

A REVIEW OF THE SUBGENUS *BULLADACUS* DREW & HANCOCK OF *BACTROCERA* MACQUART (DIPTERA: TEPHTRITIDAE: DACINAE), WITH DESCRIPTION OF TWO NEW SPECIES FROM PAPUA NEW GUINEA

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Abstract

The *Bactrocera* Macquart subgenus *Bulladacus* Drew & Hancock is reviewed. *Bactrocera* (*Bulladacus*) *trilobata* sp. n. and *Bactrocera* (*Bulladacus*) *wanangiae* sp. n. are described from Papua New Guinea. *Bactrocera obrullata* White & Evenhuis, 1999, is placed as a new synonym of *B. diaphana* (Hering, 1953); both were described from Papua Province in eastern Indonesia. The Solomon Islands species *B. unipunctata* (Malloch) is transferred from subgenus *Bactrocera* to *Bulladacus*. Males of *B. aceromata* White & Evenhuis are newly described. Records of *B. mcgregori* (Bezzi) from Singapore, West Malaysia and the Andaman and Nicobar Islands are regarded as misidentifications of *B. cinnabaria* Drew & Romig. *Bactrocera pacificae* Drew & Romig is newly recorded from Papua New Guinea. A key to the 20 known species is included.

Introduction

The *Bactrocera* Macquart subgenus *Bulladacus* Drew & Hancock is defined as having the posterior lobe of the male surstylus short, abdominal sternite V of male deeply concave on posterior margin [this combination of characters placing it in the *Bactrocera* group of subgenera], plus a combination of all or most of the following characters: antenna shorter than usual for the genus, pecten of cilia present on male abdominal tergite III, distinct oval shining spots (ceromata) on abdominal tergite V absent, one pair of scutellar setae, prescutellar acrostichal seta present, supra-alar seta present or absent, wing cell bcu with extension short, wing of male with bulla present near apex of cell bcu extension (Drew and Hancock 1995, White and Evenhuis 1999, Drew and Romig 2013). In addition, both the anatergite and katatergite are largely yellow, the notopleural lobe is often partly or entirely red-brown, fuscous or black, facial spots are often absent and most species have a broad anepisternal yellow stripe that reaches the postpronotal lobe and an isolated medial black vitta on tergite V that often crosses onto tergite IV but seldom extends onto tergite III. The male bulla and pecten of cilia on abdominal tergite III are absent in *B. aceraglans* White & Evenhuis but a patch of cilia occurs on the wing where the bulla is normally situated. In males where a distinct bulla is present, the cell bcu extension is often longer and narrower than usual. No species in the subgenus shows a response to known male lures.

Bulladacus appears to be most closely related to subgenus *Calodacus* Hancock that, like it, has comparatively short antennae, a short cell bcu extension and shows no response to known male lures (Hancock 2015); the latter subgenus differs primarily in the presence of ceromata on abdominal tergite V. Known hosts of *Bulladacus* species are primarily the fruit of

Gnetum gnemon (Gnetaceae) and *Terminalia* species (Combretaceae), with only occasional records from other plant families.

The following abbreviations have been used: QDAF – Queensland Department of Agriculture and Fisheries collection, Brisbane; QM – Queensland Museum, Brisbane. Descriptive terminology follows White *et al.* (1999), with bilateral structures (vittae, setae, etc.) listed in the singular.

Bactrocera (Bulladacus) Drew & Hancock

Bactrocera (Bulladacus) Drew & Hancock, 1995: 9. Type species: *Bactrocera gnetum* Drew & Hancock, by original designation.

Twenty species are known, the subgenus ranging from the Philippines and southern Thailand/Andaman Islands to the South Pacific as far east as Fiji and Samoa. Two species occur in Australia, five in the Pacific Islands and at least nine in Papua New Guinea.

Bactrocera (Bulladacus) aceraglans White & Evenhuis

Bactrocera (Bulladacus) aceraglans White & Evenhuis, 1999: 506 (♂). Type locality: Minj, Western Highlands, Papua New Guinea.

Description. See White and Evenhuis (1999). This species differs from all others in the presence of a patch of cilia, rather than a bulla, alongside wing cell *bcu* in males. The notopleural lobe is dark fuscous to black.

Distribution. Papua New Guinea (Western Highlands Province).

Host plant. Unknown.

Bactrocera (Bulladacus) aceromata White & Evenhuis

(Fig. 1)

Bactrocera (Bulladacus) aceromata White & Evenhuis, 1999: 509 (♀). Type locality: Tapini, Papua New Guinea.

Material examined. PAPUA NEW GUINEA: Madang Province – 29 ♂♂, 28 ♀♀, Baitabag and Ohu, March, April and September 2001, reared from *Gnetum gnemon* and *Gnetum costatum*; Morobe Province – 24 ♂♂, 28 ♀♀, Lae, February, March and April 2000, reared from *Gnetum gnemon* and *Sandoricum koetjape*. Specimens in QDAF.

Description. Male. Head: height 1.2 mm; frons length 1.3 times breadth, red-brown without dark markings; setae black: 2 frontal, 1 orbital; lunule red-brown; ocellar triangle black; vertex red-brown; face entirely fulvous without dark markings, length 0.5 mm; gena fulvous without dark markings, black seta present; occiput red-brown, fulvous along eye margins; occipital row with 3-6 strong black setae. Antenna with all segments red-brown; length of segments 0.12 mm, 0.24 mm, 0.45 mm; first flagellomere (segment 3) strongly truncate (square) across apex (not rounded as in most *Bactrocera* species).

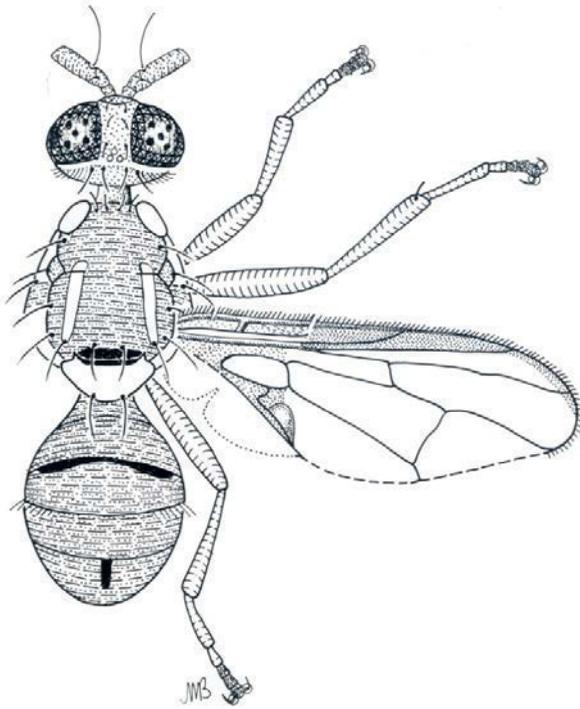


Fig. 1. *Bactrocera (Bulladacus) aceromata* White & Evenhuis, male.

Thorax. Scutum entirely red-brown with a broad transverse black band across posterior margin. Yellow markings as follows: postpronotal lobe; anepisternal stripe reaching postpronotal lobe dorsally, continuing to katapisternum as a transverse spot, anterior margin straight; anatergite (posterior apex black); anterior 2/3 of katatergite (remainder black); broad parallel-sided lateral postsutural vitta beginning with a large spot anterior to notopleural suture and ending at intra-alar seta; medial postsutural yellow vitta absent. Postnotum red-brown centrally, black laterally. Notopleural lobe red-brown. Scutellum yellow except for a narrow black basal band. Setae: 2 scapular; 2 notopleural; 1 anepisternal; 1 supra-alar; 1 postalar; 1 intra-alar; 1 prescutellar acrostichal; 1 (apical) scutellar.

Legs. All leg segments entirely fulvous except apical three segments of all tarsi dark fuscous; mid tibia with an apical black spur.

Wing. Length 4.2 mm; cells bc and c pale fuscous; dense microtrichia covering cell c only; remainder of wing colourless except fuscous cell sc, narrow fuscous costal band confluent with R_{2+3} and remaining narrow around apex of wing, a distinct large bulla across extension of cell bcu and pale

fuscous in area normally covered by anal streak; aggregation of microtrichia around A_1+Cu_2 less dense than in most species of *Bactrocera*; supernumerary lobe weak.

Abdomen. Oval; tergites free; strong black pecten present on tergite III. All tergites red-brown except for a narrow transverse black band across anterior margin of tergite III and a moderately broad medial black vitta over anterior 1/2 of tergite V. No shining spots (ceromata) on tergite V. All abdominal sternites red-brown; sternite V with a deep concavity on posterior margin. Surstylus with posterior lobe short.

Female. As for male except no bulla on wing; pecten of cilia absent from abdominal segment III; oviscapae red-brown, dorsoventrally compressed and tapering slightly in dorsal view; ratio of length of oviscapae to length of tergite V, 0.3:1; apex of aculeus needle shaped.

Distribution. Papua New Guinea (Madang, Morobe and Central Provinces north of the Owen Stanley Range).

Host plants. *Gnetum gnemon* and *Gnetum costatum*. *Bactrocera (Bulladacus)* species utilise *Gnetum* species as primary hosts across their geographic range, except in Australia where *Gnetum* is absent; the record from *Sandoricum koetjape* (Meliaceae) listed under material examined is possibly an error.

Comments. *Bactrocera aceromata* is similar to *B. (Bulladacus) cinnabaria* Drew & Romig in possessing a red-brown scutum, mostly red-brown abdominal tergites, wings without infuscation except for the costal band and anal streak and femora entirely pale (fulvous to red-brown). It differs from *B. cinnabaria* in having the costal band very narrow around the wing apex and in lacking black lateral margins on abdominal tergites IV and V.

Bactrocera (Bulladacus) aenigmatica (Malloch)

Dacus aenigmaticus Malloch, 1931: 261 (♀). Type locality: Malololelei, Upolu, Western Samoa.

Bactrocera (Bulladacus) aenigmatica (Malloch): Drew and Hancock 1995: 9 (♂♀).

Description. See Drew (1989) and Drew and Hancock (1995).

Distribution. Western Samoa (Upolu and Savaii).

Host plant. *Aglaia samoensis* (Meliaceae) (Drew and Hancock 1995).

Comments. The lengths of the antennal segments, previously unrecorded, are 0.1 mm, 0.2 mm and 0.46 mm and the first flagellomere is apically rounded.

Bactrocera (Bulladacus) bullata Drew

Bactrocera (Bactrocera) bullata Drew, 1989: 124 (♂♀). Type locality: Abelam, East Sepik district, Papua New Guinea.

Bactrocera (Bulladacus) bullata: Drew and Hancock 1995: 9.

Material examined. PAPUA NEW GUINEA: Madang Province – a large series of specimens collected at Ohu, October 2000 and February to October 2001, recorded as reared from *Phaleria macrocarpa*; a large series of specimens collected at Baitabag, May to October 2001, recorded as reared from *Phaleria macrocarpa*; Morobe Province – a large series of specimens, May 2000, reared from an unknown host at the Lae Forest Research Institute. Specimens in QDAF.

Description. See Drew (1989).

Distribution. Papua New Guinea (East Sepik, Madang and Morobe Provinces).

Host plants. *Phaleria macrocarpa* (Thymeliaceae) (Novotny *et al.* 2005 and above records) and *Gnetum gnemon* (Gnetaceae) (Leblanc *et al.* 2012). A record from *Garcinia* sp. (Clusiaceae) (Drew 1989) is probably an error.

Bactrocera (Bulladacus) bullifera (Hardy)

Dacus (Strumeta) bulliferus Hardy, 1973: 32 (♂). Type locality: Songkhla, Thailand.

Bactrocera (Bulladacus) bullifera: Drew and Hancock 1995: 9; Drew and Romig 2013 (♂♀).

Description. See Drew and Romig (2013).

Distribution. Southern Thailand, Peninsular Malaysia, East Malaysia (Sarawak), Indonesia (Java, Sumatra).

Host plant. *Gnetum gnemon* (Gnetaceae) (Drew and Romig 2013).

Bactrocera (Bulladacus) captiva Drew & Romig

Bactrocera (Bulladacus) captiva Drew & Romig, 2013: 196 (♂♀). Type locality: 'Philippines'.

Description. See Drew and Romig (2013).

Distribution. Philippines (precise locality unknown).

Host plant. *Eugenia javanica* (Myrtaceae) – possibly incorrect, the type series and host record stemming from quarantine interception at Narita Airport, Japan (Drew and Romig 2013).

Bactrocera (Bulladacus) cinnabaria Drew & Romig

Dacus (Strumeta) mcgregori: Hardy and Adachi 1954: 176 (♂♀). Singapore. Misidentification.

Bactrocera (Bulladacus) cinnabaria Drew & Romig, 2013: 197 (♂♀). Type locality: Arong, Car Nicobar, India.

Description. See Drew and Romig (2013).

Distribution. India (Andaman and Nicobar Is), West Malaysia and Singapore.

Host plants. *Gnetum gnemon* (Gnetaceae) (Hardy and Adachi 1954, Yong 1994) and *Gnetum* sp. (Drew and Romig 2013).

Comments. The abdominal pattern is a little variable, with the black medial vitta on tergites IV-V often interrupted or absent on tergite IV. Records of *B. mcgregori* from Singapore (Hardy 1973, 1974), West Malaysia (Yong 1994) and the Andaman and Nicobar Islands (David and Ramani 2011) are regarded as misidentifications of *B. cinnabaria*, with *B. mcgregori* differing in the presence of a presutural yellow vitta and longer, more parallel-sided lateral postsutural yellow vitta that extends anterior to the suture as a distinct spot.

Bactrocera (Bulladacus) diaphana (Hering)

(Fig. 2)

Strumeta diaphana Hering, 1953: 508 (♀). Type locality: Bernhard Camp, Papua Province, Indonesia.

Bactrocera (Bactrocera) diaphana: Drew 1989: 130.

Bactrocera (Bulladacus) obrullata White & Evenhuis, 1999: 510 (♂). Type locality: Dojo, Papua Province, Indonesia. **Syn. n.**

Material examined. PAPUA NEW GUINEA: Madang Province – 1 ♂, 2 ♀♀, Baitabag, 17.i.2001, reared from *Pimelodendron amboinicum*; Morobe Province – 2 ♂♂, 4 ♀♀, Lae Forest Research Institute Botanical Gardens, 29.iii.2000, reared from *Sandoricum koetjape*. Specimens in QDAF.

Description. Male. Head: Height 1.2 mm; frons length 1.4 times breadth, red-brown with pale fuscous to fuscous centrally; setae black: 2 frontal, 1 orbital; lunule fuscous; ocellar triangle black; vertex red-brown; face entirely fulvous without dark markings, length 0.5 mm; gena fulvous without dark markings, black seta present; occiput pale fuscous, fulvous along eye margins; occipital row with 2-3 weak black setae. Antenna with all segments red-brown; length of segments: 0.1 mm, 0.2 mm, 0.4 mm; first flagellomere rounded at apex.

Thorax. Scutum red-brown with two submedial black bands that are broad posteriorly and narrowing anteriorly and joined across posterior area of scutum with fuscous colouration, black on lateral margins between postpronotal lobe and notopleuron and inside notopleuron. Yellow markings as follows: postpronotal lobe; anepisternal stripe reaching to anterior notopleural seta dorsally, continuing to katapisternum as a large spot, anterior margin straight; anatergite (posterior apex black); anterior 2/3 of katatergite (remainder black); broad parallel-sided lateral postsutural vitta beginning as a large spot anterior to notopleural suture and ending at intra-alar seta; a lateral yellow band between posterior margin of postpronotal lobe and yellow spot anterior to notopleural suture; medial postsutural yellow vitta absent. Postnotum red-brown centrally, black laterally. Notopleural lobe red-brown. Scutellum yellow with a narrow black basal band that widens laterally. Setae: 2 scapular; 2 notopleural; 1 anepisternal; 1 supra-alar; 1 postalar; 1 intra-alar; 1 prescutellar acrostichal; 1 (apical) scutellar.

Legs. All leg segments entirely fulvous except hind tibiae dark fuscous basally to fuscous apically; mid tibia with an apical black spur.

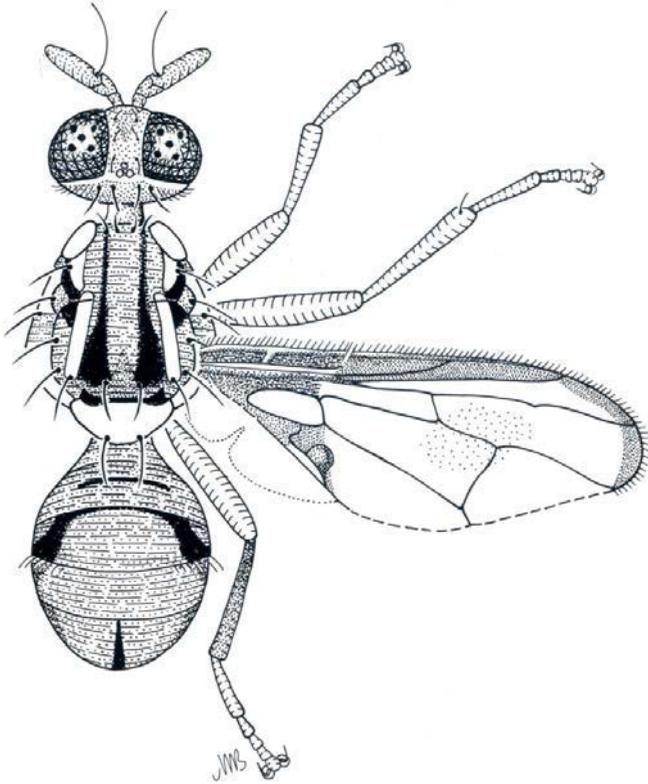


Fig. 2. *Bactrocera (Bulladacus) diaphana* (Hering), male.

Wing. Length 4.4 mm; cells bc and c dark fuscous and covered with dense microtrichia; remainder of wing colourless except dark fuscous cell sc, narrow fuscous costal band confluent with R_{2+3} and continuing around costal margin to apex of vein M, a pale tint in centre of wing, distinct large dark bulla across extension of cell bcu and fuscous in area normally covered by anal streak; a dense aggregation of microtrichia around A_1+Cu_2 ; supernumerary lobe weak.

Abdomen. Oval; tergites free; a strong black pecten present on tergite III. All tergites red-brown except for a narrow black band submedially on tergite I+II, a narrow black band across anterior margin of tergite III which expands over lateral margins, a medium width medial black vitta over tergite V and fuscous to dark fuscous anterolateral corners of tergites IV and V. No shining spots (ceromata) on tergite V. All abdominal sternites red-brown; sternite V with a deep concavity on posterior margin. Surstylus with posterior lob short.

Female. As for male except face with a pair of medium-sized oval black spots, notopleuron with anterior 1/2 fuscous and posterior 1/2 yellow, wing with cells bc and c colourless and lacking a bulla over extension of cell bcu; apex of aculeus needle shaped, ratio of length of ov scape to length of tergite V, 1:1.

Distribution. Indonesia (Papua Province); Papua New Guinea (Madang and Morobe Provinces).

Host plants. Recorded hosts are *Pimelodendron amboinicum* (Euphorbiaceae) (Novotny *et al.* 2005 and above records) and *Sandoricum koetjape* (Meliaceae). If these are correct plant identifications then they are a significant departure from those of most other *B. (Bulladacus)* species.

Comments. The female holotype of *B. diaphana* was examined, described and illustrated by Drew (1989). The rearing of both sexes from the same host fruit has now made possible the correct subgeneric placement for this species and the description of the male.

Bactrocera (Bulladacus) diaphana exhibits a low level of sexual dimorphism. It is similar to *B. (Bulladacus) mcgregori* (Bezzi) in general body and wing colour patterns and in possessing a lateral yellow vitta between the postpronotal lobe and notopleural suture. It differs from *B. mcgregori* in having apex of antennal first flagellomere rounded apically, a narrower anepisternal stripe and face fulvous with a pair of black spots in females. The original description of *B. diaphana* was based on a female specimen and that of *Bactrocera (Bulladacus) obrullata* White & Evenhuis on male specimens. Now that we have studied both sexes reared from the same host plant sample, we can confirm that *B. obrullata* is a new synonym of *B. diaphana*, being identical in all significant morphological characters.

Bactrocera (Bulladacus) eximia Drew

Bactrocera (Bactrocera) eximia Drew, 1989: 132 (♂♀). Type locality: Baku, Madang Province, Papua New Guinea.

Bactrocera (Bulladacus) eximia: Drew and Hancock 1995: 9.

Description. See Drew (1989).

Distribution. Papua New Guinea (Madang and Central Provinces).

Host plants. *Terminalia brassii* and *T. catappa* (Combretaceae) (Drew 1989, Leblanc *et al.* 2012).

Bactrocera (Bulladacus) flavinotus (May)

Afrodacus flavinotus May, 1957: 293 (♀). Type locality: Atherton, Queensland.

Bactrocera (Bulladacus) neotigrina Drew & Hancock, 1999: 7 (♂♀), in Drew *et al.* 1999. Type locality: Helenvale nr Cooktown, Queensland. Syn. Drew and Hancock 2000: 27.

Bactrocera (Bulladacus) flavinotus: Drew and Hancock 2000: 27.

Description. See May (1957) and Drew *et al.* (1999).

Distribution. Northern Queensland (Cooktown to Atherton and Gordonvale).

Host plant. *Terminalia sericocarpa* (Combretaceae) (Drew *et al.* 1999).

Bactrocera (Bulladacus) gnetum Drew & Hancock

Bactrocera (Bulladacus) gnetum Drew & Hancock, 1995: 9 (♂♀). Type locality: Saivou, Vanua Levu, Fiji.

Description. See Drew and Hancock (1995).

Distribution. Fiji.

Host plant. *Gnetum gnemon* (Gnetaceae) (Drew and Hancock 1995).

Bactrocera (Bulladacus) mcgregori (Bezzi)

Chaetodacus mcgregori Bezzi, 1919: 426 (♂♀). Type locality: Batbatan Island, Philippines.

Bactrocera (Bulladacus) mcgregori: Drew and Hancock 1995: 9.

Description. See Drew and Romig (2013).

Distribution. Philippines (Panay and Batbatan Is), Records from Singapore (Hardy and Adachi 1954, Hardy 1973, 1974), West Malaysia (Yong 1994) and the Andaman and Nicobar Islands (David and Ramani 2011) are transferred to *B. cinnabaria*.

Host plant. Unknown. Previous records of *Gnetum gnemon* (Hardy and Adachi 1954, Hardy 1973, 1974, Yong 1994) refer to *B. cinnabaria*.

Bactrocera (Bulladacus) pacificae Drew & Romig

Bactrocera (Bulladacus) pacificae Drew & Romig, 2001: 138 (♂♀). Type locality: Vatina, Guadalcanal, Solomon Islands.

Material examined. PAPUA NEW GUINEA: Central Province – 14 ♂♂, 14 ♀♀, Hiritano Highway, Doa Forest, 22.x.1999, reared from *Gnetum gnemon*; 1 ♀, Rouna Forest, 2.ii.1999, reared from *Gnetum gnemon*, coll. Drew *et al.*; Madang Province – 1 ♂, 2 ♀♀ (10.i.2001), 1 ♂ (1.ii.2001), Ohu, reared from *Gnetum gnemon*; 1 ♀, Baitabag, 25.x.2000, reared from *Gnetum gnemon*. Specimens in QDAF.

Description. See Drew and Romig (2001).

Distribution. Solomon Islands (Guadalcanal and Temotu Province (Lom Lom and Nendo Islands)) and Papua New Guinea (Central and Madang Provinces).

Host plant. *Gnetum gnemon* (Gnetaceae) (Drew and Romig 2001, Leblanc *et al.* 2012).

Comments. *Bactrocera pacificae* is distinct in possessing a red-brown scutellum with lateral yellow margins. The above new records from Papua New Guinea indicate a wider distribution than previously considered.

Bactrocera (Bulladacus) penefurva Drew

Bactrocera (Bactrocera) penefurva Drew, 1989: 151 (♂). Type locality: 20 km SE Port Moresby, Papua New Guinea.

Bactrocera (Bulladacus) penefurva: Drew and Hancock 1995: 9; Drew and Romig 2001 (♂♀).

Material examined. PAPUA NEW GUINEA: Madang Province – a large series of specimens collected at Baitabag, January to March 2001, reared from *Terminalia* sp.; Morobe Province – a large series of specimens collected at Bundun Conference Centre Lae, Lae Forest Research Institute Botanical Gardens and Oomsis Forest, February to May 2000, reared from *Terminalia* sp. Specimens in QDAF.

Description. This species has been described and illustrated by Drew (1989) and Drew and Romig (2001). One additional character is that, in both sexes, the apex of the antennal first flagellomere is rounded, not truncate as in some *B. (Bulladacus)* species.

Distribution. Papua New Guinea (Central, Morobe and Madang Provinces) and Solomon Islands (Guadalcanal).

Host plants. *Terminalia catappa* and *T. kaernbachii* (Combretaceae) (Drew and Romig 2001). A record from *Gnetum gnemon* (Gnetaceae) (Leblanc *et al.* 2012, Hollingsworth *et al.* 2003: Table 5) appears to be based on a *lapsus* for *B. pacificae*.

Bactrocera (Bulladacus) peterseni (Hardy)

Dacus (Strumeta) peterseni Hardy, 1970: 75 (♂). Type locality: Tarawakan, Tawi Tawi, Philippines.

Bactrocera (Bulladacus) peterseni: Drew and Hancock 1995: 9.

Description. See Drew and Romig (2013).

Distribution. Philippines (Tawi Tawi I.).

Host plant. Unknown.

Bactrocera (Bulladacus) tigrina (May)

Afrodacus tigrinus May, 1952: 335 (♀); 1957: 296 (♂). Type locality: Kamerunga, Cairns, Queensland.

Afrodacus furvus May, 1957: 294 (♂♀). Type locality: Atherton, Queensland. Syn. Drew 1989: 24.

Bactrocera (Bulladacus) tigrina: Drew and Hancock 1995: 9.

Description. See May (1952, 1957), Drew (1989) and Drew *et al.* (1999).

Distribution. Northern Queensland (Iron Range to Murray Falls near Tully).

Host plants. *Terminalia sericocarpa* and *T. muelleri* (Combretaceae) (Drew *et al.* 1999).

***Bactrocera (Bulladacus) trilobata* sp. n.**

(Fig. 3)

Type material. Holotype ♂, PAPUA NEW GUINEA: Madang Province, Mis Village, 5°11'S 145°47'E, 25.viii.2008, coll. Ctvrticka, Brus & Rimandai, reared from *Phaleria macrocarpa*. *Paratypes*: 1 ♂, 5 ♀♀, same data as holotype. Holotype and 1 paratype in QM (Reg. Nos T234939 (HT) and T234940 (PT)); 5 paratypes in QDAF.

Description. Male. Head: Height 1.1 mm; frons length 1.6 times breadth, red-brown without dark markings; orbital setae black: 2 frontal, 1 orbital; lunule red-brown; ocellar triangle black; vertex red-brown.; face entirely fulvous without dark markings, length 0.4 mm; gena fulvous without dark markings, weak pale seta present; occiput red-brown, fulvous along eye margins, occipital row with 1-3 dark setae. Antenna with all segments red-brown; length of segments: 0.1 mm, 0.15 mm, 0.5 mm; first flagellomere rounded at apex.

Thorax. Scutum red-brown without dark markings. Yellow markings as follows: postpronotal lobe; anepisternal stripe reaching postpronotal lobe dorsally, continuing to katapisternum as a transverse spot, anterior margin straight; anatergite (posterior apex red-brown); anterior 1/2 of katatergite (remainder red-brown); narrow lateral postsutural vitta narrowing slightly posteriorly to end just before intra-alar seta; no distinct spot anterior to notopleural suture; medial postsutural yellow vitta absent. Postnotum red-brown centrally, black laterally. Notopleural lobe red-brown. Scutellum yellow with a narrow black basal band. Setae: 2 scapular; 2 notopleural; 1 anepisternal; 1 supra-alar; 1 postalar; 1 intra-alar; 1 prescutellar acrostichal; 1 (apical) scutellar.

Legs. All leg segments entirely fulvous except apical three segments of all tarsi red-brown; mid tibia with an apical black spur.

Wing. Length 4.4 mm; cells bc and c pale fuscous with dense microtrichia in outer corner of cell c only; remainder of wing colourless except fuscous cell sc., narrow fuscous costal band confluent with R_{2+3} and remaining narrow around wing margin to end at apex of vein M, narrow fuscous transverse band enclosing DM-Cu crossvein, broad fuscous anal streak, small fuscous bulla around apex of cell bcu extension. No dense aggregation of microtrichia around A_1+Cu_2 . Supernumerary lobe weak.

Abdomen. Oval; tergites free; a strong pecten present on tergite III. All tergites red-brown except for a short, medial, narrow black vitta on posterior margin of tergite V. No shining spots (ceromata) on tergite V.

Female. As for male except bulla on wing and pecten of cilia on abdominal tergite III both absent; oviscape red-brown, dorsoventrally compressed and tapering slightly in dorsal view; ratio of length of oviscape to length of tergite V, 1:1, apex of aculeus trilobed (Fig. 3).

Etymology. Named as an adjective after the trilobed aculeus.

Distribution. Papua New Guinea (Madang Province).

Host plant. *Phaleria macrocarpa* (Thymelaeaceae).

Comments. *Bactrocera (Bulladacus) trilobata* sp. n. is similar to *B. (Bulladacus) aenigmatica* (Malloch), *B. (Bulladacus) cinnabaria* Drew & Romig and *B. (Bulladacus) pacifica* Drew & Romig in possessing a red-brown scutum, a narrow costal band confluent with R_{2+3} , lateral postsutural yellow vitta short and narrow and ending before the intra-alar seta and additionally to *B. cinnabaria* in having a broad anepisternal stripe reaching to the postpronotal lobe. It differs from all three species in having the DM-Cu crossvein enclosed with fuscous colouration and the apex of the aculeus trilobed.

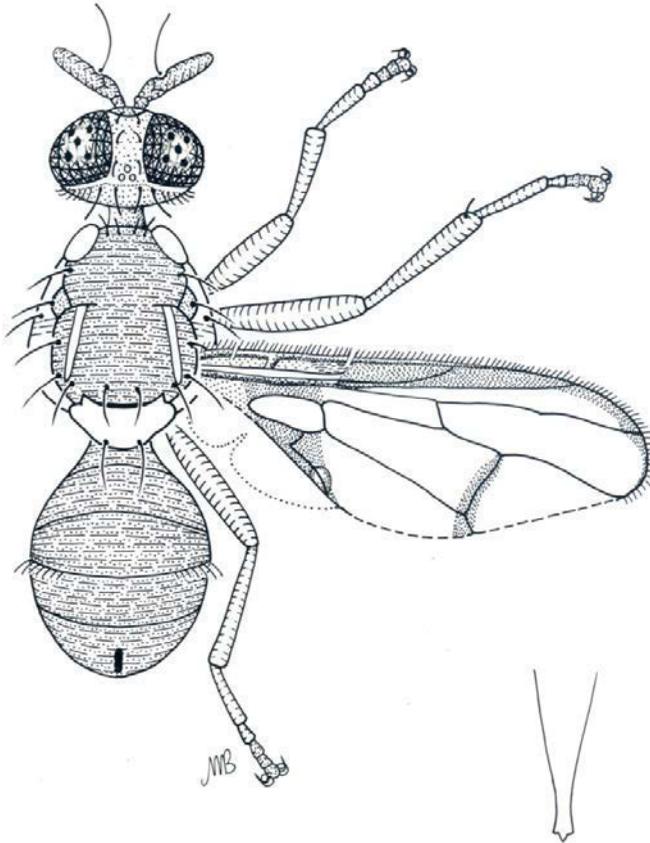


Fig. 3. *Bactrocera (Bulladacus) trilobata* sp. n., male and female aculeus.

Bactrocera (Bulladacus) unipunctata (Malloch)

Dacus unipunctatus Malloch, 1939: 245 (♂). Type locality Tulagi, Florida I., Solomon Islands.

Bactrocera (Bactrocera) unipunctata: Drew 1989: 167.

Description. See Drew (1974, 1989) and Drew and Romig (2001).

Distribution. Solomon Islands (Florida I.).

Host plant. Unknown.

Comments. The short antennal segments (0.08, 0.18, 0.5 mm), short wing cell bcu extension and lack of ceromata on abdominal tergite V place this species in *Bulladacus* and it is therefore transferred from subgenus *Bactrocera*. It also has an oval abdomen with a single black medial spot on tergite V and microtrichia over much of cells bc and c, typical of many *Bulladacus* species. The pecten of cilia and bulla appear to be absent but the only known specimen is damaged and teneral and both structures are possibly present.

Bactrocera (Bulladacus) wanangiae sp. n.

(Fig. 4)

Bactrocera (Bulladacus) sp. near *aceraglans* White & Evenhuis, 1999: 507 (♂). Wanuma, Madang Province, Papua New Guinea.

Type material. *Holotype* ♂, PAPUA NEW GUINEA: Morobe Province, Wanang, 4.xii.2008, Ctvrtcecka *et al.*, reared ex unidentified fruit. *Paratype* ♂, same data as holotype. Types in QM (Reg. Nos T234941 (HT) and T234942 (PT)).

Description. Male. Head: Height 1.2 mm; frons length 1.8 times breadth, red-brown with dark fuscous on anteromedial hump; orbital setae black: 2 frontal, 1 orbital; lunule red-brown; ocellar triangle black; vertex red-brown; face entirely fulvous, length 0.5 mm; gena red-brown; occiput red-brown, fulvous along eye margins, occipital row with 4-5 strong pale setae. Antenna abraded.

Thorax. Scutum black with red-brown bordering postpronotal lobe, around notopleural suture and below and behind lateral postsutural vitta. Yellow markings as follows: postpronotal lobe; anepisternal stripe reaching postpronotal lobe dorsally, continuing to katapisternum as a small spot, anterior margin straight; anatergite (posterior apex black); anterior 2/3 of katatergite (remainder black); broad parallel-sided lateral postsutural vitta beginning as a small spot anterior to notopleural suture and ending just behind intra-alar seta; medial postsutural yellow vitta absent. No lateral yellow area between postpronotal and notopleural lobes. Pleural areas dark fuscous to black. Postnotum red-brown centrally, black laterally. Notopleural lobe yellow. Scutellum yellow with a narrow black basal band. Setae: 2 scapular; 2 notopleural; 1 anepisternal; 1 supra-alar; 1 postalar; 1 intra-alar; 1 prescutellar acrostichal; 1 (apical) scutellar.

Legs. All segments entirely fulvous.

Wing. Length 5.4 mm; cells bc and c pale fuscous with dense microtrichia over all of cell c and outer half of cell bc; remainder of wing colourless except fuscous cell sc., narrow fuscous costal band confluent with R_{2+3} and remaining narrow around wing margin to end between apices of R_{4+5} and M, narrow infuscation enclosing R-M and DM-Cu crossveins that is also connected with infuscation along M, broad pale fuscous anal streak, distinct red-brown bulla around apex of cell bcu extension. No dense aggregation of microtrichia around A_1+CuA_2 . Supernumerary lobe of medium development.

Abdomen. Abdomen oval; tergites free; a weak pale pecten present on tergite III. All tergites red-brown except for a narrow medial black vitta over tergite V. No shining spots (ceromata) on tergite V.

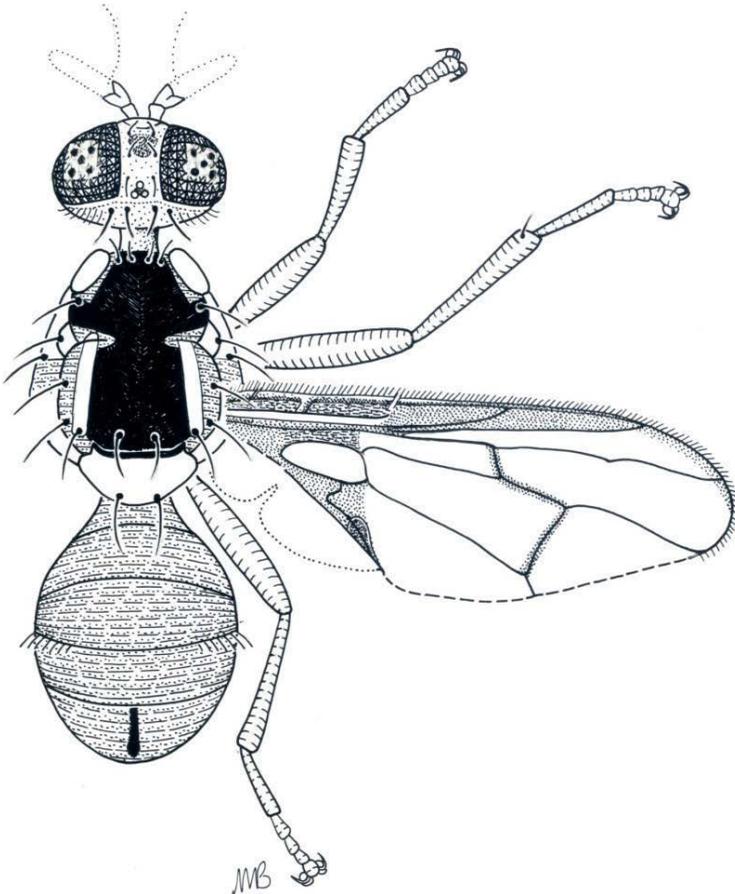


Fig. 4. *Bactrocera (Bulladacus) wanangiae* sp. n., male.

Female. Unknown.

Etymology. Named after the type locality.

Distribution. Papua New Guinea (Madang and Morobe Provinces).

Host plant. Unknown.

Comments. *Bactrocera (Bulladacus) wanangiae* sp. n. is similar to *B. (Bulladacus) gnetum* Drew & Hancock in possessing a black scutum without a medial postsutural yellow vitta, wing with a narrow fuscous costal band and fulvous leg segments. It differs from *B. gnetum* in having a broad parallel-sided lateral postsutural yellow vitta and infuscation enclosing R-M and DM-Cu crossveins that is connected by infuscation along vein M. The ‘*B. sp nr aceraglans*’ of White and Evenhuis (1999) is associated based on its original description and illustration.

Bactrocera (Bulladacus) warisensis White & Evenhuis

Bactrocera (Bulladacus) warisensis White & Evenhuis, 1999: 512 (♂). Type locality: Waris, S of Jayapura, Papua Province, Indonesia.

Description. See White and Evenhuis (1999).

Distribution. Indonesia (Papua Province).

Host plant. Unknown.

Key to species of subgenus *Bulladacus*

- 1 Scutum with a medial postsutural yellow vitta 2
- Scutum without a medial postsutural yellow vitta 7
- 2 Scutum red-brown or with a pair of submedial black vittae; male with bulla either small and distinct or weak and undeveloped 3
- Scutum mostly black; male with bulla distinct and well developed 4
- 3 Scutum with a pair of dark submedial vittae; lateral postsutural yellow vitta extending anterior to suture as a distinct spot; medial postsutural yellow vitta narrowly triangular and almost as long as lateral vitta; wing with a dark band over DM-Cu crossvein; male with a small distinct bulla over apex of cell bcu extension (Papua New Guinea) *B. bullata*
- Scutum without a pair of dark submedial vittae; lateral postsutural yellow vitta not extending anterior to suture; medial postsutural yellow vitta broadly triangular and distinctly shorter than lateral vitta; wing without a dark band over DM-Cu crossvein; male with bulla weak and undeveloped (Australia) *B. flavinotus*
- 4 Sexes similar, the costal band narrow throughout and not expanded into a broad, isolated apical patch in males; abdomen orange-brown with narrow black lateral margins on tergites III-IV and a black medial vitta on tergite V (Papua New Guinea) *B. eximia*

- Sexes dissimilar, the costal band narrow in females, expanded into a broad, isolated apical patch in males; abdomen with black areas as sublateral spots or patches on tergites III-V (males) or with black transverse bands on tergite III (and often I+II) and black lateral margins on tergites III-V (females) 5
- 5 Medial postsutural vitta reaching line of suture anteriorly; abdomen without a dark transverse band or sublateral patches on tergite I+II; male wing with apical patch crossing vein M and reaching almost to DM-Cu crossvein (Papua New Guinea and Solomon Islands) *B. penefurva*
- Medial postsutural vitta not reaching line of suture anteriorly; abdomen with a dark transverse band or sublateral patches on tergite I+II; male wing with apical patch as above or smaller and not crossing vein M 6
- 6 Medial postsutural vitta broadly triangular and distinctly shorter than lateral vitta; male wing with apical patch not crossing vein M and approaching it well distad of DM-Cu crossvein (Australia) *B. tigrina*
- Medial postsutural vitta broadly oval and almost as long as lateral vitta; male wing with apical patch crossing vein M and reaching almost to DM-Cu crossvein (Philippines) *B. captiva*
- 7 Costal band broadly expanded medially with a triangular dark band across both R-M and DM-Cu crossveins; male bulla present over apex of cell bcu extension (Papua Province, eastern Indonesia) *B. warisensis*
- Costal band narrow or expanded apically but not expanded across R-M and DM-Cu crossveins; male bulla variably placed or absent 8
- 8 Scutum black except for lateral postsutural yellow vitta; costal band very narrow and of uniform width beyond apex of vein R₂₊₃ 9
- Scutum largely fulvous to red-brown or with dark submedial and sometimes medial vittae; costal band narrow or broadened apically 11
- 9 Scutum with lateral postsutural yellow vitta short and sharply tapered posteriorly; abdomen with a broad black lateral vitta on tergites III-V and a broad medial vitta from posterior margin of tergite III to tergite V; male with bulla large and ovate (Fiji) *B. gnetum*
- Scutum with lateral postsutural yellow vitta elongate and parallel-sided, enclosing intra-alar seta; abdomen orange-brown, at most with a black medial vitta on tergite V; male bulla indistinct or absent 10
- 10 Wing with a dark posterior stripe over DM-Cu crossvein to wing margin; fore and apical halves of mid and hind femora fuscous; male with a patch of long cilia in place of bulla (Papua New Guinea) *B. aceraglans*
- Wing with a narrow infuscation over R-M and DM-Cu crossveins and intermediate portion of vein M; femora fulvous; male with bulla small and indistinct (Papua New Guinea) *B. wanangiae* **sp. n.**

- 11 Apical third of mid femur black or black-spotted, mid tibia at least partly and hind tibia entirely dark fuscous to black; costal band broadened or expanded apically; male bulla blackened; scutum with lateral postsutural yellow vitta extending anterior to suture as a distinct spot; abdomen with medial black vitta across tergites III-V connected anteriorly with a broad transverse band across tergite III; anepisternal yellow stripe narrow, not reaching postpronotal lobe anteriorly 12
 - All femora and tibiae fulvous except hind tibia often fuscous; costal band narrow, not or only weakly expanded apically; male bulla often not blackened; scutum with lateral postsutural yellow vitta often not extending anterior to suture as a distinct spot; abdomen with medial black vitta generally confined to tergites IV-V or V, seldom entering or crossing tergite III but not connected with a transverse band across it; anepisternal yellow stripe often broad and reaching postpronotal lobe anteriorly 13
- 12 Apical third of mid femur, most of mid and all of hind tibiae dark fuscous to black; costal band broadened apically and reaching vein M; scutum with the dark medial and submedial vittae not broadly connected posteriorly; a narrow presutural yellow vitta present between postpronotal lobe and sutural spot (southern Philippines: Tawi Tawi) *B. peterseni*
 - Apical third of mid femur with a black spot, basal third of mid and all of hind tibiae dark fuscous to black; costal band expanded into a distinct apical patch; scutum with the dark medial and submedial vittae broadly connected posteriorly; presutural yellow vitta absent (Southern Thailand, Peninsular Malaysia, Borneo, Sumatra and Java) *B. bullifera*
- 13 Scutum with lateral postsutural yellow vitta normally extending anterior to suture as a distinct spot; presutural lateral yellow vitta present; lateral postsutural yellow vitta parallel-sided and enclosing intra-alar seta 14
 - Scutum with lateral postsutural yellow vitta not extending anterior to suture as a distinct spot; presutural lateral yellow vitta absent, if present then reduced to a small yellowish patch immediately behind postpronotal lobe; lateral postsutural yellow vitta short and not enclosing intra-alar seta 16
- 14 Anepisternal yellow stripe narrow, only reaching anterior notopleural seta anteriorly; scutum with a broad black submedial vitta; presutural lateral yellow vitta broadly connecting presutural spot with postpronotal lobe; costal band pale and indistinct; male wing with a pale fuscous patch across vein M between R-M and DM-Cu crossveins (Papua New Guinea and Papua Province, eastern Indonesia) *B. diaphana*
 - Anepisternal yellow stripe broad, reaching postpronotal lobe anteriorly; scutum with or without a narrow black submedial vitta; presutural lateral yellow vitta not broadly connecting presutural spot with postpronotal lobe; costal band distinct; wing without a pale fuscous patch across vein M 15

- 15 Scutum with narrow dark submedial vitta and a narrow presutural lateral yellow vitta connecting or almost connecting postpronotal lobe with sutural spot; costal band reaching vein M (Philippines) *B. mcgregori*
- Scutum without dark submedial vitta and with a broad presutural lateral yellow or orange vitta between postpronotal lobe and notopleuron; costal band not reaching vein M (Papua New Guinea) *B. aceromata*
- 16 Anepisternal yellow stripe broad, reaching postpronotal lobe anteriorly; scutum red-brown; scutellum yellow with a narrow dark basal band ... 17
- Anepisternal yellow stripe narrow, not reaching postpronotal lobe anteriorly; scutum and scutellum largely orange-brown 19
- 17 Abdomen with black lateral markings; antennal first flagellomere apically truncate; male bulla large and ovate (Andaman and Nicobar Is, West Malaysia and Singapore) *B. cinnabaria*
- Abdomen without black lateral markings; antennal first flagellomere apically rounded; male bulla small and rounded or possibly absent 18
- 18 Scutum with lateral postsutural yellow vitta sharply tapered posteriorly; notopleural lobe yellow; crossvein DM-Cu not enclosed by a narrow transverse fuscous band; small facial spots present; male bulla indistinct or absent; pecten of cilia on tergite III in males weak or absent; female unknown (Solomon Islands: Florida I.) *B. unipunctata*
- Scutum with lateral postsutural yellow vitta slightly tapered posteriorly; notopleural lobe red-brown; crossvein DM-Cu enclosed by a narrow transverse fuscous band; facial spots absent; male bulla distinct; pecten of cilia on tergite III in males well developed; female aculeus apically trilobed (Papua New Guinea) *B. trilobata* **sp. n.**
- 19 Scutum with a short, medial black vitta across line of suture; lateral postsutural yellow vitta sharply tapered posteriorly; scutellum with a narrow black lateral vitta; costal band not reaching vein M; male bulla small and round and placed on vein A₁+Cu₂ beyond apex of very narrow cell bcu extension; abdomen with a narrow, interrupted black medial vitta on tergites I-V and broader sublateral markings on tergites III-IV (males) or with a distinct black medial vitta and broad lateral margins on tergites III-V (females) (Western Samoa) *B. aenigmatica*
- Scutum without a medial black vitta; lateral postsutural yellow vitta narrow but not distinctly tapered; scutellum yellow basolaterally; costal band reaching vein M; male bulla large and ovate and cell bcu extension vestigial; abdomen without lateral black bands and medial vitta confined to tergite V (Papua New Guinea and Solomon Islands, including Nendo) *B. pacificae*

Discussion

Although not all *Bulladacus* species show all the diagnostic characters, their overall similarity suggests that the subgenus is monophyletic. The lack of

shining spots (ceromata) on abdominal tergite V and the presence of either a bulla or patch of cilia at or near the apex of wing cell bcu extension appear to be synapomorphies for the subgenus. *Bactrocera aceraglans* from Papua New Guinea and possibly *B. unipunctata* from Solomon Islands lack both the bulla and abdominal pecten in males but otherwise appear to belong here.

The geographical distribution of the 20 known *Bulladacus* species is shown in Table 1, placed within the six zones recognised by Hancock and Drew (2015). Two species (*B. penefurva* and *B. pacificae*) occur in both Papua New Guinea (Zone D) and the Solomon Islands (Zone F); all other species are endemic to their particular zones. The lack of *Bulladacus* species from Wallacea (Zone C) likely reflects undercollecting rather than a genuine absence.

Table 1. Distribution of species in genus *Bactrocera* and subgenus *Bulladacus* in each biogeographic zone and percent endemism in *Bulladacus*. For a map of zones A-F see Hancock and Drew (2015).

Biogeographic Zone	No. species of <i>Bactrocera</i>	No. species of <i>Bulladacus</i>	% Endemic <i>Bulladacus</i>
(A) Indian subcontinent	75	0	–
(B) South-East Asia	225	5	100
(C) Wallacea	124	0	–
(D) New Guinea	170	10	80
(E) Australia	76	2	100
(F) South Pacific	59	5	60

The subgenus appears to be closely associated with *Gnetum gnemon*, a tropical shrub/tree distributed from NE India throughout much of SE Asia and Australasia (excluding mainland Australia) as far east as Fiji and Samoa. Some species, particularly the Australian *B. tigrina* and *B. flavinotus*, have become adapted to *Terminalia* species, while the Samoan *B. aenigmatica* utilises *Aglaia samoensis*. Although *Bulladacus* species might be expected to occur throughout the range of *Gnetum* species, so far they are only known as far west as southern peninsular Thailand and the Andaman Islands. Greatest diversity exists on the island of New Guinea, where ten species are known, suggesting that the subgenus arose there before dispersing westwards into SE Asia and eastwards into the South Pacific.

The three strongly sexually dimorphic species, *B. tigrina*, *B. penefurva* and *B. captiva*, occur in NE Australia, Papua New Guinea-Solomon Islands and the Philippines respectively, with the latter two species appearing to be the most closely allied morphologically. A similar faunal relationship between New Guinea and the Philippines exists in the closely related acanthonevrine genera *Copiolepis* Enderlein and *Picocolepis* Hancock (Hancock 2014). Of the

remaining SE Asian species, *B. bullifera* (Sundaland) and *B. peterseni* (Tawi Tawi) appear to be an allopatric species pair: both have dark areas on the mid femur and mid and hind tibiae, plus three dark scutal vittae, a complete dark medial vitta on abdominal tergites III-V, a narrow anepisternal yellow stripe that does not reach the postpronotal lobe, a broad apex to the costal band and an oval or rounded, distinctly blackened bulla. Likewise, *B. cinnabaria* (Sundaland) and *B. mcgregori* (Philippines) also appear to be an allopatric species pair: both are generally pale species with a broad anepisternal yellow stripe, a paler, ovate bulla and a short, apically truncate antennal first flagellomere especially in males. The presence or absence of a presutural lateral yellow vitta thus appears to be homoplasious, particularly since its alignment, when present, differs in the various species showing it.

In New Guinea, *B. aceraglans* (Western Highlands) stands alone, having largely fuscous femora, the bulla replaced by a patch of cilia and the pecten absent. Of the others, *B. wanangiae* (Madang and Morobe Provinces) shares with *B. aceraglans* the black scutum, while *B. diaphana* (West Sepik and Indonesian Papua) + *B. aceromata* (Central Province), both with a presutural lateral yellow vitta, and *B. bullata* (East Sepik) + *B. warisensis* (Indonesian Papua), both with the postsutural lateral yellow vitta extending anterior to the suture as a distinct spot, a black submedial scutal vitta, a dark wing band over at least DM-Cu crossvein, a small bulla at the apex of a relatively elongate cell bcu in males and an almost unpatterned abdomen, appear to be related pairs. The latter five species all have fulvous femora and all six species have a parallel-sided lateral postsutural yellow vitta that encloses the intra-alar seta. The medial postsutural yellow vitta in *B. bullata* is narrower than in other species showing this character and is presumably homoplasious, particularly since the other species lack the presutural spots.

The new species *B. trilobata* (Madang) has the lateral postsutural yellow vitta ending before the intra-alar seta and not extending anterior to the notopleural suture; it also has a red-brown scutum and fulvous femora and appears to be closest to *B. unipunctata* from the Solomon Islands. The *Terminalia* host plants, overall appearance, very short antennal first flagellomere (0.4 mm) and well developed supernumerary lobe of the male wing in *B. eximia* suggest a relationship with the *tigrina-penefurva-captiva* series.

The three South Pacific species *B. aenigmatica* (Samoa), *B. gnetum* (Fiji) and *B. pacificae* (Solomon Islands and Papua New Guinea) all have a short lateral postsutural yellow vitta and likely form a related series that possibly includes *B. unipunctata* and *B. trilobata*. In *B. gnetum* the scutum is black, the scutellum yellow, the anepisternal yellow stripe reaches the postpronotal lobe and the hind tibia is weakly fuscous. In *B. aenigmatica* and *B. pacificae* the scutum and scutellum are largely orange-brown, the anepisternal yellow stripe does not reach the postpronotal lobe and the hind tibia is dark fuscous, suggesting another allopatric species pair despite the differences in the bulla.

A similar faunal relationship between Fiji, Solomon Islands (particularly Nendo) and Western Samoa is seen in the adramine *Coelotrypes punctilabris* (Bezzi) (Hancock and Drew 2005).

The host plant switch from *Gnetum* to *Aglaia* in *B. aenigmatica* suggests that it reached Samoa prior to the arrival of *Gnetum*. The occurrence of an extended abdominal black vitta in both western and eastern outlying species suggests that this character, widespread in many *Bactrocera* species, is homoplasious and that the short vitta on tergites IV-V or V only, seen in most *Bulladacus* species, is the plesiomorphic state for the subgenus.

Relationships of the Australian *B. flavinotus*, with its red-brown scutum, rudimentary bulla and relatively weak supernumerary lobe, remain uncertain but its *Terminalia* host plant, very short antennal first flagellomere (0.4-0.44 mm) and broad medial postsutural vitta suggest a plesiomorphic relationship with the *eximia-captiva* series. As with *B. aenigmatica*, the host plant switch likely reflects the absence of *Gnetum* from Australia and suggests that the *flavinotus-captiva* series originated there. A more detailed analysis of phylogenetic relationships will be possible after all subgenera have been reviewed and the polarity of character states more accurately determined.

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