Invasive Phytophagous Pests Arising Through a Recent Tropical Evolutionary Radiation: The Bactrocera dorsalis Complex of Fruit Flies

Anthony R. Clarke,1 Karen F. Armstrong,2 Amy E. Carmichael,1 John R. Milne,3 S. Raghu,4 George K. Roderick,5 and David K. Yeates6

1School of Natural Resource Sciences, Queensland University of Technology, Brisbane, Qld 4001, Australia; email: a.clarke@qut.edu.au; ae.carmichael@qut.edu.au
2Soil, Plant and Ecological Sciences Division, Lincoln University, Canterbury, New Zealand; email: armstrong@lincoln.ac.nz
3Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand; email: frjrm@mucc.mahidol.ac.th
4Alan Fletcher Research Station, Queensland Department of Natural Resources & Mines and CRC for Australian Weed Management, Sherwood, Qld 4075, Australia; email: raghu.s@nrm.qld.gov.au
5Environmental Science, Policy and Management, Division of Insect Biology, University of California, Berkeley, California 94720-3112; email: roderick@nature.berkeley.edu
6Australian National Insect Collection, CSIRO Entomology, Canberra ACT 2601, Australia; email: david.yeates@csiro.au

Key Words diagnostics, larval host range, invasion biology, resource use, pest status

Abstract The Bactrocera dorsalis complex of tropical fruit flies (Diptera: Tephritidae: Dacinae) contains 75 described species, largely endemic to Southeast Asia. Within the complex are a small number of polyphagous pests of international significance, including B. dorsalis sensu stricto, B. papayae, B. carambolae, and B. philippinensis. Most species within the complex were described in 1994 and since then substantial research has been undertaken in developing morphological and molecular diagnostic techniques for their recognition. Such techniques can now resolve most taxa adequately. Genetic evidence suggests that the complex has evolved in only the last few million years, and development of a phylogeny of the group is considered a high priority to provide a framework for future evolutionary and ecological studies. As model systems, mating studies on B. dorsalis s.s. and B. cacuminata have substantially advanced our understanding of insect use of plant-derived chemicals for mating, but such studies have not been applied to help resolve the limits of biological species within the complex. Although they are commonly regarded as major pests, there is
little published evidence documenting economic losses caused by flies of the \textit{B. dorsalis} complex. Quantification of economic losses caused by \textit{B. dorsalis} complex species is urgently needed to prioritize research for quarantine and management. Although they have been documented as invaders, relatively little work has been done on the invasion biology of the complex and this is an area warranting further work.

\section*{INTRODUCTION}

Dacine fruit flies (Diptera: Tephritidae: Dacinae) are one of the key pest groups of Asia and the Pacific (126, 127), with the larval stages feeding on a wide range of fruits and vegetables (3). Direct fruit damage, fruit drop, and loss of export markets through quarantine restrictions are all mechanisms by which fruit fly infestation causes economic loss. With adult traits that include high mobility and dispersive powers, high fecundity, and, in some species, extreme polyphagy, dacines are well-documented invaders and rank high on quarantine target lists. Reviews of the general biology, ecology, and pest status of the dacine fruit flies can be found in a variety of sources (13, 18, 35, 91, 132, 136).

One decade ago, in a seminal taxonomic revision, Drew & Hancock (26) described 40 new species within the \textit{Bactrocera dorsalis} complex of tropical fruit flies. \textit{B. dorsalis} sensu lato had long been recognized as the most pestiferous, polyphagous, and widespread species within a group of morphologically similar, but generally nonpestiferous, dacine fruit flies (23, 44). However, the 1994 revision was critical in that \textit{B. dorsalis} sensu stricto was redescribed and multiple sibling species existing under that name were recognized. Most notable among the newly described species was a small group of pest species, \textit{B. papayae} Drew & Hancock, \textit{B. philippinensis} Drew & Hancock, and \textit{B. carambolae} Drew & Hancock. Each of these species has a different geographic and host range to \textit{B. dorsalis} s. s. The description of the new species was carried out with traditional morphological features (26), and their recognition as separate biological units was based on a suite of evidence including allozyme, geographic, host range, and pheromonal differences (26, 88, 90). These pest species, along with a number of nonpest species, form a sibling group within the \textit{B. dorsalis} complex and their discrimination based on morphological criteria alone is extremely difficult.

Incursions of flies of the \textit{B. dorsalis} complex into Australia, Central America, the continental United States, and Oceania, with resultant direct and indirect costs running into hundreds of millions of dollars, have kept the complex at the forefront of applied and quarantine research over the past decade. Because of their economic importance, much of the research on the complex has tended to be pragmatic, focusing on diagnostics (2, 50, 60, 78), quarantine (36, 56, 83), and eradication (67, 101, 119, 129). Formal systematics on the complex has been limited, although new species have been described (116) or recognized on the basis of cytogenetic grounds (10, 11). Pest management, behavioral, and related work has tended, by its nature, to concentrate on individual species within the complex, with the extensive work on \textit{B. dorsalis} in Hawaii (105, 119, 120) and Taiwan (61, 62) being excellent examples.
It is not our intent to review here all research undertaken on species belonging to the *B. dorsalis* complex. Compilations in recent publications (4, 5, 113, 115) offer a lead into much of the dacine literature, which in turn covers much of the *B. dorsalis* complex. Rather, this review focuses on studies that simultaneously treat multiple species within the complex (e.g., biogeography, systematics, and diagnostics), biological studies that allow cross-species comparisons (e.g., mating and resource utilization studies), and areas where recognition of the complex in 1994 has significantly influenced subsequent research aimed at managing the flies (e.g., invasion biology). We also include a section on the pest status of the complex within Southeast Asia, its indigenous range, an issue that has received insufficient attention when trying to interpret the risk posed by the complex as potential invaders.

**TAXONOMY, SYSTEMATICS, AND DIAGNOSTICS**

The *B. dorsalis* complex was originally defined to contain 16 species closely related to *B. dorsalis* (44). Since the early 1980s a number of additional species have been described, beginning with *B. opiliae* in 1981 (27). The *B. dorsalis* species complex was redefined (23) and expanded (26), and now contains 75 described species (Table 1), with undescribed species remaining in collections (60). The complex shows its greatest diversity in the islands of the Indonesian Archipelago. To the east of Wallace’s line the diversity of *B. dorsalis* complex species rapidly declines such that Australia, with the world’s second-most diverse *Bactrocera* fauna, contains only three endemic *B. dorsalis* complex species. Similarly, the complex becomes rapidly less diverse moving into Asia, with only two species endemic to India.

**Diagnosis and Taxonomic History of the Complex**

Originally defined by Hardy (44), the *B. dorsalis* complex was redefined as one of 20 species complexes in the subgenus *Bactrocera* of the genus *Bactrocera* (23, 26). A contemporary morphological diagnosis of the complex is as follows: species with a clear wing membrane except for a narrow costal band not reaching R\(_{4+5}\) and a narrow anal streak, costal cells colorless or pale yellow-brown and without dense microtrichia, lateral postsutural vittae present but medial postsutural vittae absent, scutellum mostly yellow with a narrow brown basal band, scutum mostly black, abdominal terga 3–5 with a median longitudinal dark band, and variable dark patterns on lateral margins (23, 26). Male flies of the complex are attracted to methyl eugenol or cue lure, but a significant percentage have no known lure response (Table 1).

As defined by Drew (23), in addition to *B. dorsalis*, the complex in 1989 contained the following eight species from the Australasian and Oceanian regions: *B. abdolonginqua* (Drew), *B. cacuminata* (Hering), *B. dapsiles* (Drew), *B. diallagma* (Drew), *B. endiandrae* (Perkins and May), *B. mimulus* (Drew), *B. nigrescens*
## TABLE 1  
*Bactrocera* species currently considered as belonging to the *B. dorsalis* complex of tropical fruit flies (23, 26, 28, 60, 116)

<table>
<thead>
<tr>
<th>Speciesa</th>
<th>Locationb</th>
<th>Family</th>
<th>Genera</th>
<th>Species</th>
<th>Economic</th>
<th>Lure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. abdolonginqua</em> (Drew)</td>
<td>l</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. aemula</em> Drew</td>
<td>l</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. affindorsalis</em> (Hardy)</td>
<td>g, m</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. arecae</em> (H&amp;A)</td>
<td>a, i, n, q</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. atrifemur</em> D&amp;H</td>
<td>i</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. bimaculata</em> D&amp;H</td>
<td>g, r</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. cacuminata</em> (Hering)</td>
<td>a</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. carambolae</em> D&amp;H</td>
<td>c, f, g, i, n, q, r</td>
<td>27</td>
<td>50</td>
<td>77</td>
<td>Yes</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. caryae</em> (Kapoor)</td>
<td>f, o</td>
<td>7</td>
<td>8</td>
<td>10</td>
<td>Yes</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. ceylanica</em> T&amp;W</td>
<td>o</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. cibodasae</em> Drew</td>
<td>g, r</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. cognata</em> (H&amp;A)</td>
<td>m</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. collita</em> D&amp;H</td>
<td>m</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. consectorata</em> Drew</td>
<td>l</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. dapsiles</em> Drew</td>
<td>l</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. diaclagma</em> Drew</td>
<td>l</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. dorsalis</em> (Hendel)</td>
<td>b, d, e, f, j, k, n, o, p, r</td>
<td>42</td>
<td>79</td>
<td>124</td>
<td>Yes</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. dorsaloides</em> (H&amp;A)</td>
<td>m</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. endiandrae</em> (Perkins &amp; May)</td>
<td>a, l</td>
<td>7</td>
<td>10</td>
<td>24</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. fernandoi</em> T&amp;W</td>
<td>o</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. floresiae</em> D&amp;H</td>
<td>g</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. fuliginus</em> (D&amp;H)</td>
<td>a, l</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. fulvifemur</em> D&amp;H</td>
<td>m</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. fuscitibia</em> D&amp;H</td>
<td>g, j, r</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. gomboakensis</em> D&amp;H</td>
<td>j, r</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. hantanae</em> T&amp;W</td>
<td>o</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. holtmanni</em> (Hardy)</td>
<td>j, m, r</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. inconstans</em> Drew</td>
<td>l</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. indecora</em> (Drew)</td>
<td>l</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. indonesiae</em> D&amp;H</td>
<td>g</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. infusata</em> D&amp;H</td>
<td>g, i</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. involuta</em> (Hardy)</td>
<td>g</td>
<td>—</td>
<td>No</td>
<td>—</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Continued)
### TABLE 1 (Continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Family</th>
<th>Genera</th>
<th>Species</th>
<th>Economic</th>
<th>Lure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. irvingiae</em> D&amp;H</td>
<td>q</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. kanchanaburi</em> D&amp;H</td>
<td>q, r</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. kandensis</em> D&amp;H</td>
<td>o</td>
<td>13</td>
<td>16</td>
<td>22</td>
<td>Yes</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. kinabalu</em> D&amp;H</td>
<td>i</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. lateritaeina</em> D&amp;H</td>
<td>i, r</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. laticosta</em> Drew</td>
<td>l</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. latilinolea</em> D&amp;H</td>
<td>i</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. lombokensis</em> D&amp;H</td>
<td>g, i, r</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. makilingensis</em> D&amp;H</td>
<td>m</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. malaysiensis</em> D&amp;H</td>
<td>j</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. melastomatos</em> D&amp;H</td>
<td>f, i, n, q</td>
<td>1 1 2</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. merapiensis</em> D&amp;H</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. mimulus</em> Drew</td>
<td>l</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. minascula</em> D&amp;H</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. maui</em> (H&amp;A)</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. neocognata</em> D&amp;H</td>
<td>g, i</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. neopropinqua</em> D&amp;H</td>
<td>m</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td><em>B. nigrescens</em> (Drew)</td>
<td>l</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. occipitalis</em> (Bezzi)</td>
<td>c, i, m</td>
<td>3 3 3</td>
<td>Yes</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. opilae</em> (Drew &amp; Hardy)</td>
<td>a</td>
<td>4 4 4</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. osbeckiae</em> D&amp;H</td>
<td>g, r</td>
<td>1 3 7</td>
<td>No</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. papayae</em> D&amp;H</td>
<td>a, g, i, l, n, q</td>
<td>51 117 209</td>
<td>Yes</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. paraverbasicifoliae</em></td>
<td>f</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td><em>B. pedestris</em> (Bezzi)</td>
<td>g, m</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. penecognata</em> D&amp;H</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. philippinensis</em> D&amp;H</td>
<td>m</td>
<td>5 5 6</td>
<td>Yes</td>
<td>Methyl eugenol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. profunda</em> T&amp;W</td>
<td>o</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
</tr>
<tr>
<td><em>B. propinqua</em> (H&amp;A)</td>
<td>d, g, i, n, q, r</td>
<td>1 1 9</td>
<td>No</td>
<td>Cue</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. pyrifoliae</em> D&amp;H</td>
<td>q, r</td>
<td>5 6 7</td>
<td>Yes</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. quasipropinqua</em> D&amp;H</td>
<td>m</td>
<td>1 2 2</td>
<td>No</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>B. raiensis</em> D&amp;H</td>
<td>q, r</td>
<td>4 4 5</td>
<td>No</td>
<td>—</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Continued)
TABLE 1 (Continued)

<table>
<thead>
<tr>
<th>Speciesa</th>
<th>Locationb</th>
<th>Family</th>
<th>Genera</th>
<th>Species</th>
<th>Economic</th>
<th>Lure</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. selenophora T&amp;W</td>
<td>o</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
</tr>
<tr>
<td>B. sembaliensis D&amp;H</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
</tr>
<tr>
<td>B. sulavesiae D&amp;H</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
</tr>
<tr>
<td>B. sumbawaensis D&amp;H</td>
<td>g</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
</tr>
<tr>
<td>B. syzygii T&amp;W</td>
<td>o</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td>B. thailandica D&amp;H</td>
<td>q, r</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>No</td>
<td>—</td>
</tr>
<tr>
<td>B. trivialis (Drew)</td>
<td>a, l</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>Yes</td>
<td>Cue</td>
</tr>
<tr>
<td>B. unimacula D&amp;H</td>
<td>g, i</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
</tr>
<tr>
<td>B. uxiata D&amp;H</td>
<td>i, m, n, r</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
</tr>
<tr>
<td>B. verbascifoliae D&amp;H</td>
<td>f, q, r</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>No</td>
<td>Methyl eugenol</td>
</tr>
<tr>
<td>B. vishnu D&amp;H</td>
<td>f</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
</tr>
<tr>
<td>B. vulgaris (Drew)</td>
<td>a, l</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Cue</td>
<td></td>
</tr>
<tr>
<td>B. anamrabalensis Drewc</td>
<td>f</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
</tr>
<tr>
<td>B. neoarecae Drewc</td>
<td>f</td>
<td>—</td>
<td>—</td>
<td>No</td>
<td>Methyl eugenol</td>
<td></td>
</tr>
</tbody>
</table>

Authors: H&A, Hardy & Adachi; D&H, Drew & Hancock; T&W, Tsuruta & White.

Location only includes countries within each species’ natural range. Country Codes: a, Australia; b, Bhutan; c, Brunei; d, Cambodia; e, China; f, India; g, Indonesia; h, Laos; i, Malaysia; j, Myanmar; k, Nepal; l, Papua New Guinea; m, Philippines; n, Singapore; o, Sri Lanka; p, Taiwan; q, Thailand; r, Vietnam.

These species fit the description of the B. dorsalis complex and are morphologically similar to other B. dorsalis complex species; however, they have not officially been placed within the complex (28). In this paper they are not treated as part of the complex.

(Drew), and B. opiliae (Drew and Hardy), which all respond to methyl eugenol. When the B. dorsalis complex from Asia was revised a few years later (26), the definition of the group was expanded to include eight species from the B. aemula species complex of Drew (23), and numerous new species from Asia were described, bringing the total to 68 species in Asia and Oceania. Concurrent with the addition of new species to the complex, a number of species originally included in the complex by Hardy (44) were removed [B. bryoniae, B. breviaculeus, B. mayi, B. moluccensis, B. rutilus (23), B. limbifera, and B. luzonae (26)] as the taxonomic scope of the complex was narrowed. Within the past four years, six new species from Sri Lanka (116) and one from India (28) belonging to the complex have been described, bringing the total number of species to 75 (Table 1). Thirty-five species respond to cue lure, 26 species respond to methyl eugenol, and 14 species have no known lure response. Identification of species in the complex is complicated because not all species are treated within a single key (26). This complication has been partly overcome with the development of an interactive, computer-based key to 68 species in the complex (60), and a similar key has been produced for the
identification of Indo-Australasian dacine fruit flies as a whole (133). However, the six Sri Lankan members of the complex and B. paraverbascifoliae (from India) are still keyed separately (28, 116).

Diagnostic Tools

Uncertainty in species limits based on the traditionally used adult morphological features, together with overlapping host and geographic ranges, significantly impacts quarantine, pest management, and general biological study. Accurate identification is essential for species found in fruit destined for export, for distinguishing exotic from native fauna, and for providing crucial data on risk and invasion pathways. Frequently, such identifications involve immature life stages, for which there are few morphologically distinguishable characters (132). Given these problems, significant effort has been spent since 1994 in developing diagnostic tools for species within the complex.

NONGENETIC DIAGNOSTIC TOOLS Species belonging to the B. dorsalis complex are morphologically similar, with species-specific diagnostic characters found in relatively minor variation in the color patterns on the wings, thorax, legs, and abdominal tergites (60). Large samples of flies, available from surveys using male lure traps or fruit rearing, reveal that many of these diagnostic characters are variable at the species level and that intermediates spanning the morphological space between distinct species are found at nontrivial frequencies.

Discriminant analyses using wing morphometrics can reliably distinguish (90% or greater correct) between small subsets of species from Sri Lanka and those from Thailand (2), although the performance of these diagnostics is likely reduced when discrimination is attempted between a larger number of species in the complex. The shape and ornamentation of the ovipositor is increasingly used as a taxonomic character system for distinguishing species of the complex (23, 26, 27). More recently, the length of the male aedeagus has also been used as a diagnostic feature at the species level in this group (50, 54). Aedeagal length and length of the female ovipositor are significantly correlated in many Bactrocera species (53, 54, 131), owing to the mechanics of mating, and these data provide a useful diagnostic for sympatric pest species of the B. dorsalis complex in Asia (50–52). Cuticular hydrocarbon analysis is also useful for distinguishing between two species of the complex from Malaysia (37).

Computer-based, multi-access keys (60, 133) have gone a substantial way toward resolving the problems of traditional dichotomous keys for flies of the B. dorsalis complex, as they have for many other taxa. Decision paths can be optimized dynamically, allowing the most discriminative character to be used at each step and thus minimizing the number of decisions needed to reach identification. Additionally, variation in character states can be accounted for in key development and can be more completely illustrated. However, the available keys are still suitable only for the identification of adult specimens in good condition. This has
driven the exploration of other character systems for more reliable diagnostics, particularly of the larval stages.

GENETIC DIAGNOSTIC TOOLS Exploitation of genetic markers has been prompted largely through the frustration of not being able to confidently distinguish between the pest species \textit{B. dorsalis}, \textit{B. carambolae}, \textit{B. papayae}, and \textit{B. philippinensis} on the basis of morphology. Genetic approaches also provide stable characters for the identification of immature life stages and an alternative tool for routine identifications that avoids adding to the strain on expert taxonomists (130). Larval polytene chromosome differences (38) and metaphase karyotypes (10–12) have been used to distinguish \textit{Bactrocera} species, including \textit{B. dorsalis}. Electrophoretic data was used initially with limited success to distinguish between five species of the \textit{dorsalis} complex, with \textit{B. dorsalis}, \textit{B. carambolae}, and \textit{B. papayae} lacking any species-specific alleles or loci (134). However, more success in finding species-specific differences has been subsequently reported between these species and \textit{B. occipitalis} and \textit{B. philippinensis} (65). Neither karyotyping nor allozyme electrophoresis are suitable for routine diagnostic testing because they are compromised by the need for reasonable amounts of good quality tissue, and allozyme analyses are vulnerable to differential expression of enzymes at different life stages and under different environmental conditions. DNA markers, however, are not restricted in this way and a number of diagnostic procedures have emerged.

The first report of DNA markers used probes from genomic extracts to hybridize anonymous repetitive DNA of \textit{B. dorsalis}, \textit{B. cucurbitae}, and \textit{Ceratitis capitata} (47). As a squash blot method, it was proposed to be a simple, rapid, and reliable method of distinguishing any life stage of these species and ideal for border quarantine application. However, it would be complicated to use for distinguishing any more than a few species and has not been developed further.

Polymerase chain reaction (PCR)-based technologies offer more flexibility, and a number of tests using PCR-RFLP (restriction fragment length polymorphism) analysis for the most pestiferous species have been described. Early methods targeting nuclear ribosomal DNA regions, 18S + ITS1 (8, 9) and ITS1 and ITS2 (68), are still used routinely within quarantine procedures to identify larvae and eggs of tephritids intercepted at the New Zealand and Australian borders, respectively. Both methods can reliably distinguish \textit{B. carambolae} from \textit{B. dorsalis} s.s. ITS1 and ITS2 use a more complicated series of primer sets with restriction analyses, but have the added benefit of distinguishing \textit{B. dorsalis} s.s. from \textit{B. papayae} and \textit{B. philippinensis} as well as from the Australian \textit{B. dorsalis} complex species, \textit{B. opiliae}, \textit{B. cacuminata}, and \textit{B. endiandrae}. Neither of the two approaches can distinguish \textit{B. papayae} from \textit{B. philippinensis}. No population-level variation in the restriction patterns for 18S + ITS1 has been observed for morphologically confirmed species (8).

Other DNA-based methods targeting mitochondrial DNA D-loop + 12S (80, 82) and 16S (77, 78, 81) gene regions appear to have greater resolution, such that the species \textit{B. dorsalis}, \textit{B. papayae}, \textit{B. philippinensis}, \textit{B. carambolae}, \textit{B. occipitalis},
and *B. kandiensis* can be distinguished. This was validated using 83 individuals across 18 *Bactrocera* species, but, in contrast to the nuclear DNA methods above, population-level variation was observed for 4 of those species (78). As restriction pattern variation occurs in only some of the 16S sections (I–IV) amplified, incorrect identification can be avoided through choice of amplicon and restriction enzyme. Of note, however, was a difficulty discriminating *B. papayae* from the majority of *B. carambolae* individuals, although PCR-RFLP analysis of the nuclear ITS region found the haplotype to be specific to *B. carambolae* (78).

Most recently, an original test based on EPIC (exon primed intron crossing)-RFLP of muscle actin to differentiate *B. dorsalis* s.s. populations (48) has been developed into a microarray-based test that can distinguish *B. dorsalis*, *B. papayae*, and *B. carambolae* (79). Allele-specific 50-mer oligonucleotides, designed from the intron sequences of each species, are hybridized to the EPIC PCR product. The detection of heterozygote individuals and intraspecific variation suggests that this is a rapid and reliable means of documenting the species and the population genotype. However, the test is anticipated to be unable to discriminate species in which alleles are shared and, as in all other tests, highlights the need for several loci to be incorporated into any one diagnostic procedure.

There is no molecular test to date that is designed to identify each of the nine Asian pest species, with *B. caryaeae* and *B. pyrifoliae* not included in any studies. A more comprehensive test, comprising more than one gene region and more taxa within the complex, is required. Further development of the oligonucleotide microarray format (79) could go some way toward this. Nonetheless, a reference nucleotide sequence database is essential to underpin this or any other advance in diagnostic capability for the complex. The collation of such data is currently underway to support an Internet-based tool for New Zealand quarantine (6) and promises to provide a more flexible means of diagnosis.

**Evolutionary History**

Because of their pest and quarantine importance, species-level taxonomic work and diagnostics in the *B. dorsalis* complex is relatively well advanced. However, few authors have addressed the evolutionary relationships of the group or to what extent the contemporary classification reflects the phylogeny of the group. None have tackled the *B. dorsalis* complex per se and there is no phylogeny (either morphological or molecular) for the complex upon which to develop an evolutionary history. Species from the complex have been included in higher taxonomic analyses, sometimes with *B. dorsalis* s.s. as the sole representative (17, 40, 41, 66).

Studies enabling direct phylogenetic comparison of species within the complex are limited, but all have used nucleotide sequence data. An early study of the nuclear genes encoding the 18S rDNA, Cu/Zn superoxide dismutase enzyme, and mitochondrial 12S rDNA gene found those loci too conserved to differentiate between *B. dorsalis*, *B. carambolae*, and *B. papayae* (130). However, differences
between the group and \( B. (B.) \)\textit{correcta} (5\% in Cu/Zn superoxide dismutase) and \( B. (Austrodacus) \) \textit{cucumis} (1.5\%, 7\%, and 18\% at the respective loci) led to the proposal that the complex had diverged within \textit{Bactrocera} less than one million years ago. This was consistent with another estimation of 87,000 years since the divergence of the complexes \( B. (B.) \) \textit{dorsalis} and \( B. (Zeugodacus) \) \textit{tau} (55).

Monophyly of the complex (\( n = 3 \) to 6 species) within \textit{Bactrocera} has been supported in analyses using 1680 bp of 16S+12S rDNA (77); 1391 bp from combined trees for 16S, 12S, and COII + tRNA\textsubscript{Lys} + tRNA\textsubscript{Asp} (111); and 841 aligned bases from combined trees for 16S and COII + tRNA\textsubscript{Lys} + tRNA\textsubscript{Asp} (110). However, in a study of five \textit{Bactrocera} subgenera, monophyly of the complex was questioned with \( B. (B.) \) \textit{musae}, from outside the complex, appearing within the clade (78). A more comprehensive phylogenetic analysis requires the inclusion of additional nucleotide characters and more taxa. Additional loci to consider may be those already examined in \( B. dorsalis \) s.s., such as the introns of muscle actin (48) and EF1-A (99) nuclear genes, as well as the mitochondrial COI gene that successfully resolved relationships within the \( B. (Z.) \) \textit{tau} complex and in which \( B. dorsalis \) and \( B. pyrifoliae \) formed the anticipated clade (55).

**ECOLOGY**

Few ecological studies have dealt concurrently with multiple species within the \( B. dorsalis \) complex and thus the known ecology of the complex is actually the ecology of a few select species, commonly pests, that have been studied in the context of pest management. Given this limitation, the following section is highly selective in the ecological areas covered and focuses only on two areas in which research during the past decade has led to theoretical developments in a wider field (see Adult Resources and Mating Systems, below), or in which compilation of species-specific research offers insights into studying and management of flies of the \( B. dorsalis \) complex (see Larval Host Range, below).

**Adult Resources and Mating Systems**

Dacine fruit flies are anautogenous, i.e., they emerge from puparia as sexually immature adults that need to forage for resources to facilitate survival and reproduction (93). Key resources include moisture for metabolism, sugars to fuel flight, protein to attain sexual maturity and, in conjunction with lipids, for egg production (35). Sugar sources include honeydew and other plant exudates. Protein is derived from sources such as phylloplane bacteria (21, 25) and bird feces (13, 35), and moisture is derived from dew and rain (70). Adult flies forage for these resources in the environment, although lipids are probably synthesized de novo (97). In addition, adults may also actively seek out certain plant-derived phenylpropanoids (e.g., methyl eugenol and raspberry ketone) (72, 73) that are
hypothesized to play a role in the mating behavior of dacine species (33, 34, 84–86, 94, 95, 103, 104, 106, 108, 114). With respect to frequency of mating, female flies are considered monandrous, whereas male flies are polygynous (93). Within the *B. dorsalis* complex, mating behavior of some of the major pest species (85, 103, 104, 106, 108, 114) and one nonpest species (93–96) has received considerable attention. Mating behavior in dacine fruit flies has been explored from two main perspectives, although both rely on the functional significance of plant-derived chemicals to which dacine flies respond.

The most common model of mating systems within those species of the complex studied suggests that mating occurs within a defined spatial arena ("lek" sensu lato) where resources for adult flies are absent (103, 107). Within these arenas sexual selection, driven by the female’s preference for males that have fed on plant-derived phenylpropanoids, is hypothesized to operate. The ingested plant chemicals are integrated into the male fly’s sex pheromone (33, 34) and this subsequently makes them more attractive to female flies (84–86, 103, 104, 106, 108). The mating behavior of *B. dorsalis* s.s. most strongly supports this view of dacine mating behavior. Male and female *B. dorsalis* aggregate on the larval host plant at dusk and females appear to choose among males that “call” to them, with males that have had prior exposure to methyl eugenol acquiring more mates than males that have not (106, 107). Contrary observations for *B. cacuminata*, a nonpest species of the complex, have been recorded, in which exposure to methyl eugenol appeared to confer no advantage in mate acquisition (94). This suggests that the physiological usage of plant-derived chemicals may vary among species.

The second model of mating behavior observed for species within the complex hypothesizes that plant-derived phenylpropanoids serve as a mate rendezvous stimulus to which male and female flies respond for mate location (73). This hypothesis has been considered unlikely in the past, as these chemicals are not common among larval host plant species to which mating was thought to be restricted (33, 34, 106). However, unmated female flies respond to lures (1, 33, 95), and with evidence indicating that mating need not be restricted to the larval host plant (95), direct experimentation has shown that natural phenylpropanoids, such as methyl eugenol, can serve as mate aggregation stimuli when resources are spatially separated (1, 33, 95).

Research on mating systems for species within the *B. dorsalis* complex is still in its infancy, with the two most-studied cases (*B. dorsalis* s.s. and *B. cacuminata*) giving different insights. Because species within the complex are thought to be recently evolved, with a high degree of genetic relatedness, the complex offers an ideal model system to study rapid speciation and the role of mate recognition, larval host plant use, and the availability of other environmental resources in limiting gene pools. Such research will not only enable us to better understand the ecology and evolution of dacine fruit flies, but may also aid in the development of sustainable management strategies, relying on mating disruption, for the pest species within the complex.
Larval Host Range

Understanding larval host range in the complex is hampered by the fact that larval rearing records are known for only 28 species (38% of the complex): Where records are known, they are found in a variety of sources (3, 23, 26, 42, 117), but have been collated (60). Of those species with rearing records, six have only one known larval host (Table 1) and it is unclear if this is because they are truly monophagous or simply undersampled. Where two or more larval hosts for a fly have been recorded, only three species are restricted to a single plant genus (B. melastomatos on two species of Melastoma; B. propinqua on nine species of Garcinia; and B. verbascifoliae on five species of Solanum) and can be regarded as narrowly oligophagous. In contrast, the more general pattern of larval host use by flies of the complex appears to be multiple plant species across genera and families (Table 1). The key plant families containing B. dorsalis complex hosts include the Anacardiaceae, Annonaceae, Clusiaceae, Lauraceae, Moraceae, Myrtaceae, Rutaceae, Sapotaceae, and Solanaceae, each with 15 or more known fruit fly host species. Excluding the three highly polyphagous species within the complex (see below), less than 5% of host plants (16 of 369) are shared by two or more fly species. Psidium guajava (common guava, exotic to Southeast Asia) is the host most utilized by flies of the B. dorsalis complex, with eight species having been reared (B. carambolae, B. caryeae, B. dorsalis, B. kandiensis, B. occipitalis, B. papayae, B. pyrifoliae, and B. trivialis). However, guava is an exceptionally common fruit fly host plant, a known host for at least 20 Bactrocera species (3, 42). The host range for most species for which larval hosts are not known can only be guessed. It is probably safe to assume that they are noncommercial, wild fruits, but whether the flies are monophagous or oligophagous is not known.

Three species within the complex are known for their extreme polyphagy: B. papayae, with 209 recorded larval hosts across 51 plant families; B. dorsalis, with 124 host species across 42 families; and B. carambolae, with 77 host species across 27 families (Table 1). Detailed examination of host use by these species is in its infancy, but what is available strongly suggests that although large numbers of different host species may be utilized, not all are utilized equally. In laboratory trials, with limited numbers of hosts, host suitability (as assessed by oviposition preference, larval development times, and survival rates) varied across hosts from different plant families (20, 59, 124) and within a family (98). From field collections the yield of flies from fruits is rarely proportional to the presence of different fruit species within samples. For example, Terminalia catappa (Pacific almond) reared 2 to 5 times more B. dorsalis and B. papayae in samples from Thailand than would have been expected on the basis of the number or weight of T. catappa fruit in overall samples (19). In stark contrast, no B. papayae were reared from rainforest fruit samples in far north Queensland during the incursion in the mid-1990s, despite the presence of plant species recorded as hosts from Southeast Asia (39), nor were any reared from fruit samples collected in tropical lowland rainforests of Papua New Guinea (87). Such results strongly imply that simple host lists themselves
are not sufficient for identifying biological host range in these polyphagous species.

PEST STATUS AND INVASION BIOLOGY

A common perception among applied entomologists and quarantine biologists is that the *B. dorsalis* complex is a major pest group, arguably one of the most important pest species complexes in world agriculture. Two core assumptions underlie this accepted pest ranking: (a) the extreme polyphagy and hence assumed pest status of species within the complex, and (b) the known invasiveness of at least some species within the complex. For quarantine and trade, particularly, the perception of risk posed by the complex is large and the presence or absence of species within a country or region can have dramatic effects. It has been estimated that the mid-1990s incursion of *B. papayae* into north Queensland caused losses of nearly AUD$100 million, most of this due to lost export markets (24). Because much of the real pest status of the *B. dorsalis* complex actually stems from these indirect trade losses, two areas crucial to understanding this issue are reviewed below. The first of these is the pest status of the complex in its native range, i.e., Southeast Asia, as an incomplete understanding of an organism’s pest status in its endemic range confounds any understanding of its potential pest status in a newly invaded region. The second area reviewed is the invasion biology of the complex: those factors that may influence invasiveness and current research methodology to understand this issue.

Pest Status in Southeast Asia

The Southeast Asian region comprises Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, the Philippines, Singapore, Thailand, and Vietnam. This region lies at the center of distribution of the *B. dorsalis* complex, with 51 of 75 species found there (Table 1). Southeast Asia is also a center for tropical fruit production, with approximately 400 edible tropical fruit and nut species grown in the region (122). Fruits are commonly grown for local consumption and domestic markets; however, several countries supply export markets with a diverse range of fresh tropical and temperate fruits. Given the coincidence of substantial fruit-growing areas with the geographic ranges of numerous frugivorous *B. dorsalis* complex species, it is not surprising that several of these fly species are fruit pests in the region.

On the basis of FAOSTAT production and export statistics (32), 28 fresh fruit commodities are of major economic importance to Southeast Asia. Using Southeast Asian literature to expand the FAOSTAT commodity categories, which combine many fruit species, lengthens the list to 42 economic fruit types (Table 2). Of the 51 *B. dorsalis* complex species present in Southeast Asia, 9 (*B. carambolae*, *B. dorsalis*, *B. irvingiae*, *B. occipitalis*, *B. papayae*, *B. philippinensis*, *B. pyrifolia*,...
TABLE 2  Fruits of economic importance to Southeast Asia and the members of the B. dorsalis complex that infest them

<table>
<thead>
<tr>
<th>Fruit species (common name)a</th>
<th>Countries in which crop is economically importantb</th>
<th>Fly species recorded to infest fruit in Southeast Asia(^{c,d})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abelmoschus esculentus (okra)</td>
<td>i</td>
<td>—</td>
</tr>
<tr>
<td>Actinidia chinensis (kiwi fruit)</td>
<td>i, n</td>
<td>—</td>
</tr>
<tr>
<td>Ananas comosus (pineapple)</td>
<td>c, d, g, h, i, m, n, q, r</td>
<td>—</td>
</tr>
<tr>
<td>Annona spp. (custard apple)</td>
<td>m, q</td>
<td>car, dor, pap</td>
</tr>
<tr>
<td>Artocarpus altilis (breadfruit)</td>
<td>i</td>
<td>car, dor, pap, phi, rai</td>
</tr>
<tr>
<td>Artocarpus heterophyllus (jackfruit)</td>
<td>i, m, q, r</td>
<td>car, dor, irv, pap</td>
</tr>
<tr>
<td>Averrhoa carambola (carambola)</td>
<td>i</td>
<td>car, dor, pap</td>
</tr>
<tr>
<td>Capsicum spp. (chile)</td>
<td>g, m, n, q</td>
<td>car, dor, pap, tri</td>
</tr>
<tr>
<td>Carica papaya (papaya)</td>
<td>g, i, m, n, q</td>
<td>dor, pap, phi</td>
</tr>
<tr>
<td>Chrysophyllum spp. (star apple)</td>
<td>m, r</td>
<td>car, dor, pap</td>
</tr>
<tr>
<td>Citrullus lanatus (watermelon)</td>
<td>g, i, m, n, q</td>
<td>—</td>
</tr>
<tr>
<td>Citrus spp. (orange, lemon, lime)</td>
<td>c, d, g, h, i, m, n, q, r</td>
<td>car, dor, occ, pap, tri</td>
</tr>
<tr>
<td>Cucumis melo (cantaloupe)</td>
<td>g, h, i, m, n, q</td>
<td>dor</td>
</tr>
<tr>
<td>Cucumis sativus (cucumber)</td>
<td>g, i, m, n, q</td>
<td>dor, pap</td>
</tr>
<tr>
<td>Cucurbita spp. (pumpkin, gourd)</td>
<td>g, i, m, q</td>
<td>—</td>
</tr>
<tr>
<td>Dimocarpus longan (longan)</td>
<td>q, r</td>
<td>dor</td>
</tr>
<tr>
<td>Durio zibethinus (durian)</td>
<td>g, i, m, q</td>
<td>—</td>
</tr>
<tr>
<td>Ficus carica (fig)</td>
<td>g</td>
<td>—</td>
</tr>
<tr>
<td>Fragaria spp. (strawberry)</td>
<td>g, i, n, q</td>
<td>—</td>
</tr>
<tr>
<td>Garcinia mangostana (mangosteen)</td>
<td>g, i, m, n, q</td>
<td>car, pap</td>
</tr>
<tr>
<td>Litchi chinensis (litchi)</td>
<td>q, r</td>
<td>dor</td>
</tr>
<tr>
<td>Lycopersicon esculentum (tomato)</td>
<td>g, i, m, n, q</td>
<td>car, pap</td>
</tr>
<tr>
<td>Malus domestica (apple)</td>
<td>g, i, m, n, q</td>
<td>dor</td>
</tr>
<tr>
<td>Mangifera indica (mango)</td>
<td>g, h, i, m, n, q</td>
<td>car, dor, occ, pap, phi</td>
</tr>
<tr>
<td>Manilkara zapota (sapodilla)</td>
<td>i, m, q</td>
<td>car, dor, pap</td>
</tr>
<tr>
<td>Musa spp. (banana and plantain)</td>
<td>c, d, g, h, i, j, m, n, q, r</td>
<td>dor, pap</td>
</tr>
<tr>
<td>Nepheleium lappaceum (rambutan)</td>
<td>g, i, m, q, r</td>
<td>dor, pap</td>
</tr>
<tr>
<td>Passiflora edulis (passion fruit)</td>
<td>i</td>
<td>pap</td>
</tr>
<tr>
<td>Persea americana (avocado)</td>
<td>g, i, m, n, q</td>
<td>car, dor, pap</td>
</tr>
<tr>
<td>Phoenix dactylifera (date)</td>
<td>g, i, n</td>
<td>—</td>
</tr>
<tr>
<td>Pouteria sapota (sapote)</td>
<td>r</td>
<td>pap</td>
</tr>
<tr>
<td>Prunus armeniaca (apricot)</td>
<td>g, n</td>
<td>—</td>
</tr>
</tbody>
</table>

(Continued)
B. dorsalis complex of fruit flies

TABLE 2  (Continued)

<table>
<thead>
<tr>
<th>Fruit species (common name)a</th>
<th>Countries in which crop is economically importantb</th>
<th>Fly species recorded to infest fruit in Southeast Asiaa,d</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prunus avium (cherry)</td>
<td>g, i, n</td>
<td>dor</td>
</tr>
<tr>
<td>Prunus domestica (plum)</td>
<td>i, n, q</td>
<td>dor</td>
</tr>
<tr>
<td>Prunus persica (peaches, nectarine)</td>
<td>i, n</td>
<td>dor, pap, pyr, tri</td>
</tr>
<tr>
<td>Prunus spp. --species not specified</td>
<td>h</td>
<td></td>
</tr>
<tr>
<td>Psidium guajava (guava)</td>
<td>i, m, q, r</td>
<td>car, dor, occ, pap, pyr, tri</td>
</tr>
<tr>
<td>Pyrus communis (pear)</td>
<td>g, i, n</td>
<td></td>
</tr>
<tr>
<td>Rubus idaeus (raspberry)</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>Solanum melongena (aubergine)</td>
<td>g, i, m, q</td>
<td>pap</td>
</tr>
<tr>
<td>Tamarindus indica (tamarind)</td>
<td>m, r</td>
<td></td>
</tr>
<tr>
<td>Vitis vinifera (grape)</td>
<td>g, i, m, n, q, r</td>
<td></td>
</tr>
</tbody>
</table>

*Plant nomenclature follows that in Reference 58.
1Country abbreviations identical to those in Table 1.
2Bactrocera dorsalis complex species infesting Southeast Asian fruit derived from Reference 60. cat, B. carabola; dor, B. dorsalis; irv, B. irvingiae; occ, B. occipitalis; pap, B. papayae; phi, B. philippinensis; pyr, B. pyrifoliae; tai, B. raiensis; tri, B. trivialis.
3Note that columns two and three are independent. They are not meant to imply that for a particular fruit every fly species listed as attacking that fruit does so in every listed country. For example, B. philippinensis attacks papaya in the Philippines, but not in other countries because it is absent from those countries (see Table 1 for country records).

B. raiensis, and B. trivialis) have been reared from 27 of these 42 commercial fruits (Table 2).

The extent to which each B. dorsalis complex species affects fruit production and agricultural economics in the Southeast Asian region is vital information for setting research priorities for these species. Several Southeast Asian species within the B. dorsalis complex have been accorded status as pests ranging from “significant” (B. occipitalis), to “serious” (B. pyrifoliae) and “major” (B. carabolaee, B. dorsalis), to the “most destructive of all dorsalis complex species” (B. papayae) (29). Similar terms have been used by others to describe the pest importance of B. dorsalis complex species (132). The justification for using these descriptors is seldom explicitly stated in the literature. Nevertheless, three ecological criteria, (the range of host fruit species, especially that of economically important hosts; geographic distribution; and fruit infestation rates) seem important in the literature for defining a fly species as an important pest. A fourth criterion for establishing pest status, their economic effects, is rarely addressed in the literature. Each of these criteria is discussed here in relation to the nine pest species in the B. dorsalis complex that infest Southeast Asian commercial fruit.

The known distributions of the nine B. dorsalis complex pest species vary tremendously, in terms of the commercial fruits they infest (Table 2) and the
countries in which they are found (Table 1). *B. dorsalis* and *B. papayae* have the greatest host ranges, with each infesting, respectively, 21 and 22 of 42 commercially important crops in Southeast Asia. *B. carambolae* also infests fruits from many plant species, having been recorded from 13 commercial fruits. The remaining six potentially pestiferous *B. dorsalis* complex species (*B. irvingiae*, *B. occipitalis*, *B. philippinensis*, *B. pyrifoliae*, *B. raiensis*, and *B. trivialis*) have each been recorded from fruits of fewer than five economically important crops. *B. occipitalis*, *B. philippinensis*, *B. pyrifoliae*, and *B. trivialis* need more extensive fruit surveys to establish their pest status (29). The addition of commercial fruits to the host fruit ranges of *B. irvingiae* (jackfruit and santol) and *B. raiensis* (breadfruit) (60) since these flies were described (26) highlights the need for further host fruit surveys.

*B. carambolae*, *B. dorsalis*, and *B. papayae*, the three members of the *B. dorsalis* complex with the greatest commercial host fruit ranges, also have the widest distributions, with each having been recorded in 4 or more of the 10 Southeast Asian countries. Each of the other six *B. dorsalis* complex pest species occurs in three or fewer countries. *B. carambolae* has been found in Vietnam and *B. occipitalis* in Brunei (60) since their first descriptions (26). The distributions of the nine *B. dorsalis* complex pest species will undoubtedly increase as more surveys are done throughout the region.

Fruit infestation rates are of vital importance for determining the pest status of fruit flies. Generally, just one larva in a fruit is enough for rejection by a consumer (or by quarantine in an export destination country). The level of infestation determines the quantity of produce that can be sold and, therefore, the economic returns to farmers. Despite the importance of knowing infestation rates, virtually no literature is available concerning *B. dorsalis* complex species in Southeast Asian fruit crops. Literature concerned with infestation from areas outside the region, where *B. dorsalis* complex species have been introduced (*B. carambolae* in Surinam and *B. dorsalis* s.s. in Hawaii), is therefore presented (Table 3).

Infestation rates for *B. carambolae* and *B. dorsalis* show a similar pattern, i.e., that infestation rates are markedly higher in some fruit species than in others. Thus, more than 40% of carambola fruit samples in Surinam were infested with *B. carambolae*, whereas only 1.2% of sweet orange samples were infested by this fly, with a wide range of infestation rates in between (Table 3). Similar infestation patterns were found for *B. dorsalis* in Hawaii, where a maximum 55% of papaya fruits were infested, compared with 0.026% for rambutan. Although infestation rates are of major importance for determining pest status, they may fluctuate considerably within the same fruit species with season and geographical location (7). Methods that consider such fluctuations need to be developed to enable comparisons of infestation rates among fruit species.

The final criterion for determining pest status of *B. dorsalis* complex species is their economic effects, e.g., losses or control costs associated with infestation. Some basic economic analyses have been conducted (123). However, these were concerned with tephritid fruit flies in general rather than individual fly species and
TABLE 3  Maximum infestation rates for \textit{B. carambolae} and \textit{B. dorsalis} in fruits of economic importance to the Southeast Asian region. Data were not available from Southeast Asia and so infestation rates from other regions of the world, where the flies have been introduced, were used

\begin{tabular}{|c|c|c|c|}
\hline
\textbf{Fruit} & \textbf{\% Infested fruit samples} & \textbf{\% Infested fruit} & \textbf{No. flies emerging kg}^{-1} \text{ fruit} \\
\hline
Carambola & 41.6 & Papaya & 54.87 & Tangerine & 42.8 \\
Star apple & 17.2 & Rambutan & 0.12 & Guava & 30.8 \\
Mango & 16.3 & Pineapple & 0.0 & Litchi & 8.2 \\
Guava & 11.4 & & & Mango & 5.8 \\
Sapodilla & 8.7 & & & Guava & 23.8 \\
Grapefruit & 8.0 & & & Mango & 10.7 \\
Mandarin & 5.7 & & & Tangerine & 6.1 \\
Sweet orange & 1.2 & & & & \\
Lime & 0 & & & & \\
Banana & 0 & & & & \\
Custard apple & 0 & & & & \\
Papaya & 0 & & & & \\
Passion fruit & 0 & & & & \\
Pineapple & 0 & & & & \\
Tamarind & 0 & & & & \\
\hline
\end{tabular}

do not ascertain the economic impact of one fly species relative to others. There is a clear need for species-specific economic analyses.

Although some \textit{B. dorsalis} complex species have been accorded status as “serious” or “major” pests in Southeast Asia, little evidence has been published that supports these descriptors being placed on them. The efficient development of research effort toward the management of pest species of the \textit{B. dorsalis} complex can only be done when such information becomes available.

\textbf{Invasion Biology}

Species within the \textit{B. dorsalis} complex vary widely in the extent of their geographical range (26). Most species are restricted (e.g., 50 of 75 species are recorded from only one country, Table 1), with relatively few species more widely distributed (e.g., only 5 of 75 are found in five or more countries). Only a few species, including \textit{B. dorsalis}, \textit{B. carambolae}, \textit{B. philippinensis}, and \textit{B. papayae}, are actively
expanding their range (15, 67, 109) and are, by definition, invasive: These species are also characterized by a relatively broad host range and are economically important. Explaining the ability of such species to invade new regions, and the consequences of these invasions, represents active areas of research, and many of the scientific tools used to study biological invasions have originated through case studies of tephritid flies, including *Bactrocera* species. The impetus for this research stems largely from active programs to develop molecular genetic methods for diagnostics, particularly in Australia (125, 135), New Zealand (9), the United States (71), and elsewhere (67, 75).

Compared with our understanding of the invasion biology of *Ceratitis capitata*, the Mediterranean fruit fly (71), and *B. tryoni*, the Queensland fruit fly (112, 135), relatively little is known about species in the *B. dorsalis* complex. However, as with these other invasive tephritids, global and regional transport of fruit and vegetable products results in constant propagule pressure by species such as *B. dorsalis* (92). Fly interceptions at airports and other points of entry bear this out but also demonstrate that actual colonization and establishment is less frequent than immigration (16). This conclusion is complicated, however, by the fact that recently established populations may persist below detection levels for some time. An important question for pest management, critical for assessing whether populations can be completely eradicated or merely controlled, is whether fruit fly populations represent transient outbreaks or have become established. To address this question, research on the historical demography of invasive fruit fly populations has prompted the development of novel approaches to determine population origins and structure, including statistical assignment tests (22) and resampling statistics based on heterozygosity and shared alleles (112). Using these approaches, studies of *C. capitata*, *B. tryoni*, and other *Bactrocera* species show that population histories are typically not simple, with established populations comprising both ancestral and invading lineages (76). For estimation of other population parameters, such as invading population size and current gene flow, new Monte Carlo approaches show much promise (14, 31).

The impacts of invasions of *Bactrocera* species on other arthropods have been little studied with the noted exception of the interaction between *B. dorsalis* and previously established *C. capitata* in the Hawaiian Islands. Because of the disappearance of Mediterranean fruit fly in low-elevation areas following the introduction of *B. dorsalis*, it had been assumed that *B. dorsalis* would displace *C. capitata* elsewhere in the Hawaiian Islands and eradication strategies were developed on the basis of this reasoning (121). However, more recent experimental work has shown that in higher-elevation coffee plantations, *C. capitata* prevails as a result of a different life history: *C. capitata* is more of an “r-selected” species, smaller and capable of rapid colonization of newly planted coffee, whereas *B. dorsalis* is more of a “K-selected” species, larger with a later onset of reproduction (120). However, the situation can be more complicated: For example, under certain conditions both species may lose in competition to another fly, *B. latifrons* (64). There is also evidence that parasitoids introduced for biological control may influence the
competitive outcome between pest fly species and may also impact indigenous fly species (30, 49). The direct impacts of Bactrocera species on indigenous arthropod species have not been well studied (39, 87).

A number of factors suggest that much will be learned about the invasion biology of the B. dorsalis group in the near future. In particular, a wealth of genetic tools is now available, active quarantine programs exist worldwide, and the infrastructure to share data concerning invasive species is rapidly growing. New molecular tools based on genetic modification will likely permit tracking of genetically marked individuals and provide alternative, albeit controversial, methods of control (43, 100).

CONCLUSIONS

Systematics and Evolutionary History

A common question that has circulated in the fruit fly community since 1994 has been, Did Dick Drew and Dave Hancock get it right when they split B. dorsalis into so many new species? Accumulated evidence now suggests that in most cases they did. By combining cytological, allozyme, and nucleotide data, there is general support for separation of even the most closely related species within the group. However, some species, such as B. carambolae and B. papayae, require molecular tools of high precision for accurate diagnosis. How these slight differences relate to species concepts has not been addressed. For example, is the level of interspecific genetic difference detected between B. carambolae and B. papayae greater than or less than the intraspecific differences between populations of other species within the complex?

Evidence to date suggests that the B. dorsalis complex represents a rapidly evolving species complex and that much of the species diversity we currently see has been generated in recent evolutionary time (past 1 to 2 million years). As such, the complex represents a good example of a phytophagous insect evolutionary radiation. Contrary to a number of other phytophagous arthropod radiations, we do not in this example have evidence of a tightly coevolving arthropod/host plant system. Rather, the radiation has probably been driven by a complicated mixture of host shifting and host range expansion, all happening within the context of a diverse rainforest plant community and a fast-evolving, Southeast Asian geological mosaic of islands and accreted terrains (74). Because of their diversity and likely evolutionary histories, these flies offer a remarkably tractable system for testing the validity of different species concepts and speciation mechanisms.

For the B. dorsalis complex to become useful as a model system for wider evolutionary-ecology questions, the development of a phylogeny for the group is critical. Phylogenetic work for the complex is in its infancy, currently relying on few morphological characters, short pieces of mitochondrial DNA, and small taxon samples. That current taxonomic treatments are geographically limited (e.g., Australia/Papua New Guinea, Asia, Sri Lanka) has also hindered an overall systematic
understanding of the group. A complete phylogeny is urgently needed, developed from a combination of molecular and morphological data, to help resolve species limits and their relationship to each other.

Hybridization, which has been reported or suspected between species within the complex (81, 128), needs to be studied further to determine if it is a rare event, with little impact on the integrity of species’ gene pools, or if it is common, in which case species limits would need to be redefined. The unresolved issue of hybridization is a reflection that little or no effort has yet been made to establish the extent to which morphologically defined species within the complex reflect biological species. Studies of mating systems within the complex, which may help resolve this issue, are still limited and, with respect to phytochemicals, give conflicting results. Studies of the mate recognition systems (89) of *B. dorsalis* complex flies are needed to help understand the functional cues by which individuals recognize potential mates and therefore set the limits to gene pools in the complex.

### Pest Status

The real pest status of flies within the *B. dorsalis* complex remains ambiguous. There is no doubt that in particular localities, and on selected crops, complex species such as *B. dorsalis*, *B. papayae*, and others cause major loss. There is also no ambiguity about the fact that the presence of even one of the pest species from the complex in a country or region can dramatically impact the freedom of market access. What is less well documented, in an economic sense, is how pestiferous are even the best known and widespread of the *B. dorsalis* complex species. Exactly how economically damaging are species such as *B. philippinensis* and *B. occipitalis*, in comparison to other flies within the complex, other daceine fruit flies, and other pests within the cropping system, has not been determined. If such information does exist, as we suspect it does for at least some localities, then it needs to be much more widely distributed in the standard literature, as such information is vital for directing research efforts for tackling the fruit fly problem.

### ACKNOWLEDGMENTS

In this review the following authors have taken lead responsibility for particular sections and are the best first contact for further discussion of those sections: ARC, overall coordination, ecology, and larval host range; KA, molecular diagnostics and evolution; AC, morphological diagnostics; JM, pest status; SR, adult resources and mating behavior; GR, invasion biology; and DKY, systematics. ARC and DKY acknowledge funding from the Australian Research Council (Large Grant A001058580), which helped support the preparation of this review. ARC and SR thank Prof. R.A.I. Drew for introducing them to fruit flies and the *B. dorsalis* complex.
The Annual Review of Entomology is online at http://ento.annualreviews.org

LITERATURE CITED

8. Armstrong KF, Cameron CM. 2000. Species identification of tephritids across a broad taxonomic range. See Ref. 113, pp. 703–10
20. Cornelius ML, Duan JJ, Messing RH.

2000. Volatile host fruit odors as attractants for the oriental fruit fly (Diptera: Tephritidae). J. Econ. Entomol. 93:93–100


34. Fitt GP. 1981. The influence of age, nutrition and time of day on the responsiveness of male Dacus opiliae to the synthetic lure, methyl eugenol. Entomol. Exp. Appl. 30:83–90


42. Hancock DL, Hamacek EL, Lloyd AC, Elson-Harris MM. 2000. The Distribution


44. Hardy DE. 1969. Taxonomy and distribution of the oriental fruit fly and related species (Tephritidae-Diptera) in Honolulu and suburban areas of Oahu, Hawaii. Environ. Entomol. 16:1273–82


46. Haymer DS, Tanaka T, Teramae C. 1994. DNA probes can be used to discriminate between tephritid species at all stages of the life cycle (Diptera: Tephritidae). J. Econ. Entomol. 87:741–46


59. Lee WY, Chang JC, Lin TL, Hwang YB.


Investigation of physiological consequences of feeding on methyl eugenol by Bactrocera cacuminata (Diptera: Tephritidae). Environ. Entomol. 31:941–46


104. Shelly TE. 2001. Feeding on methyl eugenol and Fagraea berteriana flowers increases long-range female attraction by males of the oriental fruit fly (Diptera: Tephritidae). Fla. Entomol. 84:634–40


118. van Sauers-Muller A. 1991. An overview...
of the carambola fruit fly *Bactrocera* species (Diptera: Tephritidae) found recently in Suriname. *Fla. Entomol.* 74: 432–41


130. White IM. 1996. Fruit fly taxonomy: recent advances and new approaches. See Ref. 68a, pp. 253–58

131. White IM. 2000. Morphological features of the tribe Dacini (Dacinae): their significance to behaviour and classification. See Ref. 5, pp. 505–33


# CONTENTS

**Biology and Management of Insect Pests in North American Intensively Managed Hardwood Forest Systems,**
David R. Coyle, T. Evan Nebeker, Elwood R. Hart, and William J. Mattson  

1

**The Evolution of Cotton Pest Management Practices in China,**
K.M. Wu and Y.Y. Guo  

31

**Mosquito Behavior and Vector Control,**
Helen Pates and Christopher Curtis  

53

**The Genetics and Genomics of the Silkworm, *Bombyx mori,***
Marian R. Goldsmith, Toru Shimada, and Hiroaki Abe  

71

**Tsetse Genetics: Contributions to Biology, Systematics, and Control of Tsetse Flies,**
R.H. Gooding and E.S. Krafsur  

101

**Mechanisms of Hopperburn: An Overview of Insect Taxonomy, Behavior, and Physiology,**
Elaine A. Backus, Miguel S. Serrano, and Christopher M. Ranger  

125

**Fecal Residues of Veterinary Parasitocides: Nontarget Effects in the Pasture Environment,**
Kevin D. Floate, Keith G. Wardhaugh, Alistair B.A. Boxall, and Thomas N. Sherratt  

153

**The Mevalonate Pathway and the Synthesis of Juvenile Hormone in Insects,**
Xavier Bellés, David Martín, and Maria-Dolors Piulachs  

181

**Folsomia candida (Collembola): A “Standard” Soil Arthropod,**
Michelle T. Fountain and Steve P. Hopkin  

201

**Chemical Ecology of Locusts and Related Acridids,**
Ahmed Hassanali, Peter G.N. Njagi, and Magzoub Omer Bashir  

223

**Thysanoptera: Diversity and Interactions,**
Laurence A. Mound  

247

**Effects of Plants Genetically Modified for Insect Resistance on Nontarget Organisms,**
Maureen O’Callaghan, Travis R. Glare, Elisabeth P.J. Burgess, and Louise A. Malone  

271
CONTENTS


PHEROMONE-MEDIATED AGGREGATION IN NONSOCIAL ARTHROPODS: AN EVOLUTIONARY ECOLOGICAL PERSPECTIVE, Bregje Wertheim, Erik-Jan A. van Baalen, Marcel Dicke, and Louise E.M. Vet 321

EGG DUMPING IN INSECTS, Douglas W. Tallamy 347

ECOLOGICAL, BEHAVIORAL, AND BIOCHEMICAL ASPECTS OF INSECT HYDROCARBONS, Ralph W. Howard and Gary J. Blomquist 371

THE EVOLUTION OF MALE TRAITS IN SOCIAL INSECTS, Jacobus J. Boomsma, Boris Baer, and Jürgen Heinze 395

EVOLUTIONARY AND MECHANISTIC THEORIES OF AGING, Kimberly A. Hughes and Rose M. Reynolds 421

TYRAMINE AND OCTOPAMINE: RULING BEHAVIOR AND METABOLISM, Thomas Roeder 447

ECOLOGY OF INTERACTIONS BETWEEN WEEDS AND ARTHROPODS, Robert F. Norris and Marcos Kogan 479

NATURAL HISTORY OF PLAGUE: PERSPECTIVES FROM MORE THAN A CENTURY OF RESEARCH, Kenneth L. Gage and Michael Y. Kosoy 505

EVOLUTIONARY ECOLOGY OF INSECT IMMUNE DEFENSES, Paul Schmid-Hempel 529

SYSTEMATICS, EVOLUTION, AND BIOLOGY OF SCELIONID AND PLATYGASTRID WASPS, A.D. Austin, N.F. Johnson, and M. Dowton 553

INDEXES

Subject Index 583
Cumulative Index of Contributing Authors, Volumes 41–50 611
Cumulative Index of Chapter Titles, Volumes 41–50 616

ERRATA

An online log of corrections to Annual Review of Entomology chapters may be found at http://ento.annualreviews.org/errata.shtml