

## A review of subgenus *Bactrocera* (*Bactrocera*) Macquart, 1835 (Diptera: Tephritidae: Dacinae)

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**Abstract.** The 439 described species in subgenus *Bactrocera* Macquart, 1835 of genus *Bactrocera* are referred to 90 species groups in 18 morphologically defined complexes. *Semicallantra* Drew, 1989 is placed as a new synonym of subgenus *Bactrocera*. *Bactrocera* (*Bactrocera*) *wallacei* Drew & Hancock, new species, is described from Maluku, Indonesia. *Bactrocera clarkei* Starkie, Strutt & Royer, 2022 and *B. petila* Drew, 1989 are transferred from subgenus *Bactrocera* to subgenera *Neozeugodacus* May, 1952a and *Calodacus* Hancock, 2015 respectively. *Bactrocera incognita* Doorenweerd & San Jose, 2024 and *B. borneoensis* Doorenweerd & San Jose, 2024 are regarded as new synonyms of *B. occipitalis* (Bezzi, 1919) and *B. carambolae* Drew & Hancock, 1994 respectively. *Bactrocera irvingiae* Drew & Hancock, 1994 is newly reported from Taiwan based on a previous misidentification as '*Dacus parvulus*'. Discussions are included on the history of research, biogeography, male lures, host plants and molecular evidence.

**Key words.** *Bactrocera*, taxonomy, biogeography, morphology

### INTRODUCTION

The genus *Bactrocera* Macquart, 1835 is the most speciose in the family Tephritidae, with more than 700 described species (including those often included in its synonym *Zeugodacus* Hendel, 1927a) endemic to the Afrotropical, Oriental, Australian, and Oceanian Regions. It includes some of the world's most damaging horticultural pests, several of which have become invasive beyond their normal distributions. Subgenus *Bactrocera* is the largest, with 439 described species endemic to the Oriental, Australian, and Oceanian Regions, three of which (*B. invadens* Drew, Tsuruta & White, 2005, *B. latifrons* (Hendel, 1915) and *B. zonata* (Saunders, 1842)) are invasive in Africa, with the first two also recorded from Italy but *B. latifrons* possibly not established (Gargiulo et al., 2021), two (*B. dorsalis* (Hendel, 1912) and *B. latifrons*) in Hawaii and one (*B. carambolae* Drew & Hancock, 1994) in NE South America. Comprehensive monographs covering the *Bactrocera* fauna of Southeast Asia, Australia, and the Pacific were published by Hardy (1973, 1974), Drew (1989), and Drew & Romig (2013, 2016, 2022), the latter publications resulting from extensive field collections from

1980 to 2010 across Southeast Asia and the Pacific and markedly increasing knowledge of the fauna.

Seven subgenera were included in the *Bactrocera* group of subgenera by Hancock & Drew (2018), defined by the presence of a short posterior surstylus lobe and deeply concave (emarginate) abdominal sternite V in males (Drew, 1989). This is reduced here to six subgenera by the synonymy of *Semicallantra* Drew, 1989 with typical *Bactrocera*. Other included subgenera are *Apodacus* Perkins, 1939, defined by the presence of a yellow postsutural medial vitta on the scutum and narrow, transverse ceromata (shining spots) on abdominal tergite V in both sexes, *Bulladacus* Drew & Hancock, 1995, defined by the lack of ceromata and frequent presence of a 'bullae' on the male wing, *Calodacus* Hancock, 2015, defined by the lack of the pecten of cilia on abdominal tergite III in males, the monotypic *Trypetidacus* Drew, 1989 and *Queenslandacus* Drew, 1989, also defined by the lack of the pecten of cilia on abdominal tergite III in males, and typical *Bactrocera*, defined by the lack of a medial yellow vitta, presence of oval or rounded ceromata and presence of the abdominal pecten in males. [Note that figures of female *B. (B.) daruensis* Drew, 1989 and *B. (B.) thistletoni* Drew, 1989 (figs. 66 & 70) in Drew & Romig (2022) include the abdominal pecten in error]. *Calodacus*, *Trypetidacus* and *Queenslandacus* are possibly synonyms, the presence of *B. (Trypetidacus) invisitata* Drew, 1989 in methyl eugenol-baited traps, not repeated since its original description (Drew, 1989) and possibly accidental, mirrors a situation noted for *B. (Tetradacus) minax* (Enderlein, 1920) in Bhutan by Hancock & Drew (2018). Reviews of *Calodacus*, *Bulladacus*, and *Apodacus* were provided by Hancock (2015), Drew & Hancock (2016), and Hancock

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& Drew (2018) respectively, with additional species added by David et al. (2016) and Drew & Romig (2022). The 439 species included in subgenus *Bactrocera* are referred here to 90 species groups in 18 morphological complexes. Complexes (sensu Drew & Romig, 2013) are regarded as a group of morphologically similar species which might not be monophyletic [the *quadrata* complex, for example, is likely to be polyphyletic], while species groups (some monotypic) are proposed as actual or potential monophyletic assemblages of related species.

## HISTORY OF TAXONOMIC RESEARCH WITH REFERENCE TO SUBGENUS *BACTROCERA*

Taxonomic research into the family Tephritidae has a long and valuable history dating back to the 18th century. With the expansion of European colonies across the tropics and subtropics of Africa, Southeast Asia, and the Pacific, several key biological expeditions were undertaken in the 19th century. Some of these expeditions focused on the collection of insects that included tephritid fruit flies. These specimens, including the resulting types of new species, were usually deposited in the national museums of the countries that either financed or undertook the expeditions. Consequently, many of the early type specimens are located in the Natural History Museum, London (NHML) and museums across Europe. A comprehensive list of these museums and a detailed history of taxonomic research in Tribe Dacini was published by Drew (1989) and Drew & Romig (2013).

Taxonomic studies on the genus *Bactrocera* Macquart began with the description of the olive fruit fly, *B. oleae* (Gmelin, 1790), then under the generic name *Musca* Linnaeus, 1758. This was followed by the description of *B. ferruginea* (Fabricius, 1794) from India, also under *Musca* and, due to homonymy, now known as *B. invadens* [or, incorrectly, treated as a synonym of *B. dorsalis*] (see Drew & Hancock, 2022). Additional species were described by Fabricius: *B. umbrosa* and *B. caudata* in 1805, both under genus *Dacus* Fabricius, 1805; Macquart described *B. longicornis*, the type species of genus *Bactrocera*, in 1835; Saunders described *B. zonata* in 1842 under genus *Dasyneura* Saunders, 1842; Doleschall described *B. maculigera* in 1858; and Walker, based at the NHML, described a large number of species between 1859 and 1865 under *Dacus*, the specimens having been collected by Alfred Russel Wallace in his biological expedition to the Malay Archipelago (1854–1862). Further biological expeditions to the regions we now regard as Southeast Asia and Australasia resulted in Schiner describing *B. frauenfeldi* in 1868, Weyenbergh with *B. ritsemai* in 1869, de Meijere with *B. apicalis*, *B. albistrigata* and *B. obscurata* in 1911 and *B. impunctata* in 1914, all also under *Dacus*.

Major *Bactrocera* pest species were described and/or revised during the 19th and 20th centuries. Major pest species of significance, listed in chronological order, are: *B. tau* (Walker, 1849), *B. tryoni* (Froggatt, 1897), *B. psidii* (Froggatt, 1899), *B. cucurbitae* (Coquillett, 1899), *B. diversa* (Coquillett, 1904), *B. xanthodes* (Broun, 1904), *B. cucumis* (French,

1907), *B. curvipennis* (Froggatt, 1909), *B. kirki* (Froggatt, 1910), *B. passiflorae* (Froggatt, 1910), *B. facialis* (Coquillett, 1910), *B. melanotus* (Coquillett, 1910), *B. dorsalis* (Hendel, 1912), *B. latifrons* (Hendel, 1915), *B. correcta* (Bezzi, 1916), *B. occipitalis* (Bezzi, 1919), *B. minax* (Enderlein, 1920), *B. jarvisi* (Tryon, 1927), *B. musae* (Tryon, 1927), *B. neohumeralis* (Hardy, 1951), *B. kraussi* (Hardy, 1951), *B. caryeae* (Kapoor, 1971), *B. trivialis* (Drew, 1971), *B. decipiens* (Drew, 1972), *B. carambolae* Drew & Hancock, 1994, *B. kandiensis* Drew & Hancock, 1994, *B. papayae* Drew & Hancock, 1994 and *B. pyrifoliae* Drew & Hancock, 1994, while *B. invadens* Drew, Tsuruta & White, 2005 and *B. divenderi* Maneesh, Hancock & Prabhakar, 2022 were added in the 21st century. Most of these belong in subgenus *Bactrocera*.

## MATERIAL AND METHODS

The following review is based on detailed morphological descriptions and illustrations provided in Drew (1989), Drew & Hancock (1994, 1995), Drew et al. (1999, 2011), Drew & Romig (2001, 2013, 2022), Huxham et al. (2006), Leblanc et al. (2015a, 2015b, 2018, 2021), David et al. (2017), David & Ramani (2019), Doorenweerd et al. (2020), Maneesh et al. (2022, 2023), Korneyev et al. (2024) and Abhishek et al. (2024), supplemented by biogeographical data and information from other publications that are noted in the text, together with an overall familiarity with the fauna. A morphological approach, involving the visible expression of genes in all 439 recognised species, is considered to be more comprehensive and reliable than the limited molecular studies currently available that are based on genes of unknown significance and include no more than 10–20% of the fauna in even the most detailed of studies (e.g., San Jose et al., 2018; Dupuis et al., 2018; Starkie et al., 2022b); these studies also contain numerous anomalous pairings and placements that are contrary to morphological and biogeographical evidence. Terminology follows White et al. (1999).

## SYSTEMATICS

### SYNONYMY OF SUBGENUS *SEMICALLANTRA*

*Semicallantra* Drew, which includes seven species from Indonesia (Maluku) and New Guinea, is currently defined by the presence of elongate antennae and, when present, lateral postsutural yellow vittae that are narrower anteriorly than medially (Hancock & Drew, 2018). However, re-examination of the type-species of *Bactrocera*, *B. longicornis* Macquart, 1835 (which also has elongate antennae and anteriorly narrowed lateral postsutural yellow vittae) by Drew & Romig (2022), plus the description of *B. malasaitiae* Drew & Romig, 2022 from Papua New Guinea, show that neither character is a reliable indicator of subgeneric separation. With the removal of *Semicallantra* from the subgeneric key in Drew & Romig (2022), its component species run to either subgenus *Bactrocera* or, in the case of *B. cerberae* Drew & Romig, 2022, imperfectly to subgenus *Calodacus*;

it has a short cell bcu extension on the wing and lacks the male pecten on abdominal tergite III. Elongate antennae also occur in *B. (Tetradacus) splendida* (Perkins, 1938) and *B. (Tetradacus) superba* Drew & Romig, 2013 (transferred from *Semicallantra* by Hancock & Drew, 2018) and in the *Dacus* subgenera *Callantra* Walker, 1860 and *Mellesis* Bezzi, 1916 and this character is evidently homoplasious. Furthermore, the long-antennae species appear to belong in separate complexes and do not form a monophyletic entity. Hence, we do not recognise antennal length as a subgeneric character and regard *Semicallantra* Drew, 1989 as a new synonym of subgenus *Bactrocera* Macquart, 1835. Consequently, all species with short antennae currently included in subgenus *Bactrocera* are retained there, with no resurrection of subgenus *Strumeta* Walker, 1856 required.

***Bactrocera (Bactrocera) wallacei* Drew & Hancock,  
new species  
(Fig. 1)**

*Bactrocera (Bactrocera) epicharis*: Drew & Romig, 2013: 79–80; 2016: 151; not Hardy, 1970: 119. Misidentification.

**Type material.** Holotype: male, INDONESIA: North Moluccas [North Maluku] – Maluku, North Maluku, West Halmahera, Goal, 29.v.2007, coll. Raais Abdullah, attracted to cue lure in forest, deposited in Queensland Museum (QMIC), Brisbane. Paratypes: 2 males, 5.vi.2007, same label data as holotype; 1 male (3.vi.2007), 1 male (10.vi.2007), North Maluku, Kodya Ternate, Foramadiah, coll. La Ruti, attracted to cue lure in forest. Paratypes in Department of Agriculture and Fisheries Collection (QDPC), Brisbane.

**Diagnosis.** A large species (wing 7.5 mm); face fulvous with a pair of medium-sized to large circular black spots; postpronotal lobes and notopleural calli yellow; scutum black; lateral postsutural yellow vittae present, elongate and parallel-sided; medial postsutural yellow vitta absent; no yellow spot anterior to notopleural suture; anepisternal (mesopleural) stripe reaching midway between anterior margin of notopleuron and anterior notopleural seta dorsally; scutellum yellow; wing with cells bc and c fuscous, microtrichia in anteroapical corner of cell c only; a broad dark fuscous costal band becoming paler between  $R_{2+3}$  and  $R_{4+5}$  and remaining of uniform width throughout; a broad dark fuscous anal streak; abdominal terga III–V entirely black.

**Description.** Male. Head: Height 2.0 mm. Frons length 1.57 times breadth, fuscous with fulvous along lateral and ventral margins and dark fuscous on anteromedial hump; orbital setae black: 1 s.or., 2 i.or.; lunule dark fuscous. Ocellar triangle black. Vertex fuscous. Face fulvous with a pair of medium-sized to large circular black spots; length 0.58 mm. Genae red-brown, dark fuscous subocular spot present; black seta present. Occiput fuscous, red-brown along eye margins; occipital row with 5–8 strong black setae. Antennae with segments 1 and 2 red-brown, segment 3 red-brown with fuscous on apex and outer surface; length of segments: 0.24 mm; 0.44 mm; 1.06 mm.

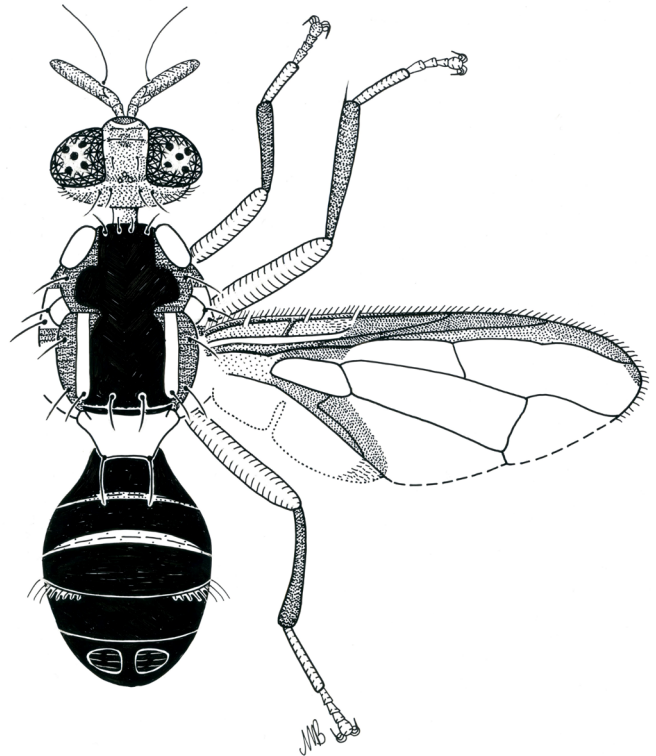


Fig. 1. Habitus of male *Bactrocera (Bactrocera) wallacei* Drew & Hancock, new species.

**Thorax:** Scutum black with dark fuscous below and behind lateral postsutural vittae, around notopleural suture, along lateral margins between postpronotal lobe and notopleuron, inside postpronotal lobe. Pleural areas entirely black. Yellow markings as follows: postpronotal lobes; notopleural calli; anepisternal stripe reaching midway between anterior margin of notopleuron and anterior notopleural seta dorsally, continuing to katapisternum as a small transverse spot, anterior margin slightly convex; anatergite (posterior apex black); anterior  $\frac{2}{3}$  katatergite (remainder black); two broad parallel-sided lateral postsutural vittae ending just behind ia. seta. Postnotum black. Scutellum yellow except for narrow black basal band. Setae (pairs): sc. 1; prsc. 1; ia. 1; p.sa. 1; a.sa. 1; mpl. 1; npl. 2; scp. 2.

**Legs:** All femora entirely fulvous; fore and hind tibiae dark fuscous, mid tibiae fuscous; fore tarsi with basal segment fulvous and apical four segments red-brown, mid and hind tarsi with all segments entirely fulvous; mid tibiae each with an apical black spur.

**Wings:** Length 7.5 mm; cells bc and c fuscous, microtrichia in anteroapical corner of cell c only; remainder of wings colourless except dark fuscous cell sc, dark fuscous costal band confluent with  $R_{4+5}$  but tending fuscous between  $R_{2+3}$  and  $R_{4+5}$  and remaining of uniform width throughout, a broad dark fuscous anal streak; a dense aggregation of microtrichia around  $A_1+CuA_2$ ; supernumerary lobe of medium development.

**Abdomen:** Oval; terga free; pecten present on tergum III. Tergum I and sterna I and II wider than long. Tergum I black

with a narrow transverse red-brown band across posterior margin but not reaching lateral margins; tergum II black with a narrow transverse fulvous band across posterior margin but not reaching lateral margins; terga III–V entirely black. A pair of oval black shining spots on tergum V. All sterna dark fuscous to black. Posterior lobe of surstylus short, sternum V with a deep concavity on posterior margin.

**Female.** No known record.

**Male attractant.** Cue lure.

**Distribution.** Known only from Halmahera and Ternate, North Maluku, Indonesia.

**Host plants.** No known record.

**Etymology.** This species is named after Alfred Russel Wallace in recognition of his pioneering field work in Wallacea and beyond.

**Remarks.** *Bactrocera (Bactrocera) wallacei* was misidentified as *B. epicharis* (Hardy, 1970) by Drew & Romig (2013, 2016), who also overlooked the description and discussion of *B. epicharis* based on new material from the Solomon Islands (Drew & Romig, 2001). It is included here in the *trivialis* group of the *nigella* complex and most resembles *B. atrabifasciata* Drew & Romig, 2001 from the Solomon Islands, differing from it in the narrower anepisternal stripe and fuscous tibiae, and from both *B. illusioscutellaris* Drew & Romig, 2013 from Bhutan and Vietnam and *B. trivialis* (Drew, 1971) from New Guinea in the broad costal band and darker abdomen.

### EXCLUDED SPECIES

*Bactrocera clarkei* Starkie, Strutt & Royer, 2022 was provisionally placed in subgenus *Bactrocera* by Starkie et al. (2022a) but sternite V is broad with a relatively shallow [moderate] posterior emargination [Starkie et al., 2022a: fig 4]; it is here transferred to subgenus *Neozeugodacus* May, 1952a, treated as a distinct subgenus in the *Melanodacus* group of subgenera by Hancock & Drew (2018). As noted in the original description, it closely resembles *B. (N.) aurea* (May, 1952a) in abdominal markings and in having the apical half of the scutellum brown but differs in the lack of basal scutellar setae and transverse wing band; it also has a narrower anepisternal stripe. Variation in the depth of the sternite V emargination in *Neozeugodacus* is similar to that seen in subgenus *Notodacus* Perkins, 1937, which also belongs in the *Melanodacus* group (Hancock & Drew, 2017b).

*Bactrocera petila* Drew, 1989, known from a single male, was placed in subgenus *Bactrocera* by Hancock (2015) but differs from all other included species in lacking the male pecten on abdominal tergite III and is provisionally included here in subgenus *Calodacus*. The original record at cue lure (Drew, 1989) has not been repeated and, as in the case of *B. (Trypetidacus) invisitata* discussed above, is also likely to

have been accidental. *Bactrocera cerberae* Drew & Romig, originally described in subgenus *Semicallantra* by Drew & Romig (2022), also lacks the male pecten on abdominal tergite III and is included here in subgenus *Calodacus*.

### INCLUDED SPECIES

The placement of *B. pseudocucurbitae* White & Evenhuis, 1999 has been uncertain. Drew & Romig (2013) and Hancock & Drew (2017c) included it in subgenus *Parasinodacus* Drew & Romig, 2013 (*Zeugodacus* group of subgenera) but Doorenweerd et al. (2018) returned it to subgenus *Bactrocera* based on its molecular affiliation with other species in that subgenus. In their original description, White & Evenhuis (1999) noted a V-shaped emargination to sternite V and lack of an elongate posterior surstylus lobe [long and stout in Drew & Romig (2013)]; the scutal and abdominal patterns are typical of several *Bactrocera (Bactrocera)* species (e.g., *B. indecora* (Drew, 1971) and *B. vulgaris* (Drew, 1971) in the *indecora* complex) and therefore we confirm its placement here.

### FURTHER NOTES ON THE *DORSALIS* COMPLEX

Of the 18 recognised complexes, the *dorsalis* complex is the second largest and has attracted the most interest due to the economic implications relating to some major pest species, with *B. citima* (Hardy, 1973), *B. ellenriederae* Korneyev, Leblanc, Hauser, General & Gaimari, 2024, *B. parafroggatti* Drew & Romig, 2001 and *B. youngi* Korneyev, Leblanc, Hauser, General & Gaimari, 2024 here added to the 79 species included by Drew & Hancock (2022).

Over the past decade, a part of the *dorsalis* complex has been left in a state of confusion that began with the erroneous synonymy of *B. invadens* and *B. papayae* with *B. dorsalis* by Schutze et al. (2015a, b), which has been followed by numerous publications that mainly focused on molecular analyses of specimens, generally without a detailed understanding of *Bactrocera* taxonomy. This limited approach has led to increased confusion in the diagnosis of species, particularly as most studies have resulted in conflicting results and incongruence between morphological and molecular data.

*Bactrocera youngi* is a possible synonym of *B. fulvifemur* Drew & Hancock, 1994. Both were described from Luzon, Philippines (Drew & Hancock, 1994; Korneyev et al., 2024) and the presence of red-brown submedial scutal vittae covered with silvery pubescence in some specimens was recorded in the description of *B. fulvifemur* by Drew & Hancock (1994). This latter species was not mentioned by Korneyev et al. (2024) and we can find no reliable characters that separate the two taxa as currently known. However, further comparison between the black and red-striped forms is needed to confirm synonymy. A second species described from Luzon by Korneyev et al. (2024), *B. ellenriederae*, is very similar to *B. lateritaenia* Drew & Hancock, 1994 and

possibly synonymous, but the latter species is not yet known from the Philippines so we provisionally accept them as separate species pending further study.

*Bactrocera papayae* and *B. invadens* were erroneously synonymised with *B. dorsalis* by Schutze et al. (2015a, b) and subsequently reestablished as valid species by Drew & Romig (2016). In his 1973 monograph, Hardy perceptively recognised *B. papayae* as a species distinct from *B. dorsalis*, although he incorrectly diagnosed it as the Philippine species *B. pedestris* (Bezzi, 1913) (see Hardy, 1973: p. 50). The specific status of both *B. papayae* and *B. invadens* was further confirmed by Drew & Hancock (2022) and Drew & Romig (2022). Contrary to Doorenweerd et al. (2024), Drew & Romig (2022) did not state that the dark foretibia stripe in *B. papayae* ‘quickly fades in deceased specimens’ but that it is more distinct in fresh specimens; it merely becomes harder to discern in dried material but is still evident, as in a specimen from Bangkok, Thailand examined by DLH (in NAQS Collection, Cairns, Queensland, Australia). Despite the study of Drew & Hancock (2022), confusion between this species, *B. dorsalis*, and *B. invadens* persists. The shorter and subovate glans of *B. dorsalis* is evident in Taiwanese specimens misidentified as ‘*Dacus pedestris*’ by Tseng et al. (1992) and is very similar to that illustrated by Drew & Hancock (2022) of Chinese *dorsalis* [cf. *B. invadens* in Maneesh et al. (2022)]. The ‘*Dacus dorsalis*’ male illustrated by Tseng et al. (1992) also differs from true *B. dorsalis* in its narrower anepisternal stripe, slight apical expansion of the costal band, short cell *bcu* extension, abdominal pattern and internal structure of the glans and appears to belong to a separate species.

Part of the belief that *B. dorsalis*, *B. papayae*, and *B. invadens* are conspecific stems from methyl eugenol response studies by Hee et al. (2015a), using the IAEA Saraburi (Thailand) colony misidentified as ‘*dorsalis*’ instead of *papayae* and originating within the known distribution of the latter species (Drew & Hancock, 2022). A study that used true *B. dorsalis* from Taiwan (Wee et al., 2002) produced conflicting results that were dismissed as regional variation by Hee et al. (2015a), but indicated that *B. dorsalis* is twice as responsive to methyl eugenol as *B. papayae*, and that these two species are, respectively, 17 and 9 times more responsive than *B. carambolae*. The similarity in lure response between the Saraburi colony and *B. papayae* supports its actual identity as the latter species, with comparison in Hee et al. (2015a) thus being made between *papayae* and *papayae*. The response of *B. invadens* is similar to that of *B. papayae* (see Hee et al., 2015a) but morphological differences are significant (Drew & Hancock, 2022).

Two ‘cryptic’ species in the *dorsalis* complex, *B. incognita* Doorenweerd & San Jose, 2024 and *B. borneoensis* Doorenweerd & San Jose, 2024, with holotypes from Cambodia and Sabah, respectively, were described recently by Doorenweerd et al. (2024) solely on molecular evidence with the bodies of the entire type series destroyed for DNA extraction, leaving only photographs of the holotypes while

they were in ethanol and legs, wings, and terminalia mounted on slides. In the absence of supporting evidence such as female morphology, host plant preference or lure difference, we are unable to support specific status for these two taxa and regard them as genetic variants and new synonyms of *B. occipitalis* and *B. carambolae* respectively. These two species have distinctive abdominal patterns identical to those in the ‘cryptic’ variants, males of all four taxa are attracted to methyl eugenol and, although synonymies represent no more than taxonomic opinion based on available evidence, validation of currently inseparable taxa requires more convincing information. Genetic variation is extensive in at least some *dorsalis* complex species (e.g., *B. carambolae*: Aketarawong et al., 2015; Drosopoulou et al., 2019) and the gene fragments analysed are either known to be unreliable (COI) (e.g., Doorenweerd et al., 2024) or their reliability is currently unknown (RAD-seq and HiMAP). The holotype of *B. incognita* has a dark fore femoral spot and, despite the statement in Doorenweerd et al. (2024) that a dark fore femoral spot is never present in *B. raiensis* Drew & Hancock, 1994, such a spot was recorded in some specimens of both it and *B. occipitalis* by Drew & Hancock (1994). However, *B. raiensis* has a narrower costal band and more extensive lateral dark markings on the abdomen. The slightly narrower costal band in ‘*incognita*’ is also seen in some Philippine specimens of *B. occipitalis* and the darker scutum regarded as morphological variation, the extent of which in the *incognita* type series can no longer be determined. The distribution of *B. occipitalis* therefore ranges from southern Thailand, Cambodia, and Vietnam to West Malaysia, Borneo and the Philippines. *Bactrocera occipitalis* was recorded previously from Brunei, Sabah, and Kalimantan by Drew & Romig (2013).

*Bactrocera carambolae* is common in the Danum Valley, Sabah [Drew & Hancock (1994) recorded 254 males], the type locality of *B. borneoensis*, and the two taxa cannot be separated morphologically. The subapical fore femoral spot is generally present in females but often absent in males; the type series of the latter is comprised solely of males and the statement that the fore femoral spot is always absent in *borneoensis* (in Doorenweerd et al., 2024) is based on too few specimens to be conclusive. The genetic similarity between *incognita* and *borneoensis* is likely due to introgression, as both taxa occur sympatrically with *B. carambolae* outside the Philippines and with each other in Borneo. It is considered inadvisable to describe species solely on molecular evidence where individual specimens cannot be identified without their destruction, leaving them unavailable for checking by taxonomists experienced in the particular fauna and thereby failing the results reproducibility test.

Taiwanese specimens of ‘*Dacus parvulus*’ illustrated in Tseng et al. (1992) are regarded here as misidentifications of *B. irvingiae* Drew & Hancock, 1994 and run to it in the key of Drew & Hancock (1994); neither has been recorded from male lures. Taiwan is thus a new country record for *B. irvingiae*.

## COMPLEXES AND SPECIES GROUPS

A long-standing convention in taxonomy where a large and diverse fauna is being researched is to group species in complexes based on morphological similarities. While a complex is not a formal category and not necessarily monophyletic, experienced researchers in taxonomic studies of large faunas often place species within such complexes. This process assists in building diagnostic keys to species and, in part, understanding evolutionary and biogeographical relationships. Definition and scope of the term ‘complex’ varies among authors, with that used here (sensu Drew, 1989; Drew & Romig, 2013) used widely in the Dacinae. Over the past decade, many papers have been published by authors inexperienced in tephritid taxonomy and the processes and practice of systematic research. An example is that by Catullo et al. (2019), who appear to have misunderstood the concept of species complexes and stated that *B. endiandrae* (Perkins & May, 1949) should not be placed in the *dorsalis* complex based on molecular data. Based on morphology and lure response, *B. endiandrae* is best placed in the *dorsalis* group, close to *B. parafroggatti* Drew & Romig, 2001 [referred to the *dorsalis* complex by Doorenweerd et al., 2024] and nowhere near either *B. aeruginosa* (Drew & Hancock, 1981 [in Drew et al., 1981]) or *B. umbrosa* (Fabricius, 1805) as indicated by Catullo et al. (2019), *B. lampabilis* (Drew, 1971) as placed by Starkie et al. (2022b), or *B. (Calodacus) calophylli* (Perkins & May, 1949) as placed by San Jose et al. (2018), all on molecular grounds. Krosch et al. (2012) placed it in an unresolved clade that also included the *dorsalis* complex, *B. murrayi* (Perkins, 1939) and *B. (C.) calophylli*, while Dupuis et al. (2018) also included it in an unresolved clade.

The following definitions of complexes and groups may be used as a ‘Key by elimination,’ reading through each complex in turn until a satisfactory placement is made and then using the group definitions for a more detailed placement. Monotypic groups reflect diversity within the complexes and might be combined with other groups when better known. Some species or groups do not fit readily in these complexes but are included to facilitate identification.

**longicornis complex:** often largely black species with a very broad transverse wing band enclosing both R-M and DM-Cu crossveins, recurved towards wing base along vein Cu<sub>1</sub> or alongside it in cell cu<sub>1</sub> and usually expanded basal to R-M crossvein in cell dm and beyond line of DM-Cu crossvein in cells r<sub>4+5</sub> and m; if wing almost entirely fuscous in apical 2/3 then with a longitudinal hyaline band in anterobasal quarter of cell dm, or without transverse bands or an isolated longitudinal hyaline band in cell dm but fuscous over all or most of wing or at least apically beyond line of R-M crossvein [17 species: Sulawesi and Maluku to New Caledonia and NE Australia].

*ampla* group: prescutellar acrostichal setae present; scutellum with basal black band narrow and not expanded; wing with transverse discal band not united with broad apical area in

cell r<sub>4+5</sub> and without a broad transverse basal band across BM-Cu crossvein; all femora fulvous; abdomen with a broad black medial vitta and lateral margins on tergites II–V; males respond to cue lure. Species: *ampla* (Drew, 1971).

*amplexiseta* group: wing without transverse bands or an isolated longitudinal hyaline band in cell dm but fuscous over all or most of wing or at least apically beyond line of R-M crossvein; postpronotal lobes entirely yellow or apically fuscous; body and leg markings variable; costal cells bc and c pale to dark fuscous with microtrichia in anteroapical corner of cell c only; males respond to methyl eugenol. Species: *amplexiseta* (May, 1962a); *ebenea* (Drew, 1971); *fumica* Drew & Romig, 2022; *fuscalata* Drew, 1989; *fuscoptera* Drew & Romig, 2013.

*biarcuata* group: prescutellar acrostichal setae present; scutellum with basal black band broadly convex or triangular but not crossing scutellum; wing with transverse discal band united with preapical band in cell r<sub>4+5</sub> or preapical band absent; at least mid and hind femora apically fuscous; abdomen mostly black, with at most a pair of small posterior pale patches on tergite II and without a broad black medial vitta and lateral margins on tergites III–V; males respond to methyl eugenol. Species: *biarcuata* (Walker, 1865); *malasaitiae* Drew & Romig, 2022; *retrorsa* Drew, 1989.

*curvifer* group: prescutellar acrostichal setae often absent; scutellum with basal black band narrow and not expanded; wing with transverse basal band across BM-Cu crossvein broad in cell dm; all femora fulvous; abdomen black or with a broad black medial vitta and lateral margins on tergites III–V and with a broad or medially intersected posterior pale band on tergite II; males respond to methyl eugenol. Species: *confluens* (Drew, 1971); *curvifer* (Walker, 1864); *pepissalae* (Froggatt, 1910); *seguyi* (Hering, 1939); *speculifer* (Walker, 1865); *ternatiae* Drew & Romig, 2013.

*longicornis* group: prescutellar acrostichal setae present; scutellum with a broad medial vitta that reaches apex of scutellum; wing with transverse discal band not united with preapical band in cell r<sub>4+5</sub>; all femora apically fuscous; abdomen mostly black, with at most a pair of small posterior pale patches on tergite II and without a broad black medial vitta and lateral margins on tergites III–V; males respond to cue lure. Species: *denigrata* (Drew, 1971); *longicornis* Macquart, 1835.

**alyxiae complex:** often largely black species with the transverse band enclosing R-M and DM-Cu crossveins either entire or separated in cell dm, not expanded basal to R-M crossvein in cell dm and beyond line of DM-Cu crossvein in cell r<sub>4+5</sub> and recurved towards wing base along vein Cu<sub>1</sub> or alongside it in cell cu<sub>1</sub>; or with the band uniformly broad and with a distinct preapical band; or with 2 separate bands over R-M and DM-Cu crossveins that are either united posteriorly or separated in cell dm into a U- or V-shaped band [16 species: Sulawesi to New Caledonia, Mariana Islands and NE Australia, with *B. umbrosa* also widespread in SE Asia.

*alyxiae* group: scutellum yellow with a narrow basal black band; transverse wing band broad and enclosing both R-M and DM-Cu crossveins and recurved towards wing base alongside vein Cu<sub>1</sub> in cell cu<sub>1</sub>; all femora fulvous; abdomen entirely pale or black with tergite II broadly pale posteriorly and a broad pale medial stripe on tergites III–V; males respond to cue lure. Species: *alyxiae* (May, 1952b); *repanda* Drew, 1989.

*halmaherae* group: scutellum yellow with a narrow basal black band; wing with 2 transverse bands over R-M and DM-Cu crossveins separated in cell dm and recurved towards wing base along vein Cu<sub>1</sub>; all femora diffusely darkened apically; all tibiae fuscous; abdomen with a narrow black T-shaped pattern on tergites III–V; males respond to cue lure. Species: *halmaherae* Drew & Romig, 2013.

*ochrosiae* group: scutellum yellow with a broadly oval black basal band; anepisternal yellow stripe horizontal and reaching postpronotal lobe; wing with transverse band over R-M and DM-Cu crossveins broad and aligned with pterostigma, with a distinct but short preapical band and with a broad basal band united with anal stripe; costal band interrupted between medial and preapical bands; all femora fulvous; abdominal tergites III–V orange-brown with broad black posterior bands; males respond to cue lure. Species: *ochrosiae* (Malloch, 1942). This species is known only from Guam and the Northern Mariana Islands, a record from Hawaii being very doubtful (Leblanc, 2022).

*reclinata* group: scutellum with either a broad black basal triangular patch or a medial stripe that reaches apex of scutellum; transverse wing band or bands enclosing both R-M and DM-Cu crossveins recurved or not towards wing base along vein Cu<sub>1</sub> and either entire and of uniform width or separated in cell dm and basal band short or absent, not reaching anal stripe; fore and hind femora with apical half black, mid femur black; abdomen black with at most a pair of small pale posterior patches on tergite II; males respond to methyl eugenol. Species: *ismayi* Drew, 1989; *lampabilis* (Drew, 1971); *reclinata* Drew, 1989.

*recurrens* group: scutellum yellow with a narrow basal black band; wing with 2 transverse bands over R-M and DM-Cu crossveins united posteriorly into a U- or V-shaped band; preapical band absent, reduced to a spot, or connected with band over DM-Cu crossvein; all femora fulvous; abdomen entirely pale, with a narrow black medial vitta on tergites II–V or III–V or with tergite II broadly pale posteriorly and tergites III–V with a black T-shaped pattern and broad black lateral margins; males respond to cue lure. Species: *absidata* Drew, 1989; *anfracta* Drew, 1989; *manskii* (Perkins & May, 1949); *nigrescentis* (Drew, 1971); *recurrens* (Hering, 1941a); *redunda* (Drew, 1971); *resima* (Drew, 1971).

*umbrosa* group: scutellum yellow with a narrow basal black band; wing with transverse band over R-M and DM-Cu crossveins broad and aligned with apex of pterostigma, with a distinct preapical band and with or without a broad basal band united with anal stripe; all femora fulvous; abdomen

with tergites III–V with variable fuscous medial and/or lateral bands; males respond to cue lure or methyl eugenol. Species: *bifasciata* (Hardy, 1982); *umbrosa* (Fabricius, 1805).

***distincta* complex:** often largely black species with costal band distinct and a transverse wing band enclosing both R-M and DM-Cu crossveins not expanded beyond line of DM-Cu crossvein in cell r<sub>4+5</sub> and sometimes absent over anterior part of R-M crossvein; preapical band absent; scutellum with a broad black medial band or mostly yellow; femora usually entirely pale or narrowly darkened apically [40 species: Maluku to New Caledonia, Fiji, and Australia].

*angustifasciata* group: scutellum with a broad black medial vitta; scutum black; males respond to cue lure. Species: *angustifasciata* Drew, 1989; *hollingsworthi* Drew & Romig, 2001; *raunsepnaensis* Drew & Romig, 2022; *rounaensis* Drew & Romig, 2022; *unilineata* Drew, 1989.

*distincta* group: scutellum yellow with at most an apical fuscous band and a narrowly concave black basal band; males respond to cue lure, zingerone or response unknown. Species: *allocalodistincta* Leblanc & Doorendeerd, 2021 [in Leblanc et al., 2021]; *anomala* (Drew, 1971); *atrilineata* Drew, 1989; *avittata* Drew & Romig, 2013; *curreyi* Drew, 1989; *decumana* (Drew, 1972); *distincta* (Malloch, 1931); *fergussoni* Drew, 1989; *furvilineata* Drew, 1989; *fuscohumeralis* White & Evenhuis, 1999; *latilineata* Drew, 1989; *monostriata* Drew & Romig, 2022; *morobiensis* Drew, 1989; *neofulvicauda* Drew & Romig, 2013; *oblineata* Drew, 1989; *penephaea* Drew & Romig, 2013; *pisinna* Drew, 1989; *propedistincta* Drew, 1989; *pseudodistincta* Drew, 1989; *pulchra* Tryon, 1927; *rhabdota* Drew, 1989; *tikelingiae* Drew & Romig, 2022; *torresiae* Huxham & Hancock, 2006 [in Huxham et al., 2006]; *tortuosa* White & Evenhuis, 1999; *truncata* Drew & Romig, 2013; *tsatsiai* Leblanc & Doorendeerd, 2021 [in Leblanc et al., 2021]; *unifasciata* (Malloch, 1939); *unitaeniola* Drew & Romig, 2001.

*fulvicauda* group: as for *distincta* group but males respond to methyl eugenol. Species: *fulvicauda* (Perkins, 1939); *inconspicua* Drew & Romig, 2013; *maculigera* Doleschall, 1858; *manusiae* Drew & Romig, 2022; *obliquivenosa* Drew & Romig, 2001; *paranigrita* Drew & Romig, 2013; *unistriata* Drew, 1989.

***frauenfeldi* complex:** largely black species with costal band very faint or absent beyond pterostigma, preapical band absent and transverse wing band distinct or faint and posteriorly diffuse and enclosing both R-M and DM-Cu crossveins; R-M crossvein distinctly oblique and less than its own length from DM-Cu crossvein; scutellum basally broadly black or with a broad black medial vitta [8 species: New Guinea to New Caledonia and Australia, except *B. albistrigata*, which is widespread from Andaman Islands and southern Thailand to Maluku and Timor].

*frauenfeldi* group: abdomen with a broad black medial vitta on tergites II–V and broad black lateral margins on tergites II–V or III–V (sometimes coalesced with medial

vitta); males respond to cue lure. Species: *albistrigata* (de Meijere, 1911); *frauenfeldi* (Schiner, 1868); *parafrauenfeldi* Drew, 1989; *trilineola* Drew, 1989. Proposed synonymy of *albistrigata* with *frauenfeldi* by Doorenweerd et al. (2023a) was considered to be based on insufficient evidence by Drew & Hancock (2022) and was not supported by the molecular studies of Yong et al. (2024).

*obliqua* group: abdomen black with or without paler areas posterolaterally on tergite II; males respond to cue lure, zingerone or possibly isoeugenol. Species: *caledoniensis* Drew, 1989; *obliqua* (Malloch, 1931); *vargasi* Leblanc & Doorenweerd, 2021 [in Leblanc et al., 2021]; *yayamiae* Drew & Romig, 2022.

**atramentata complex:** often black or mostly black species; wing with costal band very narrow and linear or pale and indistinct; preapical band absent; transverse band narrow (*strigata*) or absent, with or without a pale fuscous tint over R-M, DM-Cu or both R-M and DM-Cu crossveins; scutum with postsutural lateral yellow vittae often very narrow, narrowing anteriorly or absent; notopleural calli yellow or orange-brown to black; if scutum largely red-brown or orange-brown then postpronotal lobes brown or notopleural calli orange-brown to fuscous; scutellum black, with a broad black or red-brown medial stripe reaching apex, with a triangular black basal band not reaching apical margin, with a broad red-brown apical band or mostly yellow; legs often with femora and/or tibiae mostly black [18 species: Eastern Australia and Papua New Guinea to Cook, Marquesas, Henderson, Austral and Society Islands, and the Tuamotu Archipelago].

*atra* group: notopleural calli black; scutellum black or with lateral yellow margins and a broad medial black stripe reaching apical margin; abdomen black or with pale submedial patches apically on tergites II–IV and basally on tergites IV–V; males respond to cue lure or response unknown. Species: *atra* (Malloch, 1938); *carbonaria* (Hendel, 1927b); *melanotus* (Coquillett, 1910); *perfusca* (Aubertin, 1929); *setinervis* (Malloch, 1938).

*atramentata* group: notopleural calli yellow; scutellum with a broad medial black stripe reaching apical margin or with a broadly triangular black basal band; if costal band pale and indistinct then R-M or R-M and DM-Cu crossveins with a pale fuscous tint; abdomen black with paler apical or subapical areas on tergite V at most; males respond to cue lure. Species: *atramentata* (Hering, 1941c); *hypomelaina* Drew, 1989; *morula* Drew, 1989; *psidii* (Froggatt, 1899).

*kirki* group: notopleural calli yellow; scutellum with lateral yellow margins and a very broad medial black stripe reaching apical margin; costal band pale; transverse wing band reduced to a pale tint over R-M and DM-Cu crossveins or absent; all femora pale; abdomen with a broad black medial vitta and broad black lateral margins on tergites I–V or II–V; males respond to cue lure. Species: *enochra* (Drew, 1972); *kirki* (Froggatt, 1910); *trifaria* (Drew, 1971).

*luteola* group: scutum mostly shining orange-brown without lateral yellow vittae; notopleural calli shining orange-brown; scutellum yellow with a broad orange-brown basal band; costal cells hyaline; costal band narrow; crossveins R-M and DM-Cu with a faint infuscation; anal streak faint or absent; facial spots absent; all femora and tibiae fulvous; abdomen entirely shining orange-brown with small fuscous patches anterolaterally and medially on tergite III and medially on tergite IV; males show no response to known lures. Species: *luteola* (Malloch, 1931).

*picea* group: scutum black with elongate lateral yellow vittae; notopleural calli yellow; scutellum with a broad medial black stripe reaching apical margin; costal band pale and indistinct and R-M and DM-Cu crossveins without a pale fuscous tint; mid and hind femora black; abdomen black with small paler areas posteriorly on tergite II; males respond to methyl eugenol. Species *picea* (Drew, 1972).

*strigata* group: scutum red-brown or orange-brown with short or elongate lateral yellow vittae; notopleural calli red-brown or fuscous; costal band narrow; costal cells hyaline or fulvous; wing with or without a transverse band across R-M, DM-Cu or both R-M and DM-Cu crossveins; abdomen orange-brown with or without a narrow black medial vitta on abdominal tergites III–V or V; scutellum yellow, broadly red-brown apically or red-brown with a pair of large basolateral yellow spots; facial spots small or absent; female aculeus with 1–3 pairs of subapical lobes; males show no response to known lures. Species: *brunnea* (Perkins & May, 1949); *hispidula* (May, 1957); *phaleriae* (May, 1955); *strigata* (Perkins, 1934). These four species are restricted to Eastern Australia, with a reported response of *B. phaleriae* to isoeugenol based on a single specimen (Starkie et al., 2022a) that was possibly accidental in the trap.

**laticaudus complex:** scutum dark fuscous to black; notopleural calli yellow; wing without transverse or preapical bands but with a distinct infuscation over R-M crossvein that sometimes extends weakly into cell dm; costal band distinct and extending across vein R<sub>2+3</sub> and often reaching vein R<sub>4+5</sub>; costal cells bc and c hyaline to pale fuscous and with microtrichia confined to anteroapical corner or apical half of cell c; scutellum yellow with a narrow black basal band [6 species: Maluku to Solomon Islands and Australia].

*laticaudus* group: scutum dark fuscous to black; abdomen mostly black with a pair of large, pale posterior patches or broadly pale on tergite II; all femora apically dark fuscous to black; males respond to methyl eugenol. Species: *laticaudus* (Hardy, 1950); *melanogaster* Drew, 1989; *neonigrita* Drew, 1989; *quasineonigrita* Drew & Romig, 2013.

*phaea* group: scutum largely black; abdomen largely pale with a dark T-shaped pattern over tergites III–V; all femora apically pale fulvous; males respond to cue lure. Species: *kunwawaensis* Drew & Romig, 2022; *phaea* (Drew, 1971).



**tryoni complex:** wing without transverse or preapical bands, at most with a pale or distinct infuscation over R-M crossvein; costal band distinct and narrow or broad, often reaching or almost reaching vein  $R_{4+5}$  throughout its length; costal cells bc and c with at least a fulvous tint and at least most of cell c (and often part of cell bc) covered with microtrichia; hind tibiae often fuscous; abdominal tergite I wider than long and broadest posteriorly except in *B. incompta* [39 species: Malaysia to New Caledonia and Australia].

*assita* group: costal band broad, crossing vein  $R_{2+3}$  and often reaching or almost reaching vein  $R_{4+5}$  throughout its length; costal cells bc and c pale to dark fuscous; femora pale or at least apically fuscous; hind tibiae fuscous or pale; males respond to cue lure. Species: *apicopicta* Drew & Romig, 2013; *assita* Drew, 1989; *careofascia* Drew & Romig, 2013; *fuscolobata* Drew & Romig, 2013; *fuscoformosa* Drew & Romig, 2013; *gabensiae* Drew & Romig, 2022; *labubulu* Drew & Romig, 2022; *ochracea* Drew, 1989; *paraochracea* Drew & Romig, 2022; *pusilla* (Hardy, 1983); *ustulata* Drew, 1989.

*curvipennis* group: costal band broad, reaching vein  $R_{4+5}$  throughout its length; crossvein R-M infuscated; costal cells bc and c pale fuscous; femora pale; hind tibiae pale; males respond to cue lure, isoeugenol and dihydroeugenol. Species: *curvipennis* (Froggatt, 1909).

*incompta* group: scutum largely dull black (fuscous posteriorly) without lateral yellow vittae; postpronotal lobes and notopleural calli entirely dark fuscous; supra-alar setae absent; antennae with segment I elongate; abdomen elongate with tergite I longer than wide and almost parallel-sided, not widest posteriorly; tergites II–V red-brown without a dark T-shaped pattern and with darker lateral margins on tergite III; costal band narrow and apically linear; costal cells pale fuscous with dense microtrichia over all of cell c; all femora red-brown; all tibiae fuscous at least basally; males respond to cue lure. One species: *incompta* Drew & Romig, 2013. This species is distinct and provisionally included in the *tryoni* complex pending further study.

*mediorufula* group: costal band narrow or broadened apically; costal cells bc and c fuscous; scutum black with a broad rufous medial vitta ending before prescutellar acrostichal setae; femora fulvous or with a fuscous apical spot; fore, at least base of mid and hind tibiae fuscous; males respond to methyl eugenol. Species: *mediorufula* Drew & Romig, 2013; *tapahensis* Drew & Romig, 2013.

*notatagena* group: costal band narrow or broad, often reaching or almost reaching vein  $R_{4+5}$  throughout its length; costal cells bc and c fulvous to fuscous; femora pale, apically dark or with fore, mid and apical third to half of hind femora fuscous; male response to lures uncertain or unknown; isolated reports of *B. daruensis* at methyl eugenol (Huxham & Hancock, 2002) and *B. mutabilis* at isoeugenol (Starkie et al., 2022a) appear to be accidental. Species: *buloloensis* Drew, 1989; *caliginosa* (Hardy, 1970); *commina* Drew, 1989; *daruensis* Drew, 1989; *humilis* (Drew & Hancock, 1981) [in Drew et

al., 1981]; *kelaena* Drew, 1989; *laensis* Drew & Romig, 2022; *mendosa* (May, 1957); *mutabilis* (May, 1952a); *notatagena* (May, 1952b); *pectoralis* (Walker, 1859); *pometiae* Drew & Romig, 2022; *popondettiensis* Drew, 1989; *trivirgulata* Drew & Romig, 2022.

*romigae* group: costal band broad, reaching or almost reaching vein  $R_{4+5}$  throughout its length; costal cells bc and c pale to dark fuscous; fore and at least part of mid and hind femora fuscous; males respond to methyl eugenol or dihydroeugenol and isoeugenol. Species: *nigrovittata* Drew, 1989; *quadrisetosa* (Bezzi, 1928) [= *varipes* Drew, 1989]; *romigae* (Drew & Hancock, 1981) [in Drew et al., 1981].

*speewahensis* group: costal band narrow; costal cells bc and c fuscous; all femora fulvous; scutellum broadly red-brown posteriorly; males respond to zingerone. Species: *speewahensis* Fay & Hancock, 2006 [in Huxham et al., 2006].

*sylvania* group: costal band broad, extending well beyond vein  $R_{4+5}$  over most of its length; costal cells bc and c fuscous (cell bc paler); fore, mid and apical third of hind femora fuscous; males respond to methyl eugenol or response unknown. Species: *grandifasciata* White & Evenhuis, 1999; *sylvania* Drew & Romig, 2022.

*tryoni* group: costal band narrow, often crossing vein  $R_{2+3}$  but not reaching or almost reaching vein  $R_{4+5}$  except at apex; costal cells bc and c fulvous to fuscous; all femora pale; hind tibiae fuscous; males respond to cue lure. Species: *aquilonis* (May, 1965); *melas* (Perkins & May, 1949) [hybrid?]; *neohumeralis* (Hardy, 1951); *tryoni* (Froggatt, 1897).

**nigrotibialis complex:** wing without transverse or preapical bands or a distinct infuscation over R-M crossvein; costal band distinct and narrow to broad, often faintly reaching but not crossing vein  $R_{4+5}$  except at apex; costal cells bc and c hyaline or with a pale fulvous to fuscous tint and not covered with microtrichia; face with a pair of dark spots or black; scutum black without paler areas and with postsutural lateral yellow vittae often very narrow, narrowing anteriorly or absent; scutellum with a narrow or broad black basal band not reaching apex; legs with femora and tibiae mostly or at least partly black; abdomen black with at most pale areas posteriorly on tergites I–II and dorsocentrally-posteriorly on tergites III–V; tergite I not broadly pale medially [30 species: Pakistan and India to Japan, Solomon Islands, and northern Australia].

*aquila* group: costal band broad but not crossing vein  $R_{4+5}$  except at apex; scutellum yellow with a narrow black basal band; antennae often elongate; all femora largely or entirely black; abdomen black with at most small paler areas posteriorly on tergites II or V; males respond to cue lure or response unknown. Species: *aquila* (Drew, 1989); *epicharis* (Hardy, 1970); *exspoliata* (Hering, 1941b); *memnonia* (Drew, 1989); *nigricula* (Drew, 1989); *toxopeusi* (Hering, 1953).

*diospyri* group: costal band narrow; scutum with lateral postsutural yellow vittae short and triangular or absent;

scutellum yellow with a narrow black basal band; all femora black except extreme base or fore and mid femora partly or entirely black and hind femora black on apical third to half; abdomen black with at most paler areas posteriorly on tergites I–II and V; males respond to methyl eugenol. Species: *diospyri* Drew, 1989; *nationigrotibialis* Drew & Romig, 2013; *paradiospyri* Chen, Zhou & Li, 2011 [in Chen et al., 2011]; *wuzhishana* Lin & Yang, 2006 [in Lin et al., 2006].

*nigrotibialis* group: costal band narrow or broad but not crossing vein  $R_{4+5}$  except at apex; scutellum yellow with a narrow to relatively broad convex to subtriangular black basal band; all femora black on at least apical third (hind femora fulvous tending red-brown apically in *B. obscurata*); abdomen black with at most paler areas posteriorly on tergites I–II and dorsocentrally-posteriorly on tergites III–V; males respond to cue lure, zingerone or response unknown. Species: *anthracina* (Drew, 1971); *apiconigroscutellata* Drew, 2002 [in Drew & Raghu, 2002]; *aterrima* (Drew, 1972); *bellisi* Drew & Romig, 2013; *caccabata* Drew & Romig, 2022; *divenderi* Maneesh, Hancock & Prabhakar, 2022 [in Maneesh et al., 2022]; *dysoxyli* Drew & Romig, 2022; *kaiuiaie* Drew & Romig, 2022; *lata* (Perkins, 1938); *lineata* (Perkins, 1939); *neonigrotibialis* Drew, 2002 [in Drew & Raghu, 2002]; *nigrifemorata* Lin & Wang, 2011 [in Lin et al., 2011]; *nigrofemoralis* White & Tsuruta, 2001 [in Tsuruta & White, 2001]; *nigrotibialis* (Perkins, 1938); *obscurata* (de Meijere, 1911); *perigrapha* White & Tsuruta, 2001 [in Tsuruta & White, 2001]; *pernigra* Ito, 1983; *prabhui* David, 2019 [in David & Ramani, 2019]; *terminaliae* Drew, 1989; *thistletoni* Drew, 1989. *Bactrocera prabhui* is known only from females (David & Ramani, 2019) and is included provisionally.

***passiflorae* complex:** wing without transverse or preapical bands or a distinct infuscation over R-M crossvein; costal band narrow, linear and not expanded apically; costal cells bc and c hyaline or with a pale fulvous tint and not covered with microtrichia; scutum mostly or entirely black; postsutural lateral yellow vittae very short and narrow or absent; scutellum with narrow basal black band and sometimes a fuscous apical band; legs with all femora pale [8 species: Solomon Islands, Vanuatu, and New Caledonia to Samoa].

*obscura* group: facial spots present or absent; scutum paler laterally; postpronotal lobes mostly or entirely yellow; anepisternal stripe broad or narrow; postsutural lateral yellow vittae very short and narrow or absent; scutellum with or without a fuscous apical band; abdomen pale with broad black lateral margins on tergites III–V and no medial vitta, with a narrow black medial vitta on tergites III–V and fuscous lateral or sublateral markings on tergites I–V or III–IV, or with only a narrow fuscous vitta on tergite V; males respond to cue lure. Species: *facialis* (Coquillett, 1910) (= *virgatus* Coquillett, 1910); *obscura* (Malloch, 1931); *mucronis* (Drew, 1971); *peneobscura* Drew & Romig, 2001.

*passiflorae* group: facial spots absent; scutum entirely black; postpronotal lobes black; anepisternal stripe broad, reaching anterior notopleural seta; postsutural lateral yellow vittae

absent; scutellum without a black apical band; abdomen black, pale submedially from posterior half of tergite III to apex of tergite V and with pale posterior areas on tergite II medially divided, or entirely pale except for a narrow black medial vitta on tergites IV–V; males respond to cue lure. Species: *minuta* (Drew, 1971); *passiflorae* (Froggatt, 1910).

*samoae* group: facial spots absent; scutum entirely black; postpronotal lobes black or mostly yellow; anepisternal stripe broad, reaching anterior notopleural seta; postsutural lateral yellow vittae absent; scutellum without a black apical band; abdomen with a black medial vitta on tergites III–V and broad black lateral margins on tergites II–V, leaving tergite II broadly pale medially; males show no response to known lures. Species: *grandistylus* Drew & Hancock, 1995; *samoae* Drew, 1989.

***diallagma* complex:** wing without transverse or preapical bands or a distinct infuscation over R-M crossvein; costal band narrow or broad and reaching or almost reaching vein  $R_{4+5}$  for much of its length; costal cells bc and c hyaline or with a pale fulvous to fuscous tint and not covered with microtrichia; scutum black with pale lateral areas; postsutural lateral yellow vittae present; scutellum with narrow basal and sometimes apical black bands; legs with fore and mid femora mostly fuscous to black, or all femora with subapical black spots; at least fore and hind tibiae fuscous; abdomen with a black T-shaped pattern and often black lateral margins on tergites III–V; pale posterior band on tergite II not divided medially [6 species: India, Sri Lanka, and Southern China to Indonesia and Papua New Guinea].

*diallagma* group: costal band either narrow and confluent with vein  $R_{2+3}$  or distinctly crossing vein  $R_{2+3}$  but not reaching vein  $R_{4+5}$ ; face fulvous with a pair of dark spots; fore, mid and at least apex of hind femora mostly fuscous to black; all tibiae fuscous to dark fuscous; males respond to methyl eugenol. Species: *diallagma* Drew, 1989; *rutengiae* Drew & Romig, 2013.

*laticosta* group: costal band either narrow and confluent with vein  $R_{2+3}$  or broad and almost reaching vein  $R_{4+5}$ ; face fuscous with a pair of large black spots; fore, mid and apex of hind femora mostly fuscous to black or with black subapical spots; mid tibiae at least partly fulvous or pale fuscous; males respond to cue lure. Species: *fastigata* Tsuruta & White, 2001 [in Tsuruta & White, 2001]; *laticosta* Drew, 1989; *nigrifacia* Zhang, Ji & Chen, 2011.

*nothaphoebe* group: costal band reaching vein  $R_{4+5}$  throughout its length; face fulvous with a pair of oval spots; fore and mid femora fuscous except fulvous basally, hind femora fulvous; all tibiae fuscous; males show no response to known lures. Species: *nothaphoebe* Drew & Romig, 2013.

***indecora* complex:** wing without transverse or preapical bands and with or without separated infuscations over DM-Cu and/or R-M crossveins; costal cells bc and c hyaline or with a pale fuscous or fulvous tint and not covered with microtrichia; scutum black; postsutural lateral yellow vittae

broad and elongate; scutellum with narrow basal black band; legs with all femora fulvous; abdomen with a broad black medial vitta on tergites II–V and black lateral margins on tergites III–V, not connected across base of tergite III [4 species: Thailand to Papua New Guinea].

*abdolonginqua* group: costal band very narrow, not crossing vein  $R_{2+3}$  except at apex; abdominal vitta very narrow and linear; males respond to methyl eugenol. Species: *abdolonginqua* (Drew, 1971).

*indecora* group: costal band very narrow or almost reaching vein  $R_{4+5}$ ; abdominal vitta broad; males respond to cue lure. Species: *indecora* (Drew, 1971); *pseudocucurbitae* White & Evenhuis, 1999; *vulgaris* (Drew, 1971).

**nigella complex:** wing without transverse or preapical bands or a distinct infuscation over R-M crossvein; costal band narrow or broad; costal cells bc and c hyaline to fuscous and not covered with microtrichia; scutum black or mostly black and with elongate lateral yellow vittae; scutellum with narrow basal black band; postpronotal lobes yellow; all femora fulvous; abdominal tergites I–II black with transverse pale bands posteriorly and III–V almost or entirely black; ceromata dark fuscous or black. [6 species: Bhutan to Australia and Solomon Islands].

*nigella* group: postsutural yellow vittae that narrow posteriorly; costal band narrow or broad; costal cells hyaline to pale fulvous or fuscous; hind tibiae fuscous; males attracted to methyl eugenol. Species: *batemani* Drew, 1989; *nigella* (Drew, 1968b).

*trivialis* group: lateral postsutural yellow vittae parallel-sided; costal band narrow or broad; costal cells hyaline or fuscous; hind tibiae fulvous or fuscous; attracted to cue lure. Species: *atrabifasciata* Drew & Romig, 2001; *illusioscutellaris* Drew & Romig, 2013; *trivialis* (Drew, 1971); *wallacei* Drew & Hancock, new species.

**bryoniae complex:** wing without transverse or preapical bands; costal band broad, not expanded into a distinct apical spot and uniformly dark, almost reaching, reaching or narrowly crossing vein  $R_{4+5}$  throughout its length, sometimes paler fuscous alongside vein  $R_{4+5}$ ; costal cells bc and c hyaline to fuscous and not covered with microtrichia; face fulvous to red-brown with a pair of dark spots; scutum largely or entirely black; postsutural lateral yellow vittae present; scutellum with basal black band narrow; femora pale with at most darker apical areas or a dark subapical spot on fore femora; abdominal tergites III–V with or without a black medial vitta or broad black lateral margins, sometimes mostly but not entirely black; pale posterior band on tergite II not divided medially [25 species: Vietnam to New Guinea, Australia, and Vanuatu].

*bryoniae* group: costal cells bc and c fulvous to fuscous; abdominal tergites III–V variable but not entirely black; all femora fulvous; ceromata red-brown to fuscous; males attracted to cue lure. Species: *beckerae* (Hardy, 1982);

*bryoniae* (Tryon, 1927); *costalis* (Shiraki, 1933); *curvosterna* Drew & Romig, 2013; *eurycosta* Drew & Romig, 2013; *expandosa* Drew & Romig, 2022; *geminosimulata* Leblanc & Doorenweerd, 2021 [in Leblanc et al., 2021]; *latissima* Drew, 1989; *limbifera* (Bezzi, 1919); *linduensis* Drew & Romig, 2013; *nanoarcuata* Drew & Romig, 2013; *neoritsemiai* Drew & Romig, 2013; *paracostalis* Drew & Romig, 2001; *paralatissima* Drew & Romig, 2013; *paralimbifera* Drew & Romig, 2013; *paramusae* Drew, 1989; *ritsemiai* (Weyenbergh, 1869); *simulata* (Malloch, 1939).

*froggatti* group: costal cells bc and c fulvous; abdominal tergites III–V with a black T-shaped pattern or medial vitta not connected to lateral bands or markings at base of tergite III; all femora fulvous or with a dark subapical spot on fore femur; ceromata red-brown; males attracted to methyl eugenol. Species: *atriscuta* Drew & Romig, 2001; *bruneiae* Drew & Romig, 2013; *froggatti* (Bezzi, 1919); *meraiensis* Drew & Romig, 2022; *mimulus* Drew, 1989.

*paraendiandrae* group: costal cells bc and c fulvous; abdominal tergites III–V with a black T-shaped pattern and broad fuscous lateral margins; all femora apically fuscous; at least fore and hind tibiae fuscous; ceromata red-brown or black; males attracted to methyl eugenol. Species: *paraendiandrae* Drew & Romig, 2022; *waidoriae* Drew & Romig, 2022.

**musae complex:** wing without transverse or preapical bands; costal band narrow, not reaching vein  $R_{4+5}$  except at apex; costal cells bc and c hyaline to fulvous and with microtrichia confined to anteroapical corner of cell c; scutum largely or entirely black, sometimes dark fuscous medially; fuscous with black dorsolateral and medial vittae or largely pale with variable darker markings; postsutural lateral yellow vittae present except in *B. allwoodi*; postpronotal lobes entirely yellow; scutellum with basal black band narrow and sometimes an apical dark patch; all femora pale or apically fuscous; hind tibiae pale or fuscous; abdomen orange-brown to red-brown with or without a black medial vitta and dark lateral margins; tergites III–V usually without a distinct dark T-shaped pattern, if distinct then basal band on tergite III not reaching lateral margins or lateral margins with at most a pale or narrow infuscation or band; pale posterior band on tergite II not divided medially [32 species: India and China to New Guinea and Australia].

*aberrans* group: supra-alar setae normally absent; males attracted to iso-eugenol or methyl eugenol. Species: *aberrans* (Hardy, 1951); *melanothoracica* Drew, 1989 (= *unirufa* Drew, 1989).

*brevistriata* group: supra-alar setae present; males attracted to cue lure. Species: *allwoodi* Drew, 1989; *brevistriata* (Drew, 1968b); *bubiae* Drew & Romig, 2022; *circamusae* Drew, 1989; *inconstans* Drew, 1989; *parabancroftii* Drew, Ma, Smith & Hughes, 2011; *ramuensis* Drew, Ma, Smith & Hughes, 2011; *robertsi* Drew, 1989; *rufivitta* Drew, Ma, Smith & Hughes, 2011; *tinomiscii* Drew, 1989; *uvariae* Drew, Ma, Smith & Hughes, 2011.

*elongata* group: scutum largely black with elongate lateral yellow vittae that narrow posteriorly; postpronotal lobes entirely yellow; abdomen elongate-oval with tergite I large and almost quadrate, tergites III–V with a dark T-shaped pattern and without dark lateral margins except on tergite III; costal band narrow; costal cells hyaline; all femora fulvous; all tibiae fuscous; males respond to cue lure. One species: *elongata* Drew & Romig, 2013.

*impunctata* group: facial spots absent; supra-alar setae present; scutum with lateral yellow vittae broadly triangular; abdomen with tergite III broadly black except laterally and medially and a narrow medial vitta on tergites IV–V and posteriorly on tergite III; males attracted to methyl eugenol. Species: *impunctata* (de Meijere, 1914).

*latifrons* group: scutum largely or entirely black with elongate lateral yellow vittae; postpronotal lobes entirely yellow; costal band narrow and expanded apically; costal cells hyaline; all femora fulvous or apically fuscous; abdominal tergites III–V fulvous to broadly fuscous and with or without a narrow medial vitta; female aculeus apically trilobed; males respond to latilure or no response known. Three species: *latifrons* (Hendel, 1915); *parvula* (Hendel, 1912); *prabhakari* Maneesh, Gupta & Hancock, 2023 [in Maneesh et al., 2023]. This group is distinct and provisionally included in the *musae* complex pending further study.

*musae* group: supra-alar setae present; males attracted to methyl eugenol (sometimes weakly) or lure unrecorded. Species: *balagawii* Drew, Ma, Smith & Hughes, 2011; *bancroftii* (Tryon, 1927); *contermina* Drew, 1989; *contigua* Drew, 1989; *finitima* Drew, 1989; *musae* (Tryon, 1927); *nigrescens* (Drew, 1968a); *peneallwoodi* Drew & Romig, 2013; *penebeckerae* Drew & Romig, 2013; *prolixa* Drew, 1989.

*nigrita* group: scutum fuscous with black medial and dorsocentral vittae or fulvous with red-brown vittae, in both cases connected posteriorly; postpronotal lobes entirely yellow; supra-alar setae absent; costal band narrow and not expanded apically; costal cells hyaline; all femora fulvous; abdominal tergites III–V fulvous with a black T-shaped pattern and anteroapical patches on tergites IV (rectangular) and V (triangular), the transverse basal band on tergite III not reaching lateral margins; female aculeus needle-shaped; response to lures uncertain or unknown. Two species: *nigrita* (Hardy, 1955); *pallescentis* (Hardy, 1955); transferred from *Javadacus* Hardy, 1983 by Hancock & Drew (2017a). This group is distinct and provisionally included in the *musae* complex pending further study.

*pictipennis* group: supra-alar setae present; costal band expanded into a distinct apical spot; costal cells hyaline; all femora fulvous with fuscous subapical spots; abdominal tergites III–V pale red-brown; ceromata red-brown; males attracted to methyl eugenol. Species: *pictipennis* Lin & Zeng, 2011 [in Lin et al., 2011].

*pruniae* group: supra-alar setae present; costal band narrow and not expanded apically; costal cells hyaline; fore, mid and apical third of hind femora red-brown; abdominal tergites III–V orange-brown with narrow fuscous anteroapical bands on tergite III; ceromata fuscous; response to lures unknown. Species: *pruniae* Drew & Romig, 2013.

***dorsalis* complex:** wing without transverse or preapical bands or a distinct infuscation over R-M crossvein; costal band distinct and narrow, not or at most faintly reaching vein R<sub>4+5</sub> throughout its length and often expanded apically; costal cells bc and c hyaline or with a very pale fulvous tint and not covered with microtrichia; face fulvous to red-brown with a pair of dark spots; scutum largely or entirely black, with a pair or narrow submedial rufous vittae or with a black lanceolate pattern in at least most specimens; postsutural lateral yellow vittae present; prescutellar medial yellow patch absent; legs with femora entirely pale or with dark subapical spots or apical markings; scutellum with basal black band narrow or moderately broad and concave; hind tibiae fuscous; abdomen with a black T-shaped pattern and often black lateral margins on tergites III–V; pale posterior band on tergite II not divided medially [83 species: Pakistan and India to Australia and Solomon Islands; invasive elsewhere]. For a detailed review and discussion see Drew & Hancock (1994, 2022).

*arecae* group: scutum with narrow, parallel-sided postsutural lateral yellow vittae less than 0.15 mm in centre; males show no response to known lures. Species: *arecae* (Hardy & Adachi, 1954).

*caryeae* group: species with narrow, parallel-sided postsutural lateral yellow vittae less than 0.15 mm in centre, sometimes broader in *B. invadens* and narrower posteriorly in *B. caryeae*; femora entirely pale or with dark apical markings; males respond to methyl eugenol. Species: *amarambalensis* Drew, 2002 [in Drew & Raghu, 2002]; *caryeae* (Kapoor, 1971); *invadens* Drew, Tsuruta & White, 2005; *kandiensis* Drew & Hancock, 1994; *neoarecae* Drew, 2002 [in Drew & Raghu, 2002]; *paraarecae* Drew & Romig, 2013; *paraverbascifoliae* Drew, 2002 [in Drew & Raghu, 2002]; *verbascifoliae* Drew & Hancock, 1994.

*dorsalis* group: species with broad, parallel-sided postsutural lateral yellow vittae more than 0.15 mm in centre, sometimes narrowing posteriorly and narrower in posterior half in *B. cacuminata*; femora entirely pale or with dark apical markings; males respond to methyl eugenol or response unknown. Species: *atrifemur* Drew & Hancock, 1994; *binhduongiae* Drew & Romig, 2013; *bivittata* Lin & Wang, 2005 [in Lin et al., 2005]; *cacuminata* (Hering, 1941a); *carambolae* Drew & Hancock, 1994; *collita* Drew & Hancock, 1994; *dapsiles* Drew, 1989; *dorsalis* (Hendel, 1912); *endiandrae* (Perkins & May, 1949); *floresiae* Drew & Hancock, 1994; *indonesiae* Drew & Hancock, 1994; *infulata* Drew & Hancock, 1994; *irvingiae* Drew & Hancock, 1994 [lure unrecorded]; *kanchanaburi* Drew & Hancock,

1994; *latilineola* Drew & Hancock, 1994; *minuscula* Drew & Hancock, 1994; *muri* (Hardy & Adachi, 1954) [lure unrecorded]; *occipitalis* (Bezzi, 1919); *ochroma* Drew & Romig, 2013; *opiliae* (Drew & Hardy, 1981) [in Drew et al., 1981]; *papayae* Drew & Hancock, 1994; *parafraggatti* Drew & Romig, 2002; *raiensis* Drew & Hancock, 1994; *ranganathi* Drew & Romig, 2013; *sulawesiae* Drew & Hancock, 1994; *unimacula* Drew & Hancock, 1994.

*melastomatos* group: species with relatively long and narrow lateral yellow vittae that are not broader anteriorly than medially and taper in posterior half and extensively dark abdomens with transversely oval ceromata; at least mid and hind femora entirely pale; males respond to cue lure. Species: *melastomatos* Drew & Hancock, 1994; *osbeckiae* Drew & Hancock, 1994; both breed in the flowers of Melastomataceae.

*pedestris* group: species with subparallel to strongly tapering postsutural lateral yellow vittae; males respond to cue lure or zingerone or response unknown. Species: *aemula* Drew, 1989; *affinidorsalis* (Hardy, 1982); *bimaculata* Drew & Hancock, 1994; *bitungiae* Drew & Romig, 2013; *cibodasae* Drew & Hancock, 1994; *cognata* (Hardy & Adachi, 1954) [lure unrecorded]; *consectorata* Drew, 1989; *dongnaiiae* Drew & Romig, 2013; *dorsaloides* (Hardy & Adachi, 1954); *ellenriederae* Korneyev, Leblanc, Hauser, General & Gaimari, 2024; *fernandoi* Tsuruta & White, 2001; *flavoscutellata* Lin & Wang, 2005; *flavosterna* Drew & Romig, 2013; *fuliginus* (Drew & Hancock, 1981) [in Drew et al., 1981]; *fulvifemur* Drew & Hancock, 1994; *fuscitibia* Drew & Hancock, 1994; *gombokensis* Drew & Hancock, 1994; *hantanae* Tsuruta & White, 2001; *holtmanni* (Hardy, 1974); *involuta* (Hardy, 1982); *kalimantanae* Drew & Romig, 2013; *kinabalu* Drew & Hancock, 1994; *laithieuiiae* Drew & Romig, 2013; *lateritaenia* Drew & Hancock, 1994; *lombokensis* Drew & Hancock, 1994; *makilingensis* Drew & Hancock, 1994; *malaysiensis* Drew & Hancock, 1994; *merapiensis* Drew & Hancock, 1994; *neocognata* Drew & Hancock, 1994; *pedestris* (Bezzi, 1913); *penecognata* Drew & Hancock, 1994; *profunda* Tsuruta & White, 2001; *quasiinfulata* Drew & Romig, 2013; *sapaensis* Drew & Romig, 2013; *sembaliensis* Drew & Hancock, 1994; *sumbawaensis* Drew & Hancock, 1994; *syzygii* White & Tsuruta, 2001 [in Tsuruta & White, 2001]; *usitata* Drew & Hancock, 1994; *vishnu* Drew & Hancock, 1994; *youngi* Korneyev, Leblanc, Hauser, General & Gaimari, 2024. Yong et al. (2024) regarded *B. cheni* Zhang, Ji & Chen, 2012 as a species separate from *B. lombokensis* (synonymised by Drew & Romig, 2013) but the name is a homonym of *B. cheni* Chao, 1987, a synonym of *B. tsuneonis* (Miyake, 1919) and therefore unavailable.

*propinqua* group: species with long, subparallel lateral yellow vittae and aculeus with apex trilobed; males respond to cue lure or response unknown. Species: *neopropinqua* Drew & Hancock, 1994; *propinqua* (Hardy & Adachi, 1954); *quasipropinqua* Drew & Hancock, 1994 [lure unrecorded].

*pyrifoliae* group: species with relatively long and narrow lateral yellow vittae that are not broader anteriorly than

medially and taper in posterior half, extensively dark abdomens often with a narrow transverse basal band on tergite IV and with fuscous, broadly rounded ceromata; fore femora with a subapical black spot, mid and hind femora apically black (often narrowly); males respond to cue lure. Species: *citima* (Hardy, 1973); *pyrifoliae* Drew & Hancock, 1994; *thailandica* Drew & Hancock, 1994.

***furvescens* complex:** scutum largely black with or without a broad dark brown to fuscous medial vitta and with or without lateral yellow vittae; postpronotal lobes entirely fuscous; costal cells hyaline, fulvous or fuscous and with microtrichia confined to anteroapical corner or apical half of cell c; costal band narrow or broad; abdominal tergites III–V with or without a T-shaped pattern or medial vitta. [5 species: Ambon and Papua New Guinea].

*furvescens* group: scutum with lateral yellow vittae elongate; postpronotal lobes fuscous; costal cells hyaline, fulvous or fuscous; costal band reaching or nearly reaching vein R<sub>4+5</sub>; all femora fulvous or mid and hind femora pale fuscous over apical third; hind tibiae fuscous; abdomen mostly red-brown to fuscous without a dark medial vitta or fuscous to black with a very narrow black medial vitta on tergites IV–V; ceromata red-brown or fuscous; males respond to cue lure. Species: *furvescens* Drew, 1989; *kokodiae* Drew & Romig, 2022; *saramandiae* Drew & Romig, 2022.

*opacovitta* group: scutum with lateral yellow vittae very short and narrow or absent; postpronotal lobes fuscous; costal band broad but paler posteriorly; costal cells hyaline to very pale fulvous; all femora red-brown or fore femora with apical dark spot, mid femora fuscous and hind femora fuscous apically; hind tibiae fulvous or red-brown; abdominal tergites III–V entirely orange-brown or dark red-brown with a black T-shaped pattern; males respond to methyl eugenol or response unknown. Species: *nigroscutata* White & Evenhuis, 1999; *opacovitta* Drew & Romig, 2013.

***quadrata* complex:** wing without transverse or preapical bands; costal band narrow or broad and reaching or almost reaching vein R<sub>4+5</sub>, mostly or entirely yellow in *dispar* group; costal cells bc and c hyaline to fuscous and with confined to anteroapical corner of cell c except in *B. kyrdemkulai* and some *dispar* group species; scutum largely or entirely fulvous to pale fuscous, often with variable dark markings, mostly or entirely black in *B. absoluta* and *B. pseudobeckerae*; with a diamond-shaped prescutellar yellow patch in *B. adamantea*; postsutural lateral yellow vittae present except in *B. waaiaae*; scutellum with basal black or red-brown band narrow or broadly oval except mostly orange-brown in *B. quasienochra*; all femora fulvous except apically fuscous in *B. apicofuscans*, *B. pseudobeckerae* and *B. sari* or with elongate subapical spots in *B. andamanensis* and *B. selenophora*; hind tibiae pale or fuscous; abdomen fulvous to fuscous with or without a distinct dark T-shaped pattern and dark lateral margins [86 species: Bhutan, India, and Sri Lanka to New Guinea, Australia, and Solomon Islands]. This complex is almost certainly polyphyletic.

*abdofuscata* group: abdomen with at least tergites III–V entirely fuscous; scutum red-brown with elongate lateral yellow vittae; costal band narrow and linear; all femora pale; males attracted to cure lure or response unknown. Species: *abdofuscata* (Drew, 1971); *abdonigella* (Drew, 1971).

*adamantea* group: scutum mostly black with narrow submedial rufous vittae, elongate lateral yellow vittae and a diamond-shaped prescutellar yellow patch; costal band narrow; costal cells hyaline; all femora pale; all tibiae fuscous; abdominal tergites III–V with a broad black T-shaped pattern and broad lateral margins on tergites III–IV; ceromata dark fuscous; males respond to zingerone. Species: *adamantea* Leblanc & Dooreenweerd, 2018 [in Leblanc et al., 2018].

*andamanensis* group: scutum dark red-brown with irregular black patches and elongate lateral yellow vittae; postpronotal lobes entirely yellow; abdominal tergite III with a black posterior band interrupted medially and a narrow black medial vitta on tergites III–V; prescutellar acrostichal setae present or absent; costal cells with a fulvous tint; costal band broad and expanded into a large apical spot; all femora with subapical fuscous spots; males respond to cure lure. One species: *andamanensis* (Kapoor, 1971). This species is distinct and provisionally included in the *quadrata* complex pending further study.

*apicofuscans* group: abdominal tergites III–V with a dark T-shaped pattern; all femora apically red-brown with an elongate fuscous subapical streak on at least fore femur; scutum red-brown with or without dull black markings and with lateral yellow vittae elongate and very narrow; postpronotal lobes red-brown anterodorsally; costal band broad; costal cells fuscous; males attracted to methyl eugenol. Species: *apicofuscans* White & Tsuruta, 2001 [in Tsuruta & White, 2001].

*barringtoniae* group: abdominal tergites III–V fulvous to orange-brown without a distinct dark T-shaped pattern but often with darker lateral margins and sometimes with a narrow or indistinct medial vitta on tergites III–IV or IV–V; costal band narrow or broad; postpronotal lobes entirely yellow; males attracted to methyl eugenol, isoeugenol or response unknown. Species: *affinibancroftii* Drew & Romig, 2013; *aithogaster* Drew, 1989; *barringtoniae* (Tryon, 1927); *centraliae* Drew & Romig, 2022; *halfordiae* (Tryon, 1927); *jaceobancroftii* Drew & Romig, 2013; *keravatae* Drew & Romig, 2022; *kraussi* (Hardy, 1951); *nauliae* Drew & Romig, 2001; *neoaeroginosa* Drew & Romig, 2022; *parabarringtoniae* Drew & Hancock, 1999 [in Drew et al., 1999]; *robiginosa* (May, 1957); *waaiae* Drew & Romig, 2022.

*bidentata* group: scutum red-brown with elongate lateral yellow vittae; supra-alar and prescutellar acrostichal setae present or absent; costal cells pale fuscous; all femora fulvous; abdomen oval and mostly orange-brown with a narrow black band at base of tergite III and a narrow medial vitta on tergites IV and V; female aculeus with 3 pairs of preapical and subapical lobes; males attracted to methyl

eugenol or isoeugenol. Species: *bidentata* (May, 1962b); *decurtans* (May, 1965); both breed in the mangrove tree *Carallia brachiata* (Rhizophoraceae) (Hancock et al., 2000).

*commensurata* group: abdominal tergites III–V with a dark T-shaped pattern or with medial vitta narrowly separated from broad lateral margins; all femora fulvous; postpronotal lobes entirely yellow; costal band narrow; costal cells hyaline to pale fuscous; males attracted to methyl eugenol. Species: *blairiae* Drew & Romig, 2013; *commensurata* Drew & Romig, 2013; *ettinabhujia* Abhishek & David, 2024; *kyrdemkulai* Abhishek & David, 2024; *pseudoversicolor* Drew, 2002; *suliae* Drew & Romig, 2013.

*congener* group: scutum black with lateral yellow vittae narrowing posteriorly; postpronotal lobes entirely yellow; scutellum with a broad basal black band; wing with costal cells fuscous; costal band narrow and a pale fuscous tint over most of discal area; fore femora apically pale fuscous, mid and hind femora fulvous; abdominal tergite II broadly pale posteriorly and tergites III–V with a black T-shaped pattern and black lateral margins, broadest on tergite III; males respond to cue lure. One species: *congener* Drew, 1989. This species is distinct and provisionally included in the *quadrata* complex pending further study.

*digressa* group: scutum orange-brown with red-brown borders to elongate lateral yellow vittae; postpronotal lobes orange-brown anterodorsally; lateral yellow vittae extend across mesonotal suture anteriorly as small spots; costal band narrow and not expanded apically; supra-alar and prescutellar acrostichal setae absent; costal cells hyaline; fore and mid femora with subapical fuscous streaks and hind femora red-brown on apical half; abdominal tergites III–V fulvous with a narrow black T-shaped pattern; female aculeus apically bilobed; males attracted to cue lure. Species: *digressa* Radhakrishnan, 1999. The aculeus was illustrated by David & Ramani (2019).

*dispar* group: scutum with broad dorsolateral black vittae, large irregular black patches or mostly black; lateral yellow vittae broad, elongate and often extending across mesonotal suture anteriorly as semicircular spots (not in *absoluta* and *flavipennis*); postpronotal lobes entirely yellow; prescutellar acrostichal setae present or absent; costal band broad or narrow and yellow with or without a broad fuscous apical patch; anal stripe yellow; costal cells pale yellow and with microtrichia covering half or all of cell c or reduced to anteroapical corner; all femora and tibiae fulvous; abdominal pattern variable; males respond to cue lure or zingerone or response unknown. Species: *absoluta* (Walker, 1861); *dispar* (Hardy, 1982); *flavipennis* (Hardy, 1982); *niogreta* Dooreenweerd, 2020 [in Dooreenweerd et al., 2020]; *trifasciata* (Hardy, 1982); *dispar* and *niogreta* are very similar and possibly synonymous. This group is distinct and provisionally included in the *quadrata* complex pending further study.

*jarvisi* group: abdominal tergites III–V with a dark T-shaped pattern and without dark lateral margins; supra-alar setae

absent; postpronotal lobes entirely yellow and connected to notopleural calli by a lateral yellow vitta; males attracted to zingerone. Species: *jarvisi* (Tryon, 1927).

*mayi* group: abdominal tergites III–V with a dark T-shaped pattern and with or without dark lateral margins; postpronotal lobes entirely yellow; costal cells hyaline; all femora fulvous; males attracted to methyl eugenol. Species: *mayi* (Hardy, 1951); *pallida* (Perkins & May, 1949); *tenuifascia* (May, 1965).

*moluccensis* group: scutum red-brown with fuscous markings and elongate lateral yellow vittae; costal band narrow and not expanded apically; costal cells fulvous; all femora fulvous; abdominal tergites III–V fulvous with a narrow black band at base of tergite III and a narrow medial vitta on tergites III–V or V; female aculeus apically trilobed or with 2 pairs of subapical lobes; males attracted to cue lure and zingerone. Species: *moluccensis* (Perkins, 1939); *rutila* (Hering, 1941a).

*murrayi* group: abdominal tergites III–V with a dark T-shaped pattern and dark lateral margins; prescutellar acrostichal setae absent; postpronotal lobes entirely yellow; costal cells fulvous; males attracted to methyl isoeugenol. Species: *murrayi* (Perkins, 1939).

*obfusca* group: postpronotal lobes red-brown anteriorly; costal band broad or narrow; fore and mid femora without elongate fuscous spots; males attracted to cue lure. Species: *bogiae* Drew & Romig, 2022; *obfusca* Drew, 1989; *ohuiae* Drew & Romig, 2022; *quasi-nochra* Leblanc & Doorenweerd, 2021 [in Leblanc et al., 2021]; *rutilana* Drew & Romig, 2022.

*obscurivitta* group: abdominal tergites III–IV with a dark T-shaped pattern; postpronotal lobes entirely fuscous; scutum with lateral yellow vittae very short and narrow; males attracted to cue lure. Species: *obscurivitta* Drew & Romig, 2013.

*ochromarginis* group: abdominal tergites III–V orange-brown with or without a dark medial vitta on tergite V; prescutellar acrostichal setae present or absent; postpronotal lobes entirely yellow and connected to notopleural calli by a lateral yellow vitta; males attracted to methyl eugenol or isoeugenol. Species: *ochromarginis* (Drew, 1971); *yorkensis* Drew & Hancock, 1999 [in Drew et al., 1999].

*quadrata* group: abdominal tergites III–V without a dark T-shaped pattern but dark lateral margins and/or medial vitta often present; postpronotal lobes entirely yellow; males attracted to cue lure. Species: *aeroginosa* (Drew & Hancock, 1981) [in Drew et al., 1981]; *antigone* (Drew & Hancock, 1981) [in Drew et al., 1981]; *aurantiaca* (Drew & Hancock, 1981) [in Drew et al., 1981]; *breviaculeus* (Hardy, 1951); *dyscrita* (Drew, 1971); *fagraea* (Tryon, 1927); *kauiae* Drew & Romig, 2022; *megaspilus* (Hardy, 1982); *ochroventer* Drew & Romig, 2013; *patula* Drew & Romig, 2013; *peninsularis* (Drew & Hancock, 1981) [in Drew et al., 1981]; *quadrata*

(May, 1962b); *russeola* (Drew & Hancock, 1981) [in Drew et al., 1981].

*selenophora* group: scutum with short lateral yellow vittae extending behind supra-alar setae and narrowing posteriorly; postpronotal lobes yellow except red-brown or dark fuscous anterodorsally; scutellum with a narrow or broad black basal band; costal band narrow; costal cells hyaline; fore and mid femora with elongate fuscous spots or all femora fuscous in apical third to half; all tibiae fuscous; abdominal tergites III–V orange-brown with a fuscous anterior band on tergite III entire or interrupted medially and tergite V with a very narrow medial vitta; ceromata black; males respond to cue lure. Species: *pseudobeckerae* Drew & Romig, 2013; *selenophora* Tsuruta & White, 2001.

*silvicola* group: abdominal tergites III–V with a dark T-shaped pattern and broad or narrow dark lateral margins, or tergites III–IV mostly dark with a medial vitta on tergites IV–V; postpronotal lobes entirely yellow; males attracted to cue lure or response unknown (*B. curtivitta*). Species: *abscondita* (Drew & Hancock, 1981) [in Drew et al., 1981]; *abundans* Drew, 1989; *bhutaniae* Drew & Romig, 2013; *bisianumu* Drew & Romig, 2022; *brunneola* White & Tsuruta, 2001 [in Tsuruta & White, 2001]; *bukaensis* Drew & Romig, 2022; *ceylanica* Tsuruta & White, 2001; *cinnamea* Drew, 1989; *curtivitta* Drew & Romig, 2013; *erubescens* (Drew & Hancock, 1981) [in Drew et al., 1981]; *furfurosa* Drew, 1989; *kohkongiae* Leblanc, 2015 [in Leblanc et al., 2015a]; *mamaliae* Drew & Romig, 2022; *neoabdonigella* Drew & Romig, 2022; *paraosbeckiae* Drew, 2002; *perkinsi* (Drew & Hancock, 1981) [in Drew et al., 1981]; *quasisilvicola* Drew, 1989; *rubigina* (Wang & Zhao, 1989); *rufescens* (May, 1967); *rufofuscula* (Drew & Hancock, 1981) [in Drew et al., 1981]; *sari* Drew & Romig, 2022; *silvicola* (May, 1962a); *turneri* Drew, 1989.

**zonata complex:** scutum red-brown or black; wing with costal band narrow and linear or with an isolated apical spot; costal cells bc and c hyaline and with microtrichia absent or reduced to a narrow anteromedial stripe in or extreme anteroapical corner of cell c; anal stripe narrow and pale, confined to or just overlapping cell bcu; femora fulvous or with pale fuscous apical and subapical markings; abdominal tergites III–V black or with a black T-shaped pattern. [10 species: Indian subcontinent to Japan and Peninsular Malaysia, invasive elsewhere].

*furcata* group: scutum black with lateral yellow vittae present; costal band very narrow and linear; scutellum without a fuscous apical patch; femora fuscous on apical quarter (hind) or three-quarters (fore and mid); all tibiae fuscous; abdominal tergites III–V with a black T-shaped pattern and very broad lateral fuscous bands; ceromata black; aculeus apically bifid; response to lures unknown. Species: *furcata* David & Hancock, 2017 [in David et al., 2017].

*venefica* group: scutum with short lateral yellow vittae extending just behind supra-alar setae; postpronotal lobes

yellow with anterior black or fuscous area; scutellum with a broad black apical band or patch; abdominal tergites III–V with a black T-shaped pattern and broad lateral margins; costal band narrow and either fulvous in cell  $r_1$  or with an isolated apical spot; costal cells hyaline with microtrichia reduced to a narrow anteromedial stripe in cell c; anal stripe narrow; all femora fulvous or mid and hind femora narrowly black at apex; hind tibiae fuscous; response to male lures unknown. Species: *hyalina* (Shiraki, 1933); *venefica* (Hering, 1938).

*versicolor* group: scutum red-brown with fuscous markings; costal band very narrow and linear; scutellum with or without a fuscous apical patch; femora fulvous or with pale fuscous subapical spots on fore and mid femora and around extreme apex of hind femora; hind tibiae fuscous or all tibiae fulvous with fuscous bases; abdominal tergites III–V with a black T-shaped pattern and very broad lateral fuscous bands; ceromata dark red-brown to black; aculeus needle-like; males respond to methyl eugenol. Species: *aethriobasis* (Hardy, 1973); *versicolor* (Bezzi, 1916).

*zonata* group: scutum red-brown with pale fuscous markings or black; costal band interrupted in cell  $r_{2+3}$  and with an isolated apical spot; scutellum without a fuscous apical patch; femora fulvous; abdominal tergites III–V black, mostly black with a black medial vitta on tergites IV–V, or pale with a narrow T-shaped pattern often reduced to anterolateral streaks on tergite III and medially on tergites IV–V or V; ceromata pale or dark red-brown to black; aculeus needle-like or apically trilobed; males respond to methyl eugenol. Species: *affinis* (Hardy, 1954); *correcta* (Bezzi, 1916); *penecorrecta* Drew, 2002; *tuberculata* (Bezzi, 1916); *zonata* (Saunders, 1842).

## LIST OF SPECIES

The 439 species, their complex and group placements, male lures and distributions are listed in Table 1. Invasive, vagrant, and presumed misidentified records are excluded from the distributions. Invasive populations within the Asia-Pacific Region (i.e., excluding those noted in the Introduction) include *B. carambolae* in Bangladesh, *B. tryoni* in New Caledonia, French Polynesia and Pitcairn Island [eradicated from Easter Island], *B. dorsalis* in Tahiti, *B. latifrons* in Timor-Leste, and *B. papayae* in Palau and New Guinea (Drew, 1989; Bellis et al., 2017; Drew & Romig, 2022; Hoskins et al., 2023). Both *B. latifrons* and *B. parvula* were recorded as invasive in Japan's Ryukyu Islands by Hisaoka et al. (2024): *B. parvula* (= 'Haplotype A') on Yonaguni Island and *B. latifrons* (= 'Haplotype B') throughout. Vagrants in Australia's Torres Strait islands were noted by Huxham & Hancock (2002) and Hancock (2013). Presumed misidentifications include the Sri Lankan *B. hantanae* from Sulawesi (Doorenweerd et al., 2020). India's Andaman Islands and Australia's Christmas Island are included in Zone B and the Mariana Islands in Zone D. Most species can be identified by illustrations and keys in Drew (1989), Drew & Romig (2001, 2013, 2016, 2022), Leblanc (2022),

Korneyev et al. (2024) and Abhishek et al. (2024). Note, however, that illustrations of '*B. dorsalis*' in Korneyev et al. (2024) are of *B. invadens*.

## BIOGEOGRAPHY

The biogeography of the Dacini was discussed in detail by Drew & Hancock (1999) and Drew (2004) and, in Papua New Guinea, by Clarke et al. (2004). The endemic habitat of genus *Bactrocera* is the tropical and subtropical rainforest ecosystem recognised as the Indomalayan rainforest flora. Because there is a close association between fruit fly species and their host plants, whereby their reproductive biology is dependent upon factors within the host plant environment, Drew & Hancock (1999) proposed that the fruit fly species and their host plants continued to co-evolve over the Tertiary and Quaternary Periods. Within subgenus *Bactrocera*, there have been high levels of speciation in the Asian-Pacific Region (Table 2). The largest number of known species is in Papua New Guinea and the Melanesian Archipelago (193), followed by Southeast Asia (102), Wallacea (84), Australia (60), the Indian subcontinent (49), and the South Pacific (24). This pattern matches the distribution of Indomalayan rainforest plant species, which is at a peak in Papua New Guinea and Southeast Asia and then markedly declines to Australia and the South Pacific.

The two largest complexes within subgenus *Bactrocera* are the *dorsalis* complex (83 species) and the *quadrata* complex (86 species) (Tables 3 and 4). The distribution of species in these complexes demonstrates a concentration of the *dorsalis*-type melanic morphological characters in Southeast Asia and the *quadrata*-type pale characters in Papua New Guinea and the Pacific region. These character states overlap in Wallacea, which is a zone of integration between the two major faunas of Southeast Asia and the Pacific region.

Wallacea is now recognised as a transitional zone with shared species from West and East as well as having experienced considerable independent speciation. The *dorsalis* complex has undergone prolific speciation in the continental area of Southeast Asia, with fewer species originating in the Philippines, Indonesia, and Borneo. It is important to recognise that the Philippines and Borneo possess several *Bactrocera* species in common that are not shared with other areas of Southeast Asia. This has probably resulted from these two land areas remaining connected for a longer period after isolation from the rest of Southeast Asia. A practical consequence of this has been the inability to separate, on morphological characters, the *Bactrocera papayae* populations that currently occur in the Philippines, Borneo, and Java. Minor differences between Philippine and other populations of *B. papayae* were later judged insufficient to support species status (Drew & Romig, 2013) and thus *B. philippinensis* Drew & Hancock, 1994 is presently regarded as a synonym of *B. papayae*. Extensive speciation in the *quadrata* complex has occurred in Papua New Guinea and northeastern Australia. These two land areas also show some species indicative of periods of both isolation and unification.



Table 1. List of species in subgenus *Bactrocera*, with their complex and group placements, known lures and biogeographic zones in the Indo-Australian region (A = Indian Subcontinent; B = Southeast Asia; C = Wallacea; D = New Guinea & Solomon Islands; E = Australia; F = South Pacific) [Zones after Hancock & Drew (2015)].

Species	Complex	Group	Lure	Zone
<i>abdofuscata</i>	<i>quadrata</i>	<i>abdofuscata</i>	Unknown	D
<i>abdolonginqua</i>	<i>indecora</i>	<i>abdolonginqua</i>	ME	D
<i>abdonigella</i>	<i>quadrata</i>	<i>abdofuscata</i>	Cue	CD
<i>aberrans</i>	<i>musae</i>	<i>aberrans</i>	Isoeugenol	E
<i>abscondita</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	DE
<i>absidata</i>	<i>alyxiae</i>	<i>recurrens</i>	Unknown	D
<i>absoluta</i>	<i>quadrata</i>	<i>dispar</i>	Unknown	C
<i>abundans</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>adamantea</i>	<i>quadrata</i>	<i>adamantea</i>	Zingerone	B
<i>aemula</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	CD
<i>aeroginosa</i>	<i>quadrata</i>	<i>quadrata</i>	Cue, zingerone	DE
<i>aethriobasis</i>	<i>zonata</i>	<i>versicolor</i>	ME	AB
<i>affinibancroftii</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	C
<i>affinidorsalis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>affinis</i>	<i>zonata</i>	<i>zonata</i>	ME	A
<i>aithogaster</i>	<i>quadrata</i>	<i>barringtoniae</i>	Unknown	D
<i>albistrigata</i>	<i>frauenfeldi</i>	<i>frauenfeldi</i>	Cue	BC
<i>allostincta</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>allwoodi</i>	<i>musae</i>	<i>brevistriata</i>	Cue	E
<i>alyxiae</i>	<i>alyxiae</i>	<i>alyxiae</i>	Cue, zingerone	DE
<i>amarambalensis</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	A
<i>ampla</i>	<i>longicornis</i>	<i>ampla</i>	Cue	D
<i>amplexiseta</i>	<i>longicornis</i>	<i>amplexiseta</i>	ME	E
<i>andamanensis</i>	<i>quadrata</i>	<i>andamanensis</i>	Cue	B
<i>anfracta</i>	<i>alyxiae</i>	<i>recurrens</i>	Cue	D
<i>angustifasciata</i>	<i>distincta</i>	<i>angustifasciata</i>	Cue	D
<i>anomala</i>	<i>distincta</i>	<i>distincta</i>	Cue	F
<i>anthracina</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	D
<i>antigone</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	DE
<i>apicofuscans</i>	<i>quadrata</i>	<i>apicofuscans</i>	ME	A
<i>apiconigroscutellata</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	A
<i>apicopicta</i>	<i>tryoni</i>	<i>assita</i>	Cue	C
<i>aquila</i>	<i>nigrotibialis</i>	<i>aquila</i>	Cue	D
<i>aquilonis</i>	<i>tryoni</i>	<i>tryoni</i>	Cue	E
<i>arecae</i>	<i>dorsalis</i>	<i>arecae</i>	None	B
<i>assita</i>	<i>tryoni</i>	<i>assita</i>	Cue	D
<i>aterrima</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	D
<i>atra</i>	<i>atramentata</i>	<i>atra</i>	Cue	F
<i>atrabifasciata</i>	<i>nigella</i>	<i>trivialis</i>	Cue	D
<i>atramentata</i>	<i>atramentata</i>	<i>atramentata</i>	Cue, zingerone	D
<i>atrifemur</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>atriliniellata</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>atriscuta</i>	<i>bryoniae</i>	<i>froggatti</i>	ME	D
<i>aurantiaca</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	DE
<i>avittata</i>	<i>distincta</i>	<i>distincta</i>	Cue	C
<i>balagawii</i>	<i>musae</i>	<i>musae</i>	ME	D
<i>bancroftii</i>	<i>musae</i>	<i>musae</i>	ME weak	CE
<i>barringtoniae</i>	<i>quadrata</i>	<i>barringtoniae</i>	Isoeugenol	E
<i>batemani</i>	<i>nigella</i>	<i>nigella</i>	ME	E

Hancock & Drew: Review of subgenus *Bactrocera*

Species	Complex	Group	Lure	Zone
<i>beckerae</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>bellisi</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	C
<i>bhutanicae</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	AB
<i>biarcuata</i>	<i>longicornis</i>	<i>biarcuata</i>	ME	D
<i>bidentata</i>	<i>quadrata</i>	<i>bidentata</i>	Isoeugenol	E
<i>bifasciata</i>	<i>alyxiae</i>	<i>umbrosa</i>	Cue	C
<i>bimaculata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>binhduongiae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>bisianumu</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>bitungiae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	C
<i>bivittata</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>blairiae</i>	<i>quadrata</i>	<i>commensurata</i>	ME	B
<i>bogiae</i>	<i>quadrata</i>	<i>obfuscata</i>	Cue	D
<i>breviaculeus</i>	<i>quadrata</i>	<i>quadrata</i>	Cue, zingerone	DE
<i>brevistriata</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>bruneiae</i>	<i>bryoniae</i>	<i>froggatti</i>	ME	B
<i>brunnea</i>	<i>atramentata</i>	<i>strigata</i>	None	E
<i>brunneola</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	A
<i>bryoniae</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue, zingerone	DE
<i>bubiae</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>bukaensis</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>buloloensis</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>caccabata</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue, zingerone	D
<i>cacuminata</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	E
<i>caledoniensis</i>	<i>frauenfeldi</i>	<i>obliqua</i>	Cue	F
<i>caliginosa</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>carambolae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>carbonaria</i>	<i>atramentata</i>	<i>atra</i>	Cue	D
<i>careofascia</i>	<i>tryoni</i>	<i>assita</i>	Cue	C
<i>caryeae</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	A
<i>centraliae</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	D
<i>ceylanica</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	A
<i>cibodasae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>cinnamea</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>circamusae</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>citima</i>	<i>dorsalis</i>	<i>pyrifoliae</i>	Cue	B
<i>cognata</i>	<i>dorsalis</i>	<i>pedestris</i>	Unknown	B
<i>collita</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>commensurata</i>	<i>quadrata</i>	<i>commensurata</i>	ME	BC
<i>commina</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>confluens</i>	<i>longicornis</i>	<i>curvifer</i>	ME	D
<i>congener</i>	<i>quadrata</i>	<i>congener</i>	Cue	D
<i>consectorata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	D
<i>contermina</i>	<i>musae</i>	<i>musae</i>	ME	D
<i>contigua</i>	<i>musae</i>	<i>musae</i>	ME	CD
<i>correcta</i>	<i>zonata</i>	<i>zonata</i>	ME	AB
<i>costalis</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	B
<i>curreyi</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>curtivitta</i>	<i>quadrata</i>	<i>silvicola</i>	Unknown	B
<i>curvifer</i>	<i>longicornis</i>	<i>curvifer</i>	ME	CD
<i>curvipennis</i>	<i>tryoni</i>	<i>curvipennis</i>	Isoeugenol, cue	F
<i>curvosterna</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C

Species	Complex	Group	Lure	Zone
<i>dapsiles</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	D
<i>daruensis</i>	<i>tryoni</i>	<i>notatagena</i>	ME accidental?	DE
<i>decumana</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>decurtans</i>	<i>quadrata</i>	<i>bidentata</i>	ME	DE
<i>denigrata</i>	<i>longicornis</i>	<i>longicornis</i>	Cue	D
<i>diallagma</i>	<i>diallagma</i>	<i>diallagma</i>	ME	D
<i>digressa</i>	<i>quadrata</i>	<i>digressa</i>	Cue, zingerone	A
<i>diospyri</i>	<i>nigrotibialis</i>	<i>diospyri</i>	ME weak?	E
<i>dispar</i>	<i>quadrata</i>	<i>dispar</i>	Unknown	C
<i>distincta</i>	<i>distincta</i>	<i>distincta</i>	Cue	F
<i>divenderi</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	A
<i>dongnaiae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>dorsalis</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>dorsaloides</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>dyscrita</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	D
<i>dysoxyli</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Unknown	D
<i>ebenea</i>	<i>longicornis</i>	<i>amplexiseta</i>	ME	F
<i>ellenriederae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>elongata</i>	<i>musae</i>	<i>elongata</i>	Cue	C
<i>endiandrae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	DE
<i>enochra</i>	<i>atramentata</i>	<i>kirki</i>	Cue	D
<i>epicharis</i>	<i>nigrotibialis</i>	<i>aquila</i>	Cue	D
<i>erubescens</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	DE
<i>ettinabhujia</i>	<i>quadrata</i>	<i>commensurata</i>	ME	A
<i>eurycosta</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	B
<i>expandosa</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	D
<i>exspoliata</i>	<i>nigrotibialis</i>	<i>aquila</i>	Unknown	D
<i>facialis</i>	<i>passiflorae</i>	<i>obscura</i>	Cue	F
<i>fagraea</i>	<i>quadrata</i>	<i>quadrata</i>	Cue weak	E
<i>fastigata</i>	<i>diallagma</i>	<i>laticosta</i>	Cue	A
<i>fergussoniensis</i>	<i>distincta</i>	<i>distincta</i>	Unknown	D
<i>fernandoi</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	A
<i>finitima</i>	<i>musae</i>	<i>musae</i>	Unknown	D
<i>flavipennis</i>	<i>quadrata</i>	<i>dispar</i>	Cue	C
<i>flavoscutellata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>flavosterna</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	C
<i>floresiae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>frauenfeldi</i>	<i>frauenfeldi</i>	<i>frauenfeldi</i>	Cue, zingerone	CDE
<i>froggatti</i>	<i>bryoniae</i>	<i>froggatti</i>	ME	D
<i>fuliginus</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	DE
<i>fulvicauda</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	D
<i>fulvifemur</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>fumica</i>	<i>longicornis</i>	<i>amplexiseta</i>	ME	D
<i>furcata</i>	<i>zonata</i>	<i>furcata</i>	Unknown	A
<i>furfurosa</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>furvescens</i>	<i>furvescens</i>	<i>furvescens</i>	Cue	D
<i>furvilineata</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>fuscalata</i>	<i>longicornis</i>	<i>amplexiseta</i>	ME	D
<i>fuscitibia</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue, zingerone	BC
<i>fuscoformosa</i>	<i>tryoni</i>	<i>assita</i>	Cue	C
<i>fuscohumeralis</i>	<i>distincta</i>	<i>distincta</i>	Unknown	D
<i>fuscolobata</i>	<i>tryoni</i>	<i>assita</i>	Cue	C

Hancock & Drew: Review of subgenus *Bactrocera*

Species	Complex	Group	Lure	Zone
<i>fuscoptera</i>	<i>longicornis</i>	<i>amplexiseta</i>	ME	C
<i>gabensiae</i>	<i>tryoni</i>	<i>assita</i>	Cue	D
<i>geminosimulata</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	D
<i>gombokensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>grandifasciata</i>	<i>tryoni</i>	<i>sylvania</i>	Unknown	D
<i>grandistylus</i>	<i>passiflorae</i>	<i>samoae</i>	None	F
<i>halfordiae</i>	<i>quadrata</i>	<i>barringtoniae</i>	Isoeugenol	E
<i>halmaherae</i>	<i>alyxiae</i>	<i>halmaherae</i>	Cue	C
<i>hantanae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	A
<i>hispidula</i>	<i>atramentata</i>	<i>strigata</i>	None	E
<i>hollingsworthi</i>	<i>distincta</i>	<i>angustifasciata</i>	Cue	D
<i>holtmanni</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>humilis</i>	<i>tryoni</i>	<i>notatagena</i>	None	E
<i>hyalina</i>	<i>zonata</i>	<i>venefica</i>	None known	B
<i>hypomelaina</i>	<i>atramentata</i>	<i>atramentata</i>	Cue	D
<i>illusioscutellaris</i>	<i>nigella</i>	<i>trivialis</i>	Cue, zingerone	AB
<i>impunctata</i>	<i>musae</i>	<i>impunctata</i>	ME	BC
<i>incompta</i>	<i>tryoni</i>	<i>incompta</i>	Cue	C
<i>inconspicua</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	C
<i>inconstans</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>indecora</i>	<i>indecora</i>	<i>indecora</i>	Cue	D
<i>indonesiae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>infulata</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	C
<i>invadens</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	A
<i>involuta</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	C
<i>irvingiae</i>	<i>dorsalis</i>	<i>dorsalis</i>	Unknown	B
<i>ismayi</i>	<i>alyxiae</i>	<i>reclinata</i>	ME	D
<i>jaceobancroftii</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	B
<i>jarvisi</i>	<i>quadrata</i>	<i>jarvisi</i>	Zingerone, cue weak	DE
<i>kaiauiae</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	D
<i>kalimantanae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>kanchanaburi</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>kandiensis</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	A
<i>kauiae</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	D
<i>kelaena</i>	<i>tryoni</i>	<i>notatagena</i>	ME accidental?	D
<i>keravataiae</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	D
<i>kinabalu</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>kirki</i>	<i>atramentata</i>	<i>kirki</i>	Cue	F
<i>kohkongiae</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	B
<i>kokodiae</i>	<i>furvescens</i>	<i>furvescens</i>	Cue	D
<i>kraussi</i>	<i>quadrata</i>	<i>barringtoniae</i>	Isoeugenol	E
<i>kunvawaensis</i>	<i>laticaudus</i>	<i>phaea</i>	Cue	D
<i>kyrdemkulai</i>	<i>quadrata</i>	<i>commensurata</i>	ME	A
<i>labubulu</i>	<i>tryoni</i>	<i>assita</i>	Cue	D
<i>laensis</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>laithieuiiae</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>lampabilis</i>	<i>alyxiae</i>	<i>reclinata</i>	ME	D
<i>lata</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	B
<i>lateritaenia</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>laticaudus</i>	<i>laticaudus</i>	<i>laticaudus</i>	ME	E
<i>laticosta</i>	<i>diallagma</i>	<i>laticosta</i>	Cue	D
<i>latifrons</i>	<i>musae</i>	<i>latifrons</i>	Latilure	ABC

Species	Complex	Group	Lure	Zone
<i>latilineata</i>	<i>distincta</i>	<i>distincta</i>	Unknown	D
<i>latilineola</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>latissima</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	D
<i>limbifera</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	ABC
<i>linduensis</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>lineata</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	D
<i>lombokensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>longicornis</i>	<i>longicornis</i>	<i>longicornis</i>	Cue	D
<i>luteola</i>	<i>atramentata</i>	<i>luteola</i>	None	F
<i>maculigera</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	C
<i>makilingensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>malasaitiae</i>	<i>longicornis</i>	<i>biarcuata</i>	ME	D
<i>malaysiensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>mamaliae</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	C
<i>manskii</i>	<i>alyxiae</i>	<i>recurrens</i>	Cue	E
<i>manusiae</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	D
<i>mayi</i>	<i>quadrata</i>	<i>mayi</i>	ME	E
<i>mediorufula</i>	<i>tryoni</i>	<i>mediorufula</i>	ME	B
<i>megaspilus</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	C
<i>melanogaster</i>	<i>laticaudus</i>	<i>laticaudus</i>	ME	D
<i>melanothoracica</i>	<i>musae</i>	<i>aberrans</i>	ME	DE
<i>melanotus</i>	<i>atramentata</i>	<i>atra</i>	Cue	F
<i>melas</i>	<i>tryoni</i>	<i>tryoni</i>	Cue	E
<i>melastomatos</i>	<i>dorsalis</i>	<i>melastomatos</i>	Cue	B
<i>memnonia</i>	<i>nigrotibialis</i>	<i>aquila</i>	Cue	D
<i>mendosa</i>	<i>tryoni</i>	<i>notatagena</i>	None	E
<i>meraiensis</i>	<i>bryoniae</i>	<i>froggatti</i>	ME	D
<i>merapiensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>mimulus</i>	<i>bryoniae</i>	<i>froggatti</i>	ME	D
<i>minuscula</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	BC
<i>minuta</i>	<i>passiflorae</i>	<i>passiflorae</i>	Cue	DF
<i>moluccensis</i>	<i>quadrata</i>	<i>moluccensis</i>	Cue	BCD
<i>monostriata</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>morobiensis</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>morula</i>	<i>atramentata</i>	<i>atramentata</i>	Cue	D
<i>mucronis</i>	<i>passiflorae</i>	<i>obscura</i>	Cue	F
<i>muiri</i>	<i>dorsalis</i>	<i>dorsalis</i>	Unknown	B
<i>murrayi</i>	<i>quadrata</i>	<i>murrayi</i>	Methyl isoeugenol	E
<i>musae</i>	<i>musae</i>	<i>musae</i>	ME	DE
<i>mutabilis</i>	<i>tryoni</i>	<i>notatagena</i>	Isoeugenol?	E
<i>nanoarcuata</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>nationigrotibialis</i>	<i>nigrotibialis</i>	<i>diospyri</i>	ME	C
<i>naucleae</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	D
<i>neoabdonigella</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>neoaeruginosa</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	D
<i>neoarecae</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	A
<i>neocognata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>neofulvicauda</i>	<i>distincta</i>	<i>distincta</i>	Cue	C
<i>neohumeralis</i>	<i>tryoni</i>	<i>tryoni</i>	Cue, zingerone	DE
<i>neonigrita</i>	<i>laticaudus</i>	<i>laticaudus</i>	ME	D
<i>neonigrotibialis</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	A
<i>neopropinqua</i>	<i>dorsalis</i>	<i>propinqua</i>	Cue	B

Hancock & Drew: Review of subgenus *Bactrocera*

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<i>neoritsemai</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>nigella</i>	<i>nigella</i>	<i>nigella</i>	ME	D
<i>nigrescens</i>	<i>musae</i>	<i>musae</i>	ME	D
<i>nigrescentis</i>	<i>alyxiae</i>	<i>recurrens</i>	Cue	D
<i>nigricula</i>	<i>nigrotibialis</i>	<i>aquila</i>	Cue	D
<i>nigrifacia</i>	<i>diallagma</i>	<i>laticosta</i>	Cue	AB
<i>nigrifemorata</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	AB
<i>nigrita</i>	<i>musae</i>	<i>nigrita</i>	ME accidental?	B
<i>nigrofemorialis</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	A
<i>nigroscutata</i>	<i>furvescens</i>	<i>opacovitta</i>	Unknown	D
<i>nigrotibialis</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	BC
<i>nigrovittata</i>	<i>tryoni</i>	<i>romigae</i>	Methyl isoeugenol	DE
<i>niogreta</i>	<i>quadrata</i>	<i>dispar</i>	Zingerone	C
<i>notatagena</i>	<i>tryoni</i>	<i>notatagena</i>	None	E
<i>nothaphoebe</i>	<i>diallagma</i>	<i>nothaphoebe</i>	Unknown	B
<i>obfuscata</i>	<i>quadrata</i>	<i>obfuscata</i>	Cue	D
<i>oblineata</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>obliqua</i>	<i>frauenfeldi</i>	<i>obliqua</i>	Isoeugenol weak?	D
<i>obliquivenosa</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	D
<i>obscura</i>	<i>passiflorae</i>	<i>obscura</i>	Cue	F
<i>obscurata</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Unknown	B
<i>obscurivitta</i>	<i>quadrata</i>	<i>obscurivitta</i>	Cue	C
<i>occipitalis</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>ochracea</i>	<i>tryoni</i>	<i>assita</i>	Cue	D
<i>ochroma</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	BC
<i>ochromarginis</i>	<i>quadrata</i>	<i>ochromarginis</i>	ME	D
<i>ochrosiae</i>	<i>alyxiae</i>	<i>ochrosiae</i>	Cue	D
<i>ochroventer</i>	<i>quadrata</i>	<i>quadrata</i>	Cue?	C
<i>ohuiae</i>	<i>quadrata</i>	<i>obfuscata</i>	Cue	D
<i>opacovitta</i>	<i>furvescens</i>	<i>opacovitta</i>	ME	C
<i>opiliae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	E
<i>osbeckiae</i>	<i>dorsalis</i>	<i>melastomatos</i>	Cue	B
<i>pallescentis</i>	<i>musae</i>	<i>nigrita</i>	Unknown	A
<i>pallida</i>	<i>quadrata</i>	<i>mayi</i>	ME	E
<i>papayae</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>paraarecae</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	AB
<i>parabancroftii</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>parabarringtoniae</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	E
<i>paradiospyri</i>	<i>nigrotibialis</i>	<i>diospyri</i>	ME	A
<i>paraendiandrae</i>	<i>bryoniae</i>	<i>paraendiandrae</i>	ME	D
<i>parafrauenfeldi</i>	<i>frauenfeldi</i>	<i>frauenfeldi</i>	Cue	E
<i>parafroggatti</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	D
<i>paralatissima</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>paralimbifera</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>paramusae</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	D
<i>paranigrita</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	C
<i>paraochracea</i>	<i>tryoni</i>	<i>assita</i>	Cue	D
<i>paraosbeckiae</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	A
<i>paraverbascifoliae</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	A
<i>parvula</i>	<i>musae</i>	<i>latifrons</i>	None known	B
<i>passiflorae</i>	<i>passiflorae</i>	<i>passiflorae</i>	Cue	F
<i>patula</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	B

Species	Complex	Group	Lure	Zone
<i>pedestris</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>pectoralis</i>	<i>tryoni</i>	<i>notatagena</i>	Unknown	C
<i>peneallwoodi</i>	<i>musae</i>	<i>musae</i>	ME?	C
<i>penebeckerae</i>	<i>musae</i>	<i>musae</i>	ME?	C
<i>penecognata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>penecorrecta</i>	<i>zonata</i>	<i>zonata</i>	ME	A
<i>penecostalis</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	C
<i>peneobscura</i>	<i>passiflorae</i>	<i>obscura</i>	Cue	F
<i>penephaea</i>	<i>distincta</i>	<i>distincta</i>	Cue	C
<i>peninsularis</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	DE
<i>pepisalae</i>	<i>longicornis</i>	<i>curvifer</i>	ME	D
<i>perfusca</i>	<i>atramentata</i>	<i>atra</i>	None known	F
<i>perigrapha</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue, zingerone	A
<i>perkinsi</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	E
<i>pernigra</i>	<i>nigrotibialis</i>	<i>pernigra</i>	Cue	BC
<i>phaea</i>	<i>laticaudus</i>	<i>phaea</i>	Cue	D
<i>phaleriae</i>	<i>atramentata</i>	<i>strigata</i>	None	E
<i>picea</i>	<i>atramentata</i>	<i>picea</i>	ME	D
<i>pictipennis</i>	<i>musae</i>	<i>pictipennis</i>	ME	B
<i>pisinna</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>pometiae</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>popondettiensis</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>prabhakari</i>	<i>musae</i>	<i>latifrons</i>	None known	A
<i>prabhui</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Unknown	A
<i>profunda</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	A
<i>prolixa</i>	<i>musae</i>	<i>musae</i>	ME	D
<i>propedistincta</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>propinqua</i>	<i>dorsalis</i>	<i>propinqua</i>	Cue	BC
<i>pruniae</i>	<i>musae</i>	<i>pruniae</i>	Unknown	B
<i>pseudobeckerae</i>	<i>quadrata</i>	<i>selenophora</i>	Cue	C
<i>pseudocucurbitae</i>	<i>indecora</i>	<i>indecora</i>	Cue	BC
<i>pseudodistincta</i>	<i>distincta</i>	<i>distincta</i>	Cue	CD
<i>pseudoversicolor</i>	<i>quadrata</i>	<i>commensurata</i>	ME	A
<i>psidii</i>	<i>atramentata</i>	<i>atramentata</i>	Cue	F
<i>pulchra</i>	<i>distincta</i>	<i>distincta</i>	None	E
<i>pusilla</i>	<i>tryoni</i>	<i>assita</i>	Cue	B
<i>pyrifoliae</i>	<i>dorsalis</i>	<i>pyrifoliae</i>	Cue weak?	B
<i>quadrata</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	DE
<i>quadrusetosa</i>	<i>tryoni</i>	<i>romigae</i>	Isoeugenol	DF
<i>quasienochra</i>	<i>quadrata</i>	<i>obfuscata</i>	Cue	D
<i>quasiinfulata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>quasineonigrita</i>	<i>laticaudus</i>	<i>laticaudus</i>	ME	C
<i>quasipropinqua</i>	<i>dorsalis</i>	<i>propinqua</i>	Unknown	B
<i>quasisilvicola</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>raiensis</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>ramuensis</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>ranganathi</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>raunsepnaensis</i>	<i>distincta</i>	<i>angustifasciata</i>	Cue	D
<i>reclinata</i>	<i>alyxiae</i>	<i>reclinata</i>	ME	D
<i>recurrens</i>	<i>alyxiae</i>	<i>recurrens</i>	Cue	CD
<i>redunca</i>	<i>alyxiae</i>	<i>recurrens</i>	Cue	DF
<i>repanda</i>	<i>alyxiae</i>	<i>alyxiae</i>	Cue	D

Hancock & Drew: Review of subgenus *Bactrocera*

Species	Complex	Group	Lure	Zone
<i>resima</i>	<i>alyxiae</i>	<i>recurrens</i>	Cue	BD
<i>retrorsa</i>	<i>longicornis</i>	<i>biarcuata</i>	ME	D
<i>rhabdota</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>ritsemai</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	BC
<i>robertsi</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>robiginosa</i>	<i>quadrata</i>	<i>barringtoniae</i>	Unknown	E
<i>romigae</i>	<i>tryoni</i>	<i>romigae</i>	ME	DE
<i>rounaensis</i>	<i>distincta</i>	<i>angustifasciata</i>	Cue	D
<i>rubigina</i>	<i>quadrata</i>	<i>silvicola</i>	Cue, zingerone	AB
<i>rufescens</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	E
<i>rufivitta</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>rufofuscula</i>	<i>quadrata</i>	<i>silvicola</i>	Cue, zingerone	DE
<i>russeola</i>	<i>quadrata</i>	<i>quadrata</i>	Cue	E
<i>rutengiae</i>	<i>diallagma</i>	<i>diallagma</i>	ME	C
<i>rutila</i>	<i>quadrata</i>	<i>moluccensis</i>	Cue	D
<i>rutilana</i>	<i>quadrata</i>	<i>obfuscata</i>	Cue	D
<i>samoae</i>	<i>passiflorae</i>	<i>samoae</i>	None	F
<i>sapaensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>saramandiae</i>	<i>furvescens</i>	<i>furvescens</i>	Cue	D
<i>sari</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>seguyi</i>	<i>longicornis</i>	<i>curvifer</i>	ME	D
<i>selenophora</i>	<i>quadrata</i>	<i>selenophora</i>	Cue	A
<i>sembaliensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>setinervis</i>	<i>atramentata</i>	<i>atra</i>	None known	F
<i>silvicola</i>	<i>quadrata</i>	<i>silvicola</i>	Cue, zingerone	E
<i>simulata</i>	<i>bryoniae</i>	<i>bryoniae</i>	Cue	DF
<i>speculifer</i>	<i>longicornis</i>	<i>curvifer</i>	ME	D
<i>speewahensis</i>	<i>tryoni</i>	<i>speewahensis</i>	Zingerone	E
<i>strigata</i>	<i>atramentata</i>	<i>strigata</i>	None	E
<i>sulawesi</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	C
<i>suliae</i>	<i>quadrata</i>	<i>commensurata</i>	ME	C
<i>sumbawaensis</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>sylvania</i>	<i>tryoni</i>	<i>sylvania</i>	ME	D
<i>syzygii</i>	<i>dorsalis</i>	<i>pedestris</i>	Zingerone	ABC
<i>tapahensis</i>	<i>tryoni</i>	<i>mediorufula</i>	ME	B
<i>tenuifascia</i>	<i>quadrata</i>	<i>mayi</i>	ME	E
<i>terminaliae</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	D
<i>ternatiae</i>	<i>longicornis</i>	<i>curvifer</i>	ME	C
<i>thailandica</i>	<i>dorsalis</i>	<i>pyrifoliae</i>	Cue	AB
<i>thistletoni</i>	<i>nigrotibialis</i>	<i>nigrotibialis</i>	Cue	CD
<i>tikelingiae</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>tinomiscii</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>torresiae</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>tortuosa</i>	<i>distincta</i>	<i>distincta</i>	Unknown	D
<i>toxopeusi</i>	<i>nigrotibialis</i>	<i>aquila</i>	Unknown	D
<i>trifaria</i>	<i>atramentata</i>	<i>kirki</i>	Cue	D
<i>trifasciata</i>	<i>quadrata</i>	<i>dispar</i>	Cue	C
<i>trilineola</i>	<i>frauenfeldi</i>	<i>frauenfeldi</i>	Cue	F
<i>trivialis</i>	<i>nigella</i>	<i>trivialis</i>	Cue, zingerone	D
<i>trivirgulata</i>	<i>tryoni</i>	<i>notatagena</i>	None	D
<i>truncata</i>	<i>distincta</i>	<i>distincta</i>	Cue	C
<i>tryoni</i>	<i>tryoni</i>	<i>tryoni</i>	Cue, zingerone	E



Species	Complex	Group	Lure	Zone
<i>tsatsiai</i>	<i>distincta</i>	<i>distincta</i>	Zingerone	D
<i>tuberculata</i>	<i>zonata</i>	<i>zonata</i>	ME	AB
<i>turneri</i>	<i>quadrata</i>	<i>silvicola</i>	Cue	D
<i>umbrosa</i>	<i>alyxiae</i>	<i>umbrosa</i>	ME	BCDF
<i>unifasciata</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>unimacula</i>	<i>dorsalis</i>	<i>dorsalis</i>	ME	B
<i>unilineata</i>	<i>distincta</i>	<i>angustifasciata</i>	Cue	D
<i>unistriata</i>	<i>distincta</i>	<i>fulvicauda</i>	ME	D
<i>unitaeniola</i>	<i>distincta</i>	<i>distincta</i>	Cue	D
<i>usitata</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	BC
<i>ustulata</i>	<i>tryoni</i>	<i>assita</i>	Cue	D
<i>uvariae</i>	<i>musae</i>	<i>brevistriata</i>	Cue	D
<i>vargasi</i>	<i>frauenfeldi</i>	<i>obliqua</i>	Zingerone	D
<i>venefica</i>	<i>zonata</i>	<i>venefica</i>	None known	B
<i>verbascifoliae</i>	<i>dorsalis</i>	<i>caryeae</i>	ME	AB
<i>versicolor</i>	<i>zonata</i>	<i>versicolor</i>	ME	A
<i>vishnu</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	A
<i>vulgaris</i>	<i>indecora</i>	<i>indecora</i>	Cue	D
<i>waaiae</i>	<i>quadrata</i>	<i>barringtoniae</i>	ME	C
<i>waidoriae</i>	<i>bryoniae</i>	<i>paraendiandrae</i>	ME	D
<i>wallacei</i>	<i>nigella</i>	<i>trivialis</i>	Cue	C
<i>wuzhishana</i>	<i>nigrotibialis</i>	<i>diospyri</i>	ME	ABC
<i>yayamiae</i>	<i>frauenfeldi</i>	<i>obliqua</i>	Cue	D
<i>yorkensis</i>	<i>quadrata</i>	<i>ochromarginis</i>	M-isoeugenol, ME	E
<i>youngi</i>	<i>dorsalis</i>	<i>pedestris</i>	Cue	B
<i>zonata</i>	<i>zonata</i>	<i>zonata</i>	ME	AB

Table 2. List of species complexes in subgenus *Bactrocera*, with the total number of included species and the number of species occurring in each of the biogeographic zones in the Indo-Australian region (A = Indian Subcontinent; B = Southeast Asia; C = Wallacea; D = New Guinea & Solomon Islands; E = Australia; F = South Pacific).

Complex	Species	A	B	C	D	E	F
<i>longicornis</i>	17	–	–	3	13	1	1
<i>alyxiae</i>	16	–	2	3	13	2	1
<i>distincta</i>	40	–	–	8	29	1	2
<i>frauenfeldi</i>	8	–	1	2	5	2	2
<i>atramentata</i>	18	–	–	–	7	4	7
<i>laticaudus</i>	6	–	–	1	4	1	–
<i>tryoni</i>	39	–	3	6	22	11	2
<i>nigrotibialis</i>	30	9	6	6	14	1	–
<i>passiflorae</i>	8	–	–	–	1	–	8
<i>diallagma</i>	6	2	2	1	2	–	–
<i>indecora</i>	4	–	1	1	3	–	–
<i>nigella</i>	6	1	1	1	3	1	–
<i>bryoniae</i>	25	1	5	10	11	1	1
<i>musae</i>	32	3	6	7	18	5	–
<i>dorsalis</i>	83	13	58	18	6	4	–
<i>furvescens</i>	5	–	–	1	4	–	–
<i>quadrata</i>	86	12	11	16	38	26	–
<i>zonata</i>	10	8	6	–	–	–	–
Totals	439	49	102	84	193	60	24

Table 3. List of species-groups in the *dorsalis* complex, with the total number of included species and the number of species occurring in each of the biogeographic zones in the Indo-Australian region (A = Indian Subcontinent; B = Southeast Asia; C = Wallacea; D = New Guinea & Solomon Islands; E = Australia; F = South Pacific).

Group	Species	A	B	C	D	E	F
<i>arecae</i>	1	–	1	–	–	–	–
<i>caryeae</i>	8	8	2	–	–	–	–
<i>dorsalis</i>	26	–	17	3	3	3	–
<i>melastomatos</i>	2	–	2	–	–	–	–
<i>pedestris</i>	40	4	30	14	3	1	–
<i>propinqua</i>	3	–	3	1	–	–	–
<i>pyrifoliae</i>	3	1	3	–	–	–	–
Totals	83	13	58	18	6	4	0

 Table 4. List of species-groups in the *quadrata* complex, with the total number of included species and the number of species occurring in each of the biogeographic zones in the Indo-Australian region (A = Indian Subcontinent; B = Southeast Asia; C = Wallacea; D = New Guinea & Solomon Islands; E = Australia; F = South Pacific).

Group	Species	A	B	C	D	E	F
<i>abdofuscata</i>	2	–	–	1	2	–	–
<i>adamantea</i>	1	–	1	–	–	–	–
<i>apicofuscans</i>	1	1	–	–	–	–	–
<i>andamanensis</i>	1	–	1	–	–	–	–
<i>barringtoniae</i>	13	–	1	2	5	5	–
<i>bidentata</i>	2	–	–	–	1	2	–
<i>commensurata</i>	6	3	2	2	–	–	–
<i>congener</i>	1	–	–	–	1	–	–
<i>digressa</i>	1	1	–	–	–	–	–
<i>dispar</i>	5	–	–	5	–	–	–
<i>jarvisi</i>	1	–	–	–	1	1	–
<i>mayi</i>	3	–	–	–	–	3	–
<i>moluccensis</i>	2	–	1	1	2	–	–
<i>murrayi</i>	1	–	–	–	–	1	–
<i>obfuscata</i>	5	–	–	–	5	–	–
<i>obscurivitta</i>	1	–	–	1	–	–	–
<i>ochromarginis</i>	2	–	–	–	1	1	–
<i>quadrata</i>	13	1	1	2	8	8	–
<i>selenophora</i>	2	1	–	1	–	–	–
<i>silvicola</i>	23	5	4	1	12	5	–
Totals	86	12	11	16	38	26	0

Following an earlier study on Pacific islands biogeography by Michaux & White (1999), dispersal and speciation between New Guinea, the South Pacific islands, and Australia was discussed by Starkie et al. (2024), who noted a unidirectional west-east dispersal from New Guinea to the Pacific and multiple interchange between Papua New Guinea and NE Australia via Cape York, Queensland, with subsequent dispersal westwards from northern Queensland to the Northern Territory. It is likely, however, that the Northern Territory endemic *B. parafrauenfeldi* (and possibly others) dispersed there directly from New Guinea via Aru, given

the absence of a *frauenfeldi* group species from northern Queensland until very recently (Royer et al., 2016). A secondary NE Australia-New Caledonia link is supported by the endemic tephritid species *Austronevra irwini* Norrbom & Hancock, 2004 (Phytalmiinae) and *Oedaspis ouinensis* Hancock, 2008 (Tephritinae) in New Caledonia, which appear to be closely related to two *Austronevra* Permkam & Hancock, 1995 species and *O. mouldsi* Hardy & Drew, 1996 in NE Queensland, respectively (Hancock, 2008). However, the phylogeny used by Starkie et al. (2024) contains numerous anomalies and is regarded here as unreliable (Hancock &

Drew, 2024), so a NE Australia-New Caledonia connection in Dacini requires further investigation; it is possible that *B. ebenea* is close to the Papua New Guinean *B. fumica* and *Dacus aneuittatus* Drew, 1971 [plus *D. perpusillus* Drew, 1971] are close to *D. tauti* Drew & Romig, 2001 from Vanuatu. Neither *B. fumica* nor *D. tauti* were included in the Starkie et al. (2024) study.

**Endemism.** The Dacini are clearly of Gondwanan origin, with the parental stock having originated in the Indian block as it drifted northward before unification with Laurasia (Drew & Hancock, 1999; Krosch et al., 2012; Hancock & Drew, 2024). Given that the Indian plate was the centre of evolution for this group, it is significant to analyse the presence of endemic species across the now known zones of distribution. In defining endemic species as those that occur in a specific zone only, Drew (2004) recorded the percentages of *Bactrocera* species endemic to each major zone as follows: Indian Subcontinent (66%), Southeast Asia (89%), Papua New Guinea (90%), Australia (84%), and the Pacific Islands (100%). These high levels of endemism indicate that speciation has occurred in each zone and in isolation over a considerable period. The lower level of endemism in the Indian subcontinent probably has resulted from a relatively high level of contact between this zone and Southeast Asia. At the same time, the *caryeae* group in the Indian subcontinent is largely unique to that zone and indicates a level of isolated speciation that has resulted in species such as *B. invadens*.

**Geological background.** The geological breakup of Gondwana and the eventual collision of its Indian section with Asia has resulted in an influx of Gondwanan rainforest flora into Southeast Asia and beyond. This also explains the strong botanical relationships at the generic level among the Indomalayan forests of India, Southeast Asia, Papua New Guinea, and Australia. From this, it can be concluded that the breakup of Gondwana and the accompanying proliferation of the rainforest fruit fly host species has led to the large number of *Bactrocera* species throughout the entire Asian-Pacific region. While geological knowledge of a region is important in defining its biogeography, Hall (2001) noted that other processes actively influence the outcomes of speciation. For example, geologically induced changes in topography, localised climate, development and dissolution of land bridges, and the building of the extensive island complexes across Southeast Asia and the Pacific have all played a major role in the processes of speciation in the genus *Bactrocera*.

An assessment of the biogeography of a faunistic group requires a rigorous phylogenetic analysis of the known species and supraspecific groups, their habitat and food sources, reproductive biology that in the case of fruit flies occurs within their host plants, the geographic distribution of the species, in particular endemic species and their host plants, and the geological background from the breakup of Gondwana to the development of the numerous islands and archipelagos throughout Southeast Asia and the Pacific Region. Major geological changes also have been accompanied by changes

in localised climate, soil types that directly influence establishment of plant species, and sea level changes that result in the formation of land bridges and their subsequent decline. Only in the light of such comprehensive information can accurate taxonomic decisions be made on the status of *Bactrocera* species and their supraspecific groups.

## MALE LURES

Attractants long have been the subject of research in dacine fruit flies, leading to a wide variety of applications in faunistic surveys, pest management and pest species population eradication. The history of the development of food and synthetic fruit fly lures was reviewed by Drew (1974, 2020), Drew & Hooper (1981), and Drew & Fay (1988). Following extensive surveys using the male lures cue lure, methyl eugenol, and Willison's lure (raspberry ketone) in Steiner-type traps that included the fast knock-down insecticide Dichlorvos, Drew (1974) recorded 79 species across northeastern Australia and 26 South Pacific islands, and first noted the taxonomic implications of the species-specific responses to the lures. Within the genus *Bactrocera* in particular, groups of morphologically related species responded to the same male lure, either cue lure or methyl eugenol. This characteristic was later confirmed in a large-area survey of 55 species in Queensland and the Northern Territory (Drew & Hooper, 1981). Responses of dacine fruit flies to a variety of male lures were recorded for Queensland and Papua New Guinea by Royer (2015) and Royer et al. (2018a) respectively and included discussion of the use of some potentially new male lures, including zingerone (= vanillylacetone). The lure responses of the recognised major pest species known from Southeast Asia, Wallacea, and Australia were recorded by Drew & Romig (2013), those for all known Southeast Asian species by Drew & Romig (2016), and those for all known Dacini by Doorenweerd et al. (2018). These and subsequent records have been included in Table 1.

Faunistic surveys based on male lures, particularly cue lure and methyl eugenol, across Southeast Asia and the South Pacific over the past four decades, have made a major contribution to the discovery of previously undescribed species and a wider knowledge of the dacine fauna, taxonomic arrangements of species and biogeography. In the list of currently known species (Table 1), 240 are confirmed responders to cue lure, 122 to methyl eugenol, 23 to zingerone, 11 to isoeugenol/methyl isoeugenol, and 1 to lalilure. While the biological significance of these chemicals, especially to *Bactrocera* species, has long been questioned, there has been increasing evidence that some perform important roles in the flies' reproduction as well as rainforest orchid fertilisation (Clarke et al., 2002). Twenty-four species of subgenus *Bactrocera* were recorded in Papua New Guinea with orchid pollinaria on the dorsal midline by Clarke et al. (2002), 12 cue lure responding species, and 12 methyl eugenol responding species. They reported that in Papua New Guinea, all 13 species of *Bulbophyllum* orchid species attract and are pollinated by *Bactrocera*

species. Methyl eugenol responding species have also been trapped in northern Queensland with pollinaria attached to their eyes or scutum (DLH, pers. obs.). *Bactrocera jarvisi* in northern Queensland has a weak response to cue lure, a strong response to zingerone, and has been recorded as attracted to the flowers of *Bulbophyllum baileyi*, which contain zingerone (Fay, 2012).

Considering that the endemic habitat of the Dacini is the tropical and subtropical rainforests, we can hypothesise that the male lure responses have evolved in this ecosystem, resulting in a nutritional benefit to the flies and pollination of orchid flowers. A cue lure and/or zingerone response is known to occur only in the genera *Bactrocera* and *Dacus* and is probably inherited from a common ancestor. A methyl eugenol response occurs in *Bactrocera* and *Dacus* and also in African species of *Ceratitis* (*Pardalaspis*) Bezzi, 1918, *Nippia* Munro, 1929, and *Perilampus* Bezzi, 1920 [also with isoeugenol] in the Ceratitidini (Hancock, 1985, 1987). [Note that a record of *Nippia* attracted to trimedlure in Zambia (Hancock, 1985) is a result of contaminated traps]. Within Dacini, it is most prevalent in the *Bactrocera* group of subgenera, elsewhere occurring only weakly in the *Zeugodacus* and *Melanodacus* groups (and secondary to methyl isoeugenol: Royer et al., 2018b, 2019b) and in the Papuan-Australian *Dacus pusillus* group (Hancock & Drew, 2006). Occurring in numerous lineages, probably within two different ecosystems, we consider a methyl eugenol response to be homoplasious; it also occurs in some Chrysopidae (Neuroptera) in both Africa and Asia (DLH, pers. obs.; I.M. White, pers. comm.) and Tan & Nishida (2012) recorded it from more than 450 plant species in 80 families. While some authors believe that the attraction of male *Bactrocera* species to rainforest orchids is due to a response to zingerone (e.g., Tan & Nishida, 2007), the methyl eugenol responding species recorded at orchid flowers by Clarke et al. (2002) have never been attracted to zingerone in recent field trapping studies. It appears that other chemical cues are involved, with South American orchid-pollinating bees, for example, responding to several different lures, including eugenol and vanillin (Coswosk et al., 2019).

An attraction to zingerone is predominant in subgenus *Tetradacus* Miyake, 1919 and several of the *Melanodacus* group subgenera (*Parazeugodacus* Shiraki, 1933, *Hemizeugodacus* Hardy, 1951, *Neozeugodacus* May, 1952a), and is shared with some Asian, Australasian, and African *Dacus* species, some *Zeugodacus* group species and some species in subgenus *Bactrocera*, either exclusively or as an alternative to cue lure (Doorenweerd et al., 2018), but records of the methyl eugenol responding species *B. papayae* [as '*dorsalis*'] attracted to it in Malaysia (Tan & Nishida, 2007) are based on orchid visitation and not replicated by lure trapping, while those of *B. indonesiae* (recorded by Tan & Nishida, 2007 but not known from Malaysia) and *B. murrayi* (recorded by Doorenweerd et al., 2018) are likely to be misidentifications. As with the other lures, zingerone is likely to be environmentally induced.

In an earlier section we placed species of subgenus *Bactrocera* in morphologically similar groups within larger complexes. Most species within each group are also attracted to the same male lure. Also, there are examples where a species response to a particular male lure can be used as a taxonomic character. For example, *B. melastomatos* is attracted to cue lure whereas a similar species, *B. occipitalis*, is attracted to methyl eugenol. Attraction is generally confined to either one or other of the two lure groups (cue lure, raspberry ketone, zingerone; or methyl eugenol, isoeugenol, methyl isoeugenol, dihydroeugenol) but some weakly cue lure responding species are more strongly attracted by isoeugenol or methyl isoeugenol (Royer et al., 2019a).

## HOST PLANTS

Through several research projects, extensive host plant surveys have been carried out over the past four decades across Southeast Asia, Papua New Guinea, Australia, and 11 South Pacific islands (Allwood et al., 1999; Hancock et al., 2000; Leblanc et al., 2012), with approximately 140,000 fruit/vegetable samples collected and processed for fruit fly rearing. The sampling was designed to represent all possible floristic ecosystems and particularly the tropical and subtropical rainforests. Dacine fruit flies were reared from 71 plant families in Southeast Asia and from 63 plant families across the Pacific Region.

A knowledge of host plants, particularly the endemic hosts in the Indomalayan rainforests, has made significant contributions to the diagnosis of many species and an understanding of the process of speciation, biogeography and phylogenetic relationships. From an applied point of view, these data have led to extensive research in the areas of fruit fly biology and behaviour within the host plant, studies in parasitoids and predation, larval feeding, and chemical and physical host plant cues that attract a species to its host fruit for feeding and oviposition. Examples of useful applications to government and industry are the establishment of the Northern Australian Quarantine Fruit Fly survey in 1978, the precursor to the current Northern Australian Quarantine Survey (NAQS), the new Fruition female trap technology based on the chemistry of host fruit volatiles that attract gravid female fruit flies to oviposit in ripening fruits (Drew, 2020), and the production of the first comprehensive list of 47 major fruit fly pest species that occur across the Asian/Pacific Regions, including an assessment of their pest status and level of biosecurity risk to other countries (Drew & Romig, 2013).

In a study of the endemic plant taxa that are hosts of endemic dacine species, Drew (2004) noted that 37% of *Bactrocera* species in Australia were monophagous and 33% in Southeast Asia, while 21% in Australia were polyphagous and 14% in Southeast Asia, the polyphagous species including the major pest species. With regard to host plant families, 50% of *Bactrocera* species in Australia utilised only one plant family and in Southeast Asia 67%. Further, it was noted that the distributions of genera and species of both Indomalayan

rainforest flora and dacine species showed considerable similarities (Drew, 2004). Within the *Bactrocera* group of subgenera, the basal subgenus *Apodacus* utilises a single plant genus (*Garcinia*), while most species of subgenus *Bactrocera* where host plants are known are monophagous or stenophagous, with oligophagy and polyphagy predominant in the more derived *tryoni*, *caryeae*, *dorsalis*, and *zonata* groups. This feature was also noted by Starkie et al. (2022b).

The reproductive biology of a dacine species is dependent upon factors within the host plant environment, as Drew & Lloyd (1987) demonstrated when they defined the host plant as the ‘Centre of Activity’ for a fruit fly population. This close-knit association between a fruit fly population and its host plant has enabled the geographic distribution of dacine species to be linked with the patterns of distribution of Indomalayan rainforest plant species. Indeed, there has been considerable co-evolution of *Bactrocera* species in association with their rainforest host plants (Drew, 2004).

The number of endemic plant taxa that are hosts for endemic dacine species was listed by Drew (2004). Many dacine species utilise only one or a very few host plants. Given the close reproductive association that a species has with its host plant, the large number of fly species with single or a few hosts and the potential for co-speciation, it can be assumed that the large number of *Bactrocera* species that exist sympatrically in the tropical forests of zones such as Papua New Guinea have resulted from this process and this provides an answer as to why so many species occur in the same continental land mass. As reported by Drew & Hancock (1999), there has been considerable evolution of *Bactrocera* species in the Indomalayan rainforest ecosystem, and an understanding of the patterns of distribution of the fly and its endemic host plants will assist in the elucidation of phylogenetic relationships.

The diagnosis of cryptic species within the species complexes in subgenus *Bactrocera* has been researched and reviewed over the past two decades. The application of morphometrics, wing shape, cytology, DNA, laboratory cross-mating experiments, male pheromone chemistry, and host records was reviewed by Drew & Romig (2013, 2016). In these discussions and those of Drew & Romig (2022) and Drew & Hancock (2022), data were presented on morphology (especially new information on the male aedeagus) and endemic host plant records, which assist in the definition of cryptic species. In Australia and Southeast Asia, 37% and 33% of *Bactrocera* species, respectively, are monophagous and such data are invaluable in the diagnosis of cryptic species. For example, in the *dorsalis* group of 26 species listed above, *B. atrifemur*, *B. cacuminata*, *B. dapsiles*, *B. endiandrae*, *B. irvingiae*, *B. kanchanaburi*, *B. ochroma*, *B. opiliae*, and *B. raiensis* all utilise specific and limited hosts that provide authenticity for their specific status. Further, some polyphagous species have specialised in a limited number of hosts. For example, *B. carambolae* utilises carambola as a primary host and *B. papayae* distinctly utilises banana and papaya, especially at the mature green stage. Some species have unusual hosts, e.g., *B. arecae* in palm fruit and

the *melastomatos* group in flowers of Melastomataceae. In addition to the determination of cryptic species, such host data have proven invaluable in field pest management. In the North Queensland eradication program for *B. papayae* in the late 1990s, foreknowledge of its major hosts banana and papaya facilitated the searching for, sampling, and rearing of flies from these fruit within the first few weeks of the discovery of the presence of this major pest species. This knowledge led directly to the surveillance and early introduction of the eradication strategies that resulted in a successful eradication campaign. In the *caryeae* group of eight species listed above, *B. verbascifoliae* is monophagous, *B. kandiensis* recorded from two plant families, *B. caryeae* from seven plant families, and *B. invadens* is polyphagous.

## MOLECULAR EVIDENCE

Within the speciose subgenus *Bactrocera*, molecular evidence is especially incomplete with regard to taxon sampling. The three most detailed studies to date, San Jose et al. (2018), Dupuis et al. (2018), and Starkie et al. (2022b), examined 88 primarily Oriental, 49 primarily Oriental, and 45 primarily Australasian species of the subgenus respectively (plus others outside the subgenus), still only about 10–20% of the 439 species recorded. The widely used COI gene, known to be of limited reliability for phylogenetic analysis, is especially so in the *dorsalis* complex, where (likely ancestral) genetic introgression has confounded the results (San Jose et al., 2023; Doorenweerd et al., 2024). Proposed synonymies using these data (e.g., Schutze et al., 2015a, b), together with the misidentified IAEA Saraburi colony and misinterpreted lure responses by Hee et al. (2015a), plus imaginary clines (see Drew & Hancock, 2022), must therefore be regarded as flawed and unreliable. The inability of molecular workers to morphologically identify ‘*B. dorsalis*’ (e.g., Doorenweerd et al., 2023b) is due entirely to the false synonymisation of *B. invadens* and *B. papayae* with it and the consequent combination of morphological characters. Experienced taxonomists can readily distinguish the three separate species (Drew & Hancock, 2022) and many authors, from Schutze et al. (2015a) to Korneyev et al. (2024), have noted the absence of pale *invadens* colour forms east of the Indian subcontinent (i.e., in true *dorsalis* and *papayae*). In a similar case, the African *Ceratitidis capitata* (Wiedemann, 1824) and *C. caetrata* Munro, 1949 cannot be separated by COI data but are readily distinguishable morphologically (Giunti et al., 2023). Proposed synonymy of *B. albistrigata* with *B. frauenfeldi* by Doorenweerd et al. (2023a) was based on insufficient evidence (Drew & Hancock, 2022), since key populations in New Guinea and Timor had not been included, and was not supported by Yong et al. (2024). The problem of ‘cryptic’ species being described solely on molecular evidence was discussed above, the species ‘*incognita*’ and ‘*borneoensis*’ (see Doorenweerd et al., 2024) being regarded here as genetic variants of *B. occipitalis* and *B. carambolae* respectively. Genetic variation in many species (often reflected in morphological variation: Leblanc et al., 2015b), an overall genetic similarity and rapid speciation within subgenus *Bactrocera* also reduce the reliability of

molecular phylogenies, further exemplified by the complete lack of agreement regarding the placement of *B. endiandrae*, as discussed above under ‘Complexes and species groups.’ Three studies that focused on Australian species (Krosch et al., 2012; Catullo et al., 2019; Starkie et al., 2022b) showed very little agreement with either each other or the wider studies of San Jose et al. (2018) and Dupuis et al. (2018). For a phylogeny based on morphology, expanding that of Drew & Hancock (1999), see Hancock & Drew (2024).

Molecular studies are also being misinterpreted to expand the supposed distributions of some species. San Jose et al. (2023) mapped the distribution of *B. carambolae* as widespread from Bangladesh eastwards to southern China and Sulawesi, implying a continuous distribution. However, naturally occurring populations are known with certainty only as far north as southern parts of Thailand, Cambodia, and Vietnam, as well as the Andaman Islands; the Bangladesh population was not detected prior to 2016 (Leblanc et al., 2019) and is more likely an invasive incursion from the Andaman Islands than via Myanmar, where it is otherwise unknown. Distribution maps in Charbonnel et al. (2023) are generally inaccurate; that for ‘*B. dorsalis*’ covers three species and *B. raiensis* is not known from Myanmar or Laos, or (Doorenweerd et al., 2024) from Nepal, Cambodia, Sri Lanka, Malaysia, China and Africa; these are all undoubtedly based on misidentifications. *Bactrocera kandiensis* is not known beyond Sri Lanka and its assumed distribution in India presumably results from molecular misidentification or the ‘*kandiensis*’ genes being present ancestrally in other *caryeae* group endemics in India, such as *B. invadens* or *B. caryeae*, which Krosch et al. (2012) placed as sister to *B. kandiensis* on molecular evidence. The distributions of *B. occipitalis* for the whole of Indonesia and that of *B. carambolae* for the whole of Brazil are presumably whole country extrapolations from actual distributions that are restricted to Borneo (Kalimantan) within Indonesia and from Guyana to NE Brazil in South America, respectively.

It is clear that while molecular evidence has some value in supporting the identity and classification of *Bactrocera* species, and is useful in determining the composition and phylogenetic position of subgenera, its general unreliability, lack of agreement between studies and uncertain veracity of analysis programs suggest that it should not be the sole or dominant basis for making taxonomic decisions regarding the status of species, their geographic distributions or their phylogenetic relationships, particularly within subgenus *Bactrocera*. ‘Cryptic’ species and synonymies require more compelling evidence than mere genetic variation or similarity, while distributional assumptions require actual specimens. As an observable representation of other genes, morphology (allowing for variation) offers the most reliable evidence for species delimitation and recognition.

## DISCUSSION

Taxonomic research on the genus *Bactrocera* has transitioned from the early beginnings based purely on morphological

character states, through the 20<sup>th</sup> century where larger faunas and ecology became significant, resulting in holistic studies that also involved cryptic species. In this period, specialists researched large groups of species resulting in the production of major monographs. Since that time, we have entered a period of research based on morphological and molecular analyses of low numbers of species, primarily in cryptic species complexes. The decline in university taxonomy courses has resulted in taxonomic decisions often being based on molecular analyses that in many cases are unreliable and inaccurate. While morphological data on all known species far outweighs limited molecular data on just a few species, there is an urgent need to expand the current research to include field collecting, ecology and host fruit rearing over wide geographic zones and to make decisions on species based on an adequate Species Concept. Such a concept must be based on informed taxonomic knowledge, adequate field data, interaction with host plants, and biogeography.

Morphology remains the most reliable technique by which to diagnose species but requires considerable training and experience. Many recent papers have presented molecular data on specimens that operators found difficult to identify morphologically and in some cases were misidentified. Hee et al. (2015b) reported that 50 researchers [actually 49] from 20 countries were involved in an IAEA project that led to the synonymisation of *B. invadens* and *B. papayae* with *B. dorsalis*, yet at that time there existed no more than four specialists in the taxonomy of *Bactrocera* species, none of whom contributed to or peer-reviewed the papers of Schutze et al. (2015a, b). In a study of an invasive fruit fly population in Italy (Nugnes et al., 2018), the photographic illustration clearly can be identified as *B. invadens*, although the authors could not identify it. To add to their confusion, their molecular analyses revealed two phylogenetically distinct haplotypes, one of which represented *B. kandiensis*. Research by Taddei et al. (2023), designed to validate morphological and molecular identification protocols for *B. dorsalis*, again highlighted the lack of experience in diagnosing morphological characters but they made an unusual choice of localities for field collecting; their specimens from Africa and Taiwan would have been good representatives of *B. invadens* and *B. dorsalis* respectively, but those from Thailand and Vietnam would not necessarily be *B. dorsalis*. One abdomen photo (figure 4B) is almost certainly not *B. carambolae* and, where incongruence occurred, they correctly reflected on the inaccurate data that are on international gene data bases. Of equal concern is that Charbonnel et al. (2023) could not separate three morphologically distinct species, *B. occipitalis*, *B. carambolae*, and *B. dorsalis* based on morphology and could not separate *B. dorsalis*, *B. carambolae*, *B. kandiensis*, and *B. raiensis* based on the COI gene. This paper also stated that *B. occipitalis* could be identified on the COI gene, whereas Doorenweerd et al. (2024) could not reliably diagnose either this species or *B. kandiensis* on the COI gene. Data presented by Doorenweerd et al. (2024) throw doubt on the molecular identification of several species in the *dorsalis* complex, as did the studies of Charbonnel et al. (2023) and San Jose et al. (2023). This is understandable given that Zamani et al. (2022) reported that DNA barcodes on their

own are not enough to describe species, and Drosopoulou et al. (2019) noted the limitations of mitochondrial gene sequences for discriminating between closely related members of the *B. dorsalis* complex. Doorenweerd et al. (2023b) also reported on the inadequacy of current molecular identification protocols for the *dorsalis* complex.

Reflecting on the inconsistencies in species identifications relating specifically to the *dorsalis* complex, several aspects need to be considered: (1) The world gene data banks contain inaccurate genetic data resulting from analyses based upon incorrectly identified specimens. This is especially evident in the *dorsalis* complex, where *B. papayae* and *B. invadens* are frequently misidentified as '*B. dorsalis*'; (2) Understanding geographic distributions and the host plants of populations is vital for the establishment of consistent baseline data. This knowledge should be used when sampling for research projects. Host-reared specimens are more valuable than those trapped with male lures. The population in the Indian subcontinent is clearly *B. invadens* and carries some genes similar to those of *B. kandiensis*, most likely due to common ancestry. To lump populations together from different localities across the entire region as *B. dorsalis* is contributing to the ongoing taxonomic confusion. Some authors, including Doorenweerd et al. (2024), reported *B. kandiensis* CO1 genes in African specimens and recorded specimens identified as *B. raiensis* in Africa. The latter will be a colour variant of *B. invadens* and both records confirm that the invasive population in Africa is derived from *B. invadens* from the Indian subcontinent. Charbonnel et al. (2023) also contributed to inaccurate geographic distribution records in showing *B. carambolae* and *B. occipitalis* as present in Indonesia's West Papua and Papua Provinces; (3) In recent years there has been a misrepresentation of publications that present alternative opinions to the *B. dorsalis* complex species diagnoses. Most recently, Doorenweerd et al. (2024) stated that Drew & Romig (2022) did not present new data on the male aedeagus of these species but clearly did not consult Drew & Hancock (2022), where the statistically analysed data were presented. These new data on the male aedeagus have demonstrated the validity of *B. invadens* and *B. papayae* as distinct species; (4) The handling and storage of specimens should be a priority and the destruction of type specimens for use in molecular analyses, as done by Doorenweerd et al. (2024), is highly inappropriate. This prevents future researchers from reviewing such species. Whether specimens are used for morphological, molecular or chemical research, exact label data should be published. In a review of the dacine fruit flies of Oceania (Leblanc, 2022), photographs of colour variations of the scutum and abdomen of *B. dorsalis* were presented without specimen label data. Some of the photographs were not representative of *B. dorsalis* from Oceania, the title of the publication. Some represented *B. dorsalis* from Oceania (probably Hawaii), while others were photographs of *B. invadens*, either from the Indian subcontinent or Africa. Similarly, photographs of '*B. dorsalis*' in Korneyev et al. (2024) are also of *B. invadens*; that colour form does not occur in true *B. dorsalis* and the postsutural lateral yellow vittae are broader in the latter species. Another example is Taddei et al. (2023), who

studied specimens classified as *B. dorsalis* from Africa, Taiwan, Thailand, and Vietnam, without collection and label data. The *dorsalis* complex in Thailand and Vietnam is extensive and complex and requires intensive study by experienced taxonomists to elucidate.

Field collection of specimens is of paramount importance, particularly in respect of host-reared specimens from known major host plants within recorded geographic localities. Field collections based on male lure trapping yield many morphologically similar specimens and, without specialist diagnosis, prevent the collation of basic data on a particular species. The importance of focused field collecting and its contribution to research into the different character states was emphasised by Drew & Romig (2013). Inadequate field collecting was noted and led to significant error in the synonymies of Schutze et al. (2015a, b), whereas knowledge of host plants has proven to be a vital component of a species' diagnosis, enabled a clearer understanding of speciation, phylogeny, biogeography and host plant biology, and resulted in successful field control and eradication programs.

Laboratory-based cross-mating experiments reported by Schutze et al. (2015a, b) and Hee et al. (2015b) were shown by Drew & Romig (2016) to be inappropriate for defining species of *Bactrocera*. Drew & Romig (2016) presented examples where, as reported by these authors, pairs of distinct species had been cross-mated under laboratory conditions to produce fertile hybrid progeny. For example, when *B. tryoni* was cross-bred with *B. neohumeralis*, *B. jarvisi* with *B. tryoni* and, at the IAEA laboratory at Siebersdorf, *B. tryoni* with '*B. dorsalis*' [actually *B. papayae*], all crosses produced fertile progeny. Under field cage conditions, *B. tryoni* was recorded mating with *B. cacuminata*. This hybridisation concept was initiated by the now outdated Biological Species Concept of Wallace (1889) and, as a result of recent ecological research (see Drew & Hancock, 2022), shown to be incompatible with the courtship and mating behaviour of *Bactrocera* species within their natural host environment.

The male lure feeding and pheromone studies reported by Hee et al. (2015a) were limited to just a few of the 122 methyl eugenol responding species known in subgenus *Bactrocera*, many of which feed on and would metabolise the lure in the same manner as does *B. dorsalis*, and there are no published data that prove methyl eugenol is directly involved in host plant courtship and mating behaviour, this being significant in the process of speciation. On the contrary, Drew et al. (2008) described courtship and mating in *B. cacuminata* on its host plant in the absence of methyl eugenol. Additionally, their samples of *B. dorsalis*, *B. philippinensis*, and *B. invadens* all originated from IAEA laboratory colonies (Hee et al., 2015a), with the Saraburi (Thailand) colony of '*dorsalis*' originating from within the known distribution of *B. papayae*, which occurs at least as far north as Bangkok (Drew & Hancock, 2022; Drew & Romig, 2022). This misidentification has led to the erroneous suggestion of clines by Schutze et al. (2015a, b) and has compromised the methyl eugenol response studies by Hee et al. (2015a).

Further, the use of the COI gene by Schutze et al. (2015a, b) and Hee et al. (2015b) to argue conspecificity has been proven inadequate for accurate description of species (Zamani et al., 2022; Doorenweerd et al., 2024). Prior to their description by Drew & Hancock (1994), White & Elson-Harris (1992) referred to *papayae* as species B and *philippinensis* as species C and those two species were noted as having an aculeus length / wing cell dm ratio of 0.77–0.93; in comparison, *dorsalis* [at that time also including populations later described as *B. invadens*] and species A (= *carambolae*) only had an aculeus length / cell dm ratio of 0.57–0.75. In view of such data, coupled with morphological differences, the withdrawal of *B. invadens* and *B. papayae* from synonymy with *B. dorsalis* by Drew & Romig (2016) was justified and is further corroborated by Drew & Romig (2022) and Drew & Hancock (2022), especially in the light of a more recent understanding of the field host plant-based reproductive biology and data on the structure and function of the male genitalia. Drew & Romig (2013) had recognised *B. philippinensis* as a synonym of *B. papayae* after several years of intensive study of the *dorsalis* complex populations from the Philippines, across Borneo and into Java. Schutze et al. (2015a, b) then erroneously placed *B. papayae*, *B. philippinensis* and *B. invadens* as synonyms of *B. dorsalis*. Hee et al. (2015a, b) implied that this synonymy would significantly facilitate global trade, yet ten years later this has not eventuated. Indeed, the expanded host list has made matters worse (see Drew & Hancock, 2022). If the WTO, IPPC, and IAEA wish to aggregate several *dorsalis*-type species under one name for possible trade implications, then that is a separate matter entirely from the definition of species based on sound and consistent scientific principles.

Due to the known or potential unreliability of COI and other gene fragments, an overreliance on molecular data and a single ‘best’ tree selected from a multitude of alternatives, in many cases molecular studies have created more problems than they have resolved. This is especially the case in the large and complex subgenus *Bactrocera*, where such studies not only fail to agree with each other but also are at odds with morphology, biology and biogeography. Three allopatric species of major agricultural and biosecurity concern, *B. dorsalis*, *B. papayae*, and *B. invadens*, allegedly were synonymised to facilitate international trade. However, such trade is better served by the recognition that these three species appear to be unable to establish in each other’s territories (suggested by limited introgression and maintenance of allopatry), rather than by a false synonymy that has caused nothing but confusion and continues to compromise many recent studies (e.g., Wang et al., 2024). There is no guarantee that laboratory-reared colonies of one species will interact successfully with the others in field-based SIT programs and any comparisons between *B. papayae* and the IAEA Saraburi colony of ‘*B. dorsalis*’ will have been between *papayae* and *papayae*. Morphology-based systematics, used judiciously, still provides the best evidence of a species’ identity and phylogenetic relationships. Proper taxonomic training is essential to this process.

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