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Biogeography, Speciation and Taxonomy within the genus *Bactrocera* Macquart with application to the *Bactrocera dorsalis* (Hendel) complex of fruit flies (Diptera: Tephritidae: Dacinae)

R.A.I. DREW[1] & D.L. HANCOCK[2]
[1]*Environmental Futures Research Institute, International Centre for Management of Pest Fruit Flies, Griffith University, Nathan Campus, Brisbane, Queensland, Australia*
salome1_nbn@iinet.net.au; *https://orcid.org/0000-0003-4973-5107*
[2]*60 South Street, Carlisle, Cumbria CA1 2EP, United Kingdom.*
dlhancock20@gmail.com; *https://orcid.org/0000-0002-8478-7976*

Abstract

The genus *Bactrocera* Macquart comprises a large group of some 750 species distributed across the Asia-Pacific and Afrotropical regions. Most of these have been described and revised by Drew (1989), Drew & Hancock (1994) and Drew & Romig (2013, 2022). A taxonomic study of such a large and diverse group of species provides valuable information that can be used in the elucidation of concepts on biogeography and evolution that are presented in this paper. While a wider discussion of this genus and its many complexes of sibling species awaits a future publication, in this paper we discuss the *Bactrocera dorsalis* (Hendel) complex in light of current knowledge of biogeography and evolution in the Asia-Pacific region. Within the *dorsalis* complex, 70 species were recognized in South-East Asia by Drew & Romig (2013) and eight listed for Papua New Guinea and Australia by Drew (1989). Seventy-nine species are now included in this paper. Within this complex, two major groups occur, one with species responding to methyl eugenol and the other to cue lure. The 34 non-cue lure responding group of species are discussed, most of which respond to methyl eugenol and seven of which are recognized as having pest status, namely, *B. carambolae* Drew & Hancock, *B. caryeae* (Kapoor), *B. dorsalis* (Hendel), *B. kandiensis* Drew & Hancock, *B. occipitalis* (Bezzi), *B. ochroma* Drew & Romig and *B. papaya*e Drew & Hancock. An eighth species, *Bactrocera invadens* Drew, Tsuruta & White is included in this discussion on the basis of its molecular similarity to *B. dorsalis*. The remaining group of 45 species, mostly cue lure-responding and including the pest species *B. pyrifoliae* Drew & Hancock and *B. syzygii* White & Tsuruta, are also discussed. Morphological and ecological data are presented for each pest species and their biosecurity risks assessed. In addition, new data based on further research on the male aedeagus have demonstrated that *B. carambolae*, *B. occipitalis, B. papayae* and *B. invadens* are markedly different from *B. dorsalis* in the dimensions and shape of the glans and preglans appendix. Based on this evidence, and that presented by Drew & Romig (2016), the withdrawal of *B. papayae* and *B. invadens* from synonymy with *B. dorsalis* by Drew & Romig (2016) remains valid, while the similarity in aedeagus characters between *B. papayae* and *B. philippinensis* further supports the synonymisation of these two species. The remainder of the 34 non-cue lure responding species are distributed from the Indian subcontinent, across South-East Asia, Papua New Guinea and north-eastern Australia, some with restricted geographic distributions and specific host plant species. Comments on the reliability of molecular phylogenies in the Dacini are included, with the published mitogenome of '*Dacus longicornis*' regarded, on morphological evidence, as data based on a misidentification of *Dacus* (*Mellesis*) *polistiformis* (Senior-White), and the recent synonymy of *B. albistrigata* (de Meijere) with *B. frauenfeldi* (Schiner) considered to be based on insufficient evidence.

Key words: *Bactrocera*, *dorsalis*, host fruit, pest status, biosecurity, aedeagus

Introduction

When taxonomic research is undertaken on large taxa, valuable insights into regional biogeography and evolution are obtained. Further, groups of sibling species are encountered. These often cause serious difficulties in the specific definition of some fruit fly populations. The study of such complexes of species has become an important part of biology and requires the collation of research data from disciplines such as Biogeography, Ecology and Genetics,

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and an understanding of the Concept of Speciation based on the processes of speciation within the organisms' natural habitat. The diagnosis and definition of species is not just an academic luxury but has major contributions to make in economic arenas such as agriculture and environmental impact studies. Furthermore, as Novotny *et al.* (2007) pointed out, incomplete taxonomic knowledge not only hinders the mapping of distribution records but also the assessments of evolution and biogeography.

In the family Tephritidae, extensive speciation in the Tribe Dacini across South-East Asia and the South Pacific has led to a large number of species, particularly in the genus *Bactrocera* Macquart. Some species are placed in morphological species complexes or groups, particularly for efficiency in identification. Our understanding of the processes of speciation has been supported by our extensive knowledge of the biogeography of the fauna and its relationship with the tropical and subtropical rainforests (Drew & Hancock, 2000; Drew, 2004). One such complex, the *dorsalis* complex, is a large group of species within the genus *Bactrocera*, first studied by Hardy (1969) and later reviewed and expanded to 52 species by Drew & Hancock (1994) and recently re-examined and defined by Drew & Romig (2013, 2016). As noted by Drew (2004), the majority of species within this complex occur in South-East Asia from India to Indonesia, with a few endemics in Papua New Guinea and Australia. Because this is the largest complex of sibling species in the South-East Asian region, a further analysis of species provides us with the opportunity to further our understanding of the evolution of the Dacini. Also, because this complex contains major pest species, some with unique host plant relationships, it is important to list and define these species and reflect on their impact on international biosecurity and trade. The nine known pest species plus *B. invadens* are discussed in this paper and defined on the basis of morphological and ecological characters.

This paper brings together our current knowledge of the *Bactrocera dorsalis* (Hendel) complex of fruit fly species, our understanding of the biogeography of the group, and a discussion on the necessity of applying a Concept of Speciation that fits with the ecology of species and the process of speciation. Further, the major pest species that impact fruit and vegetable production and trade in the Asian-Pacific Region are discussed. Data have been collected from published literature and recent morphological research on the male genitalia. The published literature covers research conducted over the past five decades, particularly on species occurring in South-East Asia. Data on the morphology of the male aedeagus of five major pest species, *B. dorsalis* (Hendel), *B. carambolae* Drew & Hancock, *B. occipitalis* (Bezzi), *B. invadens* Drew, Tsuruta & White and *B. papayae* Drew & Hancock, have resulted from research at Griffith University and undertaken on specimens reared from field collected host fruits in Papua New Guinea and Sabah (East Malaysia) and specimens attracted to methyl eugenol male lure traps in China, Sri Lanka, Philippines, Borneo, Peninsular Malaysia and Indonesia.

Biogeography of the Indo-Malayan Rainforests

Given that the rainforests of the Asian-Pacific region are the native home of the Dacini and particularly the large genus *Bactrocera*, it is important to review the biogeography of this ecosystem. Worldwide there are three great blocks of tropical rainforests, the Indo-Malayan being the second largest and possessing greatest species richness with regard to plant and animal life (Whitmore, 1986). A process of co-evolution between the plant flora and the animal and insect fauna was concluded by Whitmore (1986), as did Drew (2004) for the Dacini.

The Indo-Malayan rainforest block consists of two major sections, the Western block based on the Sunda Continental Shelf and the Eastern block based on the Sahul Continental Shelf. The Western block is centred over Sumatra, the Malay Archipelago and Borneo, with small outlying pieces on Sri Lanka, the Western Ghats of India, the Andaman Islands, Myanmar, Southern Thailand, Southwest China, South Vietnam and the Philippines. The Eastern block is centred over Papua with smaller outlying pieces in northeastern Australia, Solomon Islands, Vanuatu, Fiji, Samoa, Tonga and Micronesia. The outlying pieces possess increasing floristic poverty, represented by reduced species richness with distance from the main centres.

The Indo-Malayan rainforest, at its primary centres the Western and Eastern blocks, is known for its great species richness, which supports animal and insect life (Whitmore, 1986). Over the Western block alone, 40% of plant genera and over 40% of the 25,000 recorded species are endemic. In Papua New Guinea, now representing the Eastern block, some 8,000 plant species have been recorded. Novotny *et al.* (2010) described the complex and species-rich plant-herbivore food web of Papua New Guinea. In their study, fruit flies were found to be highly specialized with regard to feeding on their host plants (Novotny *et al*., 2010), a conclusion also reached by Novotny *et al*. (2005) and Drew (2004).

An extremely valuable zone of biogeographic transition is Wallacea, bounded by Wallace's line in the West, which runs between the islands of Bali and Lombok, and Lydekker's line in the East, which runs east of Timor and Seram. Wallacea contains elements of the floras of both Malesia and Papua with additional endemic species of its own (Whitmore, 1986; Drew, 2004). An analysis of the fauna and flora in Wallacea provides an insight into the outcomes of speciation across a transition zone.

Evolutionary Geology of the Indo-Malayan Region

The influence of Gondwana on the biogeography and biology of the Asian-Pacific region has long been recognised. The most significant events of regional geology that have affected the biogeography of the Indo-Malayan region were the progressive breakup of Gondwana as the Indian fragment drifted northwards to collide with northern Laurasia, while the Australian/Papuan fragment collided with the southeast extremity of Laurasia in the area of Sulawesi (Whitmore, 1986). Under this theory, plants and animals would have reached the Indo-Malayan region via three possible routes, Laurasia, Gondwana via Australia, or Gondwana via India. The intermingling of flora and associated fauna from Gondwana and Laurasia has contributed to the high level of species richness that we know today. While these geological constructions can explain the close botanical relationships, at the generic level, between the Indo-Malayan rainforests of Australia, Papua New Guinea, southeast Asia and India, Hall (1998) stated that the present geographic distribution of plants also could have resulted from activities over the last one million years.

Within the Australian region, Drew (2004) noted that fossil records indicate that Diptera became established and speciated from 150,000 years ago, influenced by glaciation cycles. Hall (2001) noted that geologically induced changes in topography, localized climates and changes in land bridges during glaciation cycles have directly influenced speciation in plants and animals. One could add that the resulting development of the numerous islands and speciation associated with them were also a significant outcome during this period. The complex island formations associated with the Sunda Continental Shelf on one hand and the Sahul Continental Shelf on the other, mostly developed by the changes in land bridge connections, have led to a high degree of endemism across the Asian-Pacific region, on both continental areas and islands.

Species and Speciation

Experienced taxonomists studying large groups of insects generally separate species on the basis of morphological characters. However, this basis alone becomes difficult when complexes of sibling species are encountered. When making decisions on sibling species, it is important to elucidate the concept of species, and thus speciation, upon which decisions are made. The two species models most commonly used, the 'biological species concept' and the 'recognition concept of species', are diametrically opposed and are discussed here. It explains the basis upon which we and others have described species over many years.

The 'biological species concept' was initiated by A.R. Wallace (1889) and expanded by Dobzhansky (1935). Under this concept, species are defined in terms of reproductive isolation that leads to populations that cannot breed together or, if they do, produce sterile progeny. The recognised isolating mechanisms have been defined as both premating and postmating. However, because sterility arises from breeding together two parental populations, the isolation is clearly postmating and thus cannot be regarded as part of genuine isolating mechanisms leading to the development of new species. While followers of this concept have been led to define species on the basis of laboratory-based research such as crossbreeding experiments, enzyme electrophoresis and molecular analyses that measure genetic distance between species, we assert that this approach provides inconclusive results, particularly when attempting to align species with their ecological characteristics in their known habitat.

In contrast, the 'recognition concept of species', first proposed by Paterson (1973), is the one on which we base our own taxonomic decisions on species. This approach is based on considerable advances in our knowledge of dacine ecology and behaviour of populations in their host fruiting plants. The principal points in this concept are as follows—

(i) Each species possesses a 'specific mate recognition system' (SMRS), which includes courtship and mating behaviour. The mate recognition system brings the sexes of a species together to reproduce. Significant advances in our knowledge of the ecology and behaviour of *Bactrocera* species support this concept of speciation (Drew, 2004). Over four decades, we have undertaken host fruit surveys of rainforest and edible fruits across South-east Asia and the South Pacific (including Australia). Approximately 135,000 fruit samples were collected and incubated, resulting in the definition of species-specific host plants (Allwood *et al.,* 1999; Hancock *et al.,* 2000a; Leblanc *et al*., 2012). Furthermore, host plant courtship and mating are major aspects of *Bactrocera* behaviour (Drew & Lloyd, 1987; Drew *et al.,* 2008). Consequently, the SMRS for *Bactrocera* species includes chemical and visual cues that attract individuals to the host plant (the emission of pheromones and wing beat calling signals by males within the host) that attract females to the specific mating site, usually on lower surfaces of leaves.

(ii) Habitat preference is a basic species-specific character.

(iii) Ecological knowledge is fundamental to understanding speciation and defining species.

(iv) Within a species, mating partners are coadapted to finding their hosts, courtship and mating sites.

(v) The fertilisation system fits with the environment in which the species resides. This, in the case of *Bactrocera* species, equates with the host plant.

(vi) The habitat, the host plant of a species, accommodates the key factors within which speciation has occurred. Thus, significant changes in the habitat can lead to a speciation event.

(vii) Biological discontinuities such as differences in host plants can provide evidence of unsuspected sibling species.

Taxonomy and Phylogeny of the genus *Bactrocera*

The genus *Bactrocera* is a large genus comprising some 750 known species distributed across Southeast Asia (including the Indian subcontinent) and the Pacific region and, weakly, the Afrotropics. Most of the subgenera have been treated in a series of reviews in the journal *Australian Entomologist* by the present authors from 2015-2019 (e.g. Hancock & Drew, 2018: for a full list see Drew & Romig, 2022) and a review of subgenus *Bactrocera*, the largest and most speciose of the recognized subgenera, is currently under preparation.

Our extensive research into *Bactrocera* species biology, in particular adult feeding, courtship and mating behaviour, has demonstrated that these behaviours occur within the host plants and the host plant has been called the ‘Centre of Activity’ for a species population (Drew & Lloyd, 1987). In Australia 37% of species are monophagous and in Southeast Asia 33%. Similarly, 21% and 14%, respectively, are polyphagous, and those that are polyphagous generally still have a preference for one or a few host fruit sprcies. Most pest species are polyphagous within their rainforest habitat, while a few are specialists.

Because *Bactrocera* species have a close relationship with their host plants, particularly based on their reproductive behaviour, and because their endemic host plants belong primarily to the tropical and subtropical rainforests, we can map the phylogenetic relationships, evolution and distribution of species in association with our knowledge of the rainforest biogeography and geology.

The parental stock of the Dacini probably originated on the Indian block of Gondwana as it drifted northwards, and with the genus *Bactrocera* becoming established in the rainforests, before the unification of Gondwana with Laurasia. After unification, *Bactrocera* underwent prolific speciation in a pattern of co-evolution with the rainforest flora. This concept is consistent with our knowledge of geological time frames and evolution of the flowering and fruiting plants in the rainforests of Southeast Asia and the Pacific region.

Prolific speciation in this species-rich rainforest ecosystem has resulted in a large number of Dacini species and numerous morphological species complexes. Under the ‘recognition concept of species’, in fauna where non-morphological cues are used to bring individuals together in courtship and mating, such as in many *Bactrocera* species, speciation can occur without accompanying divergence in morphological characters. This clearly is the situation that has resulted in the large *Bactrocera dorsalis* (Hendel) complex of fruit flies, where difficulties occur in identifying species on morphology alone. Following, we discuss the *dorsalis* complex and the difficulties in differentiating some species.

The *Bactrocera dorsalis* complex

This is a large complex of almost 80 morphologically similar species that occur across the Asia-Pacific region.

It represents an excellent example of a species complex in which difficulties occur for workers charged with the responsibility of identifying specimens, particularly those resulting from biosecurity surveys. At the forefront, also, is the necessity for researchers to identify and describe these sibling species, using morphology as a key procedure.

The degree of divergence in genes that influence external morphological characters is not necessarily representative of the total of all genetic changes that occur during the process of speciation. In fact, the mere existence of sibling species with varying degrees of genetic similarity indicates that there is no consistent relationship between morphological and genetic change at speciation (Lambert & Paterson, 1982). This inherent problem not only raises difficulties for workers identifying species morphologically but also casts doubt on the application of molecular data based on a limited number of genes.

The highest density of *dorsalis* complex species occurs over the Sunda Continental Shelf countries, especially those centred around Peninsular Malaysia, Indonesia (especially Sumatra), Thailand, Vietnam, Cambodia and Borneo. As an example, the number of species per country of the 34 methyl eugenol plus allies subgroup defined below is shown in Table 1. This distribution pattern matches that of the species-rich Indo-Malayan rainforests described by Whitmore (1986) and, with the exception of India, with increasing distance from this centre the numbers decline.

TABLE 1. The number of *dorsalis* complex species in the 34 methyl eugenol plus allies subgroup (listed in Table 2) recorded from countries across the Asia-Pacific Region.

COUNTRY	NUMBER OF SPECIES	COUNTRY	NUMBER OF SPECIES
Thailand	8	Nepal	2
Indonesia	8	Andaman Islands	2
Vietnam	6	China	2
India	6	Papua New Guinea	2 (+ 1 adventive)
Peninsular Malaysia	6	Pakistan	1
Cambodia	5	Myanmar	1
Borneo (East Malaysia, Brunei, Kalimantan)	5	Laos	1
Sri Lanka	4	Palau	1
Bangladesh	3	Taiwan	1
Bhutan	3	Singapore	1
Philippines	3	Timor	1 (+ 3 adventives?)
Australia	3	Christmas Island	1 (+ 1 adventive)

Across the genus *Bactrocera*, the Philippines and Borneo possess a large number of species in common, with the Philippines also possessing its own level of endemism. This situation is also represented in the *dorsalis* complex, where *B. occipitalis* and *B. papayae* are shared, while *B. collita* is endemic to the Philippines. This situation is most likely a result of the Philippines splitting later from the main centre of speciation. Four species have been recorded in Wallacea, all endemic to that transition zone, i.e. *B. floresiae* Drew & Hancock, *B. infulata* Drew & Hancock, *B. minuscula* Drew & Hancock and *B. sulawesiae* Drew & Hancock. Further east in Papua New Guinea and related territories, the *dorsalis* complex is poorly represented. There are no species with *dorsalis* complex characters in the Pacific Region east of Papua New Guinea. In Australia there are three species, *B. cacuminata* (Hering), *B. endiandrae* (Perkins & May) and *B. opiliae* (Drew & Hardy).

Species in the *Bactrocera dorsalis* complex

The *dorsalis* complex is a polyphyletic assemblage of some 79 species established on morphological characters (principally a largely or entirely black scutum) as an aid to identification. Occurring primarily in the Indo-Australian Region, it has become adventive in Africa, Hawaii, Tahiti, the Mariana Islands and North-East South America. It belongs in subgenus *Bactrocera* Macquart, by far the most speciose of the subgenera included in the *Bactrocera* group of subgenera as recognised by Hancock & Drew (2018). The complex is currently defined as: species with distinct dark facial spots; scutum largely or entirely black or with a black lanceolate pattern in at least most specimens; lateral postsutural yellow vittae present; medial postsutural yellow vitta absent; wing colourless except for a narrow costal band (not or at most faintly reaching vein R_{4+5}) and anal streak; costal cells bc and c hyaline or with a very pale fulvous tint and with microtrichia only in anteroapical corner of cell c; legs with femora entirely pale or with dark subapical spots or apical markings; scutellum yellow with a dark basal band and never with other dark patterns; abdomen with pale posterior band on tergite II not divided medially and tergites III-V with a dark 'T' pattern and with or without variable dark lateral margins.

Within the complex is a group of possibly closely related species that respond to the male lure methyl eugenol or have no or an unknown response to male lures and have generally long and parallel-sided lateral postsutural yellow vittae and a needle-like, non-trilobed aculeus. *Bactrocera arecae* shows no response to known lures and the response is unknown for *B. irvingiae* and *B. muiri*. However, as interpreted here, this group contains at least eight species of economic importance, being pests of a wide range of horticultural crops. Although it usually has a largely red-brown scutum, *B. invadens* is included in this review based on its molecular similarity to *B. dorsalis*, *B. papayae* and *B. carambolae*; some specimens also have the scutum largely or entirely black. Several recent studies have suggested that these four species are virtually indistinguishable on the limited molecular data used but the species differ both morphologically and in their host plant preferences (e.g., Drew & Romig, 2022). Two Australian species, *B. cacuminata* (Hering) and *B. opiliae* (Drew & Hardy) also have some specimens with a largely red-brown scutum.

Included species: *B. amarambalensis* Drew, *B. arecae* (Hardy & Adachi), *B. atrifemur* Drew & Hancock, *B. binhduongiae* Drew & Romig, *B. bivittata* Lin & Wang, *B. cacuminata* (Hering), *B. carambolae* Drew & Hancock, *B. caryeae* (Kapoor), *B. collita* Drew & Hancock, *B. dapsiles* Drew, *B. dorsalis* (Hendel), *B. endiandrae* (Perkins & May), *B. floresiae* Drew & Hancock, *B. indonesiae* Drew & Hancock, *B. infulata* Drew & Hancock, *B. invadens* Drew, Tsuruta & White, *B. irvingiae* Drew & Hancock, *B. kanchanaburi* Drew & Hancock, *B. kandiensis* Drew & Hancock, *B. latilineola* Drew & Hancock, *B. minuscula* Drew & Hancock, *B. muiri* (Hardy & Adachi), *B. neoarecae* Drew, *B. occipitalis* (Bezzi), *B. ochroma* Drew & Romig, *B. opiliae* (Drew & Hardy), *B. papayae* Drew & Hancock, *B. paraarecae* Drew & Romig, *B. paraverbascifoliae* Drew, *B. raiensis* Drew & Hancock, *B. ranganathi* Drew & Romig, *B. sulawesiae* Drew & Hancock, *B. unimacula* Drew & Hancock, *B. verbascifoliae* Drew & Hancock. Their distribution and host plant families are listed in Table 2. The Papuan species *B. diallagma* Drew, with a relatively broad costal band and wholly fuscous femora, is distinctive and excluded from the complex. For illustrations and keys to species see Drew (1989), Drew & Hancock (1994) and Drew & Romig (2016). For host plant details see Allwood *et al*. (1999), Drew & Romig (2013) and Drew (1998).

Morphological relationships

The species in Table 2 can be divided into two groups based on the width of the lateral postsutural yellow vittae. Species with a distinct dark pattern on a red-brown scutum, such as *B. bivittata* Lin & Wang, *B. cacuminata* (Hering), *B. invadens* Drew, Tsuruta & White and *B. opiliae* (Drew & Hardy), are split between the groups. A largely black scutum is widespread in the *dorsalis* complex and the largely red-brown pattern on some specimens of the species included above, from widely disjunct localities, is assumed to be apomorphic and homoplasious. Similarly, species with a mostly black scutum and lateral postsutural yellow vittae narrowing posteriorly, such as *B. caryeae* (Kapoor), *B. dapsiles* Drew and *B. endiandrae* (Perkins & May), are also from widely disjunct localities and the posterior narrowing of the vittae is also assumed to be apomorphic and homoplasious.

Group 1. Species normally with a mostly black scutum and narrow parallel-sided lateral postsutural yellow vittae (generally less than 0.15 mm in centre): *B. amarambalensis* Drew, *B. arecae* (Hardy & Adachi), *B. kandiensis* Drew & Hancock, *B. neoarecae* Drew, *B. paraarecae* Drew & Romig, *B. paraverbascifoliae* Drew and *B. verbascifoliae* Drew & Hancock; *B. invadens* and *B. caryeae* noted above are also included. These species are largely from the Indian subcontinent and neighbouring areas of South-East Asia and the narrow vittae possibly represent a shared apomorphy, although *B. arecae*, with non-lure responding males and a non-Indian distribution, is likely to be distinct.

Group 2. Species normally with a mostly black scutum and broad parallel-sided or subparallel lateral postsutural yellow vittae (more than 0.15 mm in centre):: *B. atrifemur* Drew & Hancock, *B. binhduongiae* Drew & Romig, *B. carambolae* Drew & Hancock, *B. dorsalis* (Hendel), *B. irvingiae* Drew & Hancock, *B. kanchanaburi* Drew & Hancock, *B. latilineola* Drew & Hancock, *B. muiri* (Hardy & Adachi), *B. occipitalis* (Bezzi), *B. ochroma* Drew & Romig, *B. papayae* Drew & Hancock, *B. raiensis* Drew & Hancock, *B. ranganathi* Drew & Romig and

TABLE 2. List of species included in the methyl eugenol responding and allies subgroup of the *dorsalis* complex, their distributions and principal host plant families.

Species	Distribution	Host plant family
B. amarambalensis Drew	S. India	Unknown
B. arecae (Hardy & Adachi)	S. Thailand, W. Malaysia, Singapore & Christmas I.	Arecaceae
B. atrifemur Drew & Hancock	W. Malaysia, Indonesia (Bangka I.)	Myristicaceae
B. binhduongiae Drew & Romig	Vietnam	Unknown
B. bivittata Lin & Wang	China (Hainan I.), Cambodia, Vietnam	Unknown
B. cacuminata (Hering)	E. Australia	Solanaceae
B. carambolae Drew & Hancock	Bangladesh to Indonesia; adventive in NE South America	Polyphagous pest
B. caryeae (Kapoor)	S. India	Polyphagous pest
B. collita Drew & Hancock	Philippines	Unknown
B. dapsiles Drew	Papua New Guinea	Solanaceae
B. dorsalis (Hendel)	SE Asia from Myanmar to Taiwan; adventive in Hawaii, Tahiti and Mariana Is.	Polyphagous pest
B. endiandrae (Perkins & May)	E. Australia, Papua New Guinea	Lauraceae, Annonaceae
B. floresiae Drew & Hancock	Indonesia (Flores, Sumbawa, Timor)	Anacardiaceae, Myrtaceae
B. indonesiae Drew & Hancock	Indonesia (Java)	Unknown
B. infulata Drew & Hancock	Indonesia (Sulawesi)	Unknown
B. invadens Drew, Tsuruta & White	Bangladesh, Bhutan, India, Nepal, Pakistan, Sri Lanka; adventive in Africa	Polyphagous pest
B. irvingiae Drew & Hancock	Thailand	3 families recorded
B. kanchanaburi Drew & Hancock	Thailand, Cambodia, Vietnam	Annonaceae
B. kandiensis Drew & Hancock	Sri Lanka	Anacardiaceae, Clusiaceae
B. latilineola Drew & Hancock	W. Malaysia	Unknown
B. minuscula Drew & Hancock	Timor	Anacardiaceae, Myrtaceae
B. muiri (Hardy & Adachi)	Indonesia (Kalimantan)	Unknown
B. neoarecae Drew	S. India	Unknown
B. occipitalis (Bezzi)	Philippines, Borneo	Polyphagous pest
B. ochroma Drew & Romig	Indonesia	Anacardiaceae
B. opiliae (Drew & Hardy)	N. Australia	Opiliaceae
B. papayae Drew & Hancock	S. Thailand to Timor; adventive in New Guinea & Christmas I.	Polyphagous pest
B. paraarecae Drew & Romig	Bhutan, Cambodia	Unknown
B. paraverbascifoliae Drew	S. India, Sri Lanka	Unknown
B. raiensis Drew & Hancock	Thailand, Vietnam	4 families recorded
B. ranganathi Drew & Romig	India (Andaman Is.)	Unknown
B. sulawesiae Drew & Hancock	Indonesia (Sulawesi)	Unknown
B. unimacula Drew & Hancock	W. Malaysia, Borneo	Unknown
B. verbascifoliae Drew & Hancock	Bhutan & India to Thailand	Solanaceae

B. unimacula Drew & Hancock. This group is largely South-East Asian in distribution and appears to represent the plesiomorphic condition within the complex, the pattern of a mostly black scutum and broad postsutural vittae being widespread within the *Bactrocera* group of subgenera. The non-Indian species with a largely red-brown scutum (including *B. bivittata* Lin & Wang) or tapering lateral postsutural yellow vittae noted above are also associated with this group and the Australian *B. endiandrae*, *B. cacuminata* and *B. opiliae*, all with very narrow costal bands and entirely fulvous femora, possibly form a separate monophyletic group that might also include the Papuan *B.*

dapsiles, which also has entirely fulvous femora but a broader costal band. The largely Indonesian *B. collita* Drew & Hancock, *B. floresiae* Drew & Hancock, *B. indonesiae* Drew & Hancock, *B. infulata* Drew & Hancock, *B. minuscula* Drew & Hancock and *B. sulawesiae* Drew & Hancock, which also have tapering vittae, possibly also form a separate monophyletic group.

The remaining *dorsalis* complex species (all non-responsive to methyl eugenol) may be grouped as follows and include the pest species *B. pyrifoliae* and *B. syzygii*:

(a) Cue lure responding species with subparallel to strongly tapering postsutural lateral yellow vittae [India and Sri Lanka to Papua New Guinea and Australia]: *B. aemula* Drew, *B. affinidorsalis* (Hardy), *B. bimaculata* Drew & Hancock, *B. bitungiae* Drew & Romig, *B. cibodasae* Drew & Hancock, *B. cognata* (Hardy & Adachi) [lure unrecorded], *B. consectorata* Drew, *B. dongnaiae* Drew & Romig, *B. dorsaloides* (Hardy & Adachi) [lure unrecorded], *B. fernandoi* Tsuruta & White, *B. flavoscutellata* Lin & Wang, *B. flavosterna* Drew & Romig, *B. fuliginus* Drew & Hancock, *B. fulvifemur* Drew & Hancock, *B. fuscitibia* Drew & Hancock, *B. gombokensis* Drew & Hancock, *B. hantanae* Tsuruta & White, *B. holtmanni* (Hardy), *B. involuta* (Hardy), *B. kalimantaniae* Drew & Romig, *B. kinabalu* Drew & Hancock, *B. laithieuiae* Drew & Romig, *B. lateritaenia* Drew & Hancock, *B. lombokensis* Drew & Hancock, *B. makilingensis* Drew & Hancock, *B. malaysiensis* Drew & Hancock, *B. merapiensis* Drew & Hancock, *B. neocognata* Drew & Hancock, *B. pedestris* (Bezzi), *B. penecognata* Drew & Hancock, *B. profunda* Tsuruta & White, *B. quasiinfulata* Drew & Romig, *B. sapaensis* Drew & Romig, *B. sembaliensis* Drew & Hancock, *B. sumbawaensis* Drew & Hancock, *B. usitata* Drew & Hancock, *B. vishnu* Drew & Hancock. Leblanc *et al.* (2015) illustrated variation in scutal and abdominal patterns within this and the following two groups and included *B. kohkongiae* Leblanc, which has a variably patterned (non-lanceolate and often largely red-brown) scutum and possibly belongs elsewhere; it did not group with any other *dorsalis* complex species in their molecular phylogeny. The zingerone (=vanillylacetone) responding *B. syzygii* White & Tsuruta also appears to belong in this group.

(b) Cue lure responding species with long, subparallel lateral yellow vittae and aculeus with apex trilobed [Thailand to Philippines and Borneo]: *B. neopropinqua* Drew & Hancock, *B. propinqua* (Hardy & Adachi), *B. quasipropinqua* Drew & Hancock [lure unrecorded].

(c) Cue lure responding 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 (including fuscous ceromata) [Bhutan to Indonesia]: Two species pairs: *B. melastomatos* Drew & Hancock and *B. osbeckiae* Drew & Hancock, with transversely oval ceromata; plus *B. pyrifoliae* Drew & Hancock and *B. thailandica* Drew & Hancock, with broadly rounded ceromata.

Host plant relationships

During the 1970s we realised that dacine species could not be diagnosed on morphological characters alone and thus we began a research program into ecological aspects of some readily available species populations. This research led to an understanding that dacine species have a close association with their host plants and that their reproductive behaviour is dependent upon the host plant (Drew, 1987; Drew & Lloyd, 1987; Drew *et al*., 2008). In this research, host plant courtship and mating and oviposition were recorded as key components linking a species to its host plant and provided valuable evidence for enabling identification of some *Bactrocera* species by their hosts.

Under the Recognition Concept of Species, each species possesses a specific mate recognition system that brings the sexes together for courtship and mating. Significant advances in our knowledge of the reproductive behaviour of *Bactrocera* species on their host plants have enabled us to define the host plant as a major component of the mate recognition system of a particular fly species. Such ecological knowledge is fundamental to defining *Bactrocera* species and particularly those in morphological complexes such as the *dorsalis* complex.

The extensive host fruit sampling across South-East Asia and the South Pacific (Allwood *et al*., 1999; Hancock *et al*., 2000a; Leblanc *et al*., 2012) has provided valuable host plant records for a large number of tephritid species. From these data, Drew (2004) noted the specific host associations for 67 dacine species in South-East Asia and 53 in Australia, adding further evidence to the value of using host records as supporting evidence in the diagnosis of species.

Based on our current knowledge of host records and geographic distributions, most of the *dorsalis* complex species and all of the polyphagous species occur in India or South-East Asia. The concentration of this group within that biogeographic area is of interest from the viewpoint of speciation and biogeography. Drew (2004) noted that

33 percent of all South-East Asian *Bactrocera* species were essentially monophagous or stenophagous, either with a single or a few host species within a single plant family. Within the *dorsalis* complex, 30 percent of the South-East Asian species where host records are known are monophagous or stenophagous, demonstrating conformity with the entire genus *Bactrocera*. The strong behavioural relationship between *Bactrocera* species and their Indo-Malayan rainforest host plant species has led to prolific speciation through a process of coevolution in the South-East Asian biogeographic region (Drew, 2004), particularly after the break-up of Gondwana (Drew & Hancock, 2000). Given that South-East Asia is a 'hot spot' for dacine speciation (Drew, 2004), particularly the continental area of Thailand to Vietnam and Peninsular Malaysia and the isolated islands of the Philippines, Indonesia and Borneo, we can conclude that this group of *dorsalis* complex cryptic species has resulted in morphological similarity, often only separated by host specificity and minor morphological character states. Further, it must be understood that morphological characters are under the influence of specific genes, most of which are still to be identified.

Within Group 1, host plants have been recorded for 5 of the 9 species (Allwood *et al*., 1999; Drew & Romig, 2013). Two of the species are known from a single plant family, each with hosts in different plant families: *B. arecae* (family Arecaceae) and *B. verbascifoliae* (family Solanaceae), while *B. kandiensis* is oligophagous (families Anacardiaceae and Clusiaceae) and *B. caryeae* and *B. invadens* are polyphagous.

Within Group 2, host plants have been recorded for 15 of the 25 species (Allwood *et al*., 1999; Drew, 1989; Drew & Romig, 2013). Six of the species are known from a single plant family, most with hosts in different plant families: *B. atrifemur* (family Myristicaceae), *B. kanchanaburi* (family Annonaceae), *B. ochroma* (family Anacardiaceae), *B. cacuminata* and *B. dapsiles* (family Solanaceae: *Solanum mauritianum*) and *B. opiliae* (family Opiliaceae). For the four polyphagous species, significant host specificity is exhibited in their preferred major hosts: *B. carambolae* (carambola), *B. dorsalis* (guava), *B. occipitalis* (mango), *B. papayae* (papaya, banana). The remaining five species, which we regard as oligophagous, exhibit some specificity and some overlap in hosts: *B. irvingiae* (families Annonaceae, Meliaceae, Moraceae and Simaroubaceae), *B. raiensis* (families Asclepiadaceae, Dilleniaceae, Meliaceae and Moraceae), *B. endiandrae* (families Annonaceae and Lauraceae, especially the latter), *B. floresiae* and *B. minuscula* (families Anacardiaceae and Myrtaceae—see Bellis *et al*., 2017). Subject to further research, *B. irvingiae* and *B. raiensis* might prove to be conspecific, as also might *B. floresiae* and *B. minuscula*.

Within the cue lure-zingerone group, 11 of the 45 included species have their host plants recorded (Allwood *et al*., 1999; Drew & Romig, 2013). All except one are known from a single plant family (see Table 3); the pest species *B. pyrifoliae* is oligophagous (families Araliaceae, Euphorbiaceae, Myrtaceae, Polygalaceae and Rosaceae, especially the latter).

TABLE 3. List of species with known host plant records included in the non-methyl eugenol responding subgroup of the *dorsalis* complex, their distributions and known host plant families.

Species	**Distribution**	**Host plant family**
B. dorsaloides (Hardy & Adachi)	Philippines	Sapotaceae
B. kinabalu Drew & Hancock	West and East Malaysia	Melastomataceae
B. melastomatos Drew & Hancock	Andaman Is to Indonesia	Melastomataceae flowers
B. neocognata Drew & Hancock	Malaysia to Indonesia, Vietnam	Myrtaceae
B. osbeckiae Drew & Hancock	Thailand, Vietnam	Melastomataceae flowers
B. pedestris (Bezzi)	Philippines, Thailand	Meliaceae
B. propinqua (Hardy & Adachi)	Vietnam to East Malaysia	Clusiaceae
B. pyrifoliae Drew & Hancock	Thailand, Vietnam	5 families recorded
B. quasipropinqua Drew & Hancock	Philippines	Sapotaceae
B. syzygii White & Tsuruta	Indian subcontinent, Vietnam	Myrtaceae
B. thailandica Drew & Hancock	Bhutan to Vietnam, Brunei	Elaeocarpaceae

Molecular relationships

At the species level there has been a large number of published papers presenting molecular data on *Bactrocera* species. Most papers have produced phylogenetic trees defining relationships between species. In most publications, valuable data are presented, many confirming morphological separation of species and others questioning the definitions based on morphology. For example, the Yong *et al.* (2021) Bayesian phylogenetic and maximum likelihood trees aggregate some species that are morphologically similar, e.g., *B. dorsalis*, *B. carambolae*, *B. invadens*, *B. papayae*, while separating *B. arecae*, which morphologically is extremely close to *B. dorsalis* but has a different lure response (none). The same trees place *B. correcta* and *B. zonata* together; these are morphologically distinct species but possess similar unique wing patterns. They also place together *B. melastomatos* and *B. rubigina*, two markedly distinct species based on morphology and biology; Leblanc *et al*. (2015) grouped these two species with *B. osbeckiae* but considered them separate based on colour pattern and nucleotide gene differences.

Doorenweerd *et al.* (2020) presented comprehensive data on CO1 gene sequences for 262 species of Dacini. While they were able to identify many of the species, they still had a 12.6% non-monophyly in the data set. Further, they found that *Bactrocera dorsalis sens. lat.* could be reliably identified but that its CO1 is confused with four other species in the complex [plus '*B*. sp. OTU5353': see below]. However, their data are confounded by the incorrect synonymy and different combinations of species are involved in the introgression: *B. invadens* with *B. kandiensis* in the west, *B. papayae* with *B. carambolae*/*B. occipitalis* in the south and east, and typical *B. dorsalis* with *B. raiensis* in the north. They concluded that reliable molecular identifications with CO1 require extensive species coverage, population sampling and accurate identifications before it can be considered a valid diagnostic marker. Based on published molecular data one can make the same assessments of their value, as we do with the other taxonomic characters that are used. Over some eight character states that we have applied to defining species over several decades, i.e., adult morphology, host plant relationships, tissue enzyme electrophoresis, male pheromone chemistry, molecular analyses, scanning electron microscopy of female genitalia, larval morphology and morphometrics of adult male and female genitalia, not one character state has proven to provide accurate, complete identification in itself, thus cannot be relied upon singularly. *Bactrocera papayae*, for example, exhibits such molecular variability that some specimens sequence outside the *carambolae-papayae* clade, as demonstrated by Boykin *et al.* (2014, specimen '413') and Yaakop *et al*. (2015, as '*dorsalis*'). The widespread '*B*. sp. OTU5353' variant of Doorenweerd *et al.* (2020) occurs among scattered populations of both *B. papayae* and typical *B. dorsalis* (L. Leblanc, pers. comm.). These genetic variants, indistinguishable morphologically, are from molecularly variable cohorts and do not indicate the presence of 'cryptic' species.

The *Bactrocera* group of subgenera appears to be of Papuan origin, where all seven of the included subgenera occur (Hancock & Drew, 2018). Expansion westwards and diversification within South-East Asia is thus relatively recent and it is not surprising that many of the *dorsalis* complex species are poorly differentiated by the molecular markers currently utilised. Relatively low taxon sampling and fragmentary molecular data have resulted in suggested phylogenetic arrangements that are neither robust nor reliable. The most comprehensive study to date (San Jose *et al*., 2018) produced clades within subgenus *Bactrocera* that often contained morphologically unrelated species and were generally very weakly supported, especially the interrelationships between the various clades.

The only well supported molecular clade is that containing the pest species *B. kandiensis, B. dorsalis, B. papayae, B. invadens, B. carambolae* and *B. occipitalis*, plus the non-pest species *B. raiensis* and *B. cacuminata*, which also was recognized by Leblanc *et al*. (2015) and, largely, Dupuis *et al*. (2018), Krosch *et al*. (2012) and Zhang *et al*. (2010), although even here some non-*dorsalis* complex species (the Australian *B. musae* (Tryon) and *B. pallida* (Perkins & May)) were included by most of these authors. Boykin *et al.* (2014) and Nugnes (2018) included *B. opiliae* as sister-taxon to *B. cacuminata* and it is likely that *B. caryeae* will belong in this clade alongside *B. kandiensis*.

Of great concern in the application of molecular data to taxonomy is the fact that some published works are based on incorrectly identified fruit fly species. This results in additional confusion when such data are recorded on online data bases such as GenBank and widely reused. Several examples in the Dacini have been noted by Hancock & Drew (2006) and Kunprom & Pramual (2019). Within the *dorsalis* complex itself, Leblanc *et al.* (2021) noted that '*B. gombokensis*' of Doorenweerd *et al*. (2020) was a misidentification of *B. pedestris*. A further example is *Dacus* (*Callantra*) *longicornis* of Jiang *et al*. (2016), which, based on the provided illustration, is clearly a misidentification of *Dacus* (*Mellesis*) *polistiformis* (Senior-White): the fore femoral spines, dark apical patch of the costal band, lack of anal stripe and the abdominal pattern are all typical of the latter species but not the former. This latter example has led, in turn, to Yong *et al*. (2021), who expressed doubts about the original identification, to incorrectly indicate paraphyly in the *Dacus* subgenus *Mellesis* Bezzi. In a study on *Bactrocera ritsemai* (Weyenbergh) (Song *et al.*, 2018), no data on other character states were provided to confirm the identity of specimens studied. This species belongs to a group of closely related species that are difficult to identify. Specimens of '*B. dorsalis s.s.*' from Bangkok listed in Boykin *et al.* (2014) are likely to be misidentifications of *B. papayae* and incorrectly colour-coded in their figures 1-4. Such molecular data only should be published when the identity of specimens used can be guaranteed.

Comparative studies on the structure of the male aedeagus

Methodology. The morphology and function of the different parts of the male and female reproductive system of *Bactrocera tryoni* (Froggatt) were studied by Drew (1969). In this new study, the structure of the male aedeagus of six nominal species was examined after the method of Drew (1969). The male abdomen was removed and soaked in 10% potassium hydroxide for 24 hours, washed in 10% acetic acid before dissecting out the genitalia in water, then stained in mercurochrome for 15 minutes. The aedeagus was then mounted in a hydrated form in order to avoid distortion of membranous tissue and the preglans appendix ['basal lobe' of previous authors or 'bladder' of Drew (1969)]. This method was followed in contrast to permanent mounting, which requires removal of water using ethanol prior to setting in mounting media, causing the distortion. All specimens were preserved in a dry state before processing and treated in the same manner for study. The length of the preglans appendix and the length of the phallus from the base of the preglans appendix to the apex (including the distal portion of the distiphallus plus the glans and its apical lobe ['apical rod']) were measured using a micrometer eyepiece on a Carl Zeiss stereomicroscope. In addition to the two measurements, the ratio of the preglans appendix to the length of the phallus was calculated (Table 4). Although the shape of the glans appeared constant, the membranous nature of the preglans appendix results in variation in its observed length, so means were applied to all measurements for analysis. For each structure, i.e., the preglans appendix, phallus and the ratio, a single factor ANOVA of the measurements was conducted followed by the Tukey's test to determine which of the means in Table 4 were significantly different. Data for *B. carambolae* were not included in the analysis as only four specimens were available for study. The phallus and preglans appendix were drawn using a drawing tube on a Carl Zeiss microscope.

In addition to the above dissections, mating pairs of *B. tryoni* were collected in laboratory cages, anaesthetized and frozen for 24 hours. The flies were carefully dissected to locate the position of the ovipositor and aedeagus during the process of mating.

TABLE 4. Mean lengths (mm) of preglans appendix and phallus (from base of preglans appendix to apex of glans) and ratio of preglans appendix to phallus for *Bactrocera dorsalis* (Hendel), *Bactrocera occipitalis* (Bezzi), *Bactrocera papayae* Drew & Hancock, *Bactrocera philippinensis* Drew & Hancock and *Bactrocera invadens* Drew, Tsuruta & White.

	Preglans Appendix	Phallus	Ratio
B. dorsalis (n=26)	0.2 a	0.51 a	1:2.55 a
B. occipitalis (n=14)	0.1 b	0.53 a	1:5.3 b
B. papayae (n=20)	0.15 bc	0.59 b	1:3.93 bc
B. philippinensis (n=20)	0.15 bc	0.58 b	1:3.87 bc
B. invadens (n=20)	0.15 bc	0.56 b	1:3.73 bc

Note: For the four specimens of *B. carambolae*, the mean length of the preglans appendix was 0.13 mm, the phallus 0.54 mm, and the ratio of the length of the preglans appendix to the length of the phallus, 1:4.15.

Specimens studied. Specimens were selected from the known localities of the species and in the case of *B. papayae* reared from primary host fruits.

Bactrocera dorsalis (Hendel). 26 males, Southwest China, collector Qing Ji, January 2012, attracted to methyl eugenol.

Bactrocera occipitalis (Bezzi). 2 males, Philippines, Bagumbayan, Batangas, 17.v.1983, A.M. Arida, attracted to methyl eugenol; 1 male, Philippines, Mandane City, 19.viii.1983, V.C. Bontuyan, attracted to methyl eugenol; 1 male, Phlippines, Mt Makiling Botanic Gardens, Alt. 150 m, 12.i.2000, A. O'Toole; 6 males, Philippines, National mango research and development centre, San Miguel, Jordan, Guimaras, 30.6.2001, from laboratory colony; 3 males, Indonesia, Kalimantan, Central Kalimantan, Kota Waringin Timur, Kota Besi, 13.ix.05, Utik Darmanto & Kusyono, attracted to methyl eugenol in citrus; 1 male, Indonesia, Kalimantan, West Kalimantan, Pontianak, Pasir, 16.viii.05, A. Irom, attracted to methyl eugenol in village carambola.

Bactrocera papayae Drew & Hancock. 4 males, Papua New Guinea, Morobe Province, Lae, Bundun Conference Centre, 9.viii.1999, bred from *Citrus maxima* (Family Rutaceae); 1 male (29.ii.2000), 3 males (i.v.2000), Papua New Guinea, Morobe Province, Lae, Bubia Agric. Stn, bred from *Carica papaya* (family Caricaceae); 2 males, Papua New Guinea, Morobe Province, Lae, Markham farm, Mararumi, 6.ix.1999, bred from *Carica papaya* (family Caricaceae); 3 males, Papua New Guinea, Morobe Province, Lae, Markham farm, Mararumi, 28.vii.1999, bred from *Psidium guajava* (family Myrtaceae); 1 male, Papua New Guinea, Madang Province, Madang, Bilbil Village area, 22.vi.2000, bred from *Capsicum* sp. (family Solanaceae); 1 male, Papua New Guinea, Port Moresby, ii-iii.1998, A. Winterer, attracted to methyl eugenol; 5 males, East Malaysia, Sabah, Ulu Dusun, Sandakan, 21.vii.1992, Jinius *et al*., bred from *Garcinia forbesii*.

Bactrocera philippinensis Drew & Hancock. 10 paratypes as follows: Philippines, 3 males, Bgy San Rogue, 17.vi.1983, M. de la Cruz, attracted to methyl eugenol; l male, Bgy San Rogue, 24.vi.1983, M. de la Cruz, attracted to methyl eugenol; 2 males, Bgy San Rogue, i.vii.1983, M. de la Cruz, attracted to methyl eugenol; 1 male, Hamtik, Antigue, 25 June 1983, A.S. Nogodula, attracted to methyl eugenol; 2 males, San Miguel, Jordan, Iloilo, 17.vi.1983, A.S. Nogodula; 1 male, San Miguel, Jordan, Guimarae, July 1983, A. Tugan, attracted to methyl eugenol. Non-type specimens: 10 males, Philippines, National mango research and development centre, San Miguel, Jordan, 30.6.2001, from laboratory colony.

Bactrocera invadens Drew, Tsuruta & White. Sri Lanka: 1 male, Kandy Market, Sep. 16. 1993; 2 males, 22 Sep. 1993, 1 male, 6 Oct. 1993, 1 male, 15 Oct. 1993, 1 male, 18 Oct. 1993, 1 male, 20 Oct. 1993, 2 males, 25 Oct. 1993, Gannoruwa Mountain, Kandy, attracted to methyl eugenol; 1 male, Udawattekele, Kandy, 24 Dec. 1993, methyl eugenol; 5 males, Pelwahera, 25.x.1994; 2 males, 18.xii.1994, 2 males, 21.xii.1994, Thaladuma, methyl eugenol; 1 male, Hingurakgoda, 26.x.1994.

Bactrocera carambolae Drew & Hancock: 1 male, 18 May 1986, 1 male, 9 June 1986, RS Kuala Kangsar, Peninsular Malaysia, Ahmad Abdullah, attracted to methyl eugenol; 2 males, Central and West Java, Indonesia, 1994, Supandi, attracted to methyl eugenol.

Results. Morphometric studies conducted on large sample numbers by Drew *et al*. (2008) found that the length of the male aedeagus was significantly different between *B. dorsalis* and *B. papayae* as well as a strong correlation between length of the aedeagus and female aculeus. In this current study, major differences were recorded in the length of the preglans appendix between *B. dorsalis* (mean 0.2 mm) and *B. occipitalis* (0.1 mm), *B. papayae* (0.15 mm), *B. philippinensis* (0.15 mm) and *B. invadens* (0.15 mm) (Table 4). Further, there were significant differences in the ratio of the length of the preglans appendix to the length of the phallus, between *B. dorsalis* (1:2.55) and *B. occipitalis* (1:5.3), and between these two species and *B. papayae* (1:3.93), *B. philippinensis* (1:3.87) and *B. invadens* (1:3.73) (Table 4). The glans is medially expanded and the internal sclerotized area relatively compact in *B. dorsalis* and tubular with the internal sclerotized area elongate in the other species examined. Figure 1 illustrates the phallus and preglans appendix for: a. *B. dorsalis,* b. *B. occipitalis*, c. *B. papayae*, d. *B. philippinensis*, e. *B. invadens*.

During copulation, the aedeagus enters the ovipositor in a semi-retracted state through the gonopore and traverses the vaginal duct to a position where the apex of the phallus lies adjacent to the entrances to the spermathecae (Fig. 2). In this position, the preglans appendix aligns with the signum (sclerite), a sclerotized structure in the wall of the duct, where the sclerotized tip on the appendix interlocks with the signum. This procedure appears to maintain copulation over an extended period, often up to several hours, during which rapid vibrations of the male abdomen occur. On the basis of the measured structural differences between the species examined and our knowledge of the functional morphology of the male and female reproductive systems, we now have further evidence to show that *B. dorsalis, B. carambolae, B. occipitalis, B. papayae* and *B. invadens* are distinct species, confirming the withdrawal of the latter two species from synonymy with *B. dorsalis* by Drew & Romig (2016) and supported by Hancock *et al*. (2021). Further, these data support the synonymy of *B. papayae* and *B. philippinensis* by Drew & Romig (2016). Added confirmation of the validity of these conclusions is that the illustrations of the glans of *B. dorsalis* from Taiwan in Tseng *et al.* (1992) and *B. invadens* from India in Maneesh *et al*. (2022) and David & Ramani (2019, as *dorsalis*) match in shape those of these species in Figure 1, thus demonstrating a lack of geographic variation.

In the morphometric study of the male and female genitalia of *B. carambolae*, *B. dorsalis*, *B. occipitalis* and *B. papayae* (Drew *et al*., 2008), the length of the male aedeagus was significantly different between *B. carambolae*, *B. dorsalis* and *B. papayae*. Further, there was a strong correlation between the length of the male aedeagus and female aculeus. Moreover, there was no significant intraspecific variation with fly size or geographic distribution. This correlation between the male and female genitalia, combined with our findings above regarding the functional morphology of the two reproductive systems, adds weight to the validity of utilising these data in species definition and identification.

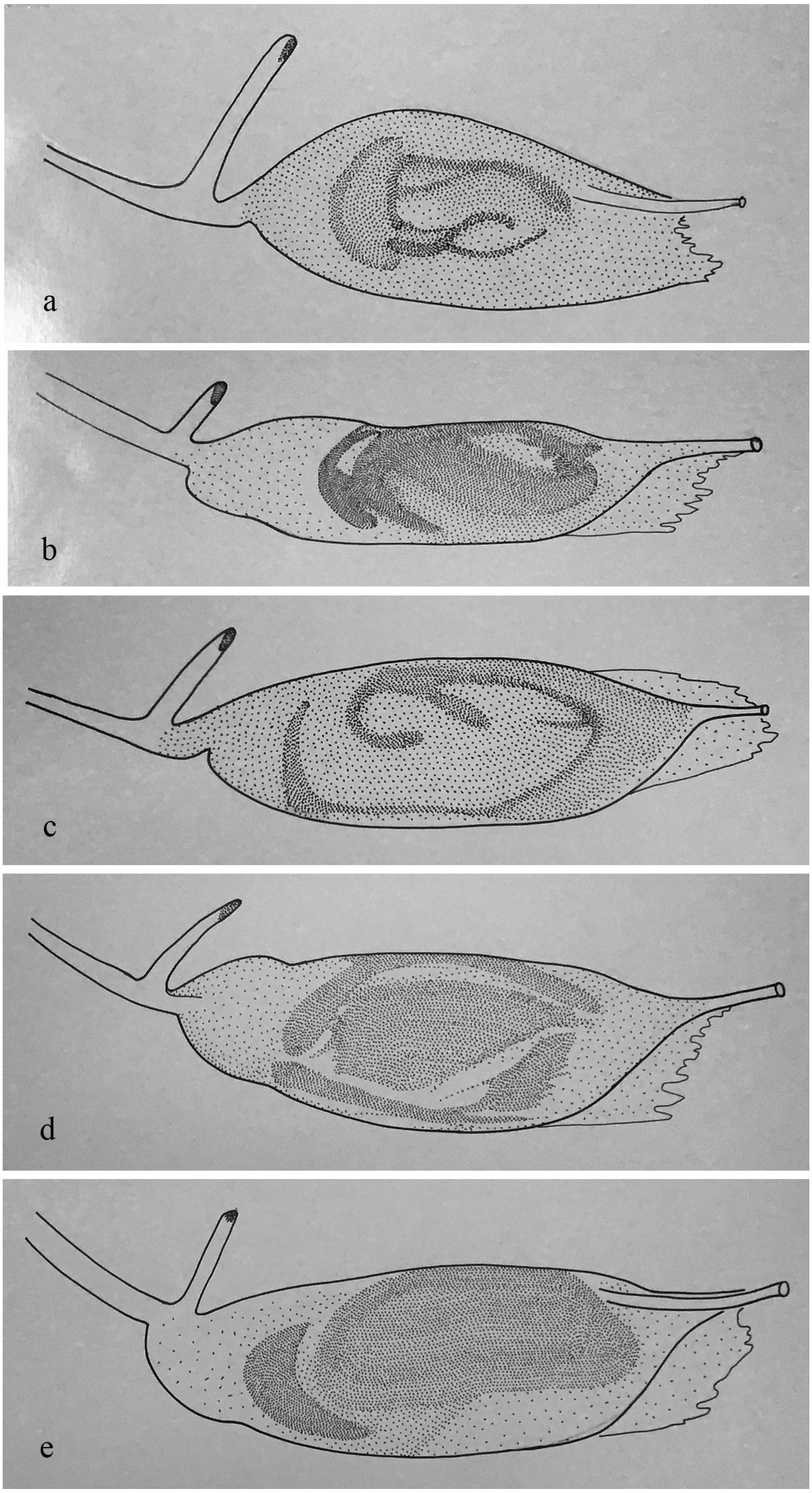

FIGURE 1. The phallus and preglans appendix of the male aedeagus: (a) *Bactrocera dorsalis* (Hendel), (b) *Bactrocera occipitalis* (Bezzi), (c) *Bactrocera papayae* Drew & Hancock, (d) *Bactrocera philippinensis* Drew & Hancock, (e) *Bactrocera invadens* Drew, Tsuruta & White.

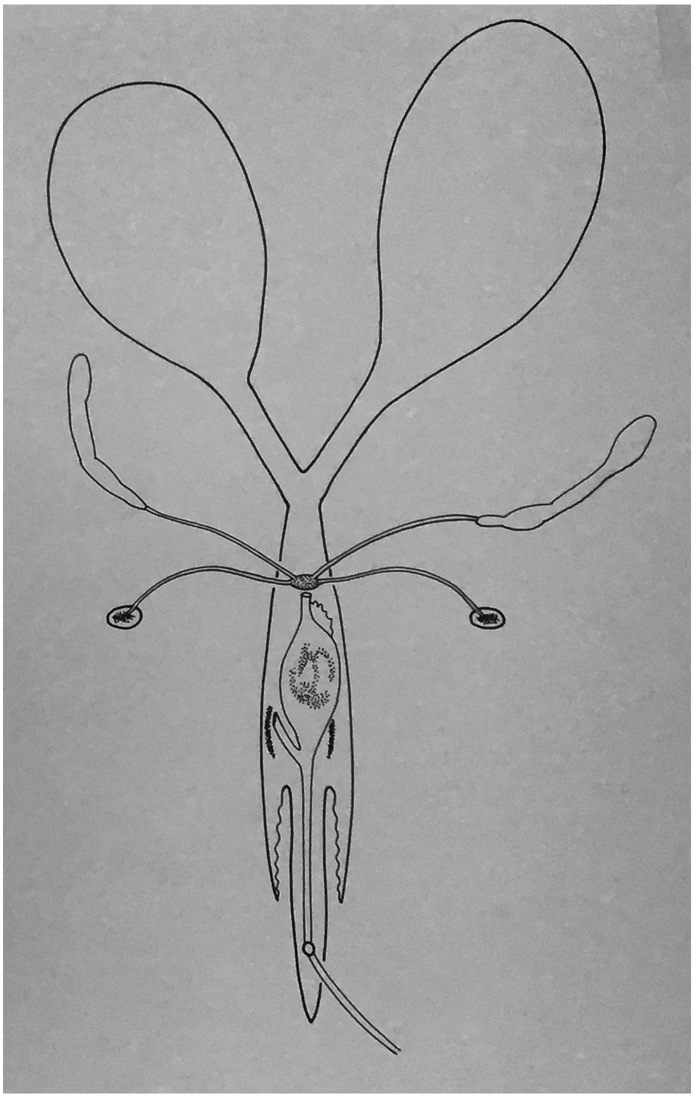

FIGURE 2. The female reproductive system of *Bactrocera tryoni* (Froggatt) showing the position of the male phallus and preglans appendix during copulation.

Bactrocera dorsalis complex pest species

Bactrocera (Bactrocera) carambolae Drew & Hancock

Bactrocera (Bactrocera) carambolae Drew & Hancock, 1994: 11; Norrbom *et al.*, 1998: 89; Drew & Romig, 2013: 61. Holotype in BMNH.

Common name: Carambola Fruit Fly.

Definition: Face fulvous with a pair of medium-sized oval black spots; postpronotal lobes and notopleura yellow; scutum black with pale lateral margins; broad parallel-sided lateral postsutural yellow vittae ending at or behind *ia*. seta; medial postsutural yellow vitta absent; anepisternal (mesopleural) stripe reaching midway between anterior margin of notopleuron and anterior *npl*. seta dorsally; scutellum yellow with a narrow dark basal band; legs with femora fulvous and with a large preapical dark spot on outer surface of fore femora in some specimens, tibiae dark fuscous; wing with cells bc and c colourless, microtrichia in outer corner of call c only, a narrow fuscous costal band overlapping R_{2+3} and expanding slightly beyond apex of this vein across apex of R_{4+5}, a narrow fuscous anal streak, supernumerary lobe of medium development; abdominal terga III-V orange-brown with a dark 'T' pattern consisting of a narrow transverse band across anterior margin of tergum III that widens to cover lateral margins, a medium width medial longitudinal band over all three terga, a dark rectangular pattern on anterolateral corners of tergum IV, anterolateral corners of tergum V dark fuscous, ceromata on tergum V orange-brown, abdominal sterna dark fuscous to black.

Distribution: Andaman Islands, Southern Thailand, Southern Vietnam, Peninsular Malaysia, East Malaysia, Indonesia. Adventive in French Guyana, Guyana, Surinam and NE Brazil. Recently recorded from Cambodia and Bangladesh (Leblanc *et al*., 2015; 2019).

Hosts: A major pest species with a preference for *Averrhoa carambola* L. See Allwood *et al*. (1999) for recorded host plants. The host range in Surinam and Guyana, a region into which *B. carambolae* was introduced, matches that recorded in South-East Asia (van Sauers-Muller, 2005).

Attractant: Methyl eugenol.

Comments: Generally, *B. carambolae* can be separated from the other *dorsalis* complex pest species in possessing the costal band broader apically and a broad medial longitudinal black band on abdominal terga III-V. Based on the mitochondrial genes COI and ND5, *B. carambolae* is separate from *B. dorsalis, B. occipitalis* and *B. papayae* (Drew & Romig, 2013). It also possesses distinct chemical components in the male pheromones (Drew & Hancock, 1994).

Bactrocera (Bactrocera) caryeae **Kapoor**

Dacus (Strumeta) caryeae Kapoor, 1971: 479. Holotype in NPC.
Dacus (Bactrocera) caryeae—Hardy, 1977: 49.
Bactrocera (Bactrocera) caryeae—Drew & Hancock, 1994: 13; Norrbom *et al*., 1998: 89.

Common Name: Careya Fruit Fly.

Definition: Face fulvous with a pair of large elongate-oval black spots; postpronotal lobes yellow with fuscous anterodorsal corners; notopleura yellow; scutum black; lateral postsutural yellow vittae narrow and parallel-sided or narrowing slightly posteriorly to end at or just before *ia*. seta; medial postsutural yellow vitta absent; anepisternal stripe reaching midway between anterior margin of notopleuron and anterior *npl.* seta dorsally; scutellum yellow with a broad back basal band; legs with femora fulvous with large dark fuscous to black preapical spots on outer surfaces of fore and inner surfaces of mid and hind femora, fore tibiae fuscous, mid tibiae fulvous, hind tibiae dark fuscous; wing with cells bc and c colourless, microtrichia in outer corner of cell c only, a narrow costal band confluent with R_{2+3} and remaining narrow around apex of wing, a narrow fuscous anal streak confined within cell bcu, supernumerary lobe of medium development; abdominal terga III-V pale with dark fuscous to black across anterior third to half of tergum III, two broad lateral longitudinal dark fuscous to black bands and a narrow medial longitudinal black band over all three terga, a pair of orange-brown ceromata on tergum V, abdominal sterna dark fuscous to black.

Distribution: Southern India (Karnataka, Kerala, western Tamil Nadu: Ramani *et al*., 2008).

Hosts: A serious economic pest recorded from seven plant families, including mango, guava, citrus and *Syzygium* spp (Allwood *et al*., 1999; Ramani *et al*., 2008; Drew & Romig, 2013). The only recorded wild host plant is *Careya arborea* (Lecythidaceae) (Ramani *et al.,* 2008).

Attractant: Methyl eugenol.

Comments: *Bactrocera caryeae* is similar to *B. arecae* (Hardy & Adachi) and *B. kandiensis* Drew & Hancock in possessing narrow lateral postsutural yellow vittae and preapical dark markings on at least one pair of femora. It differs from *B. arecae* in possessing preapical dark markings on all femora and from *B. kandiensis* in possessing a broad medial and two broad lateral longitudinal dark bands over abdominal terga III-V.

Bactrocera (Bactrocera) dorsalis **(Hendel)**

Dacus dorsalis Hendel, 1912: 18. Lectotype in NHM.
Dacus (Strumeta) dorsalis—Hardy & Adachi, 1956: 7.
Strumeta dorsalis—Hering, 1956: 63.
Dacus (Bactrocera) dorsalis—Hardy, 1977: 49.

Bactrocera (Bactrocera) dorsalis—Drew & Hancock, 1994: 17, Lectotype designation; Norrbom *et al*., 1998: 90; Drew & Romig, 2013: 76.

See Drew & Romig (2013) for comprehensive list of synonyms.

Common Name: Oriental Fruit Fly.

Definition: Face fulvous with a pair of medium-sized circular black spots; postpronotal lobes and notopleura yellow; scutum black with areas of red-brown to brown around lateral margins and notopleural suture; broad parallel-sided lateral postsutural yellow vittae ending behind *ia.* seta; medial postsutural yellow vitta absent; anepisternal stripe reaching midway between anterior margin of notopleuron and anterior *npl.* seta dorsally; scutellum yellow; legs with femora entirely fulvous, fore tibiae fuscous, mid tibiae fulvous, hind tibiae dark fuscous; wing with cells bc and c colourless, microtrichia in outer corner of cell c only; a narrow fuscous costal band confluent with R_{2+3} and remaining narrow around apex of wing (occasionally with a slight swelling around apex of R_{4+5}), a narrow fuscous anal streak, supernumerary lobe of medium development; abdominal tera III-V normally fulvous with a black 'T' pattern consisting of a narrow transverse band across anterior margin of tergum III and a narrow medial longitudinal band over all three terga, narrow fuscous to dark fuscous anterolateral corners on terga IV and V, ceromata on tergum V orange-brown to pale fuscous, abdominal sterna dark fuscous.

Distribution: Widespread across South-East Asia from Myanmar eastwards and introduced into the Hawaiian Islands, the Mariana Islands and Tahiti. It appears to be allopatric or parapatric with *B. invadens* to the west and *B. papayae* to the south.

Hosts: *B. dorsalis* is a major economic pest with a wide host range; see Allwood *et al.* (1999) for host records.

Attractant: Methyl eugenol.

Comments: *Bactrocera dorsalis* is similar to the pest species *B. carambolae* and *B. papayae* in possessing broad parallel-sided lateral postsutural yellow vittae, the costal band confluent with or slightly overlapping R_{2+3}, femora mostly or entirely fulvous and abdominal terga III-V with a general black 'T' pattern. It differs from *B. carambolae* in possessing a very narrow apical section of the costal band, a narrow medial longitudinal black band on abdominal terga III-V and triangular-shaped anterolateral dark corners on terga IV and V. It differs from *B. papayae* in having a short male aedeagus and female ovipositor (see key to species below).

Bactrocera dorsalis was the first of the *dorsalis* complex pest species to be described, with the type locality being Taiwan (Koshun). The main population appears to be concentrated around Southern and Southwestern China, Taiwan, Northern Thailand and Northern Vietnam (see Drew & Romig (2013) for details on distribution). Based on molecular studies, *B. dorsalis* from Taiwan has been proven significantly different from *B. carambolae*, *B. invadens* and *B. occipitalis* (Drew & Romig, 2013). Genetic-based studies on the *dorsalis* complex should always include specimens from the type locality.

Bactrocera (Bactrocera) invadens **Drew, Tsuruta & White**

Musca ferruginea Fabricius, 1794: 342. Preoccupied by *Musca ferruginea* Scopoli, 1763.

Bactrocera (Bactrocera) invadens Drew, Tsuruta & White, 2005: 149; Drew *et al*., 2007: 4; Drew & Romig, 2013: 99; 2016: 7. Holotype in NMKE.

Common Name: Invasive Fruit Fly.

Definition: Face fulvous with a pair of medium-sized to large oval black spots; postpronotal lobes and notopleura yellow; scutum with basic colour dark orange-brown to red-brown with a lanceolate fuscous to black pattern that varies in size (occasionally entirely black or entirely pale); narrow to medium-width lateral postsutural yellow vittae ending at or just behind *ia*. seta; medial postsutural yellow vitta absent; anepisternal stripe reaching midway between anterior margin of notopleuron and anterior *npl.* seta dorsally; scutellum yellow; legs with femora entirely fulvous, tibiae mostly fuscous; wing with cells bc and c colourless, microtrichia in outer corner of cell c only, a narrow fuscous costal band confluent with R_{2+3} and remaining narrow around apex of wing, a narrow pale fuscous anal streak, supernumerary lobe of medium development (see figure 46 in Hancock *et al*., 2021 for a photograph); abdominal terga III-V dark orange-brown with a dark fuscous to black 'T' pattern (the transverse band across anterior margin of tergum III generally broad and can cover the entire tergum), narrow lateral dark fuscous margins on terga IV and V, ceromata on tergum V dark orange-brown, abdominal sterna dark fuscous to black.

Distribution: Sri Lanka, India, Pakistan, Bhutan, Nepal and Bangladesh; introduced and widespread in Africa, Mascarenes and Grand Comore Island (see Drew & Romig, 2013; Leblanc *et al*., 2019; Hancock *et al.*, 2021). Recently detected in Italy (Nugnes *et al*., 2018).

Hosts: Recorded from a wide range of edible/commercial host fruits in Africa (see Drew & Romig, 2013; Hassani *et al*., 2022, as *dorsalis*; Rasolofoarivao *et al.*, 2022, as *dorsalis*).

Attractant: Methyl eugenol.

Comments: This species, which we now call *B. invadens*, was originally described in 1794 by Fabricius as *Musca ferruginea*, named after its red-brown appearance. We have studied the type of *M. ferrugenea* held in the Zoological Museum, Department of Entomology, Universitetsparken, Copenhagen, and we attest that this clearly is morphologically what we are now calling *B. invadens*. Due to homonomy (and thus unavailability), we could not use the name '*ferruginea'* and thus were obliged to describe the species under a new name. The closest *Bactrocera* species in appearance is the Australian *B. cacuminata* (Hering), which has a similar scutum pattern of basic red-brown coloration with a dark overlaying lanceolate marking. In *B. invadens*, over 60% of specimens possess a pale scutum whereas in *B. dorsalis* fewer than 20% do so. Further, the pale scutum pattern in *B. dorsalis* is entirely different from that in *B. invadens*, never possessing the lanceolate pattern of *B. invadens*. In analyses of the mitochondrial genes COI and ND5, *B. invadens* is considerably distant from *B. dorsalis*, *B. carambolae*, *B. ochroma, B. occipitalis* and *B. papayae* (Drew & Romig, 2013). Further, in our new studies on the male aedeagus, *B. invadens* and *B. dorsalis* are distinct in the structure of the phallus and preglans appendix. In *B. invadens* the glans is elongate and tubular and the mean length of the phallus is 3.73 times longer than the preglans appendix, whereas in *B. dorsalis* the glans is subovate and the preglans appendix is 2.55 times longer. See Drew & Romig (2013, 2016) for a detailed discussion of this species. Maneesh *et al*. (2022) illustrated the glans and preglans appendix of a specimen from northern India and Leblanc *et al*. (2013) illustrated scutal variation in specimens from Burkina Faso and (as *B. dorsalis*) from Bangladesh; they also (Leblanc *et al*., 2019) noted that the scutal pattern of specimens from Nepal showed variation typical of those from Bangladesh.

Bactrocera (Bactrocera) kandiensis Drew & Hancock

Bactrocera (Bactrocera) kandiensis Drew & Hancock, 1994: 31. Holotype in BMNH.

Common Name: Sri Lankan Fruit Fly.

Definition: Face fulvous with a pair of large oval black spots; postpronotal lobes yellow with red-brown anterodorsal corners; notopleura yellow; scutum black with brown lateral margins and around notopleural suture; narrow parallel-sided lateral postsutural yellow vittae ending at *ia.* seta; medial postsutural yellow vitta absent; anepisternal stripe slightly wider than notopleuron dorsally; scutellum yellow with a moderately broad basal band; legs with femora fulvous with large areas of dark fuscous, fore and hind tibiae with fuscous coloration; wing with cells bc and c colourless, microtrichia in outer corner of cell c only, a narrow fuscous costal band confluent with R_{2+3} and remaining narrow around apex or wing, a narrow fuscous anal streak, supernumerary lobe of medium development; abdominal terga III-V orange-brown with a narrow transverse black band across anterior margin of tergum III, a narrow fuscous to dark fuscous medial longitudinal band over all three terga and very small fuscous to dark fuscous anterolateral corners on terga IV and V, ceromata on tergum V orange-brown, abdominal sterna dark fuscous.

Distribution: Sri Lanka.

Hosts: Recorded from mango and *Garcinia* sp. in Sri Lanka (Drew & Hancock, 1994).

Attractant: Methyl eugenol.

Comments: *B. kandiensis* is similar to *B. caryeae* in possessing narrow parallel-sided lateral postsutural vittae, dark colour patterns on the apices of femora and a narrow costal band confluent with R_{2+3} and remaining narrow around apex of wing. It differs from *B. caryeae* in having a very narrow medial longitudinal dark band over abdominal terga III-V and narrow dark anterolateral corners on terga IV and V.

Bactrocera (Bactrocera) occipitalis **(Bezzi)**

Chaetodacus ferrugineus var. *occipitalis* Bezzi, 1919: 423. Lectotype in MCSNM.
Dacus (Strumeta) dorsalis var. *occipitalis*—Hardy & Adachi, 1954: 166.
Dacus (Strumeta) occipitalis—Hardy, 1974: 39.
Dacus (Bactrocera) occipitalis—Hardy, 1977: 51.
Bactrocera (Bactrocera) occipitalis—Drew & Hancock, 1994: 45; Drew & Romig, 2013: 137.
See Drew & Romig (2013) for comprehensive list of synonyms.

Common Name: Philippine Fruit Fly.

Definition: Face fulvous with a pair of large oval black spots; postpronotal lobes and notopleura yellow; scutum yellow with dark red-brown around lateral and posterior margins and along notopleural suture; broad parallel-sided or subparallel lateral postsutural yellow vittae ending at or behind *ia.* seta; medial postsutural yellow vitta absent; anepisternal stripe ending midway between anterior margin of notopleuron and anterior *npl*. seta dorsally; scutellum yellow; legs with femora entirely fulvous, tibiae with fuscous coloration; wing with cells bc and c colourless, microtrichia in outer corner of cell c only; fuscous costal band distinctly overlapping R_{2+3} and widening markedly across apex of wing, a narrow fuscous anal streak; supernumerary lobe of medium development; abdominal terga III-V with a narrow transverse black band across anterior margin of tergum III and expanding to cover lateral margins, dark fuscous to black rectangular markings anterolaterally on tergum IV and on anterolateral corners of tergum V (the lateral dark colour patterns can cover the entire lateral margins of tergum IV), a very broad medial longitudinal black band over terga III-V, ceromata on tergum V orange-brown, abdominal sterna dark fuscous.

Distribution: Philippines, Borneo.

Hosts: Host records for *B. occipitalis* are limited due to a lack of fruit-collecting field surveys in the area of geographic distribution. It has been reared from fruits of three plant families (Allwood *et al*., 1999).

Attractant: Methyl eugenol.

Comments: Within the *dorsalis* complex group of pest species, *B. occipitalis* is similar to *B. carambolae* in possessing a broader apex on the costal band and a broad medial longitudinal dark band on abdominal terga III-V. It differs from *B. carambolae* in having broader parallel-sided or subparallel lateral postsutural yellow vittae, a broader medial longitudinal black band over abdominal terga III-V, more expansive dark coloration laterally on terga III-V and generally a broader costal band overlapping R_{2+3} and widening apically over apex of R_{4+5} (see Drew & Romig, 2013 for detailed discussion on comparisons with other species).

Bactrocera (Bactrocera) ochroma **Drew & Romig**

Bactrocera (Bactrocera) ochroma Drew & Romig, 2013: 139. Holotype in BMNH.

Common Name: Indonesian Mango Fly.

Definition: Face fulvous with a pair of medium-sized circular black spots; postpronotal lobes and notopleura yellow; scutum black; two moderately broad subparallel lateral postsutural yellow vittae ending at or before *ia.* seta (may narrow sharply posteriorly); medial postsutural yellow vitta absent; anepisternal stripe ending midway between anterior margin of notopleuron and anterior *npl*. seta dorsally; scutellum yellow with a narrow black basal band; legs with femora entirely fulvous, tibiae with fuscous coloration; wing with cells bc and c colourless, microtrichia in outer corner of cell c only, narrow fuscous to dark fuscous costal band confluent with R_{2+3} and remaining narrow around apex of wing, a narrow very pale fuscous anal streak, supernumerary lobe of medium development; abdominal terga III-V orange-brown with a narrow transverse black band across anterior margin of tergum III but not reaching lateral margins, a narrow to medium-width medial longitudinal black band over all three terga, lateral margins of terga III-V generally devoid of dark patterns, ceromata on tergum V orange-brown, abdominal sterna pale orange-brown.

Distribution: Indonesia (Bali, Java, Sulawesi, Sumatra).

Hosts: Mango.

Attractant: Methyl eugenol.

Comments: *B. ochroma* is similar to *B. dorsalis* in the colour patterns on the thorax, abdomen and wings but differs in possessing tapering lateral postsutural yellow vittae ending before *ia*. seta, pale orange-brown abdominal sterna and on the mitochondrial genes COI and ND5 (see Drew & Romig, 2013).

Bactrocera (Bactrocera) papayae **Drew & Hancock**

Bactrocera (Bactrocera) papayae Drew & Hancock, 1994: 48; Norrbom *et al*., 1998: 93; Drew & Romig, 2013: 142, 2016: 7. Holotype in BMNH.

Bactrocera (Bactrocera) philippinensis Drew & Hancock, 1994: 52; Norrbom *et al*., 1998: 94. Holotype in BPBM. Syn. Drew & Romig, 2013: 142.

Common Name: Asian Papaya Fruit Fly.

Definition: Face fulvous with a pair of large oval black spots; postpronotal lobes and notopleura yellow; scutum black with dark brown laterally and around notopleural suture; broad parallel-sided lateral postsutural yellow vittae ending at or behind *ia.* seta; medial postsutural yellow vitta absent; anepisternal stripe reaching midway between anterior margin of notopleuron and anterior *npl.* seta dorsally; scutellum yellow with a narrow black basal band; legs with femora entirely fulvous, fore and hind tibiae dark fuscous, mid tibiae fuscous basally (darker stripe on ventral surface of fore tibiae more distinct on fresh specimens); wing with cells bc and c colourless, microtrichia in outer corner of cell c only, a narrow fuscous costal band confluent with R_{2+3} and may widen slightly around apex of wing, a narrow fuscous anal streak, supernumerary lobe of medium development; abdominal terga III-V orange-brown with a narrow transverse black band across anterior margin of tergum III which expands laterally into narrow margins (in some specimens this band is broken in the midline), a narrow to medium width medial longitudinal black band over all three terga, anterolateral corners of terga IV and V dark fuscous to black, ceromata on tergum V orange-brown, abdominal terga dark fuscous to black.

Distribution: Peninsular Malaysia, East Malaysia, Central to Southern Thailand (at least as far north as Bangkok), Philippines, Palau, Borneo, Indonesia, Singapore, Moluccas, Indonesian Papua, Papua New Guinea, New Britain, Christmas Island (Australian Territory).

Hosts: A wide range of commercial/edible and wild host fruits (see Allwood *et al*., 1999).

Attractant: Methyl eugenol.

Comments: Detailed discussion on the specific status of *B. papaya*e has been presented in Drew & Romig (2013, 2016, 2022). The major host preferences of this species make it a serious biosecurity risk, particularly for specific export industries such as bananas. The closest species morphologically is *B. dorsalis* and the two can be separated on the basis of aedeagus and ovipositor measurements, particularly those of host-reared specimens. In *B. papayae* the aedeagus length range is 2.54–3.4 mm and in *B. dorsalis* 2.46–2.7 mm, and in *B. papayae* the ratio of the length of the oviscape to length of tergum V is 1: 1 to 1.5: 1, whereas in *B. dorsalis* it is 0.7: 1 to 0.8: 1. The glans is elongate and tubular in *B. papayae* and sobovate in *B. dorsalis*.

Bactrocera (Bactrocera) pyrifoliae **Drew & Hancock**

Bactrocera (Bactrocera) pyrifoliae Drew & Hancock, 1994: 55; Norrbom *et al*., 1998: 94; Drew & Romig, 2013: 164. Holotype in BMNH.

Common Name: Oriental Pear Fly.

Definition: Face fulvous with a pair of medium-sized circular black spots; postpronotal lobes and notopleura yellow; scutum black with dark brown lateral margins; narrow lateral postsutural yellow vittae tapering posteriorly to end before *ia.* seta; medial postsutural yellow vitta absent; anepisternal stripe equal in width to notopleuron dorsally; scutellum yellow with a narrow black basal band; legs fulvous with a small subapical black spot on outer surfaces of fore femora and dark fuscous around apices of mid and hind femora, fore and mid tibiae dark fuscous and hind tibiae black; wings with cells bc and c colourless, microtrichia in outer corner of cell c only, a narrow fuscous costal band confluent with R_{2+3} and with a slight swelling around apex of R_{4+5}, a narrow fuscous anal streak, supernumerary lobe of medium development; abdominal terga III-V orange-brown and with each tergum with a dark fuscous to black 'T' pattern and dark fuscous to black lateral margins, ceromata on tergum V dark fuscous, abdominal sterna dark fuscous to black.

Distribution: Northern Thailand and northern Vietnam.

Hosts: Reared from five host families with a preference for peach and pear in the family Rosaceae.

Attractant: A possible weak response to cue lure (Drew & Romig, 2013).

Comments: *Bactrocera pyrifoliae* is morphologically unique within the group in possessing terga III, IV and V each with a separate dark fuscous to black 'T' pattern. In having lateral postsutural yellow vittae narrowing posteriorly, all femora with apical dark markings and an extensively dark abdomen with fuscous ceromata, it most resembles the Elaeocarpaceae-feeding *B. thailandica* (which also has a dark basal band on abdominal terga III and IV) and the Melastomataceae-feeding species *B. melastomatos* and *B. osbeckiae* and is possibly related to them.

Bactrocera (Bactrocera) syzygii **White & Tsuruta**

Bactrocera (Bactrocera) syzygii White & Tsuruta in Tsuruta & White, 2001: 85; Drew & Romig, 2013: 178. Holotype in HORDI.

Common name: Rose Apple Fruit Fly.

Definition: Face fulvous with a pair of large elongate oval back spots; postpronotal lobes and notopleura yellow; scutum entirely black; lateral postsutural yellow vittae parallel-sided and ending before *ia*. seta; medial postsutural yellow vitta absent; anepisternal stripe equal in width to notopleuron dorsally; scutellum yellow with a narrow black basal band; legs with all femora fulvous, all tibiae with dark fuscous coloration; wing with cells bc and c colourless, microtrichia in outer corner of cell c only, a narrow fuscous costal band confluent with R_{2+3} and remining narrow around apex of wing, a narrow fuscous anal streak, supernumerary lobe of medium development; abdominal terga III–V red-brown with a medium width medial and two broad lateral longitudinal dark fuscous to black bands joined along anterior margin of tergum III, ceromata on tergum V dark fuscous to black, abdominal sterna black.

Distribution: Described from Sri Lanka and subsequently recorded from India, Bangladesh, Nepal, Vietnam and possibly Borneo and Sulawesi (David *et al*., 2017; Leblanc *et al*., 2019).

Hosts: Reared from one host, *Syzygium jambos* (family Myrtaceae) (Tsuruta & White, 2001; Leblanc *et al.*, 2019).

Attractant: Zingerone (Leblanc *et al*., 2019).

Comments: *Bactrocera syzygii* is similar to *B. dorsalis* in possessing parallel-sided lateral postsutural yellow vittae, a narrow fuscous costal band confluent with R_{2+3} and remaining narrow around wing apex, and legs with all femora entirely fulvous. It differs from *B. dorsalis* in having a pair of large elongate-oval black spots on the face, dark fuscous coloration on all tibiae, broad lateral longitudinal dark fuscous to black bands over abdominal terga III–V and dark fuscous to black ceromata on tergum V. There are also differences in the female eversible membrane, the spicules being semicircular without prominent projections in *B. syzygii* (K.J. David, pers comm.) and with numerous projections in *B. dorsalis*.

Key to pest species in the *Bactrocera dorsalis* complex

1 Scutum base colour red-brown with dark lanceolate patterns similar to *Bactrocera cacuminata* (Hering), occasionally largely pale or dull black with red-brown lateral margins; lateral postsutural yellow vittae narrow (less than 0.15 mm in centre [broader in some Himalayan specimens]); all femora without dark preapical markings; dark transverse band across tergum III generally wide and covering most of tergum except in centre . . . .*B. invadens* Drew, Tsuruta & White

– Scutum base colour black with red-brown lateral margins (rarely red-brown); lateral postsutural yellow vittae broad and parallel to subparallel (greater than 0.15 mm in centre), if less then all femora with dark preapical markings; dark transverse band across tergum III narrow, not covering most of tergum 2

2 Abdominal sterna pale, approaching yellow in colour. . . . . *B. ochroma* Drew & Romig

– Abdominal sterna dark fuscous to black 3

3 Lateral postsutural yellow vittae narrowing posteriorly; abdominal terga III-V each with a separate dark fuscous to black 'T' pattern and broad dark fuscous lateral margins . . . .*B. pyrifoliae* Drew & Hancock

– Lateral postsutural yellow vittae parallel-sided or subparallel; abdominal terga III-V not as above, generally with a dark 'T' pattern over all three terga 4

4 Lateral postsutural yellow vittae narrow, less than or equal to 0.15 mm in width; all femora with dark preapical markings . . 5

– Lateral postsutural yellow vittae broad, greater than 0.15 mm wide; without preapical dark markings on all femora 6

5 Abdominal terga III-V with a moderately broad medial band and broad lateral longitudinal dark bands. . *B. caryeae* (Kapoor)

– Abdominal terga III-V with a distinct 'T' pattern, with or without narrow lateral margins . . . . *B. kandiensis* Drew & Hancock

6 Wing with costal band overlapping R_{2+3} and with some widening at apex 7

– Wing with costal band confluent with R_{2+3} and remaining narrow around apex (may have a slight swelling around apex of R_{4+5}) 9

7 Wing with costal band distinctly overlapping R_{2+3} and widening significantly at apex; abdominal terga III-V with broad medial and lateral longitudinal dark bands . . . . *B. occipitalis* (Bezzi)

– Wing with costal band only slightly overlapping R_{2+3} where it is pale in colour and widening only slightly at apex; abdominal terga III-V with a moderately broad medial longitudinal dark band and small anterolateral corners on terga IV and V 8

8 Legs with a preapical dark spot on fore femora; anterolateral dark markings on tergum IV rectangular in shape . . . .*B. carambolae* Drew & Hancock

– Legs with all femora entirely fulvous; anterolateral dark markings on tergum IV triangular in shape . . . . *B. papaya*e Drew & Hancock (some specimens: var. *philippinensis* Drew & Hancock)

9 Face with a pair of large elongate-oval black spots; abdominal terga III-V orange-brown with a broad medial and two broad lateral longitudinal dark fuscous to black bands . . . . *B. syzygii* White & Tsuruta

– Face with a pair of medium sized oval black spots; abdominal terga III-V orange-brown with a distinct ‘T’ pattern and narrow lateral dark markings 10

10 Fore tibia with a black ventral stripe; ratio of length of oviscape to length of tergum V, 1: 1 to 1.5: 1; length of male aedeagus 2.54–3.4 mm (mean 2.95 mm); ratio of length of preglans appendix to length of phallus, 1:3.93; length of aculeus 1.77–2.12 mm . . . .*B. papayae* Drew & Hancock

– Fore tibia without a black ventral stripe; ratio of length of oviscape to length of tergum V, 0.7:1 to 0.8:1; length of male aedeagus 2.46–2.7 mm (mean 2.59 mm); ratio of length of preglans appendix to length of phallus 1: 2.55; length of aculeus 1.4–1.6 mm . . . . *B. dorsalis* (Hendel)

[Note: specimens of *B. invadens* with broad lateral postsutural vittae from the Indian subcontinent that key to Couplet 10 can be separated by the combination of fore tibia without a black ventral stripe and the glans elongate and tubular]

Biosecurity and pest management considerations

The accurate diagnosis of species, pest and non-pest, is essential for reasons of biosecurity, eradication of new incursions, field pest management and international trade. The extensive speciation in the genus *Bactrocera* has resulted in a large number of morphologically similar species. While some of these have close genetic links, others are more distant. For practical identification reasons, species are placed within complexes on the basis of morphological similarity. Such groupings are not intended to reflect genetic relationships, a point not understood by Catullo *et al*. (2019) in stating that *B. endiandrae* should not be placed in the *dorsalis* complex.

The *dorsalis* complex, consisting of some 79 morphologically similar species, is the one of most interest to researchers and agriculture departments throughout the Asian-Pacific region. Species should always be defined on the basis of morphological and biological characters as top priority, and this strategy has been followed in the publications of Drew & Hancock (1994) and Drew & Romig (2013, 2016). The concept of species and speciation upon which these authors have defined species has been discussed above and by Drew & Romig (2022). The ten pest species in the *dorsalis* complex defined above are discussed below with regard to their biosecurity importance, especially reflecting on their ecological characteristics. The biosecurity risks of 47 pest species in the Dacini were discussed by Drew & Romig (2013) and an additional pest of peaches and nectarines in India was described by Maneesh *et al*. (2022).

Bactrocera carambolae Drew & Hancock

The host range of this species was recorded by Allwood *et al.* (1999). Although having a wide host range, its major hosts were carambola and guava. This species was introduced into Surinam where van Sauers-Muller (2005) recorded a similar host range to that recorded in South East Asia, its region of origin, by Allwood *et al*. (1999). In Surinam, sweet varieties of carambola were infested whereas sour varieties were not and *Syzygium samarangense* was also a major host, both species having a high moisture content (DLH pers. obs., 1989). *Bactrocera carambolae* is a major pest species with a high risk of being introduced to countries in the Asian-Pacific region and beyond, as experienced by its presence in Surinam, Guyana, French Guyana and NE Brazil. In southern South-East Asia, *B. carambolae* forms a largely sympatric species ‘pair’ with *B. papaya*e, similar to the *B. occipitalis*—*B. papayae* ‘pair’ in the Philippines.

Bactrocera caryeae **(Kapoor)**

This species is a significant pest in southern India, although having been recorded from only seven plant families (Allwood *et al.*, 1999; Ramani *et al.*, 2008). Apart from a single record from Oman (Drew & Hancock, 1994) it has never been recorded outside southern India and poses a moderate risk of being introduced to other countries. The Oman record is possibly a quarantine intercept and has not been repeated (Hancock *et al.*, 2021). Morphologically, *B. caryeae* has some similarities to *B. kandiensis* in Sri Lanka and the fuscous areas on the femora seen in these two allopatric species, visible during courtship, likely enable reproductive isolation from the sympatric *B. invadens*, which has entirely fulvous femora.

Bactrocera dorsalis **(Hendel)**

Bactrocera dorsalis was recorded from 39 plant families by Allwood *et al*. (1999). It is a major pest species causing considerable crop losses wherever it occurs and has a high risk of being introduced to countries outside South-East Asia, as demonstrated by its presence in the Hawaiian Islands and Tahiti and regular introduction to the USA mainland. The incorrect synonymization of *B. dorsalis* with *B. papaya*e has caused confusion and complexities in biosecurity and eradication programmes. For example, in the *B dorsalis* eradication campaign in Florida, 2015-2016 (Steck *et al.*, 2019), the *B. dorsalis* host list was expanded from 130 plant species to 432 species as a direct result of these synonymies (USDA, 2016), causing immense difficulties for field monitoring staff. Steck *et al.* (2019) stated: 'The timing of the host list update could not have been worse from the perspective of stakeholders, and it caused a great deal of confusion and consternation about regulated commodities'. This is an example of the importance of accurate identification of pest species to pest management and eradication campaigns. There are a number of species morphologically similar to *B. dorsalis* but with distinct host plant preferences. Some examples are *B. areceae* (Hardy & Adachi) utilizing *Areca catechu*, *B. irvingiae* Drew & Hancock breeding only in wild hosts in the families Meliaceae, Moraceae and Simaroubaceae, and *B. verbascifoliae* Drew & Hancock breeding only in wild *Solanum* species. Similarly, *B. papayae* stands apart in utilizing papaya and banana as major hosts (see discussion by Drew & Romig, 2016).

Bactrocera invadens **Drew, Tsuruta & White**

Bactrocera invadens is widespread on the Indian subcontinent (including Sri Lanka) and is invasive in much of Africa and associated islands (Hancock *et al*., 2021), where it is frequently misidentified as *B. dorsalis*. It is a major economic pest species recorded from numerous wild and cultivated hosts (Drew & Romig, 2013; Hassani *et al*., 2022, as *dorsalis*; Rasolofoarivao *et al.*, 2022, as *dorsalis*). Its rapid spread throughout much of Africa and recent detection in Italy (Nugnes *et al*., 2018, as *dorsalis*) demonstrate its high risk of being transferred to other countries and is thus of major biosecurity concern.

Bactrocera kandiensis **Drew & Hancock**

Bactrocera kandiensis occurs only in Sri Lanka where it has been misidentified as *B. dorsalis*. It is a minor economic pest species recorded from mango and *Garcinia* species. It has never been recorded from other countries in the region and appears to have a low risk of transfer out of Sri Lanka.

Bactrocera occipitalis **(Bezzi)**

Bactrocera occipitalis is a major pest species across the Philippines, East Malaysia, Brunei and Kalimantan (Indonesian Borneo). The Philippines and Borneo possess a number of *Bactrocera* species in common, *B. occipitalis* being an example. The low number of host records (Allwood *et al*., 1999) is due to a lack of field surveys in the area of distribution and not indicative of the pest status of this species: it was found to be a major pest in mangoes produced for export in Philippine plantations (Drew, pers. obs., 1983). From a biosecurity perspective, there is a high risk of *B. occipitalis* being transferred to other countries.

Bactrocera ochroma **Drew & Romig**

Bactrocera ochroma is considered a pest species, although minor, having been reared from mango, the only recorded host, in Indonesia. Morphologically it is similar to *B. dorsalis* but differs in analyses of two mitochondrial genes, COI and ND5. This species is a low risk of being spread to other countries.

Bactrocera papayae **Drew & Hancock**

Bactrocera papayae is a major pest species across much of South-East Asia and has spread into Indonesian Papua, Papua New Guinea and the Torres Strait islands. After invading northern Queensland in the late 1990s, it was successfully eradicated primarily using Male Annihilation (Hancock *et al*., 2000b). The extensive host records (Allwood *et al*., 1999) are a result of many years of host fruit surveys in a range of ecosystems in Thailand and Malaysia, and during the eradication program in northern Queensland. It shows a preference for papaya and banana (usually green to mature green) and continues to pose a major biosecurity threat in the South-East Asian and Pacific regions. Along with *B. invadens*, *B. papayae* was withdrawn from synonymy with *B. dorsalis* by Drew & Romig (2016). Before publication, that volume was peer reviewed by three researchers: a world authority on species and processes of speciation, a world authority on dacine taxonomy, and an international authority on molecular studies in the genus *Bactrocera*. It is of paramount importance that *B. dorsalis* and *B. papayae* are recognized correctly as separate species, for international biosecurity reasons and to avoid confusion such as reported by Steck *et al.* (2019).

Bactrocera pyrifoliae **Drew & Hancock**

Bactrocera pyrifoliae is a serious pest of peach and pear in northern Thailand and northern Vietnam. As it is localized in distribution and limited in host range, it is considered a low risk of spreading to other countries.

Bactrocera syzygii **White & Tsuruta**

Bactrocera syzygii is widespread from the Indian subcontinent to at least Vietnam but has only a single known host, the Rose Apple *Syzygium jambos*. It is considered a minor pest with a low risk of dispersal to other countries.

Conclusions

Prolific speciation within the dacine genus *Bactrocera* has resulted in some 750 known species across the wider area from the Indian subcontinent and South-East Asia through to the South Pacific and, to a lesser extent, Africa and its associated islands. Having studied almost all known species, we have assembled some into morphological groups called complexes. The opportunity to research this large fauna has resulted from extensive trapping and host fruit surveys conducted for more than three decades from the mid-1980s.

The majority of dacine species have been described and illustrated by Drew (1989) and Drew & Romig (2013, 2022) and these works have provided detailed information on geographic distributions, male lure records, diagnosis of pest species and their biosecurity risks. These studies have also resulted in the publication of host plant records (Allwood *et al*., 1999; Hancock *et al*., 2000a) and concepts on biogeography (Drew & Hancock, 2000; Drew, 2004). The Dacini fauna across the Asia-Pacific region has speciated in rainforests that date back to Gondwana. The close ecological relationship between *Bactrocera* species and their host plants, within which specific mate recognition systems occur, provides a fertile ground for fly speciation to be directly influenced by speciation in the flora. Consequently, prolific localized speciation in the rainforests across the entire region has resulted in large numbers of species and groups of sibling species, some of which, while morphologically similar, possess differences in the endemic host plants that they utilise. The host plant of a *Bactrocera* species thus becomes a focal point for assisting in the diagnosis of some sibling species, a principle supported by the Recognition Concept of Species proposed by Paterson (1973, 1985).

Within the genus *Bactrocera*, the *dorsalis* complex is the best known due to the inclusion of a number of pest species. This complex was first brought to prominence by Hardy (1969) and later by Drew & Hancock (1994). Because of the difficulty in diagnosing morphologically similar species, Drew & Hancock (1994) included, for the first time, host plant associations, male pheromone chemistry, enzyme electrophoresis, DNA sequencing and morphometrics of adult male and female genitalia as supporting evidence for some species.

Currently, in tephritid research there is an emphasis on sequencing a small number of genes, rather than the entire genome of a species, in order to make decisions regarding the specific status of populations. A more comprehensive and balanced approach is needed as discussed by Sasic Zoric *et al.* (2020), who recommended the inclusion of morphological data, morphometry and ecological data with molecular markers in order to determine species. Similarly, phylogenies based on a small gene pool are often contrasted with classifications based on morphological criteria. Such comparisons have little relevance until the genes that control morphological characters and the process of speciation are discovered and used in molecular analyses. Incongruence will always occur between phylogenies and classifications that are based on different criteria. Computer-based phylogenetic analyses also have their limitations, having an unrealistic dependence on minimum-length trees or the principle of parsimony, features unlikely to be matched during the actual process of evolution. Many are illogical and fail to take biogeography or homoplasy into account when associating taxa, while others appear to associate taxa on shared 'primitive' states rather than shared derived ones, the purported *Dacus-Zeugodacus* association being an example (e.g. the presence of either the TAA or TA stop codon on the COI gene: see Jiang *et al*., 2016). For the most accurate diagnosis of sibling species, it is necessary to use character states that reflect reproductive separation of populations under field conditions in addition to morphological features, some of which are also related to courtship and mating. This requires a knowledge of most species within the Dacini and the application of a broad range of biological features. For example, ecological and biogeographic studies have provided data on the significance of host plant associations, particularly in the endemic habitat, and host plant courtship and mating, which in turn emphasises the importance of host plant records in separating some species. This biological evidence was important in the comprehensive scientific analysis presented by Drew and Romig (2016) in support of *B dorsalis, B. invadens* and *B. papayae* being recognized as separate species. A largely red-brown scutum is dominant in *B. invadens*, recessive in *B. dorsalis* and unknown in *B. papayae*, while the distinct dark stripe along the underside of the fore tibia in *B. papayae*, presumably visible during courtship, would likely inhibit interspecific mating between it and the other species should they co-occur in natural situations. Hybridization studies based on laboratory or cage experiments bypass the first stage of courtship, the respective sexes first individually locating a mating site (normally a suitable host plant), by artificially uniting them in unnatural situations. Artificially uniting allopatric species is even less reliable at determining their taxonomic status, since the respective species would have faced no evolutionary pressure to develop isolating mechanisms. Different leg patterns, phallus structure and aculeus lengths likely inhibit natural matings between *B. papayae* and the sympatric *B. carambolae*, leading to little or no hybridization in the field. This suggests that sterile insect technique (SIT) eradication programs using the 'wrong' species would be unlikely to succeed, making correct identification of the target species imperative.

New data presented in this review on the differences in the structure of the male genitalia and the relationship of these structures to mating now provide additional confirmation that *B. invadens* and *B. papayae* are good species separate from *B. dorsalis*, while *B. papayae* and *B. philippinensis* are conspecific. It is recognized that molecular data often provide valuable insights into species' relationships but, in the absence of supporting evidence such as morphology and biology (and often contrary to it), they should be treated with caution and not regarded as definitive. Agreement in many published phylogenies likely results from the use of the same publicly available sequences and the same analysis programs, and genes expressed by morphology appear to be better indicators of relationships than genes about which we know nothing. Misidentifications and genetic introgression are also major problems that inhibit the reliability of molecular identification and phylogenies, especially in the rapidly evolved subgenus

Bactrocera and the *dorsalis* complex in particular, as also noted by Doorenweerd *et al*. (2020). One consequence of the erroneous synonymy of *B. papayae* and *B. invadens* with *B. dorsalis* is the widespread misidentification of sequences on public databases and their reuse in many published phylogenies, with correct identification impossible unless the source locality of the material is indicated. This study illustrates the pitfalls of basing taxonomic decisions on incomplete molecular data and imaginary clines (see Drew & Romig, 2022) that are not supported by morphology or biology and are contrary to taxonomic expertise. A similar case involves the recent synonymy of *B. albistrigata* (de Meijere) with *B. frauenfeldi* (Schiner) (Doorenweerd *et al*., 2022), in a limited molecular study of peripheral populations that failed to include examples from the key island of New Guinea or the highly complex population in Timor (Bellis *et al*., 2017), leading to unconvincing phylogenomic conclusions and with genetic introgression between two morphologically separable species along a contact zone a more likely proposition. The apparently widespread belief that if molecular data indicate one thing then everything else must be wrong, is clearly false.

For the future, there is a major need for sound molecular data that can be used to verify species diagnoses. To date, such available data are limited and incomplete and thus are unreliable indicators of the specific status of some populations. It is essential that the genes associated with speciation under field conditions be discovered in order to advance this aspect of our science. Such studies should also include much larger numbers of *Bactrocera* species, as has been achieved for our morphological and host plant association work.

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