Flower visitors and pollination in the Oriental (Indomalayan) Region

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ABSTRACT

Current knowledge of flower visitors and pollination in the Oriental Region is summarised. Much less is known about pollination than seed dispersal and the coverage of habitats and taxa in the region is very uneven. The available evidence suggests that pollination in lowland forests is dominated by highly social bees (mainly *Trigona* and *Apis* species), with beetles probably the next most important group, followed by other bees and flies. In comparison with the better-studied Neotropics, large solitary bees, moths, Lepidoptera and vertebrates are relatively less important. These differences are greatest in the canopy of the lowland dipterocarp forests of Southeast Asia, where they probably reflect the unique temporal pattern of floral resource availability resulting from 'general flowering' at supra-annual intervals. *Apis* bees (but not *Trigona* species) are also important in most montane, subtropical and non-forest habitats. Apart from the figs (*Ficus* spp.), there are few well-documented examples of plant species visited by a single potential pollinator and most plant-pollinator relationships in the region appear to be relatively generalised. The small sizes of most pollinators and the absence of direct human exploitation probably make pollination mutualisms less vulnerable to failure as a result of human impacts than dispersal mutualisms, but more subtle impacts, as a result of altered gene flows, are likely to be widespread. On current evidence, pollination systems in the Oriental Region do not require any specific conservation action, but this review reinforces arguments for making the preservation (or restoration) of habitat connectivity the major focus of Oriental conservation.

Key words: Asia, conservation, flowers, insects, Oriental Region, pollination, vertebrates.

CONTENTS

I. INTRODUCTION

The increasing interest in tropical pollination studies over the past decade has, to a large extent, been in response to fears that the failure of mutualisms may accelerate the erosion of biodiversity in disturbed and fragmented forests (Bawa, 1990; Bond, 1994; Murcia, 1996; Renner, 1998). *A priori*, plants that depend on the services of animals are expected to be in greater danger, because the vulnerabilities of the mutualist are added to those of the plant itself. It has been suggested that tropical lowland rainforest floras may be particularly vulnerable to extinction from failed pollination mutualisms because of the combination of high levels of dioecy and self-incompatibility, the low densities of many plant species, and a relatively high degree of pollinator specificity (Bond, 1994). Changes in pollinator communities may not only reduce seed set but also reduce the fitness of those offspring that are produced, through changes in the amount and composition of pollen loads (Murcia, 1996; Kearns & Inouye, 1997). Conversely, pollinators that are able to cross gaps between habitat fragments may maintain connectivity and mitigate the impact of fragmentation on genetic diversity (e.g. White & Boshier, 2000). Flower-dependent animals may be equally vulnerable to changes in flower supply resulting from deforestation, logging and the influence of climatic change on plant phenology (Corlett & LaFrankie, 1998). In theory, failed mutualisms could lead to a cascade of extinctions (Kearns & Inouye, 1997). Moreover, while loss of dispersal services in and between habitat fragments could, in theory, be mitigated by human-assisted seed dispersal, mitigation of pollinator loss is probably impossible. An additional reason for interest in pollination is that it is one of the most important ecological services provided to agriculture by wild species and eco-systems (Nabhan, 1998). Dispersal mutualisms, by contrast, have an, at most, marginal direct economic importance.

Despite the increasing level of research activity, we are little nearer than a decade ago to understanding whether or not the failure of pollination mutualisms must be added to the already long list of threats to tropical biodiversity. The first step towards both applying what is known about pollination and filling in gaps in this knowledge is to make the existing information accessible to a wider audience. In the Oriental Region, information on pollination is scattered in numerous, often obscure, mostly local or regional, publications. The major aim of this paper, therefore, is to provide an overview of pollination in the entire Oriental (or Indomalayan) Region. This region was chosen for review because it has, except near its margins, a fairly distinct and, at higher taxonomic levels, fairly uniform, flora and fauna. Moreover, I have previously reviewed frugivory and seed dispersal for this region (Corlett, 1998), providing an opportunity for comparison between the two types of mutualism. I have defined the region in the broadest sense, approximately following Corbet & Hill (1992) and Inskipp, Lindsey & Duckworth (1996) (who both call it the Indomalayan Region), to include: Pakistan, India, Nepal and Bhutan below the Himalayan treeline at approximately
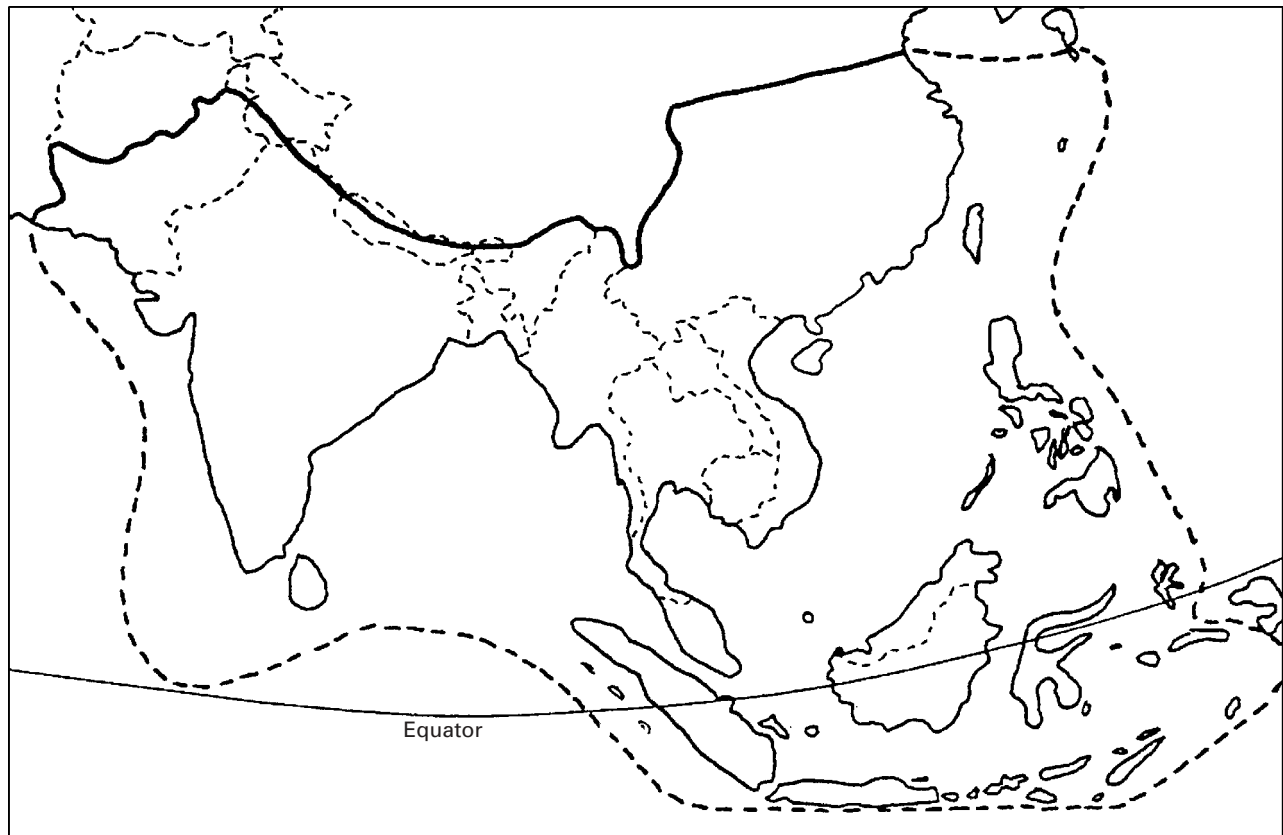
Fig. 1. Boundary of the Oriental Region as used in this paper (modified from Corbet & Hill, 1992).

3000 m; Sri Lanka; Bangladesh; Myanmar; China below 3000 m and south of 35° N; Yakushima and the Ryukyu Islands; and the whole of Southeast Asia, including Sulawesi, the Lesser Sunda Islands, Timor, and the Moluccas (Fig. 1). Pakistan and, particularly, southeastern China are transitional to the Palaearctic Region, while the islands from Sulawesi to the Moluccas are transitional to the Australian Region. Alternative boundaries, especially with the Palaearctic, are equally arbitrary.

II. METHODS

I have searched the Oriental literature for information on flower-visiting animals that appear to contribute to pollination. I have excluded studies on exotic weeds, crop plants and planted ornamentals, unless they reinforce or complement information from native wild plants. That a flower is visited by a particular species of animal does not, of course, mean that it is pollinated by it: 'floral larceny' – the removal of nectar and/or pollen without pollination – is a very widespread phenomenon (Irwin, Brody & Waser, 2001). Hardly any of the studies reviewed here meet the strictest standards of proof and the majority are based on short-term observations at a single site. Many statements on flower visitors are vague and general. Many other statements are more precise than the methods – to the extent that these are reported – justify. I have, however, completely disregarded

only the most poorly documented studies. Information is usually presented here at the generic level or above, unless enough is known to show significant differences between species. Records from outside the region were only used where they applied to Oriental taxa. Information from the literature has been confirmed or supplemented in some cases by my own observations. Classification and nomenclature for plants and animals usually follows the individual sources cited, but I have corrected and updated both where this is necessary for consistency, or where there is an obvious conflict with the currently accepted usage.

In theory, a review of a plant-animal mutualism could be ordered by either plant or animal taxa. I have chosen to focus this review on animal taxa largely because plants, in general, persist much longer in degraded landscapes (Corlett, 2000). Failures of pollination mutualisms are thus more likely to result from the biology of the animal partner. Partial reviews for some plant families already exist e.g. Gottsberger (1999) for Neotropical Annonaceae, Silberbauer-Gottsberger (1990) for palms, and Cingel (2001) for orchids.

III. ABIOTIC POLLINATION

(1) Wind

In the understorey of tropical evergreen rainforests, low wind speeds, dense evergreen foliage and regular rainfall must all reduce the effectiveness of aerial pollen transport,

and the low density and thus wide spacing of conspecifics in most plant species must strongly favour the directed movement of pollen by the animal vectors that are abundantly available year-round. Although wind-pollination of a dioecious canopy gymnosperm, *Podocarpus falcatus*, was apparently effective over at least 70 m in closed canopy evergreen forest in South Africa (Midgley, 1989), neither moss samples nor adhesive-coated slides collected any pollen in the understorey of lowland and montane forest sites in Borneo (Linskens, 1996). However, the rainforest understorey is an extreme situation and open sites, seasonal rainfall (often associated with deciduousness) and the gregarious growth of conspecifics, are all widespread in the Oriental Region.

Sampling of pollen suspended in the air, mostly in urban areas (e.g. Peng & Chen, 1997; Kuoh *et al.*, 1999; Chew *et al.*, 2000), and of the 'pollen rain' preserved in surface samples, lake sediments and pollen traps (Flenley, 1979; Payawal, 1983; Newsome, 1988; Newsome & Flenley, 1988; Stuijts, 1993; Maloney & McCormac, 1995; Satheesh *et al.*, 1996; Huang, 1998; Yu, 1998; Bonnefille *et al.*, 1999; Anupama, Ramesh & Bonnefille, 2000) gives a general picture of aerial pollen transport in the region. The taxa most consistently represented in appropriate habitats include: the conifers (*Dacrycarpus*, *Dacrydium*, *Phyllocladus*, *Pinus*, *Podocarpus*), Amaranthaceae, *Casuarina*, Chenopodiaceae, Cyperaceae, *Elaeocarpus*, *Engelhardtia*, Euphorbiaceae (*Acalypha*, *Bischofia*, *Macaranga*, *Mallotus*), Fagaceae (*Castanopsis*, *Lithocarpus*, *Quercus*), Hamamelidaceae (*Altingia*, *Symingtonia*), *Ilex*, *Juglans*, Moraceae (*Artocarpus*, *Broussonetia*, *Morus*, unidentified taxa), *Myrica*, Myrsinaceae (*Ardisia*, *Myrsine*), Myrtaceae (*Syzygium* and unidentified taxa), Palmae (*Arenga*, *Elaeis*, *Nypa*, *Oncosperma*), *Pandanus*, Poaceae, *Rhizophora*, Ulmaceae (*Celtis*, *Trema*, *Ulmus*) and Urticaceae (*Boehmeria*, *Pipturus* and unidentified taxa). Most of the woody taxa in this list are best represented in montane and subtropical forests, where lower plant diversity would be expected to favour wind-pollination.

Pollen in the air comes not only from wind-pollinated taxa, but also from some animal-pollinated taxa, particularly if they have open flower structures or 'buzz-pollinated' flowers (Bush & Rivera, 2001). In some cases, floral morphology, pollen characteristics and a tendency to gregariousness support the idea that the taxa listed above are wind-pollinated. Thus the conifers appear to be wind-pollinated even when they occur as subcanopy components of lowland rainforest. The grasses and sedges also seem to be consistently pollinated by wind, except, possibly, some rainforest understorey genera, such as *Leptaspis* and some bamboos among the grasses (Soreng & Davis, 1998) and *Mapania* and *Hypolytrum* among the sedges (Lorougnon, 1973; Simpson, 1992). Bees collect pollen from many apparently wind-pollinated taxa (e.g. Kiew, 1993; Corlett, 2001; Eltz *et al.*, 2002). Floral morphology ensures this is usually done without contacting the stigma, but in some cases pollen transfer may occur (e.g. Pant, Nautiyal & Chaturvedi, 1982; Koshy, Harikumar & Narendran, 2001). At the other extreme, both floral morphology and visits by potential pollinators make it very unlikely that wind-pollination is significant for *Elaeocarpus* or *Ilex*.

Between these extremes are many species with small, often inconspicuous, flowers, for which the relative importance of wind and insects in pollination is unclear. Corlett (2001) considered that *Myrsine seguinii* was pollinated by *Apis cerana* in Hong Kong, although bee visits were overwhelmingly to male plants, while Kato (2000) considered the same species to be wind-pollinated in the Amami Islands. Reddi (1976) and Kuruvilla (1989) consider that *Madhuca indica* (Sapotaceae), which flowers when leafless, is wind-pollinated, but other authors have suggested it is pollinated by fruit bats (Dobat & Peikert-Holle, 1985; Rajan, Nair & Subbaraj, 1999; Elangovan, Marimuthu & Kunz, 2000). Detailed studies may help resolve these conflicts. Studies in India, for instance, have shown that, although half the pollen of *Croton bonplandianum* (Euphorbiaceae) is removed by *Apis* bees, they do not visit the female flowers and the species is predominantly wind-pollinated (Reddi & Reddi, 1985). Three deciduous species of *Phyllanthus* have similarly be shown to be largely or entirely anemophilous (Reddi & Reddi, 1985) and it is possible that this applies to many other Euphorbiaceae of open sites. In Hong Kong, only the male plants of the pioneer trees *Aporosa chinensis* and *Mallotus paniculatus* are visited by pollen-collecting bees and most pollen transfer must be by wind (Corlett, 2001). However, species of the same genera in the rainforest understorey in Sarawak appear to be pollinated by insects (Momose *et al.*, 1998*c*), as is *Mallotus albus* in southern India (Krishnan & Davidar, 1993). In mid-elevation rainforest in the Western Ghats, India, four species of dioecious or monoecious Euphorbiaceae, including two understorey species, were characterised as wind-pollinated as a result of bagging experiments (Devy & Davidar, 2003).

Bees collect pollen from species of *Quercus*, but the pendulous male inflorescences, which release clouds of pollen when touched, support the assumption that this genus is anemophilous. In the same family, the erect inflorescences of *Castanopsis* and *Lithocarpus* do not visibly release pollen on contact and are visited by a variety of small insects (Kaul, Abbe & Abbe, 1986; Momose *et al.*, 1998*c*; Corlett, 2001). However, the abundance of aerial pollen from these genera suggests that a role for wind-pollination should not be ruled out. Indeed, there is no reason to think that the balance between wind and insects is constant throughout any of these genera.

Spontaneous, ballistic release of pollen into the air, by stamens held under tension until anthesis, occurs in the Urticaceae and in one tribe of the closely related Moraceae, which includes the Oriental genera *Morus*, *Broussonetia*, *Maclura*, *Malaisia*, *Streblus*, *Bleekrodea* and *Fatoua* (Friis, 1993; Rohwer, 1993). Although bees occasionally visit the flowers of many of these species, the automatic release of clouds of tiny (mostly $<20 \mu$m; Tanaka, 2000) pollen grains makes most sense as an aid to wind-pollination (Williams & Adam, 1993). Corner (1988) reported that in *Artocarpus rigidus* and *A. elasticus* – members of the Moraceae that do not have ballistic pollen release – male heads are unscented and release clouds of pollen when tapped. Other *Artocarpus* species, however, are scented, offer sugary rewards, and are apparently insect pollinated (Momose *et al.*, 1998*a*).

Both floral morphology and the aerial pollen count suggest that at least some tropical Ulmaceae may be wind-pollinated. This has been proposed for *Gironniera* species in Sarawak (Momose *et al.*, 1998*c*), although the same authors considered that *Trema tomentosa* was pollinated by bees. In Hong Kong, *Celtis sinensis* flowers while leafless and releases pollen on contact, but it is also visited by bees that sometimes contact both anthers and stigmas (R. T. Corlett, personal observations).

Coastal habitats, with their strong air movements, relative openness and tendency to single-species dominance, would be expected to favour wind-pollination more than inland areas. In fact, even here, most species have animal vectors, but the widespread Oriental seashore pioneer, *Casuarina equisetifolia*, is wind-pollinated, as may be the mangrove genus *Rhizophora* (Juncosa & Tomlinson, 1987; Aluri, Reddi & Sujatha, 1994), although the evidence for this is not entirely convincing. *R. stylosa* has a complex floral scent which suggests animal pollination (Azuma *et al.*, 2002). Cox (1990) considered that the coastal pandan, *Pandanus tectorius*, was also wind-pollinated, with the staminate inflorescences producing copious amounts of loose, dry pollen and the pistillate inflorescences acting as highly efficient pollen receivers, but Kato (2000) considered that beetles (mostly Nitidulidae) were the main pollinators in the Amami Islands.

(2) Water

Water pollination is rare, even among aquatic plants (Proctor, Yeo & Lack, 1996). Many of the 30 or so angiosperm genera in which some or all species are known to be pollinated by water occur in the Oriental Region, but there have been no detailed regional studies.

IV. INSECTS

(1) Blattodea

Cockroaches (Blattodea) are mostly omnivorous scavengers and detritus feeders, but some visit flowers and they may be the principal pollinators of *Uvaria elmeri* (Annonaceae) (Nagamitsu & Inoue, 1997*b*). In *Uvaria*, the petals do not form the floral chamber that is typical of those species of Annonaceae pollinated by beetles (Gottsberger, 1999). The flowers have spreading, creamy-white or brown petals and an odour 'like decayed wood or a mushroom'. Both flying adults and wingless nymphs of cockroaches in the family Blattelidae visited at both the female and male stages, feeding on the stigmatic exudate and the anthers. Although pollination was not proven, some cockroaches carried pollen on their heads. Blattellid cockroaches also visited both male and female heads of *Artocarpus odoratissimus* in Sarawak, and two out of three individuals collected carried pollen grains (Momose *et al.*, 1998*a*). In this case, however, the more abundant beetles and flies were probably more important as pollinators.

(2) Thysanoptera

Thrips (Thysanoptera) are tiny, short-lived insects with winged adults. Many species from at least three families (Aeolothripidae, Thripidae and Phlaeothripidae) are commonly found in flowers, feeding on sap from flower tissues and on pollen (Kirk, 1988). Both winged and wingless forms disperse between flowers with pollen attached to their bodies and their role in pollination may have been underestimated (Kirk, 1988; Williams, Adam & Mound, 2001).

The first detailed study of pollination of wild plants by thrips in the Oriental Region, was that of six co-occurring species of *Shorea* section *Mutica* at Pasoh, Malaysia (Appanah & Chan, 1981; Appanah, 1993). These outbreeding tree species flower in an overlapping sequence over 11 weeks, during episodes of general flowering that have a supra-annual periodicity (Chan & Appanah, 1980). Thus millions of flowers (up to four million per tree) are produced for a brief period at multi-year intervals. The cream-coloured flowers open at dusk and emit a 'penetrating, sickeningly sweet smell'. The corollas, with stamens attached, fall to the forest floor the next morning. Thrips (*Thrips* and *Megalurothrips*) made up more than 95 % of the floral visitors observed. They start breeding in the buds, where they may do a considerable amount of damage. The life cycle of the commonest species is only eight days so populations build up quickly. Adult thrips visit the open flowers to feed on pollen and flower tissues, and some of the sticky pollen becomes attached to their bodies (<27 grains, mean 2.4 per thrips). Many thrips are carried to the ground on the shed corollas, which spiral slowly downwards, seemingly adapted for wind dispersal (Ng, 1988). The thrips fly upwards to the heavily scented flowers the following evening. Thus air movements provide the horizontal displacement needed for cross-pollination while the thrips land directionally, presumably attracted by colour and smell. Out-crossing rates of thrips-pollinated *Shorea leprosula* trees were at least as high as for bee-pollinated species in the same genus (Nagamitsu *et al.*, 2001).

Because of their potential for explosive population increase, thrips would appear to be ideal pollinators for mast-fruiting species. They apparently pollinate one other section of *Shorea* (*Richetioides*) and at least some species of *Hopea* (Ashton, Givnish & Appanah, 1988). However, thrips did not seem to be important pollinators of dipterocarps – including some of the same species as at Pasoh – at Lambir, Sarawak (Momose *et al.*, 1998*c*). At this site, densities of thrips were much lower per flower than at Pasoh and chrysomelid beetles were the major pollinators. At Lambir, thrips (mostly the generalist *Thrips hawaiiensis*) were the most abundant insects on *Shorea parvifolia*, which is pollinated by thrips at Pasoh, but they carried less pollen than the beetles and made fewer trips between flowers (Sakai *et al.*, 1999*b*). Moreover, introduction of thrips to bagged flowers did not increase fruit set while introduction of beetles did.

Thrips were also found in the flowers of most other tree species examined at Pasoh (Appanah & Chan, 1981) but there was no evidence of a role in pollination. In Sarawak, thrips appear to pollinate two subcanopy species, in which the yellow, urceolate flowers have entrances too small for other visitors, *Popowia pisocarpa* (Annonaceae) and *Horsfieldia grandis* (Myristicaceae) (Momose *et al.*, 1998*c*). *P. pisocarpa* is self-incompatible and experiments showed that the thrips (four *Thrips* spp.) were effective pollinators

(Momose, Nagamitsu & Inoue, 1998). Compared with other, mostly beetle-pollinated, Asian Annonaceae, the floral chamber of this species is tiny, the pollen is smaller and the odour is different. In the mid-elevation rainforest at Kakachi, in the Western Ghats of India, four tree species (two each in the genera *Aglaia* and *Cinnamomum*) were apparently pollinated by thrips (Devy & Davidar, 2003). In Australian rainforests, thrips pollination has been suggested for species of *Diospyros*, *Myristica*, *Rapanea*, *Breynia* and *Smilax* – all genera that occur in Oriental forests – and *Maclura cochinchinensis*, which is widespread in Southeast Asia (Williams & Adam, 1994; Williams *et al.*, 2001).

Moog *et al.* (2002) showed that a single thrips species, *Neoheegeria* sp. (Phlaeothripidae), is the major pollinator of the dioecious pioneer tree *Macaranga hullettii* in a Malaysian rainforest. The thrips use the enclosed chambers formed by floral bracteoles of both male and female inflorescences as feeding and breeding sites. The main attractant seems to be the 'sweet vanilla-like scent' and the thrips larvae and adults feed on nectar produced by trichome patches inside the bracteolar chambers. The same mode of pollination appears to occur in other, related, *Macaranga* species with similar floral traits. Davies (1999) considered that thrips were the likely pollinators of *Macaranga velutiniflora* and other *Macaranga* species in Borneo, but, although pollen-covered thrips were abundant on staminate inflorescences, they were not seen on pistillate inflorescences.

Thrips (mostly *Taeniothrips* spp.) are apparently the exclusive pollinators of some species of *Chloranthus* in China (Luo & Li, 1999). The Chloranthaceae are one of the basal angiosperm families, with a fossil record stretching back to the late Cretaceous, so this relationship could be ancient. A single species of *Taeniothrips* was also the only pollinator of an endangered herbaceous perennial, *Ophiopogon xylorrhizus* (Liliaceae *s.l.*) in the tropical forests of southwest China, where field observations, spatial genetic structure, and paternity analysis of seeds show that pollen is rarely transferred more than 20 m (He, Rao & You, 2000; He & Smouse, 2002). All the other records of thrips pollination from the Oriental Region refer to cultivated, weedy and/or exotic species in India. Several weedy composites (*Ageratum conyzoides*, *Synedrella nodiflora*, *Tridax procumbens*, *Vernonia cinerea* and *Wedelia chinensis*) (Ananthakrishnan, Varatharajan & Gopinathan, 1981*a*,*b*), *Peltophorum inerme* (Mondal, Bhattacharya & Mandal, 1993) and *Nyctanthes arbor-tristis* (Raizada & Nangia, 1989) are apparently pollinated, at least to some extent, by thrips.

(3) Coleoptera

Pollen- and nectar-feeding is widespread among beetles and some species are as strikingly adapted to this habit as bees. In addition, some flowers have evolved attractants for beetles that primarily feed on other plant parts or carrion. Several authors have described a distinct beetle-pollination 'syndrome' of flower characters (e.g. Faegri & van der Pijl, 1979, p. 102) but, given the many, unrelated beetle families involved and the great variety of reasons for them to visit flowers, there is a risk that such generalisations can mislead more than they enlighten. Beetles are known to visit flowers

for: nectar, pollen or other food rewards; for mating and/or oviposition; and because the flower mimics food or a substrate for oviposition. The most obvious common feature of flowers that are primarily pollinated by beetles seems to be a strong odour, variously described as sweet, fruity, musty or foetid in different species (Williams & Adam, 1994). Other common features include pale colour, nocturnal or crepuscular anthesis, protogyny, a more or less closed 'floral chamber', and internal heating of the inflorescence. However, recent studies in Australia, the eastern Mediterranean, and southern Africa have shown the existence of flower types that are apparently specialised for beetle-pollination but lack most or all of the characters associated with the classical syndrome (Goldblatt, Bernhardt & Manning, 1998).

Beetles are recorded as pollinators of, or visitors to, a diverse array of angiosperms, but there have been few detailed studies in the Oriental Region. Trapping for one year in Malaysian lowland rainforest with floral fragrance chemicals (eugenol, benzyl acetate, methyl benzoate and linalool) as bait attracted a wide range of potential pollinating beetles, mainly in the families Scarabaeidae, Mordellidae, Curculionidae and Cerambycidae (Maeto *et al.*, 1995). Most studies on beetles at flowers have found a lack of specificity, with beetles of several species – and, in many cases, more than one family – visiting the same plant species and, in community-level studies, a single species of beetle visiting more than one plant species (Momose & Inoue, 1994). Since the same families of beetles visit more or less the same range of plant families, this account is structured by plant rather than beetle families. Almost all beetles that visit flowers in the region belong to the huge suborder, Polyphaga. Most records refer to plants of the families Annonaceae, Myristicaceae, Dipterocarpaceae, Araceae or Palmae.

The Annonaceae appear to be predominantly beetle-pollinated (van Heusden, 1992). Corner (1988) describes the flowers of Malaysian species as 'sweetly and often intensely fragrant' and attracting 'crowds of small beetles'. In many genera, such as *Anaxagorea*, *Cyathocalyx*, *Goniothalamus* and *Xylopia*, the inner petals form a chamber by pressing tightly over the compact stamens and carpels (Corner, 1988). Beetles, attracted by a strong scent, enter the floral chamber during the female stage and leave during the male stage. Scarabaeids, chrysomelids and curculionids are reported as visiting a *Polyalthia* species in Sumatra (Kato *et al.*, 1989). In lowland dipterocarp forest in Sarawak, 20 of 22 Annonaceae species studied were pollinated by beetles (Momose *et al.*, 1998*c*). In most species the major visitors were *Carpophilus* species (Nitidulidae), *Endaenidius* species or *Endaeus* species (Curculionidae), for which the rewards were, apparently, stigmatic secretions and mating sites. In two species, *Encosanthum coreaceum* and *Polyalthia motleyana*, the pollinators were scarabaeids and chrysomelids, which fed on the petals. Similar flowers in the Neotropics are also pollinated by scarabaeids, nitidulids, chrysomelids and curculionids (Gottsberger, 1990). All three Annonaceae trees studied in mid-elevation rainforest in the Western Ghats of India were pollinated by (unspecified) beetles (Devy & Davidar, 2003).

Beetles are apparently also the pollinators of at least some species in the related family Myristicaceae. Curculionids, staphylinids and chrysomelids are reported as pollinators of three species of *Knema* and one of *Gymnacranthera* in Sarawak (Momose *et al.*, 1998*c*). Cultivated nutmeg trees (*Myristica fragrans*) in southern India are apparently pollinated largely by an anthicid flower beetle, *Formicomus braminus* (Armstrong & Drummond, 1986). These beetles are small (3–4 mm long) and hairy, and apparently do not damage the flowers. Although the nocturnal anthesis, 'sweet musky' floral odour, and light corolla colour fit the beetle-pollination 'syndrome' the small size of the flowers is in striking contrast to the Annonaceae. The pistillate flowers apparently offer no reward and are pollinated by deceit. A study of *Myristica insipida* in northern Queensland found at least nine species in five beetle families as floral visitors (Armstrong, 1997). The author suggests that the predominance of one species on nutmeg in India is a result of rainforest destruction in the region and comments that 'it leaves the nutmeg growers in this area one beetle species away from losing a cash crop.'

In lowland forest in Sarawak, 20 dipterocarp species in the genera *Hopea*, *Shorea* and *Vatica* were pollinated by multiple species of beetles that fed on the petals and, occasionally, on pollen and the pistils (Momose *et al.*, 1998*c*; Nagamitsu, Harrison & Inoue, 1999*a*; Sakai *et al.*, 1999*b*). Chrysomelids predominated, followed by curculionids and nitidulids (but different species from those visiting the Annonaceae at the same site). Even species in *Shorea* section *Mutica*, which are pollinated by thrips at Pasoh, in the Malay Peninsula (Appanah & Chan, 1981), were pollinated by beetles in Sarawak. Several of the flower-feeding chrysomelids apparently fed on dipterocarp leaves between general flowering periods. Thus, by contrast to the thrips, which depend on explosive population growth to match the massive increase in floral resource availability during general flowering periods, the beetles may simply switch foods.

Beetles from five families were also recorded on *Dryobalanops lanceolata* flowers in Sarawak, although stingless bees were the major pollinators (Momose, Nagamitsu & Inoue, 1996). A detailed study of *Shorea megistophylla* in Sri Lanka recorded elaterid beetles consuming pollen, and chrysomelids and scarabaeids feeding on the stamens and corolla, although large bees appear to be the principal pollinators (Dayanandan *et al.*, 1990). Fourteen families of beetles visited the flowers of four individuals of *Shorea robusta* in India, with the curculionids, scarabaeids, nitidulids and phalacrids most abundant, but the authors considered their impact largely negative, and that flies and bees were the major pollinators (Khatua, Chakraborty & Mallick, 1998).

In the Araceae, the inflorescence consists of an unbranched spadix bearing numerous small flowers and is subtended by a large spathe. The lower part of the spathe typically forms a chamber that may act as a trap, temporarily retaining pollinators that enter. Heat production by the spadix has been shown in many species (Bown, 2001). In monoecious species, the female flowers are towards the base of the spadix, within the chamber, while the male flowers are in the upper part. The inflorescence is protogynous and, in trapping species, the pollinators, which are either flies, beetles or both, are retained in the lower chamber during the female phase. Beetles have been associated with many species of Araceae in the Oriental Region but details are usually lacking. The trap-inflorescences of *Cryptocoryne ciliata*, an amphibious mangrove herb, are visited by a wide range of insects but nitidulid beetles and *Drosophila* flies are most numerous (Saibeh & Mansor, 1996). The inflorescence is partly submerged, with only the entrance above water. *Alocasia macrorrhizos*, which is widespread in the Oriental Region, also traps a variety of insects in Queensland, Australia, but nitidulid and staphylinid beetles are probably the most important pollinators (Shaw & Cantrell, 1982). In the forest understorey in Sarawak, *Homalomena propinqua* was the only one of 41 species studied that was visited predominantly by beetles – a scarabaeid and a chrysomelid, which mated in the chamber (Kato, 1996). *H. pendula*, in Sumatra, by contrast, is apparently pollinated by nitidulid beetles (Kato *et al.*, 1989).

Other Araceae that are pollinated by beetles include *Plesmonium margaritiferum* in India, *Typhonium trilobatum* in Java (van der Pijl, 1953), and several species of *Amorphophallus* (van der Pijl, 1937). In *Amorphophallus* the spathe forms an open funnel around the inflorescence, rather than an enclosed trap. Beetles attracted by the fetid odour (nitidulids in *A. variabilis* and *A. muelleri*, the large silphid carrion beetle, *Diamesus*, in *A. titanum*) are apparently encouraged to stay by the presence of a superficial layer of food tissue on the interior wall of the lower part of the spathe, at least in *A. variabilis* (van der Pijl, 1937). *A. titanum* has the largest unbranched inflorescence of any plant (Bown, 2001). Analysis of the inflorescence odours of 14 Oriental species of *Amorphophallus* showed that the carrion smells of 10 species, including *A. titanum* and others known to be pollinated by beetles, consisted mainly of dimethyl oligosulphides, while the odours of the remaining species, with other smells and unknown pollinators, were dominated by other compounds (Kite & Hetterschieid, 1997).

Beetles are often associated with the inflorescences of palms in the Oriental Region (Appanah, 1990) but there have been no detailed studies on the pollination of wild palms comparable with those in the Neotropics (Silberbauer-Gottsberger, 1990). Casual observations suggest that the undergrowth palms, *Pinanga aristata* and *P. pilosa*, are pollinated by nitidulid and curculionid beetles (Ferguson *et al.*, 1983). Beetles are present at both the female and male stages of the monoecious, protogynous inflorescence, while bees visit only the male stage. Nitidulid beetles have also been reported visiting the 'penetrating, musty, sickly-sweet' smelling inflorescences of *Nenga gajah* (Dransfield, 1975) and both nitidulid and staphylinid beetles visit the variously scented inflorescences of *Johannesteijsmannia* species (Dransfield, 1972). Curculionid beetles were the most probable pollinators of the dioecious *Salacca edulis* in cultivation in Java (Mogea, 1978). Its flowers are reported to have a 'strong ginger fragrance'. Curculionid beetles have also been found in herbarium specimens of the very fragrant inflorescences of *Plectocomia* (Madulid, 1980). In the climbing palm, *Ceratolobus*, the unisexual inflorescences are entirely enclosed within a bract (prophyll) that opens at anthesis only by two, very small, apical splits (Dransfield, 1979). The probable pollinators are small staphylinid and other beetles

attracted by the 'penetrating musty aroma' that emanates from both male and female inflorescences.

Outside these five angiosperm families, beetles have been implicated in the pollination of a variety of plant species in the region. Most interesting, perhaps, in view of the supposedly 'primitive' nature of beetle pollination, is their association with many species of *Cycas* (Wang & Liang, 1996; Yang & Meerow, 1996). In Thailand and Vietnam, both male and female cones are inhabited by beetles in the genera *Tychioides* (Curculionidae) and *Hapalips* (Languriidae) (Yang & Meerow, 1996). Isozyme data showed that strong gene flow occurred between cycad populations 2–7 km apart, suggesting that this is within the foraging range of the pollinators. Beetles also visit the rather cycad-like inflorescences of *Pandanus* species: curculionids in Hong Kong (R. T. Corlett, personal observations), scarabaeids, chrysomelids and curculionids in montane Sumatra (Kato *et al.*, 1989), and mainly nitidulids in the Amami Islands (Kato, 2000).

Beetles may pollinate at least some species of *Artocarpus*, attracted by a 'sweet scent of honey and burnt sugar' (Corner, 1988). Nitidulid beetles were the second most abundant (after drosophilid flies) among the diverse insects that visited the male and female flower heads of *A. odoratissimus* in Sarawak, and 24 of 35 individuals collected carried pollen grains on their bodies (Momose *et al.*, 1998a). Other species apparently pollinated by beetles in the lowland rainforest at Lambir, Sarawak include two species of *Sterculia*, visited by chrysomelids, two species of *Heritiera* (Sterculiaceae), visited by curculionids and chrysomelids, and *Diospyros dictyoneura*, visited by staphylinids and nitidulids (Momose *et al.*, 1998c). A perennial herb, *Orchidantha inouei* (Lowiaceae), is pollinated by small scarabaeids in the genus *Onthophagus* (Sakai & Inoue, 1999). The *Orchidantha* flowers offer no reward and the dung beetles visit only for a minute or so, apparently deceived by the unpleasant odour. Beetles in various families were also a major component of the 'diverse insects' that visited 37 species in 22 families at this site.

On Yakushima Island, at the northern margins of the Oriental Region, beetles (Scarabaeidae, Oedemeridae, Cerambycidae) visited a wide range of canopy species, mostly with pale flowers, but none in the understorey, where *Bombus* bees and birds predominated (Yumoto, 1987, 1988). This may reflect a requirement by the beetles for direct sunlight to raise thoracic temperatures for flight. It is possible that the elevation of flower or inflorescence temperatures above that of the air, which is reported for several beetle-pollinated species, may, in addition to enhancing the volatilisation of floral odours, provide a direct energetic reward, enabling the beetles to remain active during cool nights without great expenditure of energy (Seymour & Schultze-Motel, 1997). In one Oriental species, the sacred lotus, *Nelumbo nucifera*, which may be beetle-pollinated, temperature is not simply increased but is thermoregulated within a narrow range (Seymour & Schultze-Motel, 1997).

(4) Hymenoptera

The Hymenoptera (wasps, ants and bees) is one of the largest and most diverse orders of insects. The phylogeny is still incompletely understood and the classification at higher levels is unstable. Instead of trying to match the heading hierarchy to the most recent phylogenies, I have divided the order into groups of similar pollination biology, rather than equivalent rank, and recognised a paraphyletic group of 'wasps' to include the rest.

(a) Wasps

The term 'wasp' is applied to all Hymenoptera that are not bees or ants and thus includes species with a great range of life histories. Although most are basically carnivorous, with animal protein the main larval food, the adults consume nectar and honeydew for energy. Pollen is not a wasp food, except for the vespid subfamily Maserinae (or Maseridae, in some classifications) which provision their larval cells with pollen and nectar. Wasps are common visitors to flowers with exposed nectar, although some species are attracted more for the opportunity to prey on other visitors (Faegri & van der Pijl, 1979; Reddi & Reddi, 1985; Dayanandan *et al.*, 1990; Corlett, 2001).

Members of the primitive suborder Symphyta (sawflies), which mostly have phytophagous larvae, are reported as common flower visitors elsewhere, but there are only a few scattered reports for the Oriental Region and no evidence that they are significant in pollination. Most wasps are in the suborder Apocrita, which also includes the ants and bees. Traditionally, the Apocrita was divided into two groups, Parasitica (stingless, with a parasitic life cycle) and Aculeata (mostly with a sting and non-parasitic), but only the second of these is now considered a natural grouping. Although there are scattered reports of non-aculeate wasps as flower visitors (Inoue *et al.*, 1990; Momose & Inoue, 1994; Bhatia *et al.*, 1995; Pedersen, 1995; Khatua *et al.*, 1998), mostly involving the closely related families Ichneumonidae and Braconidae, only one family, the Agaonidae (fig wasps), is known to be significant in pollination in the region.

The relationship between the figs (*Ficus*, Moraceae) and their short-lived pollinating wasps (Agaonidae, subfamily Agaoninae) is an obligate mutualism and the classic case of plant-insect coevolution (Bronstein, 1992; Weiblen, 2002). With a few exceptions, each species of fig has a single species of pollinator and *vice versa*. The majority of Oriental fig species are morphologically gynodioecious but functionally dioecious. Morphologically hermaphrodite plants bear closed, urn-shaped inflorescences (syconia) that contain both male and short-styled female flowers. Female plants bear syconia that contain only long-styled female flowers. Inseminated female wasps are attracted by species-specific volatile chemicals to both types of syconia (Song *et al.*, 2001; Grison-Pigé, Bessière & Hossaert-McKey, 2002) and enter through a bract-covered pore, the ostiole. Those which enter the hermaphrodite syconia pollinate and oviposit in the short-styled female flowers, while those which enter female syconia pollinate, but cannot oviposit in, the long-styled female flowers. Several weeks later, a new generation of wasps emerges and mates within the hermaphrodite syconia, and the females collect pollen from the now mature male flowers before flying off in search of syconia at the receptive stage. Seeds are normally produced only in the female syconia so the hermaphrodite syconia are

functionally male. In monoecious fig species, by contrast, all plants bear only hermaphrodite syconia in which the female flowers have a range of style lengths. When mature, these syconia produce both seeds and pollen-carrying wasps. Apart from references given above, useful entries to the voluminous Oriental fig literature include: Patel, Hossaert-McKey & McKey (1993) and Patel & McKey (1998).

The diversity and abundance of figs and fig wasps in Oriental forests demonstrates the success of this relationship. Fig wasps dominate, in terms of numbers, the nocturnal flying insect community at canopy level in lowland dipterocarp forest in Sarawak (Kato *et al.*, 1995*a*). Although figs may be pollinator-limited on small islands (Compton, Ross & Thornton, 1994), paternity analysis has shown that for several Neotropical monoecious species pollen dispersal occurs routinely over distances of 6–14 km (Nason, Herre & Hamrick, 1998). Presumably, wasp movement over these distances is aided by wind. However, such long-distance dispersal of the pollinators may not necessarily occur in Oriental dioecious figs, which mostly inhabit – and release wasps into – the forest understorey. Exceptionally severe droughts during the 1998 ENSO (El Niño Southern Oscillation) event in northern Borneo caused a break in syconia production and the consequent local extinction of the pollinators for all 25 dioecious fig species in the Lambir Hills National Park, but apparently none of the pollinators of monoecious species (Harrison, 2000). Most pollinators had not recolonized six months later, which suggests poor long-distance dispersal, although most had reappeared by two years after the drought (Harrison, 2001).

The aculeate wasps account for the great majority of flower visitation records in the region. The most important family is the Vespidae (including subfamily Eumeninae, previously treated as a separate family), which includes many social species. The genera most frequently mentioned are *Ropalidia, Vespa, Delta* and *Rhynchium* (the latter two in the non-social Eumeninae). Vespid wasps were the major visitors to *Psychotria* species in Hong Kong (22° N) (Corlett, 2001) and the Amami Islands (28.30° N) (Kato, 2000). In India, *Ropalidia* was considered a major pollinator of *Zizyphus mauritiana* (Devi, Atluri & Reddi, 1989), *Ropalidia* and *Rhynchium* were considered major pollinators of *Alangium lamarkii* (Reddy & Aruna, 1990), and *Rhynchium* and *Vespa* were considered important for moving pollen between patches in *Cardiospermum halicacabum* (Das *et al.*, 1997). Wasps in several genera are apparently major pollinators of *Santalum album* (Jyothi, Atluri & Reddi, 1991; but see Bhaskar, 1992). On *Vitex negundo* (Verbenaceae), *Rhynchium* and *Ropalidia* punctured the corolla tubes to get nectar, greatly reducing fruit set in perforated compared with non-perforated flowers (Reddy *et al.*, 1992). In lowland rainforest in Sarawak, only one of 270 species studied, *Casearia grewiaefolius* (Flacourtiaceae), was visited primarily by a wasp, *Latimenes latipennis* (Eumeninae), which was the probable pollinator (Kato, 1996; Momose *et al.*, 1998*c*).

Most other records of flower visits by aculeate wasps refer to the vespoid families Scoliidae, Tiphiidae and Pompilidae, or the huge and diverse family Sphecidae, which is allied to the bees, but these have rarely been implicated as pollinators. However, sphecid wasps (*Bembix* and *Sphex*) were frequent visitors to the small, white, cup-shaped flowers of *Allophyllus serratus* (Sapindaceae) in India and were considered to be more important than bees in cross-pollination because they made more frequent movements between plants (Aluri, Reddi & Das, 1998).

(b) Formicidae

The ant family, Formicidae, is part of the Vespoidea, but ants differ from social wasps in that the worker caste is permanently wingless. Ants are frequent – sometimes the most frequent – visitors to flowers with accessible nectar, from the ground layer to the upper canopy of the forest (R. T. Corlett, personal observations). That they are rarely mentioned in the regional literature is a reflection of the assumption that ants are, at best, poor pollinators, and, more likely, nectar thieves. Their small size, winglessness, typically smooth integument, frequent grooming, and the presence of antibiotic secretions that reduce pollen viability, all support this assumption (Proctor *et al.*, 1996). Moreover, ant-repellent chemicals in floral tissues seem to be widespread in plants (Ghazoul, 2001). However, ants have been shown to be important pollinators for low-growing plants in open, arid or high mountain, habitats (e.g. Gomez *et al.*, 1996) and might be expected to play the same role in similar Oriental habitats. Ants may also have an indirect impact on pollination – positive or negative – through their interactions with other flower visitors (Altshuler, 1999).

In India, *Camponotus* ants apparently contribute to the pollination of the herb, *Euphorbia geniculata* (Reddi & Reddi, 1984), and the largely wind-pollinated, dioecious shrub, *Phyllanthus pinnatus* (both Euphorbiaceae) (Reddi & Reddi, 1985). In the latter case, excluding insects only had a significant effect on fruit set if the male and female plants were close together, which matches expectations of ant behaviour. In the Ryukyu archipelago, selective exclusion experiments showed that ants were capable of pollination within inflorescences of *Balanophora kuroiwai*, a low-growing parasitic herb, but they were not observed to move between inflorescences (Kawakita & Kato, 2002).

(c) Bees

The bees are an apparently monophyletic group, allied to the sphecoid wasps. Like wasps, they visit flowers for nectar but, unlike wasps, most bees also gather pollen as a high-protein substitute for animal matter to feed their larvae. The number of bee progeny is directly related to the rate at which pollen can be collected, so natural selection is expected to maximise collection efficiency, to the possible detriment of pollination efficiency. Bees rarely collect pollen and nectar simultaneously because the most efficient collecting behaviours are different (Rasheed & Harder, 1997). Most bees are solitary but many nest communally and eusocial species with female castes are found in the families Halictidae and Apidae. Bees also differ widely in how much of the year they are active and how many plant species they visit. Solitary bees are often specialists for pollen but rarely for nectar (Michener, 2000). Relationships within and between bee families are still uncertain. I have here followed

Michener (2000), which differs from the older Oriental literature largely in the rank assigned to particular groups.

(*i*) *Colletidae.* A family of approximately 2000 species of solitary, short-tongued bees that is most abundant, diverse and important for pollination in Australia (Michener, 2000). The Colletidae are probably present throughout the region but are usually a minor group of little importance in pollination. However, species of *Hylaeus* are reported as major visitors to *Tectona grandis* (Verbenaceae) in Kerala, India (Mathew, Koshy & Mohanadas, 1987) and *Mosla* species (Lamiaceae) in Zhejiang, China (Zhou, Pan & Hong, 1996). On the subtropical Amami Islands in the northern Ryukyu Archipelago, another *Hylaeus* was the most abundant flower-visiting bee and a species of *Colletes* was one of only two bee species (with *Apis cerana*) active in winter (Kato, 2000).

(*ii*) *Andrenidae.* A family of over 2000 species of short-tongued, solitary, soil-nesting bees (Michener, 2000). They are primarily Holarctic and African, and are significant in the Oriental Region only in the subtropical and warm temperate north. The southern limits are in the Nilgiri Hills in southern India and the Cameron Highlands in Malaysia, in both cases above 1000 m altitude (Baker, 1995). Andrenids visit many canopy species on Yakushima (Yumoto, 1987, 1988) and are seasonally important on crop and wild flowers in northern India, particularly at high altitude (Batra, 1977; Abrol, 1991; Arif & Kumar, 1997). A single species in the Western Ghats, *Andrena bellidoides*, was reported to nest gregariously near its sole pollen source, *Pogostemon stellata* (Lamiaceae) (Batra, 1977).

(*iii*) *Halictidae.* Halictid bees ('sweat bees') are found in all terrestrial habitats from arctic tundra to desert and tropical rainforest, and in much of the world they are second in abundance only to the Apidae (Michener, 2000). However, most species are small, dark and inconspicuous, and they are probably under-recorded in many pollination studies. Most nest in the soil and most are solitary, although all intergradations from solitary, through communal, to eusocial with distinct female castes, are found. Most are short-tongued but species with a relatively long proboscis for the body size also occur (Kato *et al.*, 1989, 1991). Two (of four) subfamilies account for almost all records of flower visitors in the Oriental Region: the Nomiinae (particularly *Nomia*) are largely tropical and subtropical, while the Halictinae (*Halictus, Lasioglossum, Thrinchostoma*) are cosmopolitan but somewhat less abundant in the lowland tropics (Sakagami, Inoue & Salmah, 1990).

Although present throughout the region, halictids are numerically most important as flower visitors near the northern boundaries (Yumoto, 1987, 1988; Tadauchi & Alam, 1993; Batra, 1997; Kato, 2000). In lowland rainforest in Sarawak, 21 plant species (of 270 studied) in nine families are probably pollinated largely by *Nomia* and *Thrinchostoma* (Momose *et al.*, 1998*c*). A tentative *Nomia* pollination syndrome has been identified: white, yellow or orange flowers, bilabiate, small, with relatively long floral tube. Most of these plant species were on the forest floor, in the understorey or in forest gaps. The bees involved are described as 'shade-loving, swiftly foraging trapliners' following a set foraging route (Kato, 1996). The extreme tongue length reported in this mostly short-tongued family in the region is 15 mm, for an unusual *Thrincostoma* that is able to extract nectar from the deep spurs of *Impatiens korthalsii* in montane forest in Sumatra (Kato *et al.*, 1991; Sakagami, Kato & Itino, 1991). This bee species may specialise on this type of flower and narrow specialisation has been suggested for halictids elsewhere (e.g. *Nomia capitata* on *Indigofera linifolia* in the Punjab; Batra, 1966), although no detailed studies have been reported.

Many of the species apparently pollinated by halictids in Sarawak belong to the families Acanthaceae, Verbenaceae or Zingiberaceae (Momose *et al.*, 1998*c*) and the same three families, plus the Lamiaceae and Fabaceae, account for most of the other reported cases where halictids are major flower visitors in the region (e.g. Batra, 1966; Mathew *et al.*, 1987; Kato, Itino & Nagamitsu, 1993; Garg & Rao, 1997; Zhou *et al.*, 1996). Halictids are also minor visitors to many tree species but their small size must make them less effective pollinators of large flowers (Dayanandan *et al.*, 1990).

(*iv*) *Melittidae.* A small family of Holarctic and African soil-nesting bees. A few species in the genus *Macropis* occur in subtropical and tropical montane China, where they are reported to visit the flowers of *Lysimachia, Verbena* and *Rubus* (Wu & Michener, 1986). As far as is known, all *Macropis* species depend on *Lysimachia* flowers as a source of the oil used for larval food, but must visit other flowers for nectar (Michener, 2000).

(*v*) *Megachilidae.* A world-wide family of several thousand species, distinguished by their use of foreign materials to construct nest cells (leaf pieces in *Megachile* spp.) and their transportation of pollen on the underside of the abdomen, rather than the legs (Michener, 2000). In the Oriental Region, the family is diverse but with low average density (Sakagami *et al.*, 1990). *Megachile* (*Chalicodoma*) *pluto* in the northern Moluccas, may be the largest bee in the world, with females reaching almost 4 cm in length. The significance of members of this family as pollinators appears to come largely from their ability – shared with *Xylocopa* and *Bombus* – to force their way into flowers with tightly closed petals (Sakagami *et al.*, 1990). Most records of megachilids as sole or major visitors refer to 'flag-type' (in the sense of Faegri & van der Pijl, 1979) (or papilionaceous) flowers. These bees presumably favour such flowers, at least in part, because the sexual organs are in the lower part of the flower, thus making it easier to collect pollen on the underside of the abdomen (Faegri & van der Pijl, 1979).

In the lowland rainforest of Sarawak, four of 270 plant species studied were apparently pollinated by *Megachile* species, including three legumes and a *Xanthophyllum* (which also has papilionaceous flowers) (Momose *et al.*, 1998*c*). *Megachile* species appeared twice in the study area during the 53 month study, both times coinciding with the synchronous flowering of these plant species. Such 'episodic flushes' of megachilid abundance and diversity at peak-flowering plants have also been reported from subtropical Australia (Williams & Adam, 1997), although the reason for this behaviour is not known. Megachilid bees are recorded as visitors to a wide range of wild and crop plants in the region, but the great majority of cases, and all in which they appear to be the major pollinator, refer to Asteraceae, Fabaceae and Lamiaceae (e.g. Bhatnagar, 1986;

Abrol & Kapil, 1987; Raju & Reddi, 1989; Singh & Singh, 1993; Kato, 2000).

(*vi*) *Apidae-Xylocopinae.* Three tribes in this subfamily include important flower visitors in the Oriental Region. The Xylocopini, in the single genus *Xylocopa*, consists of large to very large bees that mostly nest in burrows excavated in wood (Michener, 2000). The Ceratinini (*Ceratina*, in the broad sense, including *Pithitis*) and Allodapini (*Braunsapis*) are mostly small, slender bees that nest in pithy dead stems or twigs.

Most species in the pantropical genus *Xylocopa* (large carpenter bees) live in tropical or subtropical climates and their activity is limited to the summer months in the northern parts of the region (Sihag, 1993; Maeta, Miyanaga & Sugiura, 1996; Kato, 2000; Corlett, 2001). Although most Oriental species seem to require temperatures above 20–25 °C for flight (e.g. Sihag, 1993; Corlett, 2001), the nocturnal *X. tranquebarica* will forage at 13 °C in northern Thailand (Burgett & Sukumalanand, 2000) and another nocturnal species, *X. tenuiscapa*, forages in temperatures as low as 2 °C in the evergreen cloud forest of the Western Ghats (Somanathan & Borges, 2001). Most species are diurnal, but the widespread *X. tranquebarica* is active on moonlit nights and *X. tenuiscapa* forages even on moonless nights. As potential pollinators, *Xylocopa* bees have the advantages of large size, fast flight, activity in strong winds (Somanathan & Borges, 2001), long flight range (<20 km in two Indian species; Kapil & Dhaliwahl, 1969), the ability to force their way into flowers with tightly closed petals (Sakagami *et al.*, 1990), and the ability to extract pollen from flowers with porose anthers by 'buzzing' (e.g. Gross, 1993; Murali, 1993; Endress, 1997; Rao *et al.*, 1998).

Although *Xylocopa* bees may visit a wide range of flower types when alternatives are unavailable, most records of pollination involve large, showy, bisexual, and usually zygomorphic, flowers of woody plants (Raju & Reddi, 1989, 2000; Momose *et al.*, 1998*c*; Kato, 2000). Legumes are particularly often mentioned. These bees appear to be the sole pollinators of some large-flowered plants with porose anthers, such as species of *Melastoma* (Gross, 1993; Corlett, 2001), *Dillenia* (Endress, 1997; Momose *et al.*, 1998*c*) and *Cassia* (Murali, 1993). They also use the same buzz-collection technique on some flowers with non-porose anthers, such as *Peltophorum pterocarpum* (Aluri & Reddi, 1996). *Xylocopa* bees apparently compete for flowers with equally large *Bombus* species towards the north of the region, where both genera occur (Yumoto, 1987; Ng & Corlett, 2000), and may compete with sunbirds in open tropical sites (Raju & Reddi, 1989, 2000; Raju, 2001).

Xylocopa bees are such conspicuous visitors to large-flowered ornamental plants in the Oriental Region that their overall importance in pollination may have been overestimated. They clearly are important pollinators of large-flowered species in relatively open habitats, from semi-desert to rainforest clearings, but, although Appanah (1990) describes them migrating into mature phase rainforest from secondary vegetation during general flowering, they seem to be relatively unimportant in extensive tracts of closed rainforest (Momose *et al.*, 1998*c*). Moreover, many species have been reported to cut open the sides of tubular flowers and collect nectar without contacting the other floral parts (e.g. Kato, 2000; Gowda *et al.*, 2001), presumably reducing the likelihood of subsequent pollination by other insects.

The genus *Ceratina* (small carpenter bees) is almost cosmopolitan in distribution and is common throughout the Oriental Region. Although these bees have been recorded as minor visitors to the flowers of numerous plant species, current evidence does not suggest that they are important pollinators. Many records refer to Asteraceae, Fabaceae or Lamiaceae (e.g. Batra, 1976; Raju, 1988; Kato *et al.*, 1989; Garg & Rao, 1997; Raju & Rao, 2002). In Thailand, *Ceratina* species are considered to be major pollinators of teak (*Tectona grandis*, Verbenaceae) (Tangmitcharoen & Owens, 1997). In the lowland dipterocarp forest of Lambir, Sarawak, a shade-loving species visited Acanthaceae and Zingiberaceae with other bees (Kato, 1996) but *Ceratina* is listed as the major pollinator of only one of 270 species studied at this site – the canopy tree, *Pometia pinnata* (Sapindaceae) (Momose *et al.*, 1998*c*). Like *Xylocopa*, *Ceratina* species sometimes pierce the sides of flowers to steal nectar (Kato, 1996) and they are frequent pollen thieves at large flowers that they are too small to pollinate.

The largely palaeotropical genus *Braunsapis* includes many social species. Although reported to be a significant pollinator of crops in India (Batra, 1976; Batra, Sakagami & Maeta, 1993) they have rather rarely been recorded as visitors to wild plants. At Lambir, *Braunsapis* was mostly recorded at flowers in gaps that were also visited by other bees and wasps (Momose *et al.*, 1998*c*). *Braunsapis* also visited flowers of *Shorea megistophylla* in Sri Lankan rainforest but was considered too small to pollinate them effectively (Dayanandan *et al.*, 1990).

(*vii*) *Apidae-Nomadinae.* These slender, wasp-like parasitic bees in the single genus *Nomada* are primarily Holarctic (Michener, 2000). They lack scopae to collect pollen but have been recorded as flower visitors in winter in the Punjab, India (30° N) (Batra, 1967).

(*viii*) *Apidae-Apinae-Ctenoplectrini.* This small group of short-tongued bees is sometimes treated as a separate family, Ctenoplectridae. Of the two genera, only *Ctenoplectra* occurs in the region. They are reported to specialise on small-flowered Cucurbitaceae from which they apparently collect oil (Michener & Greenberg, 1980). In Yunnan, *C. cornuta* visits and pollinates three dioecious species of *Thladiantha* in this family, collecting pollen and a glandular secretion from the petals (Li, 1997).

(*ix*) *Apidae-Apinae-Eucerini.* Various species of *Tetralonia* have been reported to visit flowers in the northern parts of the Oriental Region (e.g. Batra, 1967) and *Tetralonia okinawae* is an important, long-tongued pollinator on the Amami Islands in the Ryukyu Archipelago, where *Bombus* is absent (Kato, 2000).

(*x*) *Apidae-Apinae-Anthophorini.* In the Oriental literature, this tribe of robust, fast-flying, long-tongued, soil-nesting bees has usually been placed, along with some of the preceding tribes, in a separate family, Anthophoridae. Three genera are reported as flower visitors and pollinators in the region: *Anthophora*, *Elaphropoda* and *Amegilla*. *Anthophora* is primarily Holarctic and African, but is a widely reported flower visitor, usually to herbs, in the northern half of the

Oriental Region (e.g. Batra, 1980; Luo & Chen, 1999). *Elaphropoda* has been reported only as a pollinator of species of *Globba* and *Zingiber* (Zingiberaceae) and, with *Amegilla*, of three long-spurred species of *Impatiens* (Balsaminaceae) in the montane rainforest of Sumatra (Kato *et al.*, 1991, 1993). The largely palaeotropical genus *Amegilla*, by contrast, has been recorded throughout the region, visiting a variety of flower types in both open and forested habitats (e.g. Raju, 1989; Raju & Reddi, 1989; Reddy & Aruna, 1990; Atluri, Rao & Reddi, 2000; Kato, 2000; Raju & Rao, 2002). However, it appears to be most important as a pollinator in the forest understorey (Kato *et al.*, 1989, 1991, 1993; Kato, 1996, 2000; Momose *et al.*, 1998c; Sakai *et al.*, 1999a). These bees behave as classic trapliners, swiftly flying long distances between scattered patches of flowers. In the lowland rainforest of West Sumatra, the aptly named *Amegilla elephas*, with a 34 mm long proboscis, pollinates *Achasma macrocheilos* (Zingiberaceae) (Kato *et al.*, 1993). At Lambir, where *A. elephas* is absent, two *Amegilla* species pollinate 11 of the 29 species of Zingiberaceae and Costaceae, but *Achasma macrocheilos* is pollinated by long-billed spiderhunters (*Arachnothera*) (Sakai *et al.*, 1999a). *Amegilla* also pollinates a variety of other understorey taxa at Lambir that have odourless, bilabiate flowers, with nectar inaccessible to most other insects (Momose *et al.*, 1998c). A different species forages mostly at the forest edge and in gaps, often visiting *Xylocopa*-pollinated flowers. *Amegilla* species can extract pollen from porose anthers by buzzing but their smaller size must make them less effective pollinators than *Xylocopa* on large flowers. *Amegilla* species are in some ways equivalent to the euglossine bees of the Neotropics, but are much less diverse at any one site (Kato, 1996).

(*xi*) *Apidae-Apinae-Melectini.* The members of this tribe are all parasites on species of Anthophorini and do not collect pollen (Michener, 2000). Although most diverse in the Palaearctic, three genera are occasionally reported as flower visitors in the Oriental Region: *Melecta* (Singh & Singh, 1993), *Tetralonioidella* (as *Protomelissa*: Kato *et al.*, 1991), and *Thyreus* (e.g. Batra, 1967; Raju, 1989; Kato *et al.*, 1991; Singh & Singh, 1993).

(*xii*) *Apidae-Apinae-Bombini.* This tribe (the bumblebees) consists of a rather uniform group of medium to very large, hairy, primitively eusocial bees in the single genus *Bombus* (Michener, 2000). They occur throughout the northern margins of the Oriental Region and in mountains as far south as the Philippines, Java and Sumatra, but not Borneo. Where present, they are often among the dominant pollinators (Yumoto, 1987, 1988; Starr & Geronimo, 1990; Singh & Singh, 1993; Sota, Salmah & Kato, 1997). By contrast to the Neotropics, however, where a few species penetrate the lowland rainforest and cerrado, *Bombus* is absent from the tropical lowlands of the Oriental Region. In West Sumatra, two species of *Bombus* replace the anthophorine genera *Amegilla* and *Elaphropoda* and the halictid *Thrincostoma* as the dominant long-tongued bees above 1500 m (Kato *et al.*, 1993). In much of the region in which they occur, they overlap spatially with at least one species in the superficially similar genus *Xylocopa*, although these two genera show partial seasonal separation in activity in northern regions, with *Xylocopa* active only in the warmer months and *Bombus* most active in the cooler months (Kjellsson, Rasmussen & Dupuy, 1985; Corlett, 2001). In Hong Kong (22° N), *B. eximius* is active in colder weather (>8 °C) than any other bee species and flies in both strong winds and light rain (Corlett, 2001). Two species in Kashmir (32–38° N) were active above 6.5 °C.

Most reports of flower visits by *Bombus* in the Oriental Region refer to herbaceous plants, particularly in the families Asteraceae, Fabaceae, Lamiaceae and Scrophulariaceae (e.g. Michener & Amir, 1977; Singh & Singh, 1993; Sota *et al.*, 1997; Kumar & Lall, 1998), but they are also important pollinators of woody species in both forested and open sites (Yumoto, 1987; Kato, Salmah & Nagamitsu, 1992; Sota *et al.*, 1997), particularly members of the Ericaceae (Kjellsson *et al.*, 1985; Singh & Singh, 1993; Ng & Corlett, 2000). Where they are active in the same time and place, *Bombus* and *Xylocopa* often visit the same flowers (Ng & Corlett, 2000; Corlett, 2001). Like *Xylocopa*, *Bombus* species are capable of buzz-pollinating flowers with porose anthers, such as those of *Melastoma* (Starr & Geronimo, 1990; Sota *et al.*, 1997), and may steal nectar by biting through the corolla tube (Burkill, 1916).

(*xiii*) *Apidae-Apinae-Meliponini.* The stingless bees are a pantropical and southern subtropical group of highly social bees forming long-lived colonies (Michener, 2000). In the Oriental Region they are largely confined to the tropics and below 1500 m altitude (Salmah, Inoue & Sakagami, 1990). All but 3–4 Oriental species are in the genus *Trigona*. Stingless bees appear to be the single most important group of flower-visiting bees in lowland tropical rainforests worldwide and the Oriental Region is no exception. In the lowland dipterocarp forest at Lambir, Sarawak, they are the most important group of pollinators, except in the emergent layer, where beetle-pollinated dipterocarps dominate, and on the forest floor, where trap-lining solitary bees are most important (Momose *et al.*, 1998c; Sakai *et al.*, 1999a). Contrary to earlier suggestions that stingless bees are most important in the understorey (e.g. Appanah, Willemstein & Marshall, 1986), they pollinate most large, non-dipterocarp, trees at Lambir (Sakai, 2001b). Overall, 'small social bees' – largely *Trigona* species – pollinate 25% of the 305 species studied at Lambir and this proportion is even higher outside the irregular periods of mass flowering (Momose *et al.*, 1998c; Sakai *et al.*, 1999c). In the dry deciduous dipterocarp forests of Thailand, *Trigona* species are the major pollinators of one of the four dominant dipterocarp species, *Shorea siamensis* (Ghazoul & McLeish, 2001).

Although social bees with long-lived colonies must be more or less generalist foragers, 22 species (21 *Trigona*) of stingless bees coexist (with four *Apis*) in lowland rainforest at Belalong, Brunei (Roubik, 1996) and similar diversities occur at other lowland rainforest sites in Southeast Asia (Appanah, 1982; Inoue *et al.*, 1993; Nagamitsu & Inoue, 1998). Analysis of the pollen diets of three closely related *Trigona* species in Sabah showed some interspecific resource partitioning, with colonies clustering by species rather than the spatial location of the nests (Eltz *et al.*, 2001). There is evidence at Lambir of floral partitioning by height, as well as a trade-off between searching ability and defensive ability at flower patches (Nagamitsu & Inoue, 1997a; Nagamitsu *et al.*,

1999 *b*). However, interspecific aggression between bees seems to be less pronounced in Sabah than reported for the Neotropics and nests are often aggregated (Eltz *et al.*, 2003). At least some stingless bees can apparently communicate the three-dimensional location of food sources to nest mates, but the mechanism of communication and recruitment is not well understood (Nieh *et al.*, 1999; Hrncir *et al.*, 2000) and individual colonies forage on a broad array of pollen sources at any one time (Eltz *et al.*, 2001). The 17 sympatric *Trigona* species investigated at Lambir also had differences in tongue length that were associated with differences in the shape of the flowers exploited (Nagamitsu & Inoue, 1998). However, most flowers pollinated by stingless bees are small and dish-shaped, with unprotected nectar (Inoue *et al.*, 1990; Momose *et al.*, 1998 *c*). Stingless bees also harvest resources from a wide range of flower types that are pollinated principally by other, larger pollinators (e.g. Dayanandan *et al.*, 1990; Sakai *et al.*, 1999 *a*) or by wind (Eltz *et al.*, 2002). Some species make holes in the anthers of buzz-pollinated flowers to steal pollen (Roubik, 1989; Gross, 1993).

Stingless bee nests in rainforest are usually associated with large, living trees (Roubik, 1996; Eltz *et al.*, 2003) and colony density may be partly determined by nest site availability (Inoue *et al.*, 1993). A study in lowland rainforest in Sabah, however, showed that nest density was greatly enhanced where the bees had access to non-forest pollen (from *Rhizophora* mangrove or crops of maize, manioc and water melon), suggesting that the abundance of stingless bees is food-limited in these forests (Eltz *et al.*, 2002). The association of nests with commercial timber trees, coupled with the long life and low fecundity of colonies, makes stingless bees potentially vulnerable to commercial logging (Eltz *et al.*, 2003). At Lambir, Sarawak, stingless bee colonies survived during the periods of low resource availability between supra-annual general flowering episodes, but new colonies were founded in artificial nesting sites only during these episodes of massively enhanced floral resource availability (Nagamitsu, 1998, cited in Sakai, 2001 *b*). General flowering also resulted in a large increase in forager activity at each nest, presumably reflecting an increase in the number of foragers produced by the colony (Nagamitsu & Inoue, 2002).

Estimates of foraging flight distances range from <434 m (Roubik, 1989) to >1100 m (Appanah, 1982) for different species. If the positive linear relationship between maximum flight range and head width established for Neotropical species (Nieuwstadt & Iraheta, 1996) applies here, then most Oriental *Trigona* species probably forage within a radius of 1 km of their nests. In logged dry deciduous dipterocarp forest, the reduced density of *Shorea siamensis* trees resulted in lower fruit set than in undisturbed forest, because stingless bees foraging at trees separated by approximately 20 m from their nearest flowering neighbours were more likely to return to the nest than move to another tree, thus reducing the transfer of compatible cross pollen (Ghazoul, Liston & Boyle, 1998; Ghazoul & McLeish, 2001).

Stingless bees are both less diverse and less abundant in disturbed, open habitats, although some species nest in cavities in human-made structures (Salmah *et al.*, 1990; Liow, Sodhi & Elmqvist, 2001; Klein *et al.*, 2002). They also

appear to be much less important in pollination in such areas and are rarely mentioned in the Oriental literature for non-forest habitats.

(*xiv*) *Apidae-Apinae-Apini*. The true honeybees are an essentially Oriental group of eusocial bees, although there is also a single species in Africa and one of two species in much of the Palaearctic Region (Michener, 2000). There are at least eight *Apis* species in the Oriental Region, with a greater than five-fold range in worker body mass. These species can be divided into three distinct groups: small species with a single exposed comb; large species with a single exposed comb; and medium-sized, cavity-nesting species. One species from each group coexists over most of the region, but there are only two species in some peripheral areas (including most of the Philippines, Sulawesi and the higher elevation Himalayas) and there are four in some areas, although rarely in the same habitat (Otis, 1996). Although *Apis* is much less diverse than many other bee genera, the efficiency with which individual worker scouts recruit large numbers of their sisters to newly discovered floral resources makes them formidable competitors and may help explain the relatively low diversity of the Oriental bee fauna as a whole. On the other hand, even the largest *Apis* species are apparently unable to access nectar that is protected by tightly closed petals (i.e. they are not 'forceful flower visitors'; Inoue *et al.*, 1990), and honeybees have not been recorded buzzing flowers with porose anthers to extract pollen, so some floral resources are unavailable to them. In comparison with most other invertebrate pollinators in the Oriental Region, *Apis* species are capable of transferring pollen over relatively long distances. In the emergent rainforest dipterocarp, *Neobalanocarpus heimii*, pollinated by *Apis* and *Trigona*, the estimated average mating distance of five reproductive trees in a low-density population at Pasoh, Malaysia, was 524 m (Konuma *et al.*, 2000).

The two currently recognised species of small honeybees, *Apis florea* and *A. andreniformis*, are similar in size and general appearance, and were confused, as *A. florea*, in earlier literature. However, the two species differ considerably in detailed morphology, behaviour and some elements of their natural history (Wongsiri *et al.*, 1996). *A florea* is the most widespread species but only *A. andreniformis* occurs naturally in most of Malaysia and Indonesia, while the Philippines (except Palawan) and Sulawesi lack a small honeybee species. Their ranges overlap only in continental Southeast Asia and southwest China. *A. andreniformis* is mostly a lowland forest bee but *A. florea* thrives even in highly disturbed landscapes. *A. andreniformis* is slightly smaller than *A. florea* and, at least in Thailand, its proboscis is around 15 % shorter, which may facilitate their coexistence (Wongsiri *et al.*, 1996). Both species change nesting sites frequently and may migrate seasonally in at least some areas, but nothing is known about the distances travelled. *A. florea* is considered an important pollinator of field and orchard crops in the region (e.g. Batra, 1967; Rehman *et al.*, 1990; Sihag, 2000 *b*) but its significance as a pollinator of wild plants is largely unknown. In semi-arid northern India, it was active at temperatures of 18–43 °C and was the only *Apis* species still foraging above 40 °C (Sihag, 2000 *b*). Even less is known about *A. andreniformis* and it is not mentioned as a major visitor for any

species at Lambir, although it occurs there (Momose *et al.*, 1998*c*).

Of the two large *Apis* species, the Himalayan honeybee, *A. laboriosa*, is found only in remote mountain valleys in Bhutan, China, India and Nepal (Underwood, 1992). Little has been recorded about the ecology of this species. The nests are usually beneath rock overhangs and may form large aggregations at favoured sites. Some colonies migrate to higher altitudes (>3500 m) for a few months in the summer. The giant honeybee, *Apis dorsata*, by contrast, is found throughout the Oriental Region, except in the far north. It requires air temperatures of at least 17–18 °C (Dyer & Seeley, 1987), 15–19 °C (Abrol, 1992) or 16 °C (Sihag, 2000*a*) for flight, as opposed to 10.5 °C (Abrol, 1988), 12–15 °C (Abrol, 1992) or 12 °C (Corlett, 2001) for *Apis cerana*, which may set the northern and altitudinal limits of its distribution. The nests are found in forests and agricultural areas, as well as, occasionally, in cities, and are constructed on the exposed branches of large trees, on cliffs or on human-made structures. They are often, but not always, in aggregations of up to 100 colonies. Giant emergent trees of *Koompasia excelsa* (Fabaceae) are favoured nest sites in Borneo (e.g. Itioka *et al.*, 2001). Each colony has $<100 000$ workers, with most foraging flights made within 3 km radius of the nest (Batra, 2001), so these aggregations must make huge demands on local floral resources. It is not surprising, therefore, that most colonies appear to be migratory, apparently tracking the availability of sufficiently large sources of nectar and pollen. In the monsoon tropics of India, Sri Lanka, Java and Thailand, these migrations are annual (Koeniger & Koeniger, 1980; Sihag, 1993; Dyer & Seeley, 1994; Kahono, Nakamura & Amir, 1999; Thapa *et al.*, 2000; Devy & Livingstone, 2001), but in the aseasonal lowland dipterocarp forest at Lambir, Sarawak, *A. dorsata* colonies were present only during the mass-flowering episodes that occur at irregular, multi-year intervals (Itioka *et al.*, 2001). These migrations may cover distances of 50–200 km (Koeniger & Koeniger, 1980; Itioka *et al.*, 2001).

At Lambir, *A. dorsata* visited sugar solution feeders from ground level to the canopy (Roubik, Inoue & Hamid, 1995) but they were not observed on flowers in the understorey (Kato, 1996). A preference for canopy trees has also been reported from other rainforest sites (Appanah, 1990; Devy & Livingstone, 2001). In southern India, *A. dorsata* workers forage all night under a full moon, and for an hour after sunset on dark nights (Dyer, 1985), and are the major pollinators of *Pterocarpus santalinus* (Fabaceae), an endangered dry forest tree whose large yellow flowers open at midnight (Rao, Atluri & Reddi, 2001). Nocturnal foraging in these cases may be a way of avoiding excessive daytime temperatures, but this is unlikely to be true in the more equable climate of lowland rainforests. At Lambir, they were the only social bees foraging before sunrise (05:00–06:00 h) and after sunset (18:00–20:00 h) and pollinated several tree species (mostly Dipterocarpaceae) whose flowers opened during these periods (Momose *et al.*, 1998*c*). This apparent adaptation of nocturnal-flowering canopy trees to a migratory bee species that is usually absent from the site suggests that the relationship between *A. dorsata* migration and mass-flowering episodes in the lowland dipterocarp forest of Sarawak is an ancient one. In total, *A. dorsata* pollinated at least 15 species of emergent and canopy trees at Lambir. It has also been reported as among the dominant pollinators of the upper strata in rainforest in peninsular Malaysia (Appanah, 1990), in the rainforest canopy of the Western Ghats in India (Devy & Livingstone, 2001), and for canopy dipterocarps in Sri Lanka (Dayanandan *et al.*, 1990).

Despite an apparent preference for large trees, there are also records of *A. dorsata* visiting a number of orchid species (Cingel, 2001) and, in non-forest habitats, it visits a wide range of plants, including crops and herbaceous weeds (e.g. Burkill, 1919; Tadauchi & Alam, 1993; Venkatesh *et al.*, 1995). Presumably, the large population sizes of some of these plants compensate for their small individual sizes, and create resource patches big enough to sustain a giant colony.

At least four species of medium-sized, cavity-nesting honeybees are currently recognised in tropical Asia (Otis, 1996; Tanaka *et al.*, 2001). *Apis cerana* occurs almost throughout the Oriental Region and extends north into temperate East Asia. The other three species are confined to the Sunda Shelf region of Southeast Asia. Their precise geographical ranges are still unclear: *A. koschevnikovi* is the dominant cavity-nesting bee in Bornean lowland rainforests, but is apparently rare in Java, Sumatra and the Malay Peninsula; *A. nigrocincta* is widespread on Sulawesi but has also been recorded from Mindanao; *A. nuluensis* is apparently confined to the Kinabalu highlands of North Borneo above 1700 m altitude.

There is no published information on the ecology of either *A. nigrocincta* or *A. nuluensis*. Most information on *A. koschevnikovi* comes from the lowland dipterocarp forest at Lambir, Sarawak. At this site, *A. koschevnikovi* is resident, although fluctuations in the numbers of workers trapped were similar to those in the migratory *A. dorsata* (Itioka *et al.*, 2001). Presumably the much smaller colonies of *A. koschevnikovi* (1200–2000 adult bees: Roubik *et al.*, 1999) can find – or store – enough food to survive the multi-year gaps between general flowering episodes. *A. koschevnikovi* found new feeders more quickly than other social bees at Lambir and rapidly recruited additional workers (Nagamitsu & Inoue, 1997*a*). It showed a preference for the canopy, but could find and recruit to feeders at any height, although it is not clear if this ability involves communication of locations in three dimensions (Roubik *et al.*, 1999). Although described as 'one of the major pollinators' during general flowering episodes (Itioka *et al.*, 2001), it is listed as a major pollinator for only eight (of 270) species, and as the sole major pollinator for only two (Momose *et al.*, 1998*c*).

Apis cerana is the most widespread of the Oriental *Apis* species, occurring throughout the region and extending into the eastern Palaearctic to 46° N (Hepburn *et al.*, 2001). This very wide distribution in comparison with other Oriental bee taxa – totalling around 30 million km^2 – presumably reflects, at least in part, its use of protected nest sites and its ability to continue foraging at low temperatures: down to 12 °C in Hong Kong (Corlett, 2001) and 10.5 °C in Kashmir (Abrol, 1988). Although sometimes viewed as the tropical Asian equivalent of *A. mellifera*, *A. cerana* colonies

have fewer, smaller workers and a smaller foraging range (generally <1 km: Punchihewa *et al.*, 1985; Liu & Zhang, 2000).

In those parts of the Sundaland region where its range overlaps with other cavity-nesting species, *A. cerana* appears to be found mainly in disturbed and open sites. However, it is abundant in primary forests in central Sumatra up to 2500 m (Salmah *et al.*, 1990). In most areas where it is the only cavity-nesting species, it appears to occupy all habitats, including primary forests (e.g. Seeley, Seeley & Akaratanakul, 1982; Dayanandan *et al.*, 1990; Devy & Livingstone, 2001). At least some populations of *A. cerana* appear to migrate seasonally (e.g. Koeniger & Vorwohl, 1979), although the distances moved are unknown. *A. cerana* is an important canopy pollinator, with *A. dorsata*, in the rainforests of the Western Ghats (Devy & Livingstone, 2001; Devy & Davidar, 2003) and Sri Lanka (Dayanandan *et al.*, 1990), but there is virtually no information on its role in forests elsewhere in the region. For non-forest habitats, there is a vast literature on *A. cerana* as a domesticated bee and a pollinator of crops, but almost nothing on the relationship between wild colonies and wild plants. The majority of the plant species for which *A. cerana* visits have been documented are crops, ornamentals or weeds (e.g. Areekul & Rojanavongse, 1984; Kiew, 1993; Tilde, Payawal & Cervancia, 2003). A surprising number of these are considered to be wind-pollinated, with *A. cerana* presumably acting as a pollen thief.

At high altitudes in the tropics (Salmah *et al.*, 1990) and on the northeastern margins of the region, *A. cerana* is the only highly social apid bee present, and might be expected to be more important as a pollinator. Too few studies have been conducted to test this, but in the Amami Islands (28.30° N) in the northern Ryukyu archipelago, it is a significant pollinator only in winter, when few other bees are active (Kato, 2000). In Hong Kong (22 °N), by contrast, *A. cerana* was the numerically dominant visitor to 55 % of the 83 woody species studied, and probably a major pollinator for most of these (Corlett, 2001). This dominance of *A. cerana* seems to be largely a reflection of the rarity of other bees during the March–May flowering maximum, but may also be, in part, a consequence of the high degree of landscape degradation in Hong Kong resulting from several hundred years of massive human impacts. It is possible the importance of *A. cerana* increases in fragmented and degraded landscapes, as has been shown for introduced African honeybees in the Neotropics (Dick, 2001).

The many natural enemies of the native *Apis* species in the Oriental Region, including predatory wasps and bee mites, have caused problems for commercial bee-keeping with the Palaearctic and African species *Apis mellifera*, and have apparently prevented the establishment of feral colonies of this species. Introduced *A. mellifera* has, however, become established on the oceanic Bonin (Ogasawara) Islands, on the northern margins of the region, where both native social bees and predatory vespid wasps are absent (Kato *et al.*, 1999). The survival of feral colonies on these islands depends on the presence of weedy exotic plants that have greatly extended the flowering season. There is evidence for a strong, negative impact on the community of small, native, solitary bees through competition for the nectar and pollen of native flowers.

(5) Lepidoptera

Heppner (1998) estimates that there are at least 50 000 species of Lepidoptera in the Oriental Region. Almost all are dependent on flowering plants at the larval stage and most species that feed as adults depend on floral nectar for sugars and amino acids. Although the Lepidoptera are probably the best-studied invertebrate group in the region, there has been surprisingly little work on their relationships with flowers. Most studies that have been done refer to diurnal butterflies or crepuscular hawkmoths. Apparently, most Oriental pollination biologists do not work at night. With so few studies, it is dangerous to generalise, but the available evidence suggests that pollination by Lepidoptera may be considerably less important in the Oriental Region that in the Neotropics. It certainly seems to be less important in the lowland rainforest (Momose *et al.*, 1998*c*; Sakai, 2001*a*). Many lepidopteran families have been occasionally mentioned as casual flower visitors, but only for those listed below is there evidence for any role in pollination.

(a) Pyralidae

Among the 'Microlepidoptera' – a paraphyletic group of small moths – only the Pyralidae are recorded as more than casual flower visitors in the Oriental Region. Pyralids, with geometrids, were the main pollinators of the gymnosperm *Gnetum gnemon* in the understorey of the lowland dipterocarp forest at Lambir, Sarawak (Kato, Inoue & Nagamitsu, 1995*b*) and, with noctuids, of *G. luofuense* in both forest and open sites in Hong Kong (Corlett, 2001). They may also be major pollinators of *Nepenthes gracilis* in montane forest in Sumatra (Kato, 1993). Pyralids were also among the diverse insect visitors to two *Artocarpus* species at Lambir (Momose *et al.*, 1998*a*) and three *Aquilaria* species at Bogor, Java (Soehartono & Newton, 2001). Pyralids in the genera *Assara* and *Nacoleia* are considered the most likely cross-pollinators of *Balanophora kuroiwai*, in the Ryukyu archipelago (Kawakita & Kato, 2002). The moths lay eggs on the inflorescences and the larvae feed on the vegetative tissues of the developing infructescences without damaging the seeds, suggesting the existence of a complex mutualism.

(b) Geometridae

Despite their abundance and diversity in the Oriental Region, geometrids have rarely been recorded as flower visitors. At Lambir, geometrids were the main pollinators of an emergent dipterocarp, *Dipterocarpus pachyphyllus*, with nocturnal-opening, scented, white flowers (Momose *et al.*, 1998*c*), and, with pyralid moths, of *Gnetum gnemon* in the understorey (Kato *et al.*, 1995*b*). They were also among the diverse insect visitors to two species of *Artocarpus* (Momose *et al.*, 1998*a*). In the mid-elevation rainforest at Kakachi, in the Western Ghats, geometrids were the major visitors to the nine species characterized as pollinated by moths (Devy & Davidar, 2003). On subtropical Hachijo Island (33° N), the

orchid *Platanthera hachijoensis* is pollinated largely by geometrids (Inoue, 1985).

(c) *Sphingidae*

The hawkmoths are diverse and abundant in the Oriental Region, but there are few recorded examples of plants for which hawkmoths are the only or major pollinators. In hill dipterocarp forest in Sabah, hawkmoths were most abundant in the canopy and nectar-feeding species rarely penetrated the understorey (Schulze, Linsenmair & Fiedler, 2001). However, in the Sumatran rainforest understorey, a pink-flowered *Impatiens* with a long, filiform spur was pollinated by a crepuscular *Macroglossum* (Kato *et al.*, 1991). Sphingids were suspected as pollinators of only a single species in the lowland dipterocarp forest at Lambir, Sarawak: a subcanopy *Barringtonia* (Lecythidaceae) with white, scented, nocturnal brush flowers (Momose *et al.*, 1998c). On the subtropical Amami Islands (28.30° N) in the Ryukyu Archipelago, three plant species are apparently pollinated by sphingids: another species of brush-flowered *Barringtonia*, and two species with white, scented, tubular flowers, *Cerbera manghas* (Apocynaceae) and *Clerodendron trichotomum* (Verbenaceae) (Kato, 2000). *Mussaenda parviflora* (Rubiaceae), which has yellow flowers with enlarged white calyx lobes, was visited by both a crepuscular *Macroglossum* and diurnal papilionid butterflies. Further north, on Hachijo Island (33° N), the orchid *Platanthera okuboi* is apparently pollinated only by a small sphingid, *Rhagastris trilineata* (Inoue, 1985).

Other species with white, scented, tubular flowers believed to be pollinated by sphingids are *Jasminum angustifolium* (Oleaceae), *Catunaregam spinosa* (Rubiaceae) and *Carissa carandas* (Apocynaceae) in India (Raju, 1988; Raju, Reddi & Das, 1997), but this combination of floral characters is widespread in the region and many other examples of hawkmoth pollination may have been overlooked. All species believed to be pollinated by hawkmoths in Southeast Asia for which information is available have sucrose-dominated nectars (Freeman, Worthington & Jackson, 1991). Hawkmoths also visit species assumed to be pollinated by long-tongued butterflies (e.g. Balasubramanian, 1990; Corlett, 2001), as well as a wide range of other flower types. The ability to harvest nectar with a long proboscis while hovering must reduce the probability of pollen transfer in unspecialised flowers.

(d) *Noctuidae*

The Noctuidae was the most abundant and diverse family in lowland dipterocarp forest in Sabah (Willott, 1999). Although they often feature in lists of minor flower visitors, there are surprisingly few records of noctuids as pollinators or even major visitors in the Oriental Region. Large noctuids, with nocturnal hawkmoths and diurnal butterflies, were the primary pollinators of the fragrant, pink, dusk-opening flowers of *Dipterocarpus obtusifolius* in dry deciduous dipterocarp forest in Thailand (Ghazoul, 1997). Noctuids were the most common visitors to, and presumed pollinators of, *Gnetum luofuense* in Hong Kong (Corlett, 2001). Noctuids have also been reported to pollinate several species of

Asclepiadaceae in open habitats in Central India, including *Telosma pallida* and *Pergularia daemia* (Bhatnagar, 1986).

(e) *Butterflies*

At open sites throughout the region, butterflies (including Hesperiidae) are conspicuous visitors to many herbaceous plants with small, open or tubular flowers, such as members of the Asteraceae, but their role in the pollination of these species has rarely been investigated (e.g. Balasubramanian, 1989). Butterflies of several (unspecified) families pollinate six, woody, species (of 270 species studied) in the lowland dipterocarp forest at Lambir: four understorey *Ixora* species (Rubiaceae), with orange, scentless, tubular flowers, an understorey *Clerodendron* (Verbenaceae), with red brush flowers, and a climbing *Bauhinia* with orange, brush-like flowers (Momose *et al.*, 1998c). In the mid-elevation rainforest of the Western Ghats, India, butterflies visit many flowers and are considered major pollinators of four woody species (of 86 species studied), in the genera *Callicarpa*, *Clerodendrum* (both Verbenaceae), *Trichilia* (Meliaceae) and *Vernonia* (Asteraceae) (Devy & Davidar, 2003). Long-tongued butterflies from several families were the major pollinators of *Pavetta indica* (Rubiaceae) in southern India, despite the white, scented, tubular flowers suggestive of hawkmoth pollination (Balasubramanian, 1990). Butterflies were the major visitors to and probable pollinators of only two species studied on the subtropical Amami Islands, another *Bauhinia* and *Belamcanda chinensis* (Iridaceae) (Kato, 2000). In Hong Kong, six of 83 woody species studied were probably pollinated by butterflies, with two species, *Acronychia pedunculata* (Rutaceae) and *Reevesia thyrsoidea* (Sterculiaceae) attracting species from a range of families (Corlett, 2001). Butterflies are also apparently pollinators of the small-flowered species in the mangrove genus *Bruguiera* (Aluri *et al.*, 1994). Species of *Mussaenda* and *Ixora* (both Rubiaceae) that are apparently pollinated by butterflies have sucrose-dominated nectars (Freeman *et al.*, 1991).

Among the individual butterfly families, the Nymphalidae have been implicated in the pollination of *Syzygium* species in Malaysian rainforest (Appanah, 1990), but other pollinators are listed for the three canopy species studied at Lambir, Sarawak (Momose *et al.*, 1998c). The few other cases where pollination appears to depend largely on a single family of butterflies involve long-tongued Papilionidae visiting flowers with long corolla tubes (Reddy & Reddi, 1995; Kato, 1996; Corlett, 2001), although crepuscular sphingids are sometimes reported as visiting the same species and may have been overlooked in other cases. Several species of *Mussaenda*, with yellow or orange tubular flowers and one or two enlarged, white calyx lobes in each group of flowers, are visited largely or entirely by papilionids (Kato, 2000; Corlett, 2001; Gowda *et al.*, 2001). Removal of the 'pollinator flags' greatly reduced butterfly visits to *M. frondosa* (Gowda *et al.*, 2001).

(6) **Diptera**

Oosterbroek (1998) estimates that around 8800 fly species have been documented for the Malay Archipelago

(including areas east of the Oriental Region as defined here) and suggests that the total number of species present is at least three times this. The winged adults of Diptera take mainly liquid foods for which their suctorial mouthparts are specially adapted. Many species can also suck up small solid particles, such as pollen, suspended in saliva. The flies are the most likely pollinators of the ancestral angiosperms and are still probably second only to the bees in their importance as flower visitors (Endress, 2001). Many dipteran families visit flowers but most flies are confined to open flowers with exposed nectar because of their short proboscis. Specialised flower-feeders with a long proboscis, however, are found in several families, including the Bombyliidae, Empididae, Tabanidae, Nemestrinidae and Syrphidae (Proctor *et al.*, 1996). At the other extreme, many flowers use deceit to attract flies that are normally associated with decaying organic matter. Pollination by deceit appears to be particularly widespread in the family Orchidaceae, in which many Oriental species have dull-coloured flowers, often with a strong odour – that of *Bulbophyllum beccarii* has been likened to a herd of dead elephants (Pridgeon, 1994) – and sometimes with moving parts (Jongejan, 1994; Cingel, 2001). By analogy with orchid pollination systems outside the region, flies are suspected as pollinators for many of these Oriental species, but very few have been studied in any detail.

At least 25 dipteran families have been recorded visiting flowers in the Oriental Region but most reports of pollination involve the families Ceratopogonidae, Syrphidae, Drosophilidae, Muscidae, Calliphoridae, Sarcophagidae and Tachinidae. The classification used here follows Oosterbroek (1998), and differs from other classifications used in the literature mainly in the ranks assigned to taxa above the family level.

The suborder Nematocera (midges) consists of small, rather delicate flies. Although nematocerans have been reported to visit a variety of flowers, they are probably major pollinators in only a few of these. Most cases involve deceit. In open forest in northern India, the inflorescences of *Theriophonum crenatum* (Araceae) release a 'cow dung odour' which attracts a single species of *Ceratopogon* (Ceratopogonidae: biting midges) (Dakwale & Bhatnagar, 1997). Flies are trapped during the female phase and released the next evening after anther dehiscence. There is apparently no reward. In Pakistan, the trap-flowers of *Aristolochia bracteolata* (Aristolochiaceae) attract a single species of *Forcipomyia* (Ceratopogonidae) (Razzak, Ali & Ali, 1992). As with most aroid trap-inflorescences, the flowers of *Aristolochia* are protogynous and the flies are released after anther dehiscence. A range of other, mostly nematoceran, fly families have been reported as pollinators of other Aristolochiaceae (Sugawara, 1988; Razzak *et al.*, 1992). Species of *Arisaema* (Araceae) in India and Nepal are pollinated by members of the families Mycetophilidae (fungus gnats) and Sciaridae that are attracted by the odour and probably other cues (Barnes, 1934; Vogel & Martens, 2000). Unlike other aroids, most species of *Arisaema* are dioecious and, while the male inflorescence offers an exit to the flies at the bottom of the spathe, the female inflorescence does not and the pollinators die. Members of the families Sciaridae and Cecidomyiidae pollinate the lantern-like trap-flowers of three species of

Ceropegia (Asclepiadaceae) in the Western Ghats of India (Chaturvedi, 1993). These flowers have a 'mild rotten protein smell' but apparently offer no reward.

In the lowland rainforest of Sarawak, *Artocarpus integer* (Moraceae) is involved in a three-way pollination mutualism with two species of gall midges (*Contarinia* spp., Cecidomyiidae) and a fungus (*Choanephora* sp., Mucorales, Zygomycetes) (Sakai, Kato & Nagamasu, 2000). The fungus infects only the male inflorescences of this monoecious tree species. The gall midges are attracted to both male and female inflorescences by a 'fruit-like, somewhat unpleasant smell', but remain only on the male ones, where they feed on the fungal mycelia and oviposit on the inflorescence. The developing larvae then feed on the mycelia and pupate in the inflorescence. The time required to grow from an egg to an adult fly was estimated as eight days, and this could lead to a rapid build up in the population of pollinators for *A. integer*, which has a supra-annual flowering periodicity at this site.

The other reported cases of probable pollination by nematoceran flies involve small-flowered monocot herbs in the rainforest understorey. Flies from the families Ceratopogonidae, Chironomidae and Sciaridae were commonest visitors to *Dendrochilum longibracteatum* (Orchidaceae) in Sumatra (Pedersen, 1995). This orchid has a very strong 'aromatic floral' odour and secretes nectar in a minute furrow along the mid line of the labellum. In Sarawak, species of Culicidae were the probable pollinators of two mycotrophic herbs, *Sciaphila secundiflora* (Triuridaceae) and *Burmannia lutescens* (Burmanniaceae) (Kato, 1996).

All other Diptera are now placed in suborder Brachycera. The 'lower' Brachycera – traditionally, the division Orthorrhapa – includes at least 11 families with flower-visiting species including, in the Bombyliidae (bee flies), Nemestrinidae and Tabanidae (horse flies), some of the most specialised, long-tongued forms (Proctor *et al.*, 1996). Very long-tongued species of *Corizoneura* (Tabanidae) are reported to take nectar, while hovering, from flowers of Zingiberaceae, Scrophulariaceae and Lamiaceae in the hills of northern India (Fletcher & Sen, 1931). However, although these families have been recorded as minor visitors to a wide range of flowers in the Oriental Region, they have not been reported as the major pollinators of any species.

The 'higher' Brachycera, in the infraorder Muscomorpha (=Cyclorrhapha, sometimes treated as a separate suborder) is by far the largest group and also, apparently, the most important for pollination in the Oriental Region. Section Aschiza includes the family Syrphidae (hover flies), which are specialised flower visitors that consume nectar and varying amounts of pollen (Proctor *et al.*, 1996). They are the most important family of dipteran flower visitors in the northern temperate region but seem to be relatively less important at lower latitudes. Only in the forests of Yakushima (30° N), at the northern limits of the Oriental Region, are syrphids the dominant flower-visiting flies (Yumoto, 1987, 1988), while calliphorids predominate 250 km south in the Amami Islands (28.30° N) (Kato, 2000). In Hong Kong (22° N), syrphids are common flower visitors in winter and predominated on *Sageretia thea* (Rhamnaceae) (Corlett, 2001). Elsewhere in the region, they are recorded as minor visitors to flowers in a wide range of habitats but only rarely

as the major visitors. In rainforest in Sarawak, syrphids were the most abundant visitor to the understorey inflorescences of a woody climber, *Diploclisia kunstleri* (Menispermaceae) (Kato, 1996) and were second to trigonid bees as visitors to *Dryobalanops lanceolata* in the canopy (Momose *et al.*, 1996). In India, Bhaskar (1992) considered syrphids the chief pollinators of *Santalum album*, although, at another site, wasps were apparently more important (Jyothi *et al.*, 1991).

The only detailed studies of pollination by syrphids in the region involve slipper orchids in the genus *Paphiopedilum*. The large, bizarrely shaped and often luridly coloured flowers apparently offer no reward, but the nature of the deception is not entirely clear. *P. villosum*, an epiphytic species in the hill evergreen forests on northern Thailand, is pollinated by mainly females of several syrphid species (Banziger, 1996*b*). Lured by olfactory and visual cues, the fly lands on a slippery wart in the centre of a bright yellow staminode and immediately falls into the pouch-like labellum. The only escape is up a tunnel where it is pressed against the stigma and then the anther before it can fly away. Banziger (1996*b*) thinks that the principal attractant is the glittering surface of the staminode, which he suggests mimics droplets of honeydew or nectar. By contrast, Atwood (1985) suggests that, for *P. rothschildianum* in Sabah, which has an otherwise similar pollination mechanism, the staminode mimics an aphid colony on which the female syrphid flies normally deposit their eggs. The presence of up to 76 syrphid eggs on one staminode supports this suggestion, although Banziger (1996*b*) suggests that an odour mimicking that of aphid colonies may be more important in the deception. Preliminary studies of several other *Paphiopedilum* species suggest that pollination by syrphid flies may be widespread in the genus (Atwood, 1985; Banziger, 1994, 1996*b*).

The remaining section, Schizophora, is divided into two subsections. Several families in subsection Acalyptratae include flower visitors. The Drosophilidae (vinegar flies) are small flies that mostly breed in decaying organic matter, including fallen flowers. They have rarely been recorded at simple flowers in the Oriental Region, although they were frequent visitors to and potential pollinators of *Shorea robusta* in India (Khatua *et al.*, 1998) and may well have been overlooked elsewhere. Drosophilids are most often reported at inflorescences that also attract beetles: they are as common as beetles in the trap inflorescences of *Cryptocoryne ciliata* (Araceae) (Saibeh & Mansor, 1996) and non-pollinating visitors to *Homalomena propinqua* (Araceae) (Kato, 1996). Drosophilid flies also visited at both the female and male stages of the apparently cockroach-pollinated *Uvaria elmeri* in Sarawak, but rarely contacted the anthers (Nagamitsu & Inoue, 1997*b*). Drosophilids are also the commonest visitors to both male and female heads of *Artocarpus odoratissimus* (Moraceae) (Momose *et al.*, 1998*a*) and, with a species of phorid fly, to *A. heterophyllus* (van der Pijl, 1953). This latter case is particularly interesting because the flies also breed in the fallen male flower heads. Van der Pijl (1953) suggests that the 'improbably large' flower heads may be specially adapted to the breeding of their pollinators.

The best-documented case of drosophilid pollination is the highly specific relationship between *Alocasia odora* (Araceae)

and two species of *Colocasiomya* flies in Okinawa and Taiwan (Yafuso, 1993, 1994). The trap inflorescences of this species exhibit endogenous heat production during both the female and male phases. The flies are attracted by the strong odour and feed on pollen, mate and oviposit in the inflorescences. Females of both species cannot produce mature eggs without feeding on pollen. The larvae feed on the decaying tissues of the spadix. Other pairs of *Colocasiomya* species apparently have similar associations with other members of the Araceae, in the genera *Aglaonema*, *Alocasia*, *Colocasia*, *Homalomena* and *Schismatoglottis*, although none have been studied in detail and it is not clear how many are important pollinators (Yafuso & Okada, 1990; Tsacas & Chassagnard, 1992). In Sumatra, the rheophytic aroid *Furtado sumatrensis* is pollinated by a single species of *Colocasiomya* (Mori & Okada, 2001). Chemical dyes used as pollen analogues showed that pollen could be moved up to 400 m along a stream.

Several other acalyptrate families include flower visitors. In Malaysian lowland rainforest, flowers of the epiphytic orchid, *Bulbophyllum patens*, selectively attract males of several *Batrocera* species (Tephritidae : true fruit flies) with a specific fragrance, zingerone (Tan & Nishida, 2000). This relationship is apparently mutualistic, since the male flies use zingerone (a pungent component of ginger) as a sex pheromone and possibly also as a chemical defence (Tan & Nishida, 2000). Another Malaysian *Bulbophyllum* species, *B. cheiri*, uses methyl eugenol as an attractant for males of sensitive *Batrocera* species (Tan, Nishida & Toong, 2002). In this case, the flies initially feed on an unidentified material on the surface of the petals and sepals, before moving onto the finely balanced, hinged 'see-saw' lip (labellum), which throws the fly head first into a cavity in the floral column. During its struggles to escape, the fly apparently deposits any pollinia it carries and removes new ones. Males of *Batrocera papayae* metabolise the methyl eugenol into compounds that boost their pheromonal and defence systems.

Physiphora (Otitidae) was the commonest dipteran visitor and a potential pollinator of *Shorea robusta* in India (Khatua *et al.*, 1998). The Otitidae and Sepsidae were also represented in the trap inflorescences of *Sauromatum guttatum* (Araceae) in India (Dakwale & Bhatnagar, 1985). Flies in the family Lauxaniidae were the commonest insect visitors to strobili of the dioecious gymnosperm climber, *Gnetum cuspidatum*, in Sarawak (Kato *et al.*, 1995*b*). The strobili secrete nectar and produce a fungus-like odour in the evening. Members of the family Milichiidae pollinate the complex, brown-purple, lantern-like flowers of *Abroma augusta* (Sterculiaceae) (van der Pijl, 1953) and, with nematocerans, visit the lantern-like trap-flowers of three *Ceropegia* species (Asclepiadaceae) in India (Chaturvedi, 1993).

The huge subsection Calyptratae consists largely of robust flies. Five calyptrate families – Anthomyiidae, Muscidae, Calliphoridae (blow flies), Sarcophagidae (flesh flies) and Tachinidae – account for more than half the records of flower visitation and pollination by flies in the Oriental Region. The larvae of most muscids, calliphorids and sarcophagids live in carrion, dung or rotting vegetation. Flies from these families, particularly the Calliphoridae, are frequent visitors to unspecialised flowers with easily accessible

nectar throughout the region. Their importance as pollinators of such flowers has possibly been underestimated, since they are strong fliers and can carry relatively large amounts of pollen (Wickramaratne & Vitarana, 1985; Devi, Atluri & Reddi, 1989; House, 1989). A calliphorid and a muscid are believed to be the major pollinators of the mangrove *Avicennia officinalis* in southern India (Aluri, 1990) and calliphorids are apparently the major pollinators of mango (*Mangifera indica*, Anacardiaceae) in subtropical India (Bhatia *et al.*, 1995). In Sarawak, a species of *Baccaurea* (Euphorbiaceae) flowering in the forest understorey was visited only by muscid flies (Nagamitsu & Inoue, 1994). In India, the dioecious aquatic herb, *Blyxa octandra* (Hydrocharitaceae) was visited mostly by calliphorids and muscids (Cook, Luond & Nair, 1981) and, in Hong Kong, calliphorids were the commonest visitors to two species of *Lithocarpus* (Corlett, 2001). A calliphorid fly, *Stomorhina obsoleta*, was the commonest flower-visiting insect on the Amami Islands (28.30° N), although it was considered to be of only minor significance in pollination (Kato, 2000).

In addition to visiting many unspecialised flowers, calyptrate flies are major pollinators of flowers or inflorescences that apparently imitate their decaying larval substrates. These relationships usually depend on deceit, but the larvae of the anthomyiid flies that pollinate *Alocasia pubera* (Araceae) in Java complete their development in the decaying male flowers, even pupating inside the persisting spathe (van der Pijl, 1933, 1937). In the same plant family, Cleghorn (1913) reported that the trap inflorescences of *Colocasia esculenta* are pollinated by Muscidae, while Muscidae, Calliphoridae and Sarcophagidae were among the insects trapped by *Sauromatum guttatum* in India (Dakwale & Bhatnagar, 1985).

The most dramatic examples of flowers imitating rotting meat are in the family Rafflesiaceae, particularly in the genus *Rafflesia*. The huge, ephemeral flowers of these parasitic endophytes emit 'a cadaveric stench of rotting snakes' and are pollinated by calliphorid flies, mostly in the genera *Chrysomya* and *Lucilia* (Beaman, Decker & Beaman, 1988; Banziger, 1991; Hidayati *et al.*, 2000; Patiño *et al.*, 2001). Although there is no nectar, Banziger (1991) thinks that these flowers may not be entirely deceptive since the flies could consume both the pollen mush and slimy secretions. *Rafflesia* is not a trap flower, but flies remain inside for many hours, perhaps as a result of CO_2 anaesthesia (Patiño *et al.*, 2001, 2002). In the same family, *Rhizanthes infanticida* has a milder odour and nectaries (Banziger, 1996 a; as *R. zippelii*). However, it attracts the same genera of calliphorids and the fact that the pollinators are all female and sometimes oviposit on the flower suggests that it deceptively imitates carrion. The hatchlings die of starvation, hence the specific epithet! The flowers of *Rhizanthes lowii* and *Rafflesia tuan-mudae* are endothermic, maintaining tissue temperatures 7–9 °C above air temperature in *R. lowii* and 1–6 °C above in *R. tuan-mudae* (Patiño, Grace & Banziger, 2000; Patiño *et al.*, 2001, 2002). A third genus, *Sapria*, attracts flies in the same way, although in a species studied by Banziger (1996 a), the major pollinators were sarcophagids, not calliphorids.

(7) Other insects

Studies that record all insect visitors to flowers almost always report the presence of orders that are not usually considered to be pollinators (e.g. Wickramaratne & Vitarana, 1985; Khatua *et al.*, 1998; Nagamitsu *et al.*, 1999 a; Kato, 2000). The most frequently recorded of these orders is the Hemiptera, particularly the Heteroptera (true bugs), many species of which are common and conspicuous flower visitors. Heteropteran bugs in the family Miridae have been suggested as possible pollinators of *Shorea* section *Shorea* and leafhoppers (Cicadellidae) as possible pollinators of *Shorea* section *Brachypterae* (Appanah, 1985; Ashton *et al.*, 1988; Ashton, 1988). Tiny heteropteran bugs may also be involved in the pollination of some species of *Macaranga* (Moog *et al.*, 2002). Various members of the Orthoptera are also frequent flower visitors and, although these visits are probably usually destructive (e.g. Bogh, 1996), pollen must sometimes be transferred between flowers. Other orders mentioned occasionally in the Oriental literature include the Dermaptera, Neuroptera, Psocoptera and Trichoptera.

V. VERTEBRATES

(1) Birds

A wide range of plant species are visited by a wide range of bird species in the Oriental Region, but the numbers of both bird-dependent flowers and flower-dependent birds are much lower than in either the Neotropics or the Australian Region. Although representatives from at least 16 families of birds have been recorded taking nectar from flowers, the great majority of these records are from a small number of widely cultivated plant species that have large flowers with easily accessible nectar, particularly in the genera *Bombax* and *Erythrina* (e.g. Doctors van Leeuwen, 1931; Ali, 1932; Subramanya & Radhamani, 1993). The importance of bird families such as the Picidae, Megalaimidae, Cuculidae, Laniidae, Muscicapidae, Paridae, Pycnonotidae, Passeridae and Fringillidae in the pollination of wild plants is almost certainly very small. Nectar feeding seems to be more widespread in the families Corvidae (particularly *Corvus*, *Dicrurus* and *Oriolus*) and Sturnidae (many genera), and among the babblers (Sylviidae-Timaliini; many genera). Nectar seems to form a major part of the diet of some sturnids for part of the year (Ali, 1932; Ali & Ripley, 1987). The Jungle Babbler *Turdoides striatus* was the main pollinator among many avian visitors to *Helicteres isora*, a shrub with large, red tubular flowers, in degraded forest in the Western Ghats (Santharam, 1996). There may be flowers specifically adapted to pollination by these medium and large birds, but evidence is lacking.

The nectarivorous lories and lorikeets (Psittacidae-Loriinae) are widespread on the islands of Wallacea, on the eastern margins of the region, but only one species crosses Wallace's Line to Bali (Collar, 1997; Coates, Bishop & Gardner, 1997). Presumably their role in pollination is similar to that in New Guinea and Australia (Brown & Hopkins, 1996). Among the widespread tropical Asian

members of the family, the *Psittacula* parakeets are usually destructive flower feeders (e.g. Ali, 1932, Santharam, 1996) and, although they have been suggested to be significant pollinators in Indian dry forests (e.g. Murali & Sukumar, 1994), there is no direct evidence for this. The tiny, acrobatic hanging parrots in the genus *Loriculus* have narrow, prominent bills and feed non-destructively on non-tubular blossoms (Collar, 1997). They are inconspicuous birds and it is possible that their role as pollinators has been underestimated. *Loriculus philippensis*, at least, has a long, narrow, brush-tipped tongue like a lory (Collar, 1997). In the lowland dipterocarp forest at Lambir, Sarawak, the pollination of a species of *Palaquium* (Sapotaceae) with white, explosively dehiscent flowers, was attributed to *Loriculus galgulus* (Momose *et al.*, 1998*c*).

The variably nectarivorous honeyeaters, Meliphagidae, also enter the eastern margins of the Oriental Region, with 26 species in Wallacea and a single species, *Lichmera indistincta*, reaching Bali (Coates *et al.*, 1997). They may be as important pollinators there as they are in New Guinea and Australia (Brown & Hopkins, 1996), but there have been no regional studies.

The leafbirds, *Chloropsis*, in the family Irenidae, are regular visitors to flowering forest trees in the region (Ali & Ripley, 1996; Ghazoul, 1997; R. T. Corlett, personal observations) but their role in pollination has not been studied. At Lambir, *Chloropsis* is listed as a probable pollinator, with flowerpeckers, for a single species of *Macrosolen* (Loranthaceae), with explosive pollen release (Momose *et al.*, 1998*c*).

The white-eyes, *Zosterops*, and their relatives (Zosteropidae) are small, omnivorous birds that visit flowers throughout the Oriental Region. At least some species have brush-tipped tongues, like those of honeyeaters or lories, but their short bills preclude legitimate access to the nectar in long-tubed flowers, which they tend to rob. Discolouration of the forehead by pollen deposition has been widely reported in various species (e.g. Roberts, 1992; Steinheimer, 1999), and it has been suggested that a partial winter head moult in some individuals of a South African species, *Z. pallidus*, is intended to replace plumage matted by nectar and pollen (Craig & Hulley, 1996). Although Ali & Ripley (1999) consider them 'largely responsible for cross-pollinating a wide variety of flowers', white-eyes seem to be much less important in most of the region than the more nectarivorous, longer-billed sunbirds. However, at the northeastern extreme of the Oriental Region, *Zosterops japonicus* replaces the sunbirds as the dominant flower-visiting bird and may be more important in pollination (Yumoto, 1987; Chen & Chou, 1999; Corlett, 2001). On Yakushima Island, *Z. japonicus* appears to be the major pollinator of *Camellia japonica* (Theaceae) and *Taxillus yadoriki* (Loranthaceae) in the warm temperate forest (Yumoto, 1987) and *Bruguiera gymnorhiza* in the mangrove forest (Kondo *et al.*, 1991). The Zosteropidae may also be significant pollinators in montane forests in Southeast Asia, where they are sometimes very abundant. In the upper montane forest on Mount Kinabalu, Sabah, the mountain black-eye, *Chlorocharis emiliae*, regularly visits, and probably helps pollinate, the flowers of two *Rhododendron* species, although

apparently piercing the sides of the floral tube to steal nectar from a third species (Steinheimer, 1999).

The family Nectariniidae includes two distinct tribes that have usually been treated as separate families: the sunbirds (Nectariniini) and the flowerpeckers (Dicaeini) (Cheke, Mann & Allen, 2001). The sunbirds are unrivalled as flower specialists in the region, except where they overlap with the honeyeaters, lorikeets and lories in the transition to the Australian Region. Sunbirds have both morphological (Cheke *et al.*, 2001) and physiological adaptations (Lotz, 2000; Roxburgh & Pinshow, 2000) for exploiting nectar as an energy source. Most have more or less elongated bills and long, narrow, tubular tongues that can be protruded beyond the tip of the bill. Bill size and shape, and the details of tongue structure, vary considerably within and between the seven genera currently recognized in the region (Cheke *et al.*, 2001), but there is insufficient information at present to relate this variation to differences in flower-visiting behaviour, except for a crude correlation between bill and corolla lengths. Flowers are usually exploited from a perch but many sunbirds will also hover briefly, if this is necessary to access nectar. In common with other nectarivores, aggressive defence of feeding territories is common. Not only other birds but also large bees may be attacked (e.g. Doctors van Leeuwen, 1954; Roberts, 1992; Pandit & Choudhury, 2001; Raju, 2001). Individual sunbirds may forage and transfer pollen over a wide area (Sakai, 2000), with individual *Arachnothera longirostra* moving as much as 5 km in Malaysian rainforest (Wells, 1988). Some species also make large seasonal movements (Roberts, 1992; Ali & Ripley, 1999).

Sunbirds are recorded as visiting a wide range of flowers (e.g. Subramanya & Radhamani, 1993; Cheke *et al.*, 2001), but some of these are robbed by puncturing a hole at the base of the corolla (e.g. Ali, 1932; Roberts, 1992) and in many others a mismatch between flower and bird morphology probably precludes pollination (e.g. Santharam, 1996). Most cases where effective pollination has been confirmed, or is at least strongly suspected, involve the Loranthaceae (Doctors van Leeuwen, 1954; Davidar, 1985; Devkota & Acharya, 1996; Yumoto, Itino & Nagamasu, 1997; Momose *et al.*, 1998*c*; Cheke *et al.*, 2001), Zingiberaceae (Classen, 1987; Momose *et al.*, 1998*c*; Sakai, Kato & Inoue, 1999*a*; Sakai, 2000), *Musa* (Nur, 1976; Kato *et al.*, 1989; Itino, Kato & Hotta, 1991; Momose *et al.*, 1998*c*; Liu *et al.*, 2002), or large-flowered species in the mangrove tree genus *Bruguiera* (Kondo *et al.*, 1991; Noske, 1993). Sunbird pollination has also been suggested for some montane species of *Rhododendron* (Doctors van Leeuwen, 1933, 1954; Ali & Ripley, 1999), although *Aethopyga* in Hong Kong visited four large-flowered species without contacting the anthers or stigmas (Ng & Corlett, 2000), and possibly some epiphytic species of *Dendrobium* (Cingel, 2001). In the lowland dipterocarp forest at Lambir, Sarawak, sunbirds were also apparently the major pollinators of single species in the genera *Ardisia* (Myrsinaceae), *Pavetta*, *Praravinia* (Rubiaceae), *Madhuca* and *Palaquium* (Sapotaceae), and three species of *Durio* (Bombacaceae) (Momose *et al.*, 1998*c*).

Most flowers pollinated by sunbirds are bilabiate, tubular, or, in a few cases, brush-shaped. Long floral tubes

(>30 mm) are particularly common in species pollinated by members of the longest-billed genus, the spiderhunters, *Arachnothera* (e.g. Sakai *et al.*, 1999 *a*). Most flowers are brightly coloured: red is the commonest colour but others are white, orange or pink. Explosive release of pollen after the bird has contacted the flower occurs in some Loranthaceae and *Bruguiera*. Most of the flowers are scentless to humans and the only species for which floral scent chemistry has been investigated, *Bruguiera gymnorhiza*, had only trace amounts of scent chemicals, all of which could have been produced in response to mechanical damage (Azuma *et al.*, 2002). Pollen is usually deposited at the base of the bill or on the forehead, but Pauw (1998) describes the transport of asclepiad pollinia on the tongue inside the mouth of a South African sunbird, and predicts that the same may happen in some Southeast Asian *Dischidia*.

Sunbirds (as well as other Oriental flower-visiting birds) also visit, and sometimes pollinate, ornamental plants from Australia and the Neotropics, which are pollinated in their native habitats by honeyeaters and hummingbirds, respectively. This suggests a universality of the bird pollination syndrome that is perhaps surprising in view of the major differences between the bird groups involved. Honeyeaters are mostly larger than sunbirds, while hummingbirds are smaller and usually hover while visiting flowers. Although the bird and bat floral syndromes are generally distinct in the Oriental Region (e.g. Itino *et al.*, 1991), both spiderhunters and bats are effective pollinators of *Musa itinerans* in Xishuangbanna (Liu *et al.*, 2002) and, with flowerpeckers and *Apis dorsata*, *Durio kutejensis* at Lambir (Yumoto, 2000). *Sonneratia caseolaris* is apparently pollinated by sunbirds in India and bats in Malaysia (Pandit & Choudhury, 2001).

The flowerpeckers (*Dicaeum*, *Prionochilus*) have shorter bills than sunbirds and much variation between species in tongue structure (Cheke *et al.*, 2001). This variation probably reflects, at least in part, differences in the importance of nectar in the diet, but there have been insufficient observations to confirm this. Most records of flower visits and all cases in which they appear to be major pollinators involve the Loranthaceae (Doctors van Leeuwen, 1954; Subramanya & Radhamani, 1993; Cheke *et al.*, 2001). In the montane forest of the Nilgiris in southwest India, flowerpeckers visited only the unopened flowers of mistletoe species with explosive dehiscence (Davidar, 1983, 1985). These species had inconspicuous colours and the nectar was generally not replenished after depletion, thus encouraging a single visit. Mistletoe fruits made up the bulk of the flowerpecker diet, so both pollination and seed dispersal involved the same vector. Flowering and fruiting times overlap in the flowerpecker-pollinated species, and the flowers may to some extent mimic the fruits. By contrast, sunbirds at this site only visited the open flowers of brightly coloured, spontaneous-opening species with continuous nectar secretion. This contrast between flowerpecker- and sunbird-pollinated mistletoes is not universal – sunbirds elsewhere visit and pollinate many unopened flowers (Cheke *et al.*, 2001) – but the single flowerpecker-pollinated species at Lambir is an explosive *Macrosolen* (Momose *et al.*, 1998 *c*).

(2) Bats

The large literature on bat visits to flowers in tropical Asia masks a lack of detailed studies on their role in pollination. It is clear, however, that, as with the birds, bats are less important as pollinators in the Oriental Region than they are in either Australia or the Neotropics. This may reflect, in the first case, the greater openness of most Australian plant communities, and in the second, the greater ability of the Neotropical, echolocating, microchiropteran Phyllostomidae to manoeuvre in closed forests, in comparison with the megachiropteran Pteropodidae of the Old World, where no microchiropterans visit flowers. Although pteropodid bats are abundant in the canopy and subcanopy layers of Malaysian rainforest, they are virtually absent from the understorey (Francis, 1994).

Oriental members of the Pteropodidae span a huge size range (15–1500 g) and have diets consisting of fruits, nectar, pollen and leaves in proportions that differ between seasons, between sites and between species (e.g. Kitchener, Gunnell & Maharadatunkamsi, 1990). Most Oriental species that have been studied visit flowers to some extent, but the highly nectarivorous bats in the genera *Eonycteris*, *Macroglossus* and, in the eastern margins of the region, *Syconycteris*, have traditionally been placed in separate family Macroglossinae, along with other, similar, Old World genera. Recent molecular studies have shown, however, that the long narrow muzzles, delicate mandibles, reduced dentition and protrusible, brush-tipped tongues of these genera are the result of convergent adaptations to nectarivory that have arisen independently several times (Alvarez *et al.*, 1999).

On Lombok Island, the breadth of the pollen diet of the six common pteropodid species was highly positively correlated with the length of the tongue, suggesting a gradation in the extent of nectarivory, rather than a division into nectarivores and frugivores (Kitchener *et al.*, 1990). The number of pollen types recorded in gut contents of individual bats (assumed to represent feeding on the night of capture) averaged 2.5–3.3 in three *Cynopterus* species, 3.7 in a *Rousettus*, 4.5 in *Macroglossus minimus* and 5.2 (with a maximum of 10) in *Eonycteris spelaea*. Predominantly frugivorous bats often visit the same plants as the specialist nectarivores (Dobat & Peikert-Holle, 1985), but these visits tend to be more destructive, particularly when made by the larger species. However, even visits by large and clumsy *Pteropus* species can apparently be of net benefit to a plant (Cox *et al.*, 1991; Elmqvist *et al.*, 1992; Hall & Richards, 2000).

Flowers adapted for bat pollination tend to be large (or large aggregations of small flowers, as in *Parkia*) and robust, with pale or drab colouration, nocturnal anthesis, a strong nocturnal odour, and unobstructed access to flying animals (Faegri & van der Pijl, 1979). The bat-pollinated *Sonneratia alba* was the only species of eight mangrove plants tested in which the floral scent included a sulphur-containing compound, 2.4-dithiapentane (Azuma *et al.*, 2002), which has also been reported from some Neotropical bat-pollinated plants (Bestmann, Winkler & von Helversun, 1997). The reward is usually a copious supply of nectar and pollen, with the latter mainly gleaned from the bat's body after visiting the flower, but a minority of species offer a solid, sugar-rich

reward. In several species of Sapotaceae, including *Madhuca indica* (syn. *Bassia latifolia*) in the dry forests of India (Dobat & Peikert-Holle, 1985; Rajan *et al.*, 1999; Elangovan, Marimuthu & Kunz, 2000) and *Ganua beccarii* in the lowland rainforest of Sarawak (Momose *et al.*, 1998*c*), this is in the form of a detachable fleshy corolla, while in *Freycinetia* (Pandanaceae) the flowers themselves are tiny and the reward consists of edible bracts (Faegri & van der Pijl, 1979; Cox, 1990).

Oriental plant species that are known or suspected to be pollinated by bats are largely in the families Bignoniaceae (many genera, including *Markhamia*, *Nyctocalos*, *Oroxylum*, and *Stereospermum*), Bombacaceae (*Bombax, Durio*), Fabaceae (*Mucuna, Parkia*), Lecythidaceae (*Barringtonia, Careya*), Musaceae (*Musa*), Lythraceae (*Duabanga, Sonneratia*), Myrtaceae (*Syzygium*), Pandanaceae (*Freycinetia*), and Sapotaceae (*Ganua, Madhuca*) (McCann, 1938; van der Pijl, 1956; Nur, 1976; Gould, 1978; Dobat & Peikert-Holle, 1985; Marshall, 1985; Pakarnseree, 1986; Kato *et al.*, 1989; Itino *et al.*, 1991; Subramanya & Radhamani, 1993; Momose *et al.*, 1998*c*; Rajan *et al.*, 1999; Liu *et al.*, 2002; Devy & Davidar, 2003). The Old World species in the genus *Heliconia* (Heliconiaceae), which enters the eastern margins of the region, are probably also pollinated by bats (Kress, 1990). In other cases, bat behaviour and/or floral morphology make pollination unlikely. The small, nectar-rich flowers of *Mangifera indica* are eaten by bats ranging in size from the tiny, nectarivorous *Macroglossus minimus* to the huge, largely frugivorous, *Pteropus giganteus* (McCann, 1938; Marsall, 1985; Dobat & Peikert-Holle, 1985) but are probably pollinated mainly by calliphorid flies (Bhatia *et al.*, 1995). On the warm temperate Ryukyu Islands, the small, insect-pollinated, flowers of *Diospyros*, *Elaeagnus*, *Rhaphiolepis* and *Symplocos* make up a seasonally important part of the diet of *Pteropus dasymallus* (Funakoshi, Watanabe & Kunisaki, 1993).

Pteropodid bats are potentially high quality pollinators for suitably adapted flowers, able to carry large amounts of pollen for long distances between scattered plants and vegetation fragments (Law & Lean, 1999; Palmer, Price & Bach, 2000), but the Oriental species differ greatly in their foraging behaviour. In West Malaysia, *Eonycteris spelaea* roosts in large colonies in caves, can fly >38 km to feed, forages in flocks, and visits a wide variety of scattered, seasonal floral resources (Start & Marshall, 1976). The two *Macroglossus* species, by contrast, roost singly or in small groups near their gregarious, year-round food sources: *Sonneratia* species for the coastal *M. minimus* and *Musa* species for the inland *M. sobrinus*. Among the more frugivorous bats, both cave-roosting *Rousettus* and colonial *Pteropus* may fly tens of kilometres in a night (Marshall, 1983), while the tent-making *Cynopterus* species are more sedentary.

The morphological and behavioural fit between the flowers of *Oroxylon indicum* (Bignoniaceae) and its major Southeast Asian pollinator, *E. spelaea*, is so close as to suggest one to one co-evolution (Gould, 1978), yet this tree species is pollinated by unspecialized *Cynopterus* and *Rousettus* in India (Marshall, 1985). The generality of the bat-pollination syndrome is shown by the readiness with which pteropodids visit, and in some cases pollinate, Neotropical bat plants grown as ornamentals, and with which Neotropical phyllostomids visit Oriental bat plants (Marshall, 1985). The pantropical genus *Parkia* is pollinated in a very similar way by unrelated bats in the Old and New World (Hopkins, 1994).

(3) Other mammals

Flowers form part of the diet of most arboreal herbivores, but only selective feeding on floral parts is likely to result in pollination. The easily accessible nectar of *Bombax ceiba* attracts mammals from squirrels and macaques to civets and martens (Ali, 1932; Joshi, Smith & Cuthbert, 1995). Occasional pollination may result from such visits but there is no evidence that this is of any significance. Squirrels are regular visitors to many other flowers besides *Bombax*, and Balasubramanian (1995) considered that *Funambulus palmarum* could be a significant pollinator of *Rivea hypocrateriformis* (Convolvulaceae) and *Catunregam spinosa* (Rubiaceae) in southern India. Two rodents (*Plantacantho lasiurus* and *Rattus rattus*) visit flowers of an understorey treelet, *Helicia nilagirica*, in mid-elevation rainforest in the Western Ghats (Devy & Davidar, 2003). Tree shrews (*Tupaia* sp.; Tupaiidae) sometimes visit the flowers of both the bird-pollinated *Musa salaccensis* and the bat-pollinated *M. acuminata* in West Sumatra (Itino *et al.*, 1991), and separate exclusion of sunbirds and tree shrews from the former showed that both can be effective pollinators, although sunbirds are the commonest visitors (Nur, 1976).

At Lambir, Sarawak, three species of diurnal squirrel and one of nocturnal flying squirrel were the major consumers of the sweet, fleshy, detachable corollas of *Madhuca* sp. (Sapotaceae) (Yumoto, Momose & Nagamasu, 2000). Pollen was seen on the fingers and around the mouth of the squirrels, but they avoided the bitter-tasting pistil. In the Western Ghats of India, the cauliflorous *Cullenia exarillata* (Bombacaceae) produces pinkish-brown, tubular flowers with edible fleshy sepals and little nectar (Ganesh & Davidar, 1997; Ganesh & Devy, 2000). A wide range of arboreal mammals, including monkeys, squirrels, flying squirrels, civets and fruit bats, consume the flowers. All mammalian visitors were potential pollinators, but the rodents caused the most damage to the style and bats the least. Fruit set from nocturnal visitors was ten times as high as from diurnal visitors. Although pollen transfer between trees has not been confirmed in either of these species, they are the best-documented cases for pollination by non-flying mammals in the Oriental Region.

VI. DISCUSSION

(1) Pollination in the Oriental Region

The best analogy for the current state of pollination biology in the Oriental Region is one of islands of knowledge in a sea of ignorance. We have a reasonably complete picture for only a single lowland rainforest site, at Lambir, Sarawak (e.g. Kato, 1996; Momose *et al.*, 1998*c*; Sakai *et al.*, 1999*c*; Itioka *et al.*, 2001) and lack the data needed to extrapolate this even to other lowland rainforests in the region.

Table 1. *The relative importance of the major pollinator taxa* (*and wind*) *in various habitat types within the Oriental Region, on the basis of the evidence currently available. Importance*: −, *rare or absent*; +, *occasional*; ++, *widespread*; +++, *important*; ++++, *very important*; ?, *insufficient information*

	Tropical lowland rainforest	Montane (>1500 m) habitats	Tropical dry forests	Tropical non-forest habitats	Tropical coastal habitats	Subtropical/ warm temperate habitats
Wind	−	+	+	++	+	+
Thysanoptera	+	?	?	+	−	?
Coleoptera	+++	+	+	−	−	+
Vespidae	+	+	+	+	−	+
Colletidae	−	−	−	−	−	+
Andrenidae	−	−	−	−	−	+
Halictidae	++	−	+	+	−	+
Megachilidae	+	−	+	+	+	+
Xylocopinae	+	−	++	++	+	+
Anthophorinae	++	−	+	+	−	++
Bombini	−	++	−	−	−	++
Meliponini	++++	−	++	+	+	−
Apini	+++	++	+++	++	+	++
Moths	+	+	+	+	+	+
Butterflies	+	?	+	++	+	+
Diptera	+	+	+	+	+	++
Birds	++	+	++	+	+	+
Bats	+	−	+	−	+	−

Elsewhere, most research subjects appear to have been chosen on the basis of novelty, conspicuousness or convenience. A potential economic interest has also motivated many studies, particularly of bees. Any conclusions, therefore, must be tentative. Table 1 summarises the apparent relative importance of different pollinator taxa in major habitat types within the region. Tropical lowland rainforest is the best-studied habitat, but the summary relies heavily on a single site – Lambir, Sarawak – and some aspects, such as the importance of beetles as canopy pollinators, may not be generally true in other rainforests in the region. The drier forests have received little systematic attention in the Oriental Region, in contrast to the situation in the Neotropics and Australia, and the information for these and other Oriental habitats is clearly biased in favour of the more conspicuous interactions.

Pollination in lowland forests of the Oriental Region appears to be strongly dominated by social bees in the genera *Trigona* and *Apis*. Beetles are probably the second most important group, at least in rainforests, followed by other bees and flies. The relative importance of bird pollination has certainly been exaggerated by its conspicuousness, and the same may be true for *Bombus* and *Xylocopa*. Pollination by thrips, moths and small solitary bees, by contrast, may have been underreported. Fly pollination of specialised trap flowers has been widely studied but the pollination role of the numerous fly visitors to more typical flowers is virtually unknown.

(2) Comparisons with other tropical regions

In the Sundaland region of Southeast Asia, the unusual single-family dominance of dipterocarps in the forest canopy has combined with the exceptionally aseasonal climate to produce a uniquely Oriental phenomenon: the 'general flowering' of most dipterocarps species, together with numerous other plant species, at supra-annual intervals of 2–10 years. In the lowland dipterocarp forest at Lambir, Sarawak, 61% of the 257 species observed over 53 months flowered during a general flowering episode and 35% flowered only during this episode (Sakai *et al.*, 1999*c*). Among the various hypotheses put forward to explain this phenomenon, two are related to pollination. One hypothesis is that mass flowering is a simple consequence of the paucity of climatic cues for the intraspecific synchronization of flowering in aseasonal forests (Sakai *et al.*, 1999*c*). If many species are forced to depend on the same supra-annual cue to ensure intraspecific synchronization of flowering, then the observed interspecific synchronization would be an inevitable result. Another hypothesis is that pollination is enhanced during general flowering episodes because pollinator populations increase. The populations of many pollinators certainly do increase, but it is not clear if they increase enough to offset the greatly increased competition for their services. The major alternative hypothesis – that the key advantage of general flowering is the subsequent satiation of seed predators – has been strongly supported for dipterocarps (Curran & Leighton, 2000), but is much less convincing for non-dipterocarp species with very different dispersal biologies. The precise nature of the cue is still debated, but most evidence points to a low nighttime temperature event around two months before flowering (Yasuda *et al.*, 1999).

A corollary of the general flowering phenomenon is that, outside the general flowering episodes, there are far fewer floral resources available than reported for other tropical

forests (Sakai *et al.*, 1999*c*). The only major exceptions to this pattern reported from Lambir are *Ficus* species, where the unique species-specific pollination system precludes large gaps in flower availability, and the non-dipterocarp beetle-pollinated plants, which also have relatively specialised associations with pollinators. The mechanisms which ensure the availability of an adequate number of pollinators during general flowering episodes vary between taxa. The major alternatives appear to be: explosive build up of populations during general flowering episodes, as reported for the thrips pollinators of dipterocarps at Pasoh, Malaysia (Appanah, 1993); switching from non-floral resources, such as young leaves, as reported for at least some of the chrysomelid beetles that pollinate dipterocarps at Lambir (Sakai, 2001*a*, *b*); storage of floral resources in a well-protected nest, as done by most social bees (Sakai, 2001*b*); or long-distance migration, as reported for *Apis dorsata* (Itioka *et al.*, 2001).

In view of the very different patterns of floral resource availability, it is not surprising that community-level patterns of pollination biology differ considerably between the aseasonal lowland rainforests of Southeast Asia and their more seasonal counterparts elsewhere. There is insufficient information from African rainforests, but in comparison with the relatively well-studied Neotropics, the differences are generally in the expected directions. Southeast Asian rainforests appear to have fewer species pollinated by nectarivorous vertebrates, Lepidoptera and large solitary bees – the animals expected to be most vulnerable to long-term fluctuations in resource availability, because they do not store food or switch diets – and more pollinated by highly social bees, herbivorous beetles (at least at Lambir), and (at least at Pasoh) fast-breeding thrips (Bawa *et al.*, 1985; Kress & Beach, 1994; Momose *et al.*, 1998*c*; Sakai, 2001*b*). The differences appear to be smaller in the rainforest understorey, where resource availability may be relatively more similar in the two regions (Kato, 1996; Rincon *et al.*, 1999; Sakai *et al.*, 1999*c*).

The pollination systems of trees in mid-elevation (1250 m) rainforest at Kakachi, in the Western Ghats, differ somewhat from those at Lambir, with Lepidoptera, flies and thrips more important and both bees and beetles less so (Devy & Davidar, 2003). Supra-annual flowering cycles are widespread among tree species at this site, but these are not synchronised at the community level. Most parts of the Oriental Region have strongly seasonal climates and, presumably, similar patterns of resource availability to tropical ecosystems outside the region. Unfortunately, these areas have been understudied in the Oriental Region, making community-level comparisons almost impossible. The most obvious differences between the pollination systems of seasonal habitats in the Oriental and Neotropical regions involve the presence or absence of key groups of pollinators. The ecologically distinctive bee tribes Euglossini and Centridini, hummingbirds (Trochilidae), and nectarivorous microchiropteran bats (Glossophaginae) are a conspicuous feature of Neotropical pollination systems with no complete equivalents in the Old World, while the genus *Apis* was, until recently, absent from the Neotropics. A less important, but striking difference is the presence of *Bombus* at most sites in the lowland Neotropics, while it is confined to montane and subtropical areas in the Oriental Region.

Comparisons with the African and Australasian regions are limited by lack of data. Tropical Africa shares most major groups of pollinators with the Oriental Region, including *Apis* and the sunbirds, and there is no published information that suggests major differences in community patterns of pollination. Australia and New Guinea lacked *Apis* until recently, and pollination by vertebrates – particularly the near-endemic honeyeaters (Meliphagidae) – is clearly much more important than in most of the Oriental Region (e.g. Brown & Hopkins, 1996; Hansman, 2001).

(3) Vulnerability to human impacts

In theory, specialised relationships, in which a plant species depends for pollination on one or a few animal species, are likely to be more vulnerable to human impacts than more generalised ones (Bond, 1994). It has often been suggested that tropical plant-pollinator relationships are more specialised than those outside the tropics, but there is currently no evidence for this hypothesis and some which refutes it (Ollerton & Cranmer, 2002). Most studies reported in the Oriental literature, unfortunately, have been far too brief and too localized spatially to assess the true diversity of flower visitors to a single plant species.

The well-studied relationship between figs and their fig-wasp pollinators is the only known example of a strict one-to-one relationship in the region. The temporary local extinction of the pollinators of all 25 dioecious fig species in the Lambir Hills National Park, Sarawak, during the 1998 ENSO event, suggests that this extreme specificity may make figs particularly vulnerable to human impacts that reduce fig densities or increase the gaps between suitable habitat patches (Harrison, 2000). Set against this, however, is the success of many dioecious fig species in highly degraded habitats (R. T. Corlett, personal observations) and the evidence that the pollinators of at least some monoecious fig species routinely disperse over very large distances (Nason *et al.*, 1998).

In the mid-elevation rainforest at Kakachi, in the Western Ghats, the diversity within each pollination guild is lower than at lowland sites, and a quarter of the 86 tree species studied had only 1–2 species of pollinator (Devy & Davidar, 2003). In part, this reflects the very low diversity of social insects at this site – only two species. Elsewhere in the region, there are only a few non-fig species, for which only a single pollinator – in most cases a fly – has been recorded so far. There are also species of bees, moths and birds with nectar-feeding apparatus of extreme length, which implies the existence of floral rewards that are not accessible to other animals. In other cases, such as the night-flowering dipterocarps pollinated by *Apis dorsata*, flowering time may limit pollinator access. Relationships based entirely on deceit are also likely to be relatively specialised. At the other extreme, a huge range of visitors has been recorded for many plant species (e.g. Khatua *et al.*, 1998), although it is rarely known how many of these are effective pollinators. The great majority of the Oriental plant species studied fall between these extremes.

Although the potential for tight coevolution between plants and their pollinators is probably greater than between plants and seed dispersal agents (Wheelwright & Orians, 1982; Herrera, 2002), a comparison between this review and an earlier one of seed dispersal in the same region (Corlett, 1998) provides no evidence that this potential is generally realized in practice. Most plants are dispersed by fruit-eating vertebrates, which must be generalist feeders because of their long life spans, but specialisation is also precluded in long-lived colonies of social bees, the major pollinators. The most specialised dispersal mutualisms are those involving large-seeded, large fruits, which depend on very few large vertebrate species.

In general, both pollinators and seed dispersers are likely to be as vulnerable as other, similar elements of the fauna to the massive human impacts now occurring throughout the region. However, in comparison with seed dispersal agents, the usually much smaller size of pollinators will tend to make them less vulnerable to fragmentation effects (Corlett, 2000) and only *Apis* species are subject to widespread direct exploitation (e.g. Underwood, 1992), although stingless bees may be vulnerable to selective logging of their nest trees (Eltz *et al.*, 2003). The large vertebrates that disperse the largest fruits are highly vulnerable to both hunting and fragmentation, and, in some cases, such mutualisms have apparently already failed (Corlett, 1998). By contrast, the largest major pollinators in the Oriental Region are sunbirds and small fruit bats, neither of which are hunted and both of which do well in degraded landscapes. Thus there are probably fewer vulnerable pollination mutualisms than dispersal mutualisms in the Oriental Region.

Anthropogenic open habitats in the tropics appear to share few animal species with closed forests (Corlett, 2000) and there are drastic reductions in the abundance and diversity of whole groups of potential pollinators, including the stingless bees. This is the situation where failures of pollination mutualisms are most likely, but also where they are most difficult to detect, because of the many other changes which occur with deforestation. In the highly degraded landscape of Hong Kong, South China, the abundance and ubiquity of *Apis cerana* may be partly compensating for the loss of other pollinators, as has also been suggested for *A. mellifera* in tropical America (Dick, 2001).

There are no records of exotic pollinators established in the Oriental Region, except for *Apis mellifera* on the oceanic Bonin (Ogasawara) Islands, where the feral *Apis* colonies are supported largely by exotic plant species (Kato *et al.*, 1999). Invasive plant species are common throughout the region and Ghazoul (2002) suggests that their impacts on the foraging behaviour of native pollinators may be an unrecognised threat to pollination mutualisms. In disturbed dry deciduous dipterocarp forest in Thailand, the invasive American shrub, *Chromolaena odorata* (Asteraceae), was visited preferentially by the butterfly pollinators of *Dipterocarpus obtusifolius*. Fruit set was not reduced in this case, but the potential for alien invaders with prolonged production of nectar- or pollen-rich flowers to disrupt pollination is clear. The availability of extra resources from *Chromolaena* did not increase the abundance of butterfly pollinators, but, in lowland rainforest in Sabah, the nest density of stingless bees

was greatly enhanced where they had access to pollen from crops of maize, manioc and watermelon (Eltz *et al.*, 2002).

Climate change is the most pervasive and least avoidable of human impacts. Bazzaz (1998) argues that tropical forest ecosystems may be particularly sensitive to climate change, in part because of the 'high degree of specialisation' of pollination relationships and the 'fine tuned' relationship between flowering phenology and climatic patterns. This review has not directly addressed the question of climatic change, for lack of data, but it provides no support for the suggestion that tropical pollination mutualisms are particularly vulnerable. Specialisation is rare and fine-tuning to current climatic patterns is not compatible with the known history of climate change over the last few million years (Corlett & LaFrankie, 1998). However, tolerance of past climate change may not predict the impacts of future changes outside the past range of variation. In particular, changes to the frequency and/or severity of ENSO events could have a drastic impact on community-level patterns of flowering phenology, particularly the general flowering phenomenon (Yasuda *et al.*, 1999), although the impact on individual plant species is much more difficult to predict.

The key question is not whether human impacts will affect pollination – obviously they will – but whether failures of pollination mutualisms are likely to accelerate plant (and, possibly, animal) species losses in the Oriental Region. This review does not provide any evidence for this, with the possible exception of the dioecious fig species discussed above. This lack of evidence needs to be treated cautiously, however, since most pollinator relationships in the region are completely unstudied. More subtle impacts, resulting in altered gene flows and thus potential long-term changes in the fitness of plant populations, are likely to be more widespread (e.g. Konuma *et al.*, 2000; Ghazoul & McLeish, 2001), but their general importance is impossible to evaluate from the evidence currently available. Given the current pace of habitat – particularly forest – loss and degradation in the region, such subtle impacts may not be a major immediate area of concern. Overall, pollination systems in the Oriental Region do not seem to require any special conservation action. Rather, they provide yet another reason for making the preservation or restoration of habitat continuity the major focus of tropical conservation.

(4) Research needs

It is very difficult to derive useful generalisations from observations of single plant or animal species over single flowering seasons at single sites. Even the long-term, community-level study at Lambir is hard to interpret in the absence of data from replicate sites. What, for instance, is to be made of the apparent contrast between the beetle-dominated pollination of *Shorea* section *Mutica* at Lambir and the thrips-dominated system at Pasoh, involving some of the same plant species? The major research need, therefore, is the replication of the Lambir study at one or more other lowland rainforest sites, and in other ecosystem types throughout the region. For forests, the obvious sites are the network of large (typically 50 ha) forest dynamics plots established by the Centre for Tropical Forest Science (CTFS)

of the Smithsonian Tropical Research Institute throughout the region. These plots could also form the basis for a pan-tropical comparison if standardized methods were used. Similar studies are also required in the natural non-forest habitats in the west and north of the region, and in a representative sample of human-impacted and human-dominated areas. Single-species studies are justified where the plant (or its pollinator) are threatened with extinction. In these cases, the major recommendation is that the study is continued over several years. For a long-lived plant, even the total failure of pollination in a single year is of little significance.

In general, there is a need for greater rigour in pollination studies. A large majority of the results reviewed here are based on direct visual observations of flower visitors and their behaviour on the flowers. Contact with both anthers and stigmas is taken as evidence that the visitor is a pollinator. Experimental manipulations – such as the exclusion of putative pollinators – are rare. In addition, few pollination studies in the region include an estimate of how far pollen is being moved. This is rarely possible to do by observation of pollinator movements, but a variety of molecular techniques are now available for the direct or indirect estimation of gene flow through pollen (e.g. Konuma *et al.*, 2000; Dutech *et al.*, 2002; He & Smouse, 2002). Such studies will be particularly important in understanding the impact of habitat fragmentation on fitness.

VII. CONCLUSIONS

(1) Current knowledge of flower visitors and pollination in the Oriental Region is unevenly spread across habitats and taxa. In general, much less is known about pollination systems than about seed dispersal.

(2) On current evidence, highly social bees (mostly *Trigona* and *Apis*) are the most important pollinators in lowland forests, followed probably by beetles, and then by other bees and flies. Pollination by thrips, moths and small solitary bees may have been under-recorded.

(3) In comparison with the better-studied Neotropical Region, Southeast Asian rainforests appear to have fewer species pollinated by nectarivorous vertebrates, Lepidoptera and large bees, and more pollinated by highly social bees, herbivorous beetles and, possibly, thrips. These differences probably reflect the extreme fluctuations in floral resources in lowland dipterocarp forests that result from the general flowering of many plant species at intervals of 2–10 years. There is insufficient data available for similar community-level comparisons of more seasonal vegetation types, but there are striking differences in many of the key groups of pollinators involved. Africa shares most major groups of pollinators with the Oriental Region but there is little comparable data. Vertebrates, particularly birds, appear to be much more important as pollinators in New Guinea and tropical Australia.

(4) This review provides little evidence that failures of pollination mutualisms as a result of human impacts are likely to accelerate plant species losses in the Oriental Region. Specialisation is rare in the relationships studied so far and pollinators in general appear less vulnerable than do many dispersal agents. Altered gene flows must be common, however, and may results in long-term changes in plant fitness. Overall, pollination systems do not seem to require any special conservation action, but rather provide an additional reason for focusing on habitat continuity.

(5) The primary research need is for studies that look at whole plant communities in the full range of Oriental habitats. These need to be supplemented by the use of molecular techniques to measure gene flow through pollen, and its vulnerability to fragmentation and other impacts.

VIII. ACKNOWLEDGEMENTS

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