

Biogeography and Speciation in the Dacini (Diptera: Tephritidae: Dacinae)

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Abstract

The geographic distributions and host associations of the Dacini in the area from the Indian subcontinent, through South East Asia to Papua New Guinea and the South Pacific, are discussed. Included in this is the biogeographic significance of Wallacea and more detailed analysis of the Papua New Guinea and Australian fauna in relation to the rainforest flora of the same region. In summary, it is postulated that the Dacini species have cospeciated with rainforest plant species in a process fitting the Recognition Concept of species (Paterson, 1985). Although the tropical and subtropical rainforest flora are Gondwanan in origin, the Dacini fauna appear to have speciated primarily over the Tertiary Period, influenced by a combination of oscillations in topography, localized climate and land bridges during glaciation cycles.

Introduction

The Dacini, primarily comprised of species of 2 genera (*Bactrocera* Macquart and *Dacus* Fabricius), form a major part of the tropical and subtropical Tephritidae. In the Asian, South East Asian to Pacific region in particular, there has been extensive speciation. The occurrence of large numbers of sibling species, the patterns of distribution of fly species and their endemic host plants, and the strong biological relationship of species to their host plants, provide a unique opportunity to study the biogeography and speciation within this important group of flies. In this paper, a discussion of biogeography and speciation is presented from taxonomic and ecological perspectives. Hopefully, as molecular techniques advance and phylogenetic research is undertaken for large numbers of dacine species, this paper will provide some useful baseline information.

Species – The Fundamental Problem

Species are real entities, each having its own genetic makeup and usually regarded as a unit of evolution. For the taxonomist, the basic challenge is to define (and name) species in a way that will provide an understanding of their nature and origin. In other words, in the Dacini, we need to know if there is a relationship between the morphological characterizations and the real unit of evolution. This is particularly relevant when we see that large numbers of sibling species occur. What, then, is the most significant concept of species within the group that, in turn, will provide accurate species definitions?

From a practical viewpoint, dacine taxonomy began with pure morphological definitions of species and this proved satisfactory until we encountered the extensive speciation that has led to the large groups of sibling species (e.g., May, 1951, 1965; Hardy, 1951, 1973, 1974; Drew, 1989). In an attempt to elucidate the species within the *Bactrocera dorsalis*-complex of South East Asia, Drew and Hancock (1994) used host plant records, male pheromone chemistry and some molecular data to help separate the most difficult populations. In many cases, the biological and chemical data have been extremely helpful, to date, but DNA analyses have not provided definitive solutions.

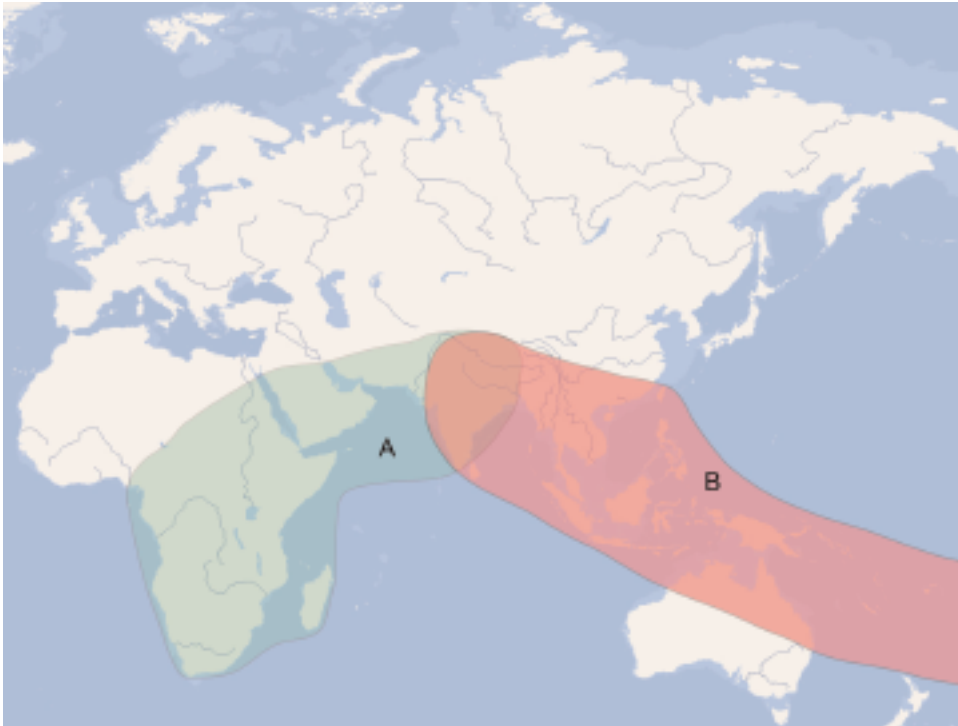


Figure 1 – The endemic distribution of Genus *Dacus* Fabricius (A) and Genus *Bactrocera* Macquart (B). Note some overlap in the area of the Indian subcontinent.

Geographic Distributions of Dacini Species

The worldwide distributions of known species within the tribe Dacini is given in Table 1. Based on current available data, there are 880 described species of which 629 belong to the genus *Bactrocera* and 248 to the genus *Dacus*. The endemic distributions of the genera *Dacus* and *Bactrocera* are shown in Figure 1. All but 10 of the *Bactrocera* are distributed in the region from India, across South East Asia to the Pacific Islands whilst the majority of *Dacus* species belong to the African continent.

Within the Asian-Pacific Dacini, primarily consisting of *Bactrocera* species, the largest number of species occur in South East Asia and Papua New Guinea. Westwards from South East Asia, to India and surrounding areas (countries) the number of species declines. Similarly, east and southeast from South East Asia and Papua New Guinea, the number of species declines. In this direction, a distinct filtering effect across islands can be observed (Table 2). This effect could be related to the decline in land area of the islands with longitude, in an easterly direction, or a combination of this and the reduced areas of rainforests that also follow the same pattern.

Endemism. For this analysis, endemic species are defined as those that occur within the specific region only. This eliminates those that are shared and those that have been more recently introduced. The percentages of species in each major genus, endemic to the Indian subcontinent, South East Asia, Papua New Guinea, Australia and the Pacific islands are listed in Table 3.

The high levels of endemism in each area indicates that speciation has occurred in relative isolation over a considerable period of time. The lower level of endemism in India, with 23 species occurring in common with South East Asia, indicates a level of contact between these 2 zones. There are 13 species shared between Australia and Papua New Guinea and 6 species shared between Papua New Guinea and South East Asia. Probably, these zones have been isolated for a very long period

Table 1. Worldwide geographic distribution of species of Dacini in each of the four genera

| | Total No. Species | Bactrocera Species | Dacus Species | Ichneumonopsis | Monacrostichus |
|--|----------------------|-----------------------|------------------|----------------|----------------|
| Africa (incl. Madagascar and Mascarene Is) | 182 | 10 | 172 | 0 | 0 |
| Indian Subcontinent | 68 | 56 | 12 | 0 | 0 |
| Southeast Asia | 256 | 218 | 35 | 1 | 2 |
| Papua New Guinea | 180 | 167 | 13 | 0 | 0 |
| Australia | 88 | 76 | 12 | 0 | 0 |
| Solomons (incl. Bougainville) | 53 | 51 | 2 | 0 | 0 |
| Vanuatu | 12 | 11 | 1 | 0 | 0 |
| New Caledonia | 11 | 10 | 1 | 0 | 0 |
| Fiji | 4 | 4 | 0 | 0 | 0 |
| Tonga | 6 | 6 | 0 | 0 | 0 |
| Samoa | 7 | 7 | 0 | 0 | 0 |
| Niue | 2 | 2 | 0 | 0 | 0 |
| Cook Islands | 2 | 2 | 0 | 0 | 0 |
| Austral Islands | 2 | 2 | 0 | 0 | 0 |
| Society Islands | 2 | 2 | 0 | 0 | 0 |
| Marquesas Islands | 1 | 1 | 0 | 0 | 0 |
| Tuamotu Archipelago | 2 | 2 | 0 | 0 | 0 |
| Micronesia/N. Pacific | 2 | 2 | 0 | 0 | 0 |
| Totals | 880 | 629 | 248 | 1 | 2 |

Table 2. Percentage of known species of Dacini (Diptera: Tephritidae: Dacinae) in major geographic areas

| Country | Percent of total fauna |
|-----------------------------|------------------------|
| India | 10.0 |
| South East Asia | 37.0 |
| Papua New Guinea | 26.0 |
| Australia | 13.0 |
| Solomon Islands | 8.0 |
| Vanuatu | 2.0 |
| New Caledonia | 2.0 |
| Fiji | 0.4 |
| Tonga | 0.7 |
| Western Samoa | 0.8 |
| Other South Pacific Islands | 0.1 |

Table 3. Percentages of species of Bactrocera and Dacus endemic to each major geographic area

| Genus | Indian Subcontinent | SE Asia | PNG | Australia | Pacific Is. |
|------------|---------------------|---------|-----|-----------|-------------|
| Bactrocera | 66 | 89 | 90 | 84 | 100 |
| Dacus | 67 | 86 | 92 | 92 | 100 |

with a longer break between Papua New Guinea and South East Asia. For the Dacini, the line of demarcation between the endemic Papua New Guinea fauna and that of South East Asia appears to be the eastern part of Wallacea, i.e. further east than Wallace's line. Another point to note is that there is very little difference between the percent endemism in the genus *Bactrocera* and genus *Dacus* in each zone. Although *Dacus* has been through more prolific speciation in Africa, Drew and Hancock (2000) suggested that the parent stock of all Dacinae are Gondwanan in origin and arose in the area now known as India rather than the Southeast Asian/Australasian plate. Indeed, the Asian *Dacus* subgenera *Callantra*, *Dacus* and *Didacus* appear to have arisen from the same parental stock, taking into account the endemic host plant families that they have in common. One can conclude that the Asian-Pacific *Bactrocera* and *Dacus* have been actively speciating, concurrently, for the same time period.

Geographic Distribution of the *Bactrocera dorsalis*-complex Species

During the past 2 decades, we have had extensive male lure trapping and host plant surveys across South East Asia, Papua New Guinea, Australia and the South Pacific Islands. This has resulted in detailed knowledge of the *Bactrocera dorsalis*-complex species and their geographic distributions over a wide area. Currently, the *dorsalis*-complex is known to consist of approximately 80 described species and another 20 undescribed which are held in our collections. The data summarized in Table 4 are based on the 80 species described in literature.

The low numbers recorded in Myanmar, China, Laos and Cambodia have resulted from collections not being conducted in these countries. In Peninsular Malaysia, Thailand and Vietnam, approximately 80% of species are shared.

Using the *dorsalis*-complex as an indicator, one can conclude that the real "hot spots" of dacine speciation have been the present continental area surrounded by Thailand, Vietnam and Peninsular Malaysia and the isolated land areas of the Philippines, Indonesia, "Borneo" and Papua New Guinea. Probably, the Philippines, Indonesia and Borneo are more recent separations from the continental

Table 4. Geographic distribution of sibling species within the *dorsalis*-complex (Diptera: Tephritidae: Dacinae) from the Indian subcontinent, South East Asia to Australia

| Country | No. Species |
|-----------------------------------|-------------|
| Bhutan | 1 |
| Bangladesh | 1 |
| Nepal | 1 |
| Pakistan | 1 |
| India | 4 |
| Sri Lanka | 3 |
| Andaman Islands | 2 |
| Myanmar | 1 |
| China | 1 |
| Taiwan | 1 |
| Laos | 1 |
| Cambodia | 2 |
| Vietnam | 17 |
| Thailand | 14 |
| Palau | 1 |
| Philippines | 13 |
| East Malaysia, Brunei, Kalimantan | 10 |
| Peninsular Malaysia | 18 |
| Singapore | 7 |
| Indonesia | 19 |
| Christmas Island | 2 |
| Papua New Guinea | 15 |
| Australia | 4 |

area and that this occurred after the majority of speciation was complete. Supporting this hypothesis is the presence of a number of rainforest-based *dorsalis*-complex species common to Thailand, Vietnam, Peninsular Malaysia, Indonesia and “Borneo”. The Philippines possess some endemic species in the complex, probably resulting from a longer period of isolation than that for Indonesia, “Borneo” and Papua New Guinea.

Host Plant Relationships

Over the past 2 decades there has been considerable research into adult fly feeding, courtship and mating behavior (e.g., Drew *et al.*, 1983; Drew & Romig, 2000; Drew & Lloyd, 1987; Fletcher *et al.*, 1978; Green *et al.*, 1993; Prokopy *et al.*, 1996). All studies showed that adult feeding, courtship and mating occurred on the host plants. Flies visited host plants and fed when fruit were at a developmental stage just prior to being susceptible to oviposition while courtship and mating occurred as the fruit entered the susceptible stage. A recent study on *Bactrocera cacuminata* (Hering) contradicting this extensive earlier research (Raghu *et al.*, 2002) has now been shown to be incomplete as the primary study was conducted over a very short period (December) of the entire 8-month fruiting cycle of the host plant, *Solanum mauritianum* Scop. Subsequent recordings of matings of *B. cacuminata* in 2 host plants from September 2002 to April 2003 showed that they began in early October (second month of Spring), peaked in mid-November (with 27 mating pairs on one night) and ended in late-November at which stage almost all fruit had fallen. In December when the work of Raghu *et al.* (2002) was conducted, there were post-teneral (immature) adults in the host plants that emerged from pupae from the earlier fallen fruit.

From 1986 to 1991, we conducted extensive host fruit collecting in rainforest habitats in South East Asia. Over 30,000 samples were taken and the records published by Allwood *et al.* (1999). From the mid-1970s to 1998, I established extensive host collecting in eastern and northeastern Australia, firstly with specific research projects and later with the *B. papayae* eradication program. These records have been published by Hancock *et al.* (2000). Further analyses of these data show an interesting pattern in the utilization of endemic host plants of endemic fly species (Table 5 and 6).

In both Australia and South East Asia, a similar percentage of *Bactrocera* species are monophagous (37 and 33 percent, respectively). Similarly, 21 and 14 percent respectively are polyphagous with 12 or more endemic host plant species. Most pest species are polyphagous in their native rainforest habitat, breeding in a large number of plant species in many plant families. (Note: In India, Sri Lanka and the Philippines, there has not been extensive host fruit collecting and so the records for the pest species, *B. caryae*, *B. kandiensis*, *B. occipitalis* and *B. philippinensis*, are deemed incomplete). Also, a few pest species are specialists, e.g. *B. cucumis* (primarily breeding in Cucurbitaceae species), *B. minax* (in citrus), *B. musae* (in *Musa*), *B. pyriformis* (in Rosaceae) and *B. umbrosa* (in *Artocarpus* spp.). *Dacus* species in the South East Asian and Pacific regions have limited host ranges (Tables 5, 6) and none has developed to significant pest status.

At the plant family level, 67% of *Bactrocera* species in South East Asia and 50% in Australia utilize hosts in one family only. An example is the *Bulladacus* species recorded from India, through South East Asia, Papua New Guinea to Samoa in the central South East Pacific. All species over this area have evolved in species of Gnetaceae.

With our knowledge of the strong fly-species/host-plant behavioral relationships, the consistent patterns of monophagy and polyphagy across biogeographic regions and speciation within single plant families, we can propose with some confidence, that a process of cospeciation or coevolution has existed [see Page (2003) for definitions of cospeciation and coevolution].

Geological Background

The break-up of Gondwana led to an eventual collision of India with Asia. This resulted in an influx of Gondwanan flora into Asia and explains why there are strong botanical relationships, at the generic level, among the rainforests of Australia, Papua New Guinea, parts of South East Asia and India. However, Hall (1998) stated that the present distribution of plants (and animals) in South East Asia might owe much more to activities of the last 1 million years than the preceding 30 million years.

Table 5. Number of endemic plant taxa recorded as hosts of endemic fruit fly species (Diptera: Tephritidae: Dacinae) in South East Asia

| Fruit Fly Species | No. Plant Families | No. Plant Genera | No. Plant Species |
|-----------------------------|--------------------|------------------|-------------------|
| Genus <i>Bactrocera</i> | | | |
| atrifemur | 1 | 1 | 1 |
| apicalis | 1 | 1 | 1 |
| calophylli | 1 | 1 | 1 |
| caudata | 1 | 1 | 1 |
| cilifera | 1 | 1 | 1 |
| kinabalu | 1 | 1 | 1 |
| lata | 1 | 1 | 1 |
| maculifacies | 1 | 1 | 1 |
| matsumurai | 1 | 1 | 1 |
| mcgregori | 1 | 1 | 1 |
| munda | 1 | 1 | 1 |
| nigrotibialis | 1 | 1 | 1 |
| quasipropinqua | 1 | 1 | 1 |
| rubella | 1 | 1 | 1 |
| rubigina | 1 | 1 | 1 |
| thailandica | 1 | 1 | 1 |
| trilineata | 1 | 1 | 1 |
| verbascifoliae | 1 | 1 | 1 |
| versicolor | 1 | 1 | 1 |
| dorsaloides | 1 | 1 | 2 |
| melastomatos | 1 | 1 | 2 |
| trimaculata | 1 | 1 | 2 |
| garciniae | 1 | 1 | 4 |
| umbrosa | 1 | 1 | 4 |
| propinqua | 1 | 1 | 8 |
| abbreviata | 1 | 2 | 2 |
| kanchanaburi | 1 | 2 | 2 |
| scutellata | 1 | 2 | 2 |
| arecae | 1 | 2 | 3 |
| depressa | 1 | 2 | 3 |
| isolata | 1 | 2 | 7 |
| tsuneonis | 1 | 2 | 7 |
| minax | 1 | 2 | 8 |
| hochii | 1 | 3 | 3 |
| scutellaris | 1 | 3 | 4 |
| osbeckiae | 1 | 3 | 6 |
| hyalina | 1 | 4 | 5 |
| diversa | 1 | 6 | 9 |
| kandiensis | 2 | 2 | 2 |
| limbifera | 2 | 2 | 2 |
| occipitalis | 2 | 2 | 2 |
| pendleburyi | 2 | 2 | 3 |
| irvingiae | 3 | 3 | 3 |
| pyrifoliae | 3 | 3 | 3 |
| philippinensis | 4 | 4 | 4 |
| sp.n. (not incisa) | 4 | 4 | 4 |
| raiensis | 4 | 4 | 5 |
| caryae | 5 | 5 | 5 |
| tuberculata | 6 | 8 | 9 |
| albistrigata | 7 | 7 | 10 |
| tau | 7 | 19 | 32 |
| latifrons | 8 | 9 | 20 |
| cucurbitae | 10 | 22 | 36 |
| zonata | 12 | 13 | 13 |
| correcta | 22 | 36 | 50 |
| carambolae | 24 | 44 | 68 |
| dorsalis | 31 | 65 | 97 |
| papayae | 45 | 100 | 166 |
| Genus <i>Dacus</i> | | | |
| esakii | 1 | 1 | 1 |
| polistiformis | 1 | 1 | 1 |
| sphaeroidalis | 1 | 1 | 1 |
| longistylus | 1 | 1 | 2 |
| keiseri | 1 | 2 | 2 |
| longicornis | 1 | 3 | 4 |
| ciliatus | 1 | 5 | 6 |
| Genus <i>Monacrostichus</i> | | | |
| malaysiae | 1 | 1 | 1 |
| citricola | 1 | 1 | 6 |

Table 6. Number of endemic plant taxa recorded as hosts of endemic fruit fly species (Diptera: Tephritidae: Dacinae) in Australia

| Fruit Fly Species | No. Plant Families | No. Plant Genera | No. Plant Species |
|--------------------------------------|--------------------|------------------|-------------------|
| Genus <i>Bactrocera</i> | | | |
| <i>aeruginosa</i> | 1 | 1 | 1 |
| <i>alyxiae</i> | 1 | 1 | 1 |
| <i>aurea</i> | 1 | 1 | 1 |
| <i>bancroftii</i> | 1 | 1 | 1 |
| <i>bidentata</i> | 1 | 1 | 1 |
| <i>calophylli</i> | 1 | 1 | 1 |
| <i>chorista</i> | 1 | 1 | 1 |
| <i>decurtans</i> | 1 | 1 | 1 |
| <i>diospyri</i> | 1 | 1 | 1 |
| <i>ektoalangiae</i> | 1 | 1 | 1 |
| <i>hispidula</i> | 1 | 1 | 1 |
| <i>humilis</i> | 1 | 1 | 1 |
| <i>melas</i> | 1 | 1 | 1 |
| <i>mendosa</i> | 1 | 1 | 1 |
| <i>parabarringtoniae</i> | 1 | 1 | 1 |
| <i>phaleriae</i> | 1 | 1 | 1 |
| <i>pulchra</i> | 1 | 1 | 1 |
| <i>robiginosa</i> | 1 | 1 | 1 |
| <i>breviaculeus</i> | 1 | 1 | 2 |
| <i>tigrina</i> | 1 | 1 | 2 |
| <i>visenda</i> | 1 | 1 | 2 |
| <i>fagraea</i> | 1 | 1 | 3 |
| <i>expandens</i> | 1 | 1 | 4 |
| <i>tenuifascia</i> | 1 | 2 | 2 |
| <i>pallida</i> | 2 | 2 | 2 |
| <i>barringtoniae</i> | 2 | 2 | 2 |
| <i>turneri</i> | 2 | 2 | 2 |
| <i>signatifera</i> | 2 | 2 | 3 |
| <i>aglaiae</i> | 2 | 2 | 3 |
| <i>aberrans</i> | 2 | 4 | 6 |
| <i>opiliae</i> | 3 | 3 | 3 |
| <i>mayi</i> | 3 | 4 | 7 |
| <i>bryoniae</i> | 3 | 5 | 6 |
| <i>murrayi</i> | 4 | 4 | 4 |
| <i>laticaudus</i> | 4 | 5 | 5 |
| <i>rufofuscula</i> | 4 | 5 | 7 |
| <i>musae</i> | 5 | 5 | 5 |
| <i>nigra</i> | 5 | 6 | 6 |
| <i>cacuminata</i> | 6 | 6 | 6 |
| <i>manskii</i> | 6 | 6 | 6 |
| <i>cucumis</i> | 6 | 6 | 8 |
| <i>endiandrae</i> | 6 | 9 | 23 |
| <i>aquilonis</i> | 7 | 10 | 13 |
| <i>halfordiae</i> | 8 | 10 | 12 |
| <i>jarvisi</i> | 15 | 19 | 33 |
| <i>kraussi</i> | 27 | 43 | 74 |
| <i>neohumeralis</i> | 36 | 59 | 91 |
| <i>tyoni</i> | 39 | 73 | 133 |
| Genus <i>Dacus</i> | | | |
| (<i>Callantra</i>) <i>axanus</i> | 1 | 1 | 2 |
| (<i>Dacus</i>) <i>absonifacies</i> | 1 | 1 | 1 |
| (<i>Dacus</i>) <i>secamoneae</i> | 1 | 1 | 1 |
| (<i>Didacus</i>) <i>aequalis</i> | 1 | 1 | 1 |
| (<i>Didacus</i>) <i>hardyi</i> | 1 | 1 | 1 |

This statement could also be applied to the Australian Region where our fossil records indicate establishment of Diptera and active speciation during the late Quaternary, especially associated with glaciation cycles over the past 150,000 years.

We can conclude that the break-up of Gondwana laid the foundation through the distribution of established rainforest habitats within which active speciation of, at least, the genus *Bactrocera* could later occur. Hall (2001) emphasized that the geological understanding of a region is useful in elucidating its biogeography but may only provide an essential background to what is a complex process of evolution. That is, other processes have, more recently, influenced speciation. For example, geologically induced changes in topography and localized climate, together with changes in land bridges during the glaciation cycles, have directly influenced speciation processes. The extensive island systems throughout South East Asia and the South Pacific region experienced these glaciation-induced changes and this laid a fertile ground for speciation in the Dacini.

Biogeography of Rainforests

Given that the endemic habitat of the Dacini is the rainforest ecosystem of the tropics and subtropics, we need to analyze the distribution of this flora. Basically, the Indomalayan rainforests (tropical rainforests in contrast to Temperate rainforests) occur in a band that includes the Indonesian archipelago, the southern Thailand isthmus, Malaysia and Papua New Guinea. In addition, there are current outlier groups in northwestern and southeastern Thailand, Indo-China (especially Vietnam), southern China, Philippines, Borneo, the Andaman Islands, southwest Sri Lanka and the Western Ghats of southwest India. Elements of the same tropical rainforests also extend to northeastern Australia, the Melanesian archipelago (Solomon Islands, Vanuatu, Fiji, Samoa, Tonga) and into Micronesia and Polynesia (Whitmore, 1986). In all of these locations, species of Dacini are endemic.

These rainforests have many endemic Dacini host plant families that date back to the Cretaceous and Tertiary Periods (Cronquist, 1981). They are extremely rich in number of species, due to considerable localization of evolution at the species level (Whitmore, 1986) and contain large numbers of plant sibling species and endemic plant species with localized distributions. The numbers of rainforest plant species decline from S.E. Asia to Papua New Guinea, and then markedly to Australia and the South Pacific Islands. Drew and Hancock (2000) proposed that the dacine species and their host plants have continued to coevolve over the Tertiary and Quaternary Periods.

Case Study – The Australian Region

Because of a reasonably comprehensive knowledge of the biogeography and ecology of the rainforest flora in the Australian region (Webb & Tracey, 1981; Barlow, 1981) combined with sound geological assessments (Hall, 1998, 2001), the biogeography and speciation in the Dacini in this zone can be discussed in more detail. Also, the broad area of biogeographic transition, called Wallacea, forms a zone of differentiation between South East Asia on the one side (Sundaland) and Australia/Papua New Guinea on the other (Hall, 2001). Wallacea was first recognized by Wallace (1869) and is bound by Wallace's Line running between Bali and Lombok in the West and Lydekker's Line east of Timor and Seram (Figure 2). Consequently, Wallacea includes Lombok and islands in the Indonesian archipelago to the East, Timor, Kai Island, Sulawesi and the Moluccas (which include Seram, Buru and Halmahera), localities from which we have good records of Dacini, in addition to the extensive records in Papua New Guinea, Australia and other Indonesian islands.

The rainforests of Australia are comprised of a series of pockets along the East coast and across parts of the northern coastline, separated by dry corridors. Prior to European settlement these forests covered approximately 1% of the total Australian land surface compared with 100% in Papua New Guinea, 32% in the neotropics and 9% in Africa.

Although the forests are Gondwanan in origin and date back to the Cretaceous, the distribution patterns at present are estimated to be some 4,000–12,000 years old (Webb & Tracey, 1981). They possess an Indomalayan element, as do those of Papua New Guinea and contain many Dacini host plants. We have recorded some 56 plant families in Australia and 65 families in South East Asia (Allwood *et al.*, 1999; Hancock *et al.*, 2000) that contain host plants of *Bactrocera* and *Dacus* species.



Figure 2. The biogeographic region of Wallacea, bounded by Wallace's Line in the West and Lydekker's Line in the East.

Four glaciation periods have been recorded during the late Quaternary and these resulted in climatic oscillations, ecological differentiation and periods of geographical isolation, leading to considerable speciation in the forests (Webb & Tracey, 1981).

Papua New Guinea and Australia were joined into a large and ecologically diverse continent until the end of the last glaciation, 10,000–8,000 years ago. (Webb & Tracey, 1981). The rainforests of Papua New Guinea, after separation, must have experienced a more humid, moist and higher temperature climate than their counterparts in Australia as they covered most of the land area and underwent more prolific speciation. It is also believed that Papua New Guinea received considerable floristic influence from the Malaysian region at the end of the Oligocene Period, at the same time as Australia joined to Sundaland (Barlow, 1981).

During the late Tertiary, Australia was in contact with the Indomalayan region (Barlow, 1981) and today Wallacea contains elements of both the South East Asian and Australian-Papua New Guinea floras, in addition to its own endemic species.

The numbers of plant species and areas of land covered by these rainforests decline markedly with increasing distance South and East from Papua New Guinea. A comparison of the rainforest communities between Papua New Guinea and Australia provides valuable background information. The current estimates of numbers of rainforest plant genera and species are as follows (data provided by Queensland Herbarium) –

| | Papua New Guinea | Australia |
|-------------|-------------------------|------------------|
| No. Genera | 716 | 545 |
| No. Species | 8000 | 1600 |

The following are significant features of the rainforest floras of Papua New Guinea and Australia –

- There are close relationships at the generic level, indicating a common phylogenetic ancestry.
- There are low numbers of shared species and large numbers of endemic species, suggesting more recent speciation uninfluenced by migration. This speciation has been more vigorous in Papua New Guinea than Australia.
- There is some evidence of close relationships between the 2 areas at the species level when comparing similar environmental ecosystems.
- Within Australia, the composition of the flora changes markedly from North to South along the East coast.
- The Papua New Guinea and Australian floras are probably the result of long climatic sifting of a single ancestral stock. Superimposed on this is the impact of the Indomalayan element which has formed a significant part of the Papua New Guinea flora but not the Australian flora.
- During the last glacial period, the PNG-Australia land bridge would have been as arid as is that area adjacent to the Gulf of Carpentaria today and which separates, ecologically, northeastern and northwestern Australia.

A comparison of the dacine fauna of Papua New Guinea, northeastern and northwestern Australia shows features similar to the floristic patterns. These 3 areas are currently ecologically isolated, one from the other, and the number of endemic dacine species known to occur are as follows:

Papua New Guinea — 164 species*
 Northeastern Australia — 70 species
 Northwestern Australia — 7 species

*(Our recent extensive surveys in PNG have collected at least 50 more undescribed species not included here).

The following observations can be made:

- The endemic dacine faunas of Papua New Guinea and Australia are each unique and different.
- There is a low level of similarity between all three areas in species character states and with only a few species shared.
- In general, there is little change in species distributions with altitude.
- Within Australia most species occur in the northeastern area and there is marked decline in numbers of species from North to South along the eastern coast.
- The distributions of genera and species of both the rainforest flora and dacine fauna show considerable similarities.

The Dacini fauna within Wallacea has been reported by Hardy (1982, 1983), Drew and Hancock (1994) and Drew *et al.* (1998). There are 37 species endemic to Wallacea, 11 shared with South East Asia, 6 shared with Irian Jaya/Papua New Guinea and 2 with Australia.

Generally, the character states of the endemic species show more relationship with species in South East Asia. Based on these data, Wallacea, as well as being a transitional zone has experienced considerable independent speciation.

Speciation – Process and Concept

The extensive speciation, particularly in the Genus *Bactrocera* throughout Asia, South East Asia and the Pacific, appears to have proceeded within the rainforest habitat. Further, the fly species have probably evolved in association with speciation of the flora. The question remains – what are the influences on the processes of speciation in the Dacini?

Hall (1998) stated that “no single factor will account for the distribution of plants and animals in South East Asia. Tectonic movements may be a control but their importance is still far from clear”.

As noted above, there is a strong relationship between a dacine species and its host plant to a point where courtship and mating occurs within the host species. Consequently, evolving host plants and associated changes within the host environment would have a significant direct influence on the fruit fly species reproductive behavior. The term cospeciation as defined by Page (2003) as “the joint

speciation of 2 or more lineages that are ecologically associated” could be applied here. Given that a fly population could cospeciate with its host plant and that many fly species have specific host plants, a number of such events could have proceeded simultaneously within separate fly lineages, in the same forest area. This concept, based on the “Center of Activity” model of dacine behavior, provides an understanding of how many species of fruit flies have arisen in the same continental land areas. Bush (1975) described this as sympatric speciation in his *Rhagoletis* studies. The tectonic movements, associated topographic changes, oscillations in climatic patterns, ecological and geographic isolations all led to long periods of independent evolution of rainforest plant taxa, large numbers of species and considerable endemism. This pattern of events could also have resulted in the large number of dacine species that we know today. Clayton *et al.* (2003) also recorded that changing ecological factors can have an influence on coevolution and cospeciation.

It is interesting to note that the large sibling species complexes, the *dorsalis*-complex and the *tau*-complex, contain some species with wide host ranges. It is possible that species such as or similar to *Bactrocera dorsalis* (Hendel) and *Bactrocera papayae* Drew & Hancock, with extensive host ranges in the rainforests, were the precursors of more than one lineage within the *dorsalis*-complex.

In speciation, population behavior and genetic changes must proceed simultaneously. In applying the isolation concept of Dobzhansky (1935) and Mayr (1963, 1970) to the Dacinae, it is difficult to assess the relative importance of genetic and habitat changes. Whether or not basic genetic changes are needed first is debatable. It has been proposed that if a segment (part) of a population becomes geographically isolated, one of 3 possibilities can result: survival, extinction, speciation.

Fruit flies appear to have the genetic capacity to survive climatic or environmental changes and thus such changes are more likely to influence behavioral divergence before genetic divergence. For Dacinae, the isolation concept of Dobzhansky and Mayr causes problems in that it begins with genetic changes leading to reproductive isolation. It leaves little scope for relating changes in the host plant environment to those in the insect population. Similarly it leaves no opportunity for understanding a relationship between the perceived isolating mechanisms and the habitat changes. Further, for the large number of sibling species of Dacinae to have developed over a region such as the Indonesian Archipelago where often only 1 species occurs per land unit (e.g. island), either these species evolved in sympatry and then the land units divided or the units of land divided and speciation was completed in allopatry without the need for reinforcement. In other words, it is difficult to imagine that over many islands, separation and reuniting always occurred in order to allow reinforcement. Probably, large fruit fly complexes such as the *dorsalis*-complex have originated in allopatry, after geographic or ecological isolation of the units of land or habitat.

The recognition concept of species (Paterson 1985) relates geographic isolation and habitat change to changes in the courtship and mating behavior of the population. Thus it accommodates changes or speciation in the rainforest habitat. Because dacine mating occurs on the host plant and mate recognition is dependent on the host, e.g. the release of pheromones while on the host during courtship, it seems plausible that plant speciation in the rainforests have influenced changes in mate recognition systems of fruit fly species. In this model, genetic changes in the fruit fly occur secondarily, induced by changes in host plant influences on fruit fly mate recognition systems. It is interesting that some sibling fruit fly species e.g. *B. tryoni* and *B. neohumeralis* reveal no detectable genetic differences in molecular and cytological studies (Morrow *et al.*, 2000).

The recognition system also forecasts that the rate and scope of speciation is inversely proportional to population size, i.e. widespread populous species are more evolutionarily inert. This relates to the Dacini where large numbers of sibling species occur in small populations over narrow geographical ranges.

Under the recognition concept, it has been predicted that more sibling species will occur in groups where the mate recognition systems are dominated by olfactory and auditory signals (i.e. non-visual signals). The extensive sibling speciation in the Dacini, which depend on olfactory and auditory mate recognition, also supports this theory.

In comparing the 2 concepts and their applicability to the Dacinae, it is clear that the recognition system is a better fit. A practical advantage of this system is that it leads us to place emphasis on certain biological characters for identifying sibling species. In particular, key factors in Mate

Recognition such as specific endemic host plants and male pheromones have been used and are essential for accurate species identifications. This is also applicable to allopatric populations of sibling species such as *B. tryoni* in eastern Australia and *B. aquilonis* in northwestern Australia. Such a valid species concept also guides biologists into researching important aspects of field biology. This is probably the major contribution of the recognition concept to taxonomists interested in understanding the biology of the organisms that they are studying. Pertinent biological characters for species identification assist in the evaluation of morphological characters that often reveal only minor differences.

Taxonomists depend heavily on morphological characters although they are often secondary signs of speciation. It is essential, therefore, to develop an understanding of the speciation process and related biological and reproductive processes that are the primary criteria in determining species. In the Dacinae, the Recognition Concept provides this opportunity.

Conclusions

Clearly, the Dacini fauna of the Asian, South East Asian and Pacific regions have speciated over the Tertiary Period in the rainforests that date back to Gondwana. The close ecological relationship between fruit fly species and their host plants, especially in the area of host plant based courtship and mating, would result in the fly speciation process being directly influenced by speciation in the flora. Consequently, prolific localized speciation in the forests across South East Asia and Irian Jaya/Papua New Guinea, in particular, has resulted in large numbers of species of Dacini, including groups of sibling species with significant differences in the endemic host plants that they utilize. Between South East Asia (Sundaland) and the Australian Region (Irian Jaya/Papua New Guinea through to the South Pacific Islands), the area called Wallacea forms a transitional zone with a large endemic fauna and a small number of species shared with either South East Asia or Papua New Guinea/Australia. The identification of habitat based mate recognition systems in the Dacini and the potential for allopatric speciation throughout the extensive island systems, support the Recognition Concept of species proposed by Paterson (1985).

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