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Review of the stalked barnacle genus *Koleolepas* (Cirripedia: Thoracica: Koleolepadidae), with new records from Australian waters

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ABSTRACT – The stalked barnacle family Koleolepadidae is found exclusively in association with hermit crabs (*Dardanus* spp.) carrying sea anemones (*Calliactis* spp.). New records of *Koleolepas avis* and *K. willeyi* are herein reported, respectively, from near Ningaloo, Western Australia, and Christmas Island, an Australian territory in the Indian Ocean. Previously these species were known only from the East China Sea and southern Japan (*K. avis*), and the Loyalty Islands (*K. willeyi*). Both species are redescribed and figured. Type material of *K. tinkeri* and *K. willeyi* were examined and *K. tinkeri* is considered a junior subjective synonym of *K. willeyi*.

KEYWORDS: Crustacea, Diogenidae, Hormathiidae, epibiotic, symbiosis, parasitism, Ningaloo Marine Park, Christmas Island, Western Australia

INTRODUCTION

Members of the little known stalked barnacle family Koleolepadidae Hiro, 1933 are notable for being the third wheel in the well known symbiotic relationship between hermit crabs and sea anemones. These barnacles attach to the gastropod shell inhabited by the hermit crab, typically underneath the sea anemone's pedal disc. This peculiar habit is enabled by the unique, expanded, adherent pad that forms a sheath into which the peduncle and capitulum can retract. Thus, by fully retracting and extending the capitulum from under the sea anemone, they mitigate predation and are able to feed. Their unusual habitat has led to an unusual parasitic diet of feeding on the tentacles of the host sea anemone (Yusa and Yamato 1999). To date, the Koleolepadidae have only been found associated with sea anemones of the genus *Calliactis* Verrill, 1869, attached to gastropod shells inhabited by hermit crabs of the genus *Dardanus* Paulson, 1875.

This monogeneric family contained three nominal species, *Koleolepas avis* (Hiro, 1931), *K. tinkeri* Edmondson, 1951 and *K. willeyi* Stebbing, 1900. Only *Koleolepas avis* has been recorded since its original description (e.g. Liu and Ren 1985, 2007; Yusa and Yamato 1999; Yusa et al. 2001). Recent material from Australian waters in the Indian Ocean has prompted a reassessment of these species.

METHODS

Specimens were examined from the Natural History Museum (NHM), London, the Bernice Pauahi Bishop Museum (BPBM), Honolulu and the Western Australian Museum (WAM), Perth. Specimens were examined and dissected under a Leica MZ16 microscope. The total length (TL) was measured from the base of the adherent pad to the apex of the capitulum. Cirri and mouthparts were stained with lignin pink, mounted on slides and examined under an Olympus BX50 microscope. Line drawings were prepared using a camera lucida and digitally inked using a Wacom Intuos II drawing tablet and Adobe Illustrator. Photographs were taken using a Leica DC500 and DFC420. The map (Figure 1) was produced using the ArcGIS online mapping tool (www.arcgis.com).

SYSTEMATICS

Order Lepadiformes Buckeridge and Newman, 2006

Suborder Heteralepadomorpha Newman, 1987

Family Koleolepadidae Hiro, 1933

Genus *Koleolepas* Stebbing, 1900

TYPE SPECIES

Koleolepas willeyi Stebbing, 1900, by monotypy.

DIAGNOSIS

Hermaphrodites; capitular plates absent except for slender chitinous scuta, often further reduced or absent on one or both sides; crest running from orifice along distal-posterior margin. Peduncle naked, retractable into expanded oval, sheath-like, adherent pad. Mandible quadripartite, two medial processes serrate. Cirrus I pedicel with filamentary appendage; rami subequal, posterior rami of cirri II–VI much narrower than anterior rami; anterior rami of cirri II–VI with distal segments bearing stout, acute setae at postero-distal angles. Caudal appendages much shorter than pedicel, uni-articulate.

Complemental male globular, crest and sheath absent; scuta present. Mouthparts and cirri similar to hermaphrodite; penis well developed.

REMARKS

The complemental males retain seemingly functional cirri and mouthparts. Owing to their small size it is doubtful that they are still able to independently feed on tentacles. Surprisingly, the complemental males were not recognised as such when the species of *Koleolepas* were described, but were referred to as a 'projecting bulb' (Stebbing 1900; Hiro 1933) or 'bulbous process' (Edmondson 1951) and suggested to provide support for the capitulum (Stebbing 1900). This, even though Hiro (1933) reported a metamorphosing cypris larva attached near the orifice of a small individual of *K. avis*.

The members of *Koleolepas* have been recorded from Japan, East China Sea, Hawaii and the Loyalty Islands and are reported herein from Australia and Australian territorial waters in the Indian Ocean (Figure 1).

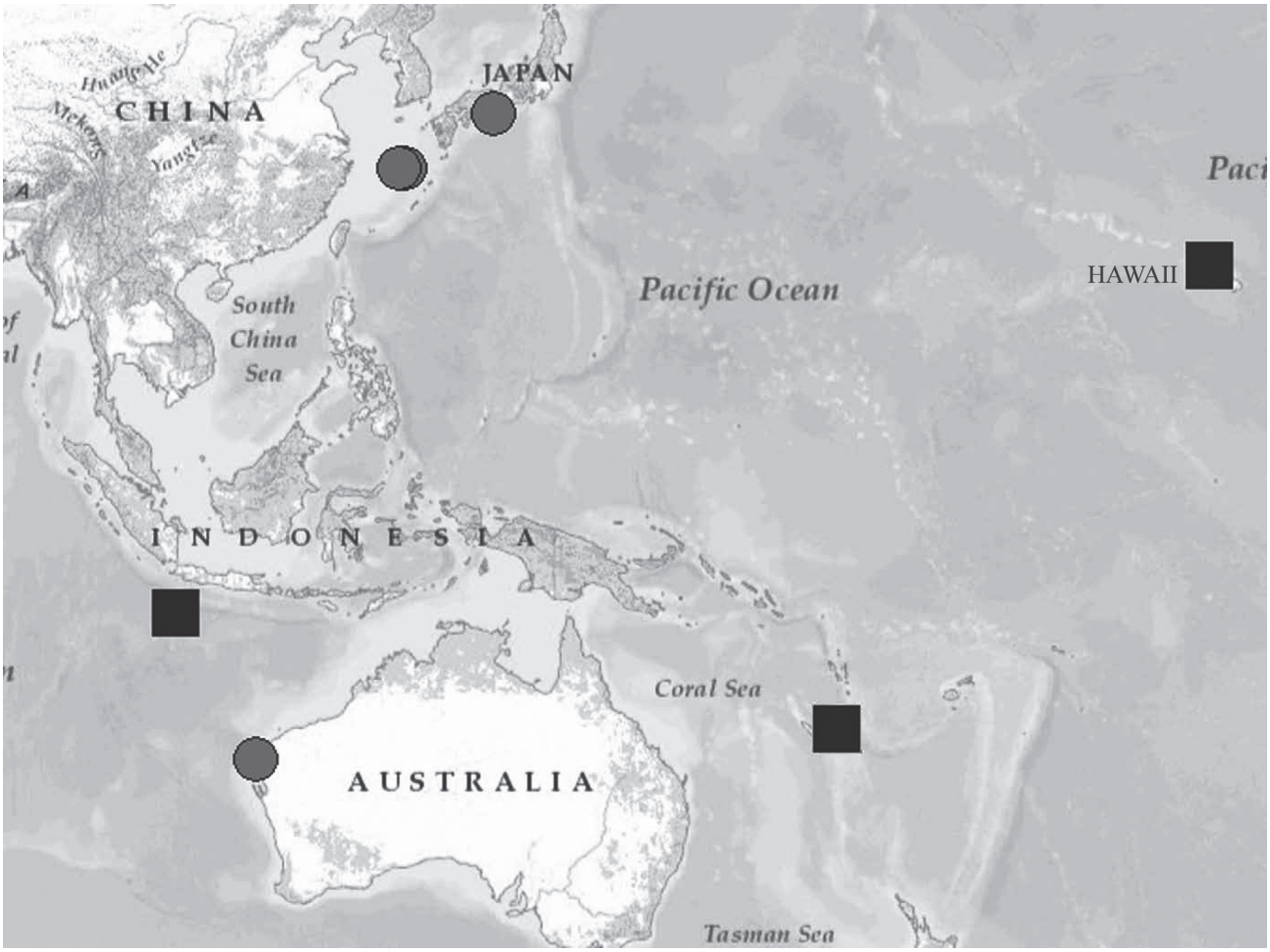

FIGURE 1 Map of known records of *Koleolepas avis* (Hiro, 1931) (□) and *K. willeyi* Stebbings, 1900 (■).

***Koleolepas avis* (Hiro, 1931)**

Figures 2, 3

Heteralepas avis Hiro 1931: 147, figures 4, 5, plate 11, figure 3.

Koleolepas avis (Hiro): Hiro 1933: 239, figure 4, plate 9 figures 4–6; Utinomi 1958: 307; Utinomi 1971: 510, figure 621; Zevina 1982: 145, figure 132; Liu and Ren 1985: 271, figure 53, plate 7; Liu and Ren 2007: 130, fig. 44.

MATERIAL EXAMINED

Australia: *Western Australia*: WAM C45480, 3 hermaphrodites, TL 15.6–25.9 mm, ~72 km SW of Coral Bay, 23°26′30″S 113°08′00″E, 220–230 m depth, G. McKewan, 18 February 2010.

DIAGNOSIS

Koleolepas hermaphrodites with orifice lips characteristically projecting beyond capitular crest, internally bearing 3 teeth near apical margin; scuta crescent shaped, present on at least one side; labrum with cutting edge bluntly V-shaped; cirrus I with long, posteriorly directed filamentary appendage at base of pedicel.

DESCRIPTION

Hermaphrodites

Capitulum smooth, not clearly demarcated from peduncle, distinctive capitular crest extending from orifice along postero-distal margin. Scutum chitinous, crescent shaped, curving away from orifice apically, reduced or absent on lower capitular side. Orifice lips triangular, projecting beyond crest, internally 3 teeth on apical margin. Peduncle smooth, 3 times longer than capitulum. Adherent disc ovoid, approximately two thirds total length.

Labrum with crest deeply concave, bluntly V-shaped, with row of 47 acute teeth, 23 straight medial teeth, lateral teeth curved medially. Palps short, subtriangular not extending medially beyond lateral edge of labral crest, single row of simple setae on margins. Mandible quadripartite, superior angle molariform followed by pectinate notch with 8 teeth, medial processes approximately equal in size, serrate with 7 and 8 teeth on upper and lower processes, respectively, separated by small pectinate notch with 4 acute teeth; inferior angle projecting, with 3 acute teeth. Maxilla I with cutting margin almost straight, 3 teeth of descending size located at superior angle, midpoint and half way between midpoint and inferior angle of margin; 2 stout setae immediately below superior tooth, separated from following stout setae by slight notch, remaining 13 stout setae more or less evenly distributed along cutting margin. Maxilla II subrectangular, sparsely setose along margins.

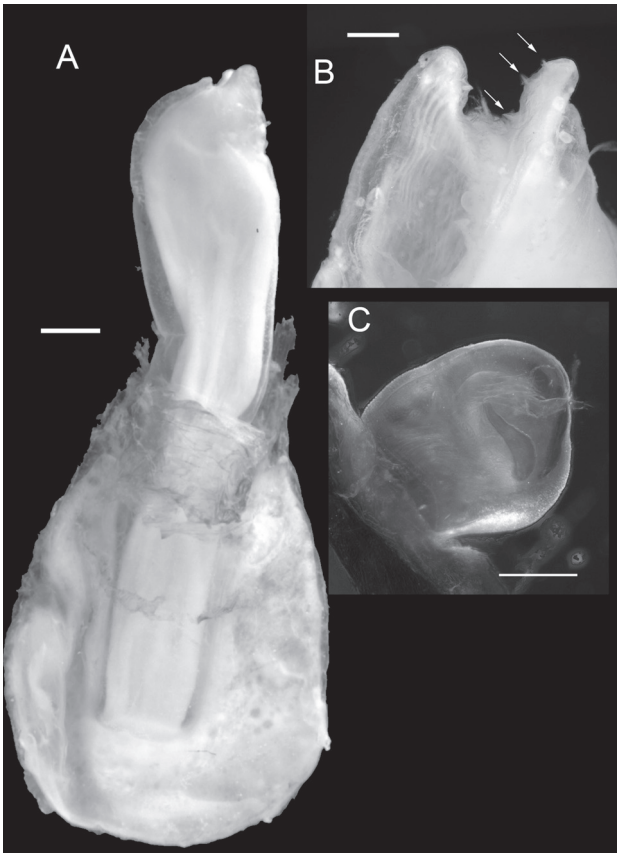

FIGURE 2 *Koleolepas avis* from west of Coral Bay, Western Australia (WAM C45480, TL = 25.9 mm). A, lateral view of hermaphrodite; B, close up of orifice, arrows indicate the orifice teeth; C, complemental male. Scale bars: A = 2 mm; B and C = 0.5 mm.

Cirrus I well separated from posterior pairs; posteriorly directed filamentary appendage near base of basal segment of pedicel, approximately as long as pedicel, tapering distally; rami subequal, approximately equal in length to pedicel, densely setose with simple and finely plumose setae. Cirri II–VI similar, pedicels becoming progressively smaller posteriorly; cirrus II with width of basal segment of pedicel 2 times width of distal segment; cirrus VI with width of pedicel basal segment 1.3 times width of distal segment; cirri II–VI with rami equal or shorter than pedicel length; anterior rami segments 1.5 times wider than respective posterior rami segments, chaetotaxy acanthopod, anterior margins sparsely setose, postero-distal margins of 4 distal-most segments armed with stout, acute, claw-like setae, antero-distal margins with 1–2 long, simple setae; posterior segments of rami becoming

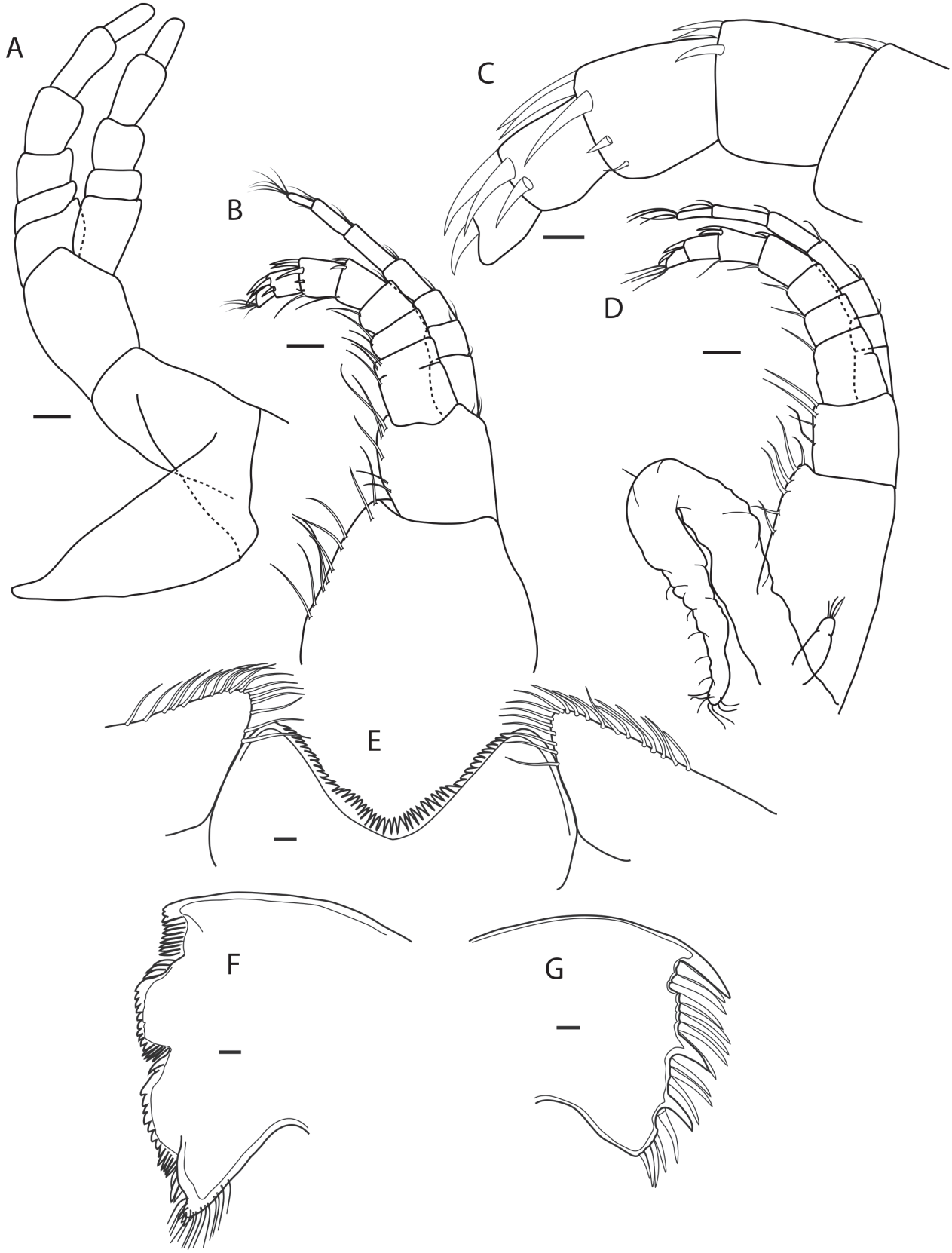

FIGURE 3 Cirri and mouthparts of *Koleolepas avis* hermaphrodite (WAM C45480, TL = 25.9 mm). A, right cirrus I; B, right cirrus II; C, terminal segments of anterior ramus of right cirrus II; D, right cirrus VI with penis and caudal appendage; E, labrum and mandibular palps; F, right mandible; G, left maxilla I;. Setation completely omitted from A; only claw-like setae shown in C; fine setae omitted from F and G. Scale bars: A, B and D = 150 µm; C, E–G = 50 µm.

elongate distally, chaetotaxy sparse, 1–2 simple setae present at postero-distal and antero-distal margins, terminal segment with tuft of 4–6 setae distally. Cirral segment counts as follows (* denotes damaged cirri):

	CI	CII	CIII	CIV	CV	CVI
L	5,5	8,7	8,8	8,8	8,8	8,7
R	6,5	8,7	8,7	8,5*	8,7	8,7

Caudal appendage uni-articulate, less than half length of basal segment of pedicel of cirrus VI, small tuft of setae apically. Penis approximately as long as cirrus VI, obscurely annulated, sparsely setose.

Complemental males

Globular, attached to hermaphrodite scuta near orifice. Capitular crest absent; peduncle very short, sheath absent; scuta bent, tapering apically. Cirri and mouthparts similar to hermaphrodites; penis longer than cirri.

HOSTS

Calliactis japonica Carlgren, 1928 (Yusa and Yamato 1999; present specimens WAM Z27714) attached to *Bufonaria bufo* (Bruguière, 1792) shell inhabited by *Dardanus arrosor* (Herbst, 1796) (WAM C45477). Other hosts include *D. crassimanus* (H. Milne-Edwards, 1836) (see Yusa et al. 2001 for details on inhabited gastropod shells). Hiro (1931) did not mention any sea anemones in his description of *K. avis*, but later, erroneously identified the host as *Calliactis parasitica* (Couch, 1842) (as *Adamsia rondeleti* Delle Chiaje, 1841), an Atlantic species (Hiro 1933).

DISTRIBUTION

Sagami Bay, Japan (type locality), East China Sea (Liu and Ren 1985), northern Western Australia. 10–230 m.

REMARKS

This is the most studied species of *Koleolepas*, having also been the subject of behavioural and ecological studies (Yusa and Yamato 1999; Yusa et al. 2001). These studies showed that the barnacles feed by cropping the tentacles from the sea anemones and that the asymmetry of the scuta develops with ontogeny, with the reduced scutum occurring on the lower side of the capitulum of older individuals. The barnacles tend to lie on their side along the lower edge of the anemone, with their orifices typically oriented towards the shell's aperture (Yusa et al. 2001).

The material agrees well with previous figures and descriptions. However, Hiro (1933) states that the first pair of cirri are shorter than the remaining pairs, but in the current specimens the rami are subequal in length. The figures of *K. avis* presented by Liu and Ren (1985, 2007) show the terminal segment of the anterior rami of cirri II and III as lacking the single claw-like seta. A slight constriction about one third from the apex of the right caudal appendage (Figure 3D) gives the impression that it may be bi-articulate, rather than uni-articulate as is the left caudal appendage and as described by Hiro (1931, 1933).

***Koleolepas willeyi* Stebbing, 1900**

Figures 4, 5

Koleolepas willeyi Stebbing 1900: Stebbing, 1900: 677, plates LXXIII, LXXIVD; Zevina 1982: 146, figure 133.

Koleolepas tinkeri Edmondson 1951: 185, figure 1; Zevina 1982: 146, figure 133.

MATERIAL EXAMINED

Loyalty Islands: NHM 1906.4.19.148, 1906.4.19.164 and 1906.4.19.165, Holotype, hermaphrodite, TL ~26 mm, Lifu Islands, depth unknown, A. Willey, 10 February 1897. **Hawaii:** BPBM B351, holotype of *K. tinkeri*, TL 28.5 mm, Oahu, off Ewa, 29 m, S.W. Tinker, 31 May 1948; BPBM B354, 3 dry hermaphrodites, TL 15–16 mm, Oahu, off Ewa, depth unknown, S.W. Tinker, 19 October 1948; BPBM B767, 1 hermaphrodite, TL 17.5 mm, Hawaii, depth unknown. **Christmas Island (Indian Ocean)**: WAM C49720, 3 hermaphrodites, TL 11.7–28.6 mm, Flying Fish Cove, 10°25′42″S 105°40′7″E, depth unknown, G.J. Morgan, 22 February 1987.

DIAGNOSIS

Koleolepas hermaphrodites with orifice lips not projecting beyond capitular crest, bearing 2 internal teeth near apical margin; scuta present on at least one side; labrum with cutting edge broadly U-shaped; cirrus I with long, posteriorly directed filamentary appendage at base of pedicel.

DESCRIPTION

Hermaphrodites

Capitulum smooth, not clearly demarcated from peduncle, capitular crest extending from orifice along postero-distal margin. Scutum chitinous, apically bent away from orifice, reduced or absent on lower capitular edge. Orifice lips not projecting beyond crest, internally 2 teeth apically. Peduncle smooth, cylindrical, 3 times longer than capitulum. Adherent pad subcircular to ovate, up to 0.5 times total length.

Labrum crest deeply concave, broadly U-shaped with row of 44 acute teeth, 32 straight medial teeth, lateral teeth curved medially. Palps subtriangular, short, not extending medially beyond lateral edge of labral crest, single row of simple setae evenly spaced on margins. Mandible quadripartite, superior angle molariform followed by pectinate notch with 5 acute teeth, medial processes serrate with 6 and 8 teeth on upper and lower

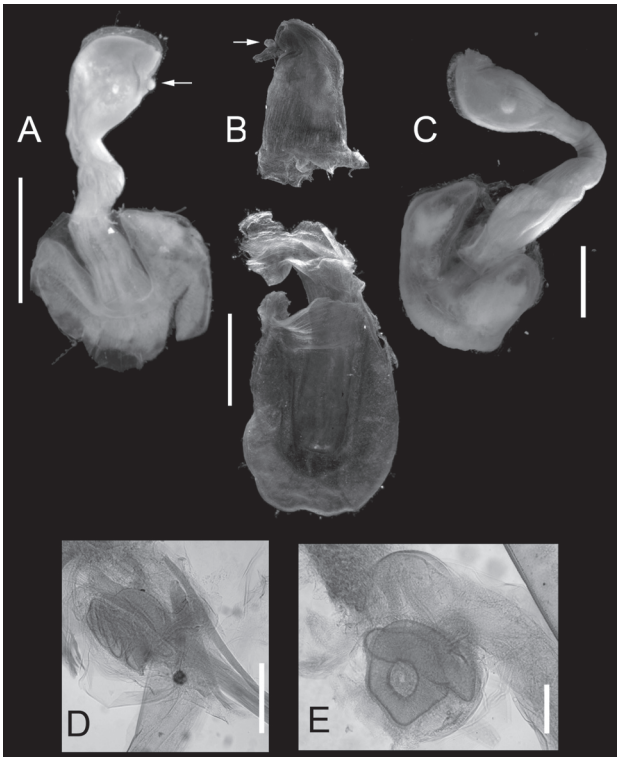

FIGURE 4 *Koleolepas willeyi* Stebbing, 1900. A, lateral view of hermaphrodite from Christmas Island (WAM C49720 TL = 11.7 mm); B, detached capitulum and peduncle of holotype of *K. willeyi* (NHM 1906.4.19.148); C, holotype of *K. tinkeri* Edmondson, 1951 (BPBM B351); D and E, coiled structure presumed to be the oviducal gland at the base of the right and left cirrus I, respectively. Arrow indicates position of complemental males. Scale bars: A = 5 mm; B and C = 200 µm.

processes, respectively, bordered by small pectinate notches with acute teeth; inferior angle projecting with 1 acute tooth and long simple setae. Maxilla I with cutting margin almost straight, 3 teeth of descending size located at superior angle, midpoint, and half way between midpoint and inferior angle of cutting margin; 2 stout setae immediately below superior tooth, separated from following setae by slight notch; remaining 14 stout setae more or less evenly spaced along cutting margin. Maxilla II subrectangular, sparsely setose on margins.

Cirrus I well separated from posterior pairs; posteriorly directed filamentary appendage near base of basal segment of pedicel, approximately as long as pedicel, tapering distally; pedicel approximately as long as rami; coiled oviducal gland prominent, located basally on basal segment of pedicel; rami equal, densely setose with plumose setae. Cirri II–VI similar, pedicels becoming progressively smaller posteriorly. Cirrus II and VI with width of pedicel of basal segment 2.4 and 1.4 times width of distal segment, respectively. Chaetotaxy of cirri II–VI anterior rami acanthopod, segments broad, up to 2 times corresponding width of segment of posterior ramus, anterior margins sometimes with 1–2 simple setae, postero-distal margins of 4 terminal segments armed with claw-like, stout acute setae; posterior ramal segments becoming elongate distally, chaetotaxy sparse, antero-distal and postero-distal margins sometimes with 1–2 simple setae. Cirral segment counts as follows (* denotes damaged cirri):

		CI	CII	CIII	CIV	CV	CVI
WAM C49720	L	5,5	7,6	7,8	7,6	7,6	7,6
(TL 18.2 mm)	R	5,5	7,6	8,7	8,6	7,6	7,6
BPBM B767	L	5,3*	7,6	8,7	8,7	7,7	7,7
(TL 17.5 mm)	R	5,5	7,7	8,7	8,7	7,7	7,7

Caudal appendages uni-articulate, approximately half length of basal segment of pedicel, tuft of simple setae apically. Penis thick, length subequal to cirrus VI, obscurely annulated.

Complemental males

Globular, attached to hermaphrodite scuta near orifice. Capitular crest absent; peduncle very short, sheath absent; scuta bent, width similar throughout length. Cirri and mouthparts similar to hermaphrodites; penis longer than cirri.

HOSTS

The type hosts were only recorded as being ‘Pagurid‘ and ‘Actinian‘ by Stebbing (1900). In Hawaii, this species is associated with *Calliactis polypus* (identified as *C. armillatas* Verrill, 1928 in Edmondson 1951) but the host hermit crab is unknown. The Australian material is associated with *Calliactis polypus* (Forsskål, 1775) (WAM Z27715) attached to the shell of *Turbo lajonkairii* Deshayes, 1839 inhabited by *Dardanus gemmatus* (H. Milne-Edwards, 1848) (WAM C42013).

DISTRIBUTION

Lifu, Loyalty Islands (type locality); southwest Oahu, Hawaii (Edmondson 1951); Christmas Island, Indian Ocean; to 30 m depth.

REMARKS

The holotype is represented by the empty capitulum, peduncle and sheath in ethanol as well as two slides with the mouthparts and cirri on one, and an egg mass and section of peduncle integument on the other. The slide bearing the mouthparts and cirri has deteriorated, with the mountant retracting around many of the limbs, however many details are still recognisable allowing a reasonable comparison with the Hawaiian and Australian material.

Stebbing’s (1900) original description specifically stated that the capitulum had no valves, however, the holotype clearly has paired, chitinous scuta. He also omitted the presence of the large filamentary appendage

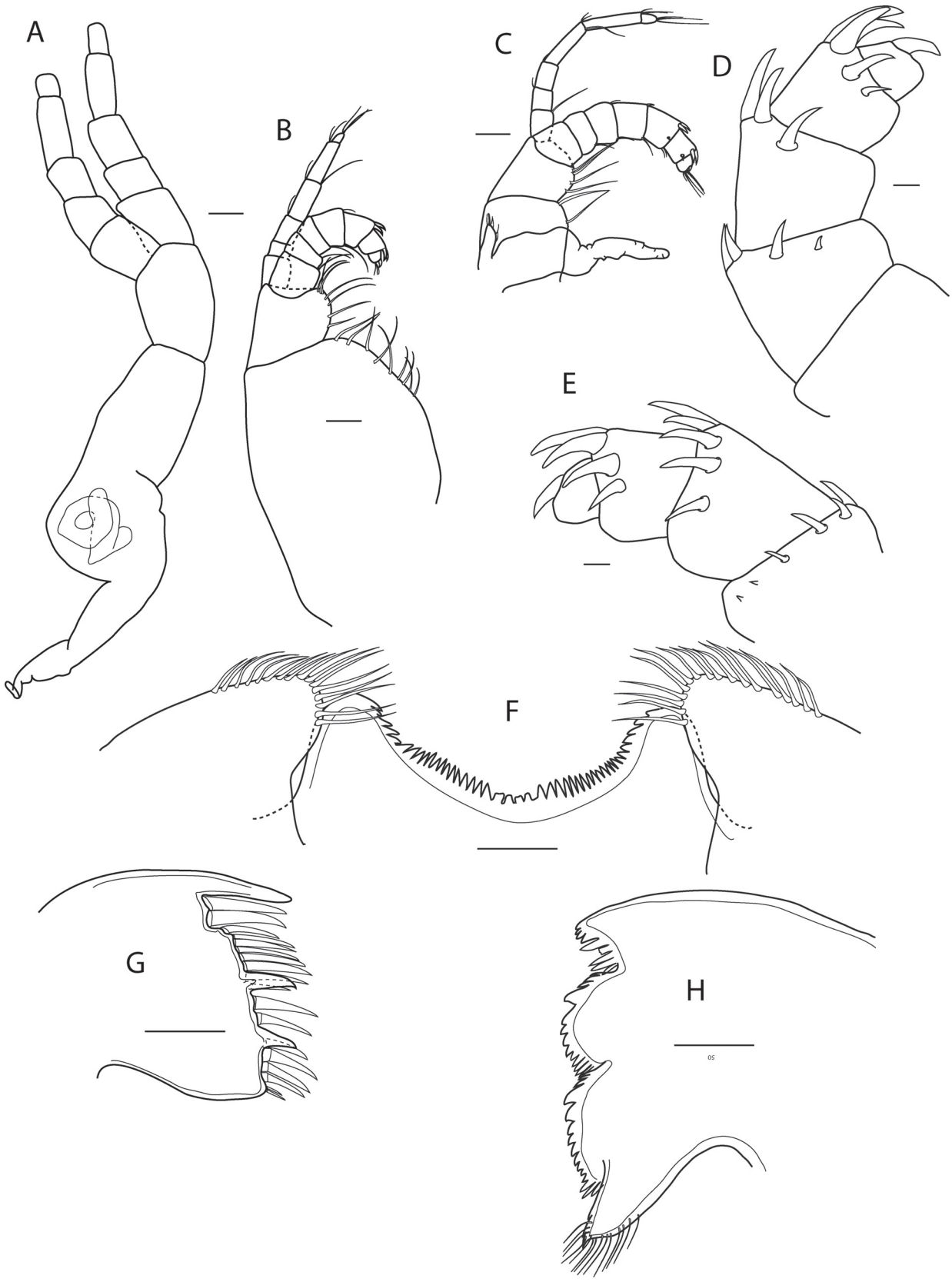

FIGURE 5 Cirri and mouthparts of *Koleolepas willeyi* hermaphrodite (WAM C49720, TL = 18.2 mm). A, right cirrus I; B, left cirrus II; C, left cirrus VI with penis and caudal appendage; D and E, terminal segments of anterior rami of cirri II (left) and III (right), respectively; F, labrum and mandibular palps; G, left maxilla I; H, right mandible. Setation completely omitted from A; only claw-like setae shown in D and E; fine setae omitted from G and H. Scale bars: A–C and F–H = 150 μm; D and E = 50 μm.

on the pedicel of cirrus I which is visible on only one of the first cirri, albeit mostly obscured by the retracting mountant. There is also no mention of a penis in his account, and there appears to be no trace of this organ on the slide. However, one of the cirri, possibly the sixth, is also missing from the slide, and perhaps had the penis attached to it. The Hawaiian specimens examined also appeared to lack a penis, but no other differences in the specimens were seen. The penis is absent in the smallest specimen from Christmas Island, but this individual does have a complemental male. Gonochoristic specimens, identified as *Koleolepas* sp., were reported by Yusa et al. (2011), but no further detail was given. As all of the dissected Hawaiian specimens are smaller than the specimen in Figure 4, it is suggested that penis development occurs at maturation, or is linked to the reproductive cycle as has been reported in other barnacles (e.g. Klepal 1990; Brickner et al. 2010).

The holotype of *K. tinkeri* was not dissected by Edmondson and nor was it in this study. The specimen, or specimens, that were dissected could not be located within the BPBM. Edmondson separated his species from *K. willeyi* on the grounds that Stebbing makes no mention of the filamentary and caudal appendages. However, the filamentary appendage was simply omitted as described above and Stebbing described the 'pleon', as being minute, and they are uni-articulate in his figure (Stebbing 1900, LXXIIIT), which is herein interpreted as referring to the caudal appendages. Further distinguishing characters listed by Edmondson included *K. tinkeri* having smaller palps that do not extend medially past the lateral borders of the labrum, and the lower serrate process of the mandible being truncate (as opposed to convex in *K. willeyi*). However, differences between the shape of the mandible and the relative size of the palps could be a result of differences in how they were examined or mounted on slides. The specimens examined in this study showed no appreciable differences between the palps, labrum or mandibles of the holotype of *K. willeyi*. Therefore, *K. tinkeri* is considered to be a junior subjective synonym of *K. willeyi.*

Characters distinguishing *K. avis* from the present species are subtle, with the exception of the projecting orifice, which gives the former species a distinctive appearance. In the present material, *K. willeyi* has relatively stouter cirri and, correspondingly, the claw-like setae are also more robust. The margin of the labrum in *K. willeyi* is more evenly curved compared with *K. avis*, which is more v-shaped. The serrations on the mandibles are also coarser and there are less pectinate spines in the notch between the superior angle and the upper serrate process of *K. willeyi*.

At the base of the pedicel of cirrus I is a coiled structure that is presumed to be the oviducal gland through which oviposition occurs (see Figures 4D, E and 5A). This prominent structure is not mentioned in the original description of *K. tinkeri* or for *K. avis*, but is clearly evident in the figure of *K. willeyi* by Stebbing although not described in the text (1900, pl. LXXIII, Cir. 1). The dissected specimen of *K. avis* was ovigerous but lacked this coiled gland. This, coupled with the prominence of the oviducal glands in the present species suggests that the *K. tinkeri* individual was entering a reproductive phase when collected (Walker 1980).

DISCUSSION

The present specimens of *Koleolepas avis* and *K. willeyi* represent significant range extensions from the East China Sea and Loyalty Islands, respectively, by several thousand kilometres into Australian territorial waters of the Indian Ocean. Based on known ranges of the hosts, however, both of these species can be expected to be found throughout the tropical Indo Pacific region.

To date, only two host species have been identified, *Calliactis japonica* and *C. polypus*. Yusa et al. (2001) found that *K. avis* was present on ~44% of shells with *C. japonica*, but none with *C. polypus* in Tanabe Bay, Japan, suggesting that at least *Koleolepas avis* is restricted to a single host species. The current material supports this hypothesis, but further studies would be required to confirm this.

The genus *Pagurolepas* Stubbings 1940 is also found in association with hermit crabs, but are instead attached to the interior of the gastropod shell and are not known to be associated with sea anemones. The trophi in this genus are of a more normal shape with the exception of the much reduced cutting margin of maxilla I (see Keeley and Newman 1974). The cirri are reduced even further than *Koleolepas* but are densely setose with long fine setae, similar to cirrus I of *Koleolepas* spp. The terminal segments of each cirri also bear smaller acute, stout spines. These features show clear adaptations to different modes of feeding between *Pagurolepas* and *Koleolepas* although the diet of *Pagurolepas* is unknown. The capitular plates on the side of the *Pagurolepas* that lies against the gastropod shell become reduced with size, in much the same way as species of *Koleolepas*.

While the koleolepadids have a unique morphology for a unique life history, similarities can be seen in the saw-like mandibles of species of the pyrgomatid tribe Hoekini Ross and Newman, 1995, which is parasitic on its coral hosts, and in the stout acanthopod first and second cirri of *Poecilasma crassa* Gray, 1848 (see Young 2001, Figure 8), which attaches on and around the mouthparts of deep sea decapods where it grabs scraps of food as the host feeds. Despite these adaptations that make the koleolepadids well suited to their unusual diet of feeding on the tentacles of *Calliactis* (Yusa and Yamato 1999), the soft chitin of the naked peduncle and capitulum suggests that they would be vulnerable to the host's nematocysts.

ACKNOWLEDGEMENTS

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