Brachylicoa lui, a New Species of Parapseudid Tanaidacean (Crustacea: Peracarida: Apseudomorpha), From the Hawaiian Islands, With a Taxonomic Key

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Brachylicoa lui, a new species of parapseudid tanaidacean (Crustacea: Peracarida: Apseudomorpha), from the Hawaiian Islands, with a taxonomic key

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Abstract

*Brachylicoa lui* sp. n. is described from the coastal waters of the Hawaiian island of O‘ahu. It is distinguished from the other four nominal members of *Brachylicoa* by a combination of characters including (1) an incised margin between base of rostrum and carapace, (2) mandible palp article-1 with cluster of 20–25 simple setae, (3) maxillule biarticulate palp ending in eight “cleaning’ setae, (4) maxilliped inner sub-distal margin with two stout spiniform seta, and (5) pereopod-6 with carpus having three plumose setae on mid-dorsal margin. *Brachylicoa* (= *Apseudes*) *babelmandebensis* sensu Guţu is tentatively transferred to the genus *Saltipedis* Guţu s.l. *Brachylicoa lui* is the only member of the genus known from the mid-Pacific Region and the Northern Hemisphere; the other species of the genus are known from the western Pacific and Indian Ocean in the Southern Hemisphere. A key to separate the four nominal species of *Brachylicoa* species is presented.

Key Words

*Brachylicoa lui* sp. n.
Parapseudidae
O‘ahu
Mid-Pacific Region
taxonomy

Introduction


An examination of the Tanaidacea holdings of the Bernice Pauahi Bishop Museum, Honolulu, Hawai‘i (BPBM) in 2015, revealed the presence of an apparently undescribed species belonging to the parapseudid genus *Brachylicoa* Guţu, 2006. Guţu (2006) established this genus designating *Saltipedis muelleri* Guţu, 1998 as the type species. In the same publication, he also described a second species, *B. indonesiana* Guţu, 2006 and a year later he emended the genus to include a third species, *B. estasiatica* Guţu, 2007 (Guţu 2007). In his revision of the family Parapseudidae Guţu, 1981, Guţu (2008) transferred *Apseudes babelmandebensis* (Băcescu, 1978) to this family and, with reservations he tentatively listed this species under the genus *Brachylicoa*; however, he listed several morphological...
differences (e.g., a distinctive pair of lateral spines on the anterior margin of the carapace and the morphology of pereopod-1), which could preclude its inclusion in this genus.

The description of the new Hawaiian species of *Brachylicoa* is the subject of this paper and represents the fourth in a series of publications dealing with the Tanaidacea of these mid-Pacific islands mentioned above.

**Materials and methods**

The material examined during this study came from the Bernice Pauahi Bishop Museum, Honolulu, Hawai‘i (BPBM), the Bohart Museum of Entomology (BME), University of California at Davis, and a collection made by the authors. Specimens from BPBM came from material collected from three coastal sites; (1) an ocean-water settling chamber in 1978 located at a now abandoned Naval Experimental site on the oceanic side of Mokapu Peninsula (type locality), (2) Kāne‘ohe Bay (adjacent to the type locality), and (3) Waikīkī. Material from the type locality was scraped by hand from sediment collection trays. Specimens from Kāne‘ohe Bay and Waikīkī were collected with sediment cores (12.5 cm diameter by 15 cm deep) pushed into the substratum and sieved through a 0.5 mm mesh screen (Coles et al. 2002 a, b). Material collected by the authors came from Makupu‘u Tidepools and was collected by “rock washings”. The late M. A. Miller collected the specimens from BME by hand from Coconut Island Reef, Kāne‘ohe Bay.

Other material (“*Brachylicoa cf. lui*”) from the eastern Hawaiian Islands [i.e., Hawai‘i (Big Island), Moloka‘i, and Maui] was collected by the same methods used for Kāne‘ohe Bay and Waikīkī studies (see Cole et al. 2004).

All the material was initially preserved in 10% formalin and then stored in ethanol. Specimens were dissected under an Olympus ZS-16 stereomicroscope. Appendages were mounted on glass slides in glycerin and observed with an Olympus BX41 microscope, and drawings were made with a *camera lucida*. Illustrations were prepared with Adobe Illustrator CC 2017. Photographs were taken using an Olympus DP73 digital camera mounted on a stereomicroscope and/or compound microscope and all specimens were measured with CellSens Dimension 1.11 Imaging Software (Olympus). Map was created using ArcGIS 10.4.1 software (University of Maryland Eastern Shore (UMES)).

The total lengths for all specimens in the type series of the new species of *Brachylicoa* were measured. Notwithstanding the presence on pereonite-6 of a male genital cone, hermaphroditic specimens having oostegites (marsupia) or oostegite buds are considered functional females. The various stages or forms observed were placed into six categories: (1) subadult <3.5 mm TL without distinctive secondary characters (e.g. oostegites and genital cone), (2) adult females with oostegites and genital cone, (3) adult ovigerous females and genital cone, (4) adult females with marsupium, (5) adult females with marsupium and genital cone, and (6) adult males having a genital cone with no indication of oostegites.

Type material is deposited in the Bernice Pauahi Bishop Museum, Honolulu, Hawai‘i (BPBM); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); and Gulf Coast Research Laboratory Museum (GCRL). All measurements are in millimeters (mm). Total body length (TL) is measured from the tip of the rostrum to the tip of the pleotelson. Terminology used in this description generally follows that of Larsen (2003). In our descriptions, the unguis is included in the total length of the dactylus.

**Abbreviations**

BPBM: Bernice Pauahi Bishop Museum, Honolulu, Hawai‘i; BME: Bohart Museum of Entomology, University of California at Davis; USNM: National Museum of Natural History, Smithsonian Institution, Washington DC; GCRL: Gulf Coast Research Laboratory Museum; TL: Total body length; Stn: Station

**Results**

**Systematics**

Order Tanaidacea Dana, 1849
Suborder Apsedomorpha Leach, 1814
Superfamily Apseduoidae Leach, 1814
Family Parapseudidae Guţu, 1981
Subfamily Parapseudinae Guţu, 2006
Tribe Parapseudini Guţu, 1981
*Brachylicoa Guţu*, 2006


**Emended diagnosis.** Hermaphroditism common with many adults having both oostegites and male genital cone. *Rostrum* weakly incised or entire at interface with carapace, broad posteriorly and with lateral margins entire or serrate, becoming greatly compressed anteriorly to form small, narrow, acute tip. *Carapace* ventral margins with row of 9–13 spiniform setae. *Pereonite-6* and *pleonites* 1–5 lacking transverse row of setae on dorsal surface. *Antennule* with peduncle article-1 having 2–3 distinctive spiniform setae on inner margin and with flagella nearly equal in length. Ventral margins of carapace with row of 9–13 spiniform setae. *Maxilliped* basis with one or two, spiniform, stout seta on or near inner distal margin. *Pereopod-1* with length of basis about equal to combined lengths of ischium-merus-carpus; merus with spiniform setae.
on distoventral margin; carpus with spiniform seta on distodorsal and distoventral margins; propodus having distodorsal margin with large spiniform seta (immediately adjacent to dactylus) and ventral margin with two to four spiniform setae. Pereopod-4 with propodus having sub-distal crown of setulate spiniform, lanceolate setae. Pereopod-6 having basis with long setae (plumose and/or simple) on dorsal and ventral margins; propodus with oblique semi-circle of setulate spiniform, lanceolate setae distally.

Male. Cheliped robust, with dorsal margin of basis armed small, but distinct spinose process.

**Type species.** *Brachylicoa muelleri* (Guţu, 1998)

**Composition (four species).** *Brachylicoa estasiatica* Guţu, 2007; *B. indonesiana* Guţu, 2006; *B. lui* sp. n. (see below); *B. muelleri* (Guţu, 1998).

**Remarks.** Based on our observations, we conclude that the questionable species “*B. babelmandebensis*” (Băcescu, 1978) described from the North west Indian Ocean, is not congenic with *Brachylicoa sensu stricto*. It is immediately distinguished from the other nominal members of *Brachylicoa* by having an acutely tipped rostrum with a unique pair of anteriorly directed, lateral spines and by the first pleonite having a distinct transverse, dorsal row of small setae near its anterior margin (see Băcescu 1978: Fig 4D). Based on these pleonal setae, “*B. babelmandebensis*” appears to be most similar to the genus *Saltipedis sensu lato* or it may represent a new but related genus. Pending examination of type or topotypic material, we herein tentatively transfer “*Apseudes babelmandebensis*” Băcescu, 1978 to the genus *Saltipedis* Guţu 1995, as *Saltipedis babelmandebensis* (Băcescu, 1978) comb. n.

Blażewicz-Paszkowycz and Bamber (2012: p. 62) commented that Guţu (2006) “somewhat tenuously separated [Brachylicoa] from Saltipedis.” Based on our study and the emended diagnosis presented herein, we follow Guţu (2006, 2008) in considering *Brachylicoa* as a distinct genus. The presence of a crown of setulate spiniform, lanceolate setae near the distal margin on the propodus of pereopod-4 (see Fig. 8F, below) appears to be a reliable generic character for *Brachylicoa* and it is included in the emended generic diagnosis. This character was used by Guţu (1998: p. 192) when separating *Saltipedis muelleri* from the genus *Saltipedis* Guţu, 1995 to become the type species of *Brachylicoa*. Besides the type species, this setal configuration occurs on the new Hawaiian species described herein and is present in the illustration of pereopod-4 for *B. estasiatica* (Guţu 2007: p. 81). Its occurrence on *B. indonesiana* cannot be verified since pereopod-4 for this species remains undescribed (Guţu 2006).

Although not prominent, we consider another reliable generic character, originally noted by Guţu (2006), to be the presence of one or two spiniform seta on the inner distal corner of the maxilliped basis. This, among other previously mentioned characters, including the setation of pereopod-4, appears to distinguish *Brachylicoa* from all other known parapseudid genera.

**Brachylicoa lui sp. n.**

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Figures 2–12, 13E, N, J, O, T, and V

**Material examined.** Holotype. Ovigerous hemaphroditic with male genital cone (BPBM S17058), TL 8.3 mm, Station (Stn) Ulupau (Head), Tray10, (780041H1 – jar #23102, labelled as *Apseudes* sp. #2), (21°27’24.26”N, 157°44’10.29”W), from Naval Experimental site (no longer extant), Mokapu Peninsula, O’ahu, Hawai‘i, 05-Dec-1978.

Paratypes. Same collection data as for holotype. One ♀ with marsupium and genital cone (BPBM S17059), TL 7.56 mm; one ♂ without oostegites but with genital cone (BPBM S17060), TL 8.4 mm; one ♀ with marsupium (USNM 1422441), TL 8.8 mm; one ♀ with marsupium and genital cone, TL 6.47 mm (USNM 1422412); one ♀ with eggs and genital cone (USNM 1422413), TL 7.5 mm; one ♀ with oostegites and genital cone, TL 6.83 mm (GCRL 06586); one ♀ with eggs and genital cone, TL 6.80 mm; (GCRL 06587).

Additional specimens from the type locality are in the collection of the Bernice Pauahi Bishop Museum, Honolulu, Hawai‘i (BPBM).

**Additional material examined.** Same collection data as for holotype. One subadult, TL 3.03 mm; one ♀ with oostegites and genital cone, TL 5.15 mm; one ♀ with oostegites and genital cone, TL 6.02 mm. Additional specimens from the type locality are in the collection of the authors.

**Additional BPBM material examined:** Kāne‘ohe Bay, O‘ahu (collectors: Coles et al. 2002a). — One ♂ (damaged), four ♀♀ (two incubatory, one with ten well-developed mancae; two pre-incubatory), Sta 1 (21°30’22.1”N, 157°57’1.7”W), North Channel KYC Patch Reef, depth 1-6 m, 17 Nov 1999. — One non-incubatory ♀, three subadults, Sta 9 (21°27’35.2”N, 157°49’22.1”W), Channel Marker “12”, depth 0.5-15 m, 28 Jan 2000. — Six ovigerous ♀♀, eight subadults, Sta 12 (21°26’36.8”N, 157°48’40.3”W), Heeia Kea Pier, depth 0-7 m, 19 Jan 2000. — Adult ♀♀, TL 6.1 mm, Sta 14 (21°26’23.1”N, 157°47’30.2”W), Floating City, depth 0-4 m, 10 Nov 1999. — Three ♀♀ (2 ovigerous), four subadults, Sta 16 (21°26’13.2”N, 157°48’15.2”W), Heeia Fish Pond Reef, 10 Nov 1999. — One ovigerous ♀ (14 undeveloped ova), TL 5.2 mm, Sta 22 (21°26’15.3”N, 157°45’55.1”W), Marine Corps Base (MCB) Fuel Dock, depth 0.5-8 m, 25 Jan 2000. — One adult incubatory ♀, Sta 23 (21°26’53.0”N, 157°46’W 58.9”W), Rubble Island, depth 0-2 m, 26 Jan 2000.


Makupuʻu Tidepools, Oʻahu. — One manca, two subadults, (21°19′0.95″N, 157°39′52.13″W ), depth 0-1 m, coll. by Andrés G. Morales-Núñez and Richard W. Heard, 22 Oct 2015


Diagnosis. Often hermaphroditic, having both four pairs of oostegites and male penal cone mid-ventrally on pereonite-6. Rostrum weakly incised at base, with slightly rounded, non-serrate shoulders, becoming immediately constricted distally to form, short, acute tip. Left mandible with lacinia mobilis having five denticles (proximal being most minute). Mandibular palp with article-1 having cluster of 20–25 simple setae. Pereopod-1 with propodus having ventral margin bearing two, rarely three, stout spiniform setae. Pereopod-6 with basis having row of plumose setae on dorsal and ventral margins; carpus with row of three plumose setae on mid-dorsal margin. Cheliped on both sexes and on hermaphroditic forms with exopod bearing five terminal plumose setae.

Female. Cheliped exhibiting two forms; first form typical of parapseudid females, having narrow carpus length three to four times width and chela lacking teeth; second form robust and similar to male cheliped, but with dorsal margin of basis lacking blunt spinose process.

Male. Cheliped robust, with dorsal margin of basis armed small, but distinct spinose process; carpus massive, length about twice width, widest distally; fixed finger of propodus and moveable finger each with tooth.

Hermaphrodites having cheliped similar to those of male, with sub-proximal anterior margin of basis with or without blunt spinose process.

Etymology. This species is named in honor of the late Lu Eldredge, a true gentleman and scholar, who contributed greatly to our understanding of the zoogeography, natural history, and marine ecology of the Pacific Ocean. Lu, also, is remembered fondly by colleagues and friends for his warm hospitality, generosity, kindness, and willingness to share his vast knowledge of the natural history and culture of the Mid and West Pacific.

Type locality. Oceanic water settling sediment chamber (now closed and abandoned), Naval Experimental site (21°27′24.26″N, 157°44′10.29″W), Mokapu Peninsula (Ulupau Head), Oʻahu, Hawai‘i.

Distribution. Known with certainty from the shallow coastal waters of the Oʻahu island, Hawaiian Archipelago.

We examined similar, possibly conspecific, BPBM material of Brachylica from the eastern Hawaiian Islands of Hawai‘i (Big Island), Moloka‘i, and Maui. Most of the relatively few specimens available for study were damaged subadults and females. We did not include specimens from these three islands in the distribution records for B. lui sensu stricto because of their relatively poor condition and geographical isolation from the Oʻahu population of B. lui. To determine if cryptic species are represented or if the specimens from the Big Island, Moloka‘i, and Maui represent a single variable species will have to resolved with certainty using molecular genetic comparisons.

Description. Hermaphrodite adult. With oostegites present on pereonites 1–4 and pereonite-6 with genital cone.

Body (Fig. 2A). Length about 8.3 mm, about 5.0 times that of width.

Cephalothorax (Fig. 2A–C). About 20% of TL and roughly as broad as long, with simple setae on sub-distal lateral face; rostrum short, pointed, with two small simple setae on each margin (Fig. 2B); ocular lobes bearing pigmented eyes. Carapace, ventral-inner margin with row of 13 irregular spiniform setae and simple seta (Fig. 2C).

Pereon (Fig. 2A). About 57% of TL, all pereonites wider than long; slightly decreasing in width, posteriorly; pereonites 1 to 3 shorter than other pereonites, with lateral lobes; pereonite-1 with one simple seta on each anterolateral corner; pereonites 2 to 3 with simple setae of unequal length on anterolateral corner and posterolateral lobe; pereonites 4–6 large, with posterolateral rounded lobe, with several simple setae of varying length on lobe, dorsal and lateral margins.

Pleon (Fig. 2A, D–E). About 15% of TL, shorter than pereonites 5 and 6 combined, all pleonites wider than long; pleonites 1–4 same length; pleonite-5 longer than others; each pleonite with several simple setae on dorsal surface and lateral lobes (Fig. 2D), each lobe with three to four long plumose setae (Fig. 2E); pleonites 4 to 5 with lateral epimeral lobes ending in posterolateral spine.

Pleotelson (Fig. 2A). About 8% of TL, sub-rectangular, shorter than pleonites 3 to 5 combined, weakly pointed at terminus with four simple setae distally, and bears several simple setae on all margins and dorsal surface.
Figure 1. Map of O‘ahu Island, indicating where *Brachylicoa lui* sp. n. was found.

Antennule (Fig. 3A). Peduncle article-1, 3.7 times as long as wide; inner margin with two or three spiniform setae and three simple setae in the middle margin, with three simple setae distally; outer margin with seven sensory setae proximally, with one tiny and nine simple setae, with a cluster of five simple setae sub-distally, dorsal surface with two sub-distal setae. Articles 2 and 3 longer than wide; inner and outer margins with several simple
setae distally. Article-4 (common) longer than broad; distal medial margin with two sensory setae. Outer flagellum with 17 articles, articles 1, 3, 5, 7, 9, 11, 13, and 15 with cluster of three to four long simple setae, articles 4, 6, 8, 10, 12, 14 with sensory seta, last article with three distal simple setae and two sensory setae. Inner flagellum of 13 articles, each with 1–3 simple setae, articles 6, 8 and 10 each with single aesthetasc.

Antenna (Fig. 3B). Composed of 18 articles. Article-1, inner margin with three (two in ventral view) simple setae and large spine distally; outer distal margin setulose. Article-2 longest, inner mid margin with two simple setae of unequal lengths; outer margin with four (two mid and two distal) small simple setae; squama present, well-developed, 5.0 times as long as wide, with 15 simple setae of varying lengths. Article-3, inner sub-distal margin with spiniform seta. Article-4, inner distal margin with two sensory setae. Article-5, inner sub-distal margin with one simple seta and two sensory setae; outer sub-distal margin with two sensory setae. Articles 6–17, with simple setae of unequal lengths on inner and outer margins. Article-18, with five distal setae of varying lengths.

Mouthparts. Labrum (Fig. 3C). Trapezoidal shallow-conical, with medial small process and finely setose. Mandibles (Fig. 4A–I). Right: incisor (Fig. 4A–B) and lacinia mobilis (Fig. 4A, C) with three denticles; setiferous lobe with five (four multi-furcate and one simple) setae (Fig. 4A, H); molar process robust, with ridged, grinding surface, and setulate spiniform setae distally (Fig. 4A, H), ventral and dorsal margins setulate (Fig. 4A, H), dorsal margin with two spiniform setae (Fig. 4H). Palp (Fig. 4D–E) with three articles; article-1 shortest bearing 20–25 simple setae; article-2 twice as long as first, with four (three long and one short) simple setae, with row of 14–16 pectinate setae (Fig. 4E), and two to three lateral pectinate setae; article-3 shorter than second, with row of 18–20 pectinate setae, and ten lateral pectinate setae, and distal margin with three simple setae. Left: incisor with five denticles (Fig. 4F, I), lacinia mobilis with four denticles (Fig. 4F, G); molar process similar to that of right mandible, except less robust (Fig. 4F, I) and dorsal margin with five spiniform setae (Fig. 4I). Labium (Fig. 4J). Outer margin with spiniform setae. Palp: with rows of small spiniform setae and simple setae along outer margin; distal margin with two pectinate setae, one apophysis, and two simple setae; inner margin with a rounded setulose expansion. Maxillule (Fig. 5A–B). Inner endite with five setulate setae and one inner setulose-pentafurcate spiniform seta (Fig. 5B), outer margin of inner endite finely setose with sub-proximal tubercle. Outer endite with twelve (one very small) spiniform setae and two sub-distal setulose setae, margins finely setose (setae longer on lateral margin); palp biarticulated with seven sub-distal and one distal whip-like “cleaning” setae. Maxilla (Fig. 5C–K). Moveable endite, outer lobe with two long inner pinnate-inner setulose spiniform setae (Fig. 5D) and nine slightly shortest inner pinnate-inner setulose spiniform setae (Fig. 5E); inner lobe with seven simple setae and seven inner pinnate-inner setulose spiniform setae (Fig. 5F). Fixed endite, outer lobe with six simple setae, two bipinnate-plumose spiniform setae (Fig. 5G), and three tri-rarcufurate-plumose spiniform setae (Fig. 5H), and one outer pectinate and outer setulose spiniform seta (Fig. 5I); inner lobe with eight bipinnate spiniform setae (Fig. 5J), and with ~40 basally swollen setae with bifid tip, sub-terminally (Fig. 5K).

Maxilliped (Fig. 5L–Q). With short and wide coxa, inner margin with small denticles. Basis longer than broad, inner proximal margin with some small denticles, with small spiniform setae, inner sub-distal margin with two stout, spiniform seta, inner and outer distal margins serrate. Palp: article-1, inner sub-distal margin with two (one long and one short) spiniform setae; outer margin with one spiniform seta and two spines forming a U-shape (Fig. 5M). Article-2; inner margin with six spiniform setae, 13–15 small setulate setae, and ~35 reduced simple setae; medial margin with four spiniform setae of varying lengths; outer margin with five spiniform setae. Article-3, inner margin with 17 inner setulate spiniform setae (Fig. 5N); medial margin with one to two spiniform setae. Article-4, inner margin with ten setulate setae, medial margin with one setulate seta; distal margin with two strongly-developed setulose seta. Endite inner margin with four coupling hooks (Fig. 5O), row of eleven basally-swollen setulate setae (Fig. 5O), with eight apically-bidentate spiniform setae (Fig. 5P), with one leaf-shaped bifid spiniform seta (Fig. 5Q), with six spiniform setae; outer margin setulose with small denticles on proximal margin. Epignath (Fig. 5R). Cup-shaped, with strong setulate spiniform seta.

Cheliped (Fig. 6A–B). Exopod with three articles, third article bearing five plumose setae. Basis, 2.5 times as long as wide; ventral margin with four small spines (three sub-proximal and one in the middle (sometimes bigger than others)), with two spiniform setae on distoventral margin, and two simple setae terminally; dorsal margin with distinct denticle on mid-margin (sometimes the denticle is not well developed) and one small spiniform setae distally. Merus sub-rectangular, ventral margin with simple seta medially and cluster of six simple setae sub-distally; mid-outer margin with four simple setae; dorsal margin with sub-proximal spiniform seta. Carpus, 1.6 times as long as wide, same length than basis, widest distally; ventral margin with five to six simple setae; outer margin with six simple setae; dorsal margin with five simple setae. Propodus, 1.4 times as long as wide; outer margin with two (one near articulation of dactylus) simple setae; dorsal margin with two simple setae distally; fixed finger with four ventral simple setae, with 16 to 18 sub-marginal simple setae on outer incisive margin, with tooth, with crenulate dorsal margin before tooth, claw short. Dactylus longer than fixed finger, with large proximal well-developed tooth, and with row of seven spines ventrally. Inner surface (Fig. 6B); basis with two ventral spiniform setae sub-distally; dorsal margin with spiniform seta distally. Merus with one spiniform setae on sub-proximal dorsal margin. Carpus with row of seven dorsolateral spiniform
Figure 2. Brachylicoa lui sp. n. holotype female with oostegites and genital cone. A dorsal view; B enlargement of rostrum; C anteroventral fold of carapace; D lateral view of pleonites; E enlargement of lateral view of pleonite-5 tip. Scale bars = 1.0 mm for A and 0.5 for B–C.
Figure 3. *Brachylicoa lui* sp. n. holotype female with oostegites and genital cone. A antennule; B antenna; C labrum. Scale bars = 0.5 mm for A–B and 0.1 mm for C.
setae; with five spiniform setae distally (three dorsolateral and two ventrolateral). Propodus palm having “comb row” of four simple setae of unequal length just proximal to articulation with dactylus, with three simple setae. Fixed finger with mid-ventrolateral spiniform seta, edge between tooth and claw with row of nine small denticles. Dactylus with one spiniform seta and a cluster of five simple setae on sub-distal lateral margin.
Figure 5. *Brachylicoa lui* sp. n. holotype female with oostegites and genital cone. A maxillule; B enlargement of penta-furcate spiniform setae; C maxilla; D–F, enlargement of inner pinnate-plumose spiniform setae; G enlargement of bipinnate-outer setulose spiniform seta; H enlargement of trifurcate-plumose spiniform seta; I enlargement of outer pectinate-outer setulose spiniform seta; J enlargement of bipinnate spiniform setae K enlargement of bifid basally-swollen seta; L maxilliped; M enlargement of distal outer margin of maxilliped palp-1; N enlargement of inner-setulate spiniform seta; O endite, P apically-bidentate spiniform setae; Q enlargement of leaf-shaped bifid spiniform seta; R epignath. Scale bars = 0.1 mm for A, C, L, O, R.
Figure 6. Brachylicoa lui sp. n. holotype female with oostegites and genital cone. A cheliped, lateral view; B cheliped, inner view. Scale bar = 0.5 mm.

Pereopod-1 (Fig. 7A−C). Exopod with three articles, third article bearing five plumose setae. Basis, 2.9 times as long as wide; ventral margin with seven small spiniform setae, terminal cluster of ten simple setae of unequal lengths; dorsal margin with ten small spiniform setae; inner margin with a cluster of eleven simple setae, and one proximal apophysis (Fig. 7B). Ischium wider than long; distoventral margin with twelve simple setae of varying lengths; distodorsal margin with one simple setae at each side. Merus, 1.5 times as long as wide; ventral margin with cluster of 7−10 simple setae, three distal simple setae, and one terminal spiniform seta; outer margin with
four sub-distal simple setae; dorsal margin with one small simple seta and with five sub-distal simple setae. Carpus, same length as merus; ventral margin with seven simple and one spiniform setae; outer margin with four (two ventrolateral and two mid-lateral) sub-distal simple setae; dorsal margin with oblique row of eleven simple and one spiniform setae. Propodus, shorter than carpus; ventral margin with 4–5 simple setae and two, rarely three, stout spiniform setae; outer margin with one simple seta just proximal to articulation with dactylus; dorsal margin with oblique row of seven setae and one spiniform seta; inner margin with three small simple setae and one sensory seta, and three sub-distal simple setae of unequal lengths, just proximal to articulation with dactylus (Fig. 7C). Dactylus and unguis combined longer than propodus, serrate (with row of 7–8 spines) ventrally, with simple seta distally; mid-dorsal margin with two small simple setae; dactylus 4.3 times longer than unguis.

**Pereopod-2** (Fig. 7D–F). Basis, 3.3 times as long as wide; ventral margin with four small spiniform setae and terminal cluster of eleven simple setae of unequal lengths; dorsal margin with seven small spiniform setae and three sensory setae; inner margin with one proximal apophysis (Fig. 7E). Ischium wider than long; sub-distal ventral margin with ten simple setae of varying lengths; distodorsal margin with two simple setae at each side (inner setae not shown). Merus, 1.5 times as long as wide; ventral margin with seven simple and two spiniform setae; outer margin with two (one of them longer than merus) simple and one spiniform sub-distal setae; distodorsal margin with one simple and one spiniform seta. Carpus, 2.2 times as long as wide; ventral margin with five simple and five spiniform setae; dorsal margin with oblique row of eleven simple and three spiniform setae. Propodus, 2.9 times as long as wide; ventral margin with six simple and four spiniform setae; dorsal margin with oblique row of seven setae and two spiniform setae; inner margin with five small simple setae, one sensory seta, and one sub-distal spiniform setae, just proximal to articulation with dactylus (Fig. 7F). Dactylus and unguis combined shorter than propodus, sub-distal outer margin with a cluster of five simple setae; mid-dorsal margin with one small simple seta; dactylus 3.0 times longer than unguis.

**Pereopod-3** (Fig. 8A–C). Basis, 3.7 times as long as wide; ventral margin with two small spiniform setae and terminal cluster of twelve simple setae of unequal lengths; dorsal margin with three small spiniform setae and two sensory setae; inner margin with one proximal apophysis (Fig. 8B). Ischium wider than long; sub-distal ventral margin with 13 simple setae of varying lengths; distodorsal margin with one simple seta at each side. Merus, 1.5 times as long as wide; ventral margin with six simple and two spiniform setae; outer margin with two spiniform and one simple sub-distal setae; distodorsal margin with one spiniform seta. Carpus, 2.9 times as long as wide; ventral margin with five simple and five spiniform setae; outer margin with oblique row of six spiniform and six simple setae. Propodus, 3.7 times as long as wide; ventral margin with five simple and four spiniform setae; outer and dorsal margin with oblique row of seven setae and two spiniform setae; dorsal margin with mid-dorsal sensory-seta; inner margin with two small simple setae, and one sub-distal spiniform setae, just proximal to articulation with dactylus (Fig. 8C). Dactylus and unguis combined longer than propodus, sub-distal outer margin with a cluster of five simple setae; mid-dorsal margin with one small simple setae; dactylus 3.0 times longer than unguis.

**Pereopod-4** (Fig. 8D–F). Basis, 2.4 times as long as wide; ventral margin with one sensory-seta and terminal cluster of nine simple setae of unequal lengths; outer margin with five small spiniform setae; dorsal margin with three sensory-setae. Ischium wider than long; distoventral margin with ten simple setae of varying lengths; distodorsal margin with one simple seta at each side. Merus, 1.7 times as long as wide; ventral margin with four (one small) simple and four spiniform setae; outer margin with two spiniform and one simple sub-distal setae; distodorsal margin with one spiniform seta. Carpus, 3.5 times as long as wide; ventral margin with five simple and eleven spiniform setae; distodorsal margin with three simple and two spiniform setae; inner distolateral margin with two spiniform setae (Fig. 8E). Propodus, 3.7 times as long as wide; ventral margin with three simple and five spiniform setae; dorsal margin with mid-proximal sensory-seta, and three distal spiniform setae (longer than dactylus and unguis combined), sub-distally with crown of 32 (14 of them on inner view (Fig. 8E)) setulate spiniform, lanceolate setae (Fig. 8F); inner margin with four simple setae; distodorsal margin with one spiniform seta (Fig. 8E). Dactylus and unguis combined shorter than propodus, mid-outer margin with one simple seta, ventral margin with two tiny setae distally; dactylus 2.0 times longer than unguis; unguis with two parallel rows of minute fine setae along posterior grasping margin.

**Pereopod-5** (Fig. 9A–B). Basis, 2.4 times as long as wide; ventral margin with terminal cluster of nine simple setae of unequal lengths; outer margin with eleven small spiniform setae and three sensory-setae. Ischium wider than long; distoventral margin with a cluster of twelve simple setae of varying lengths; distodorsal margin with one simple seta at each side. Merus, 1.8 times as long as wide; ventral margin with ten simple and three spiniform setae; distodorsal margin with one spiniform seta. Carpus, 3.2 times as long as wide; ventral margin with eight simple and nine spiniform setae; distodorsal margin with two spiniform setae. Propodus, 3.0 times as long as wide; ventral margin with six simple and five spiniform setae; dorsal margin with mid-distal simple and sensory-seta, and two distal spiniform setae (same length than dactylus and unguis combined); inner margin with two simple setae and four spiniform setae; distodorsal margin with one simple (just proximal to articulation with dactylus), and two spiniform setae (Fig. 9B). Dactylus and unguis combined shorter than propodus, mid-outer margin with
Figure 7. *Brachylicoa lui* sp. n. holotype female with oostegites and genital cone. 

A. pereopod-1, lateral view; 
B. basis of pereopod-1, inner view; 
C. propodus and dactylus of pereopod-1, inner view; 
D. pereopod-2, lateral view; 
E. basis of pereopod-2, inner view; 
F. propodus and dactylus of pereopod-2, inner view. Scale bar = 0.5 mm.
Figure 8. *Brachylica* *lui* sp. n. holotype female with oostegites and genital cone. A pereopod-3, lateral view; B basis of pereopod-3, inner view; C propodus and dactylus of pereopod-3, inner view; D pereopod-4, lateral view; E propodus and dactylus of pereopod-4, inner view; F enlargement of setulate spiniform, lanceolate setae. Scale bar = 0.5 mm for A–E.
one simple setae, distoventral margin with two tiny setae distally; dactylus 2.0 times longer than unguis; unguis with two parallel rows of minute fine setae along posterior or grasping margin.

**Pereopod-6** (Fig. 9C−D). Basis, 2.3 times as long as wide; ventral margin with one small spiniform seta proximally, and terminal cluster of seven simple setae of unequal lengths; outer margin with five small spiniform setae and 34 (12 ventrolateral and 22 dorsolateral) sensory-setae. Ischiium wider than long; distoventral margin with a cluster of eleven simple setae of varying lengths; distoskeletal margin with one simple setae at each side. Merus, 1.6 times as long as wide; ventral margin with five simple and five spiniform setae; distodorsal margin with one spiniform seta. Carpus, 2.4 times as long as wide; ventral margin with seven simple and eleven spiniform setae; dorsal margin with three simple and three plumose setae, with one simple and one spiniform setae distally; inner sub-dorsal margin with two simple setae. Propodus, 2.8 times as long as wide; ventral margin with three simple and ten spiniform setae; dorsal margin with mid-distal simple and sensory-seta; inner margin distal margin with two spiniform setae; distally with oblique semi-circle of 36 (four of them on inner view (Fig. 9C)) setulate spiniform, lanceolate setae (Fig. 9D). Dactylus and unguis combined shorter than propodus, mid-outter margin with one simple setae, disostal margin with two tiny setae distally; dactylus 1.3 times longer than unguis; unguis with two parallel rows of minute fine setae along posterior grasping margin.

**Pleopods** (Fig. 10A−B). Five well-developed, biramous pairs. Basal article, 3.2 times as long as wide, shorter than both rami, inner margin with six plumose, and outer margin with eight plumose setae. Exopod shorter than endopod, with 29 plumose setae. Endopod with 32 plumose setae (one seta with whiplike serrate tip (Fig. 11B)). Number of plumose setae (e.g. from 14 to 11) on peduncles and rami decreases from pleopod-1 to pleopod-5 and number of plumose whiplike serrate tip setae on endopod increase from one on pleopod-1 to two on pleopod-5.

**Uropods** (Fig. 10C). Peduncle well-developed, with simple setae. Exopod of 11−12 articles (twelve in the holotype, n = 10), with several simple setae, last article with 4−7 distal simple setae of varying lengths. Endopod of 33−47 articles (34−37 in the holotype, n = 9), article-2 apparently longest (but it is very difficult to determine if this article has division), with numerous simple setae; articles 7, 11, 15, and 20 with sensory setae, last article with six distal simple setae of varying lengths.

**Mucus glands/storage sites** (Fig. 11). Occurring within ischiium, merus, carpus and propodus of pereopods 1−5; and merus, carpus, and propodus of cheliped; number of glands decreasing posteriorly from pereopod-1 to pereopod-5; glands absent in pereopod-6.

**Dimorphism.** The adult male cheliped is robust and distinctly more massive than those described for the females of other members of the genus. As in the other known males of Brachylicoa, the dorsalproximal margin of the cheliped basis of B. lui bears a relatively small, blunt spiniform process (Fig. 12A) and there is a distinct mid-ventral, genital cone on pereonite-6. There are no indications of oostegites. The female cheliped exhibits two morphotypes; one having a narrow carpus with length more than three to four times width (Fig. 12B), and the other being robust and similar to that of male. Both female cheliped forms lack a blunt spine on the dorsoproximal margin of the basis (Fig. 12B−C), and there is no indication of a genital cone on pereonite-6. Adult hermaphrodites have oostegites present on pereonites 1 to 4 and a mid-ventral genital cone on pereonite-6; as in the male their chelipeds are enlarged with or without blunt spinose process on dorsoproximal margin of the basis.

**Intraspecific variation.** Brachylicoa lui exhibited some degree of variation among the individuals especially in the number of articles in uropodal exopod and endopod articles varied ontogenically, i.e., subadult and females with oostegites and genital cone have fewer articles than females with eggs/marsupium and a genital cone (7−11 versus 11−12, respectively) (Table 1).

**Size-distribution of material from Naval experimental site.** The body sizes of individual Brachylicoa lui measured during this study are presented in Table 1. The smallest observed ovigerous female and genital cone was 6.80 mm, while the largest was 7.54 mm, mean TL was 7.06 ± 0.24 (n = 3). Female with marsupium TL 8.82 mm. Females with marsupium and genital cone ranged from 6.47 to 8.13 mm; mean TL was 7.39 ± 0.49 (n = 3). Adult male without oostegites, but with genital cone TL 8.35.

**Remarks.** The adult female of Brachylicoa lui sp. n. (Fig. 13A−B), differs from other species of the genus by a combination of characters including (1) mandible palp article-1 with cluster of 20−25 simple setae, (2) the maxillule biarticulated palp ended in eight “cleaning” setae, (3) maxilliped inner sub-distal margin with two stout spiniform setae, and (4) pereopod-6 with carpus having three plumose setae on mid-dorsal margin.

The new Hawaiian species differs from B. muelleri by having the ventral margin of the carapace with a row of 13 spiniform setae (nine in muelleri), antenna with 18 articles (13 in muelleri), and more setae on the first article of the mandibular palp (20−25 versus 6). Brachylicoa lui closely resembles B. indonesiana by having a mandibular palp article-1 with a cluster of more than ten simple setae, but it can be distinguished by (1) carapace having ventral margin with row of 13 spiniform setae (nine in indonesiana), (2) the maxillule biarticulated palp with total of eight sub-terminal and terminal “cleaning” setae (five in indonesiana), (3) female cheliped basis lacking a blunt spine on the dorsal margin of the basis (one present in indonesiana), (4) pereopod-1 with distoventral margin of
Figure 9. *Brachylicoa lui* sp. n. holotype female with oostegites and genital cone. **A** pereopod-5, lateral view; **B** propodus and dactyulus of pereopod-5, inner view; **C** pereopod-6, lateral view; **D** propodus and dactyulus of pereopod-6, inner view. Scale bar = 0.5 mm.
Figure 10. *Brachylicoa lui* sp. n. holotype female with oostegites and genital cone. A pleopod; B enlargement of plumose seta with whiplike serrate tip; C uropod. Scale bars = 0.5 mm for A, C.

Table 1. TL, mean ± SE, and comparison of morphological features of sexual stages of *Brachylicoa lui* sp. n. from the Naval experimental site.

<table>
<thead>
<tr>
<th>Stages</th>
<th>TL (mm)</th>
<th>No. of uropodal exopod articles</th>
<th>No. of uropodal endopod articles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subadult</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>3.03</td>
<td>7 – 8</td>
<td>33 – 33</td>
</tr>
<tr>
<td>Adult females with oostegites and genital cone</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>5.15</td>
<td>7 – 8</td>
<td>Missing</td>
</tr>
<tr>
<td>2</td>
<td>6.02</td>
<td>11</td>
<td>33 – 35</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>5.59 ± 0.44</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult ovigerous females and genital cone</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>6.80</td>
<td>11</td>
<td>40 – 42</td>
</tr>
<tr>
<td>2</td>
<td>6.83</td>
<td>Missing</td>
<td>Missing</td>
</tr>
<tr>
<td>3</td>
<td>7.54</td>
<td>11</td>
<td>34 – 37</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>7.06 ± 0.24</td>
<td></td>
<td></td>
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<tr>
<td>Adult females with marsupium, no indication of male cone</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8.82</td>
<td>12</td>
<td>43 – 45</td>
</tr>
<tr>
<td>Adult females with marsupium and genital cone</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>6.47</td>
<td>11</td>
<td>36 – 38</td>
</tr>
<tr>
<td>2</td>
<td>7.56</td>
<td>12</td>
<td>44 – 47</td>
</tr>
<tr>
<td>3</td>
<td>8.13</td>
<td>12</td>
<td>34 – 37</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>7.39 ± 0.49</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male with genital cone, no indication of oostegites</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8.35</td>
<td>12</td>
<td>31 (damaged)</td>
</tr>
</tbody>
</table>
basis lacking a stout spiniform seta (one present in *indonesiana*) and merus without distodorsal stout spiniform seta (one present in *indonesiana*), (5) pereopod-1 with distoventral margin of basis lacking a stout spiniform setae (one present in *indonesiana*), and (6) the basal article of pleopod with plumose setae (without plumose setae in *indonesiana*). *Brachylicoa lui* is distinguished from *B. estasiatica* by the absence of an acute rostrum with serrate margins, antenna having 18 articles, and a mandible without tubercles on the outer surface. In contrast, *B. estasiatica* has 15 antennal articles, an acute rostrum with serrate margins, and a mandible with tubercles on the outer surface. The following key may be used to separate the species within the genus *Brachylicoa*.

![Figure 11. Digital images of *Brachylicoa lui* sp. n. paratype female with oostegites and genital cone (dissected). A–F pereopod 1–6. Arrows shown the presence of glands. Scale bar = 0.5 mm.](image-url)
Figure 12. *Brachylica* sp. n. paratypes chelipeds: A, male; B, C female. Scale bar = 0.5 mm.
Figure 13. Digital images of *Brachylica* *lai* sp. n. A holotype (female with oostegites and genital cone), lateral view of habitus, length 8.13 mm; B paratype (female with marsupium and genital cone) lateral view of habitus, length. Scale bar = 2.0 mm.
Key for the separation of the four currently recognized species of *Brachylicoa*

1  Tip of rostrum relatively long (over 1/3 length of rest of rostrum), posterior lateral margins distinctly serrate (Fig. 14A) .................................................................................................................. *B. estasiatica* [South China Sea: Malaysia]
   - Tip of rostrum small (less than 1/4 length of rest of rostrum), lateral margins of rostrum not distinctly serrate (Fig. 14B–D) ................................................................. 2

2  Rostrum not basally incised (Fig. 14B). Pereopod-6, ventral margin of basis with row of simple setae only (Fig. 14E).
Pleopod-1, basal article lacking plumose setae (Fig. 14H) .................................................. *B. indonesiana* [Indonesia: Celebes Sea]
   - Rostrum basally incised (Fig. 14C–D). Pereopod-6, ventral margin of basis with row of plumose setae (Fig. 14F–G).
Pleopod-1, basal article with three or more plumose setae (Fig. 14I–J) .................................................. 3

3  Mandibular palp, article-1 with cluster of six or fewer simple setae (Fig. 14K). Pereopod-6, dorsal margin of carpus lacking plumose setae (Fig. 14F) ............................................................. *B. muelleri* [Western Indian Ocean: Tanzania]
   - Mandibular palp, article-1 having cluster of 20–25 simple setae (Fig. 14L). Pereopod-6, dorsal margin of carpus with 2–3 plumose setae (Fig. 14G) ............................................................. *B. lui* sp. n. [North Central Pacific: O‘ahu Island]

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**Figure 14.** Tip of rostrum: A *Brachylica estasiatica*; B *B. indonesiana*; C *B. muelleri*; D *B. lui* sp. n. Pereopod-6: E *B. indonesiana*; F *B. muelleri*; G *B. lui* sp. n. Pleopod: H *B. indonesiana*; I *B. muelleri*; J *B. lui* sp. n. Mandible palp: K *B. muelleri*; L *B. lui* sp. n. Figures modified from [Băcescu 1978 (A); Guţu 2007 (B, E, H); Guţu 2006 (C, F, I, K); and this study (D, G, J, L)]; not to scale.
Mucus glands

We suspect the mucus secretions produced by the glands or mucus storage sites (see Fig. 11) on the appendages of *B. lui* are used in forming temporary or permanent tubular domiciles for *B. lui* and possibly in the process of feeding. We observed thin, fragile mucus tubes mixed with silt and fine detritus the material examined, sometimes still containing a specimen, from the type locality and in some instances from material collected at the Kane‘ohe Bay sites. William Cook (per. comm. 2015) indicated that during its use by the United States Navy, when the tank was periodically cleaned, the settling trays often contained thousands of *B. lui* inhabiting tube-like domiciles. Some of these “tubes,” which appear to be composed of a mixture of mucus and fine sediment and/or detritus, were mixed with the preserved specimens that we examined from Navy sites.

Possibly due to being overlooked, the presence of mucus glands and tub-like domiciles has not been reported previously for the genus *Brachylica*. We suspect that upon re-examination of the other species of the genus their presence will be confirmed. Similar glandular structures are prominent within the parapseudid genera *Halmyrapseudes* Băcescu & Guţu, 1974 and *Discapseudes* Băcescu & Guţu, 1976. In these genera, mucus is used in the thin walled tube domiciles (e.g., *H. bahamensis*: R. Heard, per. observ.) and in the lining of the burrows (e.g., *D. holthuisi*: see Băcescu and Guţu (1975, Plate 1), respectively. The mucus glands within these genera stain a distinctive dark pink when Rose Bengal is added to formalin fixed material for sorting purposes (R. Heard, per. observ.). Such glands are also prominent in the parapseudid genus *Psammokalliapseudes* Guţu, 1981 (R. Heard, pers. observ.) and we suspect that many other parapseudid genera will be found to have such homologous glandular structures in varying degrees of development.

We further suspect that these glands are analogous, or possibly homologous, to those reported for the suspension/filtered feeding members of the subfamily Kalliapseuidae. In *Mesokalliapseudes macsweenyi* (Drumm, 2003) and *Psammokalliapseudes grandulosus* Silva Brum 1973, similar mucus glands are involved in the construction of their fragile mucus tubes (Drumm 2005). Also, Kakui and Hiruta (2014) reported that such glands are involved in the production of the fine, thread-producing mucus strands in *Phoxokalliapseudes tomiokaensis* (Shiino, 1966).

Discussion

The occurrence of two distinct cheliped forms for adult females of *B. lui* may indicate the presence of both primary females and hermaphroditic forms in this species. The basis of the male cheliped has a characteristic sub-acute process on its mid-dorsal margin, which is absent on that of the female. If the presence of this process is indicative of terminal development of the cheliped, it may indicate protogynic development of the male. To support this conjecture, further observations are needed to determine if the functional females (i.e. those which produce viable young) for the other three species of the genus also exhibit two different female cheliped morphotypes. The males of *B. lui* and those of *B. muelleri* and *B. indonesiana* are characterized by the presence of a distinctive sub-acute process on cheliped basis, while the male cheliped for *B. estasiatica* remains unknown (Guţu 1998, 2006, 2007).

The presence of *B. lui* in the Hawaiian waters represents the first record for the genus from the mid-Pacific and northern Hemisphere. The other species of this genus are known from the Southern Hemisphere in coastal waters of the Indian and western South Pacific Oceans: *B. muelleri* from Tanzania, western Indian Ocean (Guţu 1998); *B. indonesiana* from Indonesia, Celebes Sea (Guţu 2006); and *B. estasiatica* from Malaysia, South China Sea (Guţu 2007).

Our observations and comparisons with other *Brachylica* species go with the caveat that ontogenetic factors may skew some taxonomic characters used in some of the earlier descriptions. For this reason, we chose the holotype and paratype series for *B. lui*, from specimens collected from the Naval experimental site. Many appeared to have reached terminal sizes, usually much greater than those of specimens collected from surveys of natural habitats on O‘ahu. Thus, the largest specimens from the type locality should quantitatively express the maximum development of characters for defining *B. lui*. In contrast, most of the specimens collected from natural habitats in Kane‘ohe Bay and Waikīkī were usually smaller and mostly damaged to varying degrees from the collection and sorting processes.

Though we did not have many terminal size adult *B. lui* from the natural habitats from O‘ahu, there appeared to be fewer hermaphrodites present than in the population occurring in the settling tank at the Naval experimental site. There is a possibility that the “unnatural” biotic environmental factors experienced by the population of *B. lui* within the settling tank may have been a contributing factor to the high percentage of the adults being hermaphroditic. For instance, this might have been an effect of the concentrations of pheromones released by the dense population of *B. lui* within the restricted confines of the settling tank habitat. Notwithstanding the role of such altered conditions or abiotic factors in inducing hermaphroditism in *B. lui* is beyond the scope of our study.

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William Cook kindly facilitated our access to the large series of B. l. i., including the holotype, collected by the U. S. Navy on O’ahu. Also, we wish to express our appreciation to Holly Bolick, Invertebrate Collections Manager, Bishop Museum, for her assistance in obtaining ecological and location data for some of the collection sites. Lynn Kimsey and Steve Heydon, Bohart Museum of Entomology, University of California at Davis, graciously gave the third author (RWH) access to the Hawaiian collections of the late Miller. This research was initially supported by NSF grant DEB-0529749. Lu Eldredge facilitated this financial support and graciously provided RWH living accommodations during his visit to the Bishop Museum in May 2012. We would like to thank Wilmelie Cruz-Marre-ro for help in drafting the study map. We are most grateful for the helpful and constructive criticism provided by the three anonymous reviews. We take full responsibility for any differing systematic or taxonomic interpretations. The open access publication of this paper was generously supported by the Museum für Naturkunde, Berlin.

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