antarctic family Notaeolidiidae have single cnidosacs in their cerata and phylogenetically appear as a basal group within Aeolidacea (Korshunova et al. 2017a; Goodheart et al. 2018), they also possess a multiserial radula similar to the dendronotacean and arminacean nudibranchs. Such a super-lumping approach thus would immediately ruin any possibility to make an integrative molecular and morphological taxonomy, because under the same family "roof" such morphologically drastically different groups as Aeolidiidae, Paracoryphellidae, or Pseudovermidae would have to be united.

For the taxonomy of the traditional family Facelinidae this means that it can be further divided into several more narrowly defined families that will integrate both morphology and molecular data instead of disintegrating it. The genus *Myja* possesses a unique combination of external and internal characters that distinguish it from any other families of the Aeolidacea (see also remarks above). Particularly, the presence of a permanent acleioproctic anus (a common feature in such families as Tergipedidae and Trinchesiidae) in combination with a small reduced radula readily differentiate the genus *Myja* from all the numerous facelinid taxa so far described. The presence of a narrow foot with a rounded anterior edge and the smooth masticatory edges of jaws in the genus *Myja* also rarely occur among facelinids. It is therefore possible that this genus should be separated into a new family to accommodate both morphological and molecular phylogenetic data in an integrative way; however, this is being left for a further study when more data on other traditional facelinids can be included. The paraphyly of the traditional facelinids indeed should be also addressed. There are two family names available for the ex-facelinid paraphyletic clade (Fig. 5) that contains several facelinid genera. One is Myrrhinidae Bergh, 1905 (Bergh 1905) and the other is Phyllodesmiidae Thiele, 1931 (originally suggested as a subfamily, Thiele 1931: 749). According to Rudman (1981) the genus *Myrrhine* Bergh, 1905 is a synonym of the genus *Phyllodesmium* and these two family names are thus referred to the same taxonomic group, but Myrrhinidae Bergh, 1905 has precedence over Phyllodesmiidae Thiele, 1931. According to the ICZN (1999) article 40.1, synonymy of the type genus in the family group does not affect validity of family-group name (if the junior family name is not in prevailing usage and the senior name was not substituted before 1961). Neither Myrrhinidae Bergh, 1905 (Bergh 1905) nor Phyllodesmiidae Thiele, 1931 were ever in prevailing usage. Both these family names were rarely used (e.g., Risso-Dominguez 1964), never synonymised with each other when listed in reviews (e.g., Thiele 1931; Parker 1982; Vaught 1989), but only with Facelinidae s. l. or Glaucidae s. l. (e.g., Rudman 1981). Therefore, we apply provision of the ICZN article 40.1 and hereby restore Myrrhinidae Bergh, 1905 (= Phyllodesmiidae Thiele, 1931) for the ex-facelinid paraphyletic group of genera including *Phyllodesmium* (= *Myrrhine*), *Hermissenda*, *Dondice*, and *Godiva* according to the priority principle. Usage of the resurrected family name Myrrhinidae Bergh, 1905 can preliminarily solve the problem of paraphyly of the traditional Facelinidae. However, the genus *Phyllodesmium* is very different indeed from the other members of this clade (e.g., absence of cnidosacs, modified cerata) such as *Hermissenda*, *Dondice*, and *Godiva* and thus does not fulfil the criteria for morphological and molecular consistency. The taxon sampling in the present study is not targeted to be exhaustive, and there are some more potential paraphyletic events also within the superclade of "Facelinidae" s. str. (see Fig. 5). Therefore, we leave further narrow-taxon based delimitation of these paraphyletic facelinid groups to a later study.

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References

Alder J, Hancock A (1845–1855) A monograph of the British nudibranchiate Mollusca. Pt I–VII. Ray Society, London.

Bergh R (1861) Om Forekomsten af Neldfiim hos Mollusker. Videnskabelige Meddelelser fra Naturhistorisk Forening Kjöbenhavn 22[1860]: 309–331.

Bergh R (1896) Eolidiens d'Amboine. Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais. Revue Suisse de Zoologie et Annales de Musée d'Histoire Naturelle de Geneve 4: 385–394.

Bergh R (1905) Die Opisthobranchiata der Siboga-Expedition. Monographie 50: 1–248.

Carmona L, Pola M, Gosliner TM, Cervera JL (2011) a molecular approach to the phylogenetic status of the aeolid genus *Babakina* Roller, 1973 (Nudibranchia). Journal of Molluscan Studies 77: 417–422. https://doi.org/10.1093/mollus/eyr029

Carmona L, Pola M, Gosliner TM, Cervera JL (2013) A tale that morphology fails to tell: a molecular phylogeny of Aeolidiidae (Aeolidida, Nudibranchia, Gastropoda). PLoS ONE 8(5): e63000. https://doi.org/10.1371/journal.pone.0063000

Churchill CKC, Valdés Á, Foighil DÓ (2014) Molecular and morphological systematics of neustonic nudibranchs (Mollusca: Gastropoda: Glaucidae: *Glaucus*), with descriptions of three new cryptic species. Invertebrate Systematics 28: 174–195. https://doi.org/10.1071/IS13038

Churchill CKC, Alejandrino A, Valdés Á, Foighil DÓ (2013) Parallel changes in genital morphology delineate cryptic diversification of planktonic nudibranchs. Proceedings of the Royal Society B 280: 20131224. https://doi.org/10.1098/rspb.2013.1224

Cobb G, Willan RC (2006) Undersea jewels: a colour guide to nudibranchs. Australian Biological Resources Study, Canberra, 310 pp.

Coleman N (2008) Nudibranchs encyclopedia, catalogue of Asia/Indo-Pacific sea slugs. Neville Coleman's Underwater Geographic Pty Ltd., Rochedale South, 416 pp.

Edmunds M (1970) Opisthobranchiate Mollusca from Tanzania. II. (Cuthonidae, Piseinotecidae and Facelinidae). Proceedings of the Malacological Society of London 39: 15–57.

Ekimova I, Carmona L, Mikhlina A, Antokhina T, Deart Y, Schepetov D (2018) Well-known, but poorly studied nudibranch: a resolving of *Myja longicornis* (Bergh, 1896) phylogenetic placement. VI International Heterobranch Workshop abstract.

Goodheart JA, Bazinet AL, Valdés Á, Collins AG, Cummings MP (2017) Prey preference follows phylogeny: evolutionary dietary patterns within the marine gastropod group Cladobranchia (Gastropoda: Heterobranchia: Nudibranchia). BMC Evolutionary Biology 17: 221. https://doi.org/10.1186/s12862-017-1066-0

Goodheart JA, Bleidißel S, Schillo D, Strong EE, Ayres DL, Preisfeld A, Collins AG, Cummings MP, Wägele H (2018) Comparative morphology and evolution of the cnidosac in Cladobranchia (Gastropoda: Heterobranchia: Nudibranchia). Frontiers in Zoology 15: 43. https://doi.org/10.1186/s12983-018-0289-2

Gosliner TM, Behrens D (1986) Two new species and genera of aeolid nudibranchs from the tropical eastern Pacific. The Veliger 29: 101–113.

Gosliner TM, Behrens DW, Valdés Á (2015) Nudibranch and Sea Slug Identification – Indo-Pacific. New World Publications, Jacksonville, 408 pp.

Hirano YJ (1999) Two new species of *Sakuraeolis* (Aeolidacea, Facelinidae) from Japan. Venus, Japanese Journal of Malacology 58: 191–199.

ICZN (1999) International Code of Zoological Nomenclature. The International Trust for Zoological Nomenclature, London, 306 pp.

Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30(14): 3059–3066. https://doi.org/10.1093/nar/gkf436

Kienberger K, Carmona L, Pola M, Padula V, Gosliner TM, Cervera JL (2016) *Aeolidia papillosa* (Linnaeus, 1761) (Mollusca: Heterobranchia: Nudibranchia), single species or a cryptic species complex? A morphological and molecular study. Zoological Journal of the Linnean Society 177: 481–506. https://doi.org/10.1111/zoj.12379

Korshunova TA, Martynov AV, Bakken T, Evertsen J, Fletcher K, Mudianta WI, Lundin K, Schrödl M, Picton B (2017a) Polyphyly of the traditional family Flabellinidae affects a major group of Nudibranchia: aeolidacean taxonomic reassessment with descriptions of several new families, genera, and species (Mollusca, Gastropoda). ZooKeys 717: 1–139. https://doi.org/10.3897/zookeys.717.21885

Korshunova T, Zimina O, Martynov A (2017b) Unique pleuroproctic taxa of the nudibranch family Aeolidiidae from the Atlantic and Pacific Oceans, with description of a new genus and species. Journal of Molluscan Studies 83: 409–421. https://doi.org/10.1093/mollus/eyx036

Korshunova T, Martynov A, Picton B (2017c) Ontogeny as an important part of integrative taxonomy in tergipedid aeolidaceans (Gastropoda: Nudibranchia) with a description of a new genus and species from the Barents Sea. Zootaxa 4324(1): 1–22. https://doi.org/10.11646/zootaxa.4324.1.1

Korshunova TA, Lundin K, Malmberg K, Picton B, Martynov AV (2018a) First true brackish-water nudibranch mollusc provides new insights for phylogeny and biogeography and reveals paedomorphosis-driven evolution. PLoS ONE 13: e0192177. https://doi.org/10.1371/journal.pone.0192177

Korshunova TA, Fletcher K, Lundin K, Picton B, Martynov AV (2018b) The genus *Zelentia* is an amphi-boreal taxon expanded to include three new species from the North Pacific and Atlantic oceans (Gastropoda: Nudibranchia: Trinchesiidae). Zootaxa 4482: 297–321. https://doi.org/10.11646/zootaxa.4482.2.4

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. https://doi.org/10.1093/molbev/msw054

Lemche H (1964) *Facelina* Alder & Hancock, 1855 (Gastropoda): added to the official list of generic names. Bulletin of Zoological Nomenclature 23: 91–92.

Marcus E (1965) Some Opisthobranchia from Micronesia. Malacologia 3: 263–286.

Millen SV, Hamann JC (1992) A new genus and species of Facelinidae (Opisthobranchia, Aeolidacea) from the Caribbean Sea. The Veliger 35: 205–214.

Millen SV, Hermosillo A (2012) Three new species of aeolid nudibranchs (Opisthobranchia) from the Pacific coast of Mexico, Panama and the Indopacific, with a redescription and redesignation of a fourth species. The Veliger 51: 145–164.

Miller MC (1974) Aeolid nudibranchs (Gastropoda: Opisthobranchia) of the family Glaucidae from New Zealand waters. Zoological Journal of the Linnean Society 54: 31–61. https://doi.org/10.1111/j.1096-3642.1974.tb00792.x

MolluscaBase (2018a) Facelinidae Bergh, 1889. World Register of Marine Species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=191

MolluscaBase (2018b) Glaucidae Gray, 1827. World Register of Marine Species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=23046

Müller OF (1776) Zoologiae Danicae. Prodromus seu animalium Daniae et Norvegiae ingenarum characteres, nomina, et synonyma imprimis popularium. Hallageriis, Havniae, 282 pp.

Müller OF, Abildgaard PC, Holten JS, Vahl M, Rathke J (1806). Zoologica Danica sev animalium Daniae et Norvegiae rariorum ac minus rotorum descriptiones et historia. Vol. 4. Christensen, Havniae.

Nakano R (2004) Opisthobranchs of Japan Islands. Rutles, Inc., Tokyo, 304 pp.

Nakano R (2018) Field Guide to Sea Slugs and Nudibranchs of Japan. Bun-ichi Co., Ltd., Tokyo, 544 pp.

Nylander JA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey JL (2004) Bayesian phylogenetic analysis of combined data. Systematic Biology 53: 47–67. https://doi.org/10.1080/10635150490264699

Odhner NH (1939) Opisthobranchiate mollusca from the western and northern coasts of Norway. Norske Videnskabelige Selskap Skrifter 1: 1–92.

Padula V, Araújo AK, Matthews-Cascon H, Schrödl M (2014) Is the Mediterranean nudibranch *Cratena peregrina* (Gmelin, 1791) present on the Brazilian coast? Integrative species delimitation and description of *Cratena minor* n. sp. Journal of Molluscan Studies 80: 575–584. https://doi.org/10.1093/mollus/eyu052

Parker SP (1982) Synopsis and classification of living organisms. McGraw-Hill, New York, 1166 pp.

Picton BE (1979) *Caloria elegans*, (Alder & Hancock) comb. nov. Gastropoda, Opisthobranchia, an interesting rediscovery from S. W. England. Journal of Molluscan Studies 45: 125–130.

Picton B (2001) *Facelina coronata* or *F. auriculata*?. [Message in] Sea Slug Forum. Australian Museum, Sydney. http://www.seaslugforum.net/find/4854

Picton BE, Morrow C (1994) A field guide to the nudibranchs of the British Isles. Immel Publishing, London, 143 pp.

Risso-Dominguez CJ (1962) Notes on the Facelinacea. I. Introduction. Annali del Museo Civico di Storia Naturale 73: 141–171.

Risso-Dominguez CJ (1964) Notes on the Facelinacea. II. On the systematic position of *Hervia serrata* Baba, 1949 and *Favorinus horridus* Macnae, 1954 (Mollusca Nudibranchia). Beaufortia, Zoological Museum University of Amsterdam 10: 222–238.

Roller RA (1972) Three new species of eolid nudibranchs from the west coast of North America. The Veliger 14: 416–423.

Roller RA (1973) *Babakina*, new name for *Babaina* Roller, 1972, preoccupied. The Veliger 16: 117–118.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard M, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rudman WB (1980) Aeolid opisthobranch molluscs (Glaucidae) from the Indian Ocean and the south-west Pacific. Zoological Journal of the Linnean Society 68: 139–172. https://doi.org/10.1111/j.1096-3642.1980.tb01923.x

Rudman WB (1981) The anatomy and biology of alcyonarian-feeding aeolid opisthobranch molluscs and their development of a symbiosis with zooxanthellae. Zoological Journal of the Linnean Society 72: 219–262. https://doi.org/10.1111/j.1096-3642.1981.tb01571.x

Rudman WB (1991) Further studies on the taxonomy and biology of the octocoral-feeding genus *Phyllodesmium* Ehrenberg, 1831 (Nudibranchia: Aeolidoidea). Journal of Molluscan Studies 57: 167–203. https://doi.org/10.1093/mollus/57.2.167

Schmekel L (1966) Zwei neue Facelinidae aus dem Golf von Neapel: *Facelina* (*A.*) *fusca* n. sp. und *Antonietta luteorufa* n. sp. n. gen. (Gastr. Opisthobranchia). Pubblicacioni della Stazione Zoologica di Napoli 35: 29–46.

Schmekel L (1967) *Dicata odhneri*, n. sp., n. gen., ein neuer Favorinide (Gastr. Opisthobranchia) aus dem Golf von Neapel. Pubblicacioni della Stazione Zoologica di Napoli 35: 263–273.

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML webwervers. Systematic Biology 75: 758–771. https://doi.org/10.1080/10635150802429642

Ström H (1765–1769) Beskrivelse over Norske Insecter. Skrifter som udi det Kiøbenhavnske Selskab 10: 1–28.

Thiele J (1931) Handbuch der Systematischen Weichtierkunde. Band 1. A. Asher & Co., Amsterdam, 778 pp.

Thompson TE (1976) Biology of opisthobranch molluscs, vol. 1. Ray Society Publishing, London, 207 pp.

Thompson TE, Brown GH (1984) Biology of Opisthobranch Molluscs (vol. 2). Ray Society Publishing, London, 229 pp.

Valdés Á, Campillo AO (2004) Systematics of pelagic aeolid nudibranchs of the family Glaucidae (Mollusca: Gastropoda). Bulletin of Marine Science 75: 381–389.

Vaught KC (1989) A Classification of the Living Mollusca. American Malacologists, Melbourne, 195 pp.

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A pictorial key to differentiate the recently detected exotic *Haemaphysalis longicornis* Neumann, 1901 (Acari, Ixodidae) from native congeners in North America

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Abstract

Until recently, only two haemaphysaline species, *Haemaphysalis chordeilis* (Packard, 1869) and *Haemaphysalis leporispalustris* (Packard, 1869), were known to occur in the United States, and neither was considered to be of significant medical or veterinary importance. In 2017–2018 established populations of the Asian longhorned tick, *Haemaphysalis longicornis* Neumann, 1901, were detected in the eastern US for the first time. *Haemaphysalis longicornis* has the potential to be a significant threat to human and animal health, and the urgent need to determine the full extent of its distribution and host range requires availability of a straightforward and practical guide to differentiate it from native species. We created a pictorial dichotomous key to all stages of *Haemaphysalis* spp. known to occur in North America with scanning electron photomicrographs of all *H. longicornis* life stages, including rarely seen males, to aid researchers in differentiating these species. The largely Neotropical species *Haemaphysalis juxtakochi* Cooley, 1946, with established populations in Mexico and sporadic detections in the US on migrating birds is also included.

Keywords

Asian longhorned tick, haemaphysaline fauna, dichotomous key, scanning electron microscopy, invasive species

Introduction

Only two native species of *Haemaphysalis* ticks are known to occur in the United States: the rabbit tick, *Haemaphysalis leporispalustris* (Packard, 1869) and the bird tick, *Haemaphysalis chordeilis* (Packard, 1869) (Keirans and Litwak 1989). *Haemaphysalis leporispalustris* is common and widespread in North America, and is frequently collected from lagomorphs (rabbits and hares) (Bishopp and Trembley 1945). Its full distribution extends from Alaska and Canada southward to Argentina (Kohls 1960, Guglielmone et al. 2003). The agents of tularemia (*Francisella tularensis*) and of Rocky Mountain spotted fever (*Rickettsia rickettsii*) have been isolated from this tick (Eremeeva et al. 2018) although its role, if any, as a vector of human disease appears to be minor. *Haemaphysalis chordeilis* is far less often collected but nonetheless assumed to have a broad distribution in North America, based on sporadic avian records spanning the US and southern Canada (Bishopp and Trembley 1945, Kohls 1960, Lindquist et al. 2016). Because these two species have historically been considered specialists on rabbits and birds, respectively, and are not significant pests of humans or domestic animals, relatively little attention has been paid to their ecology and geographical distribution.

In 1993, a single specimen of the Central/South American species *Haemaphysalis juxtakochi* Cooley, 1946 (*Haemaphysalis kochi* Aragão, 1908 is a junior synonym) was detected in Ohio, USA, on a white-tailed deer at a deer-checking station (Keirans and Restifo 1993). While the current northern limit of this species' distribution appears to be Mexico, immatures may occasionally be brought into the US by northward migrating birds (Mukherjee et al. 2014). At present there is no indication that such encounters are common or that the species has become established in the US. Adult *H. juxtakochi* are chiefly parasites of deer (Kohls 1960, Guglielmone et al. 2005) and may be able to transmit some species of *Rickettsia* (Souza et al. 2018).

In 2017, established populations of the East Asian/Australasian species *Haemaphysalis longicornis* Neumann, 1901, were discovered in New Jersey (Rainey et al. 2018) and subsequently throughout a large part of the eastern US, including Arkansas, Connecticut, Maryland, New York, North Carolina, Pennsylvania, Virginia, and West Virginia (Beard et al. 2018). This species, native to East Asia and invasive in Australia/New Zealand, is associated with disease transmission to humans in the former region (e.g., Zhuang et al. 2018) and is a serious pest of livestock in the latter (Heath 2016). Invasive populations of this species appear to be parthenogenetic, which may facilitate their establishment and spread (Heath 2013). As a result, there is now much concern over this species' potential effect on human and animal health in the United States, and studies are under way to clarify its current geographic range and preferred host species.

In order to study potential impacts of *H. longicornis* on North America, a critical first step is being able to differentiate this species from co-occurring *Haemaphysalis* spp. Here we present scanning electron photomicrographs of all stages of *H. longicornis*, as well as a simple, usable dichotomous key to differentiate the four *Haemaphysalis* species that may be encountered in North America: *H. leporispalustris*, *H. chordeilis*, *H. longicornis*, and *H. juxtakochi*. While the rarity of *H. juxtakochi* detections in the US does not suggest that this species will often be sympatric with *H. longicornis*, we feel it is important to include it in our key for three reasons: (1) climate change is predicted to alter the distribution of many tick species (Ostfeld and Brunner 2015), therefore the distribution of *H. juxtakochi* may one day shift north of Mexico; (2) unlike some of the exotic species imported by birds (Mukherjee et al. 2014), *H. juxtakochi* could easily find suitable host species in the US; and (3) as it continues its invasion of North America, *H. longicornis* may eventually be collected farther south, coinciding with *H. juxtakochi*'s existing range.

Materials and methods

Scanning electron microscopy (SEM)

Specimens of *H. longicornis* were obtained from US National Tick Collection archives for imaging. Males, females, and nymphs were sent from a laboratory colony started with specimens collected in Jeju-teukbyeoljachido, Republic of Korea (Accession # RML48803). Larvae originated from a colony started with specimens from Queensland, Australia (Accession # RML58949). Specimens were coated with gold and imaged with a JEOL JSM-6610LV scanning electron microscope (JEOL USA, Inc., Peabody, MA) (Figs 1–4). Larval and nymphal *H. juxtakochi* were collected by flagging in Guanacaste National Park, Costa Rica, and imaged in the same manner (Accession # USNMENT 986092).

Additional photomicrographs of *H. juxtakochi* (adult), *H. leporispalustris* (all stages) and *H. chordeilis* (all stages) were obtained from the US National Tick Collection archives (http://www.discoverlife.org).

Pictorial dichotomous key

A literature search was conducted and key characters useful for distinguishing the four species were gleaned from the following: Cooley (1946), Kohls (1960), Clifford et al. (1961), Fairchild et el. (1966), Hoogstraal et al. (1968), and Hoogstraal and Kim (1985). Of note, characters chosen to distinguish adult stages are present in both males and females of their respective species.

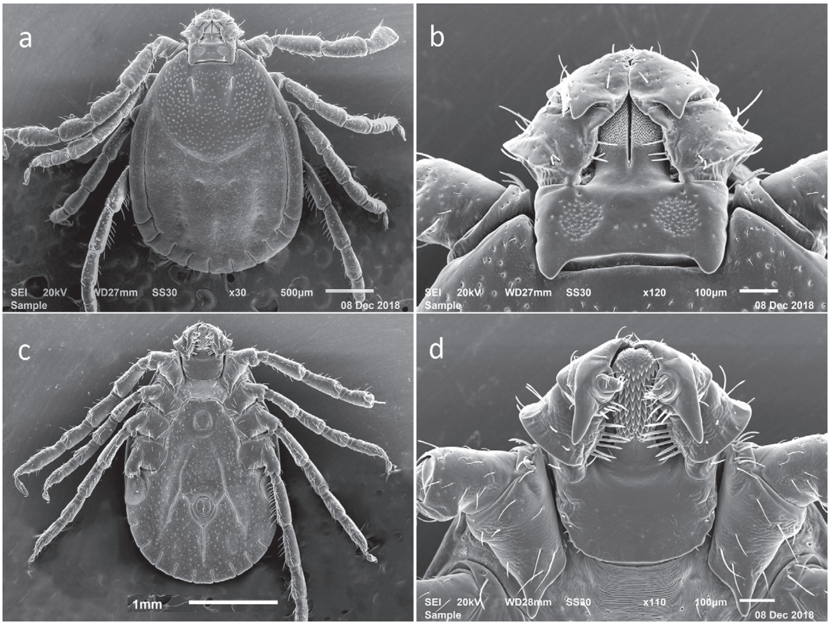


Figure 1. SEM photos of female *H. longicornis* from a colony started with specimens from Jeju-teukbyeoljachido, Republic of Korea (Accession # RML48803) **a** dorsal full body **b** dorsal capitulum **c** ventral full body **d** ventral capitulum.

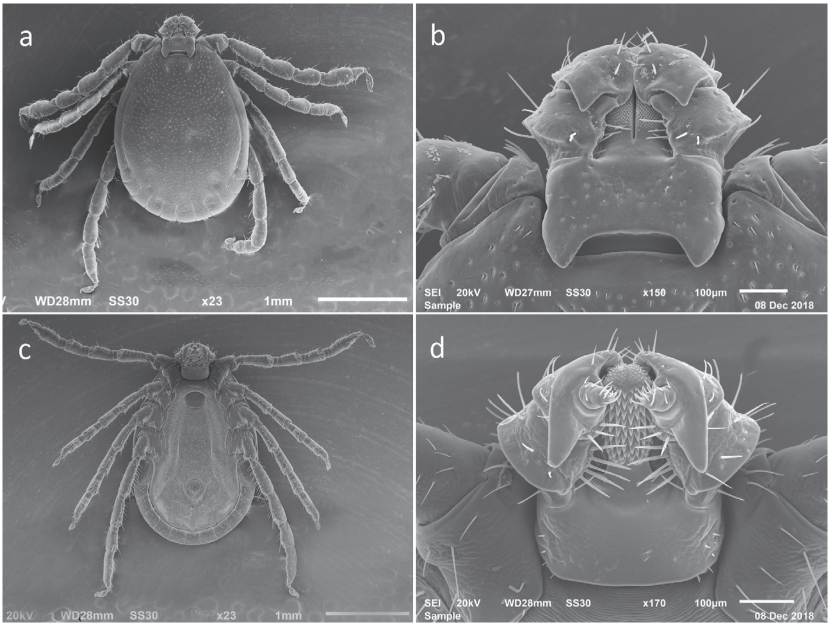


Figure 2. SEM photos of male *H. longicornis* from a colony started with specimens from Jeju-teukbyeoljachido, Republic of Korea. (Accession # RML48803) **a** dorsal full body **b** dorsal capitulum **c** ventral full body **d** ventral capitulum.

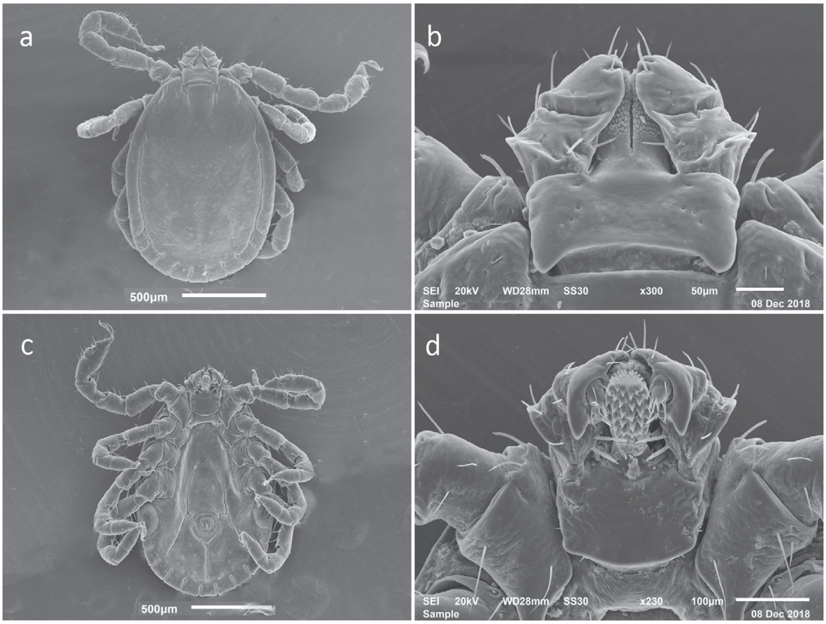


Figure 3. SEM photos of nymphal *H. longicornis* from a colony started with specimens from Jejuteukbyeoljachido, Republic of Korea (Accession # RML48803). **a** dorsal full body **b** dorsal capitulum **c** ventral full body **d** ventral capitulum.

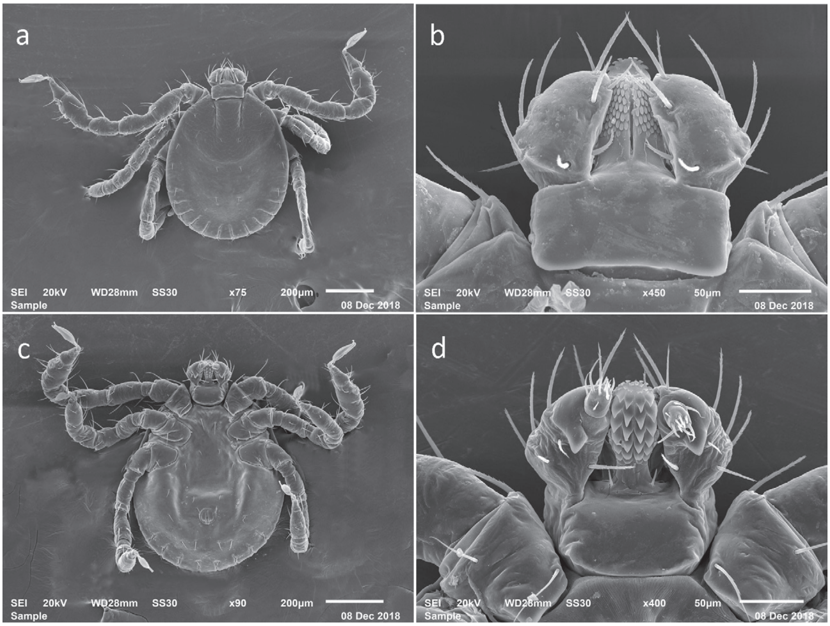


Figure 4. SEM photos of larval *H. longicornis* from a colony started with specimens from Queensland, Australia (Accession # RML58949). **a** dorsal full body **b** dorsal capitulum **c** ventral full body **d** ventral capitulum.

Key to *Haemaphysalis* spp. of North America

Adults (Fig. 5)

1 Palpal segment 3 dorsally with prominent retrograde spur (Fig. 5a) ....***Haemaphysalis* (*Kaiseriana*) *longicornis* Neumann, 1901**

– Palpal segment 3 without dorsal spur (Fig. 5b)..**2**

2 Palpal segment 3 ventrally with long, slender, retrograde spur extending at least to middle of segment 2 (Fig. 5d)... .... ***Haemaphysalis* (*Gonixodes*) *juxtakochi* Cooley, 1946**

– Palpal segment 3 ventrally with short spur, not reaching segment 2 (Fig. 5c) **3**

3 Basis capituli ventrally with cornua at postero-lateral margins; dental formula 3/3 (Fig. 5e) ....***Haemaphysalis* (*Gonixodes*) *leporispalustris* (Packard, 1869)**

– Basis capituli ventrally without cornua; dental formula 5/5 (Fig. 5f).................. .... ***Haemaphysalis* (*Aboimisalis*) *chordeilis* (Packard, 1869)**

Nymphs (Fig. 6)

1 Basis capituli ventrally with cornua at postero-lateral margins (Fig. 6a) **2**

– Basis capituli ventrally without cornua at postero-lateral margins (Fig. 6b)....... **3**

2 Palpal segment 2 ventrally with 4–8 stout hairs along internal margin; palpal segment 3 ventrally with a short, blunt spur, not reaching anterior margin of segment 2 (Fig. 6c).......... ***Haemaphysalis* (*Gonixodes*) *leporispalustris* (Packard, 1869)**

– Palpal segment 2 ventrally with 2 fine hairs along internal margin; palpal segment 3 ventrally with a longer, sharp, retrograde spur, extending to or beyond anterior margin of segment 2 (Fig. 6d) ....***Haemaphysalis* (*Gonixodes*) *juxtakochi* Cooley, 1946**

3 Dorsally, lateral margins of basis capituli straight (Fig. 6e); hypostomal dental formula 3/3............***Haemaphysalis* (*Kaiseriana*) *longicornis* Neumann, 1901**

– Dorsally, lateral margins of basis capituli pointed (Fig. 6f); hypostomal dental formula 2/2.............***Haemaphysalis* (*Aboimisalis*) *chordeilis* (Packard, 1869)**

Larvae (Fig. 7)

1 Basis capituli ventrally with cornua at postero-lateral margins (Fig. 7a).............**2**

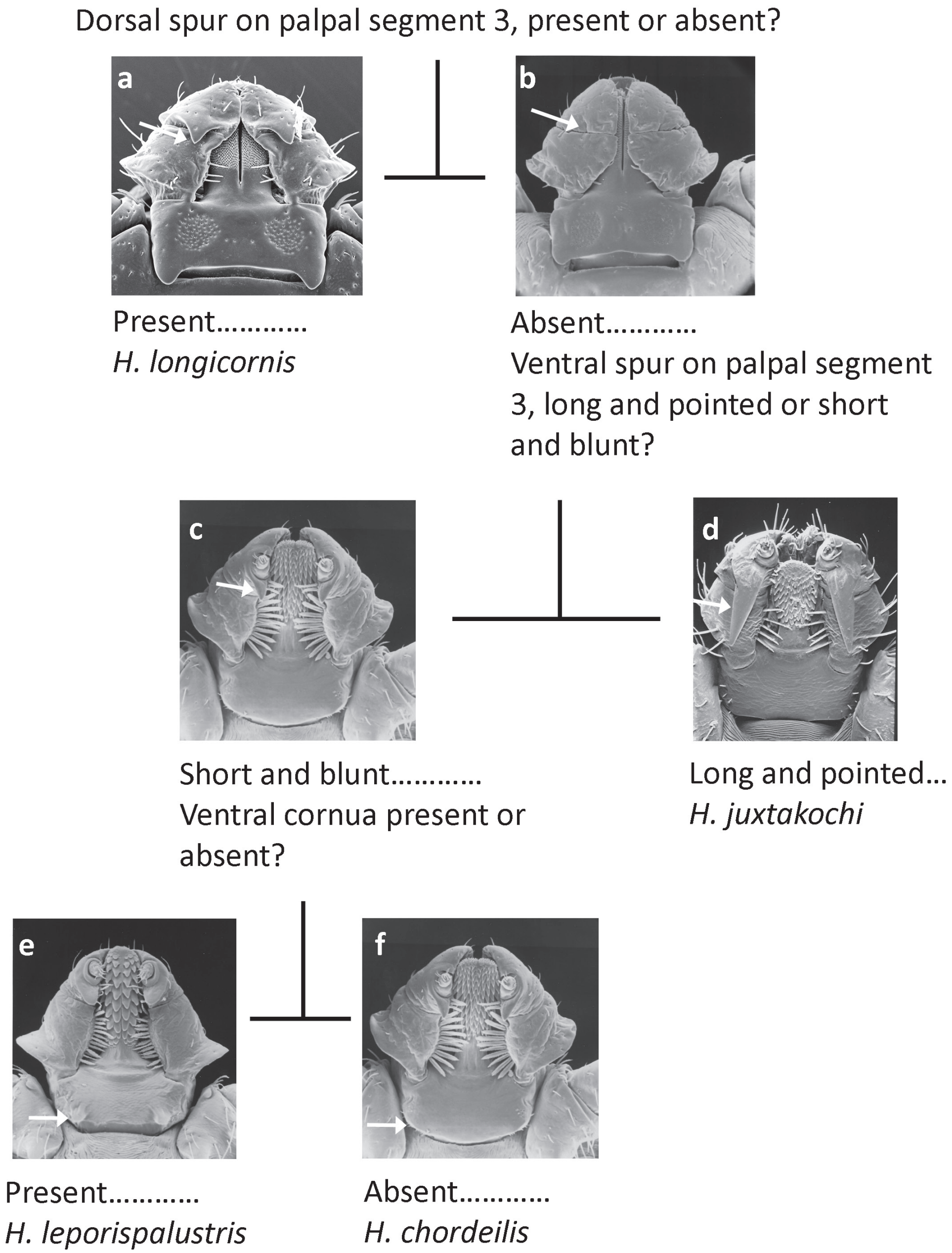
– Basis capituli ventrally without cornua at postero-lateral margins (Fig. 7b) **3**

2 Basis capituli dorsally with prominent posteriorly directed cornua (Fig. 7c)........ ....***Haemaphysalis* (*Gonixodes*) *leporispalustris* (Packard, 1869)**

– Basis capituli dorsally with cornua faint or absent (Fig. 7d)................................ .... ***Haemaphysalis* (*Gonixodes*) *juxtakochi* Cooley, 1946**

3 Dorsally, lateral margins of basis capituli straight (Fig. 7e) ....***Haemaphysalis* (*Kaiseriana*) *longicornis* Neumann, 1901**

– Dorsally, lateral margins of basis capituli pointed (Fig. 7f)................................. .... ***Haemaphysalis* (*Aboimisalis*) *chordeilis* (Packard, 1869)**



Dorsal spur on palpal segment 3, present or absent?

Present………… *H. longicornis*

Absent………… Ventral spur on palpal segment 3, long and pointed or short and blunt?

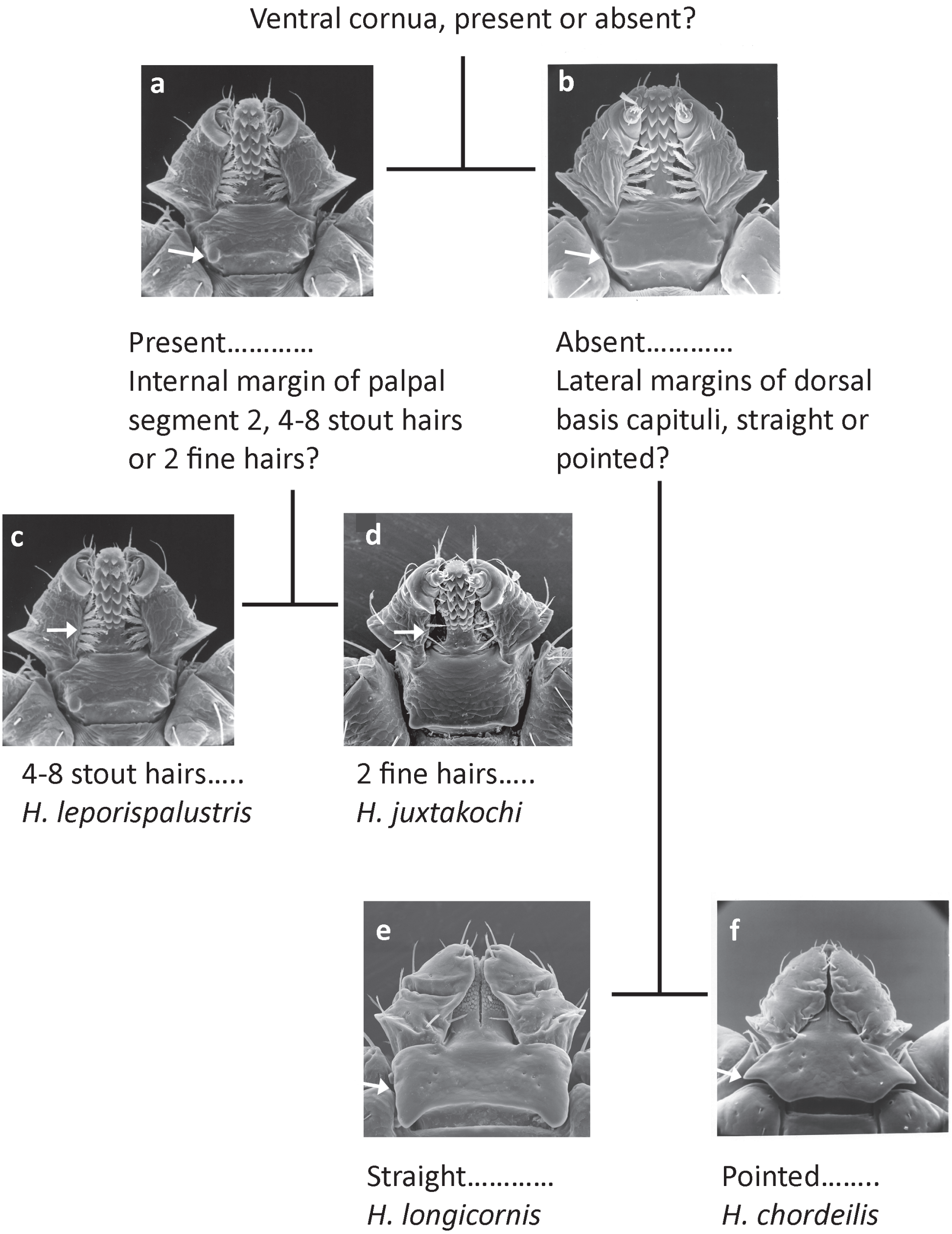
Short and blunt………… Ventral cornua present or absent?

Long and pointed… *H. juxtakochi*

Present………… *H. leporispalustris*

Absent………… *H. chordeilis*

Figure 5. Pictorial key to adults of *Haemaphysalis* spp. occurring in North America.



Ventral cornua, present or absent?

Present…………
Internal margin of palpal segment 2, 4-8 stout hairs or 2 fine hairs?

Absent…………
Lateral margins of dorsal basis capituli, straight or pointed?

4-8 stout hairs…..
H. leporispalustris

2 fine hairs…..
H. juxtakochi

Straight…………
H. longicornis

Pointed……..
H. chordeilis

Figure 6. Pictorial key to nymphs of *Haemaphysalis* spp. occurring in North America.

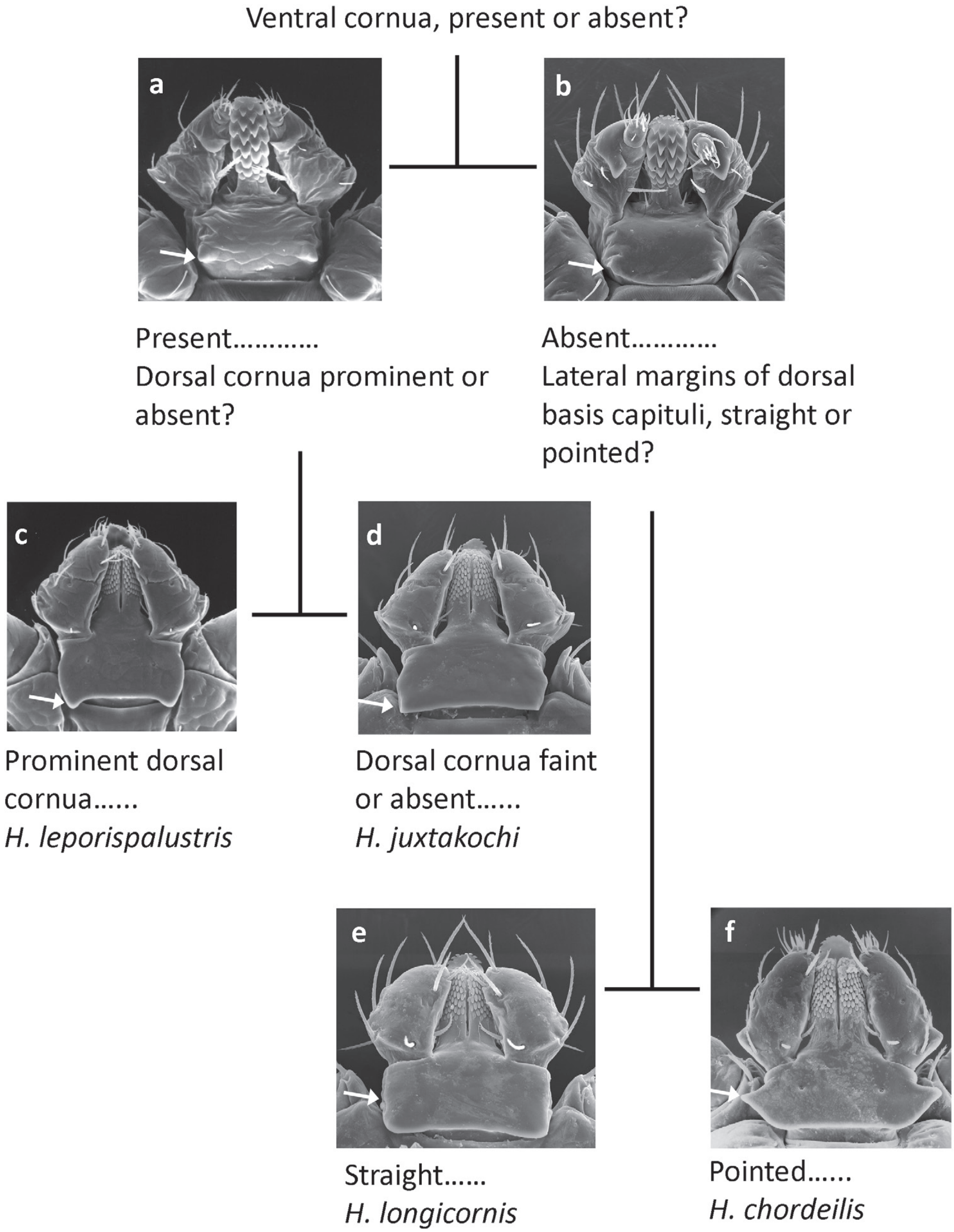


Figure 7. Pictorial key to larvae of *Haemaphysalis* spp. occurring in North America.

Conclusions

This key enables researchers to distinguish the four species of *Haemaphysalis* that may be encountered in North America in all life stages. Previously, readers would have had to peruse keys from several distinct parts of the world in order to compare the morphology of these four species, e.g. US keys containing *H. chordeilis* (Furman and Loomis 1984, Keirans and Litwak 1989); Old World keys with *H. longicornis*, including Japan (Yamaguti et al. 1971) and Australia (Roberts 1970, Barker and Walker 2014); and Central and South American keys for *H. juxtakochi* (Fairchild et al. 1966, Nava et al. 2017).

The ability to easily distinguish these four species will contribute to ongoing efforts to map the distribution of *Haemaphysalis longicornis* in North America and understand the potential risks posed by this recently discovered exotic tick species (Rainey et al. 2018). This tool will also help to improve our understanding of the biology and ecology of native *Haemaphysalis* spp., which have been relatively poorly studied compared to other native ixodids, and will promote the early detection of any northward expansions of *H. juxtakochi*. In this manner we can capitalize on the interest generated by the arrival of *H. longicornis* to augment our understanding of the existing New World haemaphysaline fauna.

However, as *Haemaphysalis* is the second largest genus in the tick family Ixodidae (so-called hard ticks), with over 160 additional species in the Old World (Petney et al. 2007, Guglielmone et al. 2014), including important disease vectors (de la Fuente et al. 2008), careful monitoring to detect the potential arrival of other members of this genus is encouraged. Should additional *Haemaphysalis* species establish themselves in North America, this key will require revision.

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References

Barker SC, Walker AR (2014) Ticks of Australia: The species that infest domestic animals and humans. Zootaxa 3816: 1–144.

Beard CB, Occi J, Bonilla DL, Egizi AM, Fonseca DM, Mertins JW, Backenson BP, Bajwa WI, Barbarin AM, Bertone MA, Brown J, Connally NP, Connell ND, Eisen RJ, Falco RC, James AM, Krell RK, Lahmers K, Lewis N, Little SE, Neault M, Pérez de León AA, Randall AR, Ruder MG, Saleh MN, Schappach BL, Schroeder BA, Seraphin LL, Wehtje M, Wormser GP, Yabsley MJ, Halperin W (2018) Multistate Infestation with the Exotic Disease–Vector Tick *Haemaphysalis longicornis* – United States, August 2017 – September 2018. MMWR Morbidity and Mortality Weekly Report 67: 1310–1313.

Bishopp F, Trembley L (1945) Distribution and hosts of certain North American ticks. Journal of Parasitology 31: 1–41.

Clifford CM, Anastos G, Elbl A (1961) The larval ixodid ticks of the eastern United States (Acarina-Ixodidae). Miscellaneous Publications of the Entomological Society of America 2: 213–237.

Cooley RA (1946) The genera *Boophilus*, *Rhipicephalus*, and *Haemaphysalis* (Ixodidae) of the New World. National Institute of Health Bulletin No. 187, 54 pp.

de la Fuente J, Estrada-Peña A, Venzal JM, Kocan KM, Soneshine DE (2008) Overview: Ticks as vectors of pathogens that cause disease in humans and animals. Frontiers in Bioscience 13: 6938–6946.

Eremeeva ME, Weiner LM, Zambrano ML, Dasch GA, Hu R, Vilcins I, Castro MB, Bonilla DL, Padgett KA (2018) Detection and characterization of a novel spotted fever group *Rickettsia* genotype in *Haemaphysalis leporispalustris* from California, USA. Ticks and Tick-borne Diseases 9: 814–818.

Fairchild G, Kohls G, Tipton V (1966) The Ticks of Panama (Acarina: Ixodidae). In: Wenzel RL, Tipton VJ (Eds) Ectoparasites of Panama. Field Museum of Natural History, Chicago, Illinois, 167–219.

Furman DP, Loomis EC (1984) The Ticks of California (Acari:Ixodida). Bulletin of the California Insect Survey Vol. 25, University of California Press, 239 pp.

Guglielmone AA, Estrada-Peña A, Keirans JE, Robbins RG (2003) Ticks (Acari: Ixodida) of the Neotropical Zoogeographic Region. Special publication of the International Consortium on Ticks and Tick-borne Diseases. Atalanta, Houten, 173 pp.

Guglielmone AA, Romero J, Venzal JM, Nava S, Mangold AJ, Villavicencio J (2005) First record of *Haemaphysalis juxtakochi* Cooley, 1946 (Acari: Ixodidae) from Peru. Systematic & Applied Acarology 10: 33–35.

Guglielmone AA, Robbins RG, Apanaskevich DA, Petney TN, Estrada-Peña A, Horak IG (2014) The Hard Ticks of the World (Acari: Ixodida: Ixodidae). Springer, Dordrecht, 738 pp.

Heath ACG (2013) Implications for New Zealand of potentially invasive ticks sympatric with *Haemaphysalis longicornis* Neumann, 1901 (Acari: Ixodidae). Systematic & Applied Acarology 18: 1–26.

Heath ACG (2016) Biology, ecology and distribution of the tick, *Haemaphysalis longicornis* Neumann (Acari: Ixodidae) in New Zealand. New Zealand Veterinary Journal 64: 10–20. https://doi.org/10.1080/00480169.2015.1035769

Hoogstraal H, Kim KC (1985) Tick and mammal coevolution, with emphasis on *Haemaphysalis*. In: Kim KC (Ed.) Coevolution of Parasitic Arthropods and Mammals. John Wiley & Sons, New York, 505–568.

Hoogstraal H, Roberts FHS, Kohls GM, Tipton VJ (1968) Review of *Haemaphysalis* (*Kaiseriana*) *longicornis* Neumann (resurrected) of Australia, New Zealand, New Caledonia, Fiji, Japan, Korea, and northeastern China and USSR, and its parthenogenetic and bisexual populations (Ixodoidea, Ixodidae). Journal of Parasitology 54: 1197–1213.

Keirans JE, Litwak TR (1989) Pictorial key to the adults of hard ticks, family Ixodidae (Ixodida: Ixodoidea), east of the Mississippi River. Journal of Medical Entomology 26: 435–448. https://doi.org/10.1093/jmedent/26.5.435

Keirans JE, Restifo RA (1993) *Haemaphysalis juxtakochi* Cooley (Acari: Ixodidae), a Neotropical tick species, found in Ohio. Journal of Medical Entomology 30: 1074–1075.

Kohls GM (1960) Records and new synonymy of New World *Haemaphysalis* ticks, with descriptions of the nymph and larva of *H. juxtakochi* Cooley. Journal of Parasitology 46: 355–361.

Lindquist EE, Galloway TD, Artsob H, Lindsay LR, Drebot M, Wood H, Robbins RG (2016) A Handbook to the Ticks of Canada (Ixodida: Ixodidae, Argasidae). Biological Survey of Canada Monograph No. 7, Ottawa, 317 pp.

Mukherjee N, Beati L, Sellers M, Burton L, Adamson S, Robbins RG, Moore F, Karim S (2014) Importation of exotic ticks and tick-borne spotted fever group rickettsiae into the United States by migrating songbirds. Ticks and Tick-borne Diseases 5: 127–134. https://doi.org/10.1016/j.ttbdis.2013.09.009

Nava S, Venzal JM, González-Acuña D, Martins TF, Guglielmone AA (2017) Ticks of the Southern Cone of America: Diagnosis, Distribution, and Hosts with Taxonomy, Ecology and Sanitary Importance. Academic Press, 372 pp.

Ostfeld RS, Brunner JL (2015) Climate change and *Ixodes* tick-borne diseases of humans. Philosophical Transactions of the Royal Society B 370: 20140051. https://doi.org/10.1098/rstb.2014.0051

Petney TN, Kolonin GV, Robbins RG (2007) Southeast Asian ticks (Acari: Ixodida): a historical perspective. Parasitology Research 101(Suppl. 2): S201–205. https://doi.org/10.1007/s00436-007-0687-4

Rainey T, Occi JL, Robbins RG, Egizi A (2018) Discovery of *Haemaphysalis longicornis* (Ixodida: Ixodidae) parasitizing a sheep in New Jersey, United States. Journal of Medical Entomology 55: 757–759. https://doi.org/10.1093/jme/tjy006

Roberts FHS (1970) Australian Ticks. Commonwealth Scientific and Industrial Research Organization, Melbourne, 267 pp.

Souza U, Dall'Agnol B, Michel T, Webster A, Weck B, Doyle R, Kasper CB, Soares J, Martins JR, Trigo TC, Ott R, Jardim MMA, Reck J (2018) Molecular survey of *Rickettsia* spp. in the Neotropical deer tick *Haemaphysalis juxtakochi* from Brazilian Pampa. Parasitology Research. https://doi.org/10.1007/s00436-018-5996-2

Yamaguti N, Tipton VJ, Keegan HL, Toshioka S (1971) Ticks of Japan, Korea, and the Ryukyu Islands. Brigham Young University Science Bulletin, Biological Series 15(1): 1–226.

Zhuang L, Sun Y, Cui XM, Tang F, Hu JG, Wang LY, Cui N, Yang ZD, Huang DD, Zhang XA, Liu W, Cao WC (2018) Transmission of severe fever with thrombocytopenia syndrome virus by *Haemaphysalis longicornis* ticks, China. Emerging Infectious Diseases 24: 868–871. https://doi.org/10.3201/eid2405.151435

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Description of *Callophylla macrocephala* sp. n. from southern Tanzania

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Abstract

A male cetoniine specimen from the old Schürhoff collection currently deposited in the Ditsong National Museum of Natural History (Pretoria, South Africa), was recently submitted for identification and has been found to represent a yet undescribed species of the poorly-known genus *Callophylla* Moser, 1916. The species is named *C. macrocephala* **sp. n.**, in recognition of its wider than average head, particularly at the level of the clypeus, and originates from the southern Tanzanian highlands, near the Tanzania-Zambia border town of Nakonde. This brings the total number of species now known for this genus to four, two from West Africa and two from East-Central Africa. All species were described on the basis of a male only, or this and a few extra specimens. The female is only known for the two West African species, *C. costata* Moser, 1916 and *C. lamottei* Antoine, 2007. A dichotomous key for the identification of the species of this genus is presented for the first time. It is suggested that the genus may be constituted of high altitude specialists, with a short period of activity and no ability to feed at the adult stage.

Keywords

Afrotropical region, *Callophylla*, Cetoniinae, new species, Tanzania

Introduction

The genus *Callophylla* Moser, 1916 was described along with the type species *C. costata* Moser, 1916, based on a male from central Cameroon. What was at first believed to be the female of the same species was described much later by Ruter (1954), on the basis of a specimen collected on Mount Nimba in Guinea. It was only in 2007 that sufficient material had finally become available to allow Antoine (2007) to describe the correct female of *C. costata* along with a new species, *C. lamottei* Antoine, 2007, to which the female described earlier by Ruter (1954) was recognised to belong. Further to this, a third species, *C. takanoi* Legrand, 2015 was recently described on the basis of a single male collected in western Zambia during a survey undertaken to the region by the British Natural History Museum. Thus, so far only a handful of specimens are known for the entire genus and of these apparently only two are female, one belonging to *C. costata* and the second to *C. lamottei*. The female of *C. takanoi* is undescribed and information on habitat and distribution of the three species of the genus is extremely limited.

A new species, recently recognised from an old specimen originating from the "Deutsch-Ostafrika" collection of Schürhoff and currently preserved in the Ditsong National Museum of Natural History (formerly Transvaal Museum, Pretoria, South Africa), is here described, thus providing additional, valuable information on the diversity of this poorly known genus.

Materials and methods

The holotype and only known specimen for this new species was submitted by Ms Ruth Müller of the Ditsong National Museum of Natural History (Pretoria, South Africa) for identification, as part of a loan to the author of several cetoniine specimens which are currently under review. The usual terminology of Krikken (1984) and Holm and Marais (1992) is followed in this study for the description of morphological characters. Specimen total length and maximum width were measured using a Vernier calliper, from the anterior margin of the clypeus to the apex of the pygidium and at the widest point of the elytra, respectively.

Photos of whole specimen dorsal and ventral habitus were taken with a Nikon CoolPix S9700 digital camera with macro setting, while photos of the male genitalia and other anatomical details were obtained using a Nikon DigitalSight DS-Fi2 camera attached to a Nikon SMZ25 dissecting microscope. The background was removed from the photos using Microsoft Word 2010 (Picture Tools), in order to increase clarity of resolution. The Combine ZP Image Stacking Software by Alan Hadley (alan@micropics.org.uk) was used to obtain z-stacking composite images.

Data on distribution and period of adult activity of the various species of the genus *Callophylla* were obtained from Moser (1916), Ruter (1954), Sakai and Nagai 1998, Antoine (2007), Legrand (2015), Beinhundner (2017) and from holders and curators of relevant collections (as per Acknowledgements section).

Taxonomy

Callophylla macrocephala sp. n.

http://zoobank.org/8DE7C0D2-AEC8-4351-8841-D69D44A8D9BF
Figures 1, 2

Diagnosis. This species can easily be separated from all the other species currently known in the genus by its remarkably wide clypeus, the brightness of its body surface and the scattered round to horseshoe punctures on the pronotum (dense and rugose in all the other species). Of the four species currently known in the genus *Callophylla*, *C. macrocephala* appears to be most closely related to *C. takanoi*, which occurs in Zambia (Ikelenge), but on its northwestern corner at the border with the DRC and Angola. Conversely, the only record currently known for *C. macrocephala* (“Nakonde Hochland”) is from the border region between southern Tanzania and north-eastern Zambia.

The two species can easily be separated on the basis of their key differences at the level of the clypeal width, pronotal tubercle and sculpture, aedeagal parameres and the general body colour and ornamentation. In particular, the clypeus of *C. macrocephala* is as wide as the total length of its head (from the tip of the clypeus to the anterior margin of the pronotum), while in *C. takanoi* it is shorter by about 30%. The pronotum of *C. macrocephala* exhibits a very prominent tubercle on its mid anterior margin, while this is absent in *C. takanoi*. Additionally, the pronotum of *C. macrocepala* is completely black and characterized by scattered, round to horseshoe punctures, while in *C. takanoi* it is brickred on the sides and black at middle, with dense rugose sculpture throughout the surface. Finally, the parameres of *C. macrocephala* are much longer and narrower than those of *C. takanoi* and also with very few, short setae at the apex.

Description of holotype. Male. (Fig. 1A–F) *Size*. Length 12.8 mm; width 5.3 mm.

Body: Shiny and elongate, black to light brown and ochreous in colour; with remarkable punctuation and long but scattered setae through most of dorsal surface (Fig. 1A).

Head. Wide and completely black; clypeus deeply concave and sharply upturned at anterior margin, sinuate at centre (Fig. 1C); entire surface covered in round to horseshoe punctures, with exception of ocular canthus, with tawny-coloured setae emerging at centre of each puncture and becoming particularly long towards vertex (Fig. 1C); antennal club dark brown and black, slightly longer than flagellum; flagellum dark brown; pedicel dark brown with lighter head attachment and bearing clusters of long, erected yellowish setae.

Pronotum. Surface entirely black and shiny with numerous but well-spaced punctures; punctures round on disc becoming horseshoe towards pre-scutellar arch; shape heptagonal and remarkably elevated at anterior margin, forming prominent tubercle at centre; antero-lateral margins carinate, postero-lateral smooth; posterior margin slightly sinuate with pre-scutellar arch smooth; medium to long yellowish setae scattered throughout lateral declivity and margins (Fig. 1A).

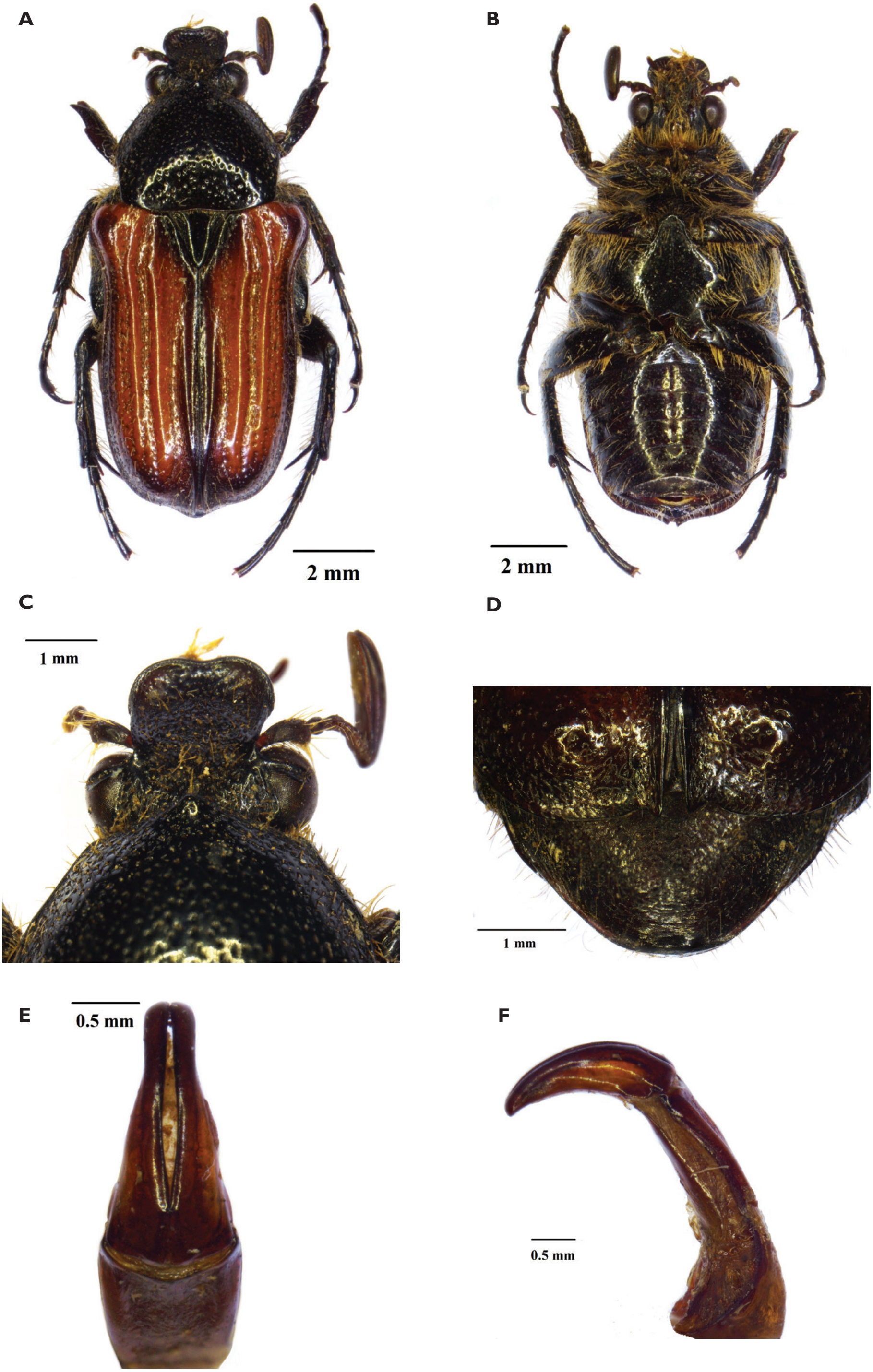

Figure 1. Dorsal (**A**) and ventral (**B**) habitus of *Callophylla macrocephala* sp. n., with details of clypeus (**C**), pygidium (**D**) and aedeagus in dorsal (**E**) and lateral (**F**) view (photographs Lynette Clennell).

Scutellum. Completely black and shiny; smooth on disc and exhibiting only minor geminate striae on antero-lateral margin; narrowly triangular with lateral margins much longer than base and sharp apex; lateral grooves exceptionally deep and wide (Fig. 1A).

Elytron. Shiny throughout; ochreous on disc, but dark brown to black on all margins except behind pronotal extra-scutellar area; costae very pronounced and typical of members of the genus; sub-humeral arch very deep, but both humeral and apical calluses poorly developed; paired horseshoe punctures lining entire surface of intercostal area, with long and erect tawny-coloured setae emerging at centre of most punctures; apical margin smoothly rounded, with a moderately-developed proximal spine; apical and postero-lateral declivities remarkably steep (Fig. 1A).

Pygidium. Closer to semicircular than triangular in shape and slightly convex; Dark brown to black and covered in dense rugose sculpture; short to medium yellow setae scattered around the disc, becoming longer and more numerous on apico-lateral margins.

Legs. Slender and elongate, with apical tarsal segments approximately twice as long as preceding ones; protibia bidentate, with second tooth blunt and poorly developed, with fine longitudinal ridges, coarse horseshoe punctures and short yellow setae, becoming longer and denser on inner margin; meso- and metatibia with longer and denser yellow setae, with striolate surfaces and mid spine on outer carina moderately developed; spurs long and acuminate, approximately twice as long in metatibia than in mesotibia (Fig. 1A, B).

Ventral surface. Completely black and shiny; with small and scattered horseshoe to round punctures throughout surface, except on mesometasternal lobe and on central area of abdominal sternites; pubescence long and dense, but shorter and scattered on abdomen and absent on mesometasternal lobe; mesosternal lobe smoothly rounded and slightly projecting anteriorly; abdominal sternites with visible concavity and groove at centre; metacoxa with remarkable carina separating ventral from lateral portion.

Aedeagus. Parameres elongate and slender, with apex smoothly rounded and bearing few scattered setae at centre (Fig. 1C); dorsal lobes of same width of ventral lobes and perfectly parallel throughout length (Fig. 1C).

Derivatio nominis. The name of this species reflects its particularly wide head, in comparison to that of all other known congeneric species.

Female. The female of this species, like that of its closest relative *C. takanoi*, is unknown, but is expected to exhibit a remarkable dimorphism, with broad characteristics similar to those previously described for *C. costata* and *C. lamottei* from West Africa (Antoine 2007). In those species, the main differences lie in the female exhibiting a tridentate and substantially enlarged protibia, in comparison to the male. The antennal clubs are almost twice as long in the male, while the general body shape is generally broader and more globose in the female. Additionally, typically the female meso- and metatibial teeth are more pronounced than those of the male.

Distribution. The only known specimen of *C. macrocephala* was collected in the "Nakonde Hochland" area of the old "Deutsch-Ostafrika". This colony included the present day mainland part of Tanzania and although the town of Nakonde falls within Zambia, the highlands area formed part of the Lindi District of the old German colony

Figure 2. Type localities of *Callophylla macrocephala* sp. n. (blue circle) and *Callophylla takanoi* Legrand, 2015 (red circle) in Central – East Africa.

(Schnee 1920, Vol II, p. 457). Thus, the type locality is obviously just across the Zambian border town of Nakonde. It is most likely though that the distribution range of this species extends to the nearby mountainous regions of both Zambia and Malawi.

Remarks. It may be of interest to note that despite the specimen carrying an unequivocal label ("Sammlung Schürhoff"), that identifies it as having belonged to the collection of this prolific entomologist of the early 20th century, no reference to it could be found in his extensive series of publications on the Cetoniinae of the World ("Beiträge zur kenntnis der Cetoniden").

Type material. Holotype (♂): Tanzania ("D. O. Afr"), Nakonde Hockland, Sammlung Schürhoff (TMSA "F", "7").

Identification key to the species of the genus *Callophylla*

1	Internal elytral costae fully developed and raised, external costae poorly raised to obsolete; body shape moderately elongate; West African distribution	**2**
–	Internal and external elytral costae equally well-developed and raised; body shape remarkably elongate; Central to East African distribution	**3**

2 Anterior margin of clypeus straight in male and weakly sinuate in female; antero-lateral angles of pronotum situated anteriad of mid pronotal length; lateral margin of metacoxae carinate; recorded from Cameroon, Gabon, Congo and Democratic Republic of Congo......................... ***C. costata* Moser, 1916**

– Anterior margin of clypeus indented in both sexes; antero-lateral angles of pronotum situated at middle of pronotal length; lateral margin of metacoxae smoothly rounded; recorded from Guinea and Ivory Coast.......................... .... ***C. lamottei* Antoine, 2007**

3 Body surface partly shiny; clypeal width shorter than total head length; pronotum without tubercle on anterior margin; recorded from Zambia (Ikelenge) .... ***C. takanoi* Legrand, 2015**

– Body surface completely shiny; clypeal width as long as total head length; pronotum with prominent tubercle on anterior margin; recorded from Tanzania (Nakonde Highlands) .... ***C. macrocephala* sp. n.**

Discussion

Callophylla macrocephala sp. n. represents the fourth species described within a very unique and poorly known genus. Very few specimens are known for this genus, and most are from Cameroon and belong to the species *C. costata*. The female of *C. takanoi* and *C. macrocephala* remains unknown, while only one female of each *C. costata* and *C. lamottei* are known with certainty (Ruter 1954, Antoine 2007, Beinhundner 2017).

A remarkable colour variation has been observed in the dorsal habitus of *C. costata*, with specimens ranging from completely reddish-ochre to dark brown and even completely black. Most specimens, however, exhibit a combinations of the lighter colours with a variable degree of black ornamentation on pronotum and elytra (Moser 1916, Beinhundner 2017). The head and scutellum appear to show the most conservative trend, in that they are always predominantly black, with few outstanding exceptions. The antennal clubs are invariably reddish to brown, even in the darkest specimens (Beinhundner 2017). Unfortunately, no similar conclusions can be drawn for the other three species, due to lack of material beyond the holotypes. However, in *C. lamottei* the male paratype is completely black, while the female holotype is reddish-brown with black areas across part of the dorsal surface (Antoine 2007). It seems likely, therefore, that a wide variability in colour pattern may be a typical feature of the entire genus.

The apparent rarity that characterises all species of the genus *Callophylla* is probably related to their unusual life cycle and ecology. Unfortunately, little information is yet available on the habitat and feeding habits of adults. One specimen of *C. costata* was reportedly collected inside a termite nest in southern Cameroon (Thierry Garnier, pers. comm.), while the label accompanying the only known specimen of *C. takanoi* explicitly states that it was collected in a "yellow pan trap" at an altitude of 1400 m (Legrand 2015). There is no evidence, however, to suggest that adults may feed on either flowers, fruits or sap flows. These and other details (e.g., "Nakonde Hochland", "Mont Kala", "Mont Nimba"), also seem to point towards a mountainous habitat for the genus.

Concerning period of adult activity, the scarce records available in the literature and collections in general indicate that adults of this genus may only be active for short periods, possibly after major rainfall events. Collection records range from March to December, with most in March/April (Sakai and Nagai 1998, Antoine 2007, Legrand 2015, Thierry Garnier and Gerhard Beinhundner pers. comm.).

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References

Antoine P (2007) Un nouveau *Callophylla* Moser, 1916 d'Afrique occidentale. Coleopteres 13(4): 43–46.

Beinhundner G (2017) The Cetoniinae of Africa. Gerhard Beinhundner, Euerbach, 1199 pp.

Legrand J-P (2015) Une nouvelle espèce de *Callophylla* Moser, 1916 de Zambie (Coleoptera, Scarabaeoidea, Cetoniidae, Cetoniinae). Cetoniimania NS 7: 32–34.

Moser J (1916) Beitrag zur Kenntnis der Cetoniden (Col.). Stettiner Entomologische Zeitung 77: 139–157.

Ruter G (1954) La reserve naturelle integrale du Mont Nimba, Fasc. II, 18 : Coleopteres Cetonides. Memoires de l'Institut francais de l'Afrique noire 40: 213–232.

Holm E, Marais E (1992) Fruit chafers of southern Africa (Scarabaeidae: Cetoniini). Ekogilde, Hartbeespoort, 326 pp.

Krikken J (1984) A new key to the suprageneric taxa in the beetle family Cetoniidae, with annotated lists of the known genera. Zoologische Verhandelingen Leiden 210: 3–75.

Sakai K, Nagai S (1998) The Cetoniine Beetles of the World.Mushi-Sha's Iconographic Series of Insects, Vol. 3. Mushi-Sha, Tokyo, 4221 pp.

Schnee H (1920) Deutsches Kolonial-Lexikon. Band II. Quelle & Meyer, Leipzig, 698 pp.