SYNONYMIZATION OF KEY PEST SPECIES WITHIN THE

BACTROCERA DORSALIS SPECIES COMPLEX (DIPTERA: TEPHRITIDAE): TAXONOMIC CHANGES BASED ON A REVIEW OF 20 YEARS OF INTEGRATIVE MORPHOLOGICAL, MOLECULAR, CYTOGENETIC, BEHAVIOURAL AND CHEMOECOLOGICAL DATA

Presented by

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AUSTRALIA
Synonymization of key pest species within the *Bactrocera dorsalis* species complex (Diptera: Tephritidae): taxonomic changes based on a review of 20 years of integrative morphological, molecular, cytogenetic, behavioural and chemoeconomic data

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Abstract. Bactrocera papayae Drew & Hancock, Bactrocera philippinensis Drew & Hancock, Bactrocera carambolae Drew & Hancock, and Bactrocera invadens Drew, Tsuruta & White are four horticultural pest tephritid fruit fly species that are highly similar, morphologically and genetically, to the destructive pest, the Oriental fruit fly, Bactrocera dorsalis (Hendel) (Diptera: Tephritidae). This similarity has rendered the discovery of reliable diagnostic characters problematic, which, in view of the economic importance of these taxa and the international trade implications, has resulted in ongoing difficulties for many areas of plant protection and food security. Consequently, a major international collaborative and integrated multidisciplinary research effort was initiated in 2009 to build upon existing literature with the specific aim of resolving biological species limits among B. papayae, B. philippinensis, B. carambolae, B. invadens and B. dorsalis to overcome constraints to pest management and international trade. Bactrocera philippinensis has recently been synonymized with B. papayae as a result of this initiative and this review corroborates that finding; however, the other names remain in use. While consistent characters have been found to reliably distinguish B. carambolae from B. dorsalis, B. invadens and B. papayae, no such characters have been found to differentiate the latter three putative species. We conclude that B. carambolae is a valid species and that the remaining taxa, B. dorsalis, B. invadens and B. papayae, represent the same species. Thus, we consider B. dorsalis (Hendel) as the senior synonym of B. papayae Drew and Hancock syn.n, and B. invadens Drew, Tsuruta & White syn.n. A redescription of B. dorsalis is provided. Given the agricultural importance of B. dorsalis, this taxonomic decision will have significant global plant biosecurity implications, affecting pest management, quarantine, international trade, postharvest treatment and basic research. Throughout the paper, we emphasize the value of independent and multidisciplinary tools in delimiting species, particularly in complicated cases involving morphologically cryptic taxa.

Introduction

The Bactrocera dorsalis species complex is a group of true fruit flies (Diptera: Tephritidae) that contains almost 100 morphologically similar taxa (Drew & Hancock, 1994; Drew & Romig, 2013). Most species in this complex are of no economic concern; however, the Oriental fruit fly, Bactrocera dorsalis (Hendel), and closely related species in this complex, namely the Asian Papaya fruit fly, Bactrocera papayae Drew & Hancock, the Philippine fruit fly, Bactrocera philippinensis Drew & Hancock, the Carambola fruit fly, Bactrocera carambolae Drew & Hancock, and the Invasive fruit fly, Bactrocera invadens Drew, Tsuruta & White (Fig. 1), are arguably amongst the world’s most important pests of horticulture (Clarke et al., 2005; Khamis et al., 2012). The native geographic distributions of these taxa span three continents: B. dorsalis ranges from the Indian subcontinent...
of *B. dorsalis* is strictly defined as mostly black (Drew & Hancock, 1994). Debate over the relationship between *B. invadens* and *B. dorsalis* has persisted, particularly as some specimens of *B. invadens* possess a black scutum and are ‘almost inseparable’ from *B. dorsalis* (Drew et al., 2005: 153). This situation is further compounded, as ‘occasionally the thorax [of *B. dorsalis*] is almost entirely red-brown’ (Drew & Hancock, 1994: 18), with ‘pale forms of *B. dorsalis* [occurring] in less than 20% of the population’ (Drew & Romig, 2013: 100). Confusion over the unreliable discrimination between *B. dorsalis* and *B. invadens* has resulted in significant problems with African horticulture and food security (Khamis et al., 2012).

Although the search for discriminatory characters has failed to yield universally accepted diagnoses, research into the biological relationships among these taxa has generated considerable evidence that *B. papayae*, *B. philippinensis*, and *B. invadens* – but not *B. carambola* – are the same biological species as *B. dorsalis*. Here, we review previous literature, in addition to that generated from recent research, much of which was carried out in conjunction with a 6-year FAO/International Atomic Energy Agency (IAEA) Coordinated Research Project (CRP) on the ‘Resolution of cryptic species complexes of tephritid pests to overcome constraints to SIT [Sterile Insect Technique] application and international trade’ involving more than 40 researchers from 20 countries. As will be shown, this multidisciplinary approach has generated consistent findings that form the basis for our taxonomic reassignments. Our work is done within an integrative taxonomic framework (sensu Schlick-Steiner et al., 2010) and we stress that while each individual dataset may be debated with respect to its relative value for species delimitation, the multiple lines of evidence across a range of disciplines undertaken by independent research groups spanning a period of 20 years provide a compelling case for taxonomic revision. In defining biological species limits through integrative taxonomy, we follow here the unified species concept of de Queiroz (2007), which defines species as separately evolving metapopulation lineages. In line with this theory, we predict that at least one attribute (e.g. mating isolation, reciprocal genetic monophyly or morphological discontinuity) would be consistent with current taxonomy if these taxa are different biological species. If they are the same biological species, we expect no such differences. Discussions of the theoretical and practical approaches underpinning the current study can be found in de Queiroz (2007) and Schlick-Steiner (2010), respectively, and as applied specifically to tephritids in Clarke & Schutze (in press).

Our review is broken into three major sections: (i) evidence for the synonymization of *B. papayae* and *B. philippinensis* with *B. dorsalis*; (ii) evidence for the synonymization of *B. invadens* with *B. dorsalis*; and (iii) evidence for maintaining *B. carambola* as a distinct species. Additionally, given that the recent revision by Drew & Romig (2013) synonymized *B. philippinensis* with *B. papayae*, but retained the other taxa, we include a summary that explicitly addresses the arguments made by Drew & Romig (2013) against synonymizing *B. papayae* and *B. invadens* with *B. dorsalis*. Following the review component of the paper, we provide the taxonomic component of the work which makes formal statements of synonymization.

Fig. 1. *Bactrocera* (Bactrocera) *dorsalis* female. Photo credit: Ana Rodriguez.

(and Andaman Island), across into southern China and mainland South-east Asia, and as far as southern Thailand (Aketarawong et al., 2007; Drew & Romig, 2013); *B. papayae* occurs from southern Thailand into much of the Indo/Malay Archipelago; *B. carambola* is largely sympatric with *B. papayae*, in addition to being widespread in the Andaman and Nicobar Islands (David & Ramani, 2011); *B. philippinensis* occurs only in the Philippines; and *B. invadens* is presumed native to parts of the Indian subcontinent (Drew & Hancock, 1994; Drew et al., 2005; Drew & Romig, 2013). More recently, the range of *B. dorsalis* has expanded into Hawaii and a number of South Pacific Islands (Stephens et al., 2007), *B. carambola* into northern South America (van Saurers-Muller, 1991), *B. papayae* into the island of New Guinea (Drew & Romig, 1997), and *B. invadens* across most of sub-Saharan Africa (Khamis et al., 2009). These highly disjunct geographic distributions, combined with prolonged difficulties in differentiating putative species and developing reliable diagnostic markers, have resulted in significant problems associated with international trade, quarantine, phytosanitation, food security and fundamental research with respect to these highly damaging and invasive pest taxa.

*Bactrocera papayae*, *B. philippinensis*, and *B. carambola* were described in a major revision of the *B. dorsalis* complex by Drew & Hancock (1994). With the exception of *B. carambola* (see later), characters provided in the descriptions of these taxa are often variable and inadequate for confident species identification, and the search for consistent diagnostic characters has been extremely problematic (Clarke et al., 2005).

*Bactrocera invadens* was detected in Kenya in 2003, at which point it was considered likely to represent a morphologically variable form of *B. dorsalis* (Lux et al., 2003). Nevertheless, *B. invadens* was described as a new species following comparison of Kenyan material with specimens from the purported native range of Sri Lanka (Drew et al., 2005). With the holotype designated from the invasive population in Kenya, *B. invadens* was determined to be a new species, due in particular to a scutum colour ranging from pale red-brown to black, with the existence of variable lanceolate-patterned intermediates; the scutum
At points we refer to two additional taxa in this review, namely *Bactrocera occipitalis* Drew & Hancock and *Bactrocera kandiensis* Drew & Hancock. *Bactrocera occipitalis* occurs in the Philippines and is sympatric with *B. philippinensis*, while *B. kandiensis* is endemic to Sri Lanka and sympatric with *B. invadens*. Both are members of the *B. dorsalis* complex, are pest species in their own right, and are morphologically similar to *B. dorsalis* (Drew & Hancock, 1994; Clarke et al., 2005; Khamis et al., 2012). This has resulted in some confusion as to their biological relationship with *B. dorsalis*, akin to that of *B. papayae*, *B. philippinensis*, and *B. invadens*. However, as for *B. kandiensis*, they possess subtle yet consistent differences in morphology (Drew & Hancock, 1994; Iwahashi, 1999a; Drew et al., 2008; Drew & Romig, 2013) and molecular genetics (Boykin et al., 2014; Schutze et al., 2014), sufficient to regard them as distinct species. They are, therefore, not a focus of this review, but occasionally they are closely associated with a particular data set and are thus discussed.

**Evidence for the synonymy of *B. papayae* with *B. dorsalis***

**Morphology**

*Bactrocera papayae* and *B. philippinensis* were separated from *B. dorsalis* based on the former two taxa having longer aculei (1.77–2.12 mm) than *B. dorsalis* (1.4–1.6 mm). The pleural area immediately below the postpronotal lobe was described as brown (i.e. pale) in *B. dorsalis* and brown to fuscous (i.e. dark) in *B. papayae* (Drew & Hancock, 1994). *Bactrocera papayae* and *B. philippinensis* were, in turn, separated from each other by the shape of scales on the distal end of the eversible membrane of the ovipositor, being long and narrow in *B. papayae* and short in *B. philippinensis* (Drew & Hancock, 1994). Drew et al. (2008) provided an additional morphological character state for the separation of *B. papayae* and *B. philippinensis*: the latter species had a costal band ‘usually expanding into a fish-hook barb pattern around apex of R1+2’ (p. 220), but the authors did note that ‘intraspecific variation in these characters … causes difficulties in successful diagnosis’ (p. 219).

Subsequent studies on external morphology have failed to detect any consistent differences between *B. papayae* and *B. philippinensis* (Mahmood, 2004; Drew & Romig, 2013), leading Drew & Romig (2013) to synonymize *B. philippinensis* with *B. papayae*. Geometric morphometric analysis of wing shape variation also failed to detect any species-level variation between these two taxa and *B. dorsalis* (Schutze et al., 2012b; Krosch et al., 2013).

The issue of genitalia length is more complex. *Bactrocera dorsalis*, *B. papayae* and *B. philippinensis* have been differentiated based on female aculeus length (Drew & Hancock, 1994) and male aedeagus length (Drew et al., 2008) [NB: male aedeagus and female aculeus lengths are closely correlated in these taxa (Iwaizumi et al., 1997)]. However, although Mahmood (2004) could separate *B. dorsalis* from *B. papayae* and *B. philippinensis* based on aculeus length, he was unable to separate the latter two species from each other. Further, while Iwahashi (2001) found significant differences in aedeagus length between *B. dorsalis* and *B. papayae* populations, there was substantial intraspecific variation and overlap in aedeagus size range for these taxa (Iwahashi, 2000). To resolve these apparent inconsistencies among previous studies, a more recent analysis used a structured latitudinal transect design running from northern Thailand to southern Peninsular Malaysia (Krosch et al., 2013), the reputed area of overlap or abutment of these taxa according to location data recorded by Drew & Hancock (1994). In this study, Krosch et al. (2013) showed aedeagus length to be a continuous clinal variable significantly correlated with latitude (Fig. 2). This result did not disagree with earlier literature, in that northern *B. dorsalis* had shorter aedeagi than southern *B. papayae*, but intermediate populations had no obvious disjunction in aedeagus length that could be attributed to a species break. Rather, there was a continuous and significant linear decrease in aedeagus length with increasing latitude northwards. We conclude that genitalia length variation among populations of *B. dorsalis* and *B. papayae* should be regarded as intraspecific variation.

**Molecular genetics**

A range of genetic tools have been applied to the pest species of the *B. dorsalis* complex since the 1994 revision; the relevant literature is reviewed in Clarke et al. (2005) and Boykin et al. (2014). There has, however, remained ongoing uncertainty over species limits among these taxa because, while some studies identified significant genetic differences between and among taxa (Muraji & Nakahara, 2002; Naeole & Haymer, 2003), others found none (Yong, 1995; Armstrong & Ball, 2005; Tan et al., 2011, 2013). Importantly, many of these studies...
were unable to differentiate population-level from species-level variation, because only relatively few individuals were analysed or only a limited number of geographic locations were sampled. This has been addressed by recent studies (see later) that have incorporated greater numbers of specimens collected from virtually the entire geographic range of the target taxa, with results failing to find evidence for genetic differentiation among *B. dorsalis*, *B. papayae* and *B. philippinensis*, except at a level commensurate with intraspecific variation.

Two independent multi-locus phylogenetic analyses, using different sets of nuclear and mitochondrial loci, could not differentiate *B. dorsalis*, *B. philippinensis*, and *B. papayae* from each other, even though these tests could separate these taxa from 12 other *Bactrocera* species from outside the complex (San Jose et al., 2013), and from other members of the *B. dorsalis* complex, including *B. carambolae* and *B. occultalis* (Boykin et al., 2014). This result led San Jose et al. (2013: 684) to conclude that *B. dorsalis*, *B. papayae* and *B. philippinensis* (along with *B. invadens*) ‘… probably represent a single genetically indistinguishable, phenotypically plastic, pest species that has spread throughout the world’. In other forms of genetic analyses, a population-level study using *cox1* sequence data identified haplotypes common to *B. dorsalis*, *B. papayae* and *B. philippinensis*, failing to identify genetic structure indicative of two or more species (Schutze et al., 2012b). Similar results were found in two independent microsatellite studies on *B. dorsalis* and *B. papayae* populations from Thailand and west Malaysia, which also found no evidence of population structure commensurate with the presence of two species (Krosch et al., 2013; Aketarawong et al., 2014). Rather, both studies revealed one panmictic population across the Thai/Malay Peninsula with a very weak or absent isolation by distance signal. We conclude that published comprehensive genetic evidence is insufficient to maintain the separation of *B. dorsalis* and *B. papayae*.

**Cytogenetics**

Mitotic and polytene chromosomes of Philippine *B. philippinensis* and Malaysian *B. papayae* maintained at the FAO/IAEA Insect Pest Control Laboratory (IPCL) at Seibersdorf, Austria, have been analysed and compared with mitotic chromosomes and polytene chromosome maps published for *B. dorsalis* (Zacharopolou et al., 2011). *Bactrocera philippinensis* and *B. papayae* presented the typical number of mitotic chromosomes and polytene elements as described for *B. dorsalis*. The comparative analysis of polytene chromosome structure and banding pattern failed to identify any differences that could be used as species-diagnostic markers. There was no evidence of chromosomal rearrangements, such as inversions, that could support the existence of well-separated species among these three entities of the complex (Augustinos et al., in press).

**Sexual compatibility**

Field-cage mate choice tests revealed that *B. dorsalis*, *B. papayae* and *B. philippinensis* mate randomly with each other (Medina et al., 1998; Tan, 2000; Schutze et al., 2013). These field-cage tests included a host tree and were carried out following internationally agreed standards used to determine mating compatibility in support of fruit fly Sterile Insect Technique (SIT) programmes (FAO/IAEA/USDA, 2003). Assessment of egg hatch rates, survival to adult emergence, sex ratios and hybrid fertility in this study found no evidence of postzygotic incompatibility to the *F*1 generation following hybridization of *B. dorsalis*, *B. papayae* and *B. philippinensis*.

**Chemoecology**

Males of *B. papayae*, *B. philippinensis* and *B. dorsalis* consume the potent male attractant methyl eugenol (ME) and bio-transform it to two oxidized analogues (2-allyl-4,5-dimethoxyphenol and (E)-coniferyl alcohol) for storage in the rectal gland and subsequent use in courtship interactions (Nishida et al., 1988; Tan & Nishida, 1996, 2012; Pee et al., 2002; Tan et al., 2013, in press). This results in a mating advantage for males that consume ME (Shelly & Dewire, 1994; Shelly et al., 1996; Tan & Nishida, 1996). Perkins et al. (1990) recorded minor differences in the rectal volatiles of *B. papayae* (then known as ‘Mal B’ prior to its formal description), *B. philippinensis* (= ‘Phil B’) and *B. dorsalis*, but nevertheless concluded that ‘… Mal B, Phil B, and B. dorsalis have similar glandular components’ (Perkins et al., 1990: 2486). Importantly, when referring to these minor differences, Perkins et al. (1990: 2486) concluded that ‘the analysis of Phil B is most similar to that of *B. dorsalis*’, as there were relatively greater differences between *B. philippinensis* and *B. papayae* than between *B. philippinensis* and *B. dorsalis*. This similarity, again with minor differences among these three taxa, was also reported by Fletcher & Kitching (1995). Considering *B. philippinensis* has now been synonymized with *B. papayae*, for which relatively greater differences were reported, we cannot maintain *B. papayae* as distinct from *B. dorsalis* based on glandular chemistry. We conclude there are insufficient differences in the pheromone chemistry of *B. papayae*, *B. philippinensis* and *B. dorsalis* to render them different biological species.

**Summary**

A large body of multidisciplinary research has failed to detect species-level differences among *B. dorsalis*, *B. papayae* and *B. philippinensis*. There is some population-level genetic structure and morphological variation consistent with isolation by distance for *B. dorsalis* s.l. in South-east Asia (Schutze et al., 2012b), but a lack of other genetic differentiation, absence of chemoecological differences, identical banding pattern of polytene chromosomes, minimal population-level morphological differences across the geographic distribution, and no evidence for mating isolation lead us to conclude that *B. dorsalis*, *B. papayae* and *B. philippinensis* constitute one biological species.
Evidence for the synonymy of B. invadens with B. dorsalis

Morphology

According to Drew & Romig (2013), diagnostic characters that distinguish B. invadens from B. dorsalis are scutum colour, width of postsutural lateral vitiae and aedeagus length. Bactrocera invadens has a scutum colour ranging from pale brown to black, whereas B. dorsalis is predominantly black, with less than 20% of specimens exhibiting a pale-coloured scutum. Also, B. invadens has narrower postsutural lateral vitiae than B. dorsalis, and B. invadens males have longer aedeagi than B. dorsalis, averaging 2.84 versus 2.69 mm, respectively (Drew et al., 2008; Drew & Romig, 2013). Difference in aedeagus length was reported by White (2006), with B. dorsalis averaging 2.59 mm, compared with 2.84 mm for B. invadens; note, however, that the range of aedeagus lengths overlapped (2.46–2.70 and 2.61–2.96 mm, respectively). Bactrocera dorsalis and B. invadens are different in their abdominal colour pattern (White, 2006).

A recent and comprehensive morphological survey of B. invadens and B. dorsalis from across their respective ranges (Africa, Indian subcontinent and Eastern Asia) by Schutze et al. (2014) revealed that aedeagus length of B. invadens and B. dorsalis ranged from 2.41 to 2.97 mm and 2.35 to 3.00 mm, respectively, while postsutural vitiae width ranged from 0.13 to 0.21 mm and 0.15 to 0.23 mm, respectively. Hence, there is significant overlap in these characters and neither separates the two entities based on current taxonomy. Further, Schutze et al. (2014) showed scutum colour to vary from brown to black in all specimens from Africa and the Indian subcontinent, with those from eastern Asia predominantly black. The full range of scutum colour variation (red-brown to black) was found in populations in which B. dorsalis, but not B. invadens, are recorded to occur, e.g. Pakistan (Schutze et al., 2014), India (David & Ramani, 2011; Schutze et al., 2014) and Bangladesh (Leblanc et al., 2013) (Fig. 3).

Morphometric analyses of wings and legs of B. invadens and B. dorsalis reveal very small differences between these two taxa relative to other Bactrocera species examined, particularly those from outside the B. dorsalis complex (Khamis et al., 2012). However, Khamis et al. (2012) found B. invadens to be highly similar to another member of the complex from Sri Lanka, B. kandiensis. Wing shape analysis of multiple populations of B. dorsalis and B. invadens from across their native and introduced ranges showed a high degree of similarity between B. dorsalis and B. invadens, particularly between African B. invadens and B. dorsalis from China (Schutze et al., 2014).

While variation in abdominal colour pattern has been reported, there is significant overlap between B. dorsalis and B. invadens. White (2006), for example, noted that the transverse band on tergum III in B. dorsalis is always narrow and never broadly extended along the lateral margin, whereas B. invadens
possesses a transverse band that often extends ‘broadly along the lateral margin so that much of the hind marking is black’ (White, 2006: 138). Abdominal colour pattern in *B. invadens* is, however, very variable (White, 2006), with Drew & Romig (2013) noting the transverse band of tergum III for *B. invadens* to range from narrow to broad. *Bactrocera dorsalis* similarly exhibits wide variation, with some forms clearly possessing broad lateral margins on tergum III. Narrow markings are similarly found on terga IV and V in *B. dorsalis*; yet, again they are often broad in *B. invadens* (White, 2006). As for tergum III, however, *B. invadens* possesses narrow lateral dark fuscous markings on terga IV and V (Drew & Romig, 2013) and some forms of *B. dorsalis* can possess broader markings on these terga (fig. 60B, Drew & Romig, 2013). Abdominal colour pattern is highly variable, with significant overlap between *B. dorsalis* and *B. invadens* that cannot discriminate between them or be used as evidence to maintain them as distinct species.

**Molecular phylogenetics**

Several molecular phylogenetic studies have evaluated the relationship between *B. invadens* and *B. dorsalis* (Tan et al., 2011; Khamis et al., 2012; Frey et al., 2013; San Jose et al., 2013; Schütze et al., 2014), the operational details of which are provided in Table 1. Frey et al. (2013) could not resolve *B. invadens* from *B. dorsalis* and recommended their synonymy. The multi-locus studies by San Jose et al. (2013) and Schütze et al. (2014) found *B. invadens* to be polyphyletic with other members of the *B. dorsalis* complex and both studies considered them genetically indistinguishable. Khamis et al. (2012) showed that *B. invadens* split into two clades following analysis of the *cox1* barcoding gene region, with Sri Lankan and African specimens grouping with *B. dorsalis* and some individuals of *B. invadens* from Sri Lanka grouping with *B. kandiensis*. Like Khamis et al. (2012), Schütze et al. (2014) incorporated *B. kandiensis* in their study; however, *B. kandiensis* resolved as a well-supported clade emerging from the broader *B. dorsalis/invadens* group and without any *B. invadens* individuals.

**Cytogenetics**

Mitotic and polytene chromosomes of Kenyan *B. invadens* have been compared with mitotic chromosomes and polytene chromosome maps published for *B. dorsalis* (Zacharopoulou et al., 2011). *Bactrocera invadens* presented the typical number of mitotic chromosomes and polytene elements as described for *B. dorsalis*. Comparative analysis of polytene chromosome structure and banding pattern failed to identify any differences that could be used as species-diagnostic markers. The lack of chromosomal differences was further supported by the analysis of polytene chromosomes of F1 bidirectional hybrids among *B. dorsalis* (Thai order) and *B. invadens* (Kenyan origin). The lack of detectable asynapses among the homologous chromosomes of these two entities supports the hypothesis that these two entities do not represent different species (Augustinos et al., in press).

**Sexual compatibility**

Field-cage mating tests and subsequent postzygotic compatibility analysis of hybrid viability, survival, fertility and sex ratios demonstrated that *B. invadens* from Kenya mated randomly with *B. dorsalis* from Pakistan and China under semi-natural conditions, producing fully viable offspring to the hybrid F2 generation (Bo et al., 2014).

**Chemoeckology**

As is the case for *B. papayae* and *B. philippinensis*, male *B. invadens* flies respond to and consume ME and biosynthesize the same rectal gland pheromone constituents (2-allyl-4,5-dimethoxyphenol and (E)-coniferyl alcohol) as *B. dorsalis* (Tan et al., 2011, in press; Tan & Nishida, 2012).

**Summary**

Similar to *B. papayae* and *B. philippinensis*, a considerable body of evidence spanning morphological, molecular,
Table 2. Arguments for maintaining the separation of *Bactrocera dorsalis*, *Bactrocera papayae* and *Bactrocera invadens* as provided in Drew & Romig (2013) and counter-evidence as detailed in the main text.

<table>
<thead>
<tr>
<th>Arguments against synonymization</th>
<th>Counter-arguments</th>
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<td>(Drew &amp; Romig, 2013)</td>
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<td>Male aedeagus and female aculeus length are significantly different between <em>B. papayae</em> (mean length 3.00 mm) and <em>B. dorsalis</em> (mean length 2.69 mm) (original data from Drew et al., 2008).</td>
<td>Genitalia lengths of these two species overlap (Iwahashi, 2001), are significantly variable among intraspecific populations (Mahmood, 1999; Drew et al., 2008), and vary clinally with geography (Krosch et al., 2013).</td>
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<tr>
<td>Wing shape variation allows the accurate separation of <em>B. dorsalis</em> from <em>B. papayae</em> (original data from Schutze et al., 2012a).</td>
<td>Schutze et al. (2012a) concluded that [these wing shape data] may support them [<em>B. papayae</em> and <em>B. dorsalis</em>] being considered conspecific.</td>
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<td><em>B. invadens</em> can be separated from <em>B. dorsalis</em> based on scutum colour range, aedeagus length and postsutural lateral vittae width.</td>
<td>Subsequent data and analyses found that wing shape between <em>B. dorsalis</em> and <em>B. papayae</em> (and <em>B. philippinensis</em>) varies along a geographic cline (Krosch et al., 2013) and is strongly correlated with regional biogeography (Schutze et al., 2012b).</td>
</tr>
<tr>
<td>Two mitochondrial DNA genes (<em>cox1</em> and <em>nad5</em>) render <em>B. invadens</em> as markedly different from <em>B. dorsalis</em> (unpublished data referred to in Drew &amp; Romig, 2013).</td>
<td>Scutum colour varies from red-brown to black in <em>B. invadens</em> (Drew et al., 2005) and <em>B. dorsalis</em> (LeBlanc et al., 2013; Schutze et al., 2014).</td>
</tr>
</tbody>
</table>

Cytenetic, sexual compatibility and chemoecological data now exist to reject the current taxonomy of *B. invadens* as a species distinct from *B. dorsalis*. Existing morphological diagnostic characters, particularly aedeagus length and postsutural lateral vittae, vary continuously across *B. dorsalis* and *B. invadens* geographic distributions. Scutum colour is highly variable across Africa and the Indian subcontinent but becomes predominantly black in populations of East and South-east Asia. While the underlying mechanisms for this intraspecific variation are unknown, preliminary experiments by the authors (M.K. Schutze, W. Bo and C. Caceres, unpublished data) on Pakistan-origin *B. dorsalis* with variable scutum colours at the FAO-IAEA Insect Pest Control Laboratory (Seibersdorf) have revealed scutum colour to be a simple heritable trait. Moreover, in a published niche overlap study, Hill & Terblanche (2014) combined new data with those available for *B. invadens* (De Meyer et al., 2010) and *B. dorsalis* (Stephens et al., 2007), revealing highly overlapping niches for these two taxa (including *B. papayae* and *B. philippinensis*), leading the authors to conclude that these taxa probably constitute the same biological species. In their recent treatment of *B. papayae*, *B. invadens* and *B. dorsalis*, Drew & Romig (2013) maintain their status as distinct species. Given the economic implications of the taxonomic status of these species, we address the specific points made by Drew & Romig (2013) in Table 2.

**Evidence for the maintenance of *B. carambolae***

*Bactrocera carambolae* has been included in studies examining pest members of the *B. dorsalis* complex due to its morphological similarity to *B. dorsalis* and its sympatric distribution with *B. papayae* (Drew & Hancock, 1994; Drew & Romig, 2013). Whereas much of this research effort has been directed at identifying diagnostic characters to distinguish *B. carambolae* from other *dorsalis*-complex species, recent work has increased attention on the biological relationship of *B. carambolae* with other members of the complex. Reliable, yet subtle, differences between *B. carambolae* and *B. dorsalis* have been found based on morphology, molecular genetics, chemoecology and behaviour.

*Morphology*

Drew & Romig (2013) remark that *B. carambolae* is distinguished from *B. papayae* by a broad medial longitudinal black band on abdominal terga III–V, a broader costal band apically and shorter male aedeagi and female ovipositor. Additionally, the anterolateral corners of terga IV are fuscous to black and distinctly rectangular in shape in *B. carambolae*, whereas the fuscous to black corners of terga IV of *B. dorsalis* and *B. papayae* are narrow (Drew & Romig, 2013). There is, however, considerable variation in abdominal colour pattern that does not directly correlate with aedeagus length or costal band width (Iwahashi, 1999b). For instance, individuals bearing abdominal colour patterns typical of *B. dorsalis/B. papayae* (i.e. narrow markings on terga IV) possess relatively long aedeagi (2.66–3.24 mm), whereas those with a *B. carambolae* pattern (i.e. rectangular markings on terga IV) possess both long and short aedeagi (2.37–2.68 mm; note the overlap with long aedeagi) (Iwahashi, 1999b). However, apical costal band width closely correlates with aedeagus length, in that individuals with apically broad costal bands have consistently short aedeagi, and those with distinctly narrow bands have long aedeagi (Iwahashi, 1999b). Taken together, these data led Iwahashi (1999b) to conclude that *B. carambolae* can be
distinguished from *B. papayae* by shorter aedeagi (albeit with small overlap in length) when present with a broader apical expansion of the costal band, but that terga IV markings, which are rectangular in *B. carambolae*, ranged from narrow to rectangular in *B. papayae*. Although aedeagus length is an unreliable taxonomic character, due to its variability over a wide geographic distribution, the data of Iwahashi (1999b) were recorded from individuals collected from the single locality of Singapore. The range of aedeagus length at this location was very wide (2.37–3.24 mm) and similar to that observed for *B. dorsalis* s.l. from across a large latitudinal gradient from Peninsular Malaysia to northern Thailand (see Fig. 2). Such a wide range in aedeagus length at a single location, with both short and long aedeagi correlating with additional morphological characters (e.g. apical costal band width), strongly supports the existence of two species, i.e. *B. carambolae* and *B. dorsalis*.

**Molecular genetics**

Despite *B. carambolae* being genetically similar to *B. dorsalis*, differences between these species exist for nuclear and mitochondrial DNA data. Armstrong & Cameron (2000), for instance, examined rDNA ITS1 restriction sites and showed that *B. carambolae* could be clearly separated from *B. dorsalis* [based on a ∼50 base pair (bp) insertion/deletion (indel)], whereas *B. dorsalis* remained indistinguishable from *B. papayae* or *B. philippinensis*. In a later phylogeographic study of the coxl barcode region, Armstrong & Ball (2005) found that *B. carambolae* formed a discrete but weakly supported group. Based on multi-locus phylogenetic analyses of mitochondrial DNA and nuclear DNA, Boykin *et al.* (2014) and Schutze *et al.* (2014) found that *B. carambolae* formed a reciprocally monophyletic sister group to a large clade consisting of *B. dorsalis*, *B. papayae*, *B. invadens* and *B. philippinensis* sampled from almost their entire native and invasive geographic distributions. Notably, a 44-bp indel in ITS1 is the key diagnostic feature that consistently differentiates *B. carambolae* from *B. dorsalis*, *B. papayae*, *B. philippinensis* and *B. invadens*; this was confirmed following screening of *B. carambolae* individuals from both their native distribution in South-east Asia and their invasive range of Suriname, South America (Boykin *et al*., 2014). Although the recent multi-locus phylogenetic study of San Jose *et al.* (2013) showed *B. dorsalis*, *B. papayae*, *B. philippinensis*, *B. invadens* and *B. carambolae* to be polyphyletic, six out of eight *B. carambolae* specimens (all from Malaysia) nevertheless formed a weakly supported monophyletic clade sister to remaining *B. dorsalis* s.l. specimens examined.

**Cytogenetics**

Differences in metaphase karyotype banding patterns between *B. carambolae* and *B. dorsalis* have been reported in *B. carambolae* larvae from Thailand (Baimai *et al*., 1999). Such differences between groups in mitotic chromosome heterochromatin patterns are considered indicative of cryptic species, as shown for other dipteran taxa, including other tephritids, vinegar flies and mosquitoes (Baimai, 1998). However, larvae examined by Baimai *et al.* (1999) were identified as *B. carambolae* based on the subsequent adult external morphology of other larvae that emerged from the same infested fruits; the identification of cytogenetically examined larvae as *B. carambolae* was thus inferred. Subsequent analysis of cultured *B. carambolae*, originally from Suriname, revealed that mitotic and polytene chromosomes of *B. carambolae* present the typical number of mitotic chromosomes and polytene elements as described for *B. dorsalis*, while comparative analyses of polytene chromosome structure and banding patterns failed to identify any differences that can be used as species-diagnostic markers (Augustinos *et al*., in press). The available cytogenetic data are thus inconclusive to differentiate *B. carambolae* from *B. dorsalis*.

**Sexual compatibility**

One of the principal arguments used against sexual compatibility tests made under semi-natural conditions is that such experiments are too far removed from the wild to reflect biological reality, and that ‘… little assistance can be provided from interbreeding experiments as they are unrelated to the behaviour of populations under field conditions’ (Drew & Romig, 2013: 26). We argue that despite the inherent caveats of such tests, systematically executed and analysed mating and postzygotic compatibility assessments (FAO/IAEA/USDA, 2003) provide extremely valuable insights for addressing species delimitation and their biological reality, and that ‘… interbreeding experiments are too far removed from the wild to reflect biological compatibility tests made under semi-natural conditions’ (Drew & Romig, 2013: 26).

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**Chemoecology**

Unlike *B. papayae*, *B. invadens* and *B. philippinensis*, *B. carambolae* males possess a pheromone blend that is considerably different from *B. dorsalis* s.l. (i.e. *B. dorsalis*, *B. papayae*, *B. carambolae*, *B. invadens*, and *B. dorsalis* synonymy).
Although very closely related to B. carambolae and B. invadens, this species has a glandular chemistry that is distinct from that of B. dorsalis, B. papayae and B. philippinensis. A similar result was found by Fletcher & Kitching (1995), which led them to conclude that B. carambolae and B. papayae represented distinct species. Male rectal gland compounds following ME feeding differ between B. carambolae and B. dorsalis, B. papayae and B. philippinensis. As mentioned earlier, these species accumulate 2-allyl-4,5-dimethoxyphenol and (E)-coniferyl alcohol, whereas B. carambolae males accumulate only (E)-coniferyl alcohol (Tan & Nishida, 1996; Wee & Tan, 2007). Each species has different sensitivities to, and consumption rates of, ME (Wee et al., 2002; Tan et al., in press). These differences are reflected in operational management programmes, as, while a distribution rate of four ME fibre blocks per hectare is typically used for B. dorsalis male annihilation purposes, a several-fold higher rate per hectare was needed to eradicate B. carambolae from an area in Suriname (van Sauer-Muller, 2008).

Host use

While we acknowledge the limitations of using host data as evidence for species delimitation, host range studies of B. carambolae and B. dorsalis/B. papayae nevertheless reveal distinct differences. This is particularly the case for banana (Musa sp.), which is a well documented host for B. dorsalis and B. papayae (Clarke et al., 2005) but not for B. carambolae. Two independent and comprehensive host fruit surveys conducted in the native and introduced ranges of B. carambolae (Thai-Malay Peninsula and Suriname, respectively) found that, while South-east Asian Musa sp. yielded B. papayae, no B. carambolae emerged from banana in either South-east Asia or Suriname despite large quantities of fruit being sampled (Clarke et al., 2001; van Sauer-Muller, 2005). Since these two species lack a common host, we propose the synonymy of B. carambolae under the senior name B. dorsalis (Hendel). Bactrocera philippinensis has recently been synonymized with B. papayae (Drew & Romig, 2013), and therefore B. philippinensis also becomes a new synonym of B. dorsalis. Bactrocera carambolae, while very closely related to B. dorsalis, exhibits a number of consistent differences from B. dorsalis and we consider it a valid species.

Drew & Romig (2013) argue that present-day B. invadens is probably the same species as Fabricius’s Musca ferruginea, inferring that they represent a separate species from B. dorsalis. This is inconsistent, as these authors maintain M. ferruginea as a junior synonym of B. dorsalis. Our proposal to synonymize B. invadens with B. dorsalis removes the circular ambiguity of Drew & Romig’s argument and acknowledges the considerable evidence that these taxa represent the same biological species.

In the following we provide a revised description of B. dorsalis that incorporates the morphological variation exhibited by B. papayae and B. invadens with reference to the original species descriptions and subsequent taxonomic treatments (Drew & Hancock, 1994; Drew et al., 2005; Drew & Romig, 2013) in addition to data obtained from studies listed earlier.


Bactrocera (Bactrocera) dorsalis (Hendel)


Dacus ferrugineus – Fabricius, 1805: 274.

Dacus dorsalis – Hendel, 1912: 18. Lectotype ♀ in BMNH.

Bactrocera ferruginea – Bezzi, 1913: 95.


Bactrocera (Bactrocera) dorsalis – Drew & Hancock, 1994: 17, Lectotype designation; Norrbom et al., 1998: 90; Mahmood & Hasan, 2005: 8; White, 2006: 137; Drew et al., 2007: 3.


Table 3. Summary of multidisciplinary evidence in support of the synonymization of Bactrocera papayae and Bactrocera invadens with Bactrocera dorsalis, and for the maintenance of Bactrocera carambolae as a separate species.

<table>
<thead>
<tr>
<th>Character</th>
<th>B. dorsalis compared with:</th>
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<tbody>
<tr>
<td></td>
<td>B. papayae philippinensis</td>
</tr>
<tr>
<td>Morphology</td>
<td>Clinal variation</td>
</tr>
<tr>
<td>Wing shape</td>
<td>Clinal variation</td>
</tr>
<tr>
<td>Postsutural lateral vittae</td>
<td>Same</td>
</tr>
<tr>
<td>Thoracic colour pattern</td>
<td></td>
</tr>
<tr>
<td>Abdominal colour pattern</td>
<td>Variable with overlap; often indistinguishable</td>
</tr>
<tr>
<td>Aculuspicles</td>
<td>Variable with overlap</td>
</tr>
<tr>
<td>Molecular genetics</td>
<td>Same monophyletic clade</td>
</tr>
<tr>
<td></td>
<td>Shared haplotypes</td>
</tr>
<tr>
<td>Microsatellite</td>
<td>Panmictic</td>
</tr>
<tr>
<td>Cytogenetics</td>
<td>Identical</td>
</tr>
<tr>
<td>Mitotic chromosomes</td>
<td>Fully random mating</td>
</tr>
<tr>
<td>Sexual compatibility</td>
<td>Hybrids viable and fertile</td>
</tr>
<tr>
<td>Chemoecology</td>
<td>Identical</td>
</tr>
</tbody>
</table>

Bactrocera philippinensis is included, yet note that this species has recently been synonymized with B. papayae (Drew & Romig, 2013). Grey – identical, highly variable with overlap, or clinal, and in accordance with intraspecific variation; black – consistent differences in accordance with interspecific variation.

Bactrocera (Bactrocera) papayae – Drew & Hancock, 1994: 48, syn.n.
Bactrocera (Bactrocera) invadens - Drew, Tsuruta & White, 2005: 149, syn.n.

Diagnosis. First flagellomere shorter than pilinial suture, face with a black spot in each antennal furrow. Tomentum pattern without longitudinal gap in the middle of prescutum. Scutum colour (other than vittae) red-brown to black. Lateral vittae of scutum present, parallel-sided, yellow, ending at or just behind intra-alar seta. Medial vitta of scutum absent. Scutellum largely yellow. Setae: anterior supra-alar present, prescutellar present, scutellar one pair. Anepisternal stripe not extended forward. Wing costal band width from vein subcostal to slightly below vein R_3_5 at wing apex; confluent with vein R_2_3 in depth. Cell basal costal without microtrichia. Cell costal with microtrichia in the anterodorsal corner only. Cell basal radial with microtrichiae at the base. Wing length: 5.4–6.9 mm. Foretibia pale fuscous to dark fuscous, mid-tibia pale fuscous to fuscous, hind tibia fuscous to dark fuscous. Femora largely fuscous. Abdominal terga free, except I and II. Terga markings: terga III–V with medial longitudinal black band, tergum III with a basal narrow transverse black band, terga IV and V with black triangular lateral markings, sometimes longitudinal black bands on lateral margins and sometimes without any mark. Tergum III (males) with pecten. Sternum V (males) with V-shaped notch. Posterior surstylus lobe short. Males attracted to methyl eugenol.

Note: Confident morphological diagnosis between B. dorsalis and other members of the B. dorsalis complex remains problematic. Many previously reported characters are subjective (e.g. ‘broad’ vs ‘narrow’) or have since been demonstrated to vary over geographical clines and to bear no relationship to actual species limits (e.g. genitalic morphometrics). Specific characters distinguishing B. dorsalis from other members of the complex are lacking and a consensus of evidence should be considered when differentiating this species.

Redescription. Male. Head. Vertical length 1.57–1.88 mm. Frons, of even width, length 1.36–1.57× breadth; red-brown to fuscous, with fuscous to dark-fuscous around frontal and orbital setae; anteromedial hump pale fuscous to fuscous, with short pale hairs; orbital setae dark fuscous to black: one superior orbital, two inferior orbital; lunule red-brown to fuscous. Ocellar triangle black. Vertex pale fuscous to fuscous. Face fuscous with medium- to large-sized black spot in each antennal furrow; length 0.4–0.53 mm. Gena fuscous, with brown subocular spot and red-brown to black seta present. Occiput red-brown to black, yellow to fuscous along eye margins; occipital row with two to eight dark to black postocular setae. Antenna, scape and pedicel fuscous to red-brown, first flagellomere fuscous to red-brown with fuscous on apex and outer surface; a strong red-brown to
dark dorsal seta on scape; arista black (fulvous basally); length of segments: 0.13–0.22, 0.31–0.35, 0.55–0.90 mm.

**Thorax.** Scutum colour variable red-brown to black, with lanceolate dark patterning in intermediate forms. When black, brown to orange-brown below and behind lateral poststatural vitiae, around transverse suture, between postpronotal lobes and notopleura, inside postpronotal lobes. Pleural area dark fuscous to black with red-brown below postpronotal lobe. Yellow markings as follows: postpronotal lobe; notopleural cal-lus; anepisternal stripe reaching midway between anterior margin of notopleural callus and anterior notopleural seta dorsally, continuing to katepisternum as a transverse spot, anterior margin straight to convex; anatergite (posterior apex black); anterior 55–75% katatergite (remainder black); two narrow to broad parallel-sided lateral poststatural vitiae ending at or just behind intra-alar seta; scutellum yellow with a black basal band. Postnotum black. Setae: apical scutellar; prescutellar acrostical; intra-alar; anterior and posterior supra-alar; enepisternal; anterior and posterior notopleural; and two pairs scapular.

**Legs.** Femora entirely fulvous, except for small elongate dark fuscous spot on outer apical surface of fore femur of some specimens; foretibia pale fuscous to dark fuscous, mid-tibia pale fuscous to fuscous, hind tibia fuscous to dark fuscous; mid-tibiae each with an apical black spur; tarsi fulvous.

**Wing.** Length 5.4–6.9 mm; cells basal costal and costal colourless; microtrichia in anterodistal corner of cell c only; remainder of wing colourless except fuscous cell subcostal, narrow fuscous costal band confluent with R2+3 and remaining very narrow or widening slightly if it overlaps this vein, to end just beyond apex of R4+5 (in some specimens there is an expansion around extremity of R4+5, which may be slight or expanding into a hook-like pattern), a narrow pale fuscous anal streak ending before the wing margin; with or without dense aggregation of microtrichia around A1 + CuA2; supernumerary lobe of weak to medium development.

**Abdomen.** Oval; terga free except I and II; tergum III with pecten. Tergum I, sterna I and II wider than long. Abdominal colour pattern variable: tergum I from orange-brown with pale fuscous laterally, to narrow black lateral margins, to entirely dark fuscous; tergum II orange-brown with narrow basal transverse black band, which may reach dark fuscous to black lateral margins; terg III–V orange-brown with black ‘T’-shaped pattern, comprising a transverse black band across anterior margin of tergite III, which may be shallow or deep and in some individuals reaches the lateral margins where it may expand to leave only a small postero-submedial orange-brown area, and a medial longitudinal dark fuscous to black band over terga III–V. Terga IV and V with narrow fuscous lateral margins or triangular (narrow or broad) black markings on anterolateral corners that may extend posteriorly along the lateral margin. A pair of ceromata on tergum V. Abdominal sterna dark.

**Female.** As for male, except no dense aggregation of microtrichia around A1 + CuA2; supernumerary lobe weak; no pecten present on abdominal tergite III. Oviscape orange-brown, may tend fuscous apically, dorsoventrally flattened and tapering posteriorly in dorsal view; ratio of length of oviscape to tergum V 0.7–1.2:1. Aculeus needle-shaped with four pairs of subapical setae.

**Illustrations.** Illustrations of what we now consider B. dorsalis are provided in Drew & Hancock (1994) (their figures 19, 63 and 70), Drew et al. (2005 (their figures 1 and 4) and Drew & Romig (2013 (their figures 60, 87 and 136). The variation between these figures encompasses the variation we recognize within B. dorsalis as defined here.

**Material examined.** Bactrocera (Bactrocera) dorsalis LECTOTYPE, ♀, TAIWAN (FORMOSA): Koshun, 9.v.08 (BMNH); PARALECTOTYPES, 3♀, 10♂, same data as lectotype (BMNH); PARALECTOTYPE, 1♂, Tainan, v.1912 (BMNH) (designated by Drew & Hancock, 1994).

Bactrocera (Bactrocera) invadens HOLOTYPE, ♀, KENYA: Coast, Matuga, 12.iii.2003, ICIPE sample T1, methyl eugenol trap (NMKE); PARATYPES, 4♀, KENYA: Matuga, 12.iii.2003 (MRAC); PARATYPES, 5♀, 2♂, CAMEROON: Essé, 23.viii.2004 (MRAC); PARATYPES, 3♀, 2♂, TANZANIA: Morogoro, xii.2003 (MRAC); PARATYPES, 1♂, BENIN: Cotonou (IITA Station), 16.ix.2004 (MRAC); PARATYPES, 1♀, SENEGAL: Keur Moussa, 8.vi.2004 (MRAC).


Lists of specimens examined as part of this revision are provided in earlier publications (Schutze et al., 2012a,b, 2014; Krosch et al., 2013; Boykin et al., 2014). These were collected from the entire geographic range of B. dorsalis, including all type localities of B. dorsalis (Taiwan), B. papayae (Peninsular Malaysia) and B. invadens (Kenya). Many thousands of other specimens across multiple depositories and identified as B. dorsalis, B. papayae and B. invadens have also been examined by several authors.

**Distribution.** The synonymization of B. invadens and B. papayae with B. dorsalis considerably expands the known distribution of B. dorsalis. Hence, the distribution now extends throughout much of sub-Saharan Africa, across the Indian sub-continent to China, throughout the South-east Asian Indo/Malay Archipelago, and as far east as New Guinea, the islands of the South Pacific and Hawaii, into the Philippines and Palau. Bactrocera dorsalis records from the Andaman and Nicobar Islands in the Indian Ocean are unconfirmed: Drew & Romig (2013) list B. dorsalis from Andaman Island, but it is not in the faunal lists provided by Ranganath & Veenakumari (1995a,b) and David & Ramani (2011).

**Conclusions.** This review of research data represents an example of comprehensive integrative taxonomy (sensu Schlick-Steiner et al., 2010; Yeates et al., 2011). As previously noted (e.g. Krosch et al., 2013), laboratories from countries spanning Africa, Asia, Australasia, Europe and North America have directed
independent multidisciplinary research efforts toward the resolution of *B. dorsalis* and closely related pest taxa over the past 20 years. Crucially, while such research has been ongoing for this time, a coordinated research project established by the UN-FAO/IAEA has intensified research focus over the last 5 years and fostered a more systematic and integrative approach within a significantly improved collaborative environment. Each research group has applied specific expertise to independently address questions pertaining to the biological relationships among *B. dorsalis* and related species, and virtually all lines of evidence have drawn the same conclusion: that there is insufficient evidence to maintain *B. invadens*, *B. papayae* and *B. philippinensis* as biological species distinct from *B. dorsalis*. This integrative research has further revealed complexities regarding intraspecific variation in *B. dorsalis* over its geographic distribution. In particular, this approach has shown that the greatest variability is in the Indian subcontinent, where the genus *Bactrocera* as a whole is considered to have originated and greatly diversified following its collision with Eurasia some 35–50 Ma (Krosch et al., 2012). Further, as biological data relevant to pest management have been published while these taxa existed under different names – particularly for *B. invadens*, for which considerable biological data have been generated recently – there is now a need to compile and reconcile this literature under a revised understanding that these taxa represent a single biological species.

The situation in India and Sri Lanka warrants particular attention to clarify relationships among the following species: (i) *B. kandeiensis*; (ii) *B. dorsalis*; (iii) populations previously referred to as *B. invadens*; and (iv) other *B. dorsalis* complex species. The study of Schutze et al. (2014) found that all *B. dorsalis* material examined from the subcontinent is genetically similar to *B. dorsalis* from Asia and *B. invadens* from Africa, while *B. kandeiensis* emerged as a distinct clade but with evidence of introgression with *B. dorsalis*. Khamis et al. (2012) found that *B. invadens* splits into two clades, one mixed with *B. dorsalis* and the other mixed with *B. kandeiensis*. This region is clearly fertile ground for future research into the *B. dorsalis* complex.

The applied impacts of these name changes are significant, covering aspects of trade, quarantine and field control; examples for each of these follow.

**Trade.** Currently, the distributions of *B. dorsalis* complex species dealt with in this paper are almost entirely disjoint, with most countries having only one of the species (Thailand is unique in having three – *B. dorsalis*, *B. papayae* and *B. carambolae*). Under the rules of the International Plant Protection Convention, a country with one of the species but not another has a sovereign right to impose risk reduction treatments on commodity imports from a country with another pest member of the *B. dorsalis* complex species; this reality severally restricts trade for many nations. Recognition that *B. dorsalis*, *B. invadens*, *B. papayae* and *B. philippinensis* are one species will ease restrictions to fresh commodity trade between countries where these are native or nonregulated invasive taxa.

**Quarantine.** A key element of quarantine is risk assessment. As demonstrated by Hill & Terblanche (2014), basic quarantine issues such as enhanced predictive power to determine the likely spread, and ultimate distribution, of invasive members of the *B. dorsalis* complex are greatly improved by accurately recognizing species boundaries.

**Pest management.** Many pest management tools will be improved by resolving the species limits, of which application of the SIT is one. The SIT requires mass release of sterilized male flies to mate with, and so make infertile, wild conspecific females. A great body of SIT knowledge exists for *B. dorsalis* (see chapters in Dyck et al., 2005), but much less so for the other members of the complex. The recognition of conspecificity among key pest taxa within the complex will allow *B. dorsalis* SIT to be applied in new countries and regions (Aketarawong et al., 2014).

Clarke et al. (2005) identified the *B. dorsalis* complex as not only of great economic importance, but also a group with a complex evolutionary history worthy of deeper study. We hope that, following this synonymization, attention can now focus on outstanding issues of economic importance and on elucidating the nature of intraspecific variation to further understand the evolutionary biology of *B. dorsalis* and related taxa.

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