Southeast Asian Ant-Gardens

- Diversity, ecology, ecosystematic significance, and evolution of mutualistic ant-epiphyte associations -

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Perhaps the most complex mutualism between plants and ants is the ant garden…

(B. Hölldobler and E.O. Wilson, *The Ants*, 1990)

Contents

1. Introduction

Tropical rain forest canopies are among the most complex and at the same time the least studied of all terrestrial habitats. This is mainly because access to this stratum is particularly difficult. Technical progress over the last 40 years has helped to solve this problem to some extent, and many studies have been published since. However, these revealed that a large part of total arthropod biodiversity still remains to be discovered in tropical forest canopies (Erwin, 1983; Stork, 1988).

Two groups of organisms are particularly important for canopy ecosystems (e.g. Benzing, 1990; Stuntz, 2001): Ants and epiphytes. In contrast to forests in temperate zones, epiphytes form a significant part of plant diversity in tropical rain forests (up to 30-50 % of the total vascular flora (Benzing, 1990)). They contribute to the complex structure of rain forest canopies and provide important resources for many canopy arthropods (Stuntz, 2001). On the other hand, ants make an important contribution in sheer numbers and biomass, though not in species richness (Adis et. al., 1984; Stork, 1988). Ants as eusocial insects form long-living colonies and have a major impact on many other organisms. It is not surprising, therefore, that ants and epiphytes interact in many ways. Such ant-epiphyte associations are the topic of the present thesis. Before various special types of ant-epiphyte associations are presented, an account will be given of common traits of epiphytes and some of the major problems arising from an epiphytic life style. The second section will do the same for arboricolous ants. Both chapters focus on topics relevant to ant-epiphyte interactions.

1.1. Epiphytes

About 10 % of all vascular plant species are epiphytes (Kress, 1986), most of them occurring in tropical rain forests. Growing on a host tree, these plants use the space available in the third dimension. This life style involves a number of special problems touching on more or less all aspects of plant life: First of all, the propagule has somehow to come across a suitable growing site. Depending on species-specific requirements, ‘suitability’ might be confined by habitat, tree species or bark characteristics, vertical position in a host tree, and growth substrate (e.g. Went, 1940; Johansson, 1974; Steege and Cornelissen, 1989; Benzing, 1995; Callaway et al., 2002). According to Benzing (1990), the growing conditions of canopy flora often resemble those on the ground with regard to rooting substrate. In view of the inhomogeneity of tree crown structure and especially the fragmentation and scarcity of suitable substrate for epiphytes, the way in which epiphyte seeds or spores reach a new appropriate growing site becomes a crucial question. Several problems have to be solved in connection with the growth substrate. Water supply is difficult and temporary drought is likely to be lethal, especially for seedlings (Benzing, 1991). All sorts of physiological (e.g. Winter et al., 1983; Sinclair, 1983a,b, 1984; Goh and Kluge, 1989; Griffiths, 1989; Benzing, 1995), morphological (Johansson, 1974; Benzing, 1990, 1995) and ecological (Benzing, 1990) tricks to cope with temporary aridity have been ‘invented’ by epiphytes. Supply with mineral nutrients is similarly difficult, a problem often solved by extremely slow growth (Benzing, 1991). Even pollination seems to require special strategies since epiphytes are usually hyperdispersed (Madison, 1977; Ackerman, 1986).

Associations with arboricolous ants are one possible strategy to overcome some of these problems: Ants can provide reliable seed dispersal to suitable growing sites, accumulate substrate throughout the life of an epiphyte and thus fertilize the plants. These substrate accumulations can also serve as short-term water-reservoirs, thus reducing water stress (Davidson and Epstein, 1989).

1.2. Arboricolous ants

Tropical arboricolous ants have been subject of many studies especially in the past 40 years. Fogging techniques revealed a high abundance and diversity of canopy ants (Erwin, 1983; Adis et al., 1984; Wilson, 1987; Stork, 1988; Tobin, 1991; Floren, 2000). According to Wilson (1959) and Tobin (1995), there is little overlap between ground nesting and arboricolous ant species, i.e. arboricolous ants are usually restricted to this habitat for nesting and often also for foraging. There are, however, some typical ground nesting genera also occurring in humus accumulations in the canopy (Longino and Nadkarni, 1990). Special adaptive characteristics of dominant ant species for canopy life were summarized by Tobin (1995) and Orivel and Dejean (1999a). These comprise morphological features protecting ants from desiccation (Hölldobler and Wilson, 1990; Tobin, 1995), special cognitive abilities for three-dimensional orientation (Hölldobler, 1980), and the use of a wider range of food sources in general and especially the use of plant sap as major food source (Tobin, 1994, 1995). The latter fact has consequences for the nitrogen economy of these ants[1] because nitrogen is a highly limited resource in the canopy (Orivel and Dejean, 1999a). Though dominant species account for the major part of biomass and abundance in canopy habitats, many subdominant species, not sharing all the features proposed as special adaptations for arboricolous life style, account for the major part of ant diversity in this habitat (Orivel and Dejean, 1999a).

The abundance of ants in tree crowns is surprising because ants, with their movable brood, were originally typical ground arthropods, specialized in building their nests in soil or using natural cavities in dead wood (Wilson, 1959; Sudd, 1967). Unlike bees with their comb-restricted brood, ants cannot produce waxy substances to build their own nests, and unlike wasps they usually do not have sticky gland products that enable them to construct nests from glued plant fibers. Therefore, at first glance, tree crowns seem not to be an ideal habitat for ants because sturdy and permanent nesting space – vital for social insects - is rather scarce. Dead twigs, hollow branches and stems as well as epiphytes provide the only natural – often short-lasting - cavities, suitable especially for

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[1] Modifications discussed in this context are: morphological modifications reducing the need for nitrogen; modification of the digestive system in order to process large amounts of liquid food; venom lacking nitrogen; maybe microbial endosymbionts and reduction of metapleural glands (Hölldobler and Wilson, 1990; Davidson and Patrell-Kim, 1996; Davidson, 1997; Orivel and Dejean, 1999a).

small ant species (Wilson, 1959). Thus, the development of strategies allowing ants to construct nest sites independently of available cavities was one of the most important evolutionary steps towards the permanent conquest of canopies (Orivel and Dejean, 1999a).

Southeast Asian ants have invented several different solutions for this problem (Doflein, 1905; Maschwitz and Hänel, 1985; Dumpert et al., 1995; Kaufmann et al., 2001; Weissflog, 2001; Ihl, 1984):

a) Bivouacking (e.g. *Dolichoderus* herdsmen ants). Here, the ants arrange their own bodies around queen and brood and make up a nest ball. Thus, no building material is necessary for nest construction.
b) Silk nests (e.g. *Polyrhachis*, *Oecophylla*, *Camponotus* (*Karavaievia*)). The ants use larval silk, often in combination with debris, for nest construction. Some *Dolichoderus* species cannot produce their own silk, but collect silk from spider webs and nests of other ants.
c) Pure carton nests (e.g. *Myrmicaria arachnoides*, *Crematogaster* cf. *artifex*). In the case of the latter species, the use of a sticky secretion stabilizing the nest construction could be proven for the first time in ants (Weissflog, 2001), whereas *Myrmicaria arachnoides* makes exclusive use of plant fibers for carton production.
d) Carton nests stabilized with fungi (e.g. *Monomorium*, *Technomyrmex* and *Dolichoderus*). The long and flexible hyphae provide both stable scaffolding and potentially good anchoring on the substrate.
e) Carton nests stabilized with epiphyte roots (ant-gardens). This nest category is described in detail in this thesis.

1.3. Ant-epiphyte interactions

Ant-gardens (AGs) have been defined by Corbara et al. (1999) as "*systems of epiphytes and ants, in which the ants build carton nests containing organic material. They incorporate seeds of epiphytes that then grow on the nest.*" Ernst Ule (1901) described this type of nest for the first time for *Camponotus femoratus* and *Azteca* spp. in Peru. Since then, many researchers have studied neotropical AGs (e.g. Ule, 1905a, b, 1906; Kleinfeldt, 1978, 1986; Madison, 1979; Belin-Depoux et al., 1987; Belin-Depoux and Sarthou, 1988; Davidson, 1988; Belin-Depoux, 1991; Corbara and Dejean, 1996; Orivel et al, 1998; Cedeño et al. 1999; Corbara et al., 1999; Marini-Filho, 1999; Dejean et al., 2000), but almost nothing has been published on similar phenomena in the palaeotropical region. In 1913, Leeuwen and Leeuwen-Reijnvaan described ant-epiphyte interactions in Java and stated that these might be similar to Ule's AGs (also s. Leeuwen 1929a, b, c). These papers have widely been ignored since then, and only a few more recent reports exist (Kiew and Anthonysamy, 1987, 1995; Kleijn and Donkelaar, 2001). Some scientists have explicitly denied the existence of AGs in Southeast Asia (e.g. Kleinfeldt, 1986; Orivel and Dejean, 1999b). Thus a combination of the literature data reveals a highly peculiar phenomenon: Whereas AGs are locally abundant and widespread in the neotropics, so-called ant-house epiphytes are common in Southeast Asia, where they seem to replace this type of epiphytic plant-ant interaction. Ant-house epiphytes (comprising c. 100 plant species from eight genera, three families in Australasia) provide leaf- or stem-domatia of different types as nesting space for their partner ants (e.g. *Dischidia major* Merr. (pitcher leaves)*; Dischidia imbricata* Steud. (shell leaves); *Hoya mitrata* Kerr (multileaved domatia); *Myrmecodia* spp., *Hydnophytum* spp. (hypocotyl domatia); *Lecanopteris* spp. (rhizome domatia))[2]. While the ants gain a dry and sturdy nest site, the main benefit for the plants is supposed to be nutritional (Janzen, 1974; Huxley, 1978, 1982; Longino, 1986; Davidson and Epstein, 1989; Benzing, 1991).

One aim of this study was to find at least a partial solution to this ‘ant-epiphyte puzzle’. Researchers in Southeast Asia have so far mainly concentrated on ant-house epiphytes and neglected the rest of the epiphyte flora. Interactions between ants and epiphytes are generally manifold (Davidson and Epstein, 1989), and there is no obvious reason why there should be no other relations between ants and epiphytes apart from ‘ant-house’ associations in palaeotropical regions.

1.4. Topics of the present study

Due to the lack of knowledge on the variety of SE-Asian ant epiphyte associations I focused on a wide range of thematic complexes in my approach:

1. The first step was to monitor the diversity of ant-epiphyte associations in Southeast Asia. Other organisms contributing to the symbiosis (‘partners’), such as carrier plants (= phorophytes), trophobionts and fungi, were also investigated.

2. Since many ant and epiphyte species turned out to participate in such interactions, these had to be characterized in further detail. ‘True’ mutualists were distinguished from ‘opportunists’, mutualistic interactions were studied. Moreover, I investigated whether there were any species-specific preferences between ant and epiphyte species, and which factors accounted for the detected patterns.

3. In order to assess the relative importance of ants for the establishment of epiphytes in the canopy, the proportion of epiphytes participating in ant-epiphyte associations relative to the total number of epiphytes in lowland rain forests of Peninsular Malaysia was investigated.

4. The basic interaction in all regular ant-epiphyte associations was the retrieval of epiphyte seeds by carton-constructing arboreal ants. Mechanisms and key-cues for this behavior were studied.

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[2] also see Color-Plate 4-4, p. 59, and Color-Plate 4-5, p. 69

2. Research Areas

Research was carried out at various places in tropical Southeast Asia (Figure 2-1), comprising pristine dipterocarp lowland, hill and montane forest, secondary rain forest in different degrees of disturbance and at different altitudes, heath forest and plantations (Table 2-1). The climate of all areas is principally influenced by monsoons in combination with typical equatorial phenomena. Regional details depend on many additional factors, e.g. distance from the coast or relative situation of mountains.

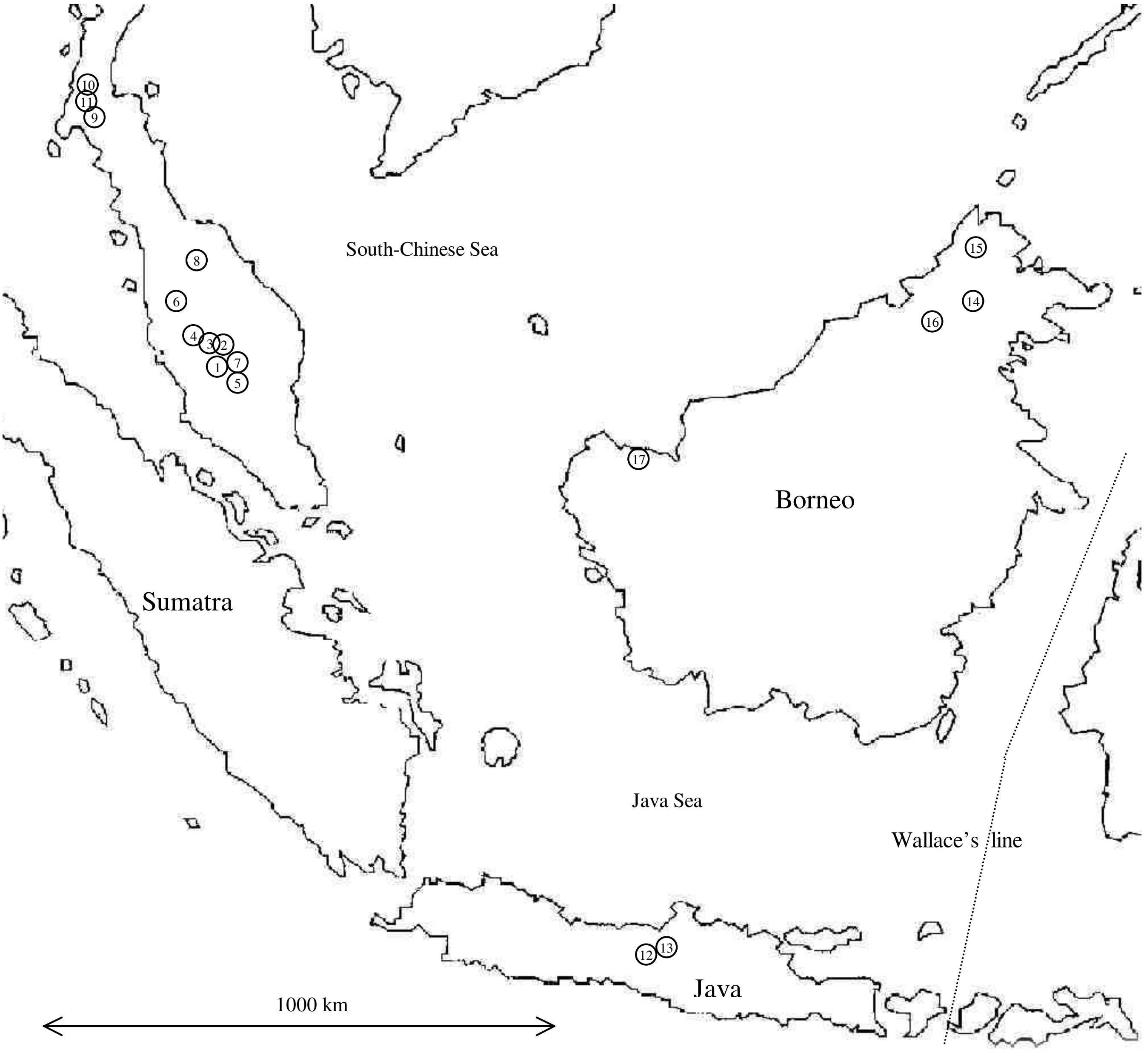

Figure 2-1: Study areas
1 Ulu Gombak; 2 Genting Tea Estate; 3 Bunga Buah; 4 Fraser's Hill; 5 Ulu Langat; 6 Cameron Highlands; 7 Karak Nature Reserve; 8 Temenggor Forest Reserve; 9 Klong Thom National Park; 10 Kao Sok National Park; 11 Klong Phanom Bencha National Park; 12 Gunung Nglimut; 13 Ambarawa/Salatiga; 14 Pedawan Valley; 15 Poring Hot Springs; 16 Long Pa Sia; 17 Bako National Park

Table 2-1: List of research areas
The numbers given in the first column refer to the pins in Figure 2-1.

Nr.	Study area	Location	Altitude	Description
Peninsular Malaysia				
1	Ulu Gombak Field Studies Center	3°19'N 101°45'E	250 m a.s.l.	secondary, heterogeneous lowland - hill forest
2	Genting Tea Estate	3°22'N 101°48'E	650 m a.s.l.	secondary hill forest
3	Bunga Buah	3°22'N 101°44'E	1400 m a.s.l.	primary montane forest
4	Fraser's Hill	3°41'N 101°45'E	800 m a.s.l.	secondary submontane forest
5	Ulu Langkat	3°07'N 101°47'E	300 m a.s.l.	primary lowland forest
6	Cameron Highlands	4°29'N 101°23'E	1500 m a.s.l.	secondary montane forest
7	Karak Nature Reserve	3°27'N 101°59'E	500 m a.s.l.	secondary hill forest
8	Temenggor Forest Reserve	5°35'N 101°41'E	550 m a.s.l.	primary hill forest
Southern Peninsular Thailand				
9	Klong Thom National Park	7°56'N 99°10'E	150 m a.s.l.	primary lowland forest
10	Kao Sok National Park	8°56'N 98°31'E	450 m a.s.l.	primary hill forest
11	Klong Phanom Bencha National Park	8°14'N 98°54'E	150 m a.s.l.	patch 1: heath forest patch 2: transition zone between heath forest and primary lowland forest
Central Java, Indonesia				
12	Gunung Nglimut	7°14'S 110°14'E	500 m a.s.l.	coffee plantation in secondary hill forest
13	Ambarawa/Salatiga	7°12'S 110°27'E	300 m a.s.l.	clove and durian plantations
NE-Borneo, Sabah, Malaysia				
14	Pedawan Valley	5°41'N 116°26'E	500 m a.s.l.	patch 1: heath forest with relatively closed canopy patch 2: heath forest with relatively open canopy
15	Poring Hot Springs	6°04'N 116°41'E	500 m a.s.l.	secondary hill forest
16	Long Pa Sia	4°26'N 115°42'E	1200 m a.s.l.	submontane heath forest
NW-Borneo, Sarawak, Malaysia				
17	Bako National Park	1°41'N 110°27'E	100 m a.s.l.	heath forest with extremely open canopy

Generally, ever-wet tropical climate is characterized by a) a maximum difference in mean temperature of 5°C between the coolest and warmest month, and b) monthly rainfall of >100 mm throughout the year with only short dry periods lasting a few days or weeks (Whitmore, 1993). The natural vegetation of such areas is evergreen tropical rain forest, large parts of which have been destroyed by human activities, mainly during the second half of the last century.

This study covered a relatively large geographical range, comprising Southern Thailand, Peninsular Malaysia, Borneo and Java, and extending from 8°56’N to 7°14’S and from 98°31’E to 116°41’E. All study-sites were located on parts of the Sunda Shelf, west of Wallace’s line.

Collections were restricted to a few sites in each area, and the amount of data collected at different sites varied greatly, from simple descriptions of ant-epiphyte associations to extensive collections and experimental investigations. Apart from the list comprising names and characteristics of all study sites (s. Table 2-1), only two areas are described in more detail here: 1) Forests around Ulu Gombak (Peninsular Malaysia) were extraordinary rich in ant-epiphyte associations, and a large part of the experiments was performed there. 2) In two heath forest areas in the Pedawan Valley near Pekan Nabawan (Sabah), ‘ant-house’ associations were closely investigated.

2.1. Ulu Gombak, Central Peninsular Malaysia

Peninsular Malaysia (Malaya) is the western part of the Federal Republic of Malaysia, and the most southerly part of the Asian continent, reaching south almost to the equator (1°10’N). Malaya separates the Indian Ocean in the west from the South-Chinese Sea in the east. The total area of Peninsular Malaysia is 131 587 km²; less than 40 % are still covered with rain forest (Aiken and Leigh, 1992). These 40 % comprise mainly montane habitats in the mountain chains, most of which extend from north to south in the northern two thirds of Peninsular Malaysia. The coastal plains east, west and south of these mountains are used for industries and agriculture.

The upper Gombak valley (Ulu Gombak, Color-Plate 2-1, p. 9) is located c. 35 km NE of Malaysia’s capital, Kuala Lumpur. The main highway from the west to east coast runs through this narrow and steep valley. However, especially on the southern slope, relatively large areas of rain forest are still conserved. The forest was selectively logged c. 40-50 years ago. Logging activities as well as more recent agricultural activities of the Orang Asli villagers left a relatively heterogeneous forest. Especially along river- and road sites as well as in side valleys, disturbance is rather high; several species of bamboo (mainly *Gigantochloa* spp.) as well as pioneer trees (e.g. *Macaranga* spp.) are the dominant plants here (Color Plate 2-1, p. 9). In steeper or more remote regions, a fairly intact forest has survived, showing a high diversity of tree species and a closed canopy with some high emergent trees in between. Details on tree flora and climate data can be found in Wiedemann (1969) and Lord Medway (1972).

The major part of ant-epiphyte associations described in this study was detected in rather disturbed areas (mainly along rivers and old logging roads), and in transition zones between such highly disturbed and less disturbed forest.

Since several colleagues have studied ants in this region during the last 25 years, it was possible to draw comparisons with their samples. This option was an additional factor making Ulu Gombak especially suitable for the present study.

2.2. Pedawan Valley, Sabah, Borneo

Three nations share Borneo, the third largest island of the world: Indonesia (Kalimantan, 539 460 km²), Brunei (5765 km²) and Malaysia (Sarawak and Sabah, 198 149 km²). Borneo is the species-richest of all Sunda Shelf islands both in flora and fauna, with a high diversity of different habitats (MacKinnon et al. 1996). Although huge areas have been destroyed, there are still large natural forests left.

For the study of ant-epiphyte associations, a certain type of forest was particularly important: heath forests or 'kerangas'[3]. Heath forests are highly distinct types of rain forest; their appearance can easily be recognized even by non-biologists (Color Plate 2-1, p. 9). The trees are much smaller than in "usual" mixed dipterocarp forests, with a single-layered, more or less open, canopy, and small, pale colored and thick leaves (MacKinnon et al., 1996). Nevertheless, depending on locality, altitude, and soil characteristics, heath forests can differ in floral composition, average height of trees, and degree of canopy-openness (Brünig, 1965 (cited from Whitmore, 1993)). Generally, heath forests grow on so-called 'white sand soils' or 'podsols', which are characterized by high acidity ($pH < 4$), poverty in bases, and a coarse texture causing free drainage (Whitmore, 1993, MacKinnon et al., 1996). The white sand is usually covered by a more or less thin layer of peat, which is high in phenols (Whitmore, 1993). This combination of soil characteristics makes heath forest areas especially vulnerable to any disturbance and unsuitable for agriculture: Once the heath forest vegetation is destroyed, the peat layer is rapidly eroded, and the land becomes so poor in nutrients and so acidic that almost nothing will grow there.[3]

A further characteristic of heath forests, described by Brünig (1969 (cited from Whitmore, 1993)), is a frequent temporary aridity even in regions with generally high rainfall (also s. Ashton, 1971). Many vegetation characteristics can be accounted for as adaptations to drought (Whitmore, 1993).

Borneo used to have the most extensive areas of tropical heath forests in Southeast Asia (c. 67,000 km²). 24,750 km² were still left in 1995 (MacKinnon et al. 1996). No recent figures are available for Sabah and Sarawak, but huge areas burned down completely during El Niño in 1997/1998. Altogether five patches (together c. 1800 ha) of heath forest still remain in Pedawan Valley in Sabah[4]. Two types of heath forests are distinguished in this area (Lamb and Wong, 1989): *Dacrydium pectinatum – Tristanopsis* sp. and *Hopea pentanervia – Shorea venulosa*. This study concentrated on two patches, both belonging to the *Dacrydium pectinatum – Tristanopsis* sp. type. Yet the two plots were clearly different in appearance. Trees on plot 1 (Table 2-1, Nr. 14) were significantly higher, the canopy was relatively closed and the peat layer was considerably thicker than on plot 2 (Table 2-1, Nr. 14), where the trees were smaller with a relatively open canopy.

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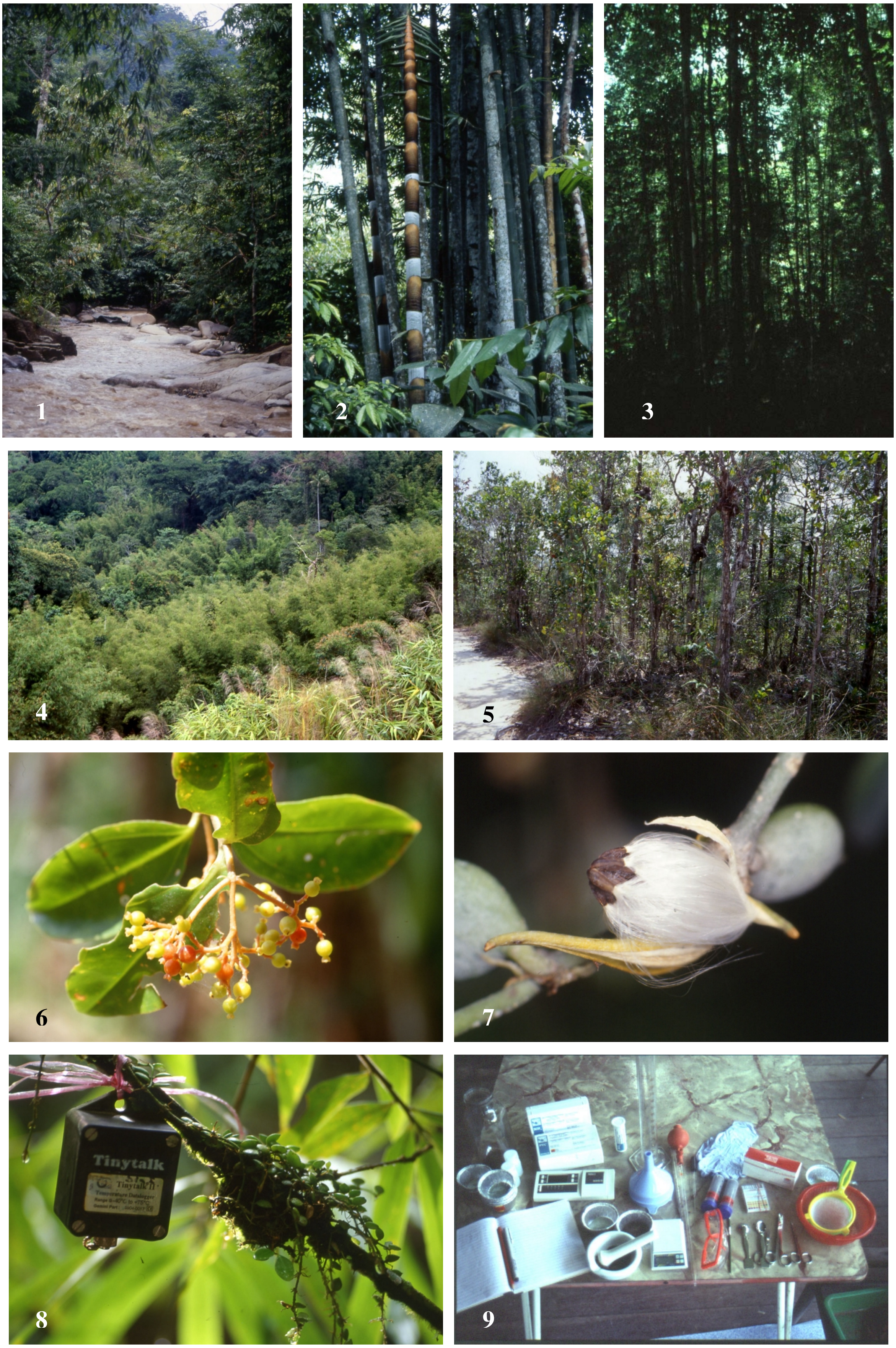
[3] Keranga is a word used by the tribe of Iban for "land that will not grow rice".

[4] As a first step to rescue these last heath forest patches in Sabah, a botanical survey was carried out in 1996-1998. The results were published by the Ministry of Culture, Environment and Tourism, Sabah (1999).



Color Plate 2-1: Typical habitats for ant-gardens and illustration of research methods
1: Gombak River; 2: *Gigantochloa scortechinii* (Poaceae), a typical plant in secondary forests in Ulu Gombak; 3: Less disturbed secondary forest in Ulu Gombak; 4: Bamboo forest near Temenggor Forest Reserve; 5: Heath forest, Bako National Park; 6: Bird-dispersed fruits of *Pachycentria constricta* (Melastomataceae); 7: Wind-dispersed seeds of *Dischidia nummularia* (Asclepiadaceae); 8: Tiny Talk Temperature Data Logger; 9: 'Field laboratory' for substrate analysis

3. Materials and Methods

3.1. Inventory methods

Epiphytes were spotted, if necessary with the aid of binoculars. Access to the epiphytes was obtained by climbing, cutting smaller trees or checking the crowns of freshly logged trees. The rooting medium of the epiphytes was examined carefully. Whenever it contained an ant nest, epiphytes, ants and substrate were collected and recorded along with a number of parameters such as host tree, exposure, associated trophobionts, etc. (Table 3-1). Frequently occurring ant species were characterized by colony size, aggressiveness, etc. (Table 3-1)[5].

Table 3-1: Main parameters recorded for descriptions of ant-epiphyte associations in Southeast-Asia, including standard methods[5]

Geographical data	
Exact locality	described on the basis of locally used reference points or places names
Altitude	Altimeter Casio Module 1282 GE, based on air pressure following ISA norm describing the relationship between altitude, air pressure and temperature; to minimize weather-effects, the altimeter was gauged whenever a point of known altitude was reached
Habitat	short description of habitat type (e.g. primary hill forest, plantation, road site, river bank, etc.)
Phorophyte	
Bark type	three classes were distinguished: rough, medium, smooth; special characteristics were noted, e.g. if the tree was constantly peeling
Diameter	diameter was measured with a custom and practice measurement tape; measured values were rounded to 0.5 cm
Height	height was either measured with a custom and practice measurement tape (rounded to 10 cm) or roughly estimated (to 0.5 m)
Trophobionts	trophobionts sucking on any places on the host plant were collected
Nest	
Height on tree	height was either measured with a custom and practice measurement tape (rounded to 10 cm) or roughly estimated (to 0.5 m)
Position	the relative position in the tree was described (stem, main branch, side branch + knothole, branching)
Size	three dimensions of size were measured with a custom and practice measurement tape; measured values were rounded to 0.5 cm
Trophobionts	trophobionts tended underneath the nests ? (yes/no)
Epiphytes	
Epiphyte species	known epiphytes were determined in the field, others were collected and herbarized, or grown for later determination (Chapter 3.2)
Degree of herbivory	degree of herbivory was estimated as leaf damage in six classes: 0%, > 0 – 20 %, > 20 – 40 %, > 40 – 60 %, > 60 – 80 %, > 80 – 100 %
Trophobionts	trophobionts sucking on any part of the epiphyte were collected

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[5] A complete list of all parameters recorded is given in the appendix (Chapter 12.5, p. 177 f.)

Ants	
Ant morphospecies	specimens were collected and determined to morphospecies (Chapter 3.2)
Colony size	colony size was estimated in four classes: <100, 100-1000, 1001-10000, >10000; for some species, inhabitant numbers of several nests (workers, alates, brood, queens) were counted
Aggressiveness	five classes of aggressiveness were distinguished, (--, -, 0, +, ++), where the lowest class described species that did not show aggressive behavior even when their nest was destroyed, while ++ described species that reacted highly aggressively to mere contact with the tree on which they were living
Nest localization	exact description of where the nest was located (e.g. inside stem, between epiphyte roots, inside domatia, etc.)
Guests	all guests found in ant nests were collected

3.2. Taxonomic classification

Epiphytes were determined by genus or species level (revisions: Burtt, 1962; Clausing, 2000; Burtt and Woods, 1974; Rintz, 1978, 1980; general monographies: Pigott, 1988; Holttum, 1968; Seidenfaden and Wood, 1992; plant collection: Herbarium of the Forest Research Institute of Malaya (FRIM)).

All ants were determined by genus level (Bolton, 1994) and sorted by morphospecies.

3.3. Microclimate of ant-gardens

To detect possible temperature preferences of certain ant species, this parameter was measured at several nests in the area around the Ulu Gombak Field Studies Center. This area was chosen because many AG ants occurred sympatrically here.

Temperature data loggers (Tinytalk II Gemini Data Loggers, Ltd. Orion Group, UK; -40 to +75°C; ±0.5°C, Color-Plate 2-1, p. 9) were installed on long bamboo culms. These were then raised to the nests of four different AG ants as well as of one non-AG ants (Chapter 5.1.2, Table 5-3, p. 96).

Temperature was recorded at 30 min intervals over a seven-day period. The positions of the loggers were repeatedly exchanged in order to eliminate systematic effects as far as possible.

3.4. Ecological significance of Southeast Asian ant-epiphyte associations

To estimate the ecological significance of ant-epiphyte interactions for the establishment of epiphytes, I carried out a closer examination of the total epiphyte flora of Peninsular Malaysia. All epiphyte species recorded in Turner (1995) were monitored for their life habits (literature data and labels from herbarium specimen in FRIM[6]). Reasonable 'candidates' for an association with ants were identified according to criteria of diaspore dispersal and establishment phase. Using such criteria, several groups could be disqualified: a) The large group of orchids and ferns was excluded because these plants use a 'micro-diaspore strategy' for (wind-)dispersal and establishment. b) Species restricted to montane regions were also excluded because they can be expected to have considerably less establishment problems due to the often extensive moss and soil accumulations and the permanently high humidity in cloud forests. Finally, c) the group of facultative epiphytes were not ranked as 'candidates', because they are not totally dependent on reaching growing sites in the canopy. With these restrictions, 55 species out of 12 genera and 8 families remain as theoretical 'candidates' (Chapter 6.1.1, Table 6-1, p. 107).

3.5. Experimental investigations

3.5.1. Seed-carrying experiments

Behavioral experiments were carried out to identify the preferences of various ant species for certain epiphyte or non-epiphyte seeds. The experiments were designed to find out a) whether the respective ant species carried any epiphyte diaspores at all, b) whether the epiphyte seeds were distinguished from non-epiphyte seeds, c) which characteristics of the seeds might account for the ants' decision (hairy appendages, chemical cues, size) and d) whether there were any detectable preferences for particular epiphyte seeds. The layout of the bioassay varied, taking different ant characteristics into account. Where relevant, details will be given together with the description of the ant species in question.

> **General description of seed retrieval bioassays:**
>
> Generally, a simultaneous setup (Color Plate 7-1, p. 121) was used, including the test items, control items already shown experimentally to be attractive (i.e. usually retrieved to ~100%), and control items known to be usually non-attractive (i.e. usually retrieved to ~0%). This double-control helped to estimate the influence of 'motivation' in an ant colony. In this way it was possible to exclude colonies that were 'in the mood' for carrying nothing but food particles or that were 'in the mood' for carrying whatever they found. Experiments were stopped and discarded if the ants had not shown any reaction after 30 minutes. Otherwise, observations were noted over a period of two hours. An experiment was marked invalid if the ants retrieved less than three items during this period, or if they retrieved everything.

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[6] A list of all epiphyte species (except ferns and orchids) occurring according to Turner (1995) in Peninsular Malaysia is given in the appendix, together with ecological reasons for classifying the species as a candidate for AG-association or not (Chapter 12.10, p. 190).

Generally, two types of epiphyte seeds were distinguished. The first group comprised primarily wind-dispersed seeds, equipped with a hairy appendage (Color-Plate 2-1, p. 9). The second group consisted of primarily bird-dispersed seeds, enclosed in a fleshy fruit pulp (Color-Plate 2-1, p. 9).

As main test items in the first group, seeds of the AG epiphytes *Dischidia nummularia*, *Hoya elliptica* (Asclepiadaceae) and *Aeschynanthus albidus* or *Aeschynanthus fecundus* (Gesneriaceae) with or without their hairy appendage were chosen. Seeds of the non-epiphytes *Emilia sonchifolia* and *Ageratum conyzoides* (Asteraceae)[7], threads and porcelain dummies were also tested[8].

Extracts of the epiphyte seeds were produced by shaking 50 intact seeds in 0.5 ml acetone in a glass vial for two minutes and leaving the vial to stand for one hour. The acetone extract was then applied to ten porcelain baits or ten non-epiphyte seeds. The acetone evaporated quickly. To make sure that the solvent was gone completely, test items were kept in shallow aluminium containers in a dry place for one hour before starting the bioassay.

Seeds of the primarily bird-dispersed AG epiphytes *Pachycentria constricta*, *Pachycentria glauca* subsp. *maingayi* and *Medinilla crassifolia* (Melastomataceae), as well as seeds of a terricolous *Medinilla* sp.[7], were offered before and after passage through the gut of a bird (*Aplonis panayensis*, ‘Philippine starling’).

3.5.2. Characterization of ant attractants in epiphyte seeds

For some ant and epiphyte species, clear evidence for chemical attractants being responsible for eliciting seed retrieval was found. Several approaches have been made to characterize these attractants:

3.5.2.1. Seed-carrying experiments with non-AG ants

In order to see whether seed attractants of AG epiphytes contain some ‘universal’ ant attractant, seeds of epiphytes (*Dischidia nummularia*, *Hoya elliptica*, *Aeschynanthus fecundus* and *Pachycentria constricta*) as well as of the non-epiphytes *Ageratum conyzoides*, *Emilia sonchifolia* and *Medinilla* sp. were offered to several non-AG ant species (Table 3-2) in a simultaneous setup. Each ant species was tested in two experiments, always using five seeds of each epiphyte species. The tested ant species were selected in order to cover a broad range of ecological types with regard to foraging habits and diet.

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[7] The none-epiphytes were chosen for their similar appearance compared to the epiphyte seeds, the two Asteraceae resembling the primarily wind-dispersed seeds, and *Medinilla* sp. resembling the primarily bird-dispersed species.

[8] A complete list of test items is given in the appendix (Chapter 12.7, p. 180 ff.). Drawings of all tested wind-dispersed seeds are also provided in the appendix (Chapter 12.6, p. 179).

Table 3-2: Non-ant-garden ants used in seed-carrying experiments

ant species	subfamily	characteristics
Anoplolepis gracilipes	Formicinae	typical ant of disturbed areas, highly efficient recruitment system, very aggressive
Camponotus $\mathrm{sp}_{\mathrm{KfmA}}239$	Formicinae	soil nesting, night-active species, feeding on honeydew and insect prey
Oecophylla smaragdina	Formicinae	arboricolous weaver ant; feeding mainly on honeydew, but also on insect prey; efficient recruitment system
Pachycondyla $\mathrm{sp}_{\mathrm{KfmA}}184$	Ponerinae	solely foraging, mainly carnivorous ant
Pheidole $\mathrm{sp}_{\mathrm{KfmA}}210$	Myrmicinae	terricolous, soil nesting species; seed harvesting; efficient recruitment system
Pheidologeton $\mathrm{sp}_{\mathrm{KfmA}}177$	Myrmicinae	army-ant-like foraging patterns

3.5.2.2. Ageing, heating, washing, and extracts with different solvents

The first steps to characterize the attractant(s) were simple mechanical treatments of epiphyte seeds. a) Seeds were kept in open aluminium containers at room temperature and used in bioassays after 8, 14 and 28 days. To prevent house-ants from eating, destroying or simply contaminating the seeds, these were stored on a table, the legs of which were placed in water-filled bowls.

b) Another approach to test the volatility and persistence of seed attractants was to heat them in open aluminium containers to 110°C and 200°C for one and for two hours and to see whether they were still attractive afterwards.

c) In order to roughly determine the polarity of the attractants, seeds were washed with different solvents. In a first attempt, 20 epiphyte seeds were washed in 20 ml of solvent (acetone, aqua dest., chloroform, cyclohexane, 70% ethanol, pentane) for one hour. The solvent was decanted, and the seeds were allowed to dry for one hour. This process was repeated twice, each time with fresh solvent. In later attempts, different solvents were used successively, and the washing time was extended to eight hours.

d) For the same purpose, seed extracts were produced using different solvents (general seed extraction method, see above). The extracts were applied to porcelain baits, wooden baits or to non-epiphyte seeds and tested in simultaneous seed-carrying experiments (also s. Chapter 12.7, p. 180).

3.5.2.3. Comparison of GC/MS profiles and IR spectra of several attractive seeds

Several analytical methods were used to identify possible attractive substances in seeds of different epiphyte species. The general idea was based on the results of the bioassays described above, as well as on literature data on other myrmecochory systems (neotropical AG epiphytes (Davidson et al, 1990; Seidel et al., 1990); terricolous myrmecochores (e.g. Berg, 1975;

Marshall et al., 1979; Hughes et al., 1994; Sheridan et al., 1996)). These provided hints that the same substances could be responsible for seed retrieval in several epiphyte species from different genera and even families (e.g. *Hoya elliptica* (Asclepiadaceae), *Dischidia nummularia, Dischidia acutifolia, Dischidia hirsuta* (Asclepiadaceae), *Aeschynanthus albidus* (Gesneriaceae) and *Aeschynanthus fecundus* (Gesneriaceae)). Therefore, extracts of these epiphyte species and of the non-attractive, terricolous Asteraceae *Emilia sonchifolia* were characterized and compared using the following methods:

Seed extracts were produced with 50 seeds (hairy appendage removed) in 50 µl solvent (acetone, CH_2Cl_2, pentane, 30 min. - 24 hrs. extraction time). The solvent was dried off with a rotary evaporator, and the oil was resolved in hexane.

Gas Chromatography / Mass Spectroscopy
GC: HP 5890 A Gas Chromatograph
MS: HP 5970 Series Mass Selective Detector
HP 59822 Ionization Gauge Controller
Splitless injection; temperature profile: 60°C start temperature, after 2 min. + 8°C/min., max. 250°C (reached after c. 24 min.), MS started after 4 min, total time: 38.25 min.

Gas Chromatography / IR Spectroscopy
GC: HP 5890 A Gas Chromatograph
IR: HP 5965 A Infrared Detector, HP 5965A IRD Flow Controller
Splitless injection; temperature profile: 60°C start temperature, after 2 min. + 8°C/min., max. 250°C (reached after c. 24 min.), total time: 38.25 min.

3.5.2.4. HPLC and LC fractions in bioassays

The third and last approach so far was to fractionate the total extract, and to test the fractions in bioassays as described above. Two methods were applied for fractionation, reverse phase HPLC (High Pressure Liquid Chromatography) and flash LC (Liquid Chromatography).

Seed extracts of *Aeschynanthus albidus* (Gesneriaceae) were used in these experiments. The extracts were produced with c. 1000 seeds in acetone. The solvent was dried off with a rotary evaporator. For HPLC, 5 mg of crude extract were solved in 25 µl hexane; for flash LC 30 mg of crude extract were solved in 50 µl hexane.

HPLC
HP 1090 II pump
Column: Phenomenex C18 prep. column, 25 cm x 10 mm
Flow: 1.0 ml/min

Solvent system: 0-3 min.: Acetonitrile (ACN) : H_2O = 60 : 40; 3-12 min.: continuous shift from ACN : H_2O = 60 : 40 to ACN : H_2O = 100 : 0; 12-24 min.: ACN : H_2O = 100 : 0

Flash-LC

EM Science Silica Gel 60 (230-440 mesh ASTM)

Ace Glassware 150 mm Ace Thred® columns

24 fractions with 1.0 ml of solvent each: increasing polarity from pure hexane, hexane : ether = 100 : 1, increasing ether concentration to hexane : ether = 1:1; last four fractions with pure methanol

3.5.3. Substrate properties

The water storing capacity and nutrient content of ant nests were investigated in order to form an impression of their suitability as a substrate for epiphyte growth. Additionally, nest building behavior and macroscopic carton composition were recorded.

3.5.3.1. Analysis of nutrient content

Three major plant nutrients were chosen for substrate analysis: ammonium (NH_4^+), nitrate (NO_3^-) and phosphate (PO_4^{3-}). For determination of the relative amount of these three substances in carton material accumulated by AG ants, a reflectometric method was used (details s. below). This method was chosen because it could be used directly in the field with relatively simple laboratory equipment and without electricity (Color-Plate 2-1, p. 9). In addition to glass bottles, glass vials and aluminium containers, the following special equipment was needed:

- Reflectometer RQflex®, Fa. Merck
- Scale Kern 466-45, max. 250 g, d=0,1 g
- Reflectoquant® Ammonium Test; 0,2-7,0 mg/l NH_4^+ (Merck Art. 1.16892.0001)
- Reflectoquant® Nitrate Test; 3-90 mg/l NO_3^- (Merck Art. 1.16995.0001)
- Reflectoquant® Phosphate Test; 5-120 mg/l PO_4^{3-} (Merck Art. 1.16978.0001)
- universal pH indicator sticks
- indicator sticks for pH 3.6
- nitrate-free paper filters
- calciumchloride dihydrate f.a.
- calcium lactate
- HCl 10M
- aqua dest. f.a.

Since the method was originally developed for larger soil samples (about 150 g), it had to be adjusted to the usually much smaller samples (about 5 g) collected from AGs. According to the developers of the test kit, this should not falsify the results. Nevertheless, I did not think it advisable to rely on the comparability of my results to those obtained by other methods. In order to achieve comparability between my own results, equal amounts of substrate were used in each test (within a single test type), and nests of non-AG ants, termites' nests, bark and forest soil were tested for comparison.

Preparation of samples

All animals living in the respective substrate were killed with chloroform. Immediately after this, the pure substrate was manually separated from (epiphyte) roots and ants / termites / other animals with forceps. The substrate was then air-dried in flat aluminium containers. Dry samples were crushed and homogenized with pestle and mortar, then weighed. Portions of 5 g (for ammonium and nitrate analyses) and 2.5 g (for phosphate analyses) were placed in 50 ml glass vials that could be tightly closed with corks.

Ammonium samples

General method: "*Ammonium ions react with a chlorinating agent to form monochloroamine. This in turn reacts with a phenol compound to form a blue indophenol derivative, the concentration of which is determined reflectometrically.*" (Merck instruction, also s. Chapter 12.8.1, p. 185)

5 g substrate sample were shaken in 30 ml 0.0125 M $CaCl_2$-solution for one hour and filtered immediately afterwards. 5 ml of the liquid fraction were measured off in a plastic test vial, which had been rinsed several times beforehand with the test solution. The pH of this solution had to be between 4 and 13, temperature between 20°C and 30°C. 10 drops of reagent NH_4-1 and 1 micro-spoon of reagent NH_4-2 were added and carefully dissolved. Test sticks were used according to the producer's instructions (Chapter 12.8.1, p. 185). The ammonium content was measured in mg/l NH_4.

Nitrate samples

General method: "*Nitrate is reduced to nitrite by a reduction agent. In the presence of an acidic buffer, this nitrite reacts with an aromatic amine to form a diazonium salt, which in turn reacts with N-(1-naphthyl)-ethylene-diamine to form a red-violet azo dye, the concentration of which is determined reflectometrically.*" (Merck instruction, also Chapter 12.8.2, p. 186)

5 g substrate sample were shaken in 30 ml 0.01 M $CaCl_2$-solution for 30 minutes. After this period, the emulsion was filtered immediately, using nitrate-free paper filters. 5 ml of the liquid fraction were measured off in a plastic test vial, which had been rinsed several times beforehand with the test solution. The pH of this solution had to be between 1 and 12, temperature between 20 and 30°C. Test sticks were used according to the producer's instructions (Chapter 12.8.2, p. 186). The nitrate content was measured in mg/l NO_3^-.

Phosphate samples

General method: "*In a solution acidified with sulphuric acid, orthophosphate ions (PO_4^{3-}) and molybdate ions form molybdophosphoric acid. This is reduced to phosphomolybdenum blue*

(PMB), the concentration of which is determined reflectometrically." (Merck instruction, also s. Chapter 12.8.3, p. 187)

The solution used for extraction of phosphate was mixed as follows: 60 g Ca-lactate (for soil analysis) were solved in 400 ml boiling water. 20 ml 10 M HCl were added to the warm solution. After reaching room temperature, the solution was diluted to a volume of 1 l with distilled water (for analysis). From this storable solution, the usable solution was produced freshly before starting the test, by diluting 12.5 ml storable solution to 250 ml, using distilled water (for analysis). A pH of 3.6 was necessary.

2.5 g substrate sample were shaken in 125 ml extraction fluid for 90 minutes. After this period, the emulsion was filtered immediately. 5 ml of the liquid fraction were measured off in a plastic test vial, which had been rinsed several times beforehand with the test solution. The pH of this solution had to be between 4 and 10, temperature between 15°C and 30°C. 10 drops of reagent PO_4-1 were added and dissolved by swirling the test vial carefully. Test sticks were used according to the producer's instructions (Chapter 12.8.3, p. 187). The phosphate content was measured in mg/l PO_4^{3-}.

3.5.3.2. Analysis of water storing capacity

In order to determine water-storing capacity under natural conditions, ant nests were collected after several days of heavy rain. The nests were weighed. After this, ants and epiphyte roots were removed and weighed separately. The pure nest-substrate was weighed after drying. Water storing capacity was estimated as factor x = wet weight of nest-substrate / dry weight of nest-substrate.

3.6. Statistical methods

Apart from the standard methods (like U-Test, t-Test, χ^2-statistics), a Monte Carlo randomization method (described in Blüthgen et al., 2000; also see Manley, 1997) was applied. This method was used to describe the ant-epiphyte distribution. It replaced χ^2-statistics whenever the expected cell entries were too low. For a matrix with r rows and c columns, the test statistic used was $T\_obs = \sum(a_{r,c} * \log a_{r,c})$. The T_obs value was compared with 25000 random matrices (T_ran) having the same row and column totals (calculation software used at http://itb.biologie.hu-berlin.de/~nils/stat/).

Sequential Bonferroni correction was generally used for experimental types containing > 4 comparisons (Rice, 1988).

4. Diversity of Southeast Asian ant-gardens

This chapter describes which organisms were involved in Southeast Asian ant-epiphyte associations and how they interacted, in order to illustrate the diversity of ant-garden systems and demonstrate the mutual benefits ants and epiphytes gain from their association.

4.1. Results

4.1.1. Inventory - True ant-garden mutualists and opportunists

Altogether 743 ant colonies comprising 67 species (5 subfamilies, 19 genera) were found in association with epiphytes. Since some of the ant species were highly polydomous, a total of 1827 nests were recorded. Sometimes two or more species lived in the same nest. 499 colonies (68 %) comprising 18 species (27 %) from 4 subfamilies, 5 genera, were identified as true AG species, i.e. for these species seed-carrying behavior and carton-building behavior were observed (Table 4-2). Most of the remaining species were identified as opportunistic, secondary inhabitants of abandoned or even still used AGs. While true AG species tended to be the only species inhabiting a nest (except for some parabiotic[9] species), secondary inhabitants were frequently found in community with several other species (Mann-Whitney U-Test: U=170 231, $p<0.001$; Figure 4-1).

All of the *Philidris* species (Dolichoderinae) and the only arboricolous *Diacamma* sp. (Ponerinae) found in this study were identified as obligate partners of epiphytes. In all the other genera with true AG ants, opportunists were recorded also (Table 4-1).

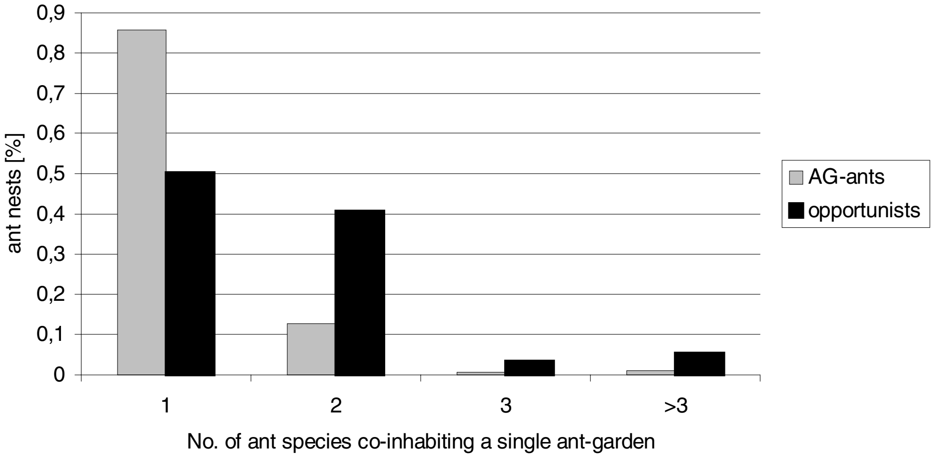

Figure 4-1: Number of ant species co-inhabiting a single ant-garden: Comparison between ant-garden ants and opportunists
Percentage of nests inhabited by 1, 2, 3, or more than three ant species. AG-ants: n=1301 ('yes' or 'yes*' in column 'true AG species' in Table 4-2); opportunists: n = 407; opportunists: n=638 ('?' or 'no' in column 'true AG species' in Table 4-2)

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[9] Definition of the term parabiosis s. Chapter 4.2.2.3, p. 91

Table 4-1: Ant-garden ant genera and opportunistic members of these genera found in the present study

		# true AG-species	# opportunist species
Dolichoderinae	*Philidris*	6	0
Formicinae	*Camponotus*	4	6
Myrmicinae	*Crematogaster*	6	6
	Pheidole	2	4
Ponerinae	*Diacamma*	1	0

On the nests of the AG ants, altogether 2048 epiphytes from 84 species (16 families, 27 genera) were found. Again, some of these species were opportunistic, secondary AG inhabitants, i.e. their seeds were not ant-dispersed (32 species, marked with '?' or 'no' in Table 4-3). As with the ants, true AG epiphytes generally occurred with a smaller number of other epiphyte species on single nests as compared to opportunistic species (U=367 457, p<0.001; Figure 4-2).

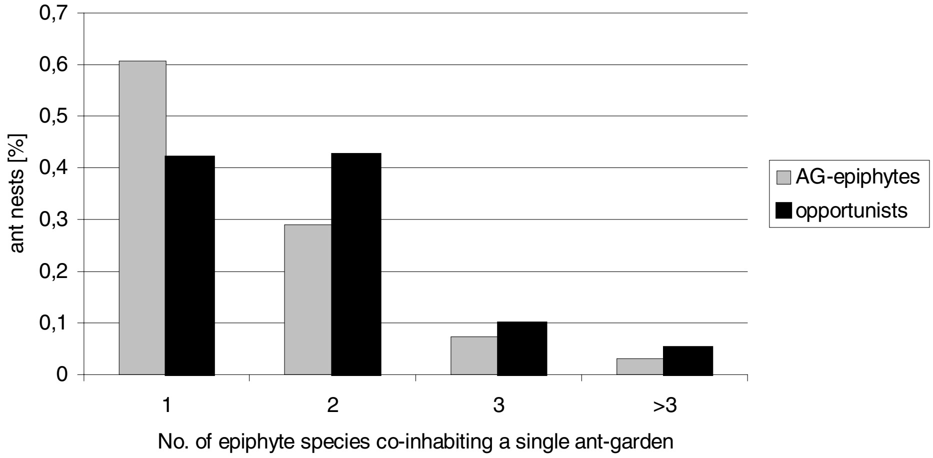

Figure 4-2: Number of epiphyte species occurring on a single nest: Comparison between ant-garden epiphytes and opportunists
Percentage of nests with 1, 2, 3, or more than three epiphyte species. AG-epiphytes: n=1417 ('yes' or 'yes*' in column 'true AG species' in Table 4-3); opportunists: n=638 ('?' or 'no' in column 'true AG species' in Table 4-3)

Table 4-3 gives a list of all epiphytes found more than once in AGs. The asclepiad genera *Dischidia* and *Hoya* were predominant with 13 and 9 species respectively (15.0 % and 10.7 % of all species).

Table 4-2: Ant-garden inhabiting ants (morphospecies).
total number of colonies: n=743; ‘occurrence’: 1 = Peninsular Malaysia, 2 = Borneo, 3 = Thailand; 4 = Java; ‘true AG-species’: yes = proved by observation of seed-carrying and carton-building behavior, yes* = probably true AG-species but final proof missing, ? = no data available, no = definitely no AG-species (no seed-retrieving and/or carton-building behavior).
Only species occurring more than once are included.

ant-subfamily	ant-species	# colonies	geographical occurrence	true AG species
Dolichoderinae	*Dolichoderus* (6 spp.)	37	1,2,4	no
	***Philidris* sp$_{\text{KfmA}}$37**	29	1,3	yes
	***Philidris* sp$_{\text{KfmA}}$85**	15	1,3,4	yes
	***Philidris* sp$_{\text{KfmA}}$159**	15	2	yes
	***Philidris* sp$_{\text{KfmA}}$160**	62	2	yes
	***Philidris* sp$_{\text{KfmA}}$208**	4	2	yes
	***Philidris* sp$_{\text{KfmA}}$209**	10	2	yes
	Plagiolepis (2 spp.)	6	1,2	no
	Tapinoma (1 sp.)	3	1	no
	Technomyrmex (6 spp.)	43	1,2,3,4	no
Formicinae	***Camponotus* sp$_{\text{KfmA}}$9**	15	1,3	yes
	Camponotus sp$_{\text{KfmA}}$168	5	2	yes*
	***Camponotus* sp$_{\text{KfmA}}$240**	22	1,2,3	yes
	***Camponotus* sp$_{\text{KfmA}}$241**	5	1	yes
	Camponotus (2 spp.)	7	1	?
	Camponotus (4 spp.)	28	1,4	no
	Echinopla (1 sp.)	2	1	no
	Myrmoteras (1 sp.)	2	1	no
	Paratrechina (2 sp.)	7	1	no
	Polyrhachis (2 sp.)	8	1,2	no
Myrmicinae	*Cataulacus* (1 sp.)	2	2	no
	***Crematogaster* sp$_{\text{KfmA}}$18**	99	1,3	yes
	***Crematogaster* sp$_{\text{KfmA}}$19**	20	1,2	yes
	***Crematogaster* sp$_{\text{KfmA}}$21**	57	1,2,3	yes
	***Crematogaster* sp$_{\text{KfmA}}$99**	5	1,3	yes
	***Crematogaster* sp$_{\text{KfmA}}$113**	9	1,2,3	yes
	***Crematogaster* sp$_{\text{KfmA}}$200**	21	4	yes
	Crematogaster (2 spp.)	28	1,2,3	?
	Crematogaster (4 spp.)	14	2	no
	Meranoplus (1 sp.)	3	1	no
	***Pheidole* sp$_{\text{KfmA}}$33**	37	1,2,4	yes
	***Pheidole* sp$_{\text{KfmA}}$120**	5	1	yes
	Pheidole (4 spp.)	13	1	no
	Smithistruma (1 sp.)	2	2	no
	Tetramorium (1 sp.)	9	1	?
	Tetramorium (4 spp.)	14	1,2,4	no
	Vollenhovia (1 sp.)	2	1	no
Ponerinae	***Diacamma* sp$_{\text{KfmA}}$111**	73	1,2	yes
Pseudomyrmecinae	*Tetraponera* (2 sp.)	15	1,2	no

Table 4-3: Ant-garden inhabiting epiphytes.
total number of epiphytes n=1989 (only one specimen/species was counted per nest, even though sometimes several specimens of one species were growing on a single nest); occurrence: 1 = Peninsular Malaysia; 2 = Borneo; 3 = Thailand; 4 = Java; 'true AG-species': yes = proved by observation of AG-ants carrying the seeds (species name printed in bold letters), yes* = probably true AG-species but final proof missing, ? = no data available, no = definitely no AG-species (diaspores not retrieved by ants). Only species occurring more than once were included, indet. genera (some orchids and seedlings) were also excluded.

		occurring with #ant nests	occurring with #ant colonies			
	epiphyte species	n	n	% of all colonies	geographical occurrence	true AG species
Araceae	*Anadendrum latifolium* Hooker	2	2	0.27	1	yes*
Araliaceae	*Schefflera* sp$_{\text{KfmE}}$75	28	28	3.77	1,3	yes*
	Schefflera sp$_{\text{KfmE}}$91	19	18	2.42	1,3	yes*
	Schefflera sp$_{\text{KfmE}}$132	17	15	2.02	4	yes*
	Schefflera sp$_{\text{KfmE}}$155	4	4	0.54	1	yes*
Asclepiadaceae	*Dischidia acutifolia* Maingay	56	16	2.15	1,3	yes
	Dischidia albida Griff.	21	19	2.56	1,2,3	yes
	Dischidia astephana Scort.	6	6	0.81	1	yes
	Dischidia bengalensis Colebr.	4	4	0.54	1	yes
	Dischidia fruticulosa Ridl.	9	5	0.67	1	yes
	Dischidia hirsuta Decne.	3	3	0.40	1,2,3	yes
	Dischidia imbricata Steud.	19	12	1.62	1,2	yes
	Dischidia major Merr.	26	21	2.83	1,2,3,4	yes
	Dischidia longepedunculata Ridl.	2	2	0.27	1	yes
	Dischidia nummularia R.Br.	532	93	12.52	1,2,3	yes
	Dischidia punctata Decne.	6	2	0.27	1	yes
	Dischidia subulata Warb.	3	2	0.27	1	yes
	Dischidia sp$_{\text{KfmE}}$115	25	23	3.10	2	yes
	Hoya elliptica Hooker	22	7	0.94	1,3	yes
	Hoya lacunosa Blume	5	5	0.67	3	yes
	Hoya micrantha Hooker	21	4	0.54	1,2	yes
	Hoya mitrata Kerr	20	17	2.29	2,3	yes
	Hoya multiflora Blume	6	4	0.54	1	yes
	Hoya parasitica Wallich	2	2	0.27	1,3	yes*
	Hoya sp$_{\text{KfmE}}$51	15	4	0.54	1,2	yes
	Hoya sp$_{\text{KfmE}}$94	6	6	0.81	1,2	yes
	Hoya sp$_{\text{KfmE}}$133	8	7	0.94	4	yes
Davalliaceae	*Humata repens* Diels	4	2	0.27	2	no
Gesneriaceae	*Aeschynanthus albidus* Steud.	150	83	11.17	1,2,4	yes
	Aeschynanthus fecundus Woods	92	25	3.36	1,3	yes
	Aeschynanthus myrmecophilus Woods	2	2	0.27	1	yes
	Aeschynanthus sp$_{\text{KfmE}}$33	6	6	0.81	1,2	yes
	Aeschynanthus sp$_{\text{KfmE}}$122	6	5	0.67	3	yes
Lycopsida	*Lycopodium* sp$_{\text{KfmE}}$125	3	3	0.40	1,2	no
Melastomataceae	*Medinilla crassifolia* Gaudich.	5	5	0.67	1	yes
	Pachycentria constricta Blume	81	62	8.34	1,2	yes
	Pachycentria glauca subsp. *maingayi* Clausing	34	13	1.75	1	yes
	Pachycentria glauca subsp. *glauca* Triana	18	12	1.62	2	yes
Moraceae	*Ficus* sp$_{\text{KfmE}}$96	7	7	0.94	1	yes
	Ficus sp$_{\text{KfmE}}$134	3	3	0.40	4	yes
	Ficus sp$_{\text{KfmE}}$144	2	2	0.27	1	yes*

		occurring with #ant nests	occurring with #ant colonies			
	epiphyte species	n	n	% of all colonies	geographical occurrence	true AG species
Orchidaceae	*Acriopsis gracilis* Mind. & deVogel	2	2	0.27	2	yes*
	Acriopsis javanica Reinw.	21	14	1.88	1,2,3	yes*
	Dendrobium crumentatum Sw.	16	10	1.35	1,2	?
	Dendrobium sp$_{\mathrm{KfmE}}$117	2	2	0.27	2	?
	Liparis lacerata Ridl.	10	9	1.21	1,2	yes*
Peperomiaceae	*Peperomia* sp$_{\mathrm{KfmE}}$135	3	3	0.40	4	yes*
Piperaceae	*Piper* sp$_{\mathrm{KfmE}}$89	3	3	0.40	1	?
Polypodiaceae	*Asplenium nidus* L.	9	9	1.21	1,2	yes*
	Drymoglossum piloselloides Presl.	73	23	3.10	1,2	?
	Drynaria rigidula Bedd.	7	5	0.67	1,2	?
	Drynaria sparsisora Moore	18	16	2.15	1,2,3	?
	Lecanopteris sinuosa Copel.	52	39	5.25	1,2,3	yes*
	Lepisorus longifolius Holttum	9	3	0.40	1	?
	Platycerium coronarium Desv.	3	2	0.27	1,2	?
	Platycerium ridleyi Desv.	12	10	1.35	1,2	yes*
	Pyrossia floccigera Ching	117	17	2.29	1,2	?
	Pyrossia lanceolata Farwell	109	36	4.85	1,2	?
Rubiaceae	*Hydnophytum formicarium* Jack	36	21	2.83	1,2,3	yes
	Hydnophytum sp$_{\mathrm{KfmE}}$104	10	7	0.94	2	yes
	Myrmecodia tuberosa Jacq.	134	42	5.65	1,2,3	yes
Urticaceae	*Poikilospermum cordifolium* Merr.	22	18	2.42	1,2,3	yes
	Poikilospermum microstachys Merr.	45	42	5.65	1,3,4	yes
Vittariaceae	*Vittaria ensiformis* Sw.	2	2	0.27	1,2	no
Zingiberaceae	*Hedychium longicornutum* Griff.	5	5	0.67	1,3	yes

The difference between AG species and opportunists can be further illustrated using the Monte Carlo randomization method described in Blüthgen et al. (2000) (Chapter 3.6, p. 19). I chose the area around the Ulu Gombak Field Studies Center (Chapter 2.1, p. 5) as an example, because here many epiphyte as well as ant species were found sympatrically. The total ant by epiphyte matrix was split to one containing only opportunists (Chapter 12.9.2, p. 189) and one containing only true AG species (Chapter 12.9.1, p. 188). For the opportunists, species distribution was not significantly different from the random matrices (T_obs=47.9, mean T_ran=44.8 ± 29.9, p=0.28), i.e. there were no specializations or preferences. In contrast, the AG matrix showed clear compartmentalization (T_obs=640.2, mean T_ran=512.5 ± 51.1, p<0.001). Details on specificities and preferences will be given in Chapter 5.1.1, p. 94 ff..

4.1.2. Detailed description of selected ant-garden systems

Altogether 18 ant species from five genera were identified as ‘true’ AG ants in this study (s. above).

The detailed presentation of descriptive data of AG systems is restricted to a selection which was studied in particularly close detail (nine species). The chosen examples cover a broad systematic range, which well represents the variety of AG systems. The main characteristics of each AG system are mentioned in the subheadings, thus permitting a quick overview. A complete synopsis comprising all the AG systems found during this research project is provided in Table 4-4.

Three partners, viz. ants, epiphytes and phorophyte, are constitutive for AGs. However, other partners can also be important: trophobionts, fungi and parabiotic ant species. Furthermore, arthropod ‘guests’ frequently inhabited AGs. Information on all these organisms is given in the first part of each description, comprising the subchapters:

- General biology of the ants
- Colony structure
- Nest architecture and carton composition
- Phorophytes
- Trophobionts
- Epiphyte partners
- Guests

As two especially important traits for a beneficial association of ants and epiphytes, carton quality and seed-carrying behavior are included in two further subchapters:

- Water storing capacity and nutritive value of the carton material
- Seed-carrying behavior

The amount of data collected for each ant species varied widely, a fact which was naturally reflected in the lengths of the various chapters. In some chapters, one or the other subchapter is missing due to lack of data.

Table 4-4: Main characteristics of the 18 ant-garden species identified in Southeast Asia
?: no data available; 'freeAG'=AG independent from preformed cavities

ant species	# colonies	range alitrunk size [mm]	gynie	median colony size	median nest size [cm³]	max. # of nests	av. weight of nesting material [mg/cm³]	nest site	phorophyte	trophobionts	50% most abundant epiphyte species	cues for seed-carrying	parabiosis
Camponotus sp$_{KfmA}$9	15	2.1-5.0	?	>>10000	470	83	13.0	free AG	variable	underneath nests and carton shelters	*Hoya elliptica* [41%] *Lepisorus longifolius* [21%]	chemical + size	*Crematogaster* sp$_{KfmA}$42 [33%] *Cr.* sp$_{KfmA}$21 [40%]
Camponotus sp$_{KfmA}$240	20	2.0-4.3	?	2500	1500	4	2.8	natural cavities	variable	underneath carton shelters	*Hoya mitrata* [50%]	chemical + size	*Crematogaster* sp$_{KfmA}$21 [100%]
Camponotus sp$_{KfmA}$241	5	3.5-5.3	?	?	2300	1	?	natural cavities	variable	underneath carton shelters	4 species in equal frequencies	?	
Crematogaster sp$_{KfmA}$18	99	0.7-1.2	mono	30000	110	25	12.7	free AG	giant bamboo	underneath nests	*Dischidia nummularia* [45%] *Pyrossia lanceolata* [9,6%]	chemical	*Dolichoderus* sp$_{KfmA}$17 ? [14%]
Crematogaster sp$_{KfmA}$19	20	0.6-0.8	mono	?	56	28	?	free AG	giant bamboo	underneath nests	*Dischidia nummularia* [47%] *Pyrossia lanceolata* [27%]	?	
Crematogaster sp$_{KfmA}$21	57	0.9-1.1	?	?	32	?	?	natural cavities	variable	sharing trophobionts with parab. species	*Hoya mitrata* [23%] *Poikilospermum microstachys* [14%] *Poikilospermum cordifolia* [10%] *Aeschynanthus albidus* [10%]	chemical + size	*Camponotus* sp$_{KfmA}$9 [11%] *Ca.* sp$_{KfmA}$240 [35%]
Crematogaster sp$_{KfmA}$99	5	0.9-1.0	?	?	?	2	?	natural cavities	variable		*Hoya multiflora* [25%] *Aeschynanthus albidus* [25%]	?	
Crematogaster sp$_{KfmA}$113	9	1.4	?	?	1860	3	?	natural cavities	variable	scattered in vegetation	*Poikilospermum microstachys* [50%]	?	
Crematogaster sp$_{KfmA}$200	21	0.8	mono	10000	271	2	?	free AG	variable	scattered in vegetation	*Aeschynanthus albidus* [71%]	?	
Diacamma sp$_{KfmA}$111	73	3.6	mono	40	134	1	2.4	natural cavities	variable	no	*Schefflera* sp$_{KfmA}$75 [28%] *Poikilospermum microstachys* [20%] *Aeschynanthus albidus* [13%]	suitability as building material	
Pheidole sp$_{KfmA}$33	37	0.7/1.1	mono	1300	218	5	40.8	natural cavities + free AG	variable	no	*Aeschynanthus albidus* [16%] *Pachycentria. constricta* [12%] *Schefflera* sp$_{KfmA}$132 [7%] *Dischidia punctata* [7%] *Dischidia albida* [6%] 24 other species with 1-5% each	chemical + suitability as building material + seed character	
Pheidole sp$_{KfmA}$120	5	0.8/1.1	?	?	960	2	?	natural cavities	variable	no	*Aeschynanthus albidus* [46%] *Pachycentria constricta* [15%]		
Philidris sp$_{KfmA}$37	29	0.9-1.6	mono	10000	46	11	15.9	natural cavities + free AG	variable	underneath nests and extensive carton shelters	*Pyrossia lanceolata* [21%] *Dischidia nummularia* [20%] *Pachycentria constricta* [7%] *Pachycentria glauca subsp. maingayi* [7%]	chemical	
Philidris sp$_{KfmA}$85	15	0.8-1.1	?	?	144	5	?	natural cavities + free AG	variable	underneath nests and extensive carton shelters	*Dischidia major* [40%] 6 other species with 10% each	?	
Philidris sp$_{KfmA}$159	15	0.8-1.3	?	?	302	8	?	natural cavities	variable	underneath nests and extensive carton shelters	*Hydnophytum formicarium* [32%] *Myrmecodia tuberosa* [22%]	?	
Philidris sp$_{KfmA}$160	62	0.8-1.2	mono	?	188	12	?	natural cavities	variable	underneath nests and extensive carton shelters	*Myrmecodia tuberosa* [34%] *Hydnophytum formicarium* [23%]	?	
Philidris sp$_{KfmA}$208	4	0.7-1.0	?	?	98	2	?	natural cavities	variable	underneath nests and extensive carton shelters	*Dischidia major* [100%]	?	
Philidris sp$_{KfmA}$209	10	0.8-1.5	?	?	65	8	?	natural cavities	variable	underneath nests and extensive carton shelters	*Myrmecodia tuberosa* [43%] *Pachycentria constricta* [29%]	?	

4.1.2.1. Myrmicinae

The Myrmicinae comprise about 150 ant genera, representing a wide variety of life-styles mainly in terricolous but also in arboricolous habitats. Members of the two species-richest genera, *Pheidole* (2 species) and *Crematogaster* (4 species), were found as AG mutualists in the present study. Three *Crematogaster* spp. and one *Pheidole* sp. are described in detail in the following sections.

Crematogaster **sp$_{\mathbf{KfmA}}$18**

A five partner system (ants, epiphytes, phorophyte, trophobionts, fungi), restricted to giant bamboo as host plant

General biology of the ant

Crematogaster sp$_{\mathrm{KfmA}}$18 (referred to as *Crematogaster* sp.1 in Kaufmann et al., 2001) is a very common AG ant in certain habitats in Peninsular Malaysia and Southern Thailand. Activity was recorded over 24 hours, with minima during the warmest/driest hours of the day as well as during rainfall, and maxima in the late morning and early night. *Crematogaster* sp$_{\mathrm{KfmA}}$18 reacts with slight aggressiveness to any disturbance, but this aggressiveness was not very effective either against larger vertebrates or against dominant ants.

Colony structure

99 colonies of *Crematogaster* sp$_{\mathrm{KfmA}}$18, nesting in 732 AGs, were collected, i.e. this species is polydomous. One colony inhabited 1 to 25 nests (median: 7). The size of single nests varied between 1 and 46 000 cm³ (median: 110 cm³). One colony occupied 6 cm³ to c. 62000 cm³ (median: 2460 cm³).

661 (> 90 %) of the 732 nests collected had epiphytes growing on them. Comparison of the two groups of nests, i.e. with and without epiphytes, revealed a difference in size: The ‘non-epiphyte nests’ (median: 16.8 cm³, range: 1-75 cm³) were significantly smaller (Mann-Whitney U-Test, $U=4651$, $p<0.001$) than the ‘epiphyte nests’ (median: 128.3 cm³; range: 1-46 000 cm³).

Crematogaster sp$_{\mathrm{KfmA}}$18 is monogynous. The number of workers, males, alate females and pupae was counted for six nests. From these numbers an average of 12 workers per cm³ was estimated, i.e. a medium-sized colony consists of about 30 000 workers, while a large colony may have up to half a million.

Nest architecture and carton composition

Different layers could be clearly distinguished in the architecture of *Crematogaster* sp$_{\mathrm{KfmA}}$18 carton nests. Generally there was a thin, outer layer, pale grayish-brown in color, consisting mainly of plant fibers. Underneath there was a zone of unidentified darker material with a few cuticular parts of prey insects and pseudococcids, and well-developed epiphyte roots. The inner part of the nest was dark brown (sometimes covered by an undetermined fungus) and chambered. Cuticular parts of pseudococcids were incorporated. Eggs, larvae and pupae of the ants were usually stored in the center. The material of this inner part was sturdy and contained only few epiphyte roots (Color Plate 4-1, p. 35).

Crematogaster $\mathrm{sp}_{\mathrm{KfmA}}18$ did not store dead colony members inside the nest but discarded them outside. The main building materials were plant fibers in 0.5-3 cm length, many of which were taken directly from dead leaves of the bamboo host.

Phorophyte

All nests of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ were located at the nodes of different species of giant bamboo, with *Gigantochloa scortechinii* as most abundant host plant (phorophyte, Color Plate 2-1, p. 9). Weissflog (2001) checked more than 1000 carton nests on trees other than giant bamboo all over Peninsular Malaysia and never found *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ (also s. Kaufmann et al., 2001). These results strongly suggest that *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ is a bamboo specialist. Interestingly, *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ never inhabited the hollow internodes of the phorophyte.

Trophobionts

Trophobionts (*Kermicus wroughtoni* Newstead, Pseudococcidae) were found underneath 89 % of the nests, sucking on the bamboo culm (Color Plate 4-1, p. 35). Their honeydew seemed to be one of the major food sources for *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ colonies. The epiphytes were always hemipteran-free. *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ moved its trophobiont to new feeding sites (underneath other nests) when the carton material covering the pseudococcids was experimentally removed.

Epiphyte partners

A list of epiphytes found in association with *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ is presented in Table 4-5. It contains 25 species from 16 genera and 7 families. The relative occurrences are noteworthy. Eight species were collected more than 20 times; they made up more than 90 % of all epiphytes associated with *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$. The asclepiad *Dischidia nummularia* (Color Plate 4-1, p. 35) was most abundant, occurring on 57 % of all nests of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$, and making up 45 % of all epiphytes found on the nests of this species. 63 of the 99 collected colonies were associated with *Dischidia nummularia*. Regarding the 378 nests with only one single epiphyte (‘single-epiphyte nests’), the significance of *Dischidia nummularia* becomes even clearer: 73 % were colonized by this species. These numbers are especially important when compared with the second most abundant epiphyte species, *Pyrossia lanceolata*. This fern was found on 9.6 % of all AGs of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$, but only on 2 % of AGs with only one epiphyte. 23 colonies (23 %) had *Pyrossia lanceolata* growing on at least one nest. Nos. 3 and 4 on the ‘hitlist’ of epiphytes, the two gesneriads *Aeschynanthus fecundus* (on 9.1 % of the nests; Color Plate 4-1) and *Aeschynanthus albidus* (on 7.2 % of the nests), occur in similar frequencies on single-epiphyte AGs (6 % and 5 %). Possibly more important for estimating the relative significance of the different plant species for *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ is the fact that in colonies with only one epiphyte species on all nests ('single species colonies', n=24), *Dischidia nummularia* was most abundant again at 58 %, followed by *Aeschynanthus fecundus* (16 %) and *Aeschynanthus albidus* (8 %), while none of the ferns and none of the orchids was found at all. Altogether 80 % of the *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ colonies were associated with at least one of the three most abundant non-fern species *Dischidia nummularia*, *Aeschynanthus albidus* and *Aeschynanthus fecundus*.

Table 4-5: Epiphyte species occurring on the nests of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ (Myrmicinae)
The table presents the total number of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ nests on which each epiphyte species was growing (# nests); of colonies with which it occurred (# colonies); of nests on which it was the only epiphyte species (# single-species nests); and of colonies with which it occurred as sole species (# single-species colonies).

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Araliaceae	*Schefflera* $\mathrm{sp}_{\mathrm{KfmE}}91$	3	2		
Asclepiadaceae	*Dischidia acutifolia*	37	9	14	1
	Dischidia albida	1	1		
	Dischidia fruticulosa	5	1		
	Dischidia nummularia.	418	63	276	14
	Hoya multiflora	1	1		
Gesneriaceae	*Aeschynanthus* $\mathrm{sp}_{\mathrm{KfmE}}122$	2	1	2	2
	Aeschynanthus albidus	53	13	18	1
	Aeschynanthus fecundus	67	18	24	4
Melastomataceae	*Pachycentria constricta*	12	4	9	
	Pachycentria glauca subsp. *maingayi*	25	6	3	1
Orchidaceae	*Acriopsis javanica*	8	2		
	Dendrobium crumentatum	1	1		
	Liparis lacerata	4	4		
Piperaceae	*Piper* $\mathrm{sp}_{\mathrm{KfmE}}89$	1	1		
Polypodiaceae	*Asplenium nidus*	1	1		
	Drymoglossum piloselloides	24	7	5	
	Lecanopteris sinuosa	3	2	1	
	Lepisorus longifolius	3	1		
	Platycerium coronarium	2	1	2	
	Platycerium ridleyi	1	1	1	
	Pyrossia floccigera	52	9	7	
	Pyrossia lanceolata	70	23	13	
Urticaceae	*Poikilospermum cordifolium*	8	6	1	1
	Poikilospermum microstachys	9	9	2	

Guests

Several arthropod guests inhabited *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ nests (Color Plate 4-2, p. 37). Cockroaches frequently lived in the innermost part (n=28). At least one species of staphilinid beetle, very similar to the ants in appearance, also lived inside the nests and additionally used the ant trails (n=12). A dolichoderine ant, *Dolichoderus* $\mathrm{sp}_{\mathrm{KfmA}}17$ was frequently observed nesting near *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ (n=14).

Two more spectacular myrmecophiles were a) stingless meliponine bees (*Trigona* (*Trigonella*) *moorei*[10]) (n=3 colonies) and b) geometrid moths (n=7 colonies; ~20 individuals). *Trigona* (*Trigonella*) *moorei* constructed its nest right in the middle of the ant nest, separated from the ants by a thick sticky layer called batumen. A long entrance tube, composed of raisin and wax, reached several centimeters out of the nest, ensuring the complete separation of both insect colonies. *Trigona* (*Trigonella*) *moorei* was not restricted to AGs of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ but frequently inhabited nests of the non-AG, carton-building myrmicine *Crematogaster* cf. *artifex* (Color Plate 4-2, p. 37).

The geometrid moth *Agathia cristifera* (Geometrinae) spent its complete juvenile life including pupation inside AGs of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$. The caterpillars fed on asclepiad epiphytes of the genus *Dischidia*, which frequently grow on these AGs. As these plants contain poisonous latex, the caterpillars need special digestive strategies to live on this diet. Like all guests, they also need special adaptations for their life in an ant nest, since the ants usually attack any nest-intruders. The caterpillars move extremely slowly, and the ants apparently do not perceive them. For resting, ecdysis and pupation, the caterpillars entered the ant nest. Pupae were frequently found in the innermost part of the AGs (Color Plate 4-2, p. 37).

Water storing capacity and nutritive value of the carton material

The dry weight of the carton material was 12.7 mg/cm³ ± 10.3 mg/cm³. Thus a large colony accumulated as much as 788 g of organic material. Water storing capacity was determined as 2.3 ± 0.4 (n=6).

The nutritive value of the carton material for the epiphytes was estimated using its relative contents (relative to total substrate weight) of ammonium, nitrate and phosphate (overview s. Table 4-6). Two groups of nests were used for the tests: those with extensive epiphyte growth and those with only little or no epiphyte growth. There were significant differences between these two groups in ammonium (t-test: $t = 4.49$, $p < 0.01$) and phosphate (t-test: $t = -8.16$, $p < 0.001$). The contents of both compounds were much higher in nests with little or no epiphyte growth (mean PO_4^{3-}: 1927.8 ± 603.5 mg/kg; mean NH_4^+: 14.9 ± 4.2 mg/kg) than in the other group (mean PO_4^{3-}: 63.9 ± 29.2 mg/kg; mean NH_4^+: 4.3 ± 1.4 mg/kg). There was no significant difference in nitrate. Concerning ammonium content, there was no significant difference between the carton material built by *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ and any of the tested comparison materials. The nitrate and phosphate values were significantly above those measured for the other materials (nitrate: t-test: $p_{max}<0.05$; $t_{min}=2.87$; phosphate: t-test: $p_{max}<0.01$; $t_{min}=-2.98$).

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[10] determined with Schwarz, 1939; Sakagami, 1975

Table 4-6: Chemical analysis of nesting substrate of several ant-garden species in comparison to a non-AG ant (*Crematogaster cf. artifex*), arboricolous termites, forest soil and bark of a variety of different trees.
For the tests, dry, pure substrate was homogenized and filled into tubes. For nitrate and ammonium tests, 5 g of substrate were used for each test, for phosphate only 2.5 g. For 'bark' and 'nests of *Diacamma* sp$_{\text{KfmA}}$111' it was difficult to obtain this amount of substrate. For this reason, bark from several trees and nesting material from several *Diacamma* colonies were combined for each test (Chapter 3.5.3, p. 17 ff.). Measured values are given as mg/kg in relation to total substrate weight.

	ammonium			nitrate			phosphate		
ant species	n	mean (mg/kg)	stdw (mg/kg)	n	mean (mg/kg)	stdw (mg/kg)	n	mean (mg/kg)	stdw (mg/kg)
Diacamma sp$_{\text{KfmA}}$111	3	8.5	4.2	3	348.0	357.8	3	623.3	565.4
Camponotus sp$_{\text{KfmA}}$9	23	15.3	6.6	24	22.0	15.8	20	107.2	167.2
Camponotus sp$_{\text{KfmA}}$240	1	27.6	-	1	90.0	-	1	300.0	-
Crematogaster sp$_{\text{KfmA}}$18	15	8.8	6.6	15	302.0	390.1	14	995.9	1050.7
without epiphytes	8	14.9	4.2	8	487.3	481.4	7	1927.8	603.5
with epiphytes	7	4.3	1.4	7	120.0	135.8	7	63.9	29.2
Pheidole sp$_{\text{KfmA}}$33	6	8.7	12.3	4	46.0	20.2	4	662.5	249.6
Philidris sp$_{\text{KfmA}}$37	6	3.2	0.7	4	73.4	33.5	4	1048.1	435.5
Crematogaster cf. *artifex*	6	7.3	2.9	6	22.2	7.2	6	115.9	226.0
nest of arboricolous termite	2	2.2	1.4	2	28.0	5.7	2	30.0	28.3
forest soil	6	15.0	14.5	6	27.9	13.9	6	27.5	31.8
Bark	2	1.9	0.4	2	31.9	16.0	2	175.0	35.4

Seed-carrying behavior

The behavior of *Crematogaster* sp$_{\text{KfmA}}$18 towards epiphyte seeds in comparison with several other items was studied in detail. Experiments were performed for the three most important epiphyte species growing on the AGs of *Crematogaster* sp$_{\text{KfmA}}$18, i.e. *Dischidia nummularia*, *Aeschynanthus fecundus* and *Aeschynanthus albidus*. All three species are primarily wind-dispersed, and their seeds thus bear a hairy appendage. Seeds (also wind-dispersed) of the asclepiad *Hoya elliptica*, which was found on the AGs of various species but never on those of *Crematogaster* sp$_{\text{KfmA}}$18, were tested in the same way. Primarily bird-dispersed fruits/seeds were represented by two species of *Pachycentria* (Melastomataceae) on AGs of *Crematogaster* sp$_{\text{KfmA}}$18. Their seeds were compared to a terricolous *Medinilla* sp. (Melastomataceae) with similar fruits, and seeds of both *Pachycentria* and *Medinilla* were tested before and after passage through a bird's gut (Table 4-7).

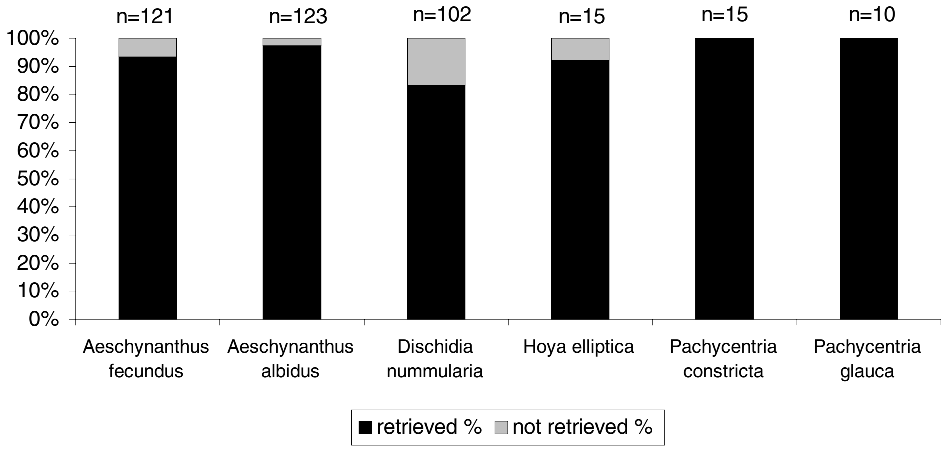

Figure 4-3: Comparison of seed-carrying behavior of *Crematogaster* sp$_{\mathrm{KfmA}}$18 towards different ant-garden epiphyte seeds

The behavior of *Crematogaster* sp$_{\mathrm{KfmA}}$18 did not vary between seeds of different epiphyte species (pairwise Fisher's exact test: $p_{\mathrm{min}} = 0.57$, Figure 4-3). Therefore, Figure 4-4 (with *Aeschynanthus fecundus* as tested seed) is representative for all the epiphyte seeds. A complete overview is given in Table 4-7. However, the two seed types[11] have to be considered separately.

A high percentage of all wind-dispersed epiphyte seeds, with or without hairy appendage, was carried into the nest. The only exception was *Hoya elliptica* with its relatively large seeds and extensive hairy appendage, though the result was not statistically significant. Here, the seeds were clearly more attractive after the appendage had been removed, for the simple reason that the ants had great difficulties in handling *Hoya* seeds with appendage. Generally, the ants removed all the hairy appendages before retrieving the seeds. Wind-dispersed non-epiphyte seeds (*Emilia sonchifolia* and *Ageratum conyzoides*, Asteraceae) were not retrieved, nor were threads and porcelain baits with pure solvent. The attractiveness of non-epiphyte seeds and baits with acetone extracts of the respective epiphyte species was comparable with that of the original seed. Pieces of paper, having a totally different shape, consistency and size compared to the original seeds, were also attractive when soaked with epiphyte seed extract (n=10). They were all retrieved as frequently as the original seed, while a control soaked with the solvent only was not attractive. I thus conclude that the main attractiveness in the seeds of the four wind-dispersed epiphyte species tested (and probably many others) must be of a chemical nature.

Seeds of berry-producing epiphytic species of *Pachycentria* (Table 4-7) and terricolous *Medinilla* were attractive both before and after passage through a bird's digestive tract. Workers of *Crematogaster* sp$_{\mathrm{KfmA}}$18 were frequently observed to retrieve small pieces of feces with or without seeds in them. However, there is some indication that a chemical attractant is also responsible at least for seed retrieval of *Pachycentria constricta*: Acetone extracts of seeds of

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[11] wind- and bird-dispersed seeds, also see Chapter 3.5.1, p. 13, and Chapter 12.6, p. 179

this species applied to porcelain baits were significantly more attractive than plain porcelain baits.

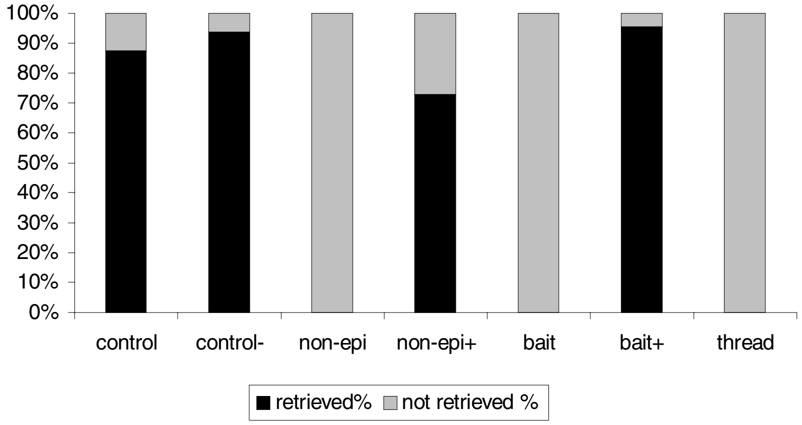


Figure 4-4: Seed-carrying behavior of *Crematogaster* sp$_{\mathrm{KfmA}}$18 towards *Aeschynanthus fecundus* (Gesneriaceae) and other test items.
control = complete seed of *Aeschynanthus fecundus*; control- = seed of *Aeschynanthus fecundus* without hairy appendage; non-epi = seed of non-epiphytic *Ageratum conyzoides* (Asteraceae) treated with pure acetone; non-epi+ = seed of *Ageratum conyzoides* treated with acetone-extract of *Aeschynanthus fecundus*; bait = porcelain bait in the size of *Aeschynanthus fecundus* treated with pure acetone; bait+ = porcelain bait in the size of *Aeschynanthus fecundus* treated with acetone-extract of *Aeschynanthus fecundus*; thread = piece of thread in the length of the hairy appendage of *Aeschynanthus fecundus*. # of items/type s. Table 4-7.

Additional experiments were performed in order to find out what happened after the ants carried seeds or other items into their nest. Therefore a large pool of seeds, baits with seed extracts and non-epiphyte seeds with seed extracts were offered next to a large nest for 48 hours. Following this period, the nest was quickly harvested and all inhabitants were killed using ethylacetate. The nests were carefully dissected (n=5), to locate the offered items in the different layers of the nest. All items were found either in the peripheral or in the second layer, in most cases securely attached to the substrate from inside the nest. It was remarkable that the non-epiphyte seeds and the baits were found in much lower numbers than the ‘real’ seeds, although especially the white porcelain baits were easy to find in the darker substrate. This might indicate that the ants notice their ‘error’ some time after they have retrieved the seeds and then dispose of them.

	Aeschynanthus fecundus, hairy appendage removed	*Aeschynanthus albidus*, control	*Aeschynanthus albidus*, hairy appendage removed	*Dischidia nummularia*, control	*Dischidia nummularia*, hairy appendage removed	*Hoya elliptica*, control	*Hoya elliptica*, hairy appendage removed	*Pachycentria constricta*, control	*P. constricta*, after passage through bird's gut	*Pachycentria glauca*, control	*P. glauca*, after passage through bird's gut	*Medinilla* sp., terricolous	*M.* sp., terricolous, after passage through bird's gut	non-epi + acetone extract *Ae. fecundus*	non-epi + acetone extract *Ae. albidus*	non-epi + acetone extract *D. nummularia*	porc.bait + acetone extract *Ae. fecundus*	porc.bait + acetone extract *Ae. albidus*	porc.bait + acetone extract *D. nummularia*	porc.bait + acetone extract *Hoya elliptica*	porc.bait + acetone extract *P. constricta* after passage through a bird's gut	thread	non-epi	non-epi + acetone	porcelain bait + acetone
Aeschynanthus fecundus, control (n=60)	n.s.	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	n.s.	n.s.	-	-	n.s.	-	-	-	-	*	*	*	*
Aeschynanthus fecundus, hairy appendage removed (n=121)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Aeschynanthus albidus, control (n=194)			n.s.	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	n.s.	-	n.s.	-	-	n.s.	-	-	-	*	*	*	*
Aeschynanthus albidus, hairy appendage removed (n=123)				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Dischidia nummularia, control (n=23)					n.s.	n.s.	-	n.s.	-	n.s.	-	n.s.	n.s.	-	-	n.s.	-	-	n.s.	-	-	*	*	*	*
Dischidia nummularia, hairy appendage removed (n=102)						-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Hoya elliptica, control (n=13)							n.s.	n.s.	-	n.s.	-	n.s.	-	-	-	-	-	-	-	n.s	-	*	*	*	*
Hoya elliptica, hairy appendage removed (n=15)								-	-	-	-	-	-	-	-	-	-	-	-	n.s	-	-	*	-	*
Pachycentria constricta, control (n=15)									n.s.	-	-	n.s.	-	-	-	-	-	-	-	-	n.s.	-	-	-	*
P. constricta, after passage through bird's gut (n=10)										-	n.s.	-	n.s.	-	-	-	-	-	-	-	n.s.	-	-	-	*
Pachycentria glauca, control (n=10)											n.s.	n.s.	-	-	-	-	-	-	-	-	-	*	*	*	*
P. glauca, after passage through bird's gut (n=10)												-	-	-	-	-	-	-	-	-	-	*	*	*	*
Medinilla sp., terricolous (n=20)													-	-	-	-	-	-	-	-	n.s.	-	-	-	*
Medinilla sp., terricolous, after passage through bird's gut (n=20)														-	-	-	-	-	-	-	n.s.	-	-	-	*
non-epi + acetone extract *Ae. fecundus* (n=28)															-	-	n.s.	-	-	-	-	-	-	*	*
non-epi + acetone extract *Ae. albidus* (n=20)																-	-	n.s.	-	-	-	-	-	*	*
non-epi + acetone extract *D. nummularia* (n=18)																	-	-	n.s.	-	-	-	-	*	*
porc.bait + acetone extract *Ae. fecundus* (n=15)																		-	-	-	-	-	-	-	*
porc.bait + acetone extract *Ae. albidus* (n=40)																			-	-	-	-	-	-	*
porc.bait + acetone extract *D. nummularia* (n=20)																				-	-	-	-	-	*
porc.bait + acetone extract *Hoya elliptica* (n=15)																					-	-	-	-	*
porc.bait + acetone extract *P. constricta* after passage through a bird's gut (n=15)																						-	-	-	*
thread (n=30)																							-	-	n.s.
non-epi (n=223)																								n.s.	n.s.
non-epi + acetone (n=96)																									n.s.
porcelain bait + acetone (n=195)																									

Table 4-7: Seed-carrying behavior of *Crematogaster* sp$_{\text{KfmA}}$18

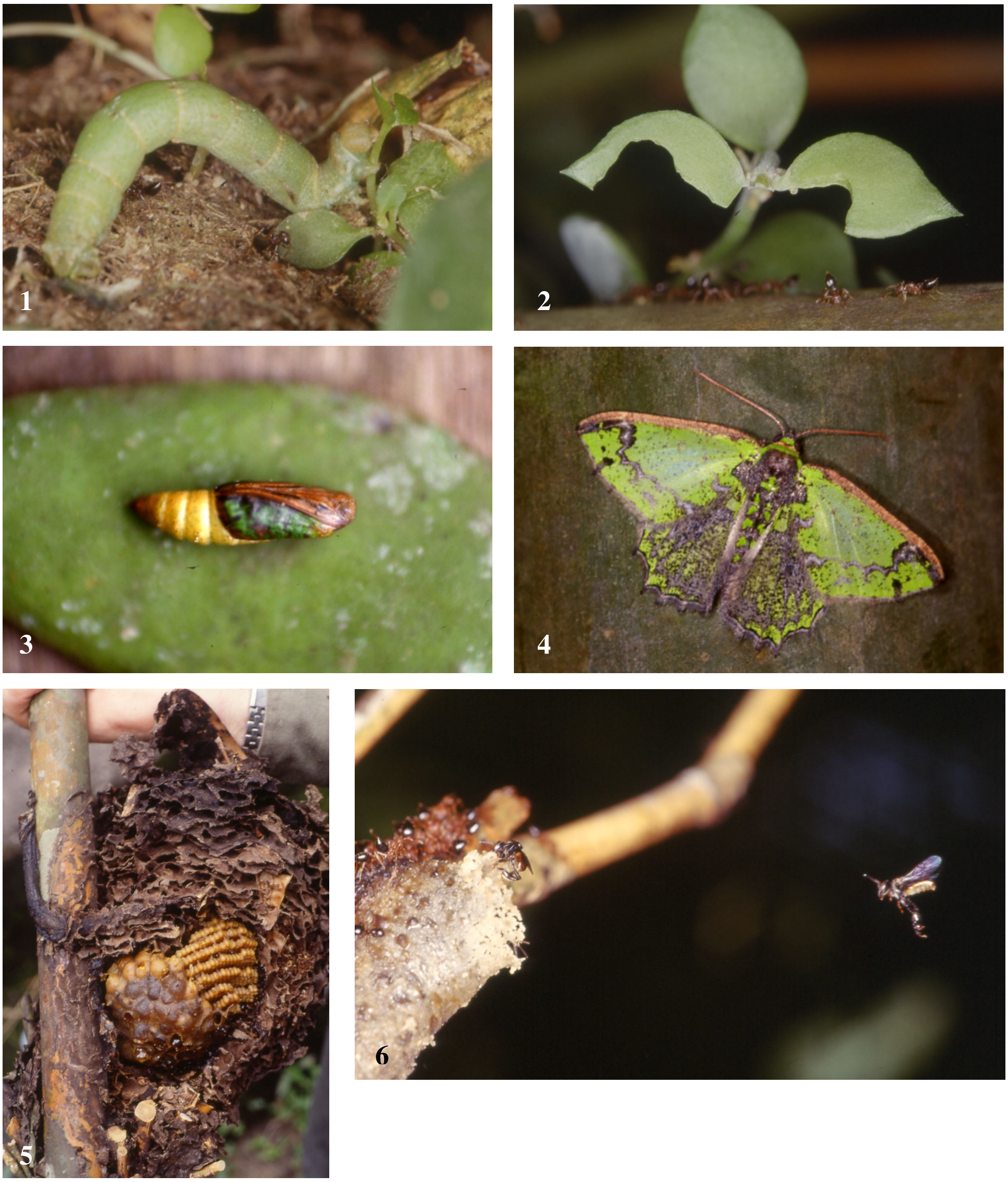
Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 97 pairwise comparisons

*: row item is significantly more attractive than column item; n.s.: no significant difference; -: not tested; non-epi=*Ageratum conyzoides* and *Emilia sonchifolia* (Asteraceae)

3-12 different items (n=3-5 of each item) were offered in a simultaneous setup in covered ice-cube boxes (s. Color-Plate 7-1, p. 121). These were installed next to a main trail of the colony, and the behavior of the ants was observed for a maximum of two hours. For further details s. Chapter 3.5.1, p. 13 and Chapter 12.7, p. 180.

Color Plate 4-1: Ant-gardens of *Crematogaster* sp$_{\text{KfmA}}$18

1: Ant-garden with *Dischidia nummularia* (Asclepiadaceae); 2: Ant-garden with *Aeschynanthus fecundus* (Gesneriaceae); 3: Structure of inner carton material; 4: Flowers of *Aeschynanthus fecundus*; 5: *Crematogaster* sp$_{\text{KfmA}}$18 feeding on honey; 6: *Kermicus wroughtoni* sucking on *Gigantochloa scortechinii* (Poaceae), tended by *Crematogaster* sp$_{\text{KfmA}}$18; 7: *Crematogaster* sp$_{\text{KfmA}}$18 collecting seeds of *Dischidia nummularia*



Color Plate 4-2: Guests in ant-gardens of *Crematogaster* sp$_{\text{KfmA}}$18
1: *Agathia cristifera* (Geometrinae, Geometridae), caterpillar; 2: Herbivore damage at *Dischidia nummularia* (Asclepiadaceae), caused by *Agathia cristifera*; 3: Pupa of *Agathia cristifera*; 4: Imago of *Agathia cristifera*; 5: Nest of *Trigona* (*Trigonella*) *moorei* (Meliponinae, Apidae), here in nest of *Crematogaster* cf. *artifex*; 6: *Trigona* (*Trigonella*) *moorei* at entrance tube

Crematogaster **sp$_{\text{KfmA}}$21**

A five partner (ants, epiphytes, phorophyte, parabiotic[12] *partner ants and trophobionts), widespread ant-garden system*

General biology of the ant

Crematogaster sp$_{\text{KfmA}}$21 colonies frequently lived in parabiosis with other ant species (n=33), mainly from the genus *Camponotus* (n=30), which usually were AG ant species also (n=26, see: *Camponotus* sp$_{\text{KfmA}}$9 and *Camponotus* sp$_{\text{KfmA}}$240). Nevertheless, as carton-building and seed-carrying behavior was observed in *Crematogaster* sp$_{\text{KfmA}}$21 as well, it is worthy of mention here.

Crematogaster sp$_{\text{KfmA}}$21 was found in Peninsular Malaysia, Southern Thailand and Sabah. It was rather aggressive but had no effective defense system against vertebrates. Though low outdoor activity was recorded during the day, the main activity period was at night.

Colony structure

Altogether 63 nests from 57 colonies were collected. 28 of these were ‘real’ nests, containing brood; the others were accumulations of workers within the nests of other ant species.

There is little information about colony size, number of nests, etc., but colonies can be very extensive, occupying several large trees as foraging area and maintaining many small nests within this area. In most cases the nests were located inside knotholes or other natural cavities in the host trees; only sometimes were they occupied by epiphytes (s. below). Some ‘nests’ were located in larger hollows right next to the *Camponotus* partner species so that the nest-sites could not be clearly distinguished. The two types of nests (only inhabited by *Crematogaster* sp$_{\text{KfmA}}$21 or in nest cavities of *Camponotus*) showed a significant difference in overall size (U-test: U=13.5, $p<0.005$). As this difference was only due to the partner species occupying the same nest, I will refer from now on to the nests inhabited by *Crematogaster* sp$_{\text{KfmA}}$21 only. When this restriction was applied and a new comparison was made between nests with epiphytes (n=20, median: 31 cm^3) and without epiphytes (n=8, median: 20 cm^3), no difference in size was found (U=8.5, p=0.45).

Phorophyte

Most nests of this ant species were located in the host trees of its parabiotic partner ant. No specificity with regard to certain tree species was detected.

Trophobionts

Crematogaster sp$_{\text{KfmA}}$21 shared its trophobionts with its parabiotic partner species. Additionally, it visited hemipterans on numerous plants within its foraging area.

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[12] For a definition of the term ‘parabiosis’, see p. 91

Epiphyte partners

A list of epiphyte species (n=21) living on the nests of *Crematogaster* sp$_{\text{KfmA}}$21 is given in Table 4-8. The asclepiad *Hoya mitrata* was most abundant (24 %, also s. *Camponotus* sp$_{\text{KfmA}}$240, p. 67), followed by two species of *Poikilospermum* (*P. microstachys*: 14 % and *P. cordifolium*: 10 %). These three epiphyte species were associated with 35 % of the colonies. The remaining ten epiphyte species represent eight plant genera and six families.

Table 4-8: Epiphyte species occurring on the nests of *Crematogaster* sp$_{\text{KfmA}}$21 (Myrmicinae)
The table presents the total numbers of *Crematogaster* sp$_{\text{KfmA}}$21 nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the only epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies).
As *Crematogaster* sp$_{\text{KfmA}}$21 is a species frequently occurring in parabiosis with several *Camponotus* spp., only the epiphytes growing on nests exclusively inhabited by *Crematogaster* sp$_{\text{KfmA}}$21 were counted here.

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Araliaceae	*Schefflera* sp$_{\text{KfmE}}$75	1	1	1	1
	Schefflera sp$_{\text{KfmE}}$91	1	1		
Asclepiadaceae	*Dischidia nummularia*	1	1	1	1
	Hoya lacunosa	1	1		
	Hoya micrantha	1	1		
	Hoya mitrata	5	5	5	5
Gesneriaceae	*Aeschynanthus* sp$_{\text{KfmE}}$122	1	1		
	Aeschynanthus albidus	2	1	2	2
Polypodiaceae	*Drynaria sparsisora*	1	1		
	Pyrossia lanceolata	1	1	1	1
Urticaceae	*Poikilospermum cordifolium*	2	2	2	2
	Poikilospermum microstachys	3	3	2	2
Zingiberaceae	*Hedychium longicornutum*	1	1		

Seed-carrying behavior

The seed-carrying behavior of *Crematogaster* sp$_{\text{KfmA}}$21 exactly resembled that of its partner-*Camponotus* species (s. *Camponotus* sp$_{\text{KfmA}}$9, p. 64, and *Camponotus* sp$_{\text{KfmA}}$240, p. 68), i.e. seeds of *Hoya elliptica*[13] were retrieved while seeds of *Dischidia nummularia* and *Aeschynanthus fecundus* were ignored. *Hoya elliptica*–sized porcelain baits with acetone extracts of any of these epiphytes were retrieved, while *Dischidia nummularia*-sized baits treated in the same way were ignored or discarded. Seeds of non-epiphytes were frequently (80 %) discarded; threads were ignored. Thus, a combination of chemical cues and seed size were responsible for selective seed-retrieval. Results of statistical comparisons are provided in Table 4-9.

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[13] *Hoya mitrata* could not be tested because no seeds were available.

Table 4-9: Seed-carrying behavior of *Crematogaster* sp$_{\text{KfmA}}$21

Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 35 pairwise comparisons

*: row item is significantly more attractive than column item; *[1]: column item is significantly more attractive than row item; n.s.: no significant difference; -: not tested; non-epi=*Ageratum conyzoides* (Asteraceae)

For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Dischidia nummularia	*Aeschynanthus fecundus*	*Hoya elliptica* baits large	*Dischidia nummularia*, baits large	*Aeschynanthus fecundus*, baits large	*Hoya elliptica* baits small	*Dischidia nummularia*, baits small	*Aeschynanthus fecundus*, baits small	non-epi	thread	porcelain bait with acetone
Hoya elliptica (n=18)	*	*	n.s.	n.s.	n.s.	*	*	*	*	*	*
Dischidia nummularia (n=20)		-	-	*^{1}	-	-	n.s.	-	-	-	n.s.
Aeschynanthus fecundus (n=20)			-	-	*^{1}	-	-	n.s.	-	-	n.s.
Hoya elliptica, porc.baits large (n=20)				n.s.	n.s.	n.s.	*	*	-	-	*
Dischidia nummularia, porc.baits large (n=20)					n.s.	-	*	-	-	-	*
Aeschynanthus fecundus, porc.baits large (n=20)						n.s.	-	*	-	-	*
Hoya elliptica, porc.baits small (n=20)							-	-	-	-	n.s.
Dischidia nummularia, porc.baits small (n=20)								-	-	-	n.s.
Aeschynanthus fecundus, porc.baits small (n=20)									-	-	n.s.
non-epi (n=20)										n.s.	n.s.
thread (n=20)											n.s.
porcelain bait + acetone (n=40)											

Crematogaster sp$_{\text{KfmA}}$200

A four partner (ants, epiphytes, phorophyte and uncovered trophobionts) monodomous ant-garden ant with intermorphs[14]

General biology of the ant

Crematogaster sp$_{\text{KfmA}}$200 was only found in Java. This morphospecies is most probably identical with *Crematogaster baduvi*, a species studied by Leeuwen early in the last century (Leeuwen and Leeuwen-Reijnvaan, 1913; Leeuwen, 1929 a, b, c). I have not seen the type specimens so far and therefore I still refer to the morphospecies mark. Studies in Java were very short-termed, consequently the set of data collected for this species is rather restricted. *Crematogaster* sp$_{\text{KfmA}}$200 was only slightly aggressive. It showed a basic activity during day and night, but no reliable data on activity rhythms were recorded. The workers were relatively

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[14] Color Plate 4-3, p. 49

monomorphic with an alitrunk length of c. 0.8 mm. The colonies also included up to 40 intermorphs (alitrunk length: 1.2 mm), i.e. females that are morphologically between workers and queens, possessing three ocelli on the head and active ovaria (Color Plate 4-3, p. 49).

Colony structure

21 colonies were recorded, ten of which were studied in detail. All dissected colonies of *Crematogaster* sp$_{\text{KfmA}}$200 were monogynous. *Crematogaster* sp$_{\text{KfmA}}$200 was usually monodomous, only one colony occupied two nests. The nests were rather small (range: 62-640 cm³; median: 272 cm³). Only two nests had no epiphytes growing on them, thus a statistical analysis of the difference between nests with and without epiphytes is impossible. It is noticeable though that these two nests both belonged to the same colony, and their size (62 and 78 cm³) was at the lowest end of the range. Mature colonies comprised about 10 000 workers.

Nest architecture and carton composition

The carton material, of which *Crematogaster* sp$_{\text{KfmA}}$200 constructed its nests, consisted of soil particles, plant fibers, and large numbers of small cuticular parts from prey insects (Color-Plate 4-3, p. 49). The outer surface had a fine-grained appearance with a fine net of roots running through it. In the interior, the nest-material was paper-like with only a few roots intruding, building up a chamber system, in which most of the brood and workers were found. In some cases, parts of the nests were built inside the stem of the host tree, in most cases in knotholes filled with carton material.

Phorophyte

The main host tree was coffee, but this is most probably only due to the forest structure in the research area. Many coffee trees had been planted in a secondary forest.

Trophobionts

Crematogaster sp$_{\text{KfmA}}$200 tended no trophobionts underneath the nests or on any of the epiphytes, but the ants visited trophobiosis sites on the leaves of their host trees and other plants in the surroundings.

Epiphyte partners

A list of epiphytes that were recorded on the nests of *Crematogaster* sp$_{\text{KfmA}}$200 is given in Table 4-10. Here we see two species making up 80 % of all epiphytes found: *Aeschynanthus albidus* (43 % of all colonies) and *Schefflera* sp$_{\text{KfmE}}$132 (48 % of all colonies). These two species are the only ones also occurring on ‘single-species nests’ and with ‘single-species colonies’. The remaining three species represent three genera and families.

Table 4-10: Epiphyte species occurring on the nests of *Crematogaster* sp$_{\text{KfmA}}$200 (Myrmicinae)
The table presents the total numbers of *Crematogaster* sp$_{\text{KfmA}}$200 nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the one epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies).

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Araliaceae	*Schefflera* sp$_{\text{KfmE}}$132	10	10	6	5
Asclepiadaceae	*Hoya* sp$_{\text{KfmE}}$133	2	2		
Gesneriaceae	*Aeschynanthus albidus*	9	9	3	2
Moraceae	*Ficus* sp$_{\text{KfmE}}$134	1	1		
Peperomiaceae	*Peperomia* sp$_{\text{KfmE}}$135	2	2		

Seed-carrying behavior

Seed-carrying behavior was tested (Table 4-11). *Aeschynanthus albidus* seeds were always carried into the nest less than 4 min after offering. Carrying *Hoya* sp$_{\text{KfmE}}$133 seeds was difficult for *Crematogaster* sp$_{\text{KfmA}}$200 because of the large size of the seeds. Nevertheless, in many cases *Hoya* sp$_{\text{KfmE}}$133 seeds were finally retrieved into the nest, while the seeds of non-epiphytic *Asclepias* sp. (Asclepiadaceae) and *Emilia sonchifolia* (Asteraceae) were always ignored.

Table 4-11: Seed-carrying behavior of *Crematogaster* sp$_{\text{KfmA}}$200
Test-statistics: Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 5 pairwise comparisons
*: row item is significantly more attractive than column item; n.s.: no significant difference; non-epi 1 was chosen because it was very similar in size to that of *Aeschynanthus albidus*, non-epi 2 was chosen because it was very similar in size to that of *Hoya* sp., and because the two species belong to the same plant family.
For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Aeschynanthus albidus	non-epi 1 (*Emilia sonchifolia*, Asteraceae)	non-epi 2 (*Asclepias* sp., Asclepiadaceae)
Hoya sp. (n=10)	n.s.	*	*
Aeschynanthus albidus (n=10)		*	*
non-epi 1 (*Emilia sonchifolia,* Asteraceae) (n=10)			-
non-epi 2 (*Asclepias* sp., Asclepiadaceae) (n=10)			

Pheidole **sp$_{\text{KfmA}}$33**

A widespread three partner (ant, epiphytes, phorophyte) ant-garden system[15]

General biology of the ant

Pheidole sp$_{\text{KfmA}}$33 was recorded in Peninsular Malaysia as well as on Borneo and Java. Thus, it is the most widespread AG species found in this study besides *Crematogaster* sp$_{\text{KfmA}}$21. It displayed a very low activity throughout day and night that could be stepped up whenever required, i.e. workers could quickly be recruited to valuable feeding sites. Workers of *Pheidole* sp$_{\text{KfmA}}$33 are dimorphic – as is typical for this genus. The alitrunk-length of a usual worker (0.7 mm) is about 1/3rd shorter than that of a soldier (1.1 mm). Aggressiveness is mainly low, the soldiers always escaped when disturbed while the normal-sized workers sometimes attacked. The adult worker : soldier ratio in a nest was about 1 : 1 (counted for six nests), while the ratio of pupae from worker : soldier was 16 : 1.

Colony structure

Altogether 37 colonies inhabited 52 nests. One colony lived in 1-5 nests (median: 1). The size of a nest ranged between 19 and 6300 cm³ (median: 218 cm³). One colony occupied 65 to 6300 cm³ (median: 370 cm³). Only one nest without epiphytes was recorded, and this nest was inside an internode of giant bamboo. In this case, therefore, it is impossible to compare nests with and without epiphytes. The nests were usually attached to the stem or located in a fork of a branch; small cavities (e.g. knotholes) underneath the AGs were frequently used as nest sites. When the phorophyte was a giant bamboo most of the nests were at the nodes, but there were also some inside the internodes.

Counting workers and soldiers for six nests, an average of about 3.5 (workers + soldiers)/cm³ was calculated. The medium size of a colony can be estimated at 1300 adult non-reproductives, with possibly about 20 000 of them in a large colony.

Nest architecture and carton composition

The nesting material of *Pheidole* sp$_{\text{KfmA}}$33 was rather fine grained, containing mainly soil particles and a high percentage of cuticular parts of prey insects as well as parts of dead colony members. The nests were completely penetrated by a dense root network; the substrate was compactly packed throughout the nest. Only small cavities, formed by roots, constituted space for brood and workers. In polycalic colonies the nests were usually connected by runways. These runways were also completely penetrated by roots and thus very stable.

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[15] Color Plate 4-3, p. 49

Phorophytes

Pheidole sp$_{\mathrm{KfmA}}$33 nested on several tree species. It was often found on *Piper aduncum* and *Gigantochloa scortechinii* in the Gombak area, but it also used at least five other tree species from several families (e.g. coffee and pine trees).

Trophobionts

Pheidole sp$_{\mathrm{KfmA}}$33 tended no trophobionts underneath its nests or on any other place; no trophobiotic behavior was observed.

Table 4-12: Epiphyte species occurring on the nests of *Pheidole* sp$_{\mathrm{KfmA}}$33 (Myrmicinae)
The table presents the total numbers of *Pheidole* sp$_{\mathrm{KfmA}}$33 nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the only epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies).

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Araliaceae	*Schefflera* sp$_{\mathrm{KfmE}}$132	6	5		
Asclepiadaceae	*Dischidia* sp$_{\mathrm{KfmE}}$115	4	4	2	2
	Dischidia albida	5	4	1	1
	Dischidia fruticulosa	1	1		
	Dischidia imbricata	1	1		
	Dischidia punctata	6	2	4	
	Hoya sp$_{\mathrm{KfmE}}$133	1	1		
	Hoya sp$_{\mathrm{KfmE}}$146	1	1		
Gesneriaceae	*Aeschynanthus* sp$_{\mathrm{KfmE}}$33	1	1	1	1
	Aeschynanthus albidus	13	11	3	
	Aeschynanthus fecundus	2	2	1	1
Lycopsida	*Lycopodium* sp$_{\mathrm{KfmE}}$125	1	1		
Melastomataceae	*Medinilla crassifolia*	2	2	1	1
	Pachycentria constricta	10	9	4	1
	Pachycentria glauca subsp. *maingayi*	4	3		
Moraceae	*Ficus* sp$_{\mathrm{KfmE}}$96	1	1		
	Ficus sp$_{\mathrm{KfmE}}$134	2	2		
Orchidaceae	*Acriopsis javanica*	1	1		
	Dendrobium crumentatum	1	1		
Peperomiaceae	*Peperomia* sp$_{\mathrm{KfmE}}$135	2	2		
Piperaceae	*Piper* sp$_{\mathrm{KfmE}}$89	1	1		
Polypodiaceae	*Asplenium nidus*	1	1	1	
	Drymoglossum piloselloides	1	1		
	Drynaria rigidula	1	1		
	Lecanopteris sinuosa	3	3	1	1
	Pyrossia floccigera	3	1	1	
	Pyrossia lanceolata	2	2	2	
Rubiaceae	*Hydnophytum formicarium*	1	1	1	1
Urticaceae	*Poikilospermum microstachys*	4	4	1	

Epiphyte partners

29 epiphyte species from 19 genera and 13 families were growing on the nests of *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}33$ (n=82, Table 4-12). *Aeschynanthus albidus* was most frequently found (16 %), followed by *Pachycentria constricta* (12 %). The abundance of all the other species ranged between 1 and 7 %. 'Single species nests' (n=24) were occupied by *Pachycentria constricta* (17 %), *Dischidia punctata* (17 %), and *Aeschynanthus albidus* (12.5 %) in most cases. With 'single species colonies' (n=9), eight different epiphyte species were found; *Aeschynanthus albidus* was not among them.

Water storing capacity and nutritive value of the carton material

The average dry weight of the nesting material was 40.8 ± 13.0 mg/cm³ (n=6). A medium sized colony accumulated about 15 g, a large colony up to 250 g of substrate for epiphytes. Water storing capacity was 3.3 ± 0.4 (n=6).

The content of ammonium, phosphate and nitrate is presented in Table 4-6, p. 31. The nesting substrate of *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}33$ contained significantly more phosphate (mean PO_4^{3-}: 662.5 ± 249.6 mg/kg) than forest soil (mean PO_4^{3-}: 27.5 ± 31.8 mg/kg) or nests of *Crematogaster* cf. *artifex* (mean PO_4^{3-}: 115.9± 226.0 mg/kg; t-test: $p_{max}<0.01$, $t_{min}=3.6$). There were no significant differences in nitrate and ammonium content compared to any of the other tested substrates.

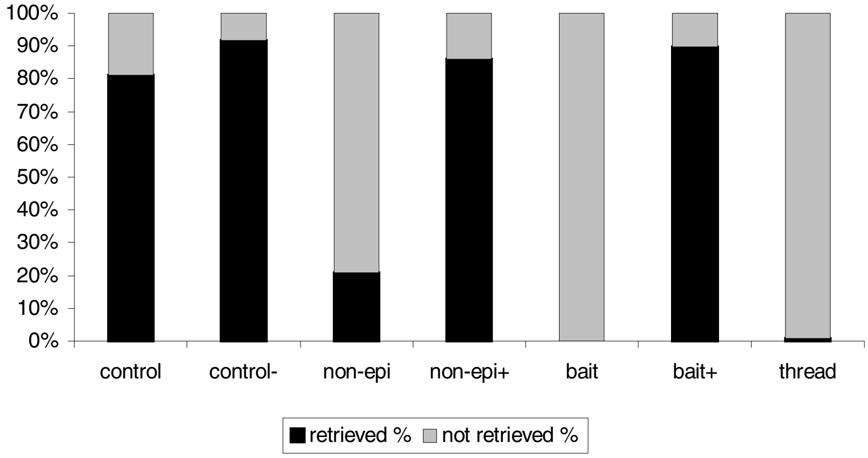


Figure 4-5: Seed-carrying behavior of *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}33$ towards *Aeschynanthus fecundus* (Gesneriaceae) and other test items.
control = complete seed of *Aeschynanthus fecundus*; control- = seed of *Aeschynanthus fecundus* without hairy appendage; non-epi = seed of *Ageratum conyzoides* (Asteraceae) treated with pure acetone; non-epi+ = seed of *Ageratum conyzoides* treated with acetone-extract of *Aeschynanthus fecundus*; bait = porcelain bait in the size of *Aeschynanthus fecundus* treated with pure acetone; bait+ = porcelain bait in the size of *Aeschynanthus fecundus* treated with acetone-extract of *Aeschynanthus fecundus*; thread = piece of thread in the length of the hairy appendage of *Aeschynanthus fecundus*. # of items/type s. Table 4-13.

Seed-carrying behavior

In extensive seed-carrying experiments (Table 4-13) *Pheidole* $sp_{KfmA}33$ showed a clear preference for the tested epiphyte seeds compared to non-epiphyte seeds (Figure 4-5). However, seeds of non-epiphytes were significantly more attractive than porcelain baits.

The carrying behavior of *Pheidole* $sp_{KfmA}33$ did not distinguish between the three wind-dispersed epiphyte species *Aeschynanthus fecundus*, *Aeschynanthus albidus* and *Dischidia nummularia*. *Hoya elliptica*-seeds were never retrieved when offered completely because the ants could not handle the large seeds with their extensive hairy appendage. Once the appendage was removed, the attractiveness was comparable to that of all the other epiphyte seeds. When baits and non-epiphyte seeds (*Ageratum conyzoides* and *Emilia sonchifolia*) were treated with extracts of any of the epiphyte seeds, their attractiveness was similar to that of the original epiphyte seeds. Threads were never retrieved.

Seeds of bird-dispersed (terricolous) *Medinilla* sp. and (epiphytic) *Pachycentria constricta* were attractive both before and after passage through a bird's gut (Table 4-13). Seeds from bird droppings were generally very attractive.

Primarily bird-dispersed seeds were thus probably attractive because of their nutritive properties, while chemical cues seemed to account for the retrieval of primarily wind-dispersed seeds. However, seeds in general were apparently distinguished from other items.

Nests were dissected 48 hrs after a large pool of test items had been offered (Chapter 4.1.2.1, p. 31). Parts of the retrieved seeds (especially non-epiphyte seeds) were found on the surface of the nests, where they were used as building material. Others were discovered deep inside the nests, next to the nest chambers of *Pheidole* $sp_{KfmA}33$. For example, porcelain baits with extract were found in this area.

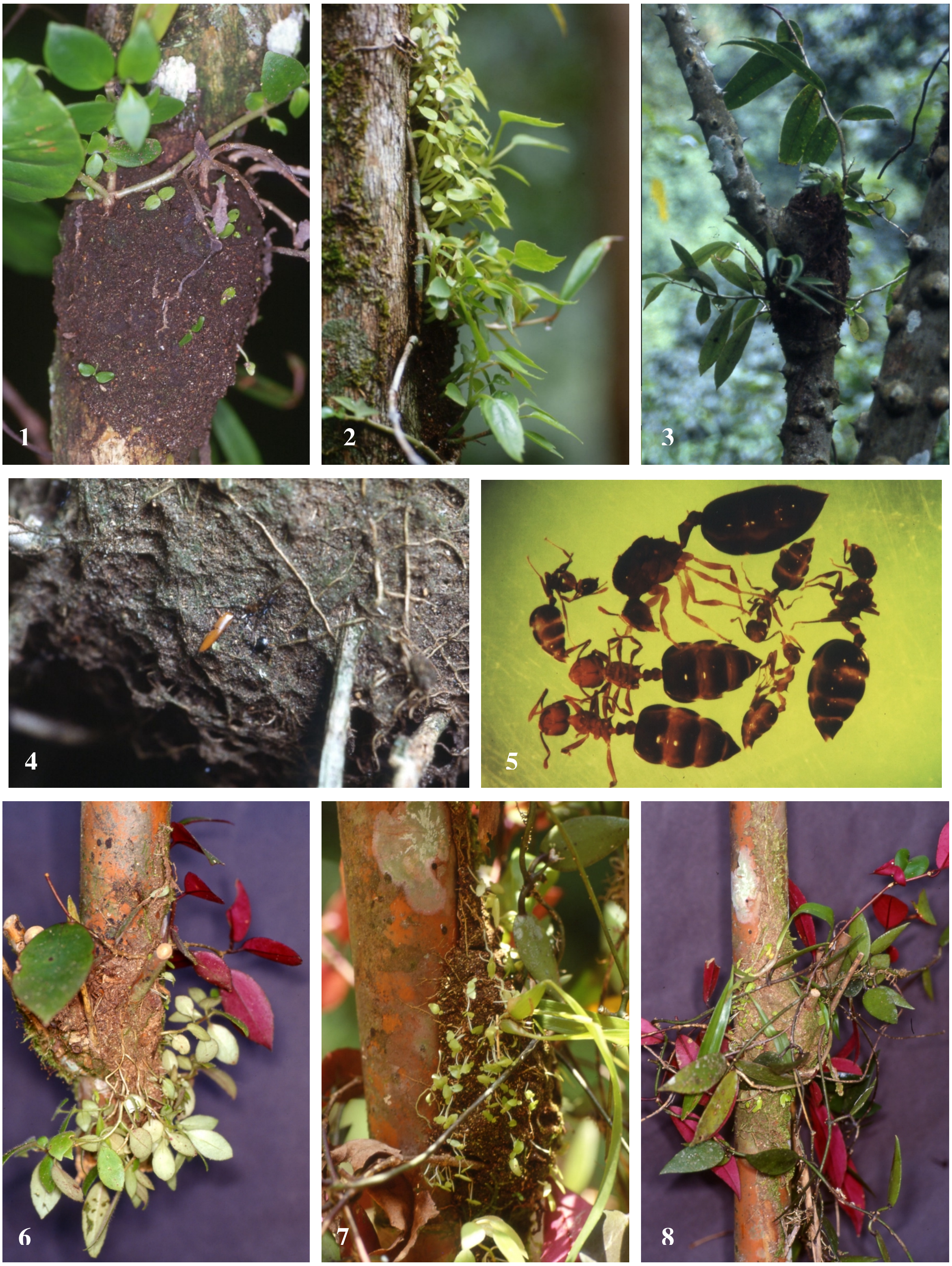
Table 4-13: Seed-carrying behavior of *Pheidole* sp$_{\text{KfmA}}$33

Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 75 pairwise comparisons

*: row item is significantly more attractive than column item; $*^1$: column item is significantly more attractive than row item; n.s.: no significant difference

For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Aeschynanthus fecundus, hairy appendage removed	*Aeschynanthus albidus*, control	*Aeschynanthus albidus*, hairy appendage removed	*Dischidia nummularia*, control	*Dischidia nummularia*, hairy appendage removed	*Hoya elliptica*, control	*Hoya elliptica*, hairy appendage removed	*Pachycentria constricta*, control	*P. constricta*, after passage through bird's gut	*Medinilla* sp., terricolous	*M.* sp., terricolous, after passage through bird's gut	non-epi + acetone extract *Ae. fecundus*	non-epi + acetone extract *D. nummularia*	porc.bait + acetone extract *Ae. fecundus*	porc.bait + acetone extract *Ae. albidus*	porc.bait + acetone extract *D. nummularia*	porc.bait + acetone extract *Hoya elliptica*	thread	non-epi	non-epi + acetone	porcelain bait + acetone
Aeschynanthus fecundus, control (n=115)	n.s.	n.s.	-	n.s.	-	*	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-	-	-	*	*	*	*
Aeschynanthus fecundus, hairy appendage removed (n=40)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Aeschynanthus albidus, control (n=40)			n.s.	n.s.	-	*	-	n.s.	-	n.s.	-	-	-	-	n.s.	-	-	*	*	*	*
Aeschynanthus albidus, hairy appendage removed (n=20)				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Dischidia nummularia, control (n=50)					n.s.	*	-	n.s.	-	n.s.	-	-	n.s.	-	-	n.s.	-	*	*	*	*
Dischidia nummularia, hairy appendage removed (n=30)						-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Hoya elliptica, control (n=15)							$*^1$	$*^1$	-	$*^1$	-	-	-	-	-	-	$*^1$	n.s.	n.s.	n.s.	n.s.
Hoya elliptica, hairy appendage removed (n=15)								n.s.	-	n.s.	-	-	-	-	-	-	n.s.	*	*	*	*
Pachycentria constricta, control (n=30)									n.s.	n.s.	-	-	-	-	-	-	-	-	-	-	*
P. constricta, after passage through bird's gut (n=10)										n.s.	n.s.	-	-	-	-	-	-	-	-	-	*
Medinilla sp., terricolous (n=20)											n.s.	-	-	-	-	-	-	-	-	-	*
Medinilla sp., terricolous, after passage through bird's gut (n=20)												-	-	-	-	-	-	-	-	-	*
non-epi + acetone extract *Ae. fecundus* (n=30)													-	n.s.	-	-	-	-	-	*	*
non-epi + acetone extract *D. nummularia* (n=30)														-	-	n.s.	-	-	-	*	*
porc.bait + acetone extract *Ae. fecundus* (n=20)															-	-	-	-	-	-	*
porc.bait + acetone extract *Ae. albidus* (n=40)																-	-	-	-	-	*
porc.bait + acetone extract *D. nummularia* (n=20)																	-	-	-	-	*
porc.bait + acetone extract *Hoya elliptica* (n=15)																		-	-	-	*
thread (n=45)																			-	-	n.s.
non-epi (n=90)																				-	*
non-epi + acetone (n=100)																					*
porcelain bait + acetone (n=100)																					



Color Plate 4-3: Ant-gardens of *Crematogaster* sp$_{\mathrm{KfmA}}$200 and *Pheidole* sp$_{\mathrm{KfmA}}$33
1-3: Ant-gardens of *Crematogaster* sp$_{\mathrm{KfmA}}$200; 4: Carton surface of *Crematogaster* sp$_{\mathrm{KfmA}}$200; 5: Workers, intermorphs and queens of *Crematogaster* sp$_{\mathrm{KfmA}}$200 (photo: A. Buschinger); 6-8: Ant-gardens of *Pheidole* sp$_{\mathrm{KfmA}}$33

4.1.2.2. Dolichoderinae

The Dolichoderinae are known as successful and abundant arboricolous ant-subfamily. However, in this study, only species of one dolichoderine genus, i.e. *Philidris*, were identified as AG mutualists. *Philidris* is entirely arboricolous (Shattuck, 1992). *Philidris cordatus* has frequently been described as a partner of typical 'ant-house epiphytes' (for example *Myrmecodia tuberosa*, *Hydnophytum formicarium* (Rubiaceae), *Lecanopteris sinuosa* (Polypodiaceae), and *Dischidia major* (Asclepiadaceae)). In this study, six morphospecies of *Philidris* were distinguished. Due to their extremely polymorphic habit it was difficult to find reliable separating characteristics. Morphospecies-splitting was handled rather conservatively, and therefore a specimen defined as belonging to one morphospecies might turn out to belong to any of two or more different species. One morphospecies, *Philidris* sp_{KfmA}37 was rarely found as partner of ant-house epiphytes but in most cases had other epiphytes growing on its nests (s. below). The remaining five morphospecies were frequently associated with ant-house epiphytes. One of these 'ant-house ants', *Philidris* sp_{KfmA}160, will be compared to the 'non-ant-house ant' *Philidris* sp_{KfmA}37. No data will be presented for other four species, which are all very similar to *Philidris* sp_{KfmA}160 in their ecology.

Philidris **sp_{KfmA}37**

A four partner system (ant, epiphytes, phorophyte, trophobionts) involving mainly non-ant-house epiphytes[16]

General biology of the ant

Philidris sp_{KfmA}37 was found in Peninsular Malaysia and Southern Thailand. It was polymorphic with an alitrunk size of 0.9 to 1.6 mm, the queens' alitrunk was 2.9 mm long. *Philidris* sp_{KfmA}37 reacted aggressively to any disturbance, using an unpleasant chemical secretion that might be an effective protection against vertebrates.

A basic outdoor activity was recorded throughout the day, but activity increased by factor ten during the night.

Colony structure

29 colonies with a total of 55 carton nests were collected. One single colony lived in 1-11 nests (median: 1). These numbers underestimate the true number of nests, because in most cases it was impossible to collect all nests.

Frequently one *Philidris* sp_{KfmA}37 colony occupied more than one phorophyte. Most of the nests were located on large branches or the stem of trees. Colonies using bamboo as host plant sometimes nested inside the internodes, but then these were also filled with carton structures.

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[16] Color Plate 4-4, p. 59

The nests were connected by runways, which often covered large areas on the surfaces of stems or branches. On 46 nests (84 %), epiphytes were growing. These nests were significantly larger (range: 3.1-2488 cm³; median: 63 cm³; U-Test: U=12.5, $p<0.001$) than those without epiphytes (range: 3.1-12.6 cm³; median: 9.4 cm³).

Based on the number of workers and brood counted for six nests, an average of seven adult workers/cm³ was estimated, i.e. a large colony may contain about 18 000 adult workers.

Nest architecture and carton composition

Nests of *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}37$ were chambered inside, with the walls consisting of rather thick and compact substrate accumulations penetrated by epiphyte roots. The carton material was fine grained and contained mainly soil particles as well as short (c. 0.5 mm) plant fibers. Numerous tiny cuticular parts of arthropods were also included.

Phorophytes

Philidris $\mathrm{sp}_{\mathrm{KfmA}}37$ was not specialized on certain phorophyte species (at least 10 different tree species were used). The suitability of the tree as host for hemipteran trophobionts appeared to be the most important criterion. Trees with either a rough bark or other structures facilitating carton construction were especially favorable phorophytes.

Trophobionts

Trophobionts were frequently covered by flat and extensive carton structures on the phorophyte as well as on neighboring plants. They were also found underneath 80 % of the nests of *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}37$. When the carton material covering the trophobionts was experimentally removed, *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}37$ was never observed moving them to new feeding sites.

Epiphyte partners

Two species of epiphytes were distinctly more abundant than the other ones (n=61, list of species s. Table 4-14): *Dischidia nummularia* (20 % of all epiphytes, 21% of colonies) and *Pyrossia longifolia* (21 % of all epiphytes, 14 % of colonies). The abundance of all the other species, belonging to 18 species, 12 genera, and 6 families, ranged between 1 and 4, i.e. 2-7 %. On ‘single-epiphyte nests’ (n=22), *Dischidia nummularia* (n=5) and *Pyrossia lanceolata* (n=7) were most abundant again, followed by *Lecanopteris sinuosa* (n=3) and *Dischidia major* (n=2). Only four ‘single epiphyte colonies’ were collected, three of which were colonizing carton nests and the rhizome of the ant-house fern *Lecanopteris sinuosa*, the latter being found in association with *Hoya lacunosa*.

Table 4-14: Epiphyte species occurring on the nests of *Philidris* sp$_{\text{KfmA}}$37 (Dolichoderinae)
The table presents the total numbers of *Philidris* sp$_{\text{KfmA}}$37 nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the only epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies).

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Araliaceae	*Schefflera* sp$_{\text{KfmE}}$91	1	1		
Asclepiadaceae	*Dischidia hirsuta*	1	1		
	Dischidia major	2	1	2	
	Dischidia nummularia	12	6	5	
	Dischidia subulata	1	1	1	
	Hoya elliptica	1	1		
	Hoya lacunosa	2	2	1	1
Gesneriaceae	*Aeschynanthus* sp$_{\text{KfmE}}$122	2	2	1	
	Aeschynanthus albidus	3	2		
	Aeschynanthus fecundus	2	1	1	
Melastomataceae	*Pachycentria constricta*	4	3		
	Pachycentria glauca subsp. *maingayi*	4	3		
Polypodiaceae	*Drymoglossum piloselloides*	2	2		
	Drynaria sparsisora	1	1	1	
	Lecanopteris sinuosa	3	3	3	3
	Lepisorus longifolius	1	1		
	Platycerium ridleyi	2	2		
	Pyrossia lanceolata	13	4	7	
Urticaceae	*Poikilospermum cordifolium*	2	1		
	Poikilospermum microstachys	2	2		

Guests

Two different guest organisms were found in the AGs of *Philidris* sp$_{\text{KfmA}}$37. The geometrid moth *Agathia cristifera* (Geometrinae) was associated with this species in the same way as with *Crematogaster* sp$_{\text{KfmA}}$18 (n=4) (Chapter 4.1.2.1, p. 29). A myrmecophilous cricket (*Myrmecophila* sp., Myrmecophilidae) was integrated into the colony and participated in trophallaxis (n=2).

Water storing capacity and nutritive value of the carton material

Dry weight of the nest-substrate was 15.9 mg/cm³. An average sized colony accumulated about 5 g, a large colony almost 100 g. Water storing capacity was determined as 2.9 ± 0.3 (n=6).

There was more phosphate (mean: 1048.1 ± 435.5 mg/kg) in the substrate of *Philidris* sp$_{\text{KfmA}}$37 than in the nests of *Crematogaster* cf. *artifex* (mean: 115.9 ± 226.0 mg/kg) and forest soil (mean: 27.5 ± 31.8 mg/kg; t-test: $p_{max}<0.01$; $t_{min}=4.5$). A comparison of the tested substrates showed no differences in ammonium and nitrate contents (Table 4-6, p. 31).

Seed-carrying behavior

In extensive seed-carrying experiments, *Philidris* $sp_{KfmA}37$ showed a clear preference for epiphyte seeds compared to seeds of non-epiphytes, porcelain baits, and threads. Seeds of the two *Aeschynanthus* spp. (Gesneriaceae) were significantly more attractive than those of *Dischidia nummularia* and *Hoya elliptica* (Asclepiadaceae). Removal of the hairy appendage of *D. nummularia* seeds significantly increased their attractiveness. This was not the case for *Hoya elliptica*. The attractiveness of non-epiphyte seeds and porcelain baits with acetone extract of any of the four tested wind-dispersed epiphyte species was comparable with that of the original seeds, i.e. chemical cues were apparently responsible for selective seed-retrieval. Seeds of bird-dispersed *Pachycentria glauca* subsp. *maingayi* and *Pachycentria constricta* as well as seeds of a terricolous *Medinilla* were retrieved both before and after passage through a bird's gut. Experiments to determine the location of seeds inside the nests (Chapter 4.1.2.1, p. 31) revealed that all items were directly used for building new carton constructions (Figure 4-6), and were therefore located in the outer part of the nest.

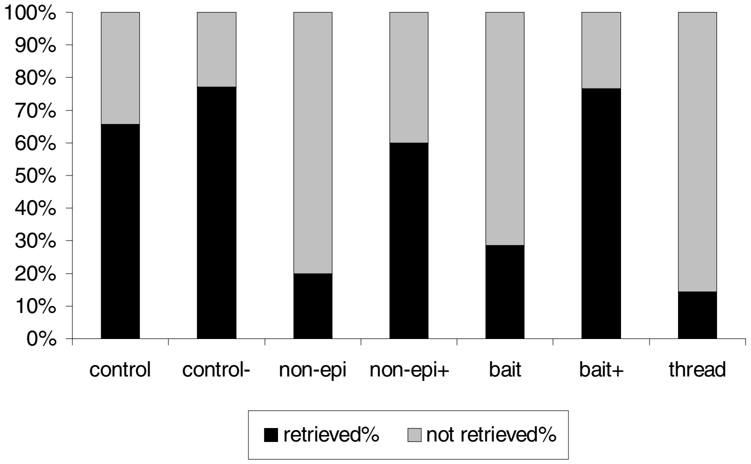

Figure 4-6: Seed-carrying behavior of *Philidris* $sp_{KfmA}37$ towards *Aeschynanthus fecundus* (Gesneriaceae).
control = complete seed of *Aeschynanthus fecundus*; control- = seed of *Aeschynanthus fecundus* without hairy appendage; non-epi = seed of *Ageratum conyzoides* treated with pure acetone; non-epi+ = seed of *Ageratum conyzoides* treated with acetone-extract of *Aeschynanthus fecundus*; bait = porcelain bait in the size of *Aeschynanthus fecundus* treated with pure acetone; bait+ = porcelain bait in the size of *Aeschynanthus fecundus* treated with acetone-extract of *Aeschynanthus fecundus*; thread = piece of thread in the length of the hairy appendage of *Aeschynanthus fecundus*. # of items/type s. Table 4-15.

Table 4-15: Seed-carrying behavior of *Philidris* sp$_{\text{KfmA}}$37

Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 90 pairwise comparisons

*: row item is significantly more attractive than column item; *^{1}: column item is significantly more attractive than row item; n.s.: no significant difference

For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Aeschynanthus fecundus, hairy appendage removed	*Aeschynanthus albidus*, control	*Aeschynanthus albidus*, hairy appendage removed	*Dischidia nummularia*, control	*Dischidia nummularia*, hairy appendage removed	*Hoya elliptica*, control	*Hoya elliptica*, hairy appendage removed	*Pachycentria constricta*, control	*P. constricta*, after passage through bird's gut	*Medinilla* sp., terricolous	*M.* sp., terricolous, after passage through bird's gut	non-epi + acetone extract *Ae. albidus*	non-epi + acetone extract *D. nummularia*	porc.bait + acetone extract *Ae. albidus*	porc.bait + acetone extract *D. nummularia*	porc.bait + acetone extract *Hoya elliptica*	thread	non-epi	non-epi + acetone	porcelain bait + acetone
Aeschynanthus fecundus, control (n=160)	n.s.	n.s.	-	*	n.s.	*	*	n.s.	-	n.s.	-	n.s.	*	n.s.	*	n.s.	*	*	*	*
Aeschynanthus fecundus, hairy appendage removed (n=25)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Aeschynanthus albidus, control (n=55)			n.s.	n.s.	-	*	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-	-	*	*	*	*
Aeschynanthus albidus, hairy appendage removed (n=55)				*	n.s.	*	*	-	-	-	-	-	-	-	-	-	-	*	-	*
Dischidia nummularia, control (n=40)					*^{1}	n.s.	-	*^{1}	-	*^{1}	-	-	n.s.	-	n.s.	-	n.s.	n.s.	n.s.	n.s.
Dischidia nummularia, hairy appendage removed (n=40)						-	-	-	-	-	-	-	-	-	-	-	-	*	-	*
Hoya elliptica, control (n=28)							n.s.	*^{1}	-	*^{1}	-	-	-	-	-	n.s.	n.s.	n.s.	n.s.	n.s.
Hoya elliptica, hairy appendage removed (n=20)								-	-	-	-	-	-	-	-	-	-	n.s.	-	n.s.
Pachycentria constricta, control (n=15)									n.s.	n.s.	-	-	-	-	-	-	*	*	*	*
P. constricta, after passage through bird's gut (n=15)										n.s.	n.s.	-	-	-	-	-	-	*	-	*
Medinilla sp., terricolous (n=20)											-	-	-	-	-	-	-	-	-	*
Medinilla sp., terricolous, after passage through bird's gut (n=15)												-	-	-	-	-	-	-	-	*
non-epi + acetone extract *Ae. albidus* (n=20)													n.s.	n.s.	-	n.s.	-	-	*	*
non-epi + acetone extract *D. nummularia* (n=30)														n.s.	n.s.	n.s.	-	-	*	*
porc.bait + acetone extract *Ae. albidus* (n=55)															n.s.	n.s.	-	-	-	*
porc.bait + acetone extract *D. nummularia* (n=37)																n.s.	-	-	-	*
porc.bait + acetone extract *Hoya elliptica* (n=55)																	-	-	-	*
thread (n=55)																		-	-	n.s.
non-epi (n=135)																			n.s.	n.s.
non-epi + acetone (n=135)																				n.s.
porcelain bait + acetone (n=150)																				

Philidris sp$_{\text{KfmA}}$160

A four partner system (ants, epiphytes, phorophyte, trophobionts), mainly with 'ant-house' epiphytes[17] *in heath forests*

General biology of the ant

Philidris sp$_{\text{KfmA}}$160 was the species of this genus most frequently found. It occurred in Sabah and Sarawak. *Philidris* sp$_{\text{KfmA}}$160 was polymorphic with an alitrunk size ranging from 0.8 mm to 1.2 mm. The ants were fairly aggressive and used a potent chemical defense that could cause trouble in (human) breathing. A basic outdoor activity was recorded throughout the day, but activity increased by factor ten during the night.

Colony structure

Altogether, 188 nests of 62 colonies were collected. One colony nested in 1-12 nests (median: 2), frequently on more than one host tree. Again, these numbers underestimate the true nest number per colony. Nests could not be clearly distinguished, because an extensive system of runways connected the whole nesting area. Accumulations of feeding sites with trophobionts and several domatia-bearing epiphytes were counted as one nest. Single colonies occupied a nesting space of 4-32 000 cm^3 (median: 576 cm^3). A comparison of the size of nests with ($n=169$) and without ($n=19$) epiphytes showed that the first group was significantly more voluminous (U-test: $U=112.5$, $p<0.01$; range: 1-23 600 cm^3, median: 217 cm^3) than the second (range: 0.5-151 cm^3, median: 7.3 cm^3). The tuber-volume of ant-house epiphytes was counted as nest volume.

As most *Philidris* sp$_{\text{KfmA}}$160 colonies (c. 92 %) were associated with 'ant-house epiphytes', it was especially interesting to see how colonies were established, i.e. whether the ants were dependent on the epiphytes from the beginning, or whether they started a colony without epiphytes and incorporated epiphyte seeds in their carton nests at a later stage. For this purpose 12 colonies were dissected, all carton material being removed and all epiphytes cut into thin slices, and a careful search was made for queens. All these colonies were monogynous, and the queen was never located in a plant domatium but always in carton structures near the bark of the host tree. Usually, the carton was extremely thick in this region. Workers and brood were always found inside carton structures and also inside domatia. Three small colonies (<1000 workers) were discovered with no epiphytes growing on their nests. Furthermore, two founding queens were hiding in bark crevices with very little carton material.

Nest architecture and carton composition

The nest architecture of most *Philidris* sp$_{\text{KfmA}}$160 colonies was widely determined by their epiphyte partners (s. below). However, even in colonies, in which a majority of the colony nested in the domatia of the associated ant-house epiphytes, parts of the colony also nested in

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[17] Color Plate 4-4, p. 59

bark crevices underneath thick carton layers. The carton was fine-grained and contained mainly soil particles, short plant fibers and cuticular parts of a variety of arthropods. The structure of the carton buildings was strongly influenced by the plants growing on them, and by the bark structure of the phorophyte. For example, the rhizome of *Lecanopteris sinuosa* frequently served as scaffolding for carton that was then built between rhizome and phorophyte or several rhizome parts (Color Plate 4-4, p. 59). *Philidris* sp$_{\text{KfmA}}$160 was clearly not able to build free carton nests independently of at least basally preformed scaffolding.

Phorophytes

More or less all the trees occurring in the habitat of *Philidris* sp$_{\text{KfmA}}$160 were used as host trees, i.e. no host specificity was detected. However, important characteristics were their suitability as food plant for trophobionts, and either a bark structure facilitating carton construction or other forms of tree cavities (e.g. knotholes).

Trophobionts

Trophobionts were found sucking on the host trees and adjacent plants, sometimes also inside tubers of ant-house epiphytes. They were always covered by extensive carton shelters. *Philidris* sp$_{\text{KfmA}}$160 was never observed moving its trophobionts to new feeding sites when the carton material covering them was experimentally removed,.

Epiphyte partners

252 epiphytes, comprising 23 species, 14 genera, and 6 families, were recorded (Table 4-16). 209 (83 %; 7 species, 5 genera) belonged to the group of ant-house epiphytes, with the rubiaceous species *Myrmecodia tuberosa* (Color Plate 4-4, p. 59), *Hydnophytum formicarium* and *Hydnophytum* sp$_{\text{KfmE}}$104 as predominant species (59 %). While ‘single-species nests’ harbored a variety of epiphyte species, the few ‘single-species colonies’ – with only one exception – were associated with domatia bearing epiphytes. Nevertheless, in five colonies, only non-ant-house epiphytes like *Dischidia* sp$_{\text{KfmE}}$115, *Dischidia nummularia*, *Pachycentria constricta*, and *Pachycentria glauca* subsp. *glauca* were found. During the investigations on *Philidris* sp$_{\text{KfmA}}$160, *Platycerium ridleyi* (Polypodiaceae) was discovered to be an ant-house epiphyte as well. The young leaves were pressed to the trunk of the host tree, forming a nest cavity for the ants (Color Plate 4-4, p. 59).

Guests

As with *Philidris* sp$_{\text{KfmA}}$37, myrmecophilous crickets (*Myrmecophila* sp., Myrmecophilidae) also lived in the nests of *Philidris* sp$_{\text{KfmA}}$160 (n=2 colonies).

Table 4-16: Epiphyte species occurring on the nests of *Philidris* sp$_{KfmA}$160 (Dolichoderinae)
The table presents the total numbers of *Philidris* sp$_{KfmA}$160 nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the only epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies). 'ant-house' epiphytes are marked with ^

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Asclepiadaceae	*Dischidia* sp$_{KfmE}$115	14	12	6	1
	Dischidia albida	3	2	1	
	Dischidia imbricata^	4	4	3	3
	Dischidia nummularia	9	4	3	
	Dischidia major^	21	9	9	
Lycopsida	*Lycopodium* sp$_{KfmE}$125	1	1		
Melastomataceae	*Pachycentria constricta*	9	8	2	
	Pachycentria glauca subsp. *glauca*	9	6		
Orchidaceae	*Acriopsis gracilis*	1	1		
	Acriopsis indica Wight	1	1	1	
	Acriopsis javanica	1	1		
	Dendrobium sp$_{KfmE}$116	1	1	1	
	Dendrobium sp$_{KfmE}$117	1	1		
	Gramatophyllum speciosum Bl.	1	1		
	Liparis lacerata	2	2		
Polypodiaceae	*Asplenium nidus*	1	1	1	
	Drynaria rigidula	1	1		
	Lecanopteris sinuosa^	30	18	18	5
	Platycerium ridleyi(^)	6	5	4	
Rubiaceae	*Hydnophytum* sp$_{KfmE}$104^	5	4	14	
	Hydnophytum formicarium^	57	19	1	
	Myrmecodia tuberosa^	86	32	35	15
Vittariaceae	*Vittaria ensiformis*	1	1	1	

Seed-carrying behavior

In seed-carrying experiments, the ants always retrieved seeds of primarily bird-dispersed *Hydnophytum formicarium*, *Myrmecodia tuberosa*, *Pachycentria constricta*, *Pachycentria glauca* subsp. *glauca*, and primarily wind-dispersed *Dischidia nummularia* and *Dischidia* sp$_{KfmE}$115 (n=10 of each species), while the seeds of a non-epiphyte (*Ageratum conyzoides*, Asteraceae) (n=10) were always ignored.

These results, together with those on colony distribution, give strong evidence that, as in AGs, ant-house associations also start with carton nests, into which seeds of certain epiphytes are then incorporated. Thus, according to our definition, ant-house associations have to be regarded as a special type of AGs. The epiphyte composition on the nests of *Philidris* sp$_{KfmA}$160 also pointed in the same direction: non-ant-house epiphytes were frequently growing on the nests in addition to ant-house epiphytes (Table 4-16)[18].

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[18] This aspect will be discussed in detail in Chapter 8.1, p. 135 ff.

Color Plate 4-4: Ant-gardens of *Philidris* sp$_{\text{KfmA}}$37 and *Philidris* sp$_{\text{KfmA}}$160 (with ant-house epiphytes)
1-2: Ant-gardens of *Philidris* sp$_{\text{KfmA}}$37; 3-4: *Myrmecodia tuberosa* (Rubiaceae); 5: Seedling of *Hydnophytum formicarium* (Rubiaceae); 6: Carton nests of *Philidris* sp$_{\text{KfmA}}$160 without epiphytes; 7: *Platycerium ridleyi* (Polypodiaceae); 8: *Lecanopteris sinuosa* (Polypodiaceae); 9: *Dischidia major* (Asclepiadaceae)

4.1.2.3. Formicinae

In the subfamily Formicinae, three species of *Camponotus* could be definitely identified as AG ants, though this might prove to be true for a number of others. The two species described here belong to the subgenus *Myrmotarsus*. Workers were large and highly polymorphic. On the basis of the few ecological data collected for it, the third species seems to have a very strong resemblance to *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$.

Camponotus $\mathbf{sp}_{\mathbf{KfmA}}\mathbf{9}$

A five to six partner system (ant, epiphytes, phorophyte, trophobionts, fungi, sometimes parabiotic Crematogaster spp.), with a strong preference for the asclepiad Hoya elliptica, and widely independent of preformed cavities

General biology of the ant

Camponotus $\mathrm{sp}_{\mathrm{KfmA}}9$ was discovered in Peninsular Malaysia and Southern Peninsular Thailand. It was highly polymorphic (range of alitrunk length: 2.1-5.0 mm) and highly aggressive. Major workers could easily penetrate the human skin with their mandibles and apply formic acid into the wounds – a very effective defense. *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ was active over the whole 24-hour period, with reduced activity in bright sunlight as well as during heavy rain. *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}42$ (n=5) or *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}21$ (n=6) were frequently found in 'parabiotic' association with *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ (Color Plate 4-6, p. 71).

Colony structure

Data on 61 nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$, belonging to 15 colonies, were recorded. Colonies of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ usually inhabited many AGs on several trees at river or road sites, 5-15 m high in the canopy. Since it was impossible to make sure that all nests of the extensive colonies had been recorded, the numbers given here must be regarded as provisional. To some extent they will be complemented by data from Weissflog (2001), who studied this association in detail. The largest colony recorded by Weissflog (2001) had 86 nests on four trees. An extensive trail system connected the nests and trophobiosis sites, which were usually also covered with carton material.

The size of a nest ranged between 4 and 29 300 cm^3 (median: 470 cm^3). The space occupied by one single colony could be estimated only roughly at about 50 000 cm^3 or more. Six nests had no epiphytes growing on them (10 %). They were significantly smaller (range: 4-66 cm^3, median: 24 cm^3; U-test: U=0.0; $p<0.001$) than those with epiphytes (range: 255-29 300 cm^3; median: 1335 cm^3).

Nest architecture and carton composition

A mature nest consisted of three clearly distinguishable layers (also s. Weissflog, 2001). The outer area was constructed with bark, soil and cuticular particles (from prey insects and dead workers), and stabilized with a dense root net (Color Plate 4-5, p. 69). It contained one layer of chambers and was walled off from the second area by a thick and stable carton layer. The second area consisted almost exclusively of a very thick and dense root net, forming several irregular chamber-layers. Almost no carton material could be distinguished. The majority of brood and workers was found in this area. In the center, only few and thick roots were found, covered and joined by thin, paper-like, dark-brown carton material. This material was covered by a black fungus.

Phorophytes

At least five different tree species from four different plant families were identified as host trees, i.e. there was no host specificity. Again, the most important characteristics appeared to be the suitability of the phorophyte as a food source for trophobionts.

Trophobionts

Trophobionts were tended underneath most of the nests (Color Plate 4-5, p. 69) and at many other places within the extensive foraging area (up to 380 m²).

Epiphyte partners

The epiphyte species predominantly growing on the nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ was *Hoya elliptica* (41 % of all epiphytes, Table 4-17; Color Plate 4-5, p. 69). The fern *Lepisorus longifolius* was also very abundant (21 %). Altogether, 11 epiphyte species from 8 genera and 7 families were found on the nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$. *Hoya elliptica* occurred on 62 % of all nests and with 87 % of all colonies, i.e. only two of the fifteen colonies were not associated with *Hoya elliptica*.

Table 4-17: Epiphyte species occurring on the nests of *Camponotus* sp$_{\mathrm{KfmA}}$9 (Formicinae)
The table presents the total numbers of *Camponotus* sp$_{\mathrm{KfmA}}$9 nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the only epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies).

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Araliaceae	*Schefflera* sp$_{\mathrm{KfmE}}$75	3	2		
Asclepiadaceae	*Hoya* sp$_{\mathrm{KfmE}}$94	1	1		
	Hoya elliptica	38	13	14	4
Gesneriaceae	*Aeschynanthus albidus*	9	3		
Melastomataceae	*Pachycentria constricta*	1	1		
	Pachycentria glauca subsp. *maingayi*	1	1		
Polypodiaceae	*Asplenium nidus*	1	1	1	
	Lepisorus longifolius	19	3		
Urticaceae	*Poikilospermum microstachys*	4	3	1	1
	Poikilospermum cordifolium	3	2		
Zingiberaceae	*Hedychium longicornutum*	12	1	5	

Guests

AGs of *Camponotus* sp$_{\mathrm{KfmA}}$9 were rich in guests (Color Plate 4-6, p. 71). A large spider rested inside the innermost part during the daytime and came out to hunt insects other than ants during the night (n=6). A myrmecophilous cricket (*Myrmecophila* sp.) was fully integrated into the ant colony, actively participating in trophallaxis. When placed into a new colony, the crickets needed some time to be accepted. In the first phase they rapidly flew when attacked by an ant, but they also sought contact with their hosts apparently in order to mimic their odor. After 1-2 hours the crickets succeeded in deceiving *Camponotus* sp$_{\mathrm{KfmA}}$9 and spent most of the time begging for food or resting, preferably underneath major workers. Like *Crematogaster* sp$_{\mathrm{KfmA}}$18, *Camponotus* sp$_{\mathrm{KfmA}}$9 AGs could also host whole colonies of social stingless bees (*Trigona* (*Lepidotrigona*) *nitidiventris*, Meliponinae[19]). The bee species was not the same as in *Crematogaster*, but the principal nest structure was alike in both cases (Chapter 4.1.2.1, p. 29).

Water storing capacity and nutritive value of the carton material

The dry weight of the pure carton material without epiphyte roots was 13.0 ± 1.7 g/cm³ in a mature nest. Thus, a medium sized nest contained about 6 g of carton material, and a large colony accumulated more than 500 g. Water storing capacity was about 5.6 ± 0.6 (n=6).

The nutritive value of this substrate for its epiphyte partners was estimated by comparing the relative contents of nitrate, ammonium and phosphate to those in forest soil, bark material and nest substrate of *Crematogaster* cf. *artifex* (Table 4-6, p. 31). It was found to contain about as much ammonium (mean: 15.3 ± 6.6 mg/kg) as forest soil (mean: 15.0 ± 14.5 mg/kg) and significantly more than nest substrate of *Crematogaster* cf. *artifex* (mean: 7.3 ± 2.9 mg/kg; t-

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[19] determined with Schwarz, 1939; Sakagami, 1975

test: p<0.01; t=2.88). There were no significant differences in the nitrate and phosphate concentrations compared to any other tested material.

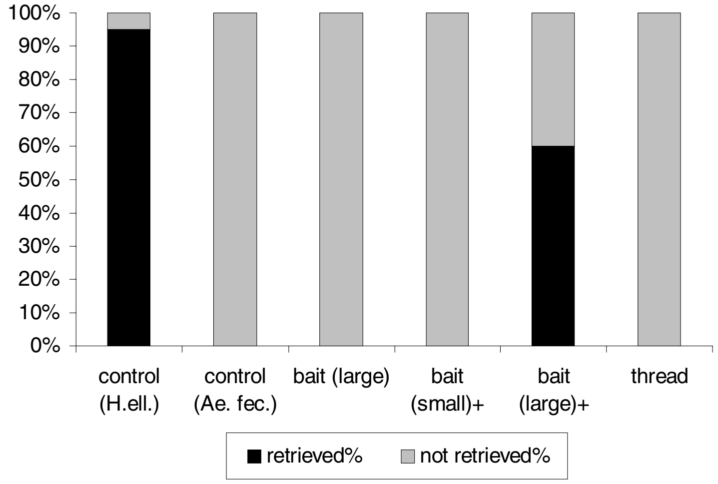


Figure 4-7: Seed-carrying behavior of *Camponotus* sp_{KfmA}9 towards *Aeschynanthus fecundus* (Gesneriaceae) and *Hoya elliptica* (Asclepiadaceae).
control (H.ell.) = complete seed of *Hoya elliptica ;* control (Ae.fec.) = complete seed of *Aeschynanthus fecundus*; bait (large) = porcelain bait in the size of *Hoya elliptica* with pure acetone; bait(small)+ = porcelain bait in the size of *Aeschynanthus fecundus* with acetone-extract of *Aeschynanthus fecundus*; bait(large)+ = porcelain bait in the size of *Hoya elliptica* with acetone-extract of *Aeschynanthus fecundus*; thread = piece of thread in the length of the hairy appendage of *Aeschynanthus fecundus*. # of items/type s. Table 4-18.

Seed-carrying behavior

Extensive seed-carrying experiments were performed (Table 4-18). Almost 100 % of the seeds of *Hoya elliptica* were retrieved, while the seeds of *Dischidia nummularia* and *Aeschynanthus fecundus* were ignored. Seeds of non-epiphytic *Emilia sonchifolia* (Asteraceae) were ignored with or without extracts of any of the three epiphyte species. Small-sized porcelain baits, resembling the seeds of *Dischidia nummularia* or *Aeschynanthus fecundus,* with extracts of any of the three epiphytes, were ignored. Large-sized porcelain baits resembling the seeds of *Hoya elliptica* were retrieved with extracts of *Hoya elliptica*, and also with those of *Dischidia nummularia* and *Aeschynanthus fecundus* (Table 4-18). To rule out the possibility that this was a concentration effect of some attractant, the extracts were diluted 1:100. The result remained the same as in the original setup. Threads were always ignored. Thus, a combination of chemical cues and seed size were responsible for selective seed-retrieval.

Whenever complete plumed seeds of *Hoya elliptica* were offered, *Camponotus* sp_{KfmA}9 attacked them first. The ants calmed down after a short while and often bit off the appendage before retrieving the seed. Seeds from which the hairy appendage had been removed beforehand were taken without attack and carried into the nest.

Table 4-18: Seed-carrying behavior of *Camponotus* sp$_{\mathbf{KfmA}}$9

Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 35 pairwise comparisons

*: row item is significantly more attractive than column item; *[1]: column item is significantly more attractive than row item; n.s.: no significant difference

For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Dischidia nummularia	*Aeschynanthus fecundus*	*Hoya elliptica* baits large	*Dischidia nummularia*, baits large	*Aeschynanthus fecundus*, baits large	*Hoya elliptica*, baits small	*Dischidia nummularia*, baits small	*Aeschynanthus fecundus*, baits small	non-epi	thread	porcelain bait with acetone
Hoya elliptica (n=25)	*	*	n.s.	n.s.	n.s.	*	*	*	*	*	*
Dischidia nummularia (n=25)		-	-	*[1]	-	-	n.s.	-	-	-	n.s.
Aeschynanthus fecundus (n=25)			-	-	*[1]	-	-	n.s.	-	-	n.s.
Hoya elliptica, porc.baits large (n=25)				n.s.	n.s.	n.s.	*	*	-	-	*
Dischidia nummularia, porc.baits large (n=25)					n.s.	-	*	-	-	-	*
Aeschynanthus fecundus, porc.baits large (n=25)						n.s.	-	*	-	-	*
Hoya elliptica, porc.baits small (n=25)							-	-	-	-	n.s.
Dischidia nummularia, porc.baits small (n=25)								-	-	-	n.s.
Aeschynanthus fecundus, porc.baits small (n=25)									-	-	n.s.
non-epi (n=25)										n.s.	n.s.
thread (n=25)											n.s.
porcelain bait + acetone (n=25)											

Camponotus sp$_{\mathrm{KfmA}}$240

A parabiotic six partner system (ants, epiphytes, phorophyte, trophobionts, fungi and parabiotic Crematogaster sp$_{KfmA}$21), with a strong dependence on large preformed cavities

General biology of the ant

Camponotus sp$_{\mathrm{KfmA}}$240 was found in Peninsular Malaysia, Sabah and Southern Thailand. Its workers were highly polymorphic (length of the alitrunk: 2.0-4.3 mm). It was active at night only, activity started at dawn and stopped shortly before sunrise. *Camponotus* sp$_{\mathrm{KfmA}}$240 always lived in a parabiotic association with *Crematogaster* sp$_{\mathrm{KfmA}}$21. In feeding experiments, both species were observed at the baits together. Nevertheless, *Crematogaster* sp$_{\mathrm{KfmA}}$21 was usually first to discover the baits. Both species used efficient recruitment systems in order to exploit the food source quickly. Workers of *Camponotus* sp$_{\mathrm{KfmA}}$240 were extremely sensitive to disturbance and retreated rather than attacked. Nevertheless, there were always major workers inside the nests at the entrance holes. This caste showed a characteristic aggressive behavior when something tried to enter the nest: They made very quick movements towards the intruder and tried to place a bite. Workers of *Crematogaster* sp$_{\text{KfmA}}$21 hurried out of the nest in relatively large numbers whenever anything unusual happened outside and made attempts at defense (Chapter 4.1.2.1, p. 39).

Colony structure

Data on 20 colonies of *Camponotus* sp$_{\text{KfmA}}$240 with altogether 27 nests was recorded. One colony lived in 1 to 4 nests (median: 1). In most cases the nests were located inside hollow stems or larger crevices in stems and branches of the host tree(s), or in domatia of a certain ant-house epiphyte (s. below). In most cases I could not be sure that I had found all nests, nor could I give good estimates of the nest sizes. Subject to these restrictions, and based on the data for seven nests, the medium nest size was 1500 cm³ (range: 230 – 8000 cm³). No reliable comparison of nests with and without epiphytes could be performed, as only one nest without epiphytes was found.

One dissected colony of *Camponotus* sp$_{\text{KfmA}}$240 consisted of c. 2500 workers. Of these, almost half belonged to the smallest group (minors), about 1/3 were medium sized, and the remaining 400 workers were categorized as majors. 550 workers and 650 pupae of *Crematogaster* sp$_{\text{KfmA}}$21 were found in small chambers next to *Camponotus* sp$_{\text{KfmA}}$240.

Nest architecture and carton composition

Camponotus sp$_{\text{KfmA}}$240 always used given cavities that were then covered with a thin layer of carton material for nest-construction. The covering consisted mainly of small woody particles, cuticular parts of ants and other insects and short plant fibers arranged in an irregular criss-cross-pattern. In most cases a net of fine roots from the epiphytes, visible on the inner surface only, stabilized the construction. Whenever the main part of a nest was located inside a hollow stem or branch, the cavity was divided into smaller chambers, often using particles of dead wood. These wooden parts were then covered with a thin layer of tiny soil particles and cuticular parts of prey insects as well as dead colony members. A black fungus was growing on this substrate.

Phorophytes

Host trees of *Camponotus* sp$_{\text{KfmA}}$240 were often directly used as nest sites and thus had to have voluminous preformed cavities. Trees with large stem cavities, due to rotting processes, were preferred nesting sites. The ants sometimes actively enlarged the cavities by removing rotten wood.

Trophobionts

Trophobionts (coccidae and pseudococcidae) were discovered within the foraging area of *Camponotus* sp$_{\text{KfmA}}$240, usually underneath carton shelters.

Epiphyte partners

Seven epiphyte species from five plant genera and four families were growing on the nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$ (Table 4-19). One to three different species were found on the same nest. *Hoya mitrata* (Asclepiadaceae) was predominant, occurring on c. 50 % of all nests and with 50 % of all colonies. Nevertheless, its geographical distribution was restricted to two areas (study area 11, patch 2, and study area 14, patch 1, Chapter 2, p. 6), in which both ant and plant were unusually abundant. *Hoya mitrata* was only recently described as an ant-house epiphyte with a special type of leaf domatium (Color Plate 4-5, p. 69; Weissflog et al., 1999). Two other species, *Poikilospermum microstachys* and *Pachycentria constricta* made up c. 30 % of the epiphytes. *Hoya mitrata* and *Poikilospermum microstachys* were the only epiphytes growing on the nests of 'single-species colonies'.

Table 4-19: Epiphyte species occurring on the nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$ (Formicinae)
The table presents the total numbers of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$ nests on which each epiphyte species was growing (# nests), of colonies with which it occurred (# colonies), of nests on which it was the only epiphyte species (# single-species nests), and of colonies with which it occurred as sole species (# single-species colonies).

plant family	plant species	# nests	# colonies	# 'single-species nests'	# 'single-species colonies'
Asclepiadaceae	*Dischidia albida*	1	1		
	Dischidia hirsuta	1	1		
	Hoya micrantha	3	2	3	
	Hoya mitrata	13	10	11	9
Melastomataceae	*Pachycentria constricta*	4	3	1	
Rubiaceae	*Hydnophytum formicarium*	1	1		
	Myrmecodia tuberosa	1	1		
Urticaceae	*Poikilospermum microstachys*	4	4	2	2

Guests

Many beetles (Hydrophilidae) and some Phoridae lived inside the nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$. In the peripheral part, nymphs of a foam-producing cicada were found (n=5). Nothing is known about their biology.

Water storing capacity and nutritive value of the carton material

A quantitative collection of nesting material was carried out for one colony only. In this colony, the ants occupied a space of c. 8000 cm³, the weight of the substrate was 22.5 g, i.e. 2.8 mg/cm³. The nutrient content of this nest's substrate was measured (Table 4-6, p. 31), but due to the low sample size no statistical comparison was possible.

Seed-carrying behavior

The seed-carrying behavior of *Camponotus* sp$_{\mathrm{KfmA}}$240 was tested during the night (with red light), using the previously described items (Table 4-20). The preferences of this ant widely resembled those of *Camponotus* sp$_{\mathrm{KfmA}}$9. Seeds of *Hoya elliptica* were retrieved, while seeds of *Dischidia nummularia*, *Aeschynanthus fecundus* and the non-epiphyte *Ageratum conyzoides* were ignored. Threads and baits with pure solvent were also ignored. *Hoya elliptica*–sized baits with acetone extracts of any of the three epiphyte species were attractive, while *Dischidia nummularia* or *Aeschynanthus fecundus*–sized baits were never retrieved. These results indicate that selective seed-retrieval was elicited by chemical cues in combination with seed size.

Table 4-20: Seed-carrying behavior of *Camponotus* sp$_{\mathrm{KfmA}}$240
Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 34 pairwise comparisons
*: row item is significantly more attractive than column item; *[1]: column item is significantly more attractive than row item; n.s.: no significant difference
For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Dischidia nummularia	*Aeschynanthus fecundus*	*Hoya elliptica* baits large	*Dischidia nummularia*, baits large	*Aeschynanthus fecundus*, baits large	*Hoya elliptica*, baits small	*Dischidia nummularia*, baits small	*Aeschynanthus fecundus*, baits small	non-epi	thread	porcelain bait with acetone
Hoya elliptica (n=25)	*	*	n.s.	*	n.s.	*	*	*	*	*	*
Dischidia nummularia (n=25)		-	-	*[1]	-	-	n.s.	-	n.s.	n.s.	n.s.
Aeschynanthus fecundus (n=25)			-	-	*[1]	-	-	n.s.	n.s.	n.s.	n.s.
Hoya elliptica, porc.baits (n=25) large				*	n.s.	*	-	-	-	-	*
Dischidia nummularia, porc.baits large (n=25)					-	-	n.s.	-	-	-	n.s.
Aeschynanthus fecundus, porc.baits large (n=25)						-	-	*	-	-	*
Hoya elliptica, porc.baits small (n=25)							-	-	-	-	n.s.
Dischidia nummularia, porc.baits small (n=25)								-	-	-	n.s.
Aeschynanthus fecundus, porc.baits small (n=25)									-	-	n.s.
non-epi (n=25)										-	n.s.
thread (n=25)											n.s.
porcelain bait + acetone (n=50)											

An interesting observation concerning the parabiotic interaction between *Camponotus* sp$_{\mathrm{KfmA}}$240 and *Crematogaster* sp$_{\mathrm{KfmA}}$21 should be mentioned here. In most cases *Crematogaster* sp$_{\mathrm{KfmA}}$21 (90 %) discovered the attractive items before *Camponotus* sp$_{\mathrm{KfmA}}$240 did, and tried to retrieve them. Again, in 90 % of all cases, a *Camponotus* worker (medium sized) discovered the item and took it over from the *Crematogaster* worker.

Color Plate 4-5: Ant-gardens of *Camponotus* sp$_{KfmA}$9 and *Camponotus* sp$_{KfmA}$240
1: Ant-garden of *Camponotus* sp$_{KfmA}$9 with *Hoya elliptica*; 2: Inflorescence of *Hoya elliptica*; 3: Root network of *Hoya elliptica*; 4: Seedlings of *Hoya elliptica* on nest of *Camponotus* sp$_{KfmA}$9; 5: Trophobionts of *Camponotus* sp$_{KfmA}$9 after a nest had been removed; 6: Ant-garden of *Camponotus* sp$_{KfmA}$240 with *Hoya mitrata*; 7: *Camponotus* sp$_{KfmA}$240 at flowers of *Hoya micrantha*

Color Plate 4-6: Guests in ant-gardens of *Camponotus* sp$_{\text{KfmA}}$9, and AGs of *Diacamma* sp$_{\text{KfmA}}$111
1: Nest of *Trigona* (*Lepidotrigona*) *nitidiventris*. (Meliponinae, Apidae) in *Camponotus* sp$_{\text{KfmA}}$9 ant-garden; 2: Entrance tube of *Trigona* (*Lepidotrigona*) *nitidiventris* nest; 3: *Myrmecophila* sp. in trophallaxis with *Camponotus* sp$_{\text{KfmA}}$9; 4: Spider on the nest surface of *Camponotus* sp$_{\text{KfmA}}$9; 5: *Camponotus* sp$_{\text{KfmA}}$9 and its parabiotic partner ant, *Crematogaster* sp$_{\text{KfmA}}$21; 6 + 7: AGs of *Diacamma* sp$_{\text{KfmA}}$111

4.1.2.4. Ponerinae

Though some exceptions exist, ponerines are usually not arboricolous. Only one species of this subfamily, *Diacamma* sp., was regularly found as AG inhabitant.

Diacamma **sp$_{\mathrm{KfmA}}$111**

A three partner system (ant, epiphytes, phorophyte) with a strong dependency on preformed cavities

General biology of the ant

Diacamma sp$_{\mathrm{KfmA}}$111 was collected in Peninsular Malaysia and on Borneo. It principally showed a low 24h-activity with a maximum in the early morning. *Diacamma* sp$_{\mathrm{KfmA}}$111 had a strong sting, but seldom used it. When a nest-site was disturbed, workers tried to escape carrying their brood with them. *Diacamma* sp$_{\mathrm{KfmA}}$111 was monomorphic with an alitrunk-size of 3.6 mm. The gamergate females were of the same size.

Colony structure

73 colonies lived in 73 nests, i.e. *Diacamma* sp$_{\mathrm{KfmA}}$111 was monocalic. The colonies were rather small with 10 to 85 workers (median: 38). *Diacamma* sp$_{\mathrm{KfmA}}$111 always nested in preformed, natural cavities. Nevertheless, the ants almost always manipulated the entrance area of their nest by building carton-like structures, on which usually epiphytes were growing (Color Plate 4-6, p. 71). In a few cases, the carton structures were also used as nests at least for parts of the colonies and at least at some times of the day. The medium volume of the entrance area, estimated as cylindrical, was 134 cm^3 (range: 0.5-63 000 cm^3). The volume of the nest could not be measured because it was often located in an irregularly formed cavity inside a stem and only parts of the cavities were used as nest.

Nest architecture and carton composition

Long plant fibers, bird feathers, seed appendages and small pieces of dead wood were the main material used for the tube-like, roughly cylindrical entrance buildings. The circular to ovoid entrance hole had an area of 0.77 ± 0.28 cm^2 (n=46). This was a very stable pattern, while the entrance hole underneath the carton material, directly into the host tree, varied very considerably in size.

Phorophytes

Diacamma sp$_{\mathrm{KfmA}}$111 depended on preformed cavities. Suitable nest sites were often located in trees with soft wood (in the study area in Peninsular Malaysia mainly in *Piper aduncum* (70 % of all host trees)), or in the internodes of giant bamboo (20 %).

Trophobionts

Diacamma sp$_{\mathrm{KfmA}}$111 was never observed visiting trophobionts.

Epiphyte partners

Epiphyte species that were found in association with *Diacamma* $sp_{KfmA}111$ are presented in Table 4-21. Altogether, 17 species from 11 genera and 9 families were growing on the nests of *Diacamma* $sp_{KfmA}111$. Again, a few predominant species contrasted with a number of other species occurring less frequently. *Schefflera* $sp_{KfmE}75$ was most abundant (28.4 %), followed by *Poikilospermum microstachys* (20 %) and *Aeschynanthus albidus* (13 %). 'Single-species' colonies (n=30) were colonized by *Schefflera* $sp_{KfmE}75$ (33 %) in most cases, followed by *Schefflera* $sp_{KfmE}91$ (10 %) and *Poikilospermum microstachys* (10 %). *Aeschynanthus albidus* was never found as sole species.

62 colonies (87 %) had epiphytes growing on their entrance constructions. The entrances of these colonies were significantly larger (range: 0.4-10 200 cm³, median: 157 cm³; U-test: U=100.0, p<0.05) than those without epiphytes (range: 0.6-98 cm³, median: 60 cm³).

Table 4-21: Epiphyte species occurring on the nests of *Diacamma* $sp_{KfmA}111$ (Myrmicinae)
The table presents the total numbers of *Diacamma* sp.1 nests on which each epiphyte species was growing (# nests), of nests on which it was the only epiphyte species (# single-species nests), also, unlike for the other ant species, the numbers of colonies with which it occurred (# colonies) and of colonies with which an epiphyte occurred as sole species (# single-species colonies) are not given here, because *Diacamma* $sp_{KfmA}111$ was monocalic.

plant family	plant species	# nests	# 'single-species nests'
Araliaceae	*Schefflera* $sp_{KfmE}75$	25	10
	Schefflera $sp_{KfmE}91$	7	3
	Schefflera $sp_{KfmE}155$	3	2
Asclepiadaceae	*Dischidia acutifolia*	6	1
	Dischidia bengalensis	1	
	Hoya $sp_{KfmE}94$	1	
	Hoya micrantha	1	1
	Hoya multiflora	1	
Gesneriaceae	*Aeschynanthus albidus*	11	
	Aeschynanthus fecundus	1	
Melastomataceae	*Pachycentria constricta*	6	
Moraceae	*Ficus* $sp_{KfmE}96$	3	
Piperaceae	*Piper* $sp_{KfmE}89$	1	
Polypodiaceae	*Drymoglossum piloselloides*	1	
	Lecanopteris sinuosa	1	
Urticaceae	*Poikilospermum microstachys*	18	3
Zingiberaceae	*Hedychium longicornutum*	1	

Guests

Many of the guests living in *Diacamma* $sp_{KfmA}111$ nests would rather have been expected in the soil, e.g. earthworms and isopods.

Water storing capacity and nutritive value of the carton material

The average dry weight of 1 cm³ substrate was 2.4 mg (n=6). A medium sized nest entrance contained 3.3 g, while a large one contained up to 150 g. There were very few entrances containing that much substrate. Thus it was difficult to collect enough material for substrate analysis and I had to combine the substrate of several nests to get a sufficient amount. To standardize this combination, equal amounts of homogenized substrate of ten nests were used for each test. With this method, the nutrient contents were measured (presented in Table 4-6, p. 31). A statistical comparison was not possible, because the available substrate was only sufficient for altogether three tests. However, the tendency was fairly clear. There was no difference in ammonium content compared to nests of *Crematogaster* cf. *artifex*, while nitrate and phosphate contents were considerably higher.

Water storing capacity was estimated as 1.9 ± 0.6 (n=6).

Seed-carrying behavior

Extensive seed-carrying experiments were performed (Table 4-22). There was no significant difference in seed attractiveness between the tested epiphyte species.

As an example for wind-dispersed seeds, the results for *Aeschynanthus fecundus* are summarized in Figure 4-8. Plumed seeds (epiphyte as well as non-epiphyte seeds) and threads were significantly more attractive than any other item. Baits with or without seed extracts showed no significant difference in attractiveness, nor did non-epiphyte seeds with or without extracts. Epiphyte seeds with or without hairy appendages were retrieved in similar frequencies.

Seeds of bird-dispersed *Medinilla* and *Pachycentria* were attractive both before and after passage through a bird's gut. Bird droppings were generally very attractive for *Diacamma* sp$_{\mathrm{KfmA}}$111. Seeds and other items offered in the experiments were most frequently used straightaway as outside building material at the entrance construction.

Thus, the main motivations of *Diacamma* sp$_{\mathrm{KfmA}}$111 to carry seeds into its nest were a) suitability as building material (wind-dispersed seeds), or b) nutritional cues.

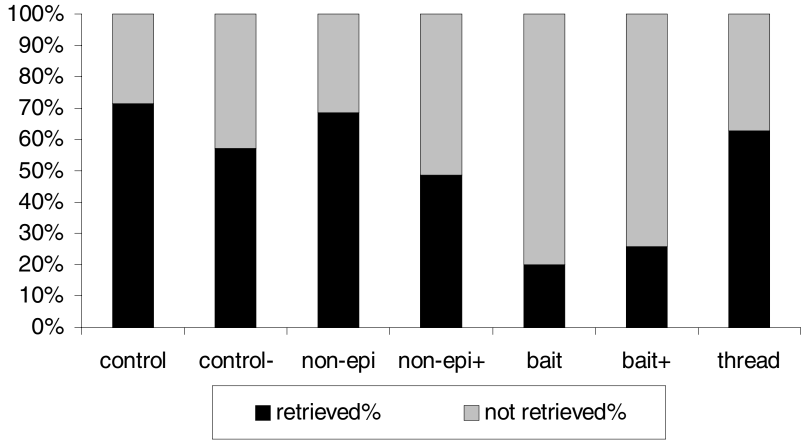


Figure 4-8: Seed-carrying behavior of *Diacamma* sp$_{\mathrm{KfmA}}$111 towards *Aeschynanthus fecundus* (Gesneriaceae).

control = complete seed of *Aeschynanthus fecundus*; control- = seed of *Aeschynanthus fecundus* without hairy appendage; non-epi = seed of *Ageratum conyzoides* (Asteraceae) treated with pure acetone; non-epi+ = seed of *Ageratum conyzoides* treated with acetone-extract of *Aeschynanthus fecundus*; bait = porcelain bait in the size of *Aeschynanthus fecundus* treated with pure acetone; bait+ = porcelain bait in the size of *Aeschynanthus fecundus* treated with acetone-extract of *Aeschynanthus fecundus*; thread = piece of thread in the length of the hairy appendage of *Aeschynanthus fecundus*. # of items/type s. Table 4-22.

Table 4-22: Seed-carrying behavior of *Diacamma* sp$_{\text{KfmA}}$111

Test-statistics: χ^2, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 58 pairwise comparisons

*: row item is significantly more attractive than column item; n.s.: no significant difference

For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	Aeschynanthus fecundus, hairy appendage removed	*Aeschynanthus albidus*, control	*Aeschynanthus albidus*, hairy appendage removed	*Dischidia nummularia*, control	*Dischidia nummularia*, hairy appendage removed	*Hoya elliptica*, control	*Hoya elliptica*, hairy appendage removed	*Pachycentria constricta*, control	non-epi + acetone extract *D. nummularia*	porc.bait + acetone extract *Ae. fecundus*	porc.bait + acetone extract *Ae. albidus*	porc.bait + acetone extract *D. nummularia*	porc.bait + acetone extract *Hoya elliptica*	thread	non-epi	non-epi + acetone	porcelain bait + acetone
Aeschynanthus fecundus, control (n=115)	n.s.	n.s.	-	n.s.	-	n.s.	-	n.s.	-	*	-	-	-	n.s.	n.s.	n.s.	*
Aeschynanthus fecundus, hairy appendage removed (n=40)		-	-	-	-	-	-	-	-	-	-	-	-	-	n.s.	-	*
Aeschynanthus albidus, control (n=40)			n.s.	n.s.	-	n.s.	-	n.s.	-	-	*	-	-	*	*	*	*
Aeschynanthus albidus, hairy appendage removed (n=20)				-	-	-	-	-	-	-	-	-	-	-	n.s.	-	*
Dischidia nummularia, control (n=50)					n.s.	n.s.	-	n.s.	n.s.	-	-	*	-	n.s.	n.s.	n.s.	*
Dischidia nummularia, hairy appendage removed (n=30)						-	-	-	-	-	-	-	-	-	n.s.	-	*
Hoya elliptica, control (n=15)							n.s.	n.s.	-	-	-	-	*	n.s.	n.s.	n.s.	n.s.
Hoya elliptica, hairy appendage removed (n=15)								-	-	-	-	-	-	-	n.s.	-	n.s.
Pachycentria constricta, control (n=30)									-	-	-	-	-	n.s.	n.s.	n.s.	*
non-epi + acetone extract *D. nummularia* (n=30)										-	-	*	-	-	n.s.	n.s.	*
porc.bait + acetone extract *Ae. fecundus* (n=20)											-	-	-	-	-	-	n.s.
porc.bait + acetone extract *Ae. albidus* (n=40)												-	-	-	-	-	n.s.
porc.bait + acetone extract *D. nummularia* (n=20)													-	-	-	-	n.s.
porc.bait + acetone extract *Hoya elliptica* (n=15)														-	-	-	n.s.
thread (n=45)															-	-	*
non-epi (n=90)																-	*
non-epi + acetone (n=100)																	*
porcelain bait + acetone (n=100)																	

4.2. Discussion

The descriptions of selected AG systems revealed that these differed from one another in many aspects as soon as attention was directed beyond the basic interactions between ants, epiphytes and phorophytes. It will therefore be necessary to find suitable criteria for classifying these highly varied AG systems. In addition, possible beneficial interactions between ants and epiphytes were studied. These will be discussed in the second part of this chapter, allowance also being made for the significance of additional partners.

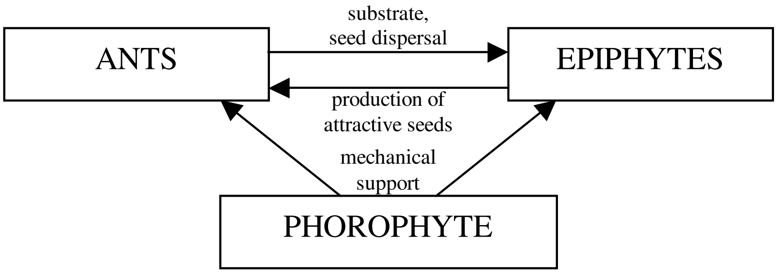
4.2.1. Towards a classification of ant-garden systems

The ant-gardens studied here diverged in many qualitatively different characteristics: Two ant species were restricted to a small group of phorophytes, while the others showed no phorophyte-specificity. The majority of ants were associated with many epiphyte species, while two species were relatively specialized on one or few epiphyte partners. Some ant species nested exclusively in carton nests with epiphytes, while others used natural cavities either in ant-house epiphytes or in the host tree. In most, but not in all systems, trophobionts were an integral partner. Motivation for seed-carrying behavior depended on chemical cues, size of the seeds, and their suitability as building material.

This high complexity of Southeast Asian AG systems arises from the wide variety of taxonomically unrelated species of both ants and plants, and from the number of partners involved in each system. Since it is difficult to keep track of general patterns when just listing the AG systems by taxonomical aspects (as was done in the previous chapter), it will be necessary to arrive at a more meaningful classification.

Generally, it seems reasonable to come to a classification reflecting a gradient from ‘primitive’ to ‘advanced’ AGs. However, it is hard to decide which characteristics could be used for the ranking of the AG systems. Due to all the divergences in Southeast Asian AGs it is impossible to choose one single criterion for a meaningful ranking. For example, increasing complexity may be expressed in increasing numbers of partner organisms as well as in decreasing numbers of associated epiphytes. Thus a classification at the present status might be best achieved with the aid of a combination of criteria. However, a ‘starting point’ has to be selected: In my approach, things will – again - be regarded from the point of view of the ants.

In order to achieve a better assessment on which characteristics might qualify for classification, a brief summary will first be given of all the basic partners and interactions constituting an AG (Scheme 4-1).



Scheme 4-1: Constitutive partners and basic interactions in ant-gardens

Three partners are indispensable: Ants, epiphytes and phorophytes. The ants provide some substrate for their epiphyte partners and disperse their seeds to this substrate; the epiphytes have merely to produce ant-attractive seeds; and the phorophyte contributes mechanical support for both the ants and the epiphytes. This is the basic scheme for any AG. It was found to be the case in all systems described during this investigation, and thus these traits are inappropriate for any further classification.

It will therefore be necessary to identify characteristics going beyond these basic ones and to consider their suitability as ranking criteria. To make it easier to understand this approach, criteria finally chosen will already be presented at this point (Table 4-23). However, some other traits will also be discussed in the following paragraphs.

Table 4-23: Criteria chosen for classification of AG ants

	top criterion	main criteria		subordinate criteria		
criterion rank	dependency on preformed cavities	trophobionts	cues for seed-carrying	# of additional partners	specialization towards phorophytes	specialization towards epiphyte partners
1	totally	no	no special 'epiphyte' cues	0	no specialization	0-25 %
2	partly	without shelters	chemical cues or seed characteristics	1	group specialization	26-50 %
3		with shelters	chemical cues only	2		51-75 %
4	independent	mainly underneath nests	chemical and mechanical cues	3	species specificity	76-100 %

The role of the phorophyte is one important characteristic: Either it offers mechanical support only, or it additionally provides nesting space for the ants. Additionally, it often even serves as a nutrient source indirectly via hemipteran trophobionts. Here, two classification criteria are touched on: One is the dependency of an ant species on preformed cavities; the other is the tending of hemipteran trophobionts. The first criterion might be particularly suitable for ranking, because gaining complete independency from preformed cavities as nest sites is one of the main benefits proposed for carton building ants in general (Wilson, 1959; Carroll, 1979; Weissflog, 2001). With the second criterion, two major groups can be distinguished: AG ants tending trophobionts and those without trophobionts[20]. Among the second group, subgroups can be distinguished: 1.The first group comprises ant species that visit trophobiosis sites at many places within their foraging area and do not cover them with carton shelters. 2. The second group comprises ants covering their trophobionts with carton shelters, but not tending the majority of trophobionts directly underneath their nests. 3. Ants of the third group tend the majority of their 'livestock' directly underneath their AGs. This might be another valid criterion, because arboreal ants mainly feed on plant saps, and this is why easy access to trophobionts as food source may be regarded as especially beneficial (Tobin, 1991, 1994; Davidson and Patrell-Kim, 1996)[21].

One of the main factors responsible for the development of an AG is the ants' seed-carrying behavior. The experiments carried out in this study revealed that there were different cues responsible for seed attractiveness. Common to all tested ant species was the attractiveness of primarily bird-dispersed seeds, both before and after passage through a bird's gut. Nutritional rewards (sugar in non-digested and minerals in digested seeds) were identified as possible responsible cues.

Thus, only the wind-dispersed seeds remain for further comparison and may provide an additional classification criterion. Four different cues for the attractiveness of wind-dispersed seeds were distinguished (Table 4-23). The ranking is not self-explanatory here; it reflects an increasing selectiveness of ants towards epiphyte seeds. Type 1 (*No special 'epiphyte' cues*) refers to the cases in which epiphyte seeds were not preferred compared to other items with similar mechanical properties or to seeds in general. This was either true for seed-eating ants, or for ants that simply used the seeds as suitable building material. The second group (*chemical cues or seed characteristics*) comprised ant species that showed a clear preference towards any seeds when compared to other items, but epiphyte seeds or baits with epiphyte seed-extracts were more attractive due to chemical characteristics. Ants in class three (*chemical cues only*) retrieved objects of any size and form when treated with epiphyte seed-extracts, but they did not retrieve non-epiphyte seeds. Finally, class four (*chemical and mechanical cues*) comprised ants that employed chemical cues, but additionally used further mechanical (e.g. size) cues. The last group was

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[20] Ants might either tend trophobionts on the phorophyte or on their epiphyte partners. Nevertheless, since trophobionts sucking on epiphytes played hardly any role in this investigation, the criterion does not distinguish between these two groups (also s. Chapter 4.2.2, p. 88 f.).

[21] A further distinction in the behavior towards trophobionts would be useful, i.e. the criterion whether the ants carry their 'livestock' to new feeding sites when disturbed. This criterion was not included here because of a lack of data for most species.

regarded as more specialized than the one before it, because here a further characteristic was added to the chemical cues, allowing a higher selectiveness towards seeds. With regard to the results of this study (esp. comparing *Crematogaster* sp$_{\text{KfmA}}$18 and *Camponotus* sp$_{\text{KfmA}}$9/sp$_{\text{KfmA}}$240 as well as *Crematogaster* sp$_{\text{KfmA}}$21), this order seems to make sense. However, once more data is available, it may turn out that this cannot be generalized.

The number of additional partners living in an AG (e.g. fungi, parabiotic ants) was regarded as less suitable for classification, because it might say more about the ecology of partner species than about the AG ants. This restriction was reflected in a subordinate classification of this criterion.

The degree of specialization towards a certain phorophyte, or at least a certain group of phorophytes, is another – though less important – criterion[22].

As a last criterion I chose the specialization towards a certain epiphyte species, which of course is at least partly dependent on seed retrieval cues and other factors independent from the ants[23]. Here, this 'specialization' is expressed by '% of colonies with which the most abundant epiphyte genus was found', divided into four classes. This trait is again assessed as subordinate, because it may be influenced by many additional factors.

Substrate quality could be estimated as degree of fertilization by the ants. My results suggest that there may be differences between the AG ants, but more data would be necessary to identify reliable patterns. This criterion will therefore not be included here.

Thus, altogether six criteria have been chosen, one 'top criterion' (dependency on preformed cavities), two main criteria and three subordinate ones (Table 4-23). Applying these six criteria to the AG ants described here resulted in Table 4-24. Each ant species was equipped with a rank number for each criterion according to Table 4-23.

Table 4-24: Ranking of AG ants due to six different characteristics
The ranks refer to the numbers given in Table 4-23. For ranks marked with *, insufficient data for a final ranking was available. The lowest possible rank according to the present data was chosen in such cases.

	dependency on preformed cavities (C_1)	trophobionts (C_2)	cues for seed-carrying (C_3)	# of additional partners (C_4)	specialization towards phorophytes (C_5)	specialization towards epiphyte partners (C_6)
Crematogaster sp$_{\text{KfmA}}$18	4	4	3	2	2.5	3
Crematogaster sp$_{\text{KfmA}}$21	1	3	4	2	1	1
Crematogaster sp$_{\text{KfmA}}$200	4	2	3^{*}	1	1	2
Pheidole sp$_{\text{KfmA}}$33	2.5	1	2	1	1	2
Philidris sp$_{\text{KfmA}}$37	2.5	3	3	1	1	2
Philidris sp$_{\text{KfmA}}$160	1	3	3^{*}	1	1	3
Camponotus sp$_{\text{KfmA}}$9	4	4	4	2	1	4
Camponotus sp$_{\text{KfmA}}$240	1	3	4	3	1	3
Diacamma sp$_{\text{KfmA}}$111	1	1	1	1	1	2

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[22] also s. the discussion on phorophyte specificity in Chapter 4.2.2, p. 88
[23] also s. Chapter 7, p. 114 ff.

Six different rankings in a row are still no integrative classification; they have to be combined in the next step. A fairly clear order is achieved by calculating the average of all ranks for each ant species. This average rank will be regarded as ‘ant-garden (AG)-index’ here. For calculating the AG-index, subordinate criteria were weighted only ½ compared to the main criteria, while the top criterion was weighted double compared to the main criteria.

According to this rules, the AG-index for each AG ant was calculated with the formula:

$$\boxed{I_{ant}=(4*C_1+2*(C_2+C_3)+(C_4+C_5+C_6))/11}$$

Equation 4-1: AG-index
C_i refers to the criteria presented in Table 4-24.

Of course this AG-index is highly artificial, and taking other criteria into account might result in somewhat different values. Additionally, data sets were incomplete for some criteria, and for a few species the sample size was relatively low. These two restrictions further reduce the meaningfulness of the index. However, the use of an index of this kind can serve to demonstrate a number of tendencies. The absolute values gain significance by comparison a) with the minimum and maximum theoretical value, and b) with the values for other AG species calculated by the same method (Table 4-25).

Table 4-25: Ranking of AG ants based on ‘AG-indices’
(s. Table 4-24 and Equation 4-1.)
Indices marked with * contain some estimated ranks and might turn out to have higher average ranks once sufficient data is available.

ant species	AG index
Diacamma $sp_{KfmA}111$	1.09
Pheidole $sp_{KfmA}33$	1.81
Philidris $sp_{KfmA}160$	1.90*
Crematogaster $sp_{KfmA}21$	2.00
Camponotus $sp_{KfmA}240$	2.27
Philidris $sp_{KfmA}37$	2.36
Crematogaster $sp_{KfmA}200$	2.73*
Crematogaster $sp_{KfmA}18$	3.41
Camponotus $sp_{KfmA}9$	3.55

The lowest theoretical value for an AG-index, $I_{min}=1$, was not realized in any of the species. The same was true for the highest value, $I_{max}=4$.

Diacamma $sp_{KfmA}111$, with an AG-index of $I_{D111}=1.09$, came quite close to the minimum. It may be regarded as the most ‘primitive’ type of AG. *Diacamma* $sp_{KfmA}111$ did not tend any hemipteran trophobionts, it was totally dependent on preformed cavities, and it was the only AG ant for which no chemical attractant was found in any of the seeds. It had no additional partners, was not specialized to any group of host trees, and specialization towards a single epiphyte genus (48 %) was at the upper end of class 2 for this criterion.

Pheidole $sp_{KfmA}33$ was not associated with trophobionts either. In contrast to *Diacamma* $sp_{KfmA}111$, *Pheidole* $sp_{KfmA}33$ was independent of preformed cavities because it was able to establish free AGs. This fact is reflected in the considerably higher I_{Ph33}. Nevertheless, it was frequently found using preformed cavities, constructing its AGs in connection with these. The seed-carrying behavior was rather specialized and apparently strongly dependent on chemical cues provided by seeds of AG epiphytes. Yet non-epiphyte seeds were sometimes also retrieved and used as building material or as food, while porcelain baits without seed extracts were always ignored. This suggests that *Pheidole* $sp_{KfmA}33$ was able to distinguish seeds of any type from other items of similar size. It further provided some indication that AG *Pheidole* spp. might have evolved from granivorous ancestors. Granivory is a fairly common trait in this genus (e.g. Ballard and Pruess, 1979; Hölldobler and Wilson, 1990). However, I never observed that any of the epiphyte seeds were consumed.

All remaining AG species tended trophobionts, usually on their host tree and sometimes also on neighboring plants.

Although *Crematogaster* $sp_{KfmA}21$ was totally dependent on preformed cavities for nest establishment, its AG-index was relatively high. The main reason for that was the fact that *Crematogaster* $sp_{KfmA}21$ was highly selective with regard to epiphyte seeds, and it lived in a five partner system. Despite the high selectiveness towards wind-dispersed seeds, *Crematogaster* $sp_{KfmA}21$ showed the lowest specialization with regard to epiphyte partners. This inconsistent result can be explained by a closer look at the epiphyte species: The majority belonged to the type of primarily bird-dispersed plants, seeds of which were carried by more or less all ant species.

Both *Philidris* spp. lived in four partner systems and had trophobionts sucking on the host tree, partly underneath their nests but mainly underneath extensive carton shelters, sometimes even covering almost the entire stem of the phorophyte or neighboring plants. *Philidris* $sp_{KfmA}160$ was the only species that had trophobionts also sucking on the rubiaceous ant-house epiphytes. All the other epiphytes growing on the nests of any of the AG ants were hemipteran-free. While *Philidris* $sp_{KfmA}160$ was highly dependent on preformed structures as scaffolding for its carton nests, *Philidris* $sp_{KfmA}37$ was capable of building free AGs. This is the main explanation for the difference between I_{Ph160} and I_{Ph37}.

A third species lived in a four partner system. *Crematogaster* $sp_{KfmA}200$ visited its trophobionts on the leaves of its host trees and adjacent plants. It never tended any hemipterans underneath its nests, and it did not cover its trophobionts with carton shelters. *Crematogaster* $sp_{KfmA}200$ was completely independent of preformed cavities. The AG-index should be regarded cautiously, since experiments concerning seed-carrying behavior provided too little information for a clear ranking in that criterion. Therefore I_{Cr200} gives the minimum value here.

Camponotus $\mathrm{sp}_{\mathrm{KfmA}}$240 was exclusively found in six partner systems, with trophobionts, a fungus and with parabiotic *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}$21. However, its AG-index is relatively low compared to *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}$9, because *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}$240 was totally dependent on living in preformed cavities. In comparison, *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}$9, also living in a five to six partner system, was able to construct large, free hanging AGs with the help of epiphytes. It can be regarded as the most advanced AG system together with *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}$18.

Crematogaster $\mathrm{sp}_{\mathrm{KfmA}}$18 was the only species that was restricted to a small and taxonomically distinct group of phorophytes (some species of giant bamboo). Trophobionts of the pseudococcid species *Kermicus wroughtoni* seemed to be an important link between ants and host plant[24]. It was astonishing that *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}$18 was the only species that never used preformed cavities but nested exclusively in free AGs. Most of the other known bamboo specialists (*Polyrhachis* (Schellerich-Kaaden et al., 1997); *Tetraponera* (Klein et al., 1992, 1993) and *Cataulacus* (Maschwitz et al., 2000)) nest inside the internodes of their host plant (exception: *Polyrhachis hodgesoni*, using bamboo-leaves for nest construction (Dorow and Maschwitz, 1990)).

4.2.2. Interspecific interactions

Interspecific interactions between AG ants and epiphytes are generally regarded as mutualistic (e.g. Ule, 1901, 1906; Kleinfeldt, 1986; Davidson, 1988). Benefits both groups obtain from their association in Southeast Asian AGs will be discussed in detail. Much less is known about the significance of the AG system for other partners and guests, and vice versa. However, a short assessment of these interactions will be provided at the end of this chapter.

4.2.2.1. Potential benefits of epiphytes to the ants

Suitable nest sites might be one of the most important limiting resources for ants in the canopy of tropical rain forests (Wilson, 1959; Carroll, 1979)[25]. This might especially be true for 'open canopy habitats': In secondary bamboo forests or heath forests, there are no high canopy trees from which dead wood could accumulate on smaller trees. Microclimatic conditions are extreme in such habitats. Huxley (1978) discussed this aspect based on her studies on ant-house epiphytes in Papua New Guinea. She found ant-house epiphytes to be highly abundant in some open canopy habitats (mangroves, heath forests, savanna forests), and rare but diverse in closed forests. The main inhabitants of the ant-house epiphytes, one or several species of *Philidris* (also s. Huxley, 1978, 1982; Janzen, 1974), are dependent on preformed cavities although they are able to construct carton shelters. Thus, the domatia provided by the plant partners might be especially beneficial to these ants.

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[24] also see Chapter 4.2.2.3, p. 88 f.

[25] also see Chapter 1.2, p. 2

Basically the same is true for all the other AG ants – dependent on natural cavities or not. They all have to achieve a dry, safe and long-lasting nest site, and they do so with the help of epiphytes. All the species tested with regard to this aspect had only small and rather fragile nests as long as epiphytes were missing, while average nest size and stability increased enormously when epiphyte roots penetrated the carton material[26]. Ule (1901) already suggested this effect for neotropical AGs in his very first description of this type of association. His idea was supported by results from Belin-Depoux et al. (1987) and Yu (1994). Yu (1994) indicated that the transpiration of the epiphytes might be important for drying and thus stabilizing the nests after heavy rainfall.

Although many ant species found in this study still need natural cavities for nest establishment, the total spectrum of suitable nest sites is increased with the help of carton-stabilizing or domatia-forming epiphytes. From the AG species studied here, seven ant species from four genera developed a high degree of independency from preformed cavities, i.e. they were capable of establishing free AGs.

The relative suitability of different epiphyte species for the purpose of nest stabilization was not investigated. At least *Dischidia* and some *Hoya* and *Aeschynanthus* species with extensive root growth are apparently highly appropriate (also see Leeuwen and Leeuwen-Reijnvaan, 1913; Khatijah and Kiew, 1986; Kiew and Anthonysamy, 1995).

A second benefit, common in many cases of terricolous myrmecophytism as well as in neotropical AGs, is a nutritional one. The plants provide extrafloral nectaries, food bodies or edible seed appendages (elaiosomes) for their partner ants (Davidson, 1988). They might also serve as food plants for hemipteran trophobionts and thus indirectly supply the ants with carbohydrate-rich plant sap in form of honeydew (Davidson, 1988).

None of these cases was common in Southeast Asian AG systems. The only exceptions were some pseudococcids, sometimes tended inside domatia of the rubiaceous ant-house plants (*Philidris* sp$_{\mathrm{KfmA}}$160, p. 57). Most AG ants had their trophobionts sucking on the host tree or adjacent plants; some did not visit trophobionts at all (*Pheidole* sp$_{\mathrm{KfmA}}$33, p. 45, and *Diacamma* sp$_{\mathrm{KfmA}}$111, p. 73). Nevertheless, there might be some nutrient supply from the epiphyte partners. Some epiphytes produced sweet and primarily bird-dispersed fruits (e.g. the Melastomataceae and the Rubiaceae), which were regularly harvested and consumed by the ants. *Pachycentria constricta* and *Pachycentria glauca* (Melastomataceae) produced pearl bodies (Clausing, 1998). Flowers of the asclepiad species of *Dischidia* and *Hoya* were extremely nectar-rich and frequently visited by AG ants (Kerr, 1912; Kleijn and Donkelaar, 2001; pers. obs.; Color Plate 4-5, p. 69). As some species flower throughout the year, highly productive floral nectaries might replace extrafloral nectaries here. Huxley (1978, 1982) observed that *Philidris cordatus* workers visited flowers of *Hydnophytum* and *Myrmecodia* after the corolla had fallen off. Davidson and Epstein (1989) even

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[26] see Chapter 4.1, Section 'Colony structure' for each species

speculate that "ants that clear some non-mutualistic epiphytes from their hosts do not eliminate seedlings of *Dischidia nummularia*, which provides no nest cavities for ants", because this species flowers constantly and the flowers "may function as analogues of extrafloral nectaries".

Leeuwen (1929a) described oil-containing tissue in the seeds of several AG epiphytes (also s. Janzen, 1974; Weir and Kiew, 1986). He suggested that these might serve as a nutritional rewards for seed-retrieving ants. However, *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ colonies, experimentally transferred to a poor nutritional condition, never retrieved any seeds (Kaufmann et al., 2001). Moreover, AG ants were never observed to gnaw on seed tissue. It therefore seems likely that the nutritional value of the seeds at least for these ants cannot be high. Unlike most other ant-dispersed plants, Southeast Asian AG epiphytes have no obvious elaiosomes.[27]

Indirectly, the association with epiphytes has a major impact on food availability for the ants. With the help of the epiphytes, large, polydomous, dominant colonies can develop. Such colonies are able to monopolize extrafloral nectaries or hemipteran trophobionts and thus improve their exploitation of these important food sources (Davidson, 1997).

A final benefit of the epiphytes for the ants might be that of providing shadow and thus compensating the presumably extreme daily temperature and humidity changes in the mostly sun-, wind- and rain-exposed nesting sites (Ule, 1901). Ants need relatively constant microclimatic conditions for brood development. Daily temperature variations of up to 12°C (Chapter 5.1.2, Table 5-3, p. 96) could cause serious problems, which might at least partly be diminished with the help of the epiphytes (Stuntz, 2001).

4.2.2.2. Potential benefits of ants to the epiphytes

Due to their life style above the ground epiphytes face several problems[28]. The association with AG ants may help to overcome at least some of them.

First of all, ants provided reliable short-distance seed dispersal to suitable growing sites. More or less selective seed retrieval was demonstrated for 18 AG ant species. All epiphytes identified as true AG mutualists were diplochorous: They either combined wind-dispersal (anemochory) with ant-dispersal (myrmecochory[29]) (e.g. Gesneriaceae, Asclepiadaceae), or myrmecochory was preceded by ornithochory (bird-dispersal; e.g. Melastomataceae, Rubiaceae). Both, anemochory

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[27] also s. Chapter 7, p. 123 ff.

[28] also s. Chapter 1.1, p. 1

[29] The term "myrmecochory" will be used in its literally and thus in an extended sense here. The original definition, designed by Sernander (1906), only included ant-dispersed plant species with an elaiosome structure attached to the seeds. The intention of Sernander's restriction was to exclude "accidental" seed dispersal, e.g. by seed harvesting ants. However, the term myrmecochory will here be used for "non-accidental seed dispersal by ants" with or without elaiosomes, because otherwise seed dispersal by Southeast Asian ant-garden ants might not be included. In view of more recent data on seed-carrying eliciting factors, Sernander's distinction becomes difficult in any case and might need redefinition in future.

and ornithochory are efficient ways of long distance seed dispersal (e.g. Kleijn and Donkelaar, 2001), but they are ineffective and not selective at all concerning the growing site on which a seed lands. Here, arboreal ants that collect the seeds and carry them into their carton nests, are ideal partners. AG ants frequently harvested epiphyte seeds before the fruit-capsules opened or birds consumed the berries. The beneficial effect seed-retrieving by ants may have for the respective plants has also been described by Beattie and Culver (1982), and the authors designated the term “inhumation” for this phenomenon. They suggest that ants and many other insects may regularly help seeds to reach a suitable growing site.

Once a seed has reached an AG, the second question becomes crucial: How favorable are ant nests as substrate for epiphytes? Do they supply the epiphytes with plant nutrients and water? In all tested cases the answer to this question was a clear ‘yes’. The substrate of ant nests has a rather high water-storing capacity (factor 2 to 5.6). This might be significant, because epiphyte habitats can be temporarily very dry (Benzing, 1990; Laman, 1995). During the mostly short and heavy tropical rainfalls, water runs down the trees quickly and therefore is available only for a very short time (Drehwald, 1995); growing on a ‘sponge’ gives epiphytes more time to absorb water. Moreover, the first rainfall after a dryer period is extraordinarily rich in nutrients (Drehwald, 1995); fast water-storing capacities may thus support nutrient supply also.

Substrate quality concerning nutrient content was high as well. Even though the epiphytes had constantly taken nutrients from their growing substrate, the nitrate, ammonium and phosphate content of AG ant nests equaled or even highly exceeded that in carton of ants with no epiphytes growing on their nests (Table 4-6, p. 31). Phosphate was factor 5-30 more concentrated in AG ant nests than in forest soil or bark. Depending on ant species and epiphyte growth, nitrate content was at least equal to that of forest soil and bark or exceeded it up to factor 10. Ammonium was more concentrated in AGs than on bark, but in some cases less concentrated than in forest soil. In contrast to other carton-building ants, AG ants actively fertilize their carton substrate by defecation and retrieval of organic material, especially of cuticular parts of prey insects. Blüthgen et al. (2001) compared substrate of neotropical AG ants with termite nests and runways of a non-AG ant. They found out that the dry weight of N, P and K was significantly higher in AGs than in any of the other substrates tested. Last but not least, the generally good condition of AG epiphytes should be sufficient evidence for the suitability of AG ant nests as substrate for these plants.

A final beneficial effect, known from many terricolous ant-plant associations (e.g. Beattie, 1985; Jolivet, 1996), is that of herbivore defense. Though no experimental data is available on this aspect, some general observations can offer hints. It was obvious that the degree of herbivore defense varied greatly between different AG ants, and the need for defense varied between different AG epiphytes. Asclepiads generally contain poisonous latex and are thus fairly well protected against most herbivores. However, some specialists are still able to feed on their leaves. Cultivating *Hoya elliptica* without its partner ants, a geometrid moth was frequently discovered feeding on the plants, while this was not the case when the ants were present (pers. obs.). This suggests some degree of herbivore protection here. *Agathia cristifera*, a geometrid moth feeding on several species of *Dischidia*, was ‘double-specialized’ and lived inside the AGs of *Crematogaster* sp$_{\text{KfmA}}$18 and *Pheidole* sp$_{\text{KfmA}}$33. Both AG ants were observed to attack other caterpillars (that had been placed artificially on the plants), but they ignored *Agathia cristifera*. This moth thus overcame both the chemical and the biological protection. Orivel and Dejean (2000) discovered a similar association in tropical American AGs. Here, the hesperid moth *Vettius tertianus* fed on the AG bromeliad *Aechmea mertensii* on AGs of *Pachycondyla goeldii* (Ponerinae). Though patrolling on the leaves of its epiphyte associates, *Pachycondyla goeldii* never attacked larvae of *Vettius tertianus*.

On AGs of *Diacamma* sp$_{\text{KfmA}}$111, an undetermined chrysomelid beetle frequently consumed large portions of the leaves of some associated epiphytes, completely unmolested by the ants. *Diacamma* sp$_{\text{KfmA}}$111 was generally never observed to keep herbivores away from any of its epiphyte partners and thus has to be regarded as a very poor defense. It might sometimes feed on herbivore eggs laid on the leaves of the epiphytes.

Generally, epiphytes growing on AGs displayed very little leave damage, thus a certain protective effect can be presumed.

4.2.2.3. Significance of additional ‘partners’ for ant-garden systems, and vice versa

Hemipteran trophobionts and phorophytes

The ecological significance of the hemipteran trophobionts will not be discussed in detail here. It is fairly clear that, except for the two species not tending any trophobionts, these played an important role for colony nutrition. Generally, dominant arboricolous ants mainly feed on honeydew for carbohydrates (Tobin, 1991, 1994; Davidson and Patrell-Kim, 1996; Blüthgen et al., 2000b); additionally, hemipteran trophobionts may also be an important protein source when consumed directly (e.g. Way, 1963). Vice versa, ants protect their ‘livestock’ from predators and parasites, sometimes carrying nymphs to new feeding sites (observed for *Crematogaster* sp$_{\text{KfmA}}$18 in this study) and providing ‘cleaning services’ (review s. Way, 1963). Since most AG ants covered their trophobionts with carton shelters, at least a basic protection can be presumed. There is no reason to doubt that further services are also common in AG ants, but no experimental investigations have been performed in this connection. It is interesting to note that AG epiphytes were used as feeding sites for trophobionts in only one case (Chapter 4.1.2.2, p. 57). Ants usually tended their ‘livestock’ on the phorophyte. This may indirectly affect the ants in two ways: Firstly, the phorophyte is a much more productive food source than the epiphytes and may thus be necessary to fulfill the ants’ nutritial demands. Secondly, the epiphytes with their relatively low biomass may severely suffer if infected with hemipterans.

Therefore, the relationship towards hemipteran trophobionts is an important link between host tree and ants, and it may explain the low phorophyte-specificity displayed by most AG ants. Generally, mutualistic associations between ants and hemipteran trophobionts tend to be non-specific, though certain preferences are common (Way, 1963; Gullan, 1997). Most AG ants tended a variety of Coccidae, Pseudococcidae and, to a lesser extent, Membracidae and Heteroptera. The lack of species-specificity between ants and hemipteran trophobionts explains the low degree of phorophyte-specialization of AG systems: There is no reason to be specialized, as long as suitable food can be found on a variety of host trees. Preformed cavities for nest establishment are limiting for species dependent on such structures; those with totally free hanging AGs are even less restricted in their phorophyte choice. The only phorophyte-specialist in the present study, *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ with its restriction to giant bamboo as host tree, also showed a high, though not exclusive, preference towards the pseudococcid *Kermicus wroughtoni* – a bamboo specialist (Hendricks and Kosztarab, 1999; Ben-Dov and German, 2002).

However, there are for sure more and less suitable phorophytes for AG associations, and patterns might become visible when collecting more data. In tropical American AGs, Orivel et al. (1996) found certain ant species-specific preferences towards phorophyte species. In addition to that, one tree species (*Vismia guyanensis*) was extraordinarily popular for AGs in general. The authors have no conclusive explanation for this phenomenon, but they suppose an influence of ant resources a tree can offer, some genetic predisposition of founding queens and a principal preference for the tree species a founding queen originates from. The latter had been shown by Dejean et al. (1992) for arboricolous non-AG ants before, and it has also been suggested for AG ants in French Guyana (Dejean et al., 1997).

Davidson (1988) found clear preferences of AG ants towards two tree species in Cocha Cashu (Peru): *Calyptranthes* cf. *lanceolata* and *Inga* sp. (also s. Davidson and Epstein, 1989). The author suggests that these preferences might be due to richness in ant resources: Large populations of hemipteran trophobionts are tended on both species, *Inga* sp. additionally provides large extrafloral nectaries. *Azteca* cf. *traili* are over-represented on *Cordia nodosa* and *Tococa* sp., which both provide nodal or foliar domatia (Davidson and Epstein, 1989).

There is no data on possible beneficial or negative effects AGs might have on their host trees, because this aspect has not been studied yet. However, at least some theoretical considerations will be addressed here. One negative effect might be simple mechanical overloading of branches that then break. Extensive phloem-sucking trophobiont populations maintained by most of the AG ants may also affect the host tree negatively. They take nutrients from the tree and additionally may be vectors of diseases or at least increase the vulnerability of the tree towards infections. Herbivore protection may be named as a possible positive effect, as has been shown by Dejean et al. (1995): Unspecific ants living in cavities of bromeliad epiphytes and orchids protected host trees from defoliators (chrysomelid beetles, leaf-cutter ants). Since herbivore defense is one of the main benefits in many mutualistic ant-plant associations (e.g. Fritz, 1983; Beattie, 1985; Fonseca, 1994; Gaume and McKey, 1999), this factor is at least worthy of consideration. Most Southeast Asian AG ants (exceptions in this study: *Diacamma* $\mathrm{sp}_{\mathrm{KfmA}}111$ and *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}200$) are polydomous and additionally have trophobiosis sites at several places in their host tree. Thus, their foraging range is relatively large. As they also feed on other arthropods as protein source, this might already be sufficient for a certain degree of herbivore defense. The relatively high aggressiveness of most AG ants further reinforces this effect.

A second beneficial factor in terricolous ant-plant systems is the pruning of climbers by the partner ants (e.g. Janzen 1967, 1969; McKey, 1984; Davidson et al., 1988; Fiala et al., 1989). The present study furnishes no evidence for such behavior. Weir and Kiew (1986) describe an ant-epiphyte-tree relationship in Malaysia, including *Crematogaster* sp., *Leptospermum flavescens* as phorophyte and *Dischidia parvifolia* as well as *D. astephana* as epiphyte partners. They suppose a tight and specific relationship and speculate that the ants keep their host tree clean of any epiphytes apart from the two associated species, but data are incomplete. However, the ants live in the central cavity of *Leptospermum flavescens*, and thus this case might be comparable rather to other myrmecophytic trees than to AG associations.

Fungi

Undetermined fungi were frequently found growing inside the nests of three AG species, *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$, *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ and *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$. As these fungi were only detected in well-developed AGs and only in the innermost part, it seems unlikely that they stabilize the nests, as it is the case in other carton building ant species[30]. As a second possibility, the fungi could form an ektomykorrhiza, providing the epiphytes with nutrients. Belin-Depoux (1991) reported the existence of ektomykorrhiza in association with the AG epiphyte *Philodendron melinonii* (Araceae) in South America. Cedeño et al. (1999) found nitrogen-fixing cyanobacteria on the roots of the AG epiphyte *Anthurium gracile* (Araceae). In the relevant Southeast Asian AGs, this nutritional significance is improbable, because there were almost no roots in the core of the nest where the fungi were found. Miehe (1911a, b) discovered a fungus in the tubers of rubiaceous ant-house epiphytes in Java and discussed its possible significance in detail – without arriving at any final conclusion. Huxley (1978, 1982) described the same from Papua New Guinea; she found two different fungi. She speculated that the ants disperse both species, because their occurrence was correlated with the occurrence of *Philidris cordatus*. Huxley (1978, 1982) further suggested that the ants might feed on the spores of one of the fungi, which was growing parasitically in the tubers of *Myrmecodia* spp. The second fungus, *Arthrocladium* sp., was supposed to secrete hydrolytic enzymes that could play a role in the process of decomposition and thus help to make nutrients available for the plants (Huxley 1978), or it might also be consumed by the ants (Huxley 1982).

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[30] also s. Chapter 1.2, p. 2 f.

As all three fungus-associated AG ant species in this study mainly fed on honeydew, the idea that they might additionally consume fungi seems questionable. However, there is no data on the ecological significance of any of the fungi found in the AGs of this study; they might just join the association commensally. Benzing (1991) described *Cladosporium myrmecophilum* as a regular inhabitant of carton nests “with no obvious impact on animal or plant inhabitants”.

Parabiotic ants

The role and significance of parabiotic[31] ant species is about as obscure as that of the fungi. It is interesting though that parabiotic associations, including identical genera, are also found in neotropical AGs. Here, *Camponotus femoratus* and *Crematogaster* cf. *limata parabiotica* frequently reside in the same AGs (Wheeler, 1921; Weber, 1943; Swain, 1980; Davidson, 1988; Orivel et al., 1997; Cedeño et al. 1999; Corbara et al., 1999; Orivel and Dejean, 1999b). In some habitats, more than 90 % of all AGs are inhabited by these two species (e.g. Davidson, 1988).

Crematogaster cf. *limata parabiotica* was additionally found in parabiotic association with five other ant species belonging to four subfamilies (Orivel et al., 1997; Corbara et al., 1999). Swain (1980) suggests that *Crematogaster* sp., associated with *Dolichoderus* sp. and referred to as *Crematogaster* cf. *limata parabiotica* in previous publications, should be regarded as a second species. It seems possible that *Crematogaster* cf. *limata parabiotica* also has been misidentified in other associations described in the literature.

This would at least partly explain why there are such great differences in the behavior of *Crematogaster* cf. *limata parabiotica* observed by different authors. For example, Wheeler (1921), Orivel et al. (1997), Corbara et al. (1999) and Orivel and Dejean (1999b) report interspecific trophallaxis of *Crematogaster* cf. *limata parabiotica* and *Camponotus femoratus*, while Swain (1980) never observed behavior of this kind. He tries to explain Wheeler’s (1921) observations as some kind of appeasement strategy, because in his experiments both species aggressively competed for protein baits. Swain (1980) presents evidence for interspecific trail following of *Camponotus femoratus* on the trails of *Crematogaster* cf. *limata parabiotica*, while Davidson (1988) could not confirm this ability. Cedeño et al. (1999) as well as Orivel and Dejean (1999b) found independent *Crematogaster* cf. *limata parabiotica* colonies inhabiting AGs, while Davidson (1988) discovered such colonies nesting exclusively in stem cavities. These ambiguous results indicate that parabiotic

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[31] Forel (1898) assigned the term ‘parabiosis’ to an association of *Dolichoderus* sp. and *Crematogaster* sp. in Colombia. Introducing this term he tried to make a clear distinction between this new case - in which both species live in common nests, keep their brood separate but show no aggression towards each other - from the ‘compound nests’ found in nearctic and palaearctic ants. In these compound nests, “two or more hostile species sometimes have interlacing but not intercommunicating galleries” (Forel 1898). Since the term parabiosis has been introduced, scientists have argued about which associations may be designated with this term and which may not. Moreover, parabiotic associations are described as one case of “compound nests” (Wilson, 1971). Nevertheless, it seems convenient to use this term here, defined as an association of two ant species that share their trails and sometimes also their nests but keep their brood in separate areas.

interactions in general are still poorly understood and that much more research is needed in this field.

However, most authors agree that parabiosis is most probably a mutualistic, though not obligate, interaction. The beneficial effect for *Crematogaster* cf. *limata parabiotica* is fairly obvious: Although these ants can live on their own and also construct (at least small) carton buildings (Davidson, 1988; Corbara et al., 1999; Orivel and Dejean, 1999b), they gain more nesting space from their parabiotic partner. Additionally, *Camponotus femoratus* is a highly effective defense against vertebrate enemies. According to Wilson (1987), *Camponotus femoratus* is (one of) the most ferocious ant species worldwide.

If *Camponotus femoratus* really follows recruitment trails of *Crematogaster* cf. *limata parabiotica,* it can exploit additional food sources and thus profit from the association (Swain, 1980). Both species together had a significant time-advantage in finding baits compared to all other sympatric ant species together (Davidson, 1988). Another benefit proposed by Davidson (1988) is nutritional also. *Camponotus femoratus* workers are too large to exploit very small food sources, and they might thus be unable to care for some nymphal stages of their trophobionts. Davidson suggests that *Crematogaster* cf. *limata parabiotica* tends these until they are big enough for *Camponotus femoratus.*

Regarding the few data collected on parabiotic interactions in the present study, similar patterns as well as fundamental differences compared to neotropical *Camponotus femoratus* - *Crematogaster* cf. *limata parabiotica* can be identified. Additionally, the parabiotic systems investigated here already vary in some aspects. There is some indication that *Camponotus* sp$_{\text{KfmA}}$9 as well as *Camponotus* sp$_{\text{KfmA}}$240 do follow the recruitment trails of *Crematogaster* sp$_{\text{KfmA}}$21, their main partner ant. In unsystematic feeding experiments with tuna baits as well as in the seed-carrying experiments, *Crematogaster* sp$_{\text{KfmA}}$21 discovered baits first, but *Camponotus* sp$_{\text{KfmA}}$9 and *Camponotus* sp$_{\text{KfmA}}$240 followed quickly and exploited the bait much faster than *Crematogaster* sp$_{\text{KfmA}}$21 could. Moreover, both *Camponotus* spp. frequently took large seeds/pieces of bait from *Crematogaster* sp$_{\text{KfmA}}$21. These observations suggest that the two *Camponotus* spp. do benefit from their parabiotic partner.

Seidel (1994) has proved experimentally that *Camponotus* sp$_{\text{KfmA}}$240 follows trails of *Crematogaster* sp$_{\text{KfmA}}$21. Vice versa, *Crematogaster* sp$_{\text{KfmA}}$21 did not follow recruitment trails of *Camponotus* sp$_{\text{KfmA}}$240.

Crematogaster sp$_{\text{KfmA}}$21 usually lives in its own small nests. It was never found in the free hanging AGs of *Camponotus* sp$_{\text{KfmA}}$9, but sometimes it co-inhabited the cavities of *Camponotus* sp$_{\text{KfmA}}$240. Thus, additional nesting space is not gained in any case, unlike the situation in the neotropics. Nevertheless, the association might still be beneficial for *Crematogaster* sp$_{\text{KfmA}}$21, because at least *Camponotus* sp$_{\text{KfmA}}$9 is extremely aggressive towards any disturbance and able to deter vertebrates effectively. *Camponotus* sp$_{\text{KfmA}}$240 is less aggressive if only slightly disturbed; in this case *Crematogaster* sp$_{\text{KfmA}}$21 starts defending the nest first. However, when severely disturbed, *Camponotus* sp$_{\text{KfmA}}$240 becomes ferocious as well. Thus, parabiotic interactions in Southeast Asian AGs might be mutualistic also.

The seed-carrying behavior is especially interesting in parabiotic species: *Camponotus* sp$_{\text{KfmA}}$9, *Camponotus* sp$_{\text{KfmA}}$240 and *Crematogaster* sp$_{\text{KfmA}}$21 all show the same preferences, relying on chemical cues and also on size cues. This is quite peculiar because *Crematogaster* sp$_{\text{KfmA}}$21 has severe difficulties in carrying the large seeds, but nevertheless it does not retrieve any smaller ones. The second *Crematogaster* sp. (*Cr.* sp$_{\text{KfmA}}$42, Chapter 4.1.2.3, p. 61) frequently observed in association with *Camponotus* sp$_{\text{KfmA}}$9 was never attracted to any seeds at all.

In the neotropics, *Camponotus femoratus* and *Crematogaster* cf. *limata parabiotica* also show common seed preferences (e.g. Orivel and Dejean, 1999b), but systematic experiments are missing. Davidson (1988) observed that *Crematogaster* cf. *limata parabiotica* was unable to carry the epiphyte seeds over long distances. None of this helps very much to account for the peculiar patterns found in this study. Possible explanations will be discussed in Chapter 7.2.2.

A further parallel between *Camponotus femoratus* - *Crematogaster* cf. *limata parabiotica* and *Camponotus* sp$_{\text{KfmA}}$240 – *Crematogaster* sp$_{\text{KfmA}}$21 is the occurrence of interspecific trophallaxis, underlining the close association. It seems, however, that trophallaxis was one-directional in Southeast Asian AGs, with *Camponotus* sp$_{\text{KfmA}}$240 begging food from *Crematogaster* sp$_{\text{KfmA}}$21, but not the other way round (also s. Seidel, 1994).

Guests

The significance of guests will not be discussed in detail here. Generally, the guests will probably benefit from the association, while neither ants nor epiphytes nor phorophytes will profit from the guests. Thus, most guests will have to be regarded as commensals or even parasites of the AG system. The high variety of guests supports the idea that AGs are of great ecological importance for many canopy organisms[32].

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[32] also see Chapter 6.2.1, p. 108

5. Species sorting of ant-garden ants and ant-garden epiphytes

Theoretically, many factors can influence the occurrence of ants and epiphytes in a certain spot in the canopy. AG ants are sensitive to microclimatic factors (humidity, temperature, 'weather-exposure'); most of them need a suitable phorophyte for hemipteran trophobionts, and some also need preformed cavities for nest construction. AG epiphytes can be expected to depend much less on phorophyte characteristics than non-AG epiphytes (Went, 1940; Johansson, 1974; Kiew and Anthonysamy, 1987; Steege and Cornelissen, 1989; Benzing, 1995; Callaway et al., 2002) because they do not grow directly on the bark but are – at least in the beginning – confined to ant nests. Microclimatic factors such as humidity and irradiance (Johansson, 1974; Sato et al., 1996) as well as 'weather exposure' might be as important as the ant species retrieving the epiphyte seeds and providing growth substrate. Furthermore, many other factors such as general habitat characteristics, competing ant and epiphyte species, predators, parasites and small-scale 'historical' events might also play a role (summarized in Benzing, 1990). The complexity of these interactions was not resolved in the present study, but three aspects were at least partly investigated: 1. The interdependences of AG ant and epiphyte species, 2. temperature-preferences of some ants, and 3. the vertical position in a tree in which AG ants and epiphytes established for preference. The latter parameter comprises a variety of changing factors with special influence on the epiphytes, e.g. irradiation, humidity, CO_2-concentration, and minerals in stem flow (Lüttge, 1989).

5.1. Results

5.1.1. Interdependences of AG ant and epiphyte species

In order to investigate species-specific preferences or specializations I tested ant-epiphyte-matrices[33] using a Monte Carlo randomization method (Chapter 3.6, p. 19) in combination with the data provided in the species descriptions.

The species descriptions already revealed that some of the ant species had strong preferences towards certain epiphyte species (e.g. 87 % of all *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ colonies with *Hoya elliptica*[34]), while others were associated with a larger variety of plants. The same is true for the epiphytes: Some were almost exclusively growing on the nests of a single ant species (e.g. 87 % of *Hoya elliptica* on *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ nests; *Hoya mitrata*[35] exclusively with either of the

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[33] The complete matrix for all AG ant species and associated epiphytes is presented in Table 5-4, p. 97.

[34] see Chapter 4.1.2.3, p. 61

[35] see Chapter 4.1.2.1, p. 39 and Chapter 4.1.2.3, p. 65

parabiotic *Camponotus* sp$_{\text{KfmA}}$240 and *Crematogaster* sp$_{\text{KfmA}}$21)[36], while others occurred in combination with several ants.

Detection of patterns becomes more difficult when considering ant species occurring with a wide variety of epiphytes. A detailed analysis was restricted to the study area around Ulu Gombak because data are most comprehensive for this area, and twelve different AG ants as well as 30 AG epiphytes occurred sympatrically. As a first step, the clear ‘specialists’, *Camponotus* sp$_{\text{KfmA}}$9 and *Hoya elliptica*, were excluded from the matrix, and the species distribution was tested for the remaining ant and epiphyte species, still revealing a clear compartmentalization (T_obs=615.8, mean T_ran=512.1 ± 46.0, p<0.001). That means that there were still certain preferences ‘hidden’ in the matrix. To identify these, the matrix of the five most common ant and epiphyte species was tested. Species sorting could be confirmed for these species also (T_obs= 481.2, mean T_ran=415.3 ± 8.4, p<0.001), and some patterns became clearly evident (Table 5-1). For example, *Aeschynanthus albidus* was growing on the nests of all the ant species but seemed to be more important for *Pheidole* sp$_{\text{KfmA}}$33 than for the other ants[37]. *Dischidia nummularia* could be identified as most important for both *Crematogaster* species (*Cr.* sp$_{\text{KfmA}}$18 and *Cr.* sp$_{\text{KfmA}}$19), and *Crematogaster* sp$_{\text{KfmA}}$18 was the most common partner of the plant also. *Poikilospermum microstachys* showed the highest relative abundance with *Pheidole* sp$_{\text{KfmA}}$33, *Pyrossia lanceolata* with *Crematogaster* sp$_{\text{KfmA}}$18. *Schefflera* sp$_{\text{KfmA}}$75 occurred predominantly with *Diacamma* sp$_{\text{KfmA}}$111 here.

Table 5-1: Relative abundance of the five most common epiphyte species and the five most common ant species in Ulu Gombak.

% col. represents the ant colonies occurring with the respective epiphyte species in relation to the total number of colonies of this ant species found in that area. % plants represents the relative occurrence of the epiphyte species with the respective ant species in relation to the total number of this epiphyte found on any ant nest in the area. (‘clear’ specialists like *Camponotus* sp$_{\text{KfmA}}$9 and *Hoya elliptica* were not included, s. text)

	Aeschynanthus albidus (n=35)		*Dischidia nummularia* (n=79)		*Poikilospermum microstachys* (n=34)		*Pyrossia lanceolata* (n=31)		*Schefflera* sp$_{\text{KfmE}}$75 (n=22)	
	% col.	% plants	% col.	% plants	% col.	% plants	% col.	% plants	% col.	% plants
Crematogaster sp$_{\text{KfmA}}$18 (n=67)	26.87	51.42	85.07	72.15	10.45	20.59	29.85	64.52	0.00	0.00
Crematogaster sp$_{\text{KfmA}}$19 (n=17)	29.41	14.29	58.82	12.66	0.00	0.00	17.65	9.68	0.00	0.00
Diacamma sp$_{\text{KfmA}}$111 (n=47)	14.89	3.23	0.00	0.00	29.79	41.18	0.00	0.00	42.55	90.91
Pheidole sp$_{\text{KfmA}}$33 (n=5)	80.00	11.43	0.00	0.00	0.00	0.00	40.00	6.45	0.00	0.00
Philidris sp$_{\text{KfmA}}$37 (n=11)	18.18	5.71	36.36	5.06	18.18	5.88	36.36	12.90	0.00	0.00

In pairwise comparison, corrected with Bonferroni correction, patterns could be confirmed as shown in Table 5-2. The epiphyte distribution on nests of *Diacamma* sp$_{\text{KfmA}}$111 differed significantly from any of the other four species, and *Crematogaster* sp$_{\text{KfmA}}$18 showed a pattern

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[36] but see Weissflog et. al., 1999

[37] This might be an artefact, because only five colonies of *Pheidole* sp$_{\text{KfmA}}$33 were collected in the Gombak Area.

significantly different from that of *Pheidole* sp$_{KfmA}$33. Between all the other species combinations, no significant species sorting could be observed.

Table 5-2: Significance levels for species sorting of the five most common ant species in Ulu Gombak
Significance means that the two ant species differed significantly in the relative occurrences of epiphyte species growing on their nests. Monte Carlo randomization method with Bonferroni correction ($p<0.01$) for 10 pairwise comparisons.

	Crematogaster sp$_{KfmA}$18	*Crematogaster* sp$_{KfmA}$19	*Diacamma* sp$_{KfmA}$111	*Pheidole* sp$_{KfmA}$33	*Philidris* sp$_{KfmA}$37
Crematogaster sp$_{KfmA}$18	-	n.s.	**	**	n.s.
Crematogaster sp$_{KfmA}$19		-	**	n.s.	n.s.
Diacamma sp$_{KfmA}$111			-	**	**
Pheidole sp$_{KfmA}$33				-	n.s.
Philidris sp$_{KfmA}$37					-

5.1.2. Temperature

The possible role of microhabitat temperature for species sorting was studied in Ulu Gombak, directly comparing mean temperature (337 measurements per week, six different colonies of each species) at nests of *Camponotus* sp$_{KfmA}$9, *Crematogaster* sp$_{KfmA}$18, *Diacamma* sp$_{KfmA}$111 and *Philidris* sp$_{KfmA}$37 (Table 5-3 and Chapter 3.3, p.12). Mean temperature/week for all species was compared using the Friedman Test, and no significant differences were detected ($\chi^2=3.0$, $p=0.39$). It cannot be ruled out, however, that small but distinct temperature differences exist but could not be resolved with the used data loggers (Chapter 3.3, p. 12). There was a significant difference when the non-AG ant *Crematogaster* cf. *artifex* was included in the test. In multiple comparisons using LSD, *Crematogaster* cf. *artifex* turned out to live in a significantly warmer microclimate than any of the other species ($p<0.05$).

Table 5-3: Temperature on the nests of four AG ants and one non-AG ant in Ulu Gombak, Malaysia

ant species	n (weeks, with 337 values per week)	mean [°C]	min [°C]	max [°C]
Camponotus sp$_{KfmA}$9	7	23.6 ± 0.33	20.3 ± 0.49	31.1 ± 1.7
Crematogaster sp$_{KfmA}$18	15	24.1 ± 0.59	20.0 ± 0.29	31.6 ± 2.37
Diacamma sp$_{KfmA}$111	15	23.5 ± 0.81	20.5 ± 0.27	30.6 ± 3.79
Philidris sp$_{KfmA}$37	15	23.6 ± 0.23	20.5 ± 0.44	30.7 ± 1.89
Crematogaster cf. *artifex*	16	24.4 ± 0.52	20.0 ± 0.34	36.1 ± 2.69

Table 5-4: Distribution of epiphyte species on ant-garden ants.

Only species that were found at least three times are included here. Ant species that were described in detail in the main text (Chapter 4.1, p. 20 ff.) are printed in bold letters. ‘Ant-house’ epiphytes are marked with ^.

	Acriopsis javanica	*Aeschynanthus* sp$_{\text{KfmE}}$122	*Aeschynanthus albidus*	*Aeschynanthus fecundus*	*Asplenium nidus*	*Dendrobium* sp$_{\text{KfmE}}$4	*Dischidia* sp$_{\text{KfmE}}$115	*Dischidia acutifolia*	*Dischidia albida*	*Dischidia bengalensis*	*Dischidia fruticulosa*	^*Dischidia imbricata*	*Dischidia nummularia*	^*Dischidia major*	*Drymoglossum piloselloides*	*Drynaria rigidula*	*Drynaria sparsisora*	*Ficus* sp$_{\text{KfmE}}$96	*Hedychium longicornutum*	*Hoya* sp$_{\text{KfmE}}$94	*Hoya elliptica*	*Hoya lacunosa*	*Hoya micrantha*	^*Hoya mitrata*	*Hoya multiflora*	^*Hydnophytum* sp$_{\text{KfmE}}$104	^*Hydnophytum formicarium*	^*Lecanopteris sinuosa*	*Liparis lacerata*	*Medinilla crassifolia*	^*Myrmecodia tuberosa*	*Pachycentria constricta*	*Pachycentria glauca* subsp. *glauca*	*Pachycentria glauca* subsp. *maingayi*	^*Platycerium ridleyi*	*Poikilospermum cordifolium*	*Poikilospermum microstachys*	*Pyrossia floccigera*	*Pyrossia lanceolata*	*Schefflera* sp$_{\text{KfmE}}$75	*Schefflera* sp$_{\text{KfmE}}$91	*Schefflera* sp$_{\text{KfmE}}$132	*Schefflera* sp$_{\text{KfmE}}$155
Camponotus **sp$_{\text{KfmA}}$9**																			1	1	13											1		1		2	3			2			
Camponotus **sp$_{\text{KfmA}}$240**									1														1	10			1					3					4						
Camponotus sp$_{\text{KfmA}}$241																	2		1											1							1						
Crematogaster **sp$_{\text{KfmA}}$18**	3	1	13	18	1	2		9	1		1		63		7										1			2	4			4		6	1	6	9	9	23		2		
Crematogaster sp$_{\text{KfmA}}$19			5										10		1																1	1						3	4				
Crematogaster **sp$_{\text{KfmA}}$21**		1	1										1				1		1			1	1	5												2	3		1	1	1		
Crematogaster sp$_{\text{KfmA}}$99			2							1	1														1							1				1							
Crematogaster sp$_{\text{KfmA}}$113																						1					1				1	1					1						
Crematogaster **sp$_{\text{KfmA}}$200**			9																																							10	
Diacamma **sp$_{\text{KfmA}}$111**			11	1				6		1					1			3	1	1			1		1			1				6					18			25	7		3
Pheidole **sp$_{\text{KfmA}}$33**	1		11	2	1	1	4		4		1	1			1	1		1									1	3		2		9		3			4	1	2			5	
Pheidole sp$_{\text{KfmA}}$120	1		4						1																1							2									2		
Philidris **sp$_{\text{KfmA}}$37**		2	2	1									6	1	2		1				2	2						3				3		3	2	1	2		4		1		
Philidris sp$_{\text{KfmA}}$85													1	4														1		1								1					
Philidris sp$_{\text{KfmA}}$159	1												5	1												1	8	4	1		8	2	6		1								
Philidris **sp$_{\text{KfmA}}$160**	1				1		12		2			4	4	9		1										4	19	18	2		32	8	6		5								
Philidris sp$_{\text{KfmA}}$208												1															1		1		1	1											
Philidris sp$_{\text{KfmA}}$209												2															2		1		3	3											

5.1.3. Vertical position in host trees

Characteristics of ants and epiphytes with regard to their usual location in the canopy are listed in Table 5-5 and Table 5-8. Two values were used to describe the vertical position in a host tree: Absolute height in a tree (nest height (NH) or growth height (GH)) as well as relative position (NH/tree height (TH), or GH/TH). Data were compared statistically among ants as well as among epiphytes. Due to a lack of data, higher trees are underrepresented in these comparisons.

5.1.3.1. Ants

In order to detect patterns in the data on the vertical position of ants in trees (Table 5-5), various groups were compared. Concerning the median of NH, three groups were defined[38]: Group 1 (0-5.2 m above the ground) comprised *Pheidole* sp$_{KfmA}$33, *Philidris* sp$_{KfmA}$160, *Camponotus* sp$_{KfmA}$240 and *Diacamma* sp$_{KfmA}$111. In group 2 (>5.2-10.4 m above the ground), *Philidris* sp$_{KfmA}$37 and *Camponotus* sp$_{KfmA}$9 were subsumed. Group 3 (>10.4 m above the ground) consisted of *Crematogaster* sp$_{KfmA}$18 and *Crematogaster* sp$_{KfmA}$19 only.

Table 5-5: Characteristics of host trees and the vertical distribution of AG ants
This table presents the absolute values for mean/median nest height (NH) per colony, standard deviation where possible, average minimum and maximum and the percentage of ant colonies with an average nest height in the lower, medium and upper third of the phorophyte. Habitat characteristics are described with L (lowland dipterocarp forest), B (bamboo-specialist), S (submontane rain forest), H (heath forest)

ant species	N	NH mean/median [m]	NH stdv. [m]	NH min [m]	NH max [m]	height of phorophyte (median) [m]	diam. of phorophyte (median) [cm]	% lower 1/3rd	% medium 1/3rd	% upper 1/3rd	habitat
Crematogaster sp$_{KfmA}$18	72	17.8/15.6	10.3	1.5	22.7	17	9.75	2	14	84	L, B
Crematogaster sp$_{KfmA}$19	13	13.0/14.6	6.4	2.0	28.0	17	11.0	0	0	100	L, B
Pheidole sp$_{KfmA}$33	19	-/1.7	-	0.8	18.0	5	7.5	33	25	42	L, S
Philidris sp$_{KfmA}$37	14	9.0/7.3	14.7	0.8	15.6	10	7.5	18	18	64	L
Philidris sp$_{KfmA}$160	50	-/1.6	-	0.1	15.0	3	5.75	15	48	37	H
Camponotus sp$_{KfmA}$9	8	7.4/8.0	4.4	2.0	13.8	23.5	21.0	25	63	12	L
Camponotus sp$_{KfmA}$240	14	2.5/2.5	1.0	0.8	4.0	6	16.5	44	33	23	L, H
Diacamma sp$_{KfmA}$111	66	-/1.9	-	0.1	2.7	7	7.5	61	30	9	L, S

Except for *Camponotus* sp$_{KfmA}$240 and *Diacamma* sp$_{KfmA}$111 all ant species were found to nest in a wide range from just above the ground to at least 15 m. Therefore it was not surprising that statistical comparisons between these species revealed few significant results (Table 5-6). *Diacamma* sp$_{KfmA}$111 was the only species with a significantly lower NH as compared to all the other species. *Camponotus* sp$_{KfmA}$240 could not be significantly distinguished from *Pheidole*

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[38] Three equally sized groups were specified by simply dividing the highest NH median by three.

sp$_{\mathrm{KfmA}}$33 and *Philidris* sp$_{\mathrm{KfmA}}$37. At the other end of the range, the two *Crematogaster* species significantly differed from most but not all of the other species.

Table 5-6: Significance levels of the nest height (NH) of AG ants
Comparison of the most important AG ants, using U-test and Bonferroni correction ($p<0.05$) for 28 pairwise tests.

	Crematogaster sp$_{\mathrm{KfmA}}$19	*Pheidole* sp$_{\mathrm{KfmA}}$33	*Philidris* sp$_{\mathrm{KfmA}}$37	*Philidris* sp$_{\mathrm{KfmA}}$160	*Camponotus* sp$_{\mathrm{KfmA}}$9	*Camponotus* sp$_{\mathrm{KfmA}}$240	*Diacamma* sp$_{\mathrm{KfmA}}$111
Crematogaster sp$_{\mathrm{KfmA}}$18	n.s.	*	*	*	n.s.	*	*
Crematogaster sp$_{\mathrm{KfmA}}$19		*	n.s.	*	n.s.	*	*
Pheidole sp$_{\mathrm{KfmA}}$33			n.s.	n.s.	n.s.	n.s.	*
Philidris sp$_{\mathrm{KfmA}}$37				n.s.	n.s.	n.s.	*
Philidris sp$_{\mathrm{KfmA}}$160					*	n.s.	*
Camponotus sp$_{\mathrm{KfmA}}$9						*	*
Camponotus sp$_{\mathrm{KfmA}}$240							*

With regard to the relative nest height of the ants in a tree, four groups were distinguished. Ants with at least 50 % of average NH/TH in one third of the phorophyte were rated as preferring this third (groups 1-3). The last group comprised species with relatively equal distribution in the whole tree (i.e. NH/TH < 50 % in all three zones). Using these criteria, *Diacamma* sp$_{\mathrm{KfmA}}$111 constituted group 1 (> 50 % in the lowest third), *Camponotus* sp$_{\mathrm{KfmA}}$9 was the only species of group 2 (> 50 % in the medium third), *Crematogaster* sp$_{\mathrm{KfmA}}$18, *Crematogaster* sp$_{\mathrm{KfmA}}$19 and *Philidris* sp$_{\mathrm{KfmA}}$37 were members of group 3 (> 50 % in the uppermost third), and *Pheidole* sp$_{\mathrm{Kfm}}$A33, *Philidris* spKfmA37 and *Camponotus* sp$_{\mathrm{KfmA}}$240 were subsumed in group 4. However, NH/TH values revealed very few significant differences in pairwise comparison (Table 5-7). Only the most distant groups, group 1 and group 3, were significantly different in all cases, all the other groups overlapped widely, indicating that the preference for certain relative vertical positions was little pronounced and/or the sample size was too small to identify such preferences.

Table 5-7: Significance levels for the relation of nest height to total tree height of AG ants
Comparison of the most important AG ants, using U-test and Bonferroni correction ($p<0.05$) for 28 pairwise comparisons

	Crematogaster sp$_{\text{KfmA}}$19	*Pheidole* sp$_{\text{KfmA}}$33	*Philidris* sp$_{\text{KfmA}}$37	*Philidris* sp$_{\text{KfmA}}$160	*Camponotus* sp$_{\text{KfmA}}$9	*Camponotus* sp$_{\text{KfmA}}$240	*Diacamma* sp$_{\text{KfmA}}$111
Crematogaster sp$_{\text{KfmA}}$18	n.s.	n.s.	n.s.	*	*	n.s.	*
Crematogaster sp$_{\text{KfmA}}$19		n.s.	n.s.	*	n.s.	n.s.	*
Pheidole sp$_{\text{KfmA}}$33			n.s.	n.s.	n.s.	n.s.	n.s.
Philidris sp$_{\text{KfmA}}$37				n.s.	n.s.	n.s.	*
Philidris sp$_{\text{KfmA}}$160					n.s.	n.s.	n.s.
Camponotus sp$_{\text{KfmA}}$9						n.s.	n.s.
Camponotus sp$_{\text{KfmA}}$240							n.s.

5.1.3.2. Epiphytes

Since the epiphytes were restricted to ant nests, they occurred in the same zones as their partner ants. However, especially for species occurring on the nests of many ant species, or for those whose partner ants were not confined to certain tree zones (which is the majority, s. above), a comparison of preferred growth zones might be interesting.

There were clear differences in the median of GH for some AG epiphytes, resulting in the following grouping and ranking (Table 5-8 and Table 5-9): Group 1[39] (0-5.2 m above the ground): *Dischidia major*, *Hoya mitrata*, *Hydnophytum formicarium*, *Lecanopteris sinuosa*, *Myrmecodia tuberosa*, *Pachycentria constricta*, *Poikilospermum microstachys* and *Schefflera* sp$_{\text{KfmA}}$75. Within this group, *Myrmecodia tuberosa*, *Pachycentria constricta* and *Poikilospermum microstachys* grew in significantly higher places than *Hydnophytum formicarium* and *Schefflera* sp$_{\text{KfmA}}$75. These two species as well as *Hoya mitrata* were the only ones that were never found above 5 m. Group 2 (>5.2-10.4 m above the ground) comprised *Aeschynanthus albidus*, *Hoya elliptica* and *Pachycentria glauca* subsp. *maingayi*. *Hoya elliptica* never grew below 5 m, while the other two species occurred from just above the ground to >15 m. However, there was no significant difference within this group. Group 3 (>10.4 m above the ground) comprised *Aeschynanthus fecundus*, *Dischidia nummularia* and *Pyrossia lanceolata*. The latter species never occurred below 6.5 m, and all three species often grew considerably above 15 m. The large range of GH in many AG epiphytes was reflected by relatively few significant results in pairwise comparisons of group 2 to groups 1 and 3 (Table 5-9). However, groups 1 and 3 were clearly separated.

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[39] In order to facilitate comparability with the ants, the group limits defined for the ants were used here as well (s. Chapter 5.1.3.1, p. 98).

Table 5-8: Characteristics of the vertical distribution of AG epiphytes
This table presents the absolute values for mean/median growth height (GH) per epiphyte species, standard deviation where possible, average minimum and maximum and the percentage of epiphytes on average growing in the lower, medium and upper third of the phorophyte. Habitat characteristics are described with L (lowland dipterocarp forest), S (submontane rain forest), H (heath forest)

epiphyte species	N	GH mean/median [m]	GH stdv. [m]	GH min [m]	GH max [m]	height of phorophyte (median) [m]	diam. of phorophyte (median) [cm]	% lower 1/3rd	% medium 1/3rd	% upper 1/3rd	habitat
Aeschynanthus albidus	47	-/5.0	-	0.8	23.0	14.5	11.0	21	24	55	L, S
Aeschynanthus fecundus	16	13.2/15.3	7.0	2.0	21.8	16.0	9.5	0	9	91	L
Dischidia major	17	2.4/1.6	2.5	0.2	10.0	3.0	8.0	25	42	33	H
Dischidia nummularia	74	12.5/13.5	6.9	0.6	27.7	14.0	7.5	10	17	73	L
Hoya elliptica	10	9.6/8.0	3.6	7.1	13.8	17.0	19.5	30	40	30	L
Hoya mitrata	10	2.4/2.5	1.4	0.5	5.0	8.0	18.0	67	33	0	H-L
Hydnophytum formicarium	31	1.2/1.2	0.6	0.3	2.5	3.0	5.0	45	34	21	H
Lecanopteris sinuosa	34	-/1.6	-	0.2	16.1	3.0	3.0	16	29	55	H
Myrmecodia tuberosa	50	-/2.2	-	0.1	25.1	4.0	6.5	21	29	50	H
Pachycentria constricta	42	-/3.0	-	0.6	16.1	6.0	7.5	33	28	39	L
Pachycentria glauca subsp. *maingayi*	8	7.1/5.5	6.3	1.0	17.3	9.0	15.0	43	29	28	L
Poikilospermum microstachys	29	5.7/3.0	5.4	0.8	16.7	13.0	10.5	29	35	36	L, S
Pyrossia lanceolata	32	14.4/14.0	4.5	6.5	27.0	17.5	10.0	0	15	85	L
Schefflera sp$_{\text{KfmA}}$75	24	1.3/1.3	0.7	0.3	2.7	6.5	14.0	70	30	0	L, S

Like in the ants, epiphytes with more than 50 % of average GH/TH in one third of the phorophyte were rated as preferring this third. Thus, four groups were distinguished: Group 1, with epiphytes preferring the lower third of the phorophyte, comprised *Hoya mitrata* and *Schefflera* sp$_{\text{KfmA}}$75. Group 2, with a preference for the medium third, was not represented by any of the epiphytes tested here. Five species usually occurred in the upper third (group 3), namely *Aeschynanthus albidus*, *Aeschynanthus fecundus*, *Dischidia nummularia*, *Lecanopteris sinuosa* and *Pyrossia lanceolata*. All remaining species belonged to group 4, with no clear preference for any zone. The statistical comparison of GH/TH values partly supported this grouping (Table 5-10): Members of group 1 and group 3 were significantly separated in most cases, while differences between species of group 4 and those of group 1 or group 3 were frequently not significant. There were no significant intra-group differences.

Table 5-9: Significance levels of the growth heights (GH) of AG epiphytes
Comparison of the most important AG epiphytes, using U-test and Bonferroni correction (p<0.05) for 92 pairwise comparisons

	Aeschynanthus fecundus	*Dischidia major*	*Dischidia nummularia*	*Hoya elliptica*	*Hoya mitrata*	*Hydnophytum formicarium*	*Lecanopteris sinuosa*	*Myrmecodia tuberosa*	*Pachycentria constricta*	*Pachycentria glauca* subsp. *maingayi*	*Poikilospermum microstachys*	*Pyrossia lanceolata*	*Schefflera* sp$_{\text{KfmA}}$75
Aeschynanthus albidus	*	*	*	n.s.	*	*	*	*	*	*	n.s.	*	*
Aeschynanthus fecundus		*	n.s.	n.s.	*	*	*	*	*	n.s.	*	n.s.	*
Dischidia major			*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Dischidia nummularia				n.s.	*	*	*	*	*	n.s.	*	n.s.	*
Hoya elliptica					n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hoya mitrata						n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Hydnophytum formicarium							n.s.	*	*	n.s.	*	*	n.s.
Lecanopteris sinuosa								n.s.	n.s.	n.s.	n.s.	*	n.s.
Myrmecodia tuberosa									n.s.	n.s.	n.s.	*	*
Pachycentria constricta										n.s.	n.s.	*	*
Pachycentria glauca subsp. *maingayi*											n.s.	*	n.s.
Poikilospermum microstachys												*	*
Pyrossia lanceolata													*

Table 5-10: Significant levels of growth height in relation to phorophyte height
Comparison of the most important AG epiphytes, using U-test and Bonferroni correction (p<0.05) for 92 pairwise comparisons

	Aeschynanthus fecundus	*Dischidia major*	*Dischidia nummularia*	*Hoya elliptica*	*Hoya mitrata*	*Hydnophytum formicarium*	*Lecanopteris sinuosa*	*Myrmecodia tuberosa*	*Pachycentria constricta*	*Pachycentria glauca* subsp. *maingayi*	*Poikilospermum microstachys*	*Pyrossia lanceolata*	*Schefflera* sp$_{\text{KfmA}}$75
Aeschynanthus albidus	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Aeschynanthus fecundus		n.s.	n.s.	n.s.	*	*	n.s.	*	n.s.	n.s.	n.s.	n.s.	*
Dischidia major			n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dischidia nummularia				n.s.	*	*	n.s.	n.s.	*	n.s.	n.s.	n.s.	*
Hoya elliptica					n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hoya mitrata						n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Hydnophytum formicarium							n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Lecanopteris sinuosa								n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Myrmecodia tuberosa									n.s.	n.s.	n.s.	*	n.s.
Pachycentria constricta										n.s.	n.s.	*	n.s.
Pachycentria glauca subsp. m*aingayi*											n.s.	n.s.	n.s.
Poikilospermum microstachys												*	n.s.
Pyrossia lanceolata													*

5.2. Discussion

The main results of this chapter are:

1. There are species-specific preferences of ant and epiphyte species occurring in association.
2. No significant differences in temperature data of four sympatrically occurring AG ants were detected. Nevertheless, four species are not enough to generally deny an influence of temperature on the ants' preferences for nest localities.
3. Although many ant and epiphyte species showed little or no preference for a certain height in host trees, some preference-patterns for absolute and relative vertical positions could be detected for both partner organisms.

Since it is hard to estimate the influence of each factor on species sorting in general, and since the relative importance of different factors is not the same for all ant and epiphyte species studied, some examples were chosen to illustrate possible patterns. In view of the fact that ants are principally responsible for the location of an AG, and at least partly influence epiphyte-species composition on their nests, the following discussion uses ant species as structuring criterion.

5.2.1. *Crematogaster* sp$_{\mathrm{KfmA}}$18 (and *Crematogaster* sp$_{\mathrm{KfmA}}$19)

Crematogaster sp$_{\mathrm{KfmA}}$18 and *Crematogaster* sp$_{\mathrm{KfmA}}$19 are the only species with a restriction to giant bamboo as phorophyte (Chapter 4.1.2.1, p. 28 and Chapter 4.2.1, p. 78 ff.). I will confine the following discussion to the first species because data are scarce for the second, and it seems to have a great resemblance to *Crematogaster* sp$_{\mathrm{KfmA}}$18.

Due to the fast growth of bamboo, and since the ants use the branches of their phorophyte for nest construction[40], it was not surprising that nests of *Crematogaster* sp$_{\mathrm{KfmA}}$18 were located in regions higher than 10 m above the ground and in most cases in the upper third of the phorophyte. However, due to polydomy and the two-dimensional extension of a single bamboo-culm, the ranges of absolute and relative heights of nests of a single colony were usually wide, sometimes covering more than 10 m. With regard to light regimes, weather-exposure and probably also humidity, *Crematogaster* sp$_{\mathrm{KfmA}}$18 thus provided a relatively high variety of microhabitats. This might be one reason why *Crematogaster* sp$_{\mathrm{KfmA}}$18 was found in association with 25 epiphyte species (Chapter 4.1.2.1, p. 28). However, a clear preference of *Dischidia nummularia* towards *Crematogaster* sp$_{\mathrm{KfmA}}$18 nests and vice versa was detected (Chapter 5.1.1, p. 94 f.); furthermore, 67 % of all *Aeschynanthus fecundus* specimens and 52 % of all *Pyrossia*

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[40] Giant bamboo reaches its final height (>20 m) within a few months. The nodes bearing branches are restricted to the upper half of the plant.

lanceolata specimens were growing on the nests of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$. These three species belonged to the same absolute and relative GH (growth height) groups as did *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ (nest height, NH), and they also remained significantly separate from most other species (Table 5-8). These results indicate that the AG association is based on some highly light-demanding, drought-tolerant epiphyte species that are enabled to colonize bamboo by an ant species with similar habitat preferences, though the reasons for this common habitat preference might be totally different in both groups. They also suggest that interspecific competition might be an important factor accounting for the epiphyte composition of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ nests, generally favoring those light-demanding and drought-tolerant species on most nests, but, due to the variable position along a bamboo culm, also supporting several other epiphyte species.

5.2.2. *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}160$

Philidris $\mathrm{sp}_{\mathrm{KfmA}}160$ (and most of the other *Philidris* spp. collected in this study) must be discussed with special respect to their predominance in an exceptional habitat: heath forests[41]. This predominance strongly suggests that these ants have competitive advantages in such sun-exposed habitats[42]. The same is true for the most abundant epiphyte species in these areas: *Myrmecodia tuberosa*, *Hydnophytum* spp., *Dischidia major* and *Lecanopteris sinuosa*. Thus, the co-occurrence of *Philidris* spp. and these epiphytes might be interpreted as due to similar habitat preferences rather than to any interdependence of these two groups (sensu Davidson, 1988), as was the case in *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ (s. above)[43].

5.2.3. *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$

Concerning interdependences of AG ants and epiphytes, the case of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ and *Hoya elliptica* is of particular interest, because these two species displayed the closest species-specific association described in this study, although many other AG ant species and AG epiphyte species occurred sympatrically. Due to the close association it is clearly evident that both species occurred in similar absolute and relative GH or NH. However, comparison to other sympatrical AG species is interesting because *Hoya elliptica* did not significantly differ from any of them in relation to these two parameters, because it lived in a wide range of GH and GH/TH. This result indicated that other species should theoretically have been able to grow on the nests of *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ also, but only very few specimens were found. One possible explanation for this phenomenon might be that the parameters used for estimating the microclimatic conditions were not suitable for detecting the differences leading to this relatively

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[41] see Chapter 2.2, p. 7 for a detailed description of heath forests.

[42] Temperature and humidity are closely correlated and might both affect the ants.

[43] also see Chapter 6.2.2.1, p. 110 and Chapter 8.3.1, p. 142 ff.

specialized association. Another, more plausible explanation is that other factors account for the phenomenon. The highly selective seed-retrieving behavior of *Camponotus* sp$_{\text{KfmA}}$9 towards *Hoya elliptica* might be one important factor. Data from neotropical AGs suggest a causal correlation of this kind (Orivel and Dejean, 1999b): The authors found clear preferences of different AG ants towards certain AG epiphyte seeds, and in consequence the respective epiphyte species were found preferentially on the AGs of the ant preferring its seeds. Data on species sorting (Chapter 5.1.1, p. 94) in combination with seed retrieving experiments performed in this study (Chapter 4.1.2.3, p. 64) suggest that the detected interdependency pattern of *Camponotus* sp$_{\text{KfmA}}$9 and *Hoya elliptica* might be interpreted as a consequence of selective seed retrieval also.

5.2.4. *Camponotus* sp$_{\text{KfmA}}$240

In *Camponotus* sp$_{\text{KfmA}}$240 and its close association to *Hoya mitrata*, the exceptional habitat again seems to play a key role. *Hoya mitrata* is an example of an epiphyte species with obviously narrow habitat preferences, because this species was only found in the transition area between heath forests and lowland dipterocarp forest. It grew exclusively on the nests of *Camponotus* sp$_{\text{KfmA}}$240. Vice versa, this ant species was frequently found with other epiphyte species and in other habitats also, but few other ant species were found in those transition areas. Moreover, *Camponotus* sp$_{\text{KfmA}}$240 was unusually abundant in these habitats. These results indicate that *Camponotus* sp$_{\text{KfmA}}$240 has competitive advantages in transition areas, which might even be a consequence of its association with *Hoya mitrata*.

Again, data of the seed-retrieving experiments (Chapter 4.1.2.3, p. 68) give further information. *Camponotus* sp$_{\text{KfmA}}$240 was as selective in its choice as *Camponotus* sp$_{\text{KfmA}}$9, but it was restricted to smaller trees and lower NH (Chapter 5.1.3, p. 98). Seeds of *Hoya mitrata* are comparable to those of *Hoya elliptica* in shape and size, and they ‘meet’ a suitable seed-dispersing species, *Camponotus* sp$_{\text{KfmA}}$240, in their habitat. Consequently, the close association between both species might be interpreted as a combination of similar habitat preferences and selective seed-retrieval.

5.2.5. *Diacamma* sp$_{\text{KfmA}}$111

The special status of *Diacamma* sp$_{\text{KfmA}}$111 as compared to other AG ants[44] was also confirmed in connection with the epiphyte flora occurring on its nests: In the case of the five most common epiphyte species occurring in Peninsular Malaysia and their distribution on ant nests, the epiphyte composition significantly differed from all the other nests (Chapter 4.1.2.4, p. 74).

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[44] also see Chapter 4.2.1, p. 78 ff.

Mature plants mainly belonged to the type of bird-dispersed epiphytes, and these plants were rarely found on the nests of other AG ants (Chapter 5.1.1, Table 5-4, p. 97).

Although temperature data at *Diacamma* nests did not significantly differ from those of other nests, the AGs were clearly established in a lower canopy stratum than any other AGs (significantly differing from the other ant species in both NH and NH/TH), and irradiance was usually lower. Light regime is one of the main factors influencing epiphyte diversity on AGs (Belin-Depoux, 1991). As *Diacamma* was least specific concerning its seed-carrying behavior (Chapter 4.1.2.4, p. 74), such microclimatic effects could account for the specific epiphyte composition. *Schefflera* $\mathrm{sp}_{\mathrm{KfmA}}75$, one of its most abundant epiphyte partners, was also distinguished from many other epiphytes by low GH and GH/TH. The predominance of this species on nests of *Diacamma* $\mathrm{sp}_{\mathrm{KfmA}}111$ can be interpreted as an effect of competition: On the nests of *Diacamma*, sun-demanding species like *Dischidia nummularia* or *Aeschynanthus fecundus* cannot survive in the presence of other, shade-tolerant species, while they have a competitive advantage on the nests of “tree-top” species, such as *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ and *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}19$. Although these explanations seem to be plausible, other factors, like carton quality (Chapter 4.1.2.1, Table 4-6, p. 31) could also play an important role.

The remaining ant species are not discussed in detail here, because explanations would be redundant. *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}33$, usually monodomous, was too rare in a single study area for reliable detection of species-specific interdependences. It inhabited AGs at low heights on small trees as well as up in the canopy of emergent rain forest trees, and it was not very selective in its seed-retrieving behavior. It is therefore not surprising that 29 epiphyte species were found on its nests. *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}37$ nested from the ground up to the high canopy, and no species-specific preferences for certain epiphyte species were detected.

Summing up, several factors examined in this study would appear to account for the species sorting of ant and epiphyte species in AGs. Common microhabitat-preferences in combination with interspecific competitive processes between epiphytes were the most likely interpretations of many patterns; however, selective seed retrieval of ants might be another important factor in some cases. At least some of the other factors named in the introduction to this chapter may also possibly play a role. The fact that species-preferences are widely lacking in species occurring at variable heights in the canopy might indicate that substrate quality plays a minor role for AG-restricted epiphytes.

6. Assessment of the ecological significance of ant-gardens

The number of species involved in Southeast-Asian ant-garden systems in itself suggests that this type of ant-plant interaction is of high ecological importance for canopy-ecosystems (Chapter 4, p. 20 ff.). The present chapter adds a further aspect to these considerations, i.e. the importance of ants for the establishment of epiphytes in Peninsular Malaysian lowland rain forests.

If all data presented so far are taken together, it may become possible to discuss the significance of ant-epiphyte associations for certain taxa on an evolutionary timescale.

6.1. Results

6.1.1. Importance of ants for the establishment of epiphytes in Peninsular Malaysia

The importance of ants for the establishment of epiphytes in Peninsular Malaysia was estimated by comparing the list of theoretical ‘epiphyte-candidates’ (non-orchids, non-ferns, no montane species, no facultative epiphytes; s. Chapter 3.1, p.11) for an association with ants in Peninsular Malaysia with the list of species found in association with ants in this area (Table 4-3 and Table 6-1).

Table 6-1: Candidates for epiphyte-ant associations in Peninsular Malaysia
This table shows all epiphyte genera occurring in Peninsular Malaysia that are good candidates for an association with ants (i.e. non-ferns, non-orchids, no genera restricted to montane regions, no genera that contain facultative epiphytes only; also s. text). The number of candidates in relation to the total species number occurring in Pen. Mal. is given as well as the number of species that were found to be associated with ants in this studies or in other studies (Kiew and Anthonysamy, 1987; marked with *). Epiphyte species that are no ‘candidates’ according to the given definition have been excluded here (Table 4-3).

plant family	plant genus	# of ‘candidates’ / total # of species in Pen.Mal.	# of species associated with ants [% of ‘candidates’]
Araliaceae	*Schefflera*	2 / 15	2 [100]
Asclepiadaceae	*Dischidia*	15 / 23	10 [66,7]
	Hoya	21 / 22	6 +1* [33,3]
Ericaceae	*Rhododendron*	1 / 11	1* [100]
	Vaccinium	1 / 9	1* [100]
Gesneriaceae	*Aeschynanthus*	3 / 9	3 [100]
Melastomataceae	*Medinilla*	4 / 11	2 [50]
	Pachycentria	2 / 2	2 [100]
Moraceae	*Ficus*	3 / 20	1 [33,3]
Rubiaceae	*Hydnophytum*	1 / 1	1 [100]
	Myrmecodia	1 / 1	1 [100]
Zingiberaceae	*Hedychium*	1 / 3	1 [100]
Total		55/127	32 [58]

This comparison revealed a rather surprising result: All epiphyte genera (100 %) in the ‘candidate’ list occurred exclusively in association with ants. At species level, app. 58 % of the ‘candidates’ were identified as AG species. The remaining 23 species were not found during the present studies, i.e. nothing is known about whether they are associated with ants or not. As certain habitats, e.g. the canopy of primary lowland forests, were underrepresented in this study, it is highly probable that even more of these ‘candidates’ are regularly associated with ants.

The principal result, indicating a high importance of ants for a major part of canopy flora, was also supported by data collected in Temenggor Primary Forest Reserve, where the crowns of 21 freshly logged high timber trees were examined. Here, some orchids and ferns were found growing independently of ants, while all the other vascular epiphyte species (8 species, 7 genera, 4 families) were associated with ants.

6.2. Discussion

6.2.1. Ecological importance of ant-epiphyte associations

Both the total species numbers of ants and plants involved in ant-epiphyte interactions in Southeast Asia (Chapter 4, p. 20 ff.), and the high proportion of ‘candidate’ epiphyte-species dependent on ants, illustrate the high ecological importance of ants and plants for each other. Possible beneficial interactions have already been discussed in Chapter 4.2.2 (p. 84 ff.).

All plant genera and more than 50 % of the plant species rated as potential candidates for ant epiphyte associations were found to be widely restricted to ant nests. Thus, activities of ants account for a large proportion of the occurrence of these epiphyte groups. Since only few and highly specialized examples of ant-epiphyte interactions in the Palaeotropis were previously known (Chapter 12.11, p. 196), this result was completely unexpected. Longino (1986) assumed that carton building ants were generally of great importance for the establishment of epiphytes in tropical rain forest canopies. My results clearly support this assumption.

Some additional remarks are necessary when comparing the true AG epiphytes identified (Chapter 4.1.1, Table 4-3, p. 23) with the theoretical criteria (Chapter 3.1, p. 11). Of all four groups that were excluded theoretically (ferns, orchids, montane species, facultative species), some members were identified as true AG partners. In the ferns, *Asplenium nidus*, *Lecanopteris sinuosa*, and *Platycerium ridleyi* (Polypodiaceae) were obligatorily associated with ants. All three species have structures that ants can inhabit: *Asplenium nidus* and *Platycerium ridleyi* are classical ‘bird nest ferns’ with leaf structures suitable for accumulating debris. However, the leaves of young *Platycerium ridleyi*, unlike its congener *Platycerium coronarium*, grow pressed to the substrate and are thus relatively poor debris collectors. Instead, ants live underneath these leaves. *Lecanopteris sinuosa* has hollow rhizome structures.

In the large orchid family, five species were found on ant nests more than once, and another c. 30 species only once. Only three orchid species were probably associated obligatorily with ants. These species possess noticeably larger seeds than other members of this family (also s. Leeuwen and Leeuwen-Reijnvaan, 1913; Benzing and Clements, 1991), and they probably grow and mature faster than their non-myrmecophilic congeners. Another case of ant-associated orchids were found in the heath forest areas of Pedawan Valley: *Gramatophyllum speciosum* and *Porphyroglottis maxwelliae* produce root- and leaf-structures in which debris accumulates. Various ants nested in this debris. These ants might collect more organic material and thus fertilize the orchids. However, further studies are needed in the special field of ant-orchid-associations.

Dischidia astephana, *Dischidia longepedunculata* and *Aeschynanthus myrmecophilus* were restricted to montane regions at about 1500 m a.s.l., where they grew exclusively in association with ants. Relatively small *Dacrydium* trees with an open canopy dominated in the habitats in which these species were found. This type of habitat was frequently found on mountain peaks.

The group of facultative epiphytes was mainly represented by two species of *Poikilospermum*, four species of *Schefflera* and three species of *Ficus*.

This occurrence of 'non-candidate' species in the list of ant-associated epiphytes further supports the idea that this type of association is extraordinarily important for the establishment of canopy-related plant growth. Furthermore, several (ca. 50)[45] opportunistic AG colonists, mainly ferns and orchids, were also found on AGs (Chapter 4.1.1, p. 20 ff.). On the side of the ants, 43 morphospecies from 17 ant genera were clearly identified as secondary, opportunistic AG inhabitants (Chapter 4.1.1, Table 4-2, p. 22). AGs can thus be regarded as 'pioneers in tree crowns', providing nesting space for other ant species and growing substrate for other epiphyte species. The numerous arthropod guests inhabiting AGs (Chapter 4.1.2 and Chapter 4.2.2, p. 93) also support this idea. AGs thus form micro-ecosystems that are highly important for ants, epiphytes, and many other organisms living in tree crowns.[46]

6.2.2. Radiation in response to ant-epiphyte interactions?

The relatively high species numbers of the asclepiads *Dischidia* and *Hoya* as well as of the Rubiaceae *Hydnophytum* and *Myrmecodia* (only three species in this study, but about 100 species in the whole region) induce the idea that the species-richness of these genera might at least partly be a consequence of their association with ants. Generally, most epiphyte taxa have not radiated (Gentry and Dodson, 1987). Species-richness in monophyletic lines can be rated as ecological success because diversified lines are more likely to survive in future (Wilson, 1987).

On the ant side, only one genus is a good candidate for radiation in response to the ant-epiphyte interactions: All *Philidris* spp. were exclusively found in association with epiphytes.

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[45] It is difficult to provide exact species numbers here, because many epiphytes were hard to distinguish when not in flower. These, together with species that were only found once, are not included in Table 4-3.

[46] Cedeño et al. (1999) point out that AGs have an impact on nutrient cycling not only in the canopy but also on the ground, because large AGs fall down during unusually strong winds or drought periods. In Venezuela, Indians use such 'fallen AGs' as fertilizer.

The low degree of species-specific associations (Chapter 5.1.1, p. 94) seems to contradict the 'radiation-hypothesis' at first glance. However, species radiation might also be triggered by other factors, e.g. particularly high reproductive success of ant and epiphyte species participating in AG associations in combination with relatively extreme and fragmented habitats, causing restricted gene flow. In that case, the mutualistic association should be regarded as a 'key innovation' (sensu Simpson, 1953), speeding up speciation in certain habitats. Associations with ants might even favor isolation of populations because successful dispersal depends on the presence of ant partners. Seeds of several AG epiphytes (e.g. *Hydnophytum formicarium*, (Janzen, 1974); *Dischidia* spp.; pers. obs.) germinated immediately as soon as they became wet, i.e. they have to be dispersed to a suitable microsite quickly. Thus, the probability of such a seed being transferred to another patch of e.g. heath forest (or some other suitable habitat) by wind or bird seems to be relatively low.

Although I am aware that my studies were not suitable in this context and did not aim to find answers to these questions, I will at least present some considerations on selected examples in the following discussion.

6.2.2.1. *Philidris* spp.

The ant genus *Philidris* was described as a new genus, derived from *Iridomyrmex*, only ten years ago (Shattuck, 1992). So far, there is no revision of *Philidris.* This is why it is impossible to present total species numbers here. According to Shattuck (1992), 14 species and subspecies, included in the genera *Iridomyrmex* and *Technomyrmex* before, were transferred to the genus *Philidris*. All species are closely related to plants and frequently inhabit myrmecodomatia (Shattuck, 1992). Janzen (1974) reports *I. myrmecodiae* even to be restricted to myrmecodomatia, but other reports contradict his observations (s. below).

In the original species descriptions (Smith, 1958, 1959; Forel, 1901, 1907; Santschi, 1928; Mann 1921; Donisthorpe, 1947; Emery, 1912), only little ecological information is given. Forel (1901, 1907) recorded *Iridomyrmex myrmecodiae* var. *andamanensis*, *I. cordatus fuscus*, *I. myrmecodiae* var. *decipiens* in domatia of *Myrmecodia* and *Hydnophytum* and in cavities in dead tree trunks and branches. Mann (1921) found *I. nagasau* in domatia of *Myrmecodia*. Donisthorpe (1941, 1943a, b) described *I. myrmecodiae* var. *nigriventris* from tuberous roots of epiphytes, leaf-bases of *Pandanus*, and rotting logs. Studies on ant-house epiphytes revealed that *Iridomyrmex myrmecodiae*, *Iridomyrmex scrutator* and *Iridomyrmex cordatus* were the principal inhabitants (Huxley, 1978).

However, since there is no revision on the genus, it is unclear how many species are subsumed under each species name, or whether these three species have correctly been identified in all cases. In the present study, six *Philidris* morphospecies were distinguished. My own observations and reports of Forel (1901, 1907), Donisthorpe (1941, 1943a, b), Karavaiev (1926) and Viehmeyer (1916) indicate that none of the described *Philidris* species is restricted to myrmecodomatia as nest-site. It seems more likely that all species of this genus are generalistic ‘cavity settlers’, with an ability to modify cavities with carton material.

The present study revealed that several *Philidris* spp. retrieve seeds of their epiphyte partners into previously constructed carton nests[47]. Present data suggest that *Philidris* spp. in association with epiphytes are particularly competitive in open-canopy habitats. Since such habitats show only patchy distribution in tropical rain forests, high reproductive success in isolated spots might lead to rapid genetic separation and thus account for speciation. Comparative ecological and genetical studies are necessary in order to find possible evidence for a radiation of the genus in response to its association with epiphytes.

6.2.2.2. The Asclepiadaceae

<u>*Dischidia*</u>

Dischidia is a large genus, comprising c. 80 exclusively epiphytic species, which are distributed from the Indo-Malayan region to Australia and the West Pacific (Kiew and Anthonysamy, 1995). As species-richness is greatest in Peninsular Malaysia, and information is most complete for this area at the moment (Rintz, 1980), I will restrict the discussion here to these 23 *Dischidia* species.

In the present study, 12 of these were recorded as true AG mutualists (Chapter 4.1.1, Table 4-3, p. 23). Others might follow. At first glance, there seems to be a developmental gradient in *Dischidia*, from species with no or few modifications for ant association to those with true ant-domatia. However, it is far from clear whether these domatia really developed in response to ant association. Leaves that are shell-shaped and pressed to the growth-substrate (*D. albiflora*, *D. astephana*, *D. cochleata*, *D. imbricata, D. longepedunculata*) could just as well be adaptations to drought as the pitcher leaves of *D. major* or *D. complex*: The stomata are concentrated on the inner surface of the leaves, and roots underneath or inside the leaves can absorb water accumulating there (Goebel, 1889; Huxley, 1980; Treseder et al., 1995).

However, an even more efficient water-economy can be reached with the help of ants in these cases. Treseder et al. (1995) found experimental evidence that, apart from nitrogen, ants also ‘fertilized’ *D. major* with respirative carbon dioxide. Thus, the leaf structure of some *Dischidia* species might be interpreted as response to drought stress and ant-occupation at the same time (Groom, 1893; Pearson, 1902; Huxley, 1980; Treseder et al., 1995). Summing up, high

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[47] also see Janzen, 1974

competitive success due to ant association in certain habitats combined with a patchy distribution of these habitats might account for the species-richness of *Dischidia*.

An ongoing taxonomic (floral morphology and molecular genetics) study at Cornell University (Livshultz, 2002; Tatyana Livshultz, pers. comm.) may very soon reveal further evidence for or against radiation in response to ant association.

Hoya

There are no reliable species numbers for *Hoya*, because new species are constantly being discovered, and revisions are lacking for important areas, e.g. Borneo. Kleijn and Donkelaar (2001) estimate that *Hoya* consists of 200 to 300 species. Rintz (1978) revised *Hoya* of Peninsular Malaysia, resulting in 25 species.

All Peninsular Malaysian *Hoya* species are epiphytic, most of them as climbers. Seven Peninsular Malaysian species are definitely known to be ant-associated. *Hoya* spp. usually have flat, rather leathery and succulent leaves. In contrast to *Dischidia*, there is only one species with shell-leaves (*Hoya imbricata*) and no species with pitcher leaves, but *Hoya darwinii* (Kloppenburg, 1993; cited from Kleijn and Donkelaar, 2001) and *Hoya mitrata* (Weissflog et al., 1999)[48] each form distinct types of multileaf-domatia. Thus, most ant-associated *Hoya* species have the ants nesting around their roots (Kleijn and Donkelaar, 2001).

According to Rintz (1978) and according to my own observations, *Hoya* spp. grow in well lighted but very humid places. They are by far not as drought-resistant as many *Dischidia* species. For the discussion of a possible radiation in response to ant association this could have two consequences:

1. If the special radiation of *Dischidia* was interpreted as a consequence of both ant association and drought resistance, there should be other reasons for the species-richness of *Hoya*. Ant association might, in this case, only account for the development of a certain group of *Hoya* species[49], like *Hoya elliptica* and *Hoya mitrata* (Chapter 5.1, p. 94). The main predisposition for the establishment of AGs, i.e. ant-attractive seeds, seems to be fulfilled for many species of *Hoya* also. However, the preference of this genus for very humid habitats might account for the lower degree of ant association as compared to *Dischidia*.

2. A second possible explanation could be that also in *Dischidia* other factors than drought-resistance/ant association were responsible for the development of species richness. To arrive at conclusions here it will ultimately be necessary to conduct comparative ecological and molecular studies.

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[48] also see Chapter 4.1.2.3, p. 67

[49] According to Kleijn and Donkelaar (2001), especially species from the section *Acanthostemma* (Blume) are associated with ants.

6.2.2.3. The Rubiaceae

There are five genera[50] in the rubiaceous subtribe Hydnophytinae, which all form hypocotyl tubers with tuber cavities frequently occupied by ants[51]. Morphological evidence (inflorescence structure, floral characters etc.) suggests that the swollen tuber is a synapomorphous trait (Huxley and Jebb, 1991a).

Especially the two genera *Hydnophytum* (50 species) and *Myrmecodia* (25 species) are exceptionally species-rich epiphyte genera, mainly occurring in seasonal, open forests (Huxley and Jebb, 1991a).

Single tubers of *Hydnophytum formicarium* weigh up to 3 kg and have a cavity volume of up to 700 ml (Janzen, 1974). The main function of the tubers is water storage (e.g. Miehe, 1911a, b); the tuber cavities are important for 1. catching and absorbing rainwater, 2. aeration, 3. insulation, and 4. harboring ants (sensu Huxley, 1978).

The argumentation for a species-radiation is similar to that for *Dischidia*[52]. Again, a structure especially benevolent for relatively dry habitats was one prerequisite for an association with ants, and this ant association may have had a further positive influence on water-economy, finally accounting for high reproductive success in open-canopied areas such as heath forests.

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[50] *Anthorriza*, *Hydnophytum*, *Myrmecodia*, *Myrmephytum* (including *Myrmedoma*), *Squamellaria* (Huxley and Jebb, 1991)

[51] Only a few species of *Hydnophytum* and one species of *Anthorrhiza* seem not to be associated with ants (Huxley and Jebb, 1991).

[52] A similar picture may also be drawn for the fern genus *Lecanopteris*. All 13 species display hollow rhizome structures (Gay, 1993) usually inhabited by ants (Yapp, 1902; Jermy and Walker, 1975; Walker, 1985a, b; Gay, 1991, 1993; Gay and Hensen, 1992). However, these hollow rhizome structures are rather of polyphyletic than of monophyletic origin according to Gay (1993). Thus, the case of *Lecanopteris* may turn out to be even more complicated than the case of the Hydnophytinae.

7. Characterization of ant attractants in epiphyte seeds

Comparative seed retrieving experiments revealed that AG ants were attracted to AG epiphyte seeds. Attraction was achieved by mechanical properties, nutritional rewards and chemical cues, depending on ant and epiphyte species.[53] The existence of certain chemical cues was previously known from terricolous myrmecochores (summarized in Beattie, 1985) and neotropical AG epiphytes (Davidson et al., 1990; Seidel et al., 1990). Chemical cues of palaeotropical AG epiphytes were characterized in the present study, using a variety of experimental approaches. These included comparative bioassays on non-AG ants and experiments on volatility and solubility in different solvents. Furthermore, analytical techniques were employed (Chapter 3.5.2, p. 14 ff.).

7.1. Results

7.1.1. Seed-carrying experiments with non-AG ants

In the group of primarily bird-dispersed plant species, epiphyte (*Pachycentria constricta*) as well as non-epiphyte (*Medinilla* sp.) seeds were attractive to all tested ant species (Table 3-2, p. 15) apart from *Oecophylla smaragdina*. The latter species did not retrieve any seeds. Nevertheless, this result suggests that primarily bird-dispersed seeds were retrieved because they directly offered food to many ants. All further studies therefore concentrated on wind-dispersed seeds.

Wind-dispersed epiphyte (*Aeschynanthus fecundus, Dischidia nummularia*, and *Hoya elliptica*) as well as non-epiphyte seeds (*Ageratum conyzoides* and *Emilia sonchifolia*) were attractive to *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}210$ – a granivorous species - only. The remaining five non-AG ant species retrieved no wind-dispersed seeds, whether epiphytic or non-epiphytic.

7.1.2. Ageing, heating, washing, and extracting

All tested wind-dispersed epiphyte seeds[54], no matter what species, were still attractive to all tested ant species[54] after the maximum ageing period of 28 days (Chapter 3.5.2, p. 15). Thus, the attractive substance(s) were clearly not volatile at ~30°C. This assumption was further supported by the observation that the ants did not perceive the seeds before touching them with their antennae.

Heating of the seeds yielded the same result[54]. All the seeds were still attractive after being heated to 110°C for one and for two hours, and they even remained attractive after being

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[53] s. Chapter 4.1, in the section 'Seed-carrying behavior' for each of the described ant species

[54] Seeds of *Aeschynanthus fecundus*, *Aeschynanthus albidus*, *Dischidia nummularia* and *Hoya elliptica* were offered to *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$, *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}33$, *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$, *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}37$ in these bioassays.

exposed to 200°C for one hour (Chapter 3.5.2, p. 15). However, seeds that had been heated up to 200°C for two hours were significantly less attractive than the controls. There were absolutely no species-specific differences in these results, with regard either to epiphyte species or to ant species.

Table 7-1: Seed-carrying behavior of *Crematogaster* sp$_{\text{KfmA}}$18 towards seed-extracts produced with different solvents

Test-statistics: $\chi 2$, Fisher's exact test, corrected with sequential Bonferroni correction ($p<0.05$) for 48 pairwise comparisons

*: row item is significantly more attractive than column item; *^{1}: column item is significantly more attractive than row item; n.s.: no significant difference; w. bait = wooden bait; non-epi=*Emilia sonchifolia* (Asteraceae); *Ae. fec.* = *Aeschynanthus fecundus, D. num.* = *Dischidia nummularia*

For detailed descriptions of the methods s. Chapter 3.5.1, p. 13, caption of Table 4-7, p. 35, and Chapter 12.7, p. 180.

	seed of *Aeschynanthus fecundus*	seed of *Dischidia nummularia*	w. bait + acetone	w. bait + cyclohexane	w. bait + pentane	w. bait + chloroform	w. bait + aqua dest.	w. bait + ethanol (70 %)	non-epi + acetone	non-epi + cyclohexane	non-epi + pentane	non-epi + chloroform	non-epi + aqua dest.	non-epi + ethanol (70 %)
w. bait + acetone extract *Ae. Fec.*	n.s.	-	*	-	-	-	-	-	-	-	-	-	-	-
w. bait + acetone extract *D. num.*	-	n.s.	*	-	-	-	-	-	-	-	-	-	-	-
w. bait + cyclohexane extract *Ae. fec.*	*^{1}	-	-	*	-	-	-	-	-	-	-	-	-	-
w. bait + cyclohexane extract *D. num.*	-	*^{1}	-	*	-	-	-	-	-	-	-	-	-	-
w. bait + pentane extract *Ae. Fec.*	n.s.	-	-	-	*	-	-	-	-	-	-	-	-	-
w. bait + pentane extract *D. num.*	-	n.s.	-	-	*	-	-	-	-	-	-	-	-	-
w. bait + chloroform extract *Ae. fec.*	*^{1}	-	-	-	-	n.s.	-	-	-		-	-	-	-
w. bait + chloroform extract *D. num.*	-	*^{1}	-	-	-	n.s.	-	-	-	-	-	-	-	-
w. bait + aqua dest. extract *Ae. fec.*	*^{1}	-	-	-	-	-	n.s.	-	-	-	-	-	-	-
w. bait + aqua dest. extract *D. num.*	-	*^{1}	-	-	-	-	n.s.	-	-	-	-	-	-	-
w. bait + ethanol (70 %) extract *Ae. fec.*	n.s.	-	-	-	-	-	-	*	-	-	-	-	-	-
w. bait + ethanol (70 %) extract *D. num.*	-	n.s.	-	-	-	-	-	*	-	-	-	-	-	-
nonepi + acetone extract *Ae. Fec.*	n.s.	-	-	-	-	-	-	-	*	-	-	-	-	-
nonepi + acetone extract *D. num.*	-	n.s.	-	-	-	-	-	-	*	-	-	-	-	-
nonepi + cyclohexane extract *Ae. fec.*	*^{1}	-	-	-	-	-	-	-	-	*	-	-	-	-
nonepi + cyclohexane extract *D. num.*	-	*^{1}	-	-	-	-	-	-	-	*	-	-	-	-
nonepi + pentane extract *Ae. Fec.*	n.s.	-	-	-	-	-	-	-	-	-	*	-	-	-
nonepi + pentane extract *D. num.*	-	n.s.	-	-	-	-	-	-	-	-	*	-	-	-
nonepi + chloroform extract *Ae. fec.*	*^{1}	-	-	-	-	-	-	-	-	-	-	n.s.	-	-
nonepi + chloroform extract *D. num.*	-	*^{1}	-	-	-	-	-	-	-	-	-	n.s.	-	-
nonepi + aqua dest. extract *Ae. fec.*	*^{1}	-	-	-	-	-	-	-	-	-	-	-	n.s.	-
nonepi + aqua dest. extract *D. num.*	-	*^{1}	-	-	-	-	-	-	-	-	-	-	n.s.	-
nonepi + ethanol (70 %) extract *Ae. fec.*	n.s.	-	-	-	-	-	-	-	-	-	-	-	-	*
nonepi + ethanol (70 %) extract *D. num.*	-	n.s.	-	-	-	-	-	-	-	-	-	-	-	*

Many approaches were needed to wash off attractiveness from the seeds[54] (Chapter 3.5.2, p. 15). Washing seeds with only one solvent never seemed to decrease attractiveness. Successive washing with four different solvents (no matter which) for eight hours each did not result in reduced attractiveness compared to the original seeds either. The only 'successful' treatment, in a somewhat desperate approach to get rid of the attractiveness, was successive washing with: acetone (2x1h), cyclohexane (2x1h), pentane (2x1h), aqua dest. (2x1h), ethanol (2x1h), dichlormethane (2x1h), acetone (1x12h).

Extracts of two AG epiphyte seeds (*Aeschynanthus fecundus*, Gesneriaceae; *Dischidia nummularia*, Asclepiadaceae), produced with various solvents (Chapter 3.5.2, p. 15), clearly differed in their attractiveness to *Crematogaster* sp_{KfmA}18 (Table 7-1). It is remarkable though that there was no difference between these two epiphyte species. Three groups could be distinguished. Group 1 (acetone, ethanol, pentane) comprised all solvents yielding extracts that were as attractive as the original seeds ('positive controls'), and significantly more attractive than the baits with pure solvent ('negative controls').

In group 2 (cyclohexane), extracts were still significantly more attractive than the baits with pure solvent, but they also were significantly less attractive than the original seeds. Finally, group 3-extracts (chloroform, aqua dest.) were significantly less attractive than the original seeds, and their attractiveness did not differ from the negative controls.

Bait types (wooden baits, non-epiphyte seeds (*Emilia sonchifolia*, Asteraceae)) did not influence the ants' response. As tests were exclusively performed with *Crematogaster* sp_{KfmA}18, a comparison of ant species was not possible here.

7.1.3. Comparison of GC/MS profiles and IR spectra of different epiphyte seeds

GC profiles of *Aeschynanthus fecundus*, *Aeschynanthus albidus*, *Dischidia acutifolia, Dischidia nummularia, Hoya* sp., and *Emilia sonchifolia* were recorded (Chapter 3.5.2, p. 15). Presumed that the seed attractant(s) was/were the same in all the epiphyte species, and if they were volatile below 250°C, there might be similar peaks in the chromatograms of different epiphyte species, even in different plant families. These peaks should not be present in the chromatogram of non-attractive *Emilia sonchifolia,* or at least significant differences in relative concentration could be expected.

Comparing the chromatograms presented in Figure 7-1 to Figure 7-6, some aspects became obvious: Within the same plant genus / plant family, many equivalent peaks can be found, though partly in differing relative concentrations. In contrast to this, there were almost no similarities between plant families. This first impression was confirmed when peaks with equivalent retention times were identified using mass spectroscopy and/or infrared spectroscopy. Thus, there is not much point in comparing epiphytes to non-epiphytes, or to list identified substances here. Squalene was common to *Aeschynanthus albidus*, *Aeschynanthus fecundus* and *Dischidia nummularia*, and it was very prominent in these species. However, it was also highly concentrated in non-attractive *Emilia sonchifolia*. Direct bioassays with synthetic squalene confirmed that it was not attractive to ants.

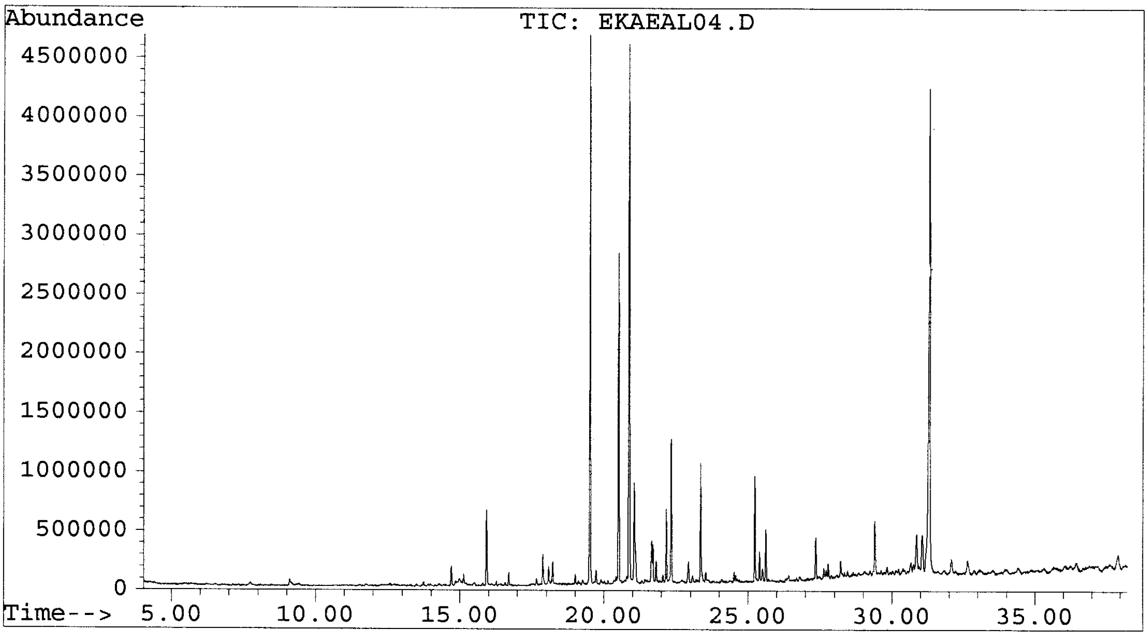


Figure 7-1: Gas chromatogram of acetone extract of *Aeschynanthus albidus* (Gesneriaceae)

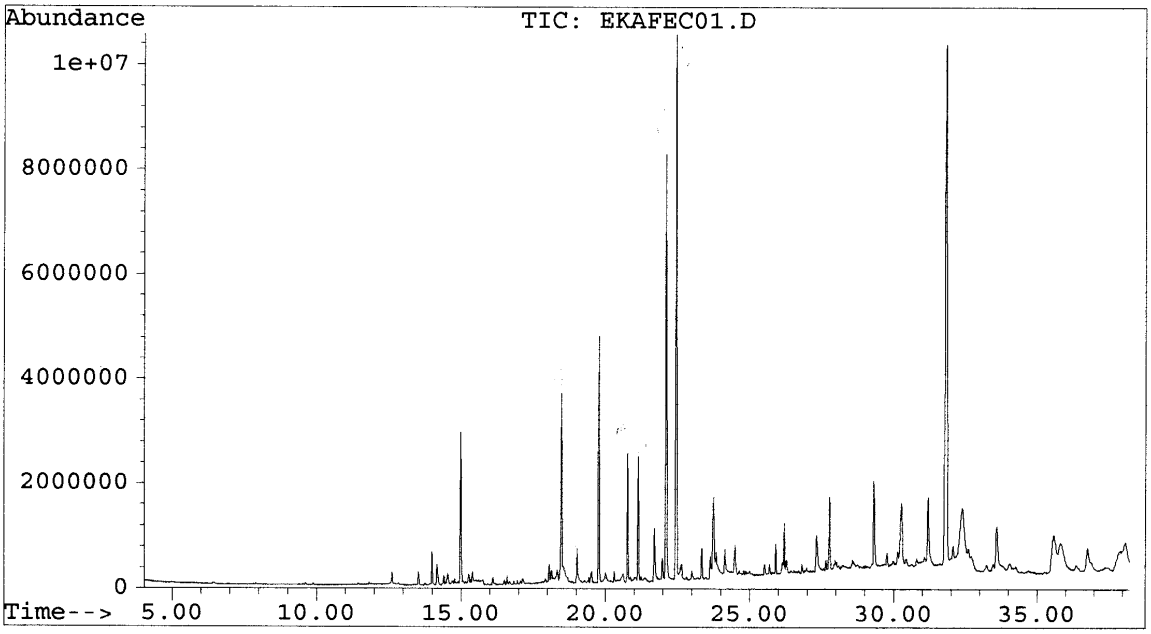


Figure 7-2: Gas chromatogram of acetone extract of *Aeschynanthus fecundus* (Gesneriaceae)

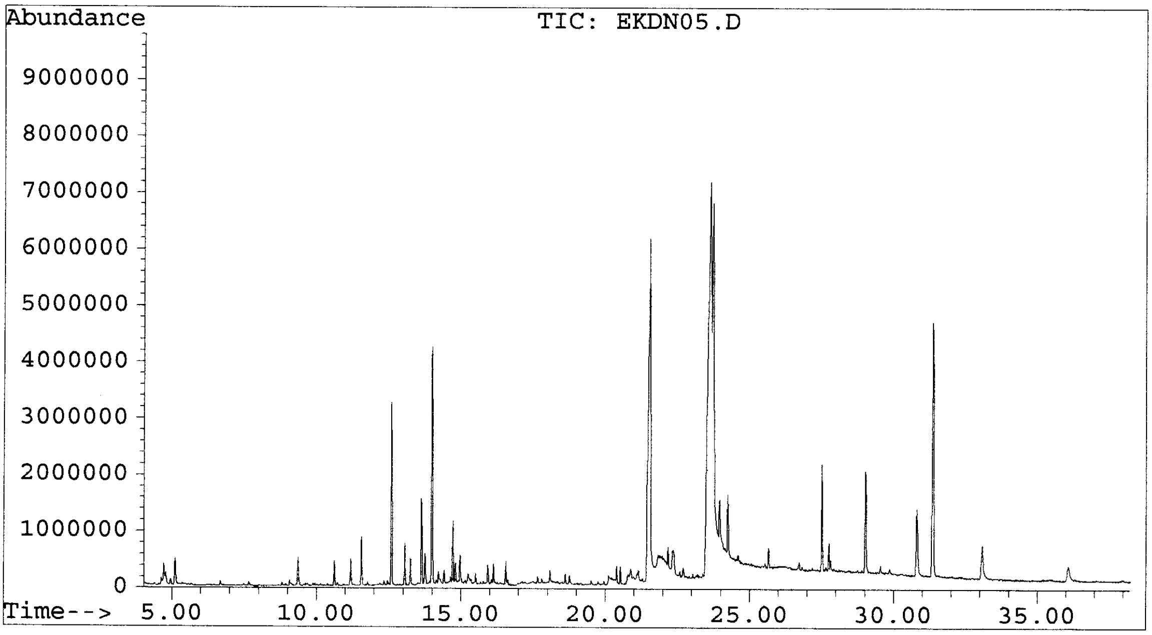


Figure 7-3: Gas chromatogram of acetone extract of *Dischidia nummularia* (Asclepiadaceae)

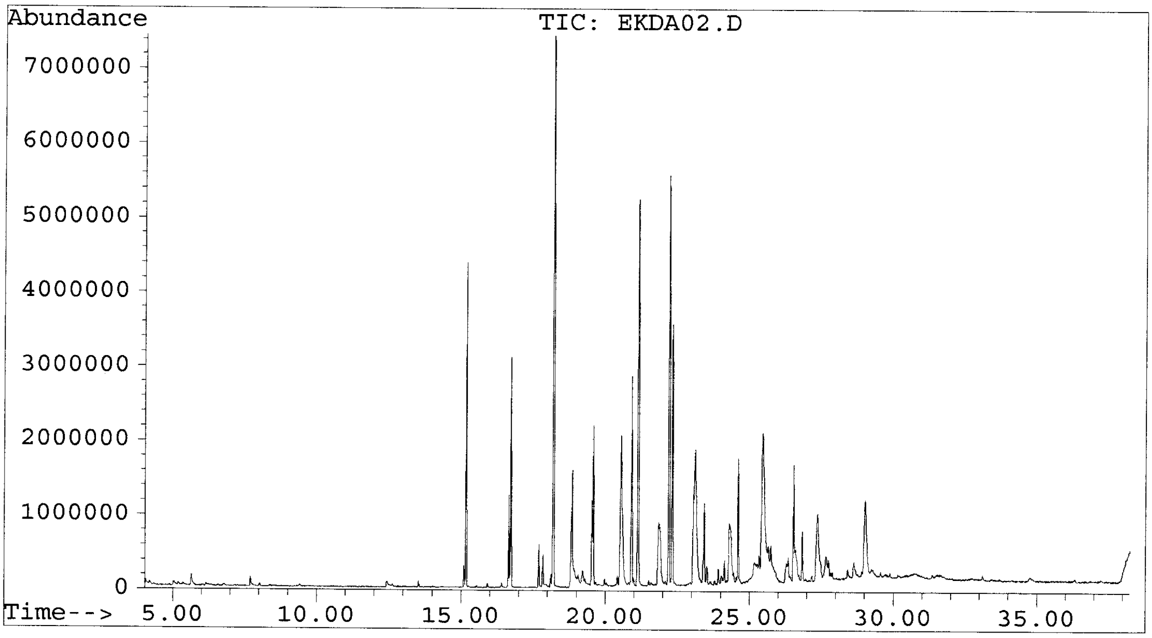


Figure 7-4: Gas chromatogram of acetone extract of *Dischidia acutifolia* (Asclepiadaceae)

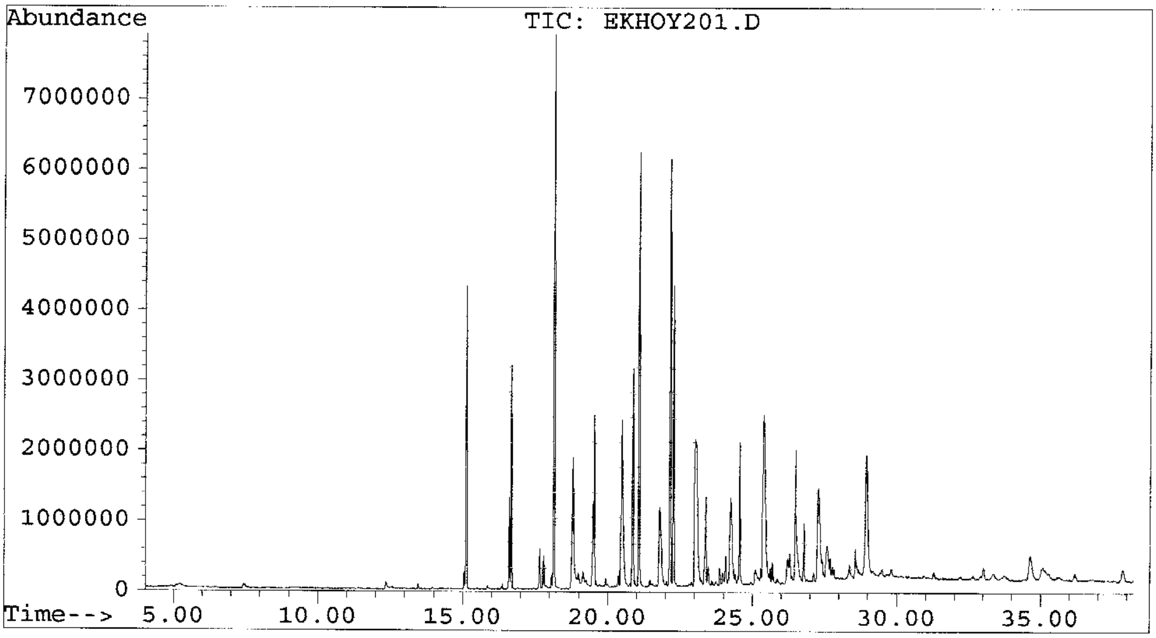


Figure 7-5: Gas chromatogram of acetone extract of *Hoya* sp. (Asclepiadaceae)

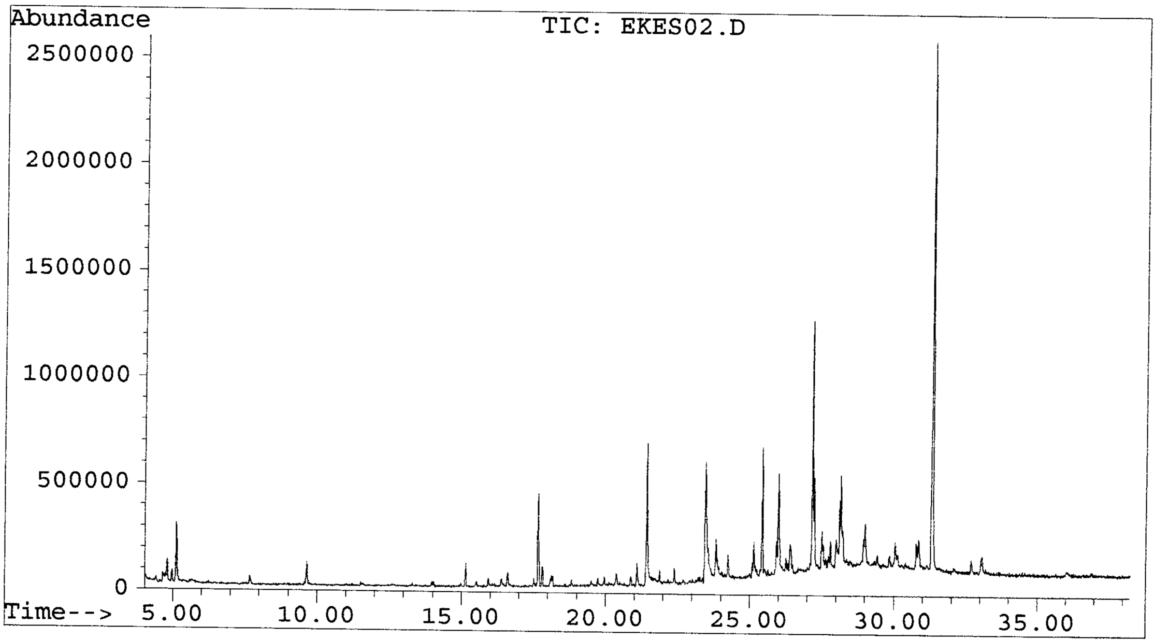


Figure 7-6: Gas chromatogram of acetone extract of *Emilia sonchifolia* (Asteraceae)

7.1.4. HPLC and LC fractions in bioassays

28 HPLC fractions (Chapter 12.4, p. 177), and ten representative LC fractions were tested in bioassays (Chapter 3.5.2, p. 16). The lowest fraction number refers to the most polar fraction in the case of HPLC (reverse-phase column) and to the least polar fraction in the case of LC. In order to give an overview over the results, HPLC fractions were therefore listed in reverse order in Scheme 7-1. The results of bioassays using these fractions were categorized in: -: 0 - 20 % retrieved; 0: > 20 - 40 % retrieved; +: > 40 - 60 % retrieved. No fraction resulted in more than 60 % bait retrieval.

increasing polarity →

HPLCfraction	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
category	0	-	0	0	0	-	0	0	0	0	+	+	+	0	+	-	+	-	+	0	0	-	+	-	0	-	0	-

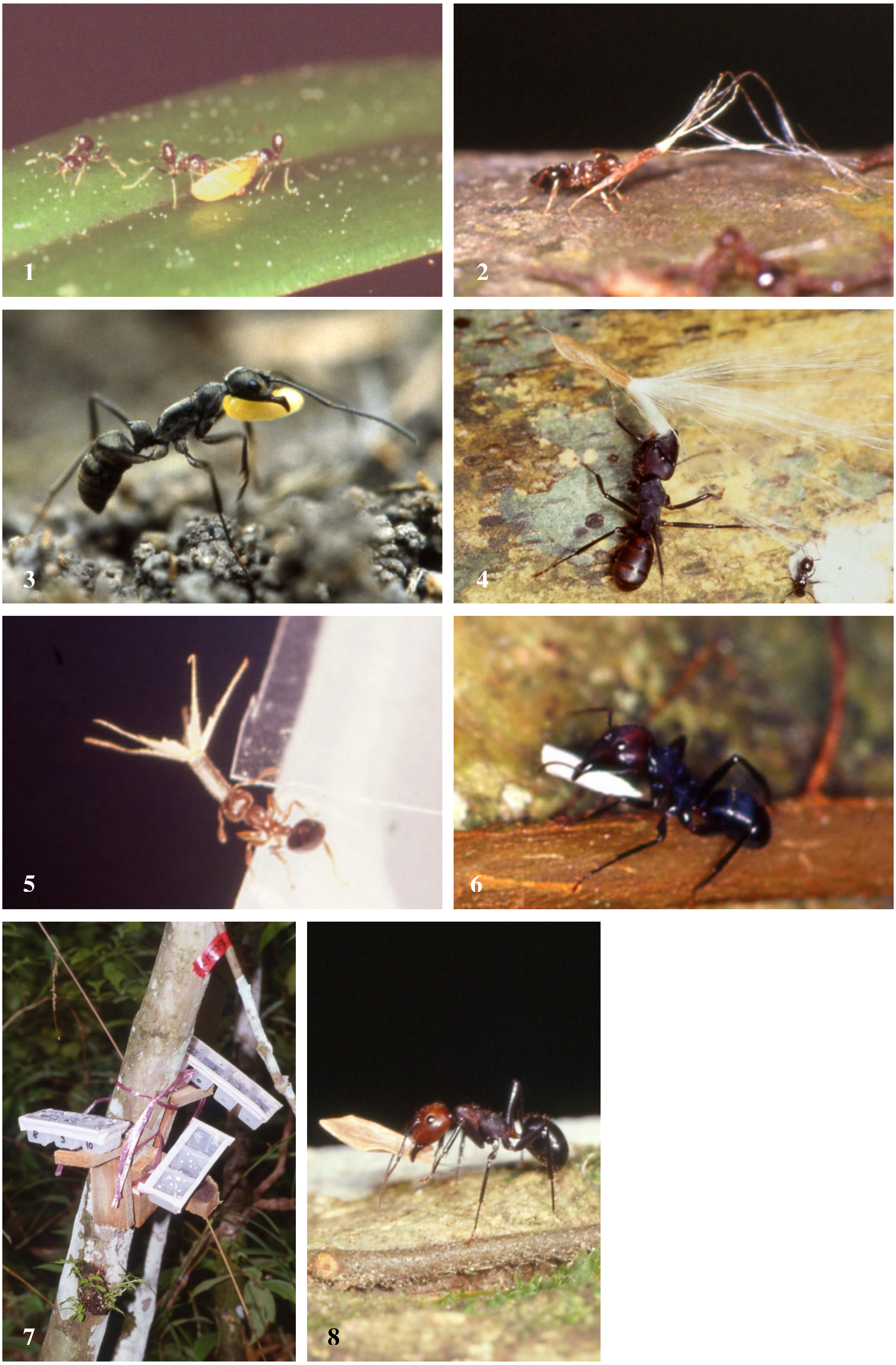
LCfraction	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
category	▨	+		▨	+	▨	▨	0	0	0	0	-	▨	0	▨	-	▨	▨	▨	-				

increasing polarity →

Scheme 7-1: Attractiveness of LC and HPLC fractions on porcelain baits
-:0 - 20 % retrieved; 0: > 20 - 40 % retrieved; +: > 40 – 60 % retrieved; the most attractive fractions are encircled; n=30 for each tested item; 'grey' LC fractions were not tested.

Maximum attractiveness was reached in the middle of the HPLC fractions, with 55.6 % retrieved seeds, and in LC fraction no.5 (57.4 %). With a recombination of all fractions retrieval was 70 % (both LC and HPLC), with control seeds 95 %. Each single fraction and the recombination of all fractions were significantly less attractive (χ^2=43.5, p<0.001) than control seeds, while the total extract (without previous separation) had been proven to be as attractive as the control seeds. HPLC fractions suggested that the main attractive compounds have a medium polarity; on the other hand, the most non-polar LC fractions were most attractive. However, due to the differences in technique, the polarity of LC fraction 5 may very well be similar to the polarity of HPLC fractions 10-18.

In both preparation types, 'biological activity' was found in several fractions. Thus, there is clearly more than one attractive substance in the extracts.



Color Plate 7-1: Seed-carrying experiments

1: *Philidris* sp$_{\text{KfmA}}$160 with seed of *Hydnophytum formicarium* 2: *Crematogaster* sp$_{\text{KfmA}}$18 with seed of *Aeschynanthus fecundus*; 3: *Diacamma* sp$_{\text{KfmA}}$111 with seed of *Pachycentria constricta*; 4: *Camponotus* sp$_{\text{KfmA}}$9 attacking seed of *Hoya elliptica* 5: *Crematogaster* sp$_{\text{KfmA}}$18 with seed of *Emilia sonchifolia* with acetone extract of *Aeschynanthus fecundus*; 6: *Camponotus* sp$_{\text{KfmA}}$9 with porcelain bait with acetone extract of *Hoya elliptica*; 7: Experimental setup for seed-carrying experiments at a nest of *Diacamma* sp$_{\text{KfmA}}$111; 8: *Camponotus* sp$_{\text{KfmA}}$9 carrying seed of *Hoya elliptica* after the hairy appendage had been removed

7.2. Discussion

Combining all results bearing on the nature of substances responsible for seed attractiveness, several characteristics can be concluded. This first part of the discussion is closely related to the results gained in the present study. The second part will be devoted to a comparison of myrmecochory 'systems' in terricolous plants and in neotropical AGs to myrmecochory in palaeotropical AGs. In the third part patterns will be discussed in an evolutionary context and finally be applied to the AG systems investigated in this study.

7.2.1. Characteristics of ant attractants in wind-dispersed epiphyte seeds

Though the characterization of ant attractants in palaeotropical AG epiphyte seeds is far from complete, some conclusions can be drawn from the present results.

The granivorous non-AG ant *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}210$ collected epiphyte as well as non-epiphyte seeds, indicating that seed attractants for AG ants were at least not repellent to non-AG ants in general (Chapter 7.1.1, p. 114).

Nevertheless, it would appear that AG ant attractants are not general ant attractants, because most non-AG ants did not retrieve any wind-dispersed seeds. It therefore seems unlikely that seed attractants are simply nutritive for their partner ants. This conclusion is further supported by the observation that colonies under 'starvation' conditions never retrieved any seeds (s. Kaufmann et al., 2001). However, Leeuwen (1929a) described oil-containing tissue in the diaspores of several AG species[55], and he concluded that these might be elaiosomes responsible for seed attractiveness. This idea cannot be totally ruled out, though it is not supported by the present results. None of the AG ants investigated during this study has ever been observed to consume seed tissue. Furthermore, if the seeds had consumable parts it would seem rather strange that the ants frequently incorporate them immediately in their nest walls (also s. Kleijn and Donkelaar, 2001). Generally, many seeds – myrmecochores as well as non-myrmecochores – contain oils.

According to my experiments (Chapter 7.1.2, p. 114), seed attractants are non-volatile at 'normal' temperature[56]: Seeds were still attractive after a period of more than four weeks, and highly resistant to heat. Moreover, washing experiments suggest that they must occur in a very high concentration: It took a long time and several solvents to get rid of activity, and extracts were even attractive to ants after very short extraction periods (shortest tested period: 3

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[55] *Lecanopteris sinuosa*, *L. curtisii*: oil droplets in thin-walled cells of sporangia; *Acriopsis javanica*: seeds with thin-walled outer cells containing oil droplets; *Dendrobium pallide-flavens*: club-like at the distal end, this structure was filled with oil-containing tissue; *Aeschynanthus angustifolia*; *Aeschynanthus albidus*: oil droplets in outer cell layers and in hairy appendage; *Dischidia nummularia*, *D. punctata*, *D. bengalensis*, *Hoya lanceolata*: epidermal seed cells filled with oil droplets (Leeuwen, 1929a)

[56] Weissflog (2001) observed that seeds of *Hoya elliptica* (Asclepiadaceae) were no longer attractive for *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ after he had stored them in paper envelopes for one week. This seems to contradict my results. One possible explanation might be that the paper envelope absorbed the active substances.

minutes). The latter result additionally indicates that ants react to comparably low concentrations. Furthermore, ants were never observed to react towards the seeds from a distance. When they found seeds, they first antennated them and then decided whether to carry them or not.

While experiments with seed extracts, using different solvents (Chapter 7.1.2, p. 114), point towards similar or equivalent attractive compounds in the seeds of different plant families, comparison of the gas chromatograms (Chapter 7.1.3, p. 116) does not support this assumption. However, this hypothesis cannot be rejected yet, because the active substance(s) might just not be visible in gas chromatograms. For example, they might become volatile at higher temperatures only. This may at first seem to contradict the results gained from heating experiments, but it might still be possible: High temperatures may trigger a degeneration process in active molecules.

Since the most polar solvent (aqua dest.) produced the least attractive extracts, polar substances like sugar and amino acids seem not to be responsible for seed attractiveness. Chloroform extracts were about as little attractive for ants as aqua dest., though it is known to be a good solvent for many organic substances, especially lipids (Leray, 2002). This may indicate that the chloroform I used was not pure and left some contamination on the seeds.

Finally, the results gained from experiments with HPLC and LC fractions (Chapter 7.1.4, p. 120) further complicate any approach to identifying active substances. They revealed that several compounds were active, and these even seemed to achieve synergistic effects when mixed. Recombination of all fractions increased activity but was still less attractive than the original extract or seed. This suggests that preparation of fractions has some effect on active substances.

Summarizing, any conclusion concerning active seed compounds still has to be highly speculative. Some relatively non-polar substances seem to be most attractive. Since activity appears in so many fractions, it is difficult to identify active compounds. One approach towards finding possible ‘candidates’ for active substances in future could be the use of simple chemical reactions allowing certain substance-classes to be modified and easily separated from the rest by methods not harming other substances (Attygalle, 1998).

7.2.2. Myrmecochory – 'Systems'

In order to discuss possible ways of evolutionary development of seed dispersal in palaeotropical AGs, these will be compared to neotropical AGs and to terricolous myrmecochores. As a first step, a summary of relevant literature data on the latter two systems will be provided.

7.2.2.1. Terricolous myrmecochores

Terricolous myrmecochores have been the subject of scientific studies for a long time. According to Berg (1975), Milewski and Bond (1982), Bond et al. (1991), and Hughes et al. (1994) altogether c. 3000 plant species from 80 plant families are myrmecochores sensu stricto, i.e. these myrmecochores all have some type of elaiosome[57]. The vast majority of these terricolous myrmecochores inhabit low-nutrient soils (sclerophyll vegetation) in Australia (Berg, 1975) and Southern Africa (Bond et al., 1991; Hughes and Westoby, 1992a); a smaller fraction grows in deciduous forests of the northern hemisphere (Europe: Sernander, 1906; Northern America: Beattie and Culver, 1981), and several species have been discovered in tropical rain forests (e.g. Horvitz, 1978; Horvitz and Beattie, 1980; Passos and Ferreira, 1996). Aronne and Wilcock (1994) give an explanation for the prevalence of myrmecochory in nutrient deficient habitats. They suppose that the costs for ant attractants are significantly lower than those for vertebrate attractants, so that the cost-benefit-relation may be better for myrmecochores compared to e.g. ornithochores in low resource habitats (also s. Westoby et al., 1991).

Another important selective pressure is the demand for favorable microhabitats (Davidson and Morton, 1981; Beattie and Culver, 1982; Beattie, 1985). This demand might also be especially high in nutrient poor habitats, favoring directed dispersal (Howe and Smallwood, 1982; Hanzawa et al., 1988) by ants as compared to haphazard dispersal by birds. Further potential benefits for ant-dispersed plants (e.g. fire protection, predator protection) are portrayed in great detail by Beattie (1985). Since plant adaptations to myrmecochory seem to be independent from the type of benefit plants obtain from their ant partners, this aspect will not be discussed here.

The diversity of plant dispersing ants has been estimated at c. 200 species from 47 ant genera, belonging to Dolichoderinae, Formicinae, Myrmicinae and Ponerinae (Gomez and Espadaler, 1995). Generally, myrmecochory is not species-specific, though certain preferences between ant and plant species are common (e.g. Beattie, 1985; Böhning-Gaese et al., 1996). Furthermore, the response of a single ant species or even a single ant colony may vary in dependence on habitat and situation (Beattie, 1985; Gordon, 1983). Reasons for behavioral variations are a)

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[57] For definition of 'myrmecochory', s. Chapter 4.2.2, p. 86

nutritional status and availability of alternative food sources (Culver and Beattie, 1978; Beattie, 1985); b) preliminary experiences of the colony (Warburg, 2000); and c) behavioral shifts due to changing worker age (age polyethism) and colony demands (Gordon, 1983).

Elaiosomes are generally thought to be responsible for seed retrieval. Morphologically, elaiosomes originate from various plant tissues (e.g. chalazal outgrowths, exostoma of raphal arils, endospermal tissues (Bresinsky, 1963; Lisci and Pacini, 1997)), and they contain lipids, proteins, amino acids, sugars and vitamins in any combination (Bresinsky, 1963; Beattie, 1985).

Fatty acids were frequently identified as major ant attractants in seeds (Morrone et al., 2000: palmitic, oleic, linoleic and stearic acids). Studies with several ant species and plant families revealed that one single compound, the diglyceride 1,2-diolein, generally elicits seed-carrying behavior (Carroll and Janzen, 1973; Marshall et al., 1979; Horvitz and Beattie, 1980; Skidmore and Heithaus, 1988; Brew et al., 1989; Kusmenoglu et al., 1989). Marshall et al. (1979) suppose that 1,2-diolein is not attractive for its nutritional value (though this cannot be totally excluded (Beattie, 1985)), but simply serves as general cue in ant behavior. They compared 1,2-diolein to 1,3-diolein, and found the first configuration to be much more attractive than the second. This should not be the case if the ants retrieved this diglyceride for its nutritional value.

Since 1,2-diolein is also found in the hemolymph of many insects, Carroll and Janzen (1973) suppose that seeds might mimic insect prey (‘dead insect analogue’). This hypothesis has been supported by observations of Horvitz and Beattie (1980), because some carnivorous ants seem to be particularly reliable seed dispersers. Hughes et al. (1994) compared the fatty acid compositions of elaiosomes to those of the seeds to which the elaiosomes were attached, and to general patterns of fatty acids in seven insect orders. Their results revealed that the fatty acid compositions of elaiosomes and insects were very similar, while those of elaiosomes and seeds were not. Hughes et al. (1994) therefore suggested that, although 1,2-diolein might be eliciting seed-retrieval in the first place, the similarity of fatty acid composition to possible prey insects might further promote seed retrieval by carnivorous and omnivorous rather than granivorous ants.

This explanation seems to be reasonable: If 1,2-diolein were the only factor influencing an ant’s response, it would be hard to explain species-specific differences in the ants’ seed preferences. In addition to this, seeds would hardly produce relatively cost-intensive elaiosomes as nutritional rewards if these had no effect on their reproductive success, and thus – in the case of myrmecochory – on ants. Generally, different ant species vary in their suitability as seed dispersers. Moreover, one ant species that is favorable for a certain plant species might turn out to be less favorable for another. Quality and quantity of nutritional rewards and possibly other chemical cues apart from 1,2-diolein are therefore necessary to modulate myrmecochorous interactions. For example, size relation of elaiosome to achene (Hughes and Westoby, 1992b;

Sheridan et al., 1996) or total elaiosome size (Mark and Olesen, 1996) seem to be important traits.

Generally, it is hard to imagine that the nutritional quality of an elaiosome directly modifies ant behavior. Foraging ants quickly decide whether they will retrieve a certain seed or not, and thus fairly simple signals are needed for this decision. However, if the ants' choice increases their own reproductive fitness, this may very well have an effect on an ant species' seed-retrieving preferences on an evolutionary timescale. Furthermore, nutritional rewards might even influence ant colonies on a very short timescale, because ants are capable of learning (e.g. Warburg, 2000). Workers may learn to distinguish between seeds of different species which they have experienced as especially 'tasty' or nutrient-rich. Some results of Davidson et al. (1990), performing experiments with zeolite baits treated with more or less attractive substances, support this idea of learning: In these experiments, the ants apparently learned that the baits were not 'real seeds' and therefore discarded all of them after a certain experimental period. Similar observations have been made while experimenting with porcelain baits in palaeotropical AG species (pers. obs.).

Simplified, conditions leading to a system consisting of a simple, rather universal seed-carrying eliciting cue in combination with other signals that modulate the ants' response may be expressed in one sentence: *For a (terricolous) myrmecochore, it is better to be dispersed by any ant than by no ant, but if certain ant species can be persuaded to retrieve seeds, this even increases reproductive success.* The main reason why plant species generally do not specialize in one single ant species may be found in a patchy distribution of ant species, so that a species-specific plant would run the risk of its seeds not being found by the 'correct' ant species in time (Brew et al., 1989; Hughes et al., 1994).

7.2.2.2. Neotropical ant-gardens

About 50 epiphyte species from 12 plant families have been reported as AG epiphytes in tropical South America (Chapter 12.12, p. 198)[58]. They are associated with c. seven to ten ant species from five genera[59] and four subfamilies. Though there are no species-specific AG associations, certain preferences have been detected by Orivel and Dejean (1999b): The distribution of epiphyte species on nests of different AG ants could at least partly be explained by seed-retrieval preferences of the respective ant species.

Most neotropical AG epiphyte seeds are equipped with an elaiosome (Davidson, 1988). Moreover, most seeds are primarily bird-, bat- or monkey-dispersed and thus enclosed in a

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[58] Some of them might be secondary, opportunistic inhabitants of ant-gardens.

[59] Dolichoderinae: *Azteca* spp.; Formicinae: *Camponotus femoratus;* Myrmicinae: *Crematogaster longispina*, *Cr.* cf. *limata parabiotica* (possibly more than one species); Ponerinae: *Odontomachus mayi*, *Pachycondyla goeldii*

sweet and sticky fruit pulp[60]. However, nutritional rewards clearly did not fully explain why ants were attracted to seeds. Firstly, non-AG ants were repelled even when nutritional rewards were present; secondly, seeds remained attractive for AG ants and repellent for non-AG ants even after passage through a frugivorous bat's digestive system (Davidson, 1988; Davidson et al., 1990; Orivel and Dejean, 1999b), while seeds of closely related non-AG plants were always rejected; thirdly, in simultaneous experiments, the ants showed clear preferences independently of direct nutritional rewards and also independently of expected long-term food rewards (extrafloral nectaries, etc.).

Davidson et al. (1990) and Seidel et al. (1990) made an attempt to identify compounds responsible for seed retrieving. In a first step, they identified common volatile seed compounds in ten AG epiphytes occurring sympatrically in Cocha Cashu, Peru. One substance, 2-hydroxy-6-methyl-benzoic acid methyl ester (=methyl-6-methyl-salicylate, 6-MMS), was detected in seeds from nine of ten tested species. Four other compounds were common to several, though not all epiphyte seeds. All five substances together constituted a major part of seed volatiles. Seidel et al. (1990) mainly concentrated on 6-MMS and found out that it also occurs in male heads of *Camponotus femoratus,* the most common AG ant in Cocha Cashu (Davidson, 1988). Seidel et al. (1990) suggested three different explanations for co-occurrence of these compounds in the epiphyte seeds: a) Convergent evolution with the ants as selective forces might be responsible. b) The plants might have produced these compounds for reasons other than ants before they were growing on AGs. The accumulation of plants with these seed traits would then be a consequence of the ants' chemical preferences. c) Epiphytes produce these compounds in consequence of their association with ants, i.e. they are infected with some symbiotic microorganisms inducing the production when growing in an AG. This last hypothesis could be easily tested using cultivation experiments, but this has not been done so far.

In subsequent bioassays, artificial seeds (made from zeolite molecular sieves) treated with 6-MMS and many other substances were offered to *Camponotus femoratus* (Davidson et al., 1990). The results were fairly ambiguous and ultimately inconclusive. Seed retrieval could hardly be elicited at all; the ants' responses were highly concentration-dependent and also varied between different years of field trials. Furthermore, whenever too many experiments were performed with a single colony, the ants discarded any test item immediately.

Nevertheless, Davidson et al. (1990) suggest that 6-MMS might at least have been responsible for seed attractiveness to AG ants during the early historical evolution of the association. There is some indication that it might play a role similar to that of 1,2-diolein in terricolous myrmecochores. Additional seed compounds might again be responsible for species-dependent modulations of attractiveness to certain ant species (Orivel and Dejean, 1999b). However,

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[60] exception: *Peperomia* spp., Piperaceae: wind-dispersed seeds

results are too meager to come to a conclusion here. In particular, responses of other South-American AG ants, which are frequently associated with the same epiphyte species, have not been tested yet.

7.2.2.3. General considerations on possible evolutionary pathways for myrmecochory

What can we learn from the two previously described myrmecochory 'systems', combined with data for palaeotropical AGs? First of all, convergences and differences must be named.

Convergences of the three known myrmecochory systems

a) Myrmecochory is apparently never strictly species-specific. In all three 'systems', a large array of ant and plant species participate.

b) Nutritional rewards play a role in terricolous myrmecochores as well as in neotropical AGs, but they are not the proximate cues responsible for seed retrieval in any case. In palaeotropical AGs, nutritional rewards seem to elicit seed retrieval in primarily bird-dispersed epiphytes. Nevertheless, the existence of cues in addition to nutritional rewards cannot be excluded. In primarily wind-dispersed seeds, nutritional rewards play – if at all – a minor role. Cues varied, depending on responding ant species, but chemical cues were most important in three of four types that were distinguished (Chapter 4.2.1, p. 80).

c) In terricolous myrmecochores and neotropical AGs, circumstantial evidence suggests one or a few basic chemical cues to be responsible for eliciting seed retrieval. Theoretical considerations on possible cues lead to the assumption that this might be a general pattern (s. p. 126) in all myrmecochory systems.

d) Signal modulation is a second step, explaining species-specific differences in seed retrieval. This is apparently achieved mainly with the help of elaiosomes (e.g. size, s. above) in terricolous myrmecochores; in neotropical AGs both elaiosomes and chemical cues (aromatic compounds, s. above) might play a role, and in palaeotropical AGs chemical cues will probably turn out to be most important. I presume that in all myrmecochory systems one or a few key-substances responsible for basic attractiveness exist or at least existed in the past, but other compounds are responsible for species-specific differences in the ants' responses.

Despite these parallels, there is at least one major factor differentiating myrmecochory in AGs from myrmecochory in terricolous habitats: While the only benefit ants gain from their 'seed-dispersal service' for terricolous myrmecochores is nutritional, it goes very much beyond this in AGs. Here, the ant colony is totally dependent on epiphytes stabilizing its nest; without its epiphyte partners, it would probably be unable to establish reproductive colonies. Thus, myrmecochory in AG systems is vital for both partners. Selective pressure should therefore be higher than in terricolous habitats. Moreover, nutritional rewards are probably less important in

AGs because the fitness of the ants is greatly improved by non-nutritional benefits. However, other factors such as competition for ant dispersal may favor plants offering additional food rewards.

Theoretical considerations on the evolutionary development

One main question arises from the foregoing considerations: How could these highly convergent myrmecochory systems develop evolution-wise? Especially the apparent existence of one or a few basic key-substances in each 'system', occurring in several plant families and attractive to several ant genera/subfamilies, seems highly peculiar on first view. Several evolutionary pathways are conceivable:

1. 'Convergent development': If convergent evolution is presumed, a hypothetical originally attractive substance ('compound A') must have two characteristics: Firstly, it has to occur as a product of normal seed-metabolism, either as intermediate product in some metabolic pathway, or with some significance for the plant independent of ants. Secondly, 'compound A' has to be something ants know from their usual life, e.g. a signal eliciting prey carrying or brood carrying. Once 'compound A' accumulates in a seed to a concentration significant to ants, these might start retrieving the seeds. If this turns out to be highly beneficial for the plants, a selective pressure towards highest concentrations of 'compound A' might cause the relevant genes to spread quickly in the population. This idea is supported by the fact that the attractive substance is apparently highly concentrated in neotropical (Davidson et al., 1990) as well as in palaeotropical AG epiphyte seeds.

In terricolous myrmecochores, 1,2-diolein is such a general ant attractant, known from prey insects and corpses to all ants that deal with these items – which is the vast majority (Carroll and Janzen, 1973; Marshall et al., 1979; Horvitz and Beattie, 1980; Brew et al., 1989). In neotropical AGs, 'compound A' may be 6-MMS (Davidson et al., 1990; Seidel et al., 1990). However, possibly 6-MMS only (?) plays a role in the biology of *Camponotus femoratus.* If this was true, 6-MMS is probably just one of the 'modulating' factors responsible for the preferential association with *Camponotus femoratus.* There is some indication, though, that 6-MMS might have broader significance: A similar substance, methyl-salicylate, has been found to be an important signal in several insect-plant interactions (Brouat et al., 2000 and references therein). Thus, 6-MMS might turn out to be significant for other ant species also. In this case, it might have all the characteristics important for a basic attractant.

Generally, the 'substance cocktail' in neotropical AG epiphyte seeds is much more specialized than in terricolous myrmecochores, attracting relatively few ant species and even repelling others (Davidson et al., 1990). Palaeotropical AGs also have a fairly specialized cocktail: Their seeds attract especially AG ants; other, e.g. granivorous ants, however, are not repelled but harvest the seeds. Altogether, AG epiphyte seeds are not attractive to as many ant species as the seeds of terricolous myrmecochores seem to be. The original ‘compound A’, attractive to many ant species, might still be present, but other compounds (‘compound B’) strongly modulate the signal to ants. On a longer timescale, a complete signal shift is conceivable. The more specialized associations between arboricolous ants and their epiphytes might support the assumption that selective pressures are stronger for both partners than in terricolous habitats.

Seidel et al. (1990) and Davidson et al. (1990) present two more ideas as to how the convergent occurrence of certain ant attractants in different plant families in neotropical AGs might be explained.

2. ‘Species accumulation’: Seeds in several plant families developed a certain compound for reasons independent of the ants. Once this compound became attractive to a certain ant species, these epiphyte species ‘accumulated’ on, in this case, the AGs of neotropical *Camponotus femoratus*.

This idea can easily be included in the previously discussed hypothesis of convergent evolution; ‘compound A’ developed independently of ants, and – contrasting the general idea of convergent evolution – was attractive to one certain ant species. This scenario may explain why the same compound occurs in different plant families, but it does not explain whether or why several ant species are attracted to the same cue[61].

3. ‘”Cultural” transmission via microorganisms’: The ants infect their epiphyte partners with some microorganism which induces the production of the attractive compound in the seeds. This idea is again easily conceivable as long as a certain compound attracts only one ant species – as was the case in the experiments on some neotropical AG epiphytes and a single partner ant species (Davidson et al., 1990; Seidel et al., 1990). Once several ant species are attracted to the same compound, things become more complicated. Southeast Asian AG ants also retrieved seeds originating from another ant species’ nest garden. Thus, if the ‘microorganism hypothesis’ was true, the relevant microorganisms should generally live in AG substrate, and thus not be species-specific. This could be the case in AGs, making ‘cultural transmission’ possible, but it seems unlikely for terricolous myrmecochores.

For myrmecochory in general, three further pathways may be discussed:

4. ‘Granivorous history’: Granivory might be the starting point for an evolutionary pathway leading to myrmecochory. O´Dowd and Hay (1980) describe the case of two desert harvester ants that collect elaiosome-bearing seeds of *Datura discolor* and discard the seeds on their

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[61] Seidel et al. propose a significance shift of 6-MMS from sexual pheromone to seed attractant in *Camponotus femoratus*. It has not been shown, though, whether a) 6-MMS is attractive to other ant-garden ants also, and b) whether these use 6-MMS in their social context.

colony midden after removing the elaiosome. These ants thus behave like perfect seed dispersing ants, not like harvester ants, in this case. *Datura discolor* gains a double benefit: Competing desert herb seeds are consumed by the ants, while its own seeds are dispersed away from the mother plant and escape from predators. Thus, once a plant has developed protection mechanisms against being eaten by harvester ants, these can be especially beneficial partners to these plant species.

Levey and Byrne (1993) presented a second, more general and much simpler example, comparing several species of the ant genus *Pheidole* and their effect on small-seeded forest herbs in Costa Rica: They compared the effect of seed-eating colonies of *Pheidole* spp. to several plant species. The experiments revealed for some plant species that most of their seeds were consumed by ants, but those harvested but not consumed significantly increased fitness by growing on the refuse piles. These 'incidental' benefits show that ants may be both antagonistic and mutualistic towards seeds. Even when most seeds are consumed, seed eating ants may thus be beneficial to a plant species at population level – the level at which selection starts.

Generally, it is even possible to achieve a similar picture as via the 'convergent evolution route' here, if a universal 'seed marker' ('compound A'[62]) is presumed. 'Compound A' marks a seed as what it is, and thus makes it attractive to granivorous ants. If the seeds manage to protect themselves from being consumed, they may still be harvested for their 'compound A'-signal. The protection mechanism may be mechanical or chemical. Generally, most myrmecochorous plants produce relatively strong seed coats, preventing granivorous ants from consuming the seeds (Rodgerson, 1998).

5. 'Ornithochorous ancestors': The evolutionary pathway leading from ornithochory to diplochory with myrmecochory as second or only system is a simple one, as Pizo and Oliveira (1998) show for the Brazil rain forest tree *Cabralea canjerana* (Meliaceae). Seeds bear a lipid-rich aril, which is highly attractive to many ants. Small species, however, are not able to carry the seeds, while large ponerines retrieve them to their nests. Both small and large ants consume the aril, thereby increasing germination success. Thus, a sweet aril may persuade ants to retrieve seeds.

6. 'Coincidental use of seeds': In a similar way, wind-dispersed seeds can simply be retrieved for their hairy appendage, which may be used for nest construction in carton-building ant species.

Several evolutionary pathways will have contributed to the myrmecochory systems we find today. In many terricolous myrmecochores, convergent evolution can be presumed. Nevertheless, the 'granivory' route as well as the 'bird-dispersal' route were also realized

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[62] 'Compound A' may also refer to a set of compounds.

several times. Little can be said about neotropical AGs, because systematic studies have not yet been conducted. The situation in palaeotropical AGs will be discussed in the following chapter.

7.2.2.4. Evolutionary ecology of myrmecochory in Southeast Asian ant-gardens

In this chapter, the six evolutionary pathways described above will be considered with regard to their probability for palaeotropical ant gardens.

Two groups of seeds (primarily wind-dispersed and primarily bird-dispersed) and four groups of ants in respect to seed-retrieval cues[63] were distinguished.

Starting with the two groups of seeds, there is some indication that the primarily bird-dispersed seeds were attractive for their nutritional cues only (pathway no.5). However, there is some indication that chemical cues might play a role in addition to nutritional ones at least for some ants. Thus, 'convergent development' and 'cultural transmission' seem to be possible pathways also. However, the remaining considerations will mainly concentrate on wind-dispersed seeds.

Concerning the four groups[63] into which AG ants have been sorted due to seed retrieval cues, *Diacamma* $\mathrm{sp}_{\mathrm{KfmA}}$111 must be regarded as a special case: This species retrieved seeds either due to nutritional rewards (fruit pulp of bird-dispersed seeds), or due to suitability as building material (wind-dispersed seeds). Thus, seeds were just carried among many other items; there was no obvious specialization (pathway no.6, s. above). Generally, this evolutionary pathway seems to be a 'dead end'; more specific cues are necessary for the development of more 'advanced' myrmecochory systems. In this context it is interesting to note that *Diacamma* is the only genus that has not been reported as seed dispersing agent before (Gomez and Espadaler, 1995) – which underlines the special status of this *Diacamma* species.

The second group of AG ants[63], retrieving seeds in general, but preferentially epiphyte seeds, may have granivorous ancestors (pathway no. 4). This seems even more likely because *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}$33 is the only member of this group. *Pheidole* is known as granivorous genus (Hölldobler and Wilson, 1992; Levey and Byrne, 1993; Laman, 1996), and *Pheidole* $\mathrm{sp}_{\mathrm{KfmA}}$33 is one of the two species not tending hemipteran trophobionts (Chapter 4.2.1, p.80). If the 'granivory-hypothesis' is true, wind-dispersed AG epiphyte seeds are still recognized as attractive items and retrieved, but not consumed – or at least only a relatively low percentage of them.

In the other two groups[63], chemical cues play a major role. Granivorous ancestors are unlikely here, because granivory has not been reported for the respective ant genera. Thus, some general ant attractant, for example marking an item as food or brood item, or having some broader significance in ant-plant 'communication', are presumed to have been originally responsible for

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[63] also see Chapter 4.2.1, p.80: group 1: no special "epiphyte" cues; group 2: chemical cues or seed characteristics; group 3: chemical cues only; group 4: chemical and mechanical cues

seed retrieval in these cases. Data is insufficient, however, to distinguish whether 'convergent development' (pathway no.1) or 'cultural transmission' (pathway no.3) was responsible for the patterns found here. Future studies, using cultivated plant seeds, might help to answer this question.[64]

'Group 4' is most remarkable, because here some mechanical cue apparently is important in addition to the chemical cue(s). This would not be particularly remarkable if the same pattern was not found in two parabiotic ant species, one of which has great difficulties in retrieving any seeds at all: *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}21$ is as selective as *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}9$ and *Camponotus* $\mathrm{sp}_{\mathrm{KfmA}}240$, although it only occasionally has epiphytes growing on its nests, and when it does, these belong to a variety of mainly bird-dispersed species (Chapter 4.1.2.1, p. 39 ff. and Chapter 4.2.2, p. 91).

The explanation for this peculiar behavior has to be found in the parabiotic association. The two *Camponotus* spp. clearly benefit from their association with epiphytes. Circumstantial evidence suggested that both *Camponotus* spp. were able to follow the recruitment trails of *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}21$. If *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}21$ was more successful in finding prey items as well as seeds, and if it benefits from its association with *Camponotus* spp., identification of the 'correct' seeds may increase the fitness of all three partners, *Camponotus* spp., *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}21$ and *Hoya* spp.

Summarizing, several different ways can be presumed for the evolution of myrmecochory in AG systems. The lack of species specificity suggests that, as in terricolous myrmecochores (s. p. 126), it is better for an epiphyte to be retrieved by any AG ant than by no ant at all, depending on the availability of ant partners. For the ants, moreover, it seems to be better to have some kind of AG epiphyte growing on their nests than none, depending on the availability of seeds. It is hard to predict, in a tropical rain forest, which ant will 'meet' which seed, and thus this relatively low specificity with potential for modulation and thus creation of preferences may be the optimal scenario for AG associations (sensu Brew et al., 1989).

All the different pathways leading to selective myrmecochory in AGs provide fruitful starting points for further specializations leading to the present diversity of AGs in Southeast Asia. Considerations on the evolutionary development, with special regard to the question of co-evolution, will be discussed in Chapter 8.3, p. 140 ff.

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[64] also see Chapter 7.2.2.3, p. 129

8. Concluding discussion

8.1. The ‘ant epiphyte puzzle’ of Southeast Asia

A perusal of the literature on ant-epiphyte interactions worldwide shows that just about as many papers have been written on neotropical AGs as on palaeotropical ant-house epiphytes. On the other hand, there have so far been relatively few anecdotal reports from palaeotropical AGs (Chapter 12.11, p. 196), and very few ant-house epiphytes have been described in tropical America[65], though this region is renowned for its highly diverse and abundant myrmecophytes and epiphytes. As a result of this imbalance, AGs were widely thought to be restricted to the neotropics (Kleinfeldt, 1986; Orivel et al., 1999). Domatia-bearing ant-house epiphytes were often regarded as a second and totally different type of ant-epiphyte interaction. Studies mainly focused on the ability of these plants to derive nutrients from the debris the ants stored in their domatia or to even use CO_2 produced by the ants (Huxley, 1978; Rickson, 1979; Gay, 1993; Treseder et al., 1995). Seed-dispersal, implantation, and cultivation on the ants’ carton nests had not been recognized as crucial for the phenomenon (Janzen, 1974; Huxley, 1978, 1982; Maeyama and Matsumoto, 2000).

The results on ant epiphyte interactions in Southeast Asia presented in this study contribute two important aspects which help to solve this ‘ant-epiphyte puzzle’:

First, AGs were discovered in a wide variety of ant and epiphyte species in Southeast Asia. The variety of species and genera involved in these systems is not smaller than in tropical America (Chapter 8.2). On the plant side, ants even seem to be partners of the majority of non-facultative vascular epiphytes in lowland forests (except for ferns and orchids, Chapter 6.1.1, p. 107). Seed dispersal as well as nutrient and water supply are the main benefits the epiphytes gain from the ants (Chapter 4.2.1, p. 86 ff.). Ants seem to be absolutely vital for their plant partners at least in the early phase of establishment in the canopy. Thus, epiphyte distribution in the canopy widely depends on formicids building carton nests and carrying epiphyte seeds. The widespread assumption that AGs do not exist or at least play a minor role in Southeast Asian lowland rain forests can now be regarded as a ‘scientific legend’.

Secondly, I suggest integrating the group of ant-house interactions to the large group of AG interactions for several reasons. *Philidris* sp$_{\mathrm{KfmA}}$160 was the main inhabitant (c. 80 %) of ant-house epiphytes in my research areas (heath forests in Borneo). Queens of this monogynous species were never found inside any of the ant-house epiphytes, but always in bark crevices

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[65] Benzing, 1970, 1991; Gomez, 1974, 1977; Fisher and Zimmerman, 1988; Rico-Gray et al., 1989; details s. below

covered by thick carton layers. This means that the essential part of the nest is not inside epiphyte domatia but in carton nests.

Small colonies frequently only had a few small seedlings growing on their nests and carton runways (Chapter 4.1.2.2, p. 56 ff.). The ants retrieved seeds of all their partner epiphytes into their carton nests. These results make the ontogenetic development of these ant-epiphyte associations fairly clear: Ants inhabiting ant-house epiphytes build carton nests and implant seeds from their partner epiphytes.

As this is exactly what happens in AG systems, the two groups can no longer be separated as they used to be. Ant-house epiphytes must be regarded as a special type of AG epiphyte, i.e. an ant-house epiphyte is an AG epiphyte producing domatia.

The fact that many ‘non-ant-house’ epiphytes can be found in combination with ant-house epiphytes further supports this idea. These are most probably not ‘parasites’ of the ant-house mutualism as suggested by Janzen (1974), but as regular AG epiphytes they stabilize carton constructions of the ants. *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}37$ is especially interesting in this respect because this ant frequently housed in AGs without any ant-house epiphytes around, while all other *Philidris* spp. collected in this study (and also those known from literature) were mainly associated with ant-house epiphytes.

My results are partly supported by genetic studies of Maeyama and Matsumoto (2000) in Papua New Guinea. They analyzed seven colonies of monogynous but polydomous *Dolichoderus* sp. (Dolichoderinae), inhabiting the rubiaceous ant-house epiphyte *Anthorriza caerulea*, in terms of the genetic similarities (using RAPD-PCR) of their plant partners. Within the territory of one ant colony, all epiphyte specimens were closely related and had apparently been dispersed by their partner ants. In this case, *Dolichoderus* queens were always found inside epiphyte tubers.

Philidris cordatus, one of the main partners of *Myrmecodia tuberosa* and *Hydnophytum formicarium*, is supposed to be polygynous (Davidson and Epstein, 1989; Davidson et al. 1991). Here, queens are also sometimes found inside the tubers of associated epiphytes, but Davidson and Epstein (1989) suspect that the main part of the colony might reside on the host tree. As c. 95% of all ant-house epiphytes are colonized by *Philidris cordatus* in certain habitats (Janzen, 1974), it seems highly probable that, in this case, at least one means of colony dispersal is budding or splitting.

Not only the ontogenetic development of traditional ant-house and AG systems is alike, but also the benefits for the ants as well as for the plants strongly resemble those in other AG associations. The ants gain safe and dry nest sites (Chapter 4.2.2, p. 84 f.) and provide nutrients and reliable short distance seed dispersal for their partner plants (Chapter 4.2.2, p. 86 f.).

Thus, the term ‘ant-house’ remains useful for describing a special type of epiphyte, but it is not suitable for describing the association between ants and these epiphytes as contrasting AGs.

The part of the puzzle I cannot solve here is: Why are there so few reports on ant-house epiphytes in tropical America? This is astonishing because domatium structures have developed independently many times in Southeast Asia. The rubiaceous subtribe Hydnophytinae contains the most complex and species rich ant-house epiphytes, with almost 100 species from five genera (Jebb, 1991; Huxley and Jebb, 1991a,b). A variety of other plant genera, like *Hoya* or *Dischidia* (Asclepiadaceae), developed different forms of ant domatia even within the same genus. Various ferns (*Lecanopteris* spp., and also *Platycerium ridleyi*, (Kaufmann and Maschwitz, unpubl.)) also contribute to this type of ant plant.

The conclusion might be drawn that it cannot be too ‘difficult’ for a plant to develop domatia. Although Hydnophytinae and the asclepiad genera *Hoya* and *Dischidia* are restricted to Southeast Asia, neotropical rain forests are extremely rich in epiphytes (e.g. Madison, 1977; Kress, 1986) and host, for example, the Bromeliaceae with a great variety of forms. Nevertheless, the only species described as domatia-bearing epiphytes are the potato-ferns *Solanopteris* spp. (Gomez, 1974, 1977), the bromeliads *Tillandsia caput-medusae* and *Tillandsia butzii* (Benzing, 1970), and some species from the orchid genera *Schomburgkia* (Rico-Gray et al., 1989) and *Caularthron* (Fisher and Zimmerman, 1988; Benzing, 1991). It is interesting that all these species have also been reported from AGs and in association with typical AG ants (Benzing, 1970; Gomez, 1977; Rico-Gray et al., 1989). Nutrient uptake from debris stored in the domatia has been experimentally shown for the two species of *Tillandsia* as well as for *Schomburgkia tibicinis*, and it is highly probable for *Solanopteris*.

Though I have not studied ant-epiphyte interactions in tropical America, and since any further discussion on this subject is therefore highly speculative, I will at least name some considerations on the phenomenon.

With regard to habitat distribution of Southeast Asian ant-house epiphytes, it becomes apparent that these plants are most abundant in relatively dry, open-canopied habitats, e.g. in heath forests, where sun-exposure is particularly strong. Jebb (1991) as well as Davidson and Epstein (1989) suggest that all the ant-house epiphytes had highly drought resistant ancestors. Indeed, all involved genera show some xeromorph features[66]. There are even some observations that ant-house epiphytes are intolerant to shadier conditions (Davidson and Epstein, 1989). If the assumption that domatia-bearing epiphytes are derived from drought-resistant ancestors is true, neotropical epiphytes occurring in similar habitats must be regarded as possible ancestors for ant-house epiphytes there.

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[66] also see Chapter 6.2.2, p. 111 ff.

Two groups are especially drought-resistant in the neotropics: The first group are orchids with their velamentous roots and pseudobulbs, the second group are bromeliads with their specialized trichome structures (Benzing, 1990). The latter family is almost completely missing in the old world (Kress, 1986; Benzing, 1990). If nutritional aspects were further necessary for promoting ant-epiphyte interactions, as has been presumed many times (e.g. Huxley, 1980; Davidson and Epstein, 1989; Benzing, 1991), this might be a possible explanation for the lack of ant-house epiphytes in tropical South America. On the one hand, orchids show little predisposition for an association with ants, mainly because of their dust-like seeds and mycotrophic establishment system. Bromeliads, on the other hand, frequently produce some debris-collecting rosettes that make them independent of ants. Moreover, they are indeed frequently ant-associated in South American ant gardens (Chapter 12.12, p. 198), and they are one of the most species-rich plant families, dominating a large part of the epiphytic flora in South America. Thus, the predominance of bromeliads under ecological conditions conductive to the development of ant-house epiphytes might at least partly explain why there are so few domatia-bearing epiphytes in the neotropics. However, this hypothesis is, if at all, just a small part of the answer; further studies are needed.

8.2. Comparison of Southeast Asian and tropical American ant-gardens

In this chapter I will stress some striking similarities as well as remarkable differences between Southeast Asian and tropical American AGs. Aspects concerning the 'ant epiphyte puzzle' (Chapter 8.1) and a detailed comparison of seed-retrieving behavior (Chapter 7.2.2) will not be repeated here.

8.2.1. Species composition

The number of ant species found in Southeast Asian AGs will probably resemble or possibly exceed the number in tropical America (Chapter 4.1.1, Table 4-2, p. 22). Their taxonomic composition seems to be similar at least at subfamily-level. In both areas, AG ants have been found in Dolichoderinae, Formicinae, Myrmicinae and Ponerinae. *Azteca* (Dolichoderinae) is restricted to the neotropics; on the other side, *Philidris* (Dolichoderinae) is restricted to Southeast Asia. *Dolichoderus* (Dolichoderinae) occurs in association with epiphytes in tropical America (Dejean and Olmstedt, 1997; Corbara et al, 1999) as well as in Southeast Asia (Maeyama and Matsumoto, 2000). *Camponotus* (Formicinae) and *Crematogaster* (Myrmicinae) are partners of epiphytes in both regions, and apparently - at least in some species - even in a similar parabiotic fashion[67]. In some tropical American regions, parabiotic *Camponotus femoratus* and *Crematogaster* cf. *limata parabiotica* are the most abundant inhabitants of AGs

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[67] also see Chapter 4.2.2, p. 91

(e.g. Wheeler, 1921; Weber, 1943; Davidson 1988; Orivel et al. 1997). There are two ponerine AG initiators in tropical America (*Pachycondyla goeldii*, *Odontomachus mayi*; Corbara and Dejean, 1996; Orivel et al., 1996, 1997). AGs of *Pachycondyla goeldii* are apparently more elaborated than those described for the ponerine *Diacamma* in this study (Chapter 4.1.2.4, p. 73 ff. and Chapter 4.2.1, p. 78 ff.).

True AG epiphytes on palaeotropical AGs apparently outnumber those on neotropical AGs in species numbers. According to Madison (1977, 1979) and Orivel and Dejean (1999b), of the 15 500 described neotropical epiphyte species, only very few regularly occur on AGs. Madison (1977, 1979) listed altogether 19 species from 10 families (mainly Araceae, Bromeliaceae, Gesneriaceae, Piperaceae). Accumulating literature data from five neotropical countries (Brazil, Costa Rica, French-Guyana, Peru, Venezuela) resulted in 53 epiphyte species from 12 families that grow on AGs (Chapter 12.12, p. 198). These numbers also include opportunistic AG epiphytes. Thus, the relative significance of AGs for the total canopy flora seems to be higher in Southeast Asia. The total number of epiphytes in the palaeotropis, including also Africa, is estimated to 12 600 species (Madison, 1977). In the present study alone, altogether 84 epiphyte species from 16 plant families were found on AGs. More than 50 species were even identified as true AG species (Chapter 6.1, Table 4-3, p. 23).

8.2.2. Ant-garden establishment

One of the main discussions with regard to neotropical AGs started with Wheeler (1921). It deals with the question: Which comes first, the ant or the epiphyte?

While Ule (1901, 1905a, b, 1906) did not question that the ants were the active constructors of AGs, building carton nests and retrieving the seeds of their partner epiphytes, Wheeler (1921) doubted these observations. He stated that young queens found their nests between the roots of previously established epiphytes; the associations were then rather casual. Research has supported Ule's hypothesis in most cases since, but apparently there are some cases which correspond to Wheeler's idea as well. These might be non-regular, secondary, opportunistic AG inhabitants (e.g. Davidson, 1988).

Using the definition of an AG employed in this study (based on Corbara et al., 1999, Chapter 1.3, p. 3), such species should not be regarded as true AG ants. Belin-Depoux et al. (1987, 1988, 1991) found *Anthurium gracile* and *Aechmea mertensii* to establish without supporting ants in open-canopy habitats. In this case, founding queens were said to colonize the roots of the epiphytes. However, this mode of establishment seems to be unusual for these plants because the results were not supported by numerous observations of other scientists. For example, Davidson (1988) observed that the seeds of *Anthurium gracile* were retrieved to the AGs of *Camponotus femoratus*. Corbara and Dejean (1996) and Orivel et al. (1998) experimentally showed that the ponerine AG ant *Pachycondyla goeldii* built small carton nests and then retrieved seeds of *Aechmea mertensii* as well as those of *Anthurium gracile*.

Thus, the main proportion of ant-epiphyte interactions in both biogeographical regions depends on carton building and seed retrieving ants. Besides these true AG mutualists, opportunistic ant and epiphyte species exist in Southeast Asia (Chapter 4.1.1, p. 20) as well as in tropical America.

8.2.3. Ant nutrition and the significance of phorophytes

The nutritive impact of neotropical AG epiphytes generally seems to be higher than that of palaeotropical AG epiphytes. Several species possess extrafloral nectaries, others provide pearl bodies (Davidson, 1988) for their partner ants. Ants have frequently been observed feeding on fruit pulps of the AG epiphytes. Furthermore, some of the epiphyte seeds carry nutritive appendages consumed by either workers or ant larvae.[68]

The use of trophobionts is common in most neotropical as well as in most palaeotropical AG ants. There is little information on whether neotropical AG ants also tend trophobionts underneath their nests, as it is frequently the case in palaeotropical AGs. Davidson (1988) reported carton shelters built by parabiotic *Camponotus femoratus* and *Crematogaster limata parabiotica* for their ‘livestock’ on several trees, including both the host tree and adjacent plants. She also mentioned trophobionts sucking on AG epiphytes, but she stressed the high significance of the phorophytes as food plants for hemipterans tended by AG ants. Principally, the phorophyte seems to be the more important and more suitable food source for large ant colonies because epiphytes will have to invest their restricted biomass and relatively small light-absorbing surface in plant growth and reproduction.[69] I suppose that there is no strong selective advantage for an epiphytic plant to provide ants with nutrients.

8.3. Evolution of palaeotropical ant-gardens

AGs represent one of the most complex asymmetric mutualistic associations (Hölldobler and Wilson, 1990), making the assessment of possible evolutionary pathways difficult: Ant and epiphyte species interact in many combinations. It is difficult to find patterns of specificity because many factors influence the distribution of both partners in different habitats and on different host trees (Chapter 5, p. 94 ff.). Additional organisms play key-roles in the interaction. Competition of the epiphytes for ant partners, and vice versa of the ants for specific epiphyte partners, is difficult to assess. And – finally – the relative benefit each partner has for the other

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[68] also see Chapter 4.2.2, p. 84 ff. and Chapter 7.2.2, p. 127

[69] also see Chapter 4.2.2, p. 88 f.

may change depending on the environment. Though most of the epiphytes may – from time to time – be found growing outside AGs, the associations generally seem to be highly obligatory for both ‘guilds’ involved. This must be regarded as an outcome of the mutualistic interaction.

As a first evolutionary indication, the high number of ant and plant taxa participating in AGs suggest that these associations have a multiple evolutionary origin. Ant-epiphyte interactions might have supported ant radiation and epiphyte radiation in one or the other case (Chapter 6.2.2, p. 109 ff.).

Secondly, AG systems have developed from loose, facultative ant-epiphyte interactions. Such interactions are still found in some neotropical species (Davidson and Epstein, 1989). Even in myrmecophytic rubiaceous epiphytes, the whole spectrum from loose and facultative interactions to highly specialized, obligate ant-epiphyte associations exists (Maeyama et al., 1997).

Thirdly, the use of plant material for nest or shelter construction is one of the main predispositions for the development of AGs. Many tropical arboricolous ant species a) construct carton shelters for hemipteran trophobionts, or b) cover their main trails with carton-runways, or c) manipulate cavities and crevices with carton material. In the latter case, only seed-retrieval to the nest has to occur in order to establish a simple AG. This applied in this study to the ponerine *Diacamma* sp$_{\mathrm{KfmA}}$111 (Chapter 4.1.2.4, p. 73 ff. and Chapter 4.2.1, p. 78 ff.). However, the other two cases might also lead to AG associations. Workers may have started to reside in carton shelters because this helped to monopolize food sources and extended nesting space. As a next step, they may have taken brood to their shelters, thus further reducing energy costs (Davidson, 1997). This step resulted in simple carton nests into which ants could again retrieve seeds, thus establishing simple AGs. The development of selective seed retrieval can be rated as the main factor accounting for a more reliable type of AG association (Davidson and Epstein, 1989). This factor has already been discussed in Chapter 7.2.2 (p. 133 ff.). However, other traits of ant and epiphyte partners may have been necessary for the interaction, or may have co-evolved during the interaction. These aspects will be discussed in the following paragraphs.

One major question which always arises in connection with ant-plant mutualism is whether the involved species have co-evolved. Due to the relatively loose character of most plant-animal associations (Schemske, 1983; Howe, 1984; Jordano, 1987; Davidson et al., 1991), co-evolution in a strict sense[70] will not be considered. The discussion will concentrate on the question whether a) the partners have evolved special traits in response to the association (diffuse co-evolution; Janzen, 1980), or whether b) they achieved their beneficial association by chance

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[70] = specific reciprocal evolutionary responses of each partner to the other (Janzen, 1980); in order to prove co-evolution sensu stricto, cladistic methods are necessary in addition to ecological data (McKey, 1991).

only due to suitable predispositions and similar ecological preferences. The latter case also includes the one-sided exploitation of a certain trait of one partner by the other.

In order to find indications for one or the other scenario, it will be necessary to identify characteristics of ants and epiphytes which are indispensable or at least highly beneficial for the association. In 'diffuse' co-evolution, a certain trait of partner 1 is advantageous only in combination with a certain trait of partner 2. Comparison with taxonomically related non-AG species might be especially helpful in this approach. The discussion will be rather speculative in most parts because no systematic investigations have been performed so far.

A general assumption, although trivial, will be stated here again before the start of any detailed discussion: None of the partners is 'interested' in increasing its mutualistic partner's fitness. Each organism participating in whatever interaction is exclusively selected for its own 'fitness'. This is naturally compatible with the fact that increasing fitness of a certain organism may sometimes also benefit the fitness of the other.

8.3.1. Ants

AG ants occur in several of the most species-rich ant genera: *Camponotus*, *Crematogaster*, *Pheidole* and *Azteca*. Within these genera, only very few species are confined to AGs. This suggests that the relevant species should show some special traits as compared to their congeners. The following traits are common to most AG ants. They have been rated as beneficial for an association with epiphytes either in earlier studies on neotropical AGs, or in view of data obtained in this study:

1. Selective retrieval of epiphyte seeds
2. Construction of nutrient-rich carton material
3. 'Dominance': polydomy, aggressiveness, and individual-rich colonies
4. Use of plant resources as main food source
5. Preference for sun-exposed habitats

<u>Selective retrieval of epiphyte seeds</u>

The selective retrieval of epiphyte seeds has already been discussed in detail in Chapter 7 and will therefore not be repeated here. In all the scenarios discussed in Chapter 7.2.2 (p. 129 ff.), important predispositions were presumed. However, further adaptations in consequence of the association cannot be excluded.

<u>Construction of nutrient-rich carton material</u>

The construction of nutrient rich plant material is beneficial for the plants' nutritive demands. In the same context, the preferential storing of debris in rough-walled chambers of myrmecophytic *Hydnophytum* and *Myrmecodia* can be discussed.

First of all, carton construction itself has to be regarded as a predisposition for the development of AGs. Many tropical arboricolous ant species are capable of building carton shelters for trophobionts, carton runways or even carton nests (Sudd, 1977; Weissflog, 2001). However, this carton material is sometimes paper-like and unsuitable for epiphyte growth (Davidson and Epstein, 1989; pers. obs.). Carton quality varies depending on AG ant species: While some species (e.g. *Camponotus* sp$_{\text{KfmA}}$9, *Crematogaster* sp$_{\text{KfmA}}$200, *Philidris* sp$_{\text{KfmA}}$160 in this study; *Camponotus femoratus* in neotropical AGs (Davidson, 1988; Davidson and Epstein, 1989)) retrieve vertebrate feces and remains of prey insects into their carton nests or into chambers of domatia-providing epiphytes, others use almost exclusively plant fibers for carton construction (e.g. *Crematogaster* sp$_{\text{KfmA}}$18). Nutrient content seemed not to differ too much in these two types (Chapter 4.1.2.1, Table 4-6, p. 31). However, further studies are necessary to obtain reliable data here.

Davidson and Epstein (1989) discuss whether the retrieval of vertebrate feces should be regarded as special adaptation of the ants, i.e. whether it only is advantageous for the ants in relation to their plant partners. This is not the case, since many ant species relying on honeydew for a large part of their diet are attracted to mineral-rich substances and retrieve them to their nests (Davidson, 1988; Davidson and Epstein, 1989).

Janzen (1974) cited the selective storing of debris in rough walled chambers of *Myrmecodia* spp. and *Hydnophytum* spp. as evidence for highly specialized ant behavior. However, other explanations might be more likely. If this behavior were specialized, it would have had to develop convergently several times in different ant genera: Apart from the usual inhabitants of these ant-house epiphytes in heath forests, *Philidris* spp., *Dolichoderus* spp. (Maeyama et al., 1997) and *Camponotus* sp$_{\text{KfmA}}$240 inhabited the domatia of *Hydnophytum* spp. The same patterns of specific brood- / debris-storage were found when the tubers were dissected.

Thus, the explanation suggested by Davidson and Epstein (1989) seems most likely: Smooth-walled chambers are most suitable for the ant brood, while rough-walled chambers are too moist or inconvenient for some other reason. This idea is supported by the fact that the ants do not follow the suggested patterns strictly. When *Philidris* sp$_{\text{KfmA}}$160 colonies in a Borneon heath forest were dissected (Chapter 4.1.2.2, p. 52), brood was indeed seldom found in warted chambers, while debris was frequently stored in smooth-walled as well as in warted chambers.

Summarizing, the construction of nutrient-rich carton material/storing of nutrient-rich material in absorptive chambers is a predisposition rather than an adaptation.

Nevertheless, although all these predispositions existed, the proportion of nutrient-rich material included in the carton construction might have increased in response to the association with epiphytes. In some cases, ants might even prefer certain nest regions for including such debris because this is a good way to manipulate the direction of epiphyte root growth (Weissflog, 2001).

Dominance: polydomy, aggressiveness, and individual-rich colonies

Arboreal dominant ants have been defined as ants that a) are polydomous, b) defend territories aggressively, and c) form individual-rich colonies (Hölldobler and Wilson, 1990; Tobin, 1995). Further on, they monopolize food resources such as extrafloral nectaries and hemipteran trophobionts (Tobin, 1991, 1994; Davidson and Patrell-Kim, 1996; Orivel and Dejean, 1999a).

Polydomous nest structure occurs in many, but by no means all, AG associations. However, numerous other arboreal ant species are polycalic also, especially those with cavity-independent nests (Weissflog, 2001). Polydomous nests are a necessity for many arboreal ants because the limited size of one single nest also restricts colony size. Thus, polydomy is a beneficial predisposition rather than an adaptation in many ant species.

Since AG ants are enabled to construct larger nests with the help of epiphytes, selective pressure for polydomy even seems to be low at first glance. However, if a monodomous ant species with relatively small colonies starts an association with epiphytes, this might favor larger colonies. That, in turn, might induce a larger demand for nutrients. In a three-dimensional environment, it might often be easier to monopolize food sources when inhabiting more than one nest. Thus, again, polydomous ants might have been especially suitable partners for the establishment of AG associations, but previously monodomous ants might also have developed polydomy in consequence of their interaction with epiphytes.

Colony size has already been touched on in the previous paragraph, because it is closely related to polydomy in arboreal species. The same considerations also hold for aggressiveness. It might be a prerequisite of an already dominant, territorial species, but it also might be a consequence of the association. Altogether, AG associations can support the development of dominant species under certain circumstances, but dominance is neither a compelling predisposition nor an inevitable consequence.

Use of plant resources as main food source

At least all the more advanced AG ants (Chapter 4.2.1, p. 78) use plant sap as their main food source. This preference for liquid food requires certain morphological modifications: In many formicine and dolichoderine ants, the proventriculus is preceded by a tiny slit, passively damming food from entering the midgut (Eisner, 1957; Davidson and Patrell-Kim, 1996; Orivel and Dejean, 1999a). Eisner (1957) suggested that only small molecules could enter the midgut, so that these ants are disproportionally fuelled by liquid food. The same mechanism is found in the myrmicine genus *Crematogaster*, in which trophallaxis is unusually common as compared to other myrmicine ants (Eisner, 1957).

Most AG ant species in both geographical regions belong to Dolichoderinae, Formicinae or *Crematogaster*. Thus, this morphological trait can be regarded as favorable predisposition for the development of ant-epiphyte interactions. However, ponerine AG ants show that this trait, again, is not inevitable.

Preference for sun-exposed habitats

Many AG associations are predominantly found in sun-exposed habitats, and therefore this trait will be discussed here. Almost nothing is known about special behavioral, morphological or physiological adaptations of ants towards high temperature. Low temperature seems to be the more important problem for ants in general (Hölldobler and Wilson, 1990; Malsch, 2002). However, high temperature and direct irradiation are closely connected with desiccation even in tropical rain forests (Hölldobler and Wilson, 1990; Kaspari, 1993; pers. obs.).

In tree-crowns, ants will almost always find some shady pathways. The most exposed ant colonies, e.g. *Philidris* spp., rarely foraged on the surface but covered their main foraging trails with carton runways and tended their trophobionts underneath carton shelters. Ant brood is known to be especially vulnerable to temperature changes (Hölldobler and Wilson, 1990). However, since ant brood is not comb-restricted, as is the case in bees and wasps, ants can simply move their brood to the most convenient places at any time of the day. After heavy rain, when the nests were partly soaked, *Crematogaster* $\mathrm{sp}_{\mathrm{KfmA}}18$ was frequently observed to accumulate larvae outside the nests, on epiphyte leaves (pers. obs.).

Altogether, there is little indication for special adaptations to high temperature in AG associated ants. Epiphytes may be directly responsible for the ants' ability to survive even in such extreme habitats as heath forests, as they have been shown to mitigate microclimatic extremes (Stuntz et al., 1999; Stuntz, 2001). No evolutionary change in the ants themselves is visible here.

Summing up, there is no ant characteristic that can only be explained in the context of AG associations. Seed retrieval seems to be the most important trait distinguishing AG species from their congeners. All the other traits can be found in non-AG species also. Nevertheless, interactions with epiphytes might have influenced the development and shaping of one or the other trait in one or the other ant species.

8.3.2. Epiphytes

Like in the ants, very species-rich plant families and genera contribute to the diversity of AG epiphytes, and only some of the species in each of these groups are confined to AGs (exceptions in the Palaeotropis are the genera *Dischidia* and *Hoya* (Asclepiadaceae), and all genera in the subtribe Hydnophytinae (Rubiaceae))[71].

The following traits are common to several AG epiphytes. They have been rated as beneficial for an association with ants either in earlier studies on neotropical AGs, or due to data obtained in this study:

1. Seed compounds attractive to ants
2. Extensive root system
3. Provisioning of food resources
4. Resistance against hemipteran trophobionts
5. Autogamy
6. Preference for sun-exposed habitats

Seed compounds attractive to ants

Again, the discussion on the development of ant-attractive seed compounds will not be repeated here[72]. It has been shown that ants are attracted in different ways, and that several scenarios for the development of such ant attractants are conceivable.

Extensive root system

An extensive root system is sometimes rated as beneficial for the ants, because it might provide a good framework for the ant nests. This may be true in those cases in which the partner ants are capable of root manipulation (e.g. *Crematogaster* sp_{KfmA}18 and *Camponotus* sp_{KfmA}9 in this study). On the other hand, exaggerated root growth might limit nesting space in ant species unable to manipulate root growth (e.g. *Philidris* spp. and *Pheidole* sp_{KfmA}33 in this study). As long as epiphyte species are growing on nests of both types of ants, extension of the root system might therefore not be promoted at population level. Moreover, extended root growth does not only have an effect on the ants, but also affects the epiphytes themselves. Extended root growth compared to ‘green’ biomass produces a shifted ratio of ‘energy traps’ to ‘mineral traps’, relatively enlarging the mineral traps. This might be beneficial for epiphytes in general, because they grow in light-exposed situations, but mineral nutrients are usually relatively scarce.

A detailed analysis of the root growth of selected plant genera, comparing species restricted to AGs to those growing independently of AGs, might reveal whether the often presumed extended root growth in AG epiphytes exists at all.

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[71] see Chapter 6.2.2.2, p. 111 f., and Chapter 6.2.2.3, p. 113 f.

[72] see Chapter 7

In the rubiaceous ant-house epiphytes, absorptive chambers replace the absorptive function of the roots (Huxley, 1978; Rickson, 1979). The development of smooth-walled and rough-walled chambers is closely related to their association with ants (Benzing, 1990; Jebb, 1991). However, since the ants' behavioral response to this chamber dimorphism can be explained without evolutionary changes (s. above), this cannot be taken as evidence for co-evolution.

Provisioning of food resources

Neotropical AG epiphytes frequently produce nutritive rewards for their partner ants. These seem, however, not to be sufficient for the demands of a dominant ant colony (Davidson and Epstein, 1989). All the ant species, in palaeotropical as well as in neotropical AGs, use additional food sources. Kleinfeldt's (1978) reports on *Crematogaster longispina*, almost exclusively feeding on extrafloral nectar provided by its partner plant *Codonanthe crassifolia*, seem to be contradictory at first glance. However, since Kleinfeldt also describes that *Crematogaster longispina* was not a dominant species[73] in her study areas, the inconsistency is at least partly resolved.

Most palaeotropical AG epiphytes provide little or no food rewards at all. Thus, food rewards are certainly not an inevitable predisposition for AG epiphytes.

Regarding different types of food rewards, nutritive seed appendages may play a role in mediating seed attractiveness (Chapter 7.2.2, p. 129 ff.). A second type comprises those food sources that are not ant-specific, i.e. fruit pulp or floral nectar. As argued above (Chapter 7.2.2, p. 129 ff.), a sweet fruit pulp might be responsible for seed attractiveness in some cases.

Floral nectar might replace extrafloral nectaries (EFN) (Chapter 4.2.2, p. 84), and, if so, has to be discussed together with other ant-specific food rewards: EFN and food bodies. EFN exist in many terricolous and epiphytic plant species, including altogether at least 68 plant families (Elias, 1983). Fiala and Linsenmair (1995) surveyed the occurrence of EFN-plants in Pasoh Forest Reserve (Peninsular Malaysia). Here, 12.3 % of all plant species bore EFN. Food bodies are much less common, but they also occur on a variety of plants often in combination with other ant attractive structures (EFN or domatia) (Beattie, 1985). Food bodies and EFN mediate ant attendance and are usually interpreted as adaptations for herbivore protection (Buckley, 1982; Beattie, 1985; Fiala and Maschwitz, 1995; Jolivet, 1996). Thus, neither food bodies nor EFN are restricted to AG epiphytes, and their presumed benefit is independent of basic AG interactions.

Davidson and Epstein (1989) suggest that these ant-specific food rewards might be some sort of 'appeasement strategy', ensuring that the respective epiphytes are not removed from the ant nests. However, this assumption seems to me to be unlikely, because a) small seedlings usually do not produce any food rewards, but the ants do nevertheless not remove them, and b) at least

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[73] but see: Davidson (1988)

palaeotropical AG epiphytes grow on the ant nests although they lack nutritional rewards in most cases. Moreover, *Crematogaster* (*Decacrema*) sp., an obligate plant-ant living in *Macaranga* sp., removed flower stalks even when these bore food bodies (Moog, 2002). This is an example illustrating that even food rewards are no protection against ants that are motivated to destruction.

Summing up, even ant-specific food rewards cannot be conclusively interpreted as special adaptations to AG associations, although the close association to ants in AGs may promote the production of such rewards.

Resistance against hemipteran trophobionts

These considerations on epiphyte-produced food resources for AG associations directly lead to a further trait of AG epiphytes: Palaeotropical AG epiphytes seemed to be highly resistant against hemipteran trophobionts. Except for a few pseudococcids sucking in the tubers of rubiaceous ant-house epiphytes, no hemipterans were ever found sucking on the AG epiphytes (Chapter 4.2.2, p. 88).

A second explanation for this phenomenon is also possible: The ants may have ‘learned’ not only not to tend any trophobionts on their epiphyte partners but possibly also even to remove them actively. However, this explanation seems to be much more unlikely than the ‘resistance-hypothesis’. This ‘resistance-hypothesis’ is further supported by the fact that poisonous substances are known to occur in some palaeotropical AG epiphytes, e.g. in all the asclepiads (latex). In neotropical AGs, hemipteran trophobionts are frequently tended on AG epiphytes (Davidson, 1988; Davidson and Epstein, 1989). Thus, ‘hemipteran resistance’ is not an absolutely necessary prerequisite for the development of AG associations. Almost nothing is known about herbivore resistance in epiphytes in general (Benzing, 1990), and therefore a comparison with non-AG epiphytes is not possible.

Autogamy

Autogamy has been reported in many neotropical AG epiphytes (Madison, 1979). At least facultative autogamy also occurs in several palaeotropical AG epiphytes, for example in *Dischidia nummularia* and *Aeschynanthus fecundus*. Nothing is known about the reproductive systems of most other palaeotropical AG epiphytes. Autogamy generally seems to be more widespread in epiphytes than in forest floor herbs (Gentry and Dodson, 1987). The predominance of autogamy in neotropical AG epiphytes has been explained by a potential conflict between aggressive ants and pollinators (Madison, 1979; Kleinfeldt, 1978). Conflicts of this type have been presumed several times in ant-plant associations, but there is no evidence that they exist in reality. For example, *Dischidia nummularia* is a facultative selfer, but its flowers are also visited by bees (pers. obs.; Liede and Ollerton, 2002). Furthermore, the flowers constantly produce high amounts of nectar, which is harvested by the associated ants and even interpreted as replacing EFNs in this plant (Chapter 4.2.2.1, p. 84 ff.). The same was observed in some *Hoya* species. However, since floral nectar production is usually a reward to pollinating insects, the ants could also be regarded as nectar thieves.

Another idea was that AGs occur in relatively resource poor habitats, in which only few pollinators live (Madison, 1979). However, such a scenario could also result in highly specialized pollination systems, particularly since AG epiphytes are usually abundant in such habitats. Benzing (1990) suggests that homozygosity, resulting from autogamy, might be less problematic for AG epiphytes than for other epiphytes, because non-AG epiphytes have to accommodate to more diverse growing substrates. However, this assumption again is not supported by any systematic investigations. Reproductive strategies are complex and depend on many factors. It therefore seems to be questionable to discuss autogamy exclusively in response to ant association. Finally, it is not clear whether autogamy is really more common in AG epiphytes than in epiphytes in general. If there is an ant-related predominance of autogamy in AG epiphytes, it will with certainty have to be regarded as a predisposition.

Preference for sun-exposed habitats

The predominance of ant-epiphyte interactions in general in highly disturbed, open areas has received a great deal of attention in the literature (Janzen, 1974; Davidson and Epstein, 1989; Benzing, 1990; Engwald et al., 2000). AG epiphytes often show succulent features, display CAM metabolism and are relatively drought-resistant (e.g. Davidson and Epstein, 1989; Benzing, 1990). The special type of ant-house epiphytes, most abundant in disturbed, relatively dry habitats, might have been derived from highly drought-resistant ancestors with water-storing tissue, later used as nesting space for ants (e.g. Groom, 1893; Huxley, 1978; Chapter 6.2.2.2, p. 111 and Chapter 6.2.2.3, p. 113 f.). Again, the ability to live in extremely sun-exposed habitats is a predisposition rather than an adaptation.

However, AGs do not exclusively inhabit disturbed areas, but are also found in undisturbed rain forest. Thus, the unusual abundance of AG epiphytes in highly disturbed areas might be explained by less competition as compared to undisturbed forests. AG epiphytes generally display features enabling them to resist drought, but their association with ants may account for the fact that they can even live in such extreme habitats as heath forests. According to Jebb (1985), non-myrmecophytic Hydnophytinae are usually shade-tolerant and slow-growing, while their myrmecophytic congeners are heliophilic and fast-growing. The latter connection between sun-exposure and growth-speed might explain why heliophilic epiphytes are generally more suitable for ant associations: ‘ant-resources’, such as roots or nest-cavities, will develop faster in this type of epiphyte, promoting an association with ants (Benzing, 1990).

Summing up, most ant and epiphyte traits can be regarded as predispositions rather than as special developments in response to the association. The best candidate for diffuse co-evolution might be seed attractiveness, but other explanations are also possible here (Chapter 7.2.2, p. 129 ff.). Nevertheless, in the course of AG development, it is possible that key innovations lay in the evolution of specialized structures particularly in the plants, or in the pronounced development of certain plant traits. Most characteristics can be interpreted as predispositions, facilitating ant-epiphyte interactions.

8.4. Perspectives for future studies

After 100 years of AG research in tropical America, many questions still remain open. Almost every year at least one new article is published on some aspect of neotropical AGs.

AG systems in Southeast Asia are as numerous and complex as neotropical AGs, and research is almost 100 years behind. To give the prospects for further studies on palaeotropical ant-epiphyte interactions, I will explicitly name some important questions that have not been answered so far.

More intensive studies must be made on all partners of AG systems. While we are just beginning to understand ant-epiphyte interactions, we hardly understand the significance of most of the other partners. We know a very small amount about the importance of trophobionts and phorophytes for the nutrition of ant colonies, we have no idea about the significance of the fungi, and the name ‘parabiosis’ describes a phenomenon about which we know almost nothing.

Many questions also remain open even in the basic interactions between ants and epiphytes. For example, little is known about differences in the suitability of epiphytes as AG plants. Vice versa, there is hardly any information about how suitable the various ant species are as partners for epiphytes.

Apart from the aspects discussed in this study, further benefits of epiphytes and ants in their mutual association should be investigated. So far, the question of herbivore protection of the ants for either their epiphyte partners or their phorophyte has not been studied. Some authors speculate about possible antibiotic substances provided by epiphyte seeds or roots that might be used by the ants (Seidel et al., 1990; Dejean et al., 2000). Here, further research is needed both in neotropical as well as in palaeotropical regions.

Myrmecochory in tropical canopies seems to be highly important for epiphyte establishment in Southeast Asia, but the factors accounting for selective seed retrieval are poorly understood. Studies on carrying behavior releasing compounds in the seeds of palaeotropical AG epiphytes, in comparison with neotropical epiphytic and terricolous myrmecochores worldwide, will be one of my main future topics.

The present study might also serve as a basis for future investigations on the importance of AGs for the ecosystem ‘tree-crown’, and for tropical canopy ecology in general. There is some evidence that AG systems play key roles as microhabitats for many organisms, but the significance for species richness and ecosystem balance in tropical rain forest canopies requires further studies.

Last but not least, it would be highly interesting to study the evolutionary development of the different types of AG systems, and to discuss this aspect with particular reference to ant behavior, characteristics of the epiphytes, and habitat criteria. The evolutionary discussion in this thesis revealed that comparative studies on non-AG congeners of ants and epiphytes are badly needed.

Evolution of ant-epiphyte associations not only occurred independently in the different taxa, but may also have had a multiple origin even within some ant as well as plant genera. Levels of interdependence between ants and epiphytes vary greatly, including the whole range from occasional and more or less random associations to highly specific mutualisms and possibly also parasitism. Ant-epiphyte interactions might thus be good models for studying general evolutionary aspects of interspecific associations.

9. Summary

For palaeotropical regions, only a few anecdotal reports had been published on the existence of ‘ant-gardens’ before this study started. As opposed to this, ‘ant-house epiphytes’ (i.e. domatia-bearing epiphytes) were reported to be highly abundant in Southeast Asia and were presumed to be a second type of ant-epiphyte interaction. In the much better studied neotropical regions the situation seemed to be the reverse: Many reports on AGs in contrast to very few reports on ant-house epiphytes. In this study, I have presented extensive data which may help towards a better understanding of the ‘Southeast Asian part’ of this ‘ant-epiphyte puzzle’.

In Peninsular Malaysia, Borneo, Java, and Southern Thailand, a great variety of formerly unknown AG systems were discovered. 18 ant species (from 5 genera, 4 subfamilies) were identified as true AG ants, i.e. these ants actively retrieved seeds of certain epiphyte species into their carton nests. Another 49 ant species inhabited AGs as secondary, opportunistic settlers. On the epiphyte side, 84 plant species were found growing on AGs, 51 (19 genera, 12 families) of which were probably true AG epiphytes, i.e. ants retrieved the seeds to their arboreal carton nests, on which the epiphytes were then cultivated. Most of the epiphyte flora of lowland forests in Peninsular Malaysia (except for ferns, orchids and facultative epiphytes) seemed to be totally dependent on ants for their establishment in the canopy. Together with the high number of opportunistic AG inhabitants (ants, epiphytes, and many arthropod guests), these facts suggest that AGs function as pioneers in the canopy of Southeast Asian rain forests. Moreover, AG-associations might even have accounted for the unusual species richness in the epiphyte genera *Dischidia*, *Hoya* (Asclepiadaceae), *Myrmecodia*, and *Hydnophytum* (Rubiaceae).

The definition of the term ant-garden only describes the basic interactions. In the ant-garden associations investigated in this study, interactions going beyond these basic ones varied depending on ant and epiphyte species. Ant-gardens initiated by *Diacamma* sp$_{\text{KfmA}}$111 were regarded as the ‘most primitive’ type, because this ponerine was totally dependent on preformed cavities for nest establishment, did not tend any trophobionts, and was the least selective in its seed-retrieving behavior. On the other end of the scale, *Crematogaster* sp$_{\text{KfmA}}$18 and *Camponotus* sp$_{\text{KfmA}}$9 were rated as ‘most advanced’ because both lived in free (i.e. cavity-independent) AGs, tended trophobionts underneath their nests, were associated with a couple of other organisms, and were highly selective in their seed-retrieving behavior. Moreover, *Camponotus* sp$_{\text{KfmA}}$9 occurred preferentially with one single epiphyte species, *Hoya elliptica* (Asclepiadaceae), and *Crematogaster* sp$_{\text{KfmA}}$18 was specialized on some species of giant bamboo as phorophyte.

Philidris sp$_{\text{KfmA}}$160, which occupied a medium position in relation to the other AGs was particularly interesting for several reasons. This ant species was mainly associated with ant-house epiphytes and occurred in the heath forests of Borneo. However, the major part of the colonies, including the queen, was located underneath carton structures near the surface of the host tree and not inside the domatia of the associated plants. Moreover, very young *Philidris* sp$_{\text{KfmA}}$160 colonies had only small seedlings growing on their carton nests. The ant workers actively retrieved the seeds of their epiphyte partners into the nests. These results indicate that associations with ant-house epiphytes must be regarded as a special case of ant-gardens. I therefore suggest using the term ‘ant-house’ only to describe the epiphytes, but not to describe the association, and to include this type of association in the group of AGs.

Strict species-specificity never occurred, but some epiphytes showed great preference for growing on the nests of certain ant species, while others occurred over a wider range. Vice versa, most ant species had several epiphytes growing on their nests, while others were mostly found with one or very few epiphyte species. These patterns were shown to be the effect of different factors, including common microclimatic preferences of ants and epiphytes, interspecific competition of epiphytes, and selective seed retrieval of AG ants.

The main behavioral trait responsible for the establishment of AGs was the selectivity shown by the ants in the epiphyte seeds they carried. However, details of the mechanisms, i.e. what characteristics of the seeds are important and what motivates the ants to retrieve them, varied widely. In many cases, seed compounds located on the surface triggered carrying behavior. Detailed experimental investigations combined with literature data from the two other known ‘myrmecochory systems’, terricolous myrmecochores and neotropical AGs, suggested that myrmecochory is frequently triggered by a two-stage system. One relatively unspecific compound (or a combination of such compounds) constitutes the basic attractiveness for a number of ant species. Other seed characteristics (elaiosomes, mechanical properties, other surface-compounds) modulate this basic signal, accounting for species-specific preferences of ants towards certain plant species.

A comparison of AGs in Southeast Asia and the neotropics shows that the numbers of AG ant and epiphyte species in each case are almost equal. Southeast Asian AG epiphytes might even turn out to outnumber the neotropical ones. Thus, not only was it possible to break down the distinction between ant-house and AG associations, but also to show that AGs in Southeast Asia are present in such high diversity and abundance as to diminish the apparent contrast between the two biogeographical regions yet further. These data help to solve at least the Southeast Asian part of the ‘ant-epiphyte puzzle’.

10. Ausführliche Zusammenfassung

Einleitung

Der Kronenraum tropischer Regenwälder gehört zu den noch immer relativ wenig erforschten Lebensräumen der Erde, auch wenn neue Zugangstechniken in den letzten Jahrzehnten zahlreiche Studien ermöglicht haben. Ein Kennzeichen tropischer Wälder im Gegensatz zu den Wäldern gemäßigter Breiten ist das Vorkommen von epiphytischen Gefäßpflanzen in großer Artenzahl und Abundanz. Insgesamt sind ca. 10 % aller Gefäßpflanzenarten Epiphyten, in manchen tropischen Habitaten leben bis zu 50 % aller vorkommenden Pflanzenarten epiphytisch. Ein weiteres Charakteristikum ist die Allgegenwart von Ameisen, die in vielen Gebieten einen vergleichsweise großen Teil der Biomasse und Individuenzahl arboricoler Insekten stellen. Weder die Häufigkeit der Ameisen in den Baumkronen noch die der Epiphyten ist selbstverständlich: Für beide Gruppen bringt ihr „erhöhter” Lebensraum auch Probleme mit sich. Ameisen sind als soziale Insekten auf einen geschützten, dauerhaften Nistraum angewiesen, der im Kronenraum relativ selten ist. Epiphytische Gefäßpflanzen brauchen ein geeignetes Wuchssubstrat, ihre Samen (oder Sporen) müssen auf einen solchen Platz hoch über dem Erdboden gelangen, die Versorgung mit Wasser und Mineralsalzen ist schwieriger als am Boden.

Ameisen und Epiphyten sind in der Lage, Eigenschaften der jeweils anderen Gruppe auszunutzen, um einige der genannten Probleme zu lösen. Hieraus ist eine Fülle verschiedener, häufig mutualistischer, Assoziationen hervorgegangen.

Ein bestimmter Assoziationstyp, die sogenannten Ameisengärten, war bislang im wesentlichen aus der Neotropis bekannt. In Ameisengartenassoziationen tragen Ameisen Samen bestimmter Epiphyten in ihre Kartonnester ein. Die Epiphyten wachsen dort und stabilisieren die Nester mit ihren Wurzeln. Ein zweiter Typ von Ameisen-Epiphyten-Assoziationen, die „echten”, domatientragenden Ameisenepiphyten der Palaeotropis, wurde den Ameisengärten gegenübergestellt (z.B. *Dischidia major* (Asclepiadaceae); *Myrmecodia* spp. und *Hydnophytum* spp. (Rubiaceae). Es war nicht klar, warum Ameisengärten in der Palaeotropis anscheinend durch „echte” Ameisenepiphyten ersetzt werden, während letztere in der Neotropis nur in wenigen Arten vorkommen. Ein Ziel dieser Arbeit war, Ameisen-Epiphyten-Assoziationen in Südostasien, und hier besonders auf der Malayischen Halbinsel, Borneo und Java, in ihrer Vielfalt zu erfassen und zu beschreiben. Der Qualität mutualistischer Interaktionen kam hierbei besondere Aufmerksamkeit zu. Ein weiterer Schwerpunkt beschäftigte sich mit dem Samentrageverhalten arboricoler Ameisen, das sich als konstitutiv für alle regelmäßigen Ameisen-Epiphyten-Assoziationen erwies.

Die Vielfalt südostasiatischer Ameisen-Epiphyten-Assoziationen

Insgesamt wurden 743 Ameisenkolonien (67 Arten, 19 Gattungen, 5 Unterfamilien) in Assoziation mit Epiphyten gefunden. Es konnte gezeigt werden, dass in Südostasien eine Vielzahl von Ameisen-Epiphyten-Assoziationen der oben genannten Definition eines Ameisengartens entspricht. Auf Seiten der Ameisen waren insgesamt 18 Arten (499 Kolonien) aus fünf Gattungen und den vier Unterfamilien Dolichoderinae, Formicinae, Myrmicinae und Ponerinae als aktive Ameisengarten-Initiatoren beteiligt. Auf Seiten der Epiphyten wurden 2048 Pflanzen (84 Arten, 27 Gattungen, 16 Familien) gesammelt. Von diesen waren ca. 50 Arten obligatorisch mit Ameisen assoziiert; ihre Samen wurden von verschiedenen Ameisenarten in ihre Kartonnester eingetragen. Um einen Überblick über die systematische und ökologische Vielfalt der südostasiatischen Ameisengärten zu geben, wurden neun Ameisengarten-Assoziationen detailliert beschrieben.

Die Definition eines Ameisengartens umfasst lediglich die grundlegenden Interaktionen zwischen Ameisen und Epiphyten. Über diese basalen Interaktionen hinaus existieren große Unterschiede zwischen verschiedenen Ameisengärten, die vor allem von den beteiligten Ameisen abzuhängen scheinen. Einige dieser Unterschiede wurden als Kriterien herangezogen, um die gefundenen Ameisengärten zu klassifizieren und einen „Ameisengarten-Index” zu definieren, dessen numerischer Wert zwischen 1 und 4 den Entwicklungsgrad einer Ameisengartenassoziation im Vergleich zu den anderen beschreibt. Wichtigste Kriterien waren 1) die Abhängigkeit der Ameisen von bereits vorhandenen Höhlungen als Nistraum, 2) die Assoziation mit Trophobionten und 3) Faktoren, die das Samentrageverhalten auslösten. Als weniger wichtige Faktoren wurden weiterhin 1) die Anzahl zusätzlicher Partner im System (beispielsweise Pilze oder parabiotische Ameisen), 2) die Spezialisierung auf einen bestimmten Trägerbaum und 3) der Spezialisierungsgrad auf eine bestimmte Epiphytenart berücksichtigt.

Die einfachste hier beschriebene Form eines Ameisengartens wurde von der Ponerine *Diacamma* sp$_{\text{KfmA}}$111 gegründet. Die kleinen Kolonien waren vollständig auf vorgeformte Höhlungen in ihrem Wirtsbaum angewiesen, sie verkleinerten den Eingangsbereich mit Kartonstrukturen und versahen ihn mit Vorbauten, die in seltenen Fällen temporär auch als zusätzlicher Nistraum verwendet wurden. Auf diesen Kartonstrukturen wuchsen Epiphyten verschiedener, hauptsächlich primär vogelverbreiteter Arten. *Diacamma* sp$_{\text{KfmA}}$111 besuchte keine Trophobionten. Das Samentrageverhalten wurde bei den vogelverbreiteten Epiphytenarten offenbar durch Nahrung (süßes Fruchtfleisch oder mineralstoffhaltige Bestandteile des Vogelkots) ausgelöst, bei primär windverbreiteten Epiphyten durch ihre Eignung als Baumaterial (durch fädige Anhänge) – es war damit sehr wenig spezialisiert.

Den höchsten Ameisengarten-Index erreichten *Camponotus* sp$_{\text{KfmA}}$9 (Formicinae) und *Crematogaster* sp$_{\text{KfmA}}$18 (Myrmicinae). Beide waren in der Lage, freie Ameisengärten unabhängig von vorhandenen Höhlungen zu etablieren. Sie hielten Trophobionten unter ihren Nestern, und in ihren Nestern kam Pilzbewuchs vor. Eine Besonderheit bei *Crematogaster* sp$_{\text{KfmA}}$18 war ihre Spezialisierung auf wenige baumförmige Bambusarten als Trägerpflanzen (insbesondere *Gigantochloa scortechinii*). *Camponotus* sp$_{\text{KfmA}}$9 zeigte eine starke Präferenz für eine einzige Epiphytenart, *Hoya elliptica* (Asclepiadaceae). Diese Spezialisierung wurde von einem hoch spezialisierten Samentrageverhalten begleitet: Neben chemischen Auslösern war hier die Größe des Samens zusätzlich entscheidend. Die gleiche Selektivität fand sich auch bei *Camponotus* sp$_{\text{KfmA}}$240 und der häufig mit diesen beiden Arten parabiotisch vorkommenden *Crematogaster* sp$_{\text{KfmA}}$21.

Von den zwischen diesen Extremen liegenden Ameisengartenassoziationen war die Dolichoderine *Philidris* sp$_{\text{KfmA}}$160 besonders interessant. Sie kam in den Heidewäldern Borneos vor und war dort vorwiegend mit Domatien tragenden Ameisenepiphyten assoziiert. Allerdings befand sich nur ein kleinerer Teil der Kolonie in den Domatien, der größere Teil, der auch die Königin einschloss, nistete in Kartonbauten, die unter Ausnutzung von Strukturen des Wirtsbaumes geschützte Räume herstellten. Da sowohl der gegenseitige Nutzen beider Partner füreinander als auch die ontogenetische Entwicklung exakt der von Ameisengärten entspricht, wurde vorgeschlagen, den Begriff der „echten“ Ameisenepiphyten nur noch für die Beschreibung dieser Pflanzen, nicht aber zur Beschreibung der Assoziation zu verwenden. Diese sollte in die Gruppe der Ameisengärten integriert werden.

Mutualistische Interaktionen

Trotz der Unterschiede in der Ausgestaltung der verschiedenen Ameisengärten waren die prinzipiellen mutualistischen Interaktionen jeweils ähnlich.

Die Ameisen verbreiteten die Samen der mit ihnen assoziierten Epiphyten in ihre Kartonnester. Diese erwiesen sich als nährstoffreich (Testgrößen: Phosphat, Nitrat, Ammonium) im Vergleich zu den Kartonnestern von Ameisen, die nicht mit Epiphyten assoziiert waren, wie auch im Vergleich zu Waldboden oder Rindensubstrat. Makroskopisch unterschied sich die Zusammensetzung des Kartons verschiedener Ameisengartenameisen deutlich: Während beispielsweise *Camponotus* sp$_{\text{KfmA}}$9 und *Crematogaster* sp$_{\text{KfmA}}$200 zahlreiche Cuticulareste von Beuteinsekten und toten Koloniemitgliedern (insbesondere Köpfe) in ihren Karton einbauten, bestanden die Nester von *Crematogaster* sp$_{\text{KfmA}}$18 fast ausschließlich aus Pflanzenfasern.

Prinzipiell waren alle untersuchten Nester in der Lage, Wasser zu speichern. Die Wasserspeicherkapazität variierte zwischen 1,9 (*Diacamma* sp$_{\text{KfmA}}$111) und 5,6 (*Camponotus* sp$_{\text{KfmA}}$9). Selbst eine geringe Wasserspeicherkapazität kann für die assoziierten Epiphyten eine überlebenswichtige Funktion haben. Dies gilt vor allem für Keimlinge, die besonders anfällig gegen temporäre Trockenheit sind, weil sie noch keine xeromorphen Strukturen ausgebildet haben.

In Analogie zu vielen terricolen Ameisen-Pflanzen-Assoziationen könnte Herbivorieschutz als Nutzeffekt der Ameisen für ihre epiphytischen Partner angenommen werden. Zu diesem Aspekt liegen bislang keine systematischen Untersuchungen vor, die meisten Epiphyten besitzen wohl einen ameisenunabhängigen, mechanischen und/oder chemischen Schutz. Dennoch lässt die hohe Aggressivität einiger Ameisengartenameisen einen gewissen Schutzeffekt vermuten.

Der Nutzen der Epiphyten für die Ameisen bezieht sich vorwiegend auf die Erweiterung des Nistraumes. „Echte“ Ameisenepiphyten stellen trockene, geschützte Hohlräume in Form ihrer Domatien bereit, Ameisengartenepiphyten stabilisieren die Nester der Ameisen, tragen durch Transpiration zum Trocknen der Nester bei und bieten Schutz vor extremen Witterungsbedingungen, in dem ihre Blätter die Nester „beschatten“. Einige Epiphyten produzieren zusätzlich in geringem Umfang Nahrung für ihre Partnerameisen. Vertreter der beiden Asclepiadaceen-Gattungen *Dischidia* und *Hoya* beispielsweise zeigten eine außergewöhnlich reichliche florale Nektarproduktion, der Nektar wurde von den Ameisen gesammelt. Die Ameisen konsumierten auch das süße Fruchtfleisch der Früchte primär vogelverbreiteter Pflanzen. All diese Beiträge zur Ameisenernährung sind allerdings nicht ausreichend für die Kolonieernährung. Im Bereich der Nahrung ist der eigentliche Nutzen der Epiphyten für ihre Ameisen der, dass sie ihnen ermöglichen, große (polydome) Kolonien zu bilden. Damit werden die Ameisen befähigt, ergiebigere Nahrungsquellen wie Trophobionten und extraflorale Nektarien im Kronenraum zu monopolisieren.

Die vorangegangenen Überlegungen leiten direkt zum Nutzen des Wirtsbaumes für die Assoziation über. Neben dem rein mechanischen Tragen bilden sie in vielen Systemen indirekt die Hauptnahrungsquelle, weil die Ameisen zahlreiche Trophobionten (insbesondere Pseudococcidae, aber auch Coccidae, Aphidae, Membracidae und Heteroptera) an ihnen besuchen. Es gibt bislang keine Untersuchungen darüber, ob die Ameisen einen Schutzeffekt für ihre Wirtsbäume haben, und damit eventuell auch zwischen Ameisen und Wirtsbaum eine mutualistische Assoziation vorstellbar ist. Es ist daher auch möglich, dass Ameisengärten die Ressourcen ihres Wirtsbaumes einseitig ausnutzen und daher eher als Parasiten zu bezeichnen wären.

Neben Ameisen, Epiphyten, Wirtsbaum und Trophobionten tragen weitere Organismen (Pilze, Parabiosepartner, Gäste) zusätzlich zur Komplexität der Systeme bei.

Artspezifische Präferenzen

Auch wenn alle Ameisengartenameisen mit mehreren Epiphytenarten assoziiert waren, und umgekehrt auch alle Epiphytenarten auf den Nestern mehrerer Ameisenarten gefunden wurden, so gab es doch einige artspezifische Präferenzen. Diese müssen jedoch nicht zwangsläufig auf ein Wahlverhalten der Ameisen (bezüglich der Epiphytensamen) zurückzuführen sein. Vielmehr könnten auch gemeinsame Habitatpräferenzen zum Aufeinandertreffen bestimmter Artzusammensetzungen führen. Als Parameter zur Aufklärung solcher Muster wurden Temperaturdaten an den Nestern verschiedener sympatrisch vorkommender Ameisenarten aufgezeichnet. Absolute und relative Besiedlungshöhe im Wirtsbaum repräsentierten zahlreiche weitere Faktoren, wie z.B. Sonneneinstrahlung, Nährstoffmenge aus am Stamm herablaufendem Regenwasser, CO_2-Konzentration etc. Die Temperaturdaten ergaben keine signifikanten Unterschiede zwischen den verschiedenen Ameisenarten. Bei den Besiedlungshöhen ließen sich einige Muster erkennen, die zur Erklärung gemeinsamen Vorkommens von Ameisen und Epiphyten herangezogen werden konnten. So gab es beispielsweise einige Ameisen- und Epiphytenarten (z.B. *Crematogaster* sp_{KfmA}18 und *Dischidia nummularia*, *Aeschynanthus fecundus*; *Philidris* sp_{KfmA}160 und *Hydnophytum formicarium*) die sehr exponierte Standorte bevorzugten. Andererseits konnte die besonders spezifische Assoziation zwischen *Camponotus* sp_{KfmA}9 und *Hoya elliptica* nicht allein durch mikroklimatische Faktoren erklärt werden, denn weder absolute noch relative Aufwuchshöhe waren eng definiert, und viele andere Ameisen- und Epiphytenarten kamen sympatrisch in gleicher Lage vor. Hier schien das hochselektive Samentrageverhalten der Ameisen ein entscheidender Faktor zu sein. Bei *Diacamma* sp_{KfmA}111 fiel auf, dass insbesondere einige primär vogelverbreitete Epiphytenarten häufig waren, obwohl die Ameisen auch die Samen windverbreiteter Epiphytenarten eintrugen. Da sich die Nester von *Diacamma* an eher schattigen Standorten im Bereich von 0 - 3 m über dem Boden befanden, wurden die Verteilungsmuster hier als Effekte interspezifischer Konkurrenz zwischen den Epiphyten, im Endeffekt also gemeinsamer Habitatpräferenz von Ameisen und Pflanzen, gedeutet.

Bedeutung von Ameisengärten für das Ökosystem Kronenraum

Bereits die Vielfalt der an Ameisen-Epiphyten-Assoziationen beteiligten Arten deutet auf eine große Bedeutung dieser Assoziationen für den Kronenraum tropischer Tieflandregenwälder hin.

Um die Bedeutung der Assoziation für die Epiphytenflora insgesamt besser einschätzen zu können, wurden die Epiphytenarten der malaysischen Halbinsel näher untersucht. Zunächst wurden gute „Kandidaten“ für eine Assoziation mit Ameisen gesucht, indem solche Arten, die „ameisenunabhängige“ Strategien zur Lösung ihrer Probleme verfolgten, identifiziert und aus der „Kandidatenliste“ gestrichen wurden. Hierzu gehörten Orchideen und Farne mit ihren staubfeinen Verbreitungseinheiten und der spezialisierten Ernährungsweise insbesondere der jungen Stadien. Fakultative Epiphyten könnten „notfalls“ auch auf dem Boden wachsen und sind für das Überleben auf Populationsniveau daher nicht in gleichem Maße auf gute Wuchssubstrate im Kronenraum angewiesen wie obligate Epiphyten. Auch montane Arten wurden nicht als Kandidaten angesehen, da die Lebensbedingungen durch eine andauernd hohe Feuchtigkeit und dicke Moospolster auf den Ästen als Aufwuchssubstrat nicht mit Tieflandregenwäldern vergleichbar sind. Mit dieser Methode blieben 55 Arten aus acht

Familien und zwölf Gattungen als potenzielle Kandidaten übrig, von denen 32 Arten, die sich auf alle Gattungen und Familien verteilten, tatsächlich als obligate Ameisengartenepiphyten identifiziert wurden. Für die übrigen 23 Arten liegen bislang noch keine Daten vor, so dass sich der Anteil noch erhöhen könnte. Dieses Ergebnis unterstreicht die besondere Bedeutung von Ameisengarten-Assoziationen für die Ansiedlung vieler Epiphyten im Kronenraum südostasiatischer Tieflandregenwälder. Auch aus den Gruppen, die nicht zu den „Kandidaten" gehörten, waren einige Vertreter obligate Ameisengartenepiphyten. Insgesamt konnte man Ameisengärten vielfach als „Pioniere in Baumkronen" ansehen, die nicht nur für die jeweiligen Mutualisten Lebensraum boten, sondern auch für zahlreiche weitere Ameisen- und Epiphytenarten sowie für Gäste aus diversen Arthropodengruppen und andere Organismen.

Betrachtet man die Liste der obligatorisch in Ameisengärten assoziierten Ameisen und Epiphyten, so fällt der besondere Artenreichtum in den Pflanzengattungen *Dischidia*, *Hoya* (Asclepiadaceae), *Hydnophytum* und *Myrmecodia* (Rubiaceae) auf, ebenso wie die Tatsache, dass offenbar alle Arten der Ameisengattung *Philidris* in Ameisengärten vorkommen. Auch wenn die vorliegende Arbeit sich nicht explizit mit dieser Frage beschäftigte, so ergeben sich unter Berücksichtigung von Literaturdaten doch Hinweise darauf, dass die Ameisengartenassoziation in Zusammenwirken mit den oft relativ extremen Lebensräumen, die Arten aufgrund der Assoziation besiedeln können, zur Radiation der genannten Gattungen zumindest beigetragen haben könnte.

Charakterisierung der Samenattraktivität

Ein besonderes Augenmerk dieser Arbeit lag auf der Charakterisierung derjenigen Sameneigenschaften, die für die Ameisen-Attraktivität verantwortlich sind. Bei den primär vogelverbreiteten Arten konnten Nährstoffe als attraktiv für eine große Zahl verschiedener Ameisenarten identifiziert werden. Bei den primär windverbreiteten Arten war die Situation komplizierter. Außer den Ameisengartenameisen trugen nur granivore Ameisen diese Samen ein, alle übrigen zeigten keine Reaktion. Oberflächennahe chemische Attraktivitätsstoffe konnten durch Versuchsreihen mit Extrakten von Samen ausgewählter Ameisengartenepiphyten aus verschiedenen Pflanzenfamilien als attraktiv für mehrere Ameisengartenameisen identifiziert werden. Offenbar trugen mehrere Substanzen zur Attraktivität bei, denn Versuche mit einzelnen Fraktionen (HPLC, LC) ergaben biologische Aktivität in mehreren, nicht immer benachbarten Fraktionen. Die Kombination aller Fraktionen zeigte, dass hierdurch synergistische Effekte erzielt werden konnten. Der Vergleich mit Literatur zu den zwei anderen bislang bekannten Myrmecochorie-Systemen, terricole Myrmecochoren und neotropische Ameisengärten, ergab Hinweise darauf, dass generell ein mindestens zweistufiges System zu vermuten ist: Ein relativ unspezifischer „Ameisenattraktionsstoff" (oder ein Gemisch solcher Substanzen) ist prinzipiell für das Samentragen verantwortlich, weitere Eigenschaften modulieren diese allgemeine Attraktivität und sind damit für artspezifische Präferenzen verantwortlich. Verschiedene evolutive Szenarien, die zu solchen Systemen führen könnten, wurden diskutiert. Für die unterschiedlichen beschriebenen Ameisengartensysteme schienen auch verschiedene dieser Szenarien wahrscheinlich.

Schlußbemerkungen

Zusammenfassend lässt sich durch die große Anzahl neu entdeckter Ameisengartensysteme in Südostasien festhalten, dass das scheinbare Ungleichgewicht zwischen Paläotropis und Neotropis in Bezug auf Ameisengärten aufgelöst ist – in beiden geografischen Räumen sind ungefähr gleich viele Ameisen- und Epiphytenarten beteiligt, es könnte nach den bisherigen Daten sogar zumindest bei den Epiphyten ein leichtes Übergewicht der südostasiatischen Artenzahlen geben.

Die Untersuchung verschiedener Charakteristika von Ameisengartenameisen und –epiphyten ergab keine Hinweise auf strenge Coevolution. Die meisten Eigenschaften konnten als Prädispositionen interpretiert werden. Zu vielen einzelnen Aspekten fehlten jedoch vergleichende Daten, so dass vielfach nicht zu entscheiden war, ob eine bestimmte Eigenschaft eine Besonderheit der entsprechenden Arten im Vergleich zu nahen Verwandten darstellte, ob solche Besonderheiten Prädispositionen waren, oder ob sie tatsächlich in Reaktion auf die Ameisengartenassoziation zu verstehen sind.

Die Ameisengärten der Neotropis werden seit ziemlich genau 100 Jahren umfassend untersucht, und trotzdem sind noch viele Fragen ungeklärt. Die Ameisengartenforschung in der Paläotropis muss daher einen erheblichen Rückstand aufholen. Mit dieser Dissertationsschrift soll ein erster Beitrag dazu geleistet werden.

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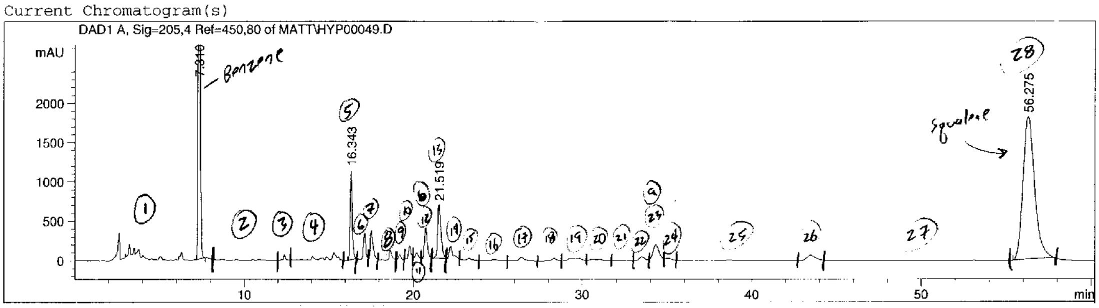
12. Appendix

12.1. Author index

12.2. Table Index

12.3. Figure Index

12.4. HPLC-Fractions



12.5. Parameters recorded for an inventory of ant-epiphyte interactions in Southeast Asia

Geographical data	
Country	
Place	county, nearest city, name of national park etc.
Exact locality	described on the basis of locally used reference points or places names
Altitude	Altimeter Casio Module 1282 GE, based on air pressure following ISA norm describing the relationship between altitude, air pressure and temperature; to minimize weather-effects, the altimeter was gauged whenever a point of known altitude was reached
Habitat	short description of habitat type (e.g. primary hill forest, plantation, road site, river bank, etc.)
Phorophyte	
Tree species	
Distance to nearest neighbor	estimated to 0.5 m
Shading from neighboring trees	estimated to five classes: 1: 0-20 %; 2: >20-40 %; 3: >40-60 %; 4: >60-80 %; 5: >80-100 %
Bark type	three classes were distinguished: rough, medium, smooth; special characteristics were noted, e.g. if the tree was constantly peeling
Diameter	diameter was measured with a custom and practice measurement tape; measured values were rounded to 0.5 cm
Height	height was either measured with a custom and practice measurement tape (rounded to 10 cm) or roughly estimated (to 0.5 m)
Trophobionts	trophobionts sucking on any places on the tree were collected
Nest	
Date of record	
Height on tree	height was either measured with a custom and practice measurement tape (rounded to 10 cm) or roughly estimated (to 0.5 m)
Position	the relative position in the tree was described (stem, main branch, side branch + knothole, branching)
Size	three dimensions of size were measured with a custom and practice measurement tape; measured values were rounded to 0.5 cm
Type	categories: AG, pure carton nest, AG + nest cavity in phorophyte, nest cavity in phorophyte
Shape	descriptive
Moss-coverage	categories: 0: 0 %; 1: >0-20 %; 2: >20-40 %; 3: >40-60 %: 4: >60-80 %; 5: >80-100 %
Enclosure of branch/stem	categories: 1: -90°; 2: >90-180°: 3: >180-270°; 4: >270-360°
Trophobionts	we recorded whether or not trophobionts were tended underneath the nests

Epiphytes	
Epiphyte species	known epiphytes were determined in the field, others were collected and herbarized, or grown for later determination (Chapter 3.2)
Detailed description	each species was described concerning morphological traits
Growth substrate	descriptive; pure bark, ant carton, debris accumulation etc.
Ant-domatia	yes/no; if yes, location of domatium
Degree of herbivory	degree of herbivory was estimated as leaf damage in six classes: 0%, > 0 – 20 %, > 20 – 40 %, > 40 – 60 %, > 60 – 80 %, > 80 – 100 %
Trophobionts	trophobionts sucking on any part of the epiphyte were collected
Ants	
Ant morphospecies	specimen were collected and determined to morphospecies (Chapter 3.2)
Detailed description	each species was described concerning morphological traits
Colony size	colony size was estimated in four classes: <100, 100-1000, 1001-10000, >10000; for some species, inhabitant numbers of several nests (workers, alates, brood, queens) were counted
Aggressiveness	five classes of aggressiveness were distinguished, (--, -, 0, +, ++), where the lowest class described species that did not show aggressive behavior even when their nest was destroyed, while ++ described species that reacted highly aggressively to mere contact with the tree on which they were living
Nest localization	exact description of where the nest was located (e.g. inside stem, between epiphyte roots, inside domatia, etc.)
Main food source	position of trophobionts, collection of retrieved food items, data from feeding experiments
Distribution of ant colony	(recorded per nest)
Alates	present / not present
Larvae	present / not present
Eggs	present / not present
Queen	present / not present
Workers	present / not present
Guests	all guests found in ant nests were collected

12.6. Wind-dispersed seeds used in seed-retrieving bioassays

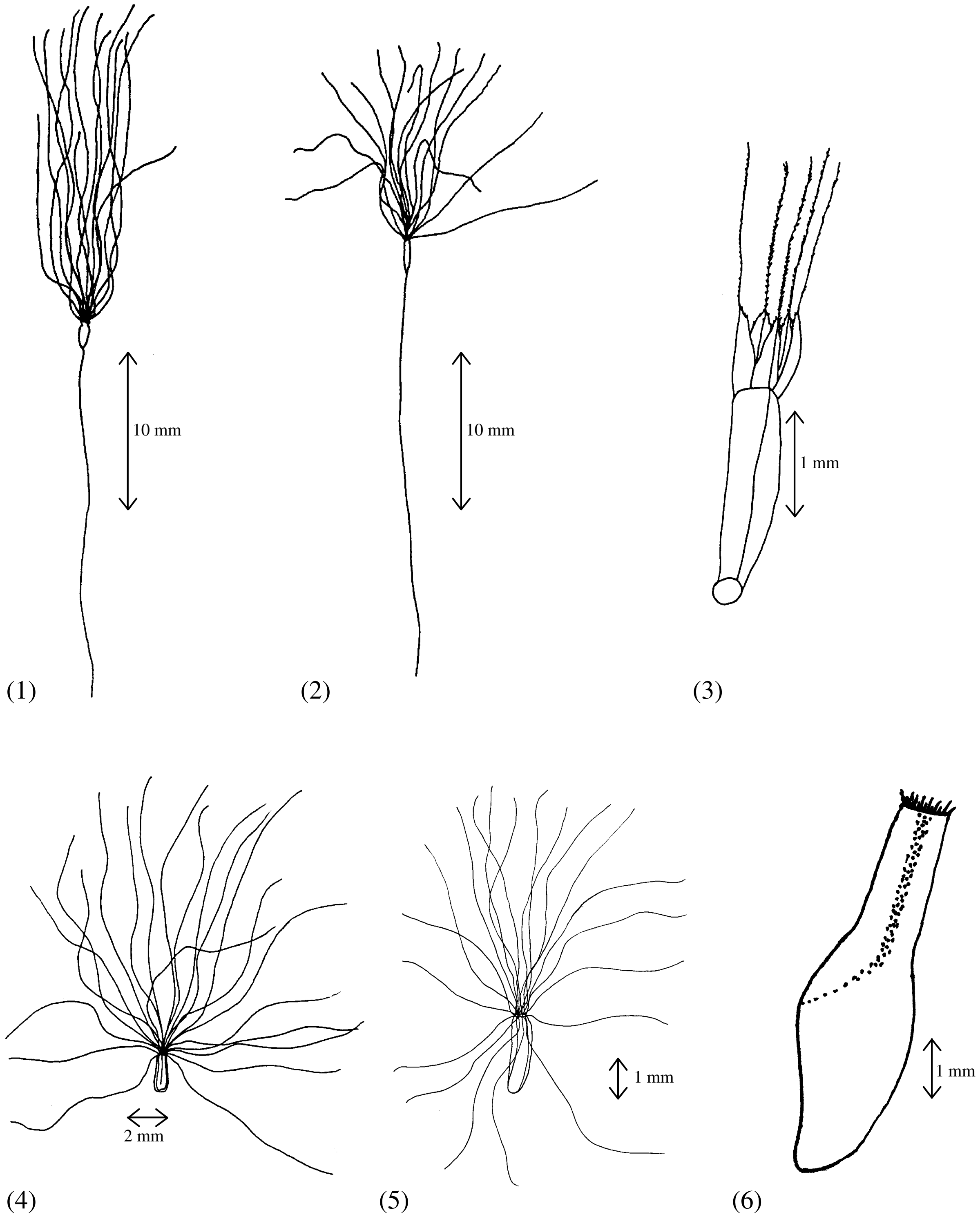


Figure 12-1: Wind-dispersed seeds used in seed-retrieving bioassays
(1) *Aeschynanthus albidus* (Gesneriaceae); (2) *Aeschynanthus fecundus* (Gesneriaceae); (3) *Ageratum conyzoides* (Asteraceae); (4) *Dischidia nummularia* (Asclepiadaceae); (5) *Emilia sonchifolia* (Asteraceae); (6) *Hoya elliptica* (Asclepiadaceae) (hairy appendage removed, each single hair may be up to 2.5 cm long)

12.7. Item list for bioassays

Table 12-1: List of items used in bioassays concerning seed-carrying behavior
Abbreviations: *D.=Dischidia*; *Ae.=Aeschynanthus*; *H.=Hoya*; *P.=Pachycentria*; LC=Liquid Chromatography; HPLC=High Pressure Liquid Chromatography

Nr.	Item	treatment
1	seed of *Aeschynanthus fecundus* (Gesneriaceae)	control
2	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in aqua dest. (1h)
3	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in acetone (1h)
4	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in chloroform (1h)
5	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in 50% ethanol (1h)
6	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in pentane (1h)
7	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in cyclohexane (1h)
8	seed of *Aeschynanthus fecundus* (Gesneriaceae)	7-14 days
9	seed of *Aeschynanthus fecundus* (Gesneriaceae)	15-21 days
10	seed of *Aeschynanthus fecundus* (Gesneriaceae)	22-28 days
11	seed of *Aeschynanthus fecundus* (Gesneriaceae)	> 28 days
12	seed of *Aeschynanthus fecundus* (Gesneriaceae)	hairy appendage removed
13	seed of *Aeschynanthus albidus* (Gesneriaceae)	control
14	seed of *Dischidia acutifolia* (Asclepiadaceae)	control
15	seed of *Dischidia nummularia* (Asclepiadaceae)	control
16	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in aqua dest. (1h)
17	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in acetone (1h)
18	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in chloroform (1h)
19	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in 50% ethanol (1h)
20	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in pentane (1h)
21	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in cyclohexane (1h)
22	seed of *Dischidia nummularia* (Asclepiadaceae)	7-14 days
23	seed of *Dischidia nummularia* (Asclepiadaceae)	15-21 days
24	seed of *Dischidia nummularia* (Asclepiadaceae)	22-28 days
25	seed of *Dischidia nummularia* (Asclepiadaceae)	> 28 days
26	wooden bait	control
27	seed of *Emilia sonchifolia* (Asteraceae)	control
28	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* acetone-extract (0,5ml/100 seeds / 60 seeds)
29	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* cyclohexane-extract (0,5ml/100 seeds / 60 seeds)
30	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* acetone+cyclohexane-extract (0,5ml/100 seeds / 60 seeds)
31	seed of *Aeschynanthus albidus* (Gesneriaceae)	hairy appendage removed
32	seed of *Aeschynanthus albidus* (Gesneriaceae)	washed in aqua. dest. (1h)
33	seed of *Aeschynanthus albidus* (Gesneriaceae)	washed in chloroform (1h)
34	seed of *Aeschynanthus albidus* (Gesneriaceae)	washed in acetone (1h)
35	seed of *Aeschynanthus albidus* (Gesneriaceae)	washed in 50% ethanol (1h)
36	seed of *Aeschynanthus albidus* (Gesneriaceae)	washed in pentane (1h)
37	seed of *Aeschynanthus albidus* (Gesneriaceae)	washed in cyclohexane (1h)
38	seed of *Aeschynanthus albidus* (Gesneriaceae)	7-14 days
39	seed of *Aeschynanthus albidus* (Gesneriaceae)	15-21 days
40	seed of *Aeschynanthus albidus* (Gesneriaceae)	22-28 days
41	seed of *Aeschynanthus albidus* (Gesneriaceae)	> 28 days
42	seed of *Aeschynanthus* sp. (Gesneriaceae), climber	control
43	hairy appendage of *Aeschynanthus fecundus* (Gesneriaceae)	control
44	seed of *Hoya micrantha* (Asclepiadaceae)	control
45	wooden bait	with *Ae. fecundus* acetone-extract (0,5ml/100 seeds / 60 baits)
46	wooden bait	with *Ae. fecundus* cyclohexane-extract (0,5ml/100 seeds / 60 baits)
47	wooden bait	with *Ae. fecundus* acetone+cyclohexane-extract (0,5ml/100 seeds / 60 baits)
48	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in cyclohexane + acetone (1h)
49	seed of *Dischidia acutifolia*(Asclepiadaceae)	washed in aqua dest. (1h)
50	seed of *Dischidia acutifolia*(Asclepiadaceae)	washed in acetone (1h)
51	seed of *Dischidia acutifolia*(Asclepiadaceae)	washed in chloroform (1h)
52	seed of *Dischidia acutifolia*(Asclepiadaceae)	washed in pentane (1h)
53	seed of *Dischidia acutifolia*(Asclepiadaceae)	washed in cyclohexane (1h)
54	seed of *Dischidia acutifolia*(Asclepiadaceae)	washed in 50% ethanol (1h)
55	seed of *Dischidia acutifolia*(Asclepiadaceae)	hairy appendage removed

Nr.	Item	treatment
56	wooden bait	with *D. nummularia* acetone-extract (0,5ml/100 seeds / 60 baits)
57	wooden bait	with *D. nummularia* cyclohexane-extract (0,5ml/100 seeds / 60 baits)
58	wooden bait	with *D. nummularia* acetone+cyclohexane-extract (0,5ml/100 seeds / 60 baits)
59	seed of *Emilia sonchifolia* (Asteraceae)	with *D. nummularia* acetone-extract (0,5ml/100 seeds / 60 seeds)
60	seed of *Emilia sonchifolia* (Asteraceae)	with *D. nummularia* cyclohexane-extract (0,5ml/100 seeds / 60 seeds)
61	seed of *Emilia sonchifolia* (Asteraceae)	with *D. nummularia* acetone+cyclohexane-extract (0,5ml/100 seeds / 60 seeds)
62	wooden bait	with *Ae. fecundus* pentane-extract (0,5ml/100 seeds / 60 baits)
63	wooden bait	with *Ae. fecundus* 50% ethanol-extract (0,5ml/100 seeds / 60 baits)
64	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* pentane-extract (0,5ml/100 seeds / 60 seeds)
65	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* 50% ethanol-extract (0,5ml/100 seeds / 60 seeds)
66	wooden bait	with *Ae. fecundus* pentane + 50% ethanol-extract (0,5ml/100 seeds / 60 baits)
67	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* pentane + 50% ethanol-extract (0,5ml/100 seeds / 60 seeds)
68	seed of *Ageratum conyzoides* (Asteraceae)	control
69	seed of *Pachycentria* sp. (Melastomataceae)	fruit pulp removed and washed with aqua dest.
70	seed of *Emilia sonchifolia* (Asteraceae)	acetone (0,5 ml / 60 seeds)
71	seed of *Emilia sonchifolia* (Asteraceae)	cyclohexane (0,5 ml / 60 seeds)
72	seed of *Emilia sonchifolia* (Asteraceae)	pentane (0,5 ml / 60 seeds)
73	seed of *Emilia sonchifolia* (Asteraceae)	50% ethanol (0,5 ml / 60 seeds)
74	seed of *Emilia sonchifolia* (Asteraceae)	aqua dest. (0,5 ml / 60 seeds)
75	seed of *Emilia sonchifolia* (Asteraceae)	chloroform (0,5 ml / 60 seeds)
76	seed of *Emilia sonchifolia* (Asteraceae)	70% ethanol (0,5 ml / 60 seeds)
77	wooden bait	acetone (0,5 ml / 60 baits)
78	wooden bait	cyclohexane (0,5 ml / 60 baits)
79	wooden bait	pentane (0,5 ml / 60 baits)
80	wooden bait	50% ethanol (0,5 ml / 60 baits)
81	wooden bait	aqua dest. (0,5 ml / 60 baits)
82	wooden bait	70% ethanol (0,5 ml / 60 baits)
83	wooden bait	with *Ae. fecundus* aqua dest.-extract (0,5ml/100 seeds / 60 baits)
84	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* aqua dest.-extract (0,5ml/100 seeds / 60 seeds)
85	wooden bait	with *Ae. fecundus* 70% ethanol-extract (0,5ml/100 seeds / 60 baits)
86	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* 70% ethanol-extract (0,5ml/100 seeds / 60 seeds)
87	wooden bait	with *Ae. fecundus* chloroform-extract (0,5ml/100 seeds / 60 baits)
88	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* chloroform-extract (0,5ml/100 seeds / 60 seeds)
89	seed of *Dischidia nummularia* (Asclepiadaceae)	hairy appendage removed
90	wooden bait	chloroform (0,5 ml / 60 baits)
91	seed of *Dischidia nummularia* (Asclepiadaceae)	washed in cyclohexane + acetone (1h)
92	seed of *Aeschynanthus fecundus* (Gesneriaceae)	washed in pentane + 50% ethanol (1h)
93	wooden bait	with *D. nummularia* 70% ethanol-extract (0,5ml/100 seeds / 60 baits)
94	seed of *Emilia sonchifolia*	with *D. nummularia* 70% ethanol-extract (0,5ml/100 seeds / 60 seeds)
95	wooden bait	with *D. nummularia* pentane-extract (0,5ml/100 seeds / 60 baits)
96	wooden bait	with *D. nummularia* aqua dest.-extract (0,5ml/100 seeds / 60 baits)
97	seed of *Emilia sonchifolia*	with *D. nummularia* pentane-extract (0,5ml/100 seeds / 60 seeds)
98	seed of *Emilia sonchifolia*	with *D. nummularia* aqua dest.-extract (0,5ml/100 seeds / 60 seeds)
99	wooden bait	petrol (0,5 ml / 60 baits)
100	seed of *Emilia sonchifolia*	petrol (0,5 ml / 60 seeds)
101	wooden bait	with *D. nummularia* petrol-extract (0,5ml/100 seeds / 60 baits)
102	seed of *Emilia sonchifolia*	with *D. nummularia* petrol-extract (0,5ml/100 seeds / 60 seeds)
103	wooden bait	with *Ae. fecundus* petrol-extract (0,5ml/100 seeds / 60 baits)
104	seed of *Emilia sonchifolia*	with *Ae. fecundus* petrol-extract (0,5ml/100 seeds / 60 seeds)
105	seed of *Emilia sonchifolia*	with *D. nummularia* chloroform-extract (0,5ml/100 seeds / 60 seeds)
106	wooden bait	with *D. nummularia* chloroform-extract (0,5ml/100 seeds / 60 baits)
107	seed of *Emilia sonchifolia*	with *D. nummularia* 95% ethanol-extract (0,5ml/100 seeds / 60 seeds)
108	wooden bait	with *D. nummularia* 95% ethanol-extract (0,5ml/100 seeds / 60 baits)
109	seed of *Emilia sonchifolia*	95% ethanol (0,5 ml / 60 seeds)
110	wooden bait	95% ethanol (0,5 ml / 60 baits)
111	seed of *Emilia sonchifolia*	with *Ae. fecundus* 95% ethanol-extract (0,5ml/100 seeds / 60 seeds)
112	wooden bait	with *Ae. fecundus* 95% ethanol-extract (0,5ml/100 seeds / 60 baits)
113	seed of *Aeschynanthus* sp. (Frasers Hill)	control
114	seed of indet. Asteraceae, Java	control
115	seed of *Hoya* sp$_{\text{KfmE}}$133	control
116	seed of *Asclepia*s sp. (Java)	control
117	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* acetone-extract (0,5ml/100 seeds / 60 seeds), 30 minutes

Nr.	Item	treatment
118	seed of *Emilia sonchifolia* (Asteraceae)	with *Ae. fecundus* acetone-extract (0,5ml/100 seeds / 60 seeds), 15 minutes
119	thread	control
120	seed of *Ageratum conyzoides*	with *Hoya elliptica* acetone-extract (5ml/20 seeds / 60 seeds)
121	porcelain bait	with *Hoya elliptica* acetone-extract (5ml/20 seeds / 60 baits)
122	seed of *Hoya elliptica*	control
123	seed of *Hoya elliptica*	with acetone (1h)
124	porcelain bait	with *D. nummularia* acetone extract (0,5ml/100 seeds / 60 baits)
125	seed of *Hoya elliptica*	hairy appendage removed
126	porcelain bait	with *Ae. fecundus* acetone extract (0,5ml/100 seeds / 60 baits)
127	seed of *Pachycentria constricta*	control
128	seed of *Pachycentria constricta*	after passage through a bird's gut
129	porcelain bait	with *P. constricta* acetone extract (0,5ml/100 seeds / 60 baits)
130	seed of *Dischidia nummularia*	washed with cyclohexane (2x8h), ethanol (2x8h), aqua dest. (2x8h) and acetone (2x8h)
131	seed of *Aeschynanthus fecundus*	washed with cyclohexane (2x8h), ethanol (2x8h), aqua dest. (2x8h) and acetone (2x8h)
132	seed of indet. Melastomataceae	after passage through a bird's gut
133	seed of *Poikilospermum* sp.	control
134	porcelain bait	with *D. nummularia* acetone extract after treatment s. 130 (0,5ml/100 seeds / 60 baits)
135	porcelain bait	with *Ae. fecundus* acetone extract after treatment s. 131 (0,5ml/100 seeds / 60 baits)
136	seed of *Hoya elliptica*	> 4 weeks
137	seed of *Dischidia nummularia*	heated to 110°C (1h)
138	seed of *Aeschynanthus fecundus*	heated to 110°C (1h)
139	seed of *Hoya elliptica*	heated to 110°C (1h)
140	seed of *Aeschynanthus fecundus*	washed in dichlormethane (2x12hrs)
141	seed of *Aeschynanthus fecundus*	heated to 110°C (2h)
142	seed of *Dischidia nummularia*	heated to 110°C (2h)
143	seed of *Dischidia nummularia*	heated to 200°C (1h)
144	seed of *Aeschynanthus fecundus*	heated to 200°C (1h)
145	seed of *Hoya elliptica*	heated to 200°C (1h)
146	seed of *Hoya elliptica*	washed with acetone (2x1h), cyclohexane (2x1h), pentane (2x1h), aqua dest. (2x1h), ethanol (2x1h), dichlormethane (2x1h)
147	seed of *Aeschynanthus fecundus*	washed with acetone (2x1h), cyclohexane (2x1h), pentane (2x1h), aqua dest. (2x1h), ethanol (2x1h), dichlormethane (2x1h)
148	seed of *Dischidia nummularia*	washed with acetone (2x1h), cyclohexane (2x1h), pentane (2x1h), aqua dest. (2x1h), ethanol (2x1h), dichlormethane (2x1h)
149	porcelain bait	with *D. nummularia* acetone extract after treatment s. 143
150	porcelain bait	with *D. nummularia* acetone extract after treatment s. 148
151	porcelain bait	with *Ae. fecundus* acetone extract after treatment s. 144
152	porcelain bait	with *Ae. fecundus* acetone extract after treatment s. 147
153	porcelain bait	with *H. elliptica* acetone extract after treatment s. 145
154	porcelain bait	with *H. elliptica* acetone extract after treatment s. 146
155	seed of *Dischidia nummularia*	washed with acetone (2x1h), cyclohexane (2x1h), pentane (2x1h), aqua dest. (2x1h), ethanol (2x1h), dichlormethane (2x1h), acetone (1x12h)
156	seed of *Aeschynanthus fecundus*	washed with acetone (2x1h), cyclohexane (2x1h), pentane (2x1h), aqua dest. (2x1h), ethanol (2x1h), dichlormethane (2x1h), acetone (1x12h)
157	seed of *Emilia sonchifolia*	with *Ae. albidus* acetone extract (0,5ml/100 seeds / 60 seeds)
200	porcelain bait	control
201	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 1 (+ 0,2ml acetone)
202	porcelain bait	*Ae. albidus* HPLC MRG III-75 (reverse phase) Fraction 2 (+ 0,2ml acetone)
203	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 3 (+ 0,2ml acetone)
204	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 4 (+ 0,2ml acetone)
205	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 5 (+ 0,2ml acetone)
206	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 6 (+ 0,2ml acetone)
207	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 7 (+ 0,2ml acetone)
208	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 8 (+ 0,2ml acetone)
209	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 9 (+ 0,2ml acetone)
210	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 10 (+ 0,2ml acetone)
211	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 11 (+ 0,2ml acetone)
212	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 12 (+ 0,2ml acetone)
213	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 13 (+ 0,2ml acetone)
214	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 14 (+ 0,2ml acetone)
215	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 15 (+ 0,2ml acetone)
216	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 16 (+ 0,2ml acetone)
217	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 17 (+ 0,2ml acetone)
218	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 18 (+ 0,2ml acetone)

Nr.	Item	treatment
219	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 19 (+ 0,2ml acetone)
220	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 20 (+ 0,2ml acetone)
221	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 21 (+ 0,2ml acetone)
222	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 22 (+ 0,2ml acetone)
223	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 23 (+ 0,2ml acetone)
224	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 24 (+ 0,2ml acetone)
225	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 25 (+ 0,2ml acetone)
226	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 26 (+ 0,2ml acetone)
227	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 27 (+ 0,2ml acetone)
228	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 28 (+ 0,2ml acetone)
297	porcelain bait	Squalen
298	porcelain bait	acetone
299	porcelain bait	*Ae. albidus* acetone-extract
302	porcelain bait	*Ae. albidus* LC (silica column) Fraction 2-3 (+ 0,1ml acetone)
305	porcelain bait	*Ae. albidus* LC (silica column) Fraction 5 (+ 0,1ml acetone)
308	porcelain bait	*Ae. albidus* LC (silica column) Fraction 8 (+ 0,1ml acetone)
309	porcelain bait	*Ae. albidus* LC (silica column) Fraction 9 (+ 0,1ml acetone)
310	porcelain bait	*Ae. albidus* LC (silica column) Fraction 10 (+ 0,1ml acetone)
311	porcelain bait	*Ae. albidus* LC (silica column) Fraction 11 (+ 0,1ml acetone)
312	porcelain bait	*Ae. albidus* LC (silica column) Fraction 12 (+ 0,1ml acetone)
314	porcelain bait	*Ae. albidus* LC (silica column) Fraction 14 (+ 0,1ml acetone)
316	porcelain bait	*Ae. albidus* LC (silica column) Fraction 16 (+ 0,1ml acetone)
320	porcelain bait	*Ae. albidus* LC (silica column) Fraction 20-24 (+ 0,1ml acetone)
402	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 2-3 (+ 0,1ml acetone)
405	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 5 (+ 0,1ml acetone)
408	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 8 (+ 0,1ml acetone)
409	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 9 (+ 0,1ml acetone)
410	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 10 (+ 0,1ml acetone)
411	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 11 (+ 0,1ml acetone)
412	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 12 (+ 0,1ml acetone)
414	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 14 (+ 0,1ml acetone)
416	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 16 (+ 0,1ml acetone)
420	seed of *Emilia sonchifolia*	*Ae. albidus* LC (silica column) Fraction 20-24 (+ 0,1ml acetone)
501	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 1 (+ 1ml acetone)
502	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 2 (+ 1ml acetone)
503	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 3 (+ 1ml acetone)
504	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 4 (+ 1ml acetone)
505	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 5 (+ 1ml acetone)
506	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 6 (+ 1ml acetone)
507	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 7 (+ 1ml acetone)
508	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 8 (+ 1ml acetone)
509	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 9 (+ 1ml acetone)
510	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 10 (+ 1ml acetone)
511	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 11 (+ 1ml acetone)
512	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 12 (+ 1ml acetone)
513	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 13 (+ 1ml acetone)
514	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 14 (+ 1ml acetone)
515	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 15 (+ 1ml acetone)
516	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 16 (+ 1ml acetone)
517	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 17 (+ 1ml acetone)
518	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 18 (+ 1ml acetone)
519	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 19 (+ 1ml acetone)
520	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 20 (+ 1ml acetone)
521	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 21 (+ 1ml acetone)
522	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 22 (+ 1ml acetone)
523	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 23 (+ 1ml acetone)
524	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 24 (+ 1ml acetone)
525	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 25 (+ 1ml acetone)
526	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 26 (+ 1ml acetone)
527	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 27 (+ 1ml acetone)
528	porcelain bait	*Ae. albidus* HPLC (reverse phase) Fraction 28 (+ 1ml acetone)
602	porcelain bait	*Ae. albidus* LC (silica column) Fraction 2-3 (+ 0,5ml acetone)

Nr.	Item	treatment
605	porcelain bait	*Ae. albidus* LC (silica column) Fraction 5 (+ 0,5ml acetone)
608	porcelain bait	*Ae. albidus* LC (silica column) Fraction 8 (+ 0,5ml acetone)
609	porcelain bait	*Ae. albidus* LC (silica column) Fraction 9 (+ 0,5ml acetone)
610	porcelain bait	*Ae. albidus* LC (silica column) Fraction 10 (+ 0,5ml acetone)
611	porcelain bait	*Ae. albidus* LC (silica column) Fraction 11 (+ 0,5ml acetone)
612	porcelain bait	*Ae. albidus* LC (silica column) Fraction 12 (+ 0,5ml acetone)
614	porcelain bait	*Ae. albidus* LC (silica column) Fraction 14 (+ 0,5ml acetone)
616	porcelain bait	*Ae. albidus* LC (silica column) Fraction 16 (+ 0,5ml acetone)
620	porcelain bait	*Ae. albidus* LC (silica column) Fraction 20-24 (+ 0,5ml acetone)

12.8. Instructions for the use of reflectometric tests

12.8.1. Ammonium

Reflectoquant®

Ammonium Test

MERCK

1.16892.0001

NH_4^+

1. Method

NH_4^+ ions react with a chlorinating agent to form monochloramine. This in turn reacts with a phenol compound to form a blue indophenol derivative, the concentration of which is determined reflectometrically.

2. Measuring range and number of determinations

Measuring range[1]	Number of determinations
0.2 – 7.0 mg/l NH_4^+	50
0.16– 5.4 mg/l N 11.1 –388 mmol/l³ NH_4^+ or N	

[1] for conversion factors see section 8
for measurement of concentrations > 7.0 mg/l NH_4^+
see section 6

3. Applications

Sample material:

Wastewater
Soils and fertilizers
Food (meats and sausages)

4. Influence of foreign substances

This was checked – in the case of interfering ions up to concentrations of 1,000 mg/l – in solutions containing 5 and 0 mg/l NH_4^+. The concentrations of foreign substances given in the table lie below the limit at which the determination is interfered with.

Concentrations of foreign substances in mg/l or %					
Al^{3+}	1.000	**Fe^{2+}**	**10**	EDTA	1,000
Ascorbate	100	**Fe^{3+}**	**100**	Anionic	
BO_3^{3-}	1,000	K^+	1,000	surfactants[1]	1,000
Br^-	1,000	Mg^{2+}	1,000	Cationic	
Ca^{2+}	1,000	Mn^{2+}	100	surfactants[2]	1,000
Citrate	1,000	Ni^{2+}	1,000	Nonionic	
Cl^-	1,000	**NO_2^-**	**50**	surfactants[3]	100
CN^-	**1**	NO_3^-	1,000	HO_2	10
CO_3^{2-}	1,000	Oxalate	1,000	Na_2SO_4	5%
Cr^{3+}	100	PO_4^{3-}	1,000		
CrO_4^{2-}	100	SO_3^{2-}	100		
Cu^{2+}	100	Tartrate	1,000		

[1] tested with Na-dodecyl sulfate
[2] tested with N-cetylpyridinium chloride
[3] tested with polyvinylpyrrolidone

5. Reagents and auxiliaries

Please note the warnings on the packaging materials!

The analytical test strips are stable at least up to the date stated on the pack when stored in the closed tube at +2 to +8 °C.

Package contents:

Tube containing 50 analytical test strips
Bar code strip
1 bottle of reagent NH_4–1
1 bottle of reagent NH_4–2
1 test vessel with stopper

Other reagents:

Merckoquant® Ammonium Test,
Cat. No. 1.10024.0001,
measuring range 10–400 mg/l NH_4^+
pH-indicator strips non-bleeding,
Universal Indicator pH 0–14, Cat. No. 1.09535.0001
Sodium hydroxide solution 1 mol/l,
Cat. No. 1.09137.
Sulfuric acid 0.5 mol/l, Cat. No. 1.09072.
Ammonium standard solution, 1,000 mg/l NH_4^+,
Cat. No. 1.19812.0500

6. Preparation

- Check whether the ammonium content is within the measuring range.
  Use the Merckoquant® Ammonium Test as a guide.
  Samples containing more than 7.0 mg/l NH_4^+ must be diluted with distilled water.
- **The pH must be within the range 4–13.**
  Check with Universal Indicator strips. If pH is lower than 4, add sodium hydroxide solution dropwise; if greater than 13, add sulfuric acid dropwise.

7. Procedure

- Observe the instructions for the RQflex reflectometer.
  The following applies to the Ammonium Test:
  Measurement procedure A.
  Stored reaction time: 480 sec.
- Rinse the test vessel several times with the pretreated sample solution (20–30 °C). Then fill to the 5-ml mark.
- Add 10 drops of reagent NH_4–1 and swirl.
- Add 1 level blue microspoon (in the cap of the NH_4–2 bottle) of reagent NH_4–2 and swirl to dissolve.
- Remove 1 analytical test strip and **immediately reclose the tube.**
- Press START button of the reflectometer and – **this is imperative – at the same time** place the test strip in the measurement solution **for 8 min.** so **that both reaction zones are completely wetted.**
- 10 sec before end of reaction time, remove the test strip from the solution and vigorously *shake off excess liquid*. ***Immediately** insert the test* strip all the way into the strip adapter with the reaction zones facing the display.
- Read off the result from the display in mg/l NH_4^+. The result is automatically stored.

Notes:

- If the test strip is inserted into the adapter after the reaction time has expired, renewed depression of the START button may result in a false reading of the ammonium concentration.
- At the end of each workday, cleanse the strip adapter thoroughly with water or ethanol.

8. Conversions

units **required** =	units **given** ×	conversion factor
mmol/m³ NH_4^+ or N	**mg/l NH_4^+**	55.4
mg/l N		0.777
mg/l NH_4^+	mmol/m³ NH_4^+ or N	0.0180
	mg/l N	1.29

9. Method control

To check analytical test strips, equipment, and procedure:
Dilute ammonium standard solution to 2.5 mg/l NH_4^+ and analyze as described in section 7.

12.8.2. Nitrate

Reflectoquant®

Nitrate Test

MERCK

1.16995.0001

NO_3^-

1. Method

Nitrate is reduced to nitrite by a reduction agent. In the presence of an acidic buffer, this nitrite reacts with an aromatic amine to form a diazonium salt, which in turn reacts with N-(1-naphthyl)-ethylenediamine to form a red-violet azo dye, the concentration of which is determined reflectometrically.

2. Measuring range and number of determinations

Measuring range[1]	Number of determinations
3 – 90 mg/l NO_3^-	50
0.7– 20.3 mg/l N 48.3–1,449 mmol/m³ NO_3^- or N	

[1] for conversion factors see section 8
for measurement of concentrations > 90 mg/l NO_3^- see section 6

3. Applications

This test is only conditionally suited for the determination of the nitrate content of seawater samples (false-low readings).

Sample material:

Groundwater, wellwater, and drinking water
Spring water and mineral water
Industrial water, wastewater, percolating water
Water in aquariums
Pressed plant and fruit juices
Food, animal fodder
Soils and fertilizers

4. Influence of foreign substances

This was checked – in the case of interfering ions up to concentrations of 1,000 mg/l – in solutions containing 50 mg/l and 0 mg/l NO_3^-. The concentrations of foreign substances given in the table lie below the limit at which the determination is interfered with.

Concentrations of foreign substances (mg/l or %)					
Al^{3+}	1,000	Fe^{2+}	10	EDTA	1,000
Ascorbate	1,000	Fe^{3+}	10	Anionic surfactants[2]	10
BO_3^{3-}	1,000	K^+	1,000	Cationic surfactants[3]	10
Ca^{2+}	1,000	Mg^{2+}	1,000	Nonionic surfactants[4]	1,000
Citrate	1,000	Mn^{2+}	1,000	H_2O_2	10
Cl^-	500	**NO_2^-**	**0.5**[1]	Na_2SO_4	1%
CO_3^{2-}	1,000	Oxalate	1,000		
Cr^{3+}	100	PO_4^{3-}	1,000		
CrO_4^{2-}	10	SO_3^{2-}	10		
Cu^{2+}	**1**	Tartrate	1,000		

[1] In cases in which the nitrite concentration is higher, eliminate nitrite ions acc. to section 6.
[2] tested with Na-dodecyl sulfate
[3] tested with N-cetylpyridinium chloride
[4] tested with polyvinylpyrrolidone

5. Reagents and auxiliaries

Store originally sealed pack in refrigerator. Opened pack: store closed tube outside refrigerator in a cool and dry place. The analytical test strips are stable at least up to the date stated on the pack when stored under these conditions.

Package contents:

Tube containing 50 analytical test strips
Bar code strip

Other reagents:

Merckoquant® Nitrite Test, Cat. No. 1.10007.0001, measuring range 2–80 mg/l NO_2^-
pH-indicator strips non-bleeding,
Universal Indicator pH 0–14, Cat. No. 1.09535.0001
Amidosulfonic acid GR, Cat. No. 1.00103.
Merckoquant® Nitrate Test, Cat. No. 1.10020.0001 or 1.10050.0001, measuring range 10–500 mg/l NO_3^-
Sodium acetate GR, Cat. No. 1.06268.
Tartaric acid GR, Cat. No. 1.00804.
Nitrate standard solution,
1,000 mg/l NO_3^-, Cat. No. 1.19811.0500

6. Preparation

- Extract solid sample materials by an appropriate method.
- If nitrite is suspected, check the nitrite content using the Merckoquant® Nitrite Test.
  If necessary, eliminate interfering nitrite ions:
  To 5 ml of sample (pH < 10) add 5 drops of a 10% aqueous amidosulfonic acid solution and shake several times.
- Check whether the nitrate content is within the measuring range.
  Use the Merckoquant® Nitrate Test as a guide.
  Samples containing more than 90 mg/l NO_3^- must be diluted with distilled water.
- **The pH must be within the range 1–12.**
  Check with universal indicator strips.
  If pH is lower than 1, buffer with sodium acetate; if greater than 12, adjust to approx. 3–5 with tartaric acid.

7. Procedure

- Observe the instructions for the RQflex reflectometer.
  The following applies to the Nitrate Test:
  Measurement procedure A. Stored reaction time: 60 sec.
- Remove 1 analytical test strip and **immediately reclose the tube.**
- Press START button of the reflectometer and at the same time immerse **both reaction zones** of the test strip in the sample solution (15–30 °C) **for approx. 2 sec.**
- Shake off excess liquid from the test strip.
- As soon as the beeper sounds (5 sec before end of reaction time), insert the test strip all the way into the strip adapter with the reaction zones facing the display.
- Read off the result from the display. The result is automatically stored.

Notes:

- If the test strip is inserted into the adapter after the reaction time has expired, renewed depression of the START button will result in a false-high reading of the nitrate concentration.
- At the end of each workday, the strip adapter must be cleansed thoroughly with water or ethanol.

8. Conversions

units **required**	= units **given**	× conversion factor
mmol/m³ NO_3^- or N	**mg/l NO_3^-**	16.1
mg/l N		0.226
mg/l NO_3^-	mmol/m³ NO_3^- or N	0.0620
	mg/l N	4.43

9. Method control

To check analytical test strips, equipment, and procedure:
Dilute nitrate standard solution to 30 mg/l NO_3^- and analyze as described in section 7.

12.8.3. Phosphate

Reflectoquant®

Phosphate Test

MERCK

1.16978.0001

PO_4^{3-}

1. Method

In a solution acidified with sulfuric acid, orthophosphate ions (PO_4^{3-}) and molybdate ions form molybdophosphoric acid. This is reduced to phosphomolybdenum blue (PMB), the concentration of which is determined reflectometrically.

2. Measuring range and number of determinations

Measuring range[1]	Number of determinations
5 – 120 mg/l PO_4^{3-}	50
1.6– 39.1 mg/l P	
52.5–1,260 mmol/m³ PO_4^{3-} or P	
3.7– 89.6 mg/l P_2O_5	

[1] for conversion factors see section 8
for measurement of concentrations > 120 mg/l PO_4^{3-} see section 6

3. Applications

This test measures only orthophosphate. Samples must be decomposed before total phosphate can be measured.

Sample material:

Wastewater
Soils and fertilizers
Food

4. Influence of foreign substances

This was checked – in the case of interfering ions up to concentrations of 1,000 mg/l – in solutions containing 50 and 0 mg/l PO_4^{3-}. The concentrations of foreign substances given in the table lie below the limit at which the determination is interfered with.

Concentrations of foreign substances in mg/l or %					
Ag^+	1,000	**Fe^{2+}**	**10**	Anionic surfactants[1]	1,000
Al^{3+}	1,000	**Fe^{3+}**	**10**	Cationic surfactants[2]	100
Ascorbate	1,000	K^+	1,000	Nonionic surfactants[3]	100
BO_3^{3-}	1,000	Mg^{2+}	1,000	H_2O_2	100
Br^-	1,000	Mn^{2+}	1,000	NaCl	10%
Ca^{2+}	1,000	NH_4^+	1,000	Na_2SO_4	10%
Cd^{2+}	100	Ni^{2+}	1,000		
Citrate	1,000	**NO_2^-**	**10**		
Cl^-	1,000	NO_3^-	1,000		
CN^-	1,000	Oxalate	1,000		
CO_3^{2-}	1,000	SO_3^{2-}	1,000		
Cr^{3+}	100	$S_2O_3^{2-}$	1,000		
CrO_4^{2-}	**10**	Tartrate	1,000		
Cu^{2+}	**10**				

[1] tested with Na-dodecyl sulfate
[2] tested with N-cetylpyridinium chloride
[3] tested with polyvinylpyrrolidone

5. Reagents and auxiliaries

Please note the warnings on the packaging materials!

The analytical test strips are stable at least up to the date stated on the pack when stored in the closed tube at +15 to +25 °C.

Package contents:

Tube containing 50 analytical test strips
Bar code strip
1 bottle of reagent PO_4–1
1 test vessel

Other reagents:

pH-indicator strips non-bleeding, Universal indicator pH 0–14, Cat. No. 1.09535.0001
Sodium hydroxide solution 1 mol/l, Cat. No. 1.09137.
Sulfuric acid 0.5 mol/l, Cat. No. 1.09072.
Phosphate standard solution, 1,000 mg/l PO_4^{3-}, Cat. No. 1.19898.0500

6. Preparation

- Check whether the phosphate content is within the measuring range. Samples containing more than 120 mg/l PO_4^{3-} must be diluted with distilled water.
- **The pH must be within the range 4–10.** Check with universal indicator strips. If pH is lower than 4, add sodium hydroxide solution dropwise; if greater than 10, add sulfuric acid dropwise.

7. Procedure

- Observe the instructions for the RQflex reflectometer. The following applies to the Phosphate Test: **Measurement procedure A.** Stored reaction time: 90 sec.
- Rinse the test vessel several times with the pretreated sample solution (15–30 °C). Then fill to the 5-ml mark.
- Add 10 drops of reagent PO_4–1 and swirl.
- Remove 1 analytical test strip and **immediately reclose the tube.**
- Press START button of the reflectometer and at the same time immerse **both reaction zones** of the test strip in the measurement solution **for approx. 2 sec.**
- Vigorously shake off excess liquid from the test strip.
- As soon as the beeper sounds (5 sec before end of reaction time), insert the test strip all the way into the strip adapter with the reaction zones facing the display.
- Read off the result from the display in mg/l PO_4^{3-}. The result is automatically stored.

Notes:

- If the test strip is inserted into the adapter after the reaction time has expired, renewed depression of the START button may result in a false reading of the phosphate concentration.
- At the end of each workday, cleanse the strip adapter thoroughly with water or ethanol.

8. Conversions

units **required** =	units **given** ×	conversion factor
mmol/m³ PO_4^{3-} or P	**mg/l PO_4^{3-}**	10.5
mg/l P		0.326
mg/l P_2O_5		0.747
mg/l PO_4^{3-}	mmol/m³ PO_4^{3-} or P	0.095
	mg/l P	3.07
	mg/l P_2O_5	1.34

9. Method control

To check analytical test strips, equipment, and procedure:
Dilute phosphate standard solution to 50 mg/l PO_4^{3-} and analyze as described in section 7.

12.9. Distribution matrices for ants and epiphytes in Ulu Gombak

12.9.1. AG-ants

Table 12-2: AG ant species in Ulu Gombak and epiphytes growing on their nests

	Acriopsis javanica	*Aeschynanthus albidus*	*Aeschynanthus fecundus*	*Asplenium nidus*	*Dendrobium crumentatum*	*Dischidia acutifolia*	*Dischidia albida*	*Dischidia hirsuta*	*Dischidia nummularia*	*Dischidia punctata*	*Dischidia subulata*	*Drymoglossum piloselloides*	*Drynaria sparsisora*	*Ficus* sp$_{\mathrm{KfmE}}$96	*Hedychium longicornutum*	*Hoya elliptica*	*Lepisorus longifolius*	*Liparis lacerata*	*Medinilla crassifolia*	*Pachycentria constricta*	*Pachycentria maingayi*	*Platycerium coronarium*	*Platycerium ridleyi*	*Poikilospermum cordifolium*	*Poikilospermum microstachys*	*Pyrossia floccigera*	*Pyrossia lanceolata*	*Schefflera* sp$_{\mathrm{KfmE}}$75	*Schefflera* sp$_{\mathrm{KfmE}}$91	*Schefflera sp*$_{\mathrm{KfmE}}$*155*
Camponotus sp$_{\mathrm{KfmA}}$9	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0	1	0	0	0	2	2	0	0	2	0	0
Camponotus sp$_{\mathrm{KfmA}}$240	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0
Camponotus sp$_{\mathrm{KfmA}}$241	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sp$_{\mathrm{KfmA}}$18	3	8	10	1	2	5	1	0	56	0	0	6	0	0	0	0	1	3	0	4	4	1	0	3	7	9	20	0	1	0
Crematogaster sp$_{\mathrm{KfmA}}$19	0	5	0	0	0	0	0	0	10	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	4	3	0	0	0
Crematogaster sp$_{\mathrm{KfmA}}$21	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	2	0
Crematogaster sp$_{\mathrm{KfmA}}$113	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Diacamma sp$_{\mathrm{KfmA}}$111	0	7	0	0	0	5	0	0	0	0	0	0	0	2	1	0	0	0	0	3	0	0	0	0	14	0	0	20	7	1
Pheidole sp$_{\mathrm{KfmA}}$33	0	4	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	2	0	0	0
Pheidole sp$_{\mathrm{KfmA}}$120	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Philidris sp$_{\mathrm{KfmA}}$37	0	2	0	0	0	0	0	0	4	0	1	2	1	0	0	1	1	0	0	3	3	0	2	0	2	0	4	0	1	0
Philidris sp$_{\mathrm{KfmA}}$85	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0

12.9.2. Opportunists

Table 12-3: Opportunistic ant species in Ulu Gombak and epiphytes growing on their nests

	Acriopsis javanica	*Aeschynanthus albidus*	*Aeschynanthus fecundus*	*Anadendrum latifolium*	*Dendrobium crumentatum*	*Dischidia acutifolia*	*Dischidia albida*	*Dischidia imbricata*	*Dischidia nummularia*	*Drymoglossum piloselloides*	*Drynaria sparsisora*	*Hedychium longicornutum*	*Hoya elliptica*	*Hoya micrantha*	*Lepisorus longifolius*	*Liparis lacerata*	*Pachycentria constricta*	*Pachycentria maingayi*	*Platycerium coronarium*	*Poikilospermum cordifolium*	*Poikilospermum microstachys*	*Pyrossia floccigera*	*Pyrossia lanceolata*	*Schefflera* sp$_{\text{KfmE}}$91
Camponotus sp$_{\text{KfmA}}$8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Camponotus sp$_{\text{KfmA}}$11	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cataulacus sp$_{\text{KfmA}}$36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Camponotus sp$_{\text{KfmA}}$38	0	2	0	0	1	0	0	0	2	0	0	0	1	0	0	0	0	0	1	0	0	1	2	0
Camponotus sp$_{\text{KfmA}}$235	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sp$_{\text{KfmA}}$22	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crematogaster sp$_{\text{KfmA}}$42	0	1	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	2	0	0	0
Crematogaster sp$_{\text{KfmA}}$142	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Crematogaster sp$_{\text{KfmA}}$203	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Dolichoderus sp$_{\text{KfmA}}$10	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Dolichoderus sp$_{\text{KfmA}}$17	0	0	2	0	0	2	0	0	7	0	0	0	0	0	0	1	0	0	0	0	1	3	4	0
Dolichoderus sp$_{\text{KfmA}}$118	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dolichoderus sp$_{\text{KfmA}}$124	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dolichoderus sp$_{\text{KfmA}}$126	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Echinopla sp$_{\text{KfmA}}$1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Echinopla sp$_{\text{KfmA}}$134	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monomorium sp$_{\text{KfmA}}$31	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myrmoteras sp$_{\text{KfmA}}$2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Paratrechina sp$_{\text{KfmA}}$28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Pheidole sp$_{\text{KfmA}}$32	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	0
Pheidole sp$_{\text{KfmA}}$145	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pheidole sp$_{\text{KfmA}}$147	0	1	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0
Podomyrma sp$_{\text{KfmA}}$108	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyrhachis sp$_{\text{KfmA}}$4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Polyrhachis sp$_{\text{KfmA}}$5	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyrhachis sp$_{\text{KfmA}}$6	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Polyrhachis sp$_{\text{KfmA}}$154	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tapinoma sp$_{\text{KfmA}}$15	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Technomyrmex sp$_{\text{KfmA}}$12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Technomyrmex sp$_{\text{KfmA}}$13	0	1	1	0	1	0	0	0	3	0	1	0	0	0	1	0	0	0	0	0	0	2	0	0
Technomyrmex sp$_{\text{KfmA}}$81	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Technomyrmex sp$_{\text{KfmA}}$86	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Technomyrmex sp$_{\text{KfmA}}$146	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Tetramorium sp$_{\text{KfmA}}$29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tetramorium sp$_{\text{KfmA}}$109	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tetramorium sp$_{\text{KfmA}}$153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1
Tetraponera sp$_{\text{KfmA}}$26	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Tetraponera sp$_{\text{KfmA}}$137	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vollenhovia sp$_{\text{KfmA}}$30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0

12.10. List of epiphytes occurring in Peninsular Malaysia

Table 12-4: List of epiphytes (except for ferns and orchids) occurring on Peninsular Malaysia (after Turner, 1995).
Apart from habit and habitat (modified after Turner, 1995) information is given on whether the species was ranked as a 'candidate' (Chapter 6.1.1, p. 107) for associations with ants, and whether it was found in this study or not.

plant family	plant species	habit	habitat	candidate	sample
Araceae	*Anadendrum latifolium* Hook.f.	epiphytic root climber to 2 m or more long	on tree trunks in lowland and hill forest	no	no
	Anadendrum montanum (Blume) Schott	epiphytic root climber to 2 m or more long	on tree trunks in lowland forest; occasionally at higher altitudes	no	no
	Epipremnum giganteum (Roxb.) Schott	stout epiphytic root climber to 20 m long	on rocks and trees in the lowlands and hills	no	no
Araliaceae	*Schefflera actinophylla* (Endl.) Harms	shrub or tree; terrestrial or epiphytic	lowland forest	no	no
	Schefflera beccariana Harms	epiphytic shrub	lowland swamp forest	yes	yes
	Schefflera cephalotes (C.B. Clarke) Harms	shrub; usually epiphytic	hill forest	no	no
	Schefflera elliptica (Blume) Harms	climber or straggling shrub; often epiphytic	lowland and hill forest; also mangroves and on limestone	no	no
	Schefflera hullettii (King) R. Vig.	epiphytic shrub or climber	lowland and hill forest	no	no
	Schefflera latifoliolata (King) R. Vig.	shrub; terrestrial or epiphytic	montane forest	no	no
	Schefflera lurida (King) Ridl.	slender epiphytic creeper or shrub	lower montane forest	no	no
	Schefflera nanocephala Frodin ined.	terrestrial or epiphytic tree to 6 m tall	montane forest	no	no
	Schefflera oxyphylla (Miq.) R. Vig.	epiphytic climber	lowland and hill forest	yes	yes
	Schefflera ridleyi (King) R. Vig.	epiphytic shrub; occasionally epilithic	lowland and hill forest; also in mangroves	no	no
	Schefflera simulans Craib	terrestrial or epiphytic shrub to 3 m tall	montane forest	no	no
	Schefflera singalensis (Miq.) R. Vig.	epiphytic shrub or liana	lowland and hill forest	no	no
	Schefflera tomentosa (Blume) Harms	shrub or climber; terrestrial or epiphytic	lowland forest; including swamps and on limestone	no	no
	Schefflera tristis (King) Ridl.	terrestrial or epiphytic shrub to 3 m tall	montane forest	no	no
Aquifoliaceae	*Ilex baasiana* B.C. Stone & Kiew	epiphytic shrub with tuberous roots	montane forest at about 1500 m	no	no
	Ilex epiphytica King	small tree or shrubby epiphyte	montane forest	no	no
Asclepiadaceae	*Dischidia acutifolia* Maing. ex Hook.f.	twining epiphyte	lowland forest understorey	yes	yes
	Dischidia albida Griff.	slender twining epiphyte	commonest in the mountains; sometimes lower	yes	yes
	Dischidia albiflora Griff.	creeping epiphyte; leaves convex	on trees near the sea	no	no
	Dischidia astephana Scort. ex King & Gamble	slender creeping epiphyte; leaves convex	montane forest to highest peaks	no	yes
	Dischidia bengalensis Colebr.	long creeping epiphyte	coasts to mountains at 1700 m	yes	yes
	Dischidia cochleata Blume	creeping epiphyte; leaves convex	lowland and hill forest	yes	no

plant family	plant species	habit	habitat	candidate	sample
	Dischidia complex Griff.	slender creeping epiphyte; some leaves pitcher-like	lowland forest	yes	yes
	Dischidia dolichantha Schltr.	wiry twining epiphyte	montane forest	no	no
	Dischidia fruticulosa Ridl.	shrubby epiphyte	hill forest	yes	yes
	Dischidia hirsuta (Blume) Decne.	hairy twining epiphyte	lowland and hill forest; also on limestone	yes	yes
	Dischidia imbricata (Blume) Steud.	slender twining epiphyte; leaves convex	lowland forest	yes	yes
	Dischidia longepedunculata Ridl.	creeping epiphyte; leaves convex	montane forest	no	yes
	Dischidia major (Vahl) Merr.	creeping epiphyte; some leaves pitcher-like	lowland and hill forest; common near the sea	yes	yes
	Dischidia nummularia R.Br.	creeping epiphyte	on trees in the open	yes	yes
	Dischidia parvifolia Ridl.	slender twining epiphyte	montane forest	no	no
	Dischidia pubescens Ridl.	creeping epiphyte	lowland forest	yes	no
	Dischidia punctata (Blume) Decne.	long twining epiphyte	lowland and hill forest	yes	yes
	Dischidia rhodantha Ridl.	slender twining epiphyte	montane forest	no	no
	Dischidia scortechinii King & Gamble	slender twining epiphyte	understorey of montane forest	no	no
	Dischidia singaporensis Ridl.	slender creeping epiphyte	on trees	no	no
	Dischidia subulata Warb.	twining epiphyte	montane forest	no	no
	Dischidia superba Rintz	creeping epiphyte	lowland and hill forest	yes	no
	Dischidia tomentella Ridl.	long slender climbing epiphyte	forest on limestone	yes	no
	Dischidia vadosa Rintz	creeping epiphyte	montane forest	no	no
	Hoya caudata Hook.f.	climbing epiphyte	lowland forest; common on limestone	yes	no
	Hoya coriacea Blume	stout twining epiphyte	forests from mangroves to hill tops; including limestone	yes	no
	Hoya coronaria Blume	hairy twining epiphyte	mangroves; lowland forest incl. quartzite and limestone ridges	yes	no
	Hoya curtisii King & Gamble	slender; fleshy creeping epiphyte	hill forest at 700 m	yes	no
	Hoya diversifolia Blume	twining epiphyte	lowland forest and limestone hills	yes	no
	Hoya elliptica Hook.f.	slender twining epiphyte	often along rivers	yes	yes
	Hoya endauensis Kiew	epiphytic climber	on riverside tree	yes	no
	Hoya erythrina Rintz	twining epiphyte	hill forest at 400-700 m	yes	no
	Hoya erythrostemma Kerr	twining epiphyte	on riverside tree	yes	no
	Hoya finlaysonii Wight	twining epiphyte	along rivers in lowland forest	yes	no
	Hoya forbesii King & Gamble	twining epiphyte	lowland forest including that on limestone	yes	no
	Hoya lacunosa Blume	slender creeping epiphyte	lowland and hill forest	yes	yes
	Hoya lasiantha Korth. ex Miq.	climbing epiphyte	lowland and hill forest	yes	no
	Hoya latifolia G. Don	long climbing and creeping epiphyte	lowland forest	yes	no
	Hoya micrantha Hook.f.	stout twining epiphyte	montane forest at 800-1000 m	yes	yes

plant family	plant species	habit	habitat	candidate	sample
	Hoya mitrata Kerr	twining epiphyte	lowland and hill forest	yes	yes
	Hoya multiflora Blume	shrubby epiphyte	mostly in hill forest at 500-900 m	yes	yes
	Hoya obtusifolia Wight	stout-stemmed twining epiphyte	mangroves	no	no
	Hoya pusilla Rintz	slender twining epiphyte	lowland forest on river banks	yes	no
	Hoya scortechinii King & Gamble	twining climbing epiphyte	lowland forest	yes	no
	Hoya verticillata (Vahl) G. Don	twining epiphyte	along lowland rivers and on limestone hills, often near the sea	yes	no
	Hoya wrayi King & Gamble	twining epiphyte	montane forest at 1000-1500 m	no	no
Ericaceae	*Agapetes scortechinii* (King & Gamble) Sleumer	sprawling shrub or epiphyte	upper montane forest above 1200 m	no	no
	Diplycosia elliptica Ridl.	epiphytic or terrestrial shrub to 1 m tall	montane forest at 900-1800 m	no	no
	Diplycosia heterophylla Blume	shrub or climber; sometimes epiphytic	montane forest at 1200-1700 m	no	no
	Pernettyopsis malayana King & Gamble	epiphytic or terrestrial shrub to 60 cm tall	upper montane forest above 1500 m	no	no
	Rhododendron jasminiflorum Hook.	scrambling shrub to 2.5 m tall; usually epiphytic	open places at 1100-1500 m	no	no
	Rhododendron javanicum (Blume) Benn.	epiphytic shrub	on riverside trees in the lowlands	yes	no
	Rhododendron longiflorum Lindl.	terrestrial or epiphytic shrub to 4.5 m tall	lowland and hill forest to 1000 m; also on rocky ridges	no	no
	Rhododendron malayanum Jack	epiphytic or terrestrial shrub to 3 m tall	montane forest at 1000-1800 m	no	no
	Rhododendron pauciflorum King & Gamble	epiphytic shrub	montane forest at 1500-1800 m	no	no
	Rhododendron pauciflorum King & Gamble	shrubby epiphyte to 2 m tall	montane forest at 1500-2100 m	no	no
	Rhododendron perakense King & Gamble	epiphytic or terrestrial shrub to 2 m tall	montane forest at 1800 m	no	no
	Rhododendron robinsonii Ridl.	epiphytic or sometimes terrestrial shrub to 3 m tall	montane forest at 1000-1800 m	no	no
	*Rhododendron scorte*chinii King & Gamble	epiphytic or terrestrial shrub to 2 m tall	upper montane forest above 1500 m	no	no
	Rhododendron seimundii J.J. Sm.	epiphytic or terrestrial shrub to 1.5 m tall	montane forest at about 1500 m	no	no
	Rhododendron spathulatum Ridl.	epiphytic or terrestrial shrub to 1.5 m tall	montane forest at 1500-2100 m	no	no
	Vaccinium acuminatissimum Miq.	epiphytic or climbing shrub	lowland forest to 460 m	no	no
	Vaccinium bancanum Miq.	shrub or small treelet; often epiphytic	montane forest	no	no
	Vaccinium dialypetalum J.J.Sm.	epiphytic climber	montane forest above 800 m	no	no
	Vaccinium glabrescens King & Gamble	shrub; sometimes epiphytic; to 5 m tall	montane forest above 1000 m	no	no
	Vaccinium leptanthum Miq.	small; usually epiphytic; shrub	lowland forest	yes	no
	Vaccinium littoreum Miq.	shrub; often epiphytic	sandy shores; rocky ridges; montane forest	no	no

plant family	plant species	habit	habitat	candidate	sample
	Vaccinium pseudodialypetalum Ng	epiphytic shrub	montane forest at 1000-1500 m	no	no
	Vaccinium scortechinii King & Gamble	epiphytic or terrestrial shrub	montane forest at 1500-1900 m	no	no
	Vaccinium viscifolium King & Gamble	shrub to 5 m tall; sometimes epiphytic	hill and montane forest	no	no
Gesneriaceae	*Aeschynanthus albidus* (Blume) Steud.	slender erect epiphyte	lowland forest	yes	yes
	Aeschynanthus angustifolius (Blume) Steud.	slender epiphyte shrub	lowlands and hills	yes	no
	Aeschynanthus fecundus P. Woods	tufted epiphyte to 30 cm tall	lowland forest near rivers	yes	yes
	Aeschynanthus lanceolatus Ridl.	slender epiphyte	montane forest	no	no
	Aeschynanthus longicaulis Wall. ex R.Br.	trailing epiphyte or epilith	on limestone	no	no
	Aeschynanthus myrmecophilus P. Woods	shrubby epiphyte to 60 cm long	montane forest	no	yes
	Aeschynanthus parvifolius R.Br.	creeping epiphyte	lowland to montane forests	no	no
	Aeschynanthus radicans Jack	creeping epiphytic or epilithic herb	lowland forest	no	no
	Agalmyla parasitica (Lam.) Kuntze	climbing epiphytic shrub	hill and montane forest	no	no
	Cyrtandra falcata Ridl.	epiphyte about 60 cm tall	lowland forest	no	no
	Micraeschynanthus dischidioides Ridl.	slender epiphyte	montane forest	no	no
Loganiaceae	*Fagraea acuminatissima* Merr.	epiphytic climber or shrub	rocky coasts and inland forests of lowland and hills	no	no
	Fagraea auriculata Jack	shrubby epiphyte or climber; sometimes free-standing	lowland and hill forest to 1200 m; sometimes cultivated	no	no
	Fagraea blumei G. Don	tree; shrub; epiphyte or climber	lowland and hill forest; often near rivers	no	no
	Fagraea carnosa Jack	epiphytic shrub or climber	lowland to montane forest	no	no
	Fagraea ceilanica Thunb.	epiphytis shrub; climber or small tree	coasts to mountain tops	no	no
	Fagraea curtisii King & Gamble	spreading tree or sometimes epiphytic	usually on limestone	no	yes
	Fagraea fastigiata Blume	liana; epiphytic shrub	hill forest	no	no
	Fagraea gardenioides Ridl.	epiphytic shrub	montane forest at 1200-1650 m	no	no
Melastomataceae	*Medinilla clarkei* King	shrub to 2.5 m tall; usually epiphytic	montane forest above 1000 m	no	no
	Medinilla crassifolia (Reinw. ex Blume) Blume	epiphytic shrub to 3 m tall	lowland to lower montane forest at 1500 m	yes	no
	Medinilla pendens Ridl.	pendent shrubby epiphyte to 1.5 m long	lowland forest	yes	no
	Medinilla penduliflora Ridl.	epiphytic shrub to 6 m tall	montane forest above 1000 m	no	no
	Medinilla scortechinii King	epiphytic shrub to 3 m tall	lowland to montane forest at 1600 m; also on limestone	yes	no
	Medinilla selangorensis J.F. Maxwell	scandent shrub; often epiphytic	montane forest at 1600-2000 m	no	no
	Medinilla speciosa (Reinw. ex Blume) Blume	shrub to 3 m tall; often epiphytic	hill forest at 500-1200 m	no	no
	Medinilla succulenta (Blume) Blume	epiphytic shrub	lowland to montane forest	yes	no

plant family	plant species	habit	habitat	candidate	sample
	Medinilla varingiifolia (Blume) M.P. Nayar	shrub to 3 m tall; often epiphytic	montane forest at 1000-2200 m	no	no
	Medinilla venusta King	shrub to 5 m tall; sometimes epiphytic	hill and montane forest at 500-1700 m	no	no
	Memecylon fruticosum King	shrub to 3 m tall; often epiphytic	lowland and hill forest	no	no
	Pachycentria maingayi (C.B. Clarke) J.F. Maxwell	epiphytic shrub to 1 m tall	lowland and hill forest	yes	yes
	Pachycentria microsperma Becc.	epiphytic shrub to 2 m tall	on limestone	yes	yes
	Plethiandra sessiliflora (Cogn.) Ridl.	epiphytic shrub to 1 m tall	mangroves or on limestone	no	no
Moraceae	*Ficus allutacea* Blume	epiphytic shrub to 12 m tall	lowland forest	no	no
	Ficus calcicola Corner	shrub or small tree to 8 m tall; sometime epiphytic	limestone hills	no	no
	Ficus deltoidea Jack	shrub to 4 m tall; sometimes epiphytic	lowland and montane forest; common on seashores	no	no
	Ficus excavata King	epiphytic climber	lowlands	yes	no
	Ficus heteropleura Blume	epiphytic shrub	lowland to montane forest	yes	no
	Ficus laevis Blume	small tree or epiphyte	lowlands	no	no
	Ficus obscura Blume	epiphyte or strangler	lowland forest	no	no
	Ficus parietalis Blume	climber or epiphytic shrub	lowland forest	no	no
	Ficus recurva Blume	epiphyte and rock climber	lowlands	no	no
	Ficus sinuata Thunb.	epiphyte or small tree	lowlands to mountains	no	no
	Ficus spathulifolia Corner	epiphytic tree	peat swamp forest	no	no
	Ficus sumatrana Miq.	tree; epiphytic when young	lowland forest	yes	yes
	Ficus uniglandulosa Wall. ex Miq.	small tree; sometimes epiphytic	lowlands	no	no
Pandanaceae	*Pandanus epiphyticus* Martelli	massive shrub; usually epiphytic	lowland forests	no	no
Rosaceae	*Sorbus corymbifera* (Miq.) Khep & Yakovlev	tree to 30 m tall; starting life as an epiphyte	montane forest at about 1200 m	no	no
Rubiaceae	*Aidiopsis orophila* (Miq.) Ridsdale	epiphytic strangler or free-standing shrub	lowland forest	no	no
	Hydnophytum formicarum Jack	large tuberous myrmecophytic epiphyte	forest near the sea; also in the mountains	yes	yes
	Lecananthus erubescens Jack	epiphytic shrub	wet lowland forest	no	no
	Lucinaea ridleyi King	epiphytic climber	montane forest	no	no
	Myrmecodia tuberosa Jack	spiny ant-inhabited tuberous epiphyte	lowland forest; usually near the sea	yes	yes
	Psychotria condensa King & Gamble	epiphytic shrub	montane forest	no	no
	Psychotria kunstleri King & Gamble	epiphyte		no	no
Santalaceae	*Phacellaria malayana* Ridl.	small leafless hyperparasitic epiphytic shrub	on mistletoes in montane forest	no	no
Scrophulariaceae	*Wightia borneensis* Hook.f.	climbing arborescent epiphyte	hill forest	no	no
Solanaceae	*Lycianthes parasitica* (Blume) Bitter	epiphytic shrub to 1 m tall	lowland forest	no	no
Urticaceae	*Poikilospermum cordifolium* (Barg.-Petr.) Merr.	hemi-epiphyte	along streams in the lowlands	no	yes

plant family	plant species	habit	habitat	candidate	sample
	Poikilospermum microstachys (Barg.-Petr.) Merr.	hemi-epiphyte	along rivers or in swamp forest	no	yes
	Poikilospermum scortechinii (King) Merr.	hemi-epiphyte	lowland forest to 300 m; near water courses and swamps	no	no
	Poikilospermum suaveolens (Blume) Merr.	hemi-epiphyte	along water courses in forest to 1500 m	no	no
Zingiberaceae	*Hedychium hirsutissimum* Holttum	herb possibly epiphytic	montane forest 1200 m	no	no
	Hedychium longicornutum Baker	herbaceous epiphyte about 60 cm tall	low down on trees in lowland and hill forest	yes	yes
	Hedychium macrorrhizum Ridl.	herbaceous epiphyte	on tall trees	yes	no

12.11. Previous reports on palaeotropical ant-gardens

Table 12-5: Previous reports on palaeotropical ant-gardens
(updated and modified from Kaufmann et al., 2001)
(*Ca.=Camponotus*, *Cr.=Crematogaster*, *Phil.=Philidris;* A=Asclepiadaceae, Ar=Araliaceae, E=Ericaceae, G=Gesneriaceae, M=Melastomataceae, O=Orchidaceae, P=Polypodiaceae)
1: Kerr, 1912; 2: Leeuwen and Leeuwen-Reijnvaan, 1913; 3: Leeuwen, 1929a; 4: Leeuwen, 1929b; 5: Leeuwen, 1929c; 6: Holttum, 1974; 7: Janzen, 1974; 8: Rintz, 1978; 9: Weir and Kiew, 1986; 10: Kiew and Anthonysamy, 1987; 11: Davidson and Epstein, 1989; 12: Benzing and Clements, 1991; 13: Kiew and Anthonysamy, 1995; 14: Clausing, 1998; 15: Kleijn and Donkelaar, 2001; 16: Weissflog, 2001

Epiphytes	referred to as ant - garden epiphyte in	reasons for assuming the plant to be an ant-garden epiphyte				with ant species	country/area
		frequently growing in runways / ant nests	always found in ant nests	ants retrieve diaspores	oil-containing diaspores		
Dischidia albida (A)	10	10		10			Malaya
Dischida albiflora	2	2				*Phil. cordatus*	Java
Dischidia astephana	13			9		*Cr. sp.*	Malaya
Dischidia bengalensis	3	3					Java
Dischidia hirsuta	3, 10, 13	3, 10		3, 13, 10			Java
Dischidia imbricata	3, 5; 15	3; 15	3			*Phil.cordatus*	Java; Sulawesi
Dischidia major	2, 3, 4, 5, 10, 13	2, 3, 10, 13	3	1, 2, 3, 10	3	*Phil. cordatus*	Java, Thailand
Dischidia nummularia	2, 3,4 , 5, 11, 13, 15	2, 3, 13, 15	3	1, 2, 3, 6, 7, 9; 15	3	*Phil. cordatus*	Borneo; Java, Malaya, Thailand, Sulawesi
Dischidia ovata	13						Malaya
Dischidia parviflora	13			9		*Cr. sp.*	Malaya
Dischidia punctata	3, 4	3	3		3	*Cr. baduvi*	Java
Dischidia singularis	1	1			1	*Cr. biroi, Cr. rogenhoferi*	Thailand
Hoya brevialata	15	15		15		*Phil. cordatus*	Sulawesi
Hoya elliptica (A)	8, 13, 14, 16	8, 13, 16	16	16		*Ca.(Myrmotarsus) sp.*	Malaya
Hoya endauensis	13	13					Malaya
Hoya imbricata	15	15					Sulawesi
Hoya lacunosa	3, 4, 8, 13	3, 8, 13			3	*Cr. baduvi*	Java
Hoya obtusifolia	13	13					Malaya
Hoya pallilimba	15			15		*Tetramorium* sp.	Sulawesi
Hoya pubera	3	3	3			*Phil. cordatus*	Java
Hoya pusilla	8, 13, 14	8, 13					Malaya
Aeschynanthus albidus (G)	3, 4, 5	3				*Cr. baduvi*	Java
Aeschynanthus angustifolia	3, 4, 5	3	3		3	*Cr. baduvi*	Java
Schefflera sp. (Ar)	5	5					Java
Pachycentria constricta (M)	10, 14	10, 14		10, 14		*Phil. sp., Cr. sp.*	Malaya, Borneo
Pachycentria glauca subsp. *glauca*	14	14		14		*Phil. sp., Cr. sp.*	Borneo
Pachycentria glauca subsp. *maingayi*	10	10					Malaya
Pachycentria tuberosa	10			7		*Phil. cordatus*	Borneo

Epiphytes	referred to as ant - garden epiphyte in	reasons for assuming the plant to be an ant-garden epiphyte				with ant species	country/area
		frequently growing in runways / ant nests	always found in ant nests	ants retrieve diaspores	oil-containing diaspores		
Vaccinium bancanum (E)	10	10		10			Malaya
Acriopsis javanica (O)	3, 5	3		3	3	*Cr. baduvi*	Java
Dendrobium bicaudatum	15	15				*Phil. cordatus*	Sulawesi
Dendrobium insigne	12	12		12		*Phil. cordatus*	Papua New Guinea
Dendrochilum pallide-flavens	3, 5	3	3		3	*Phil. cordatus*	Java
Lecanopteris curtisii (P)	3, 4	3	3	3	3	*Phil. cordatus*	Java
Phymatodes sinuosa	3, 5	3	3		3	*Phil. cordatus*	Java

12.12. Neotropical ant-garden epiphytes

Table 12-6: Neotropical ant-garden epiphytes
plant species: current nomenclature was checked using the following references: a) Index Kewensis, 1992; b) Hassler and Swale, 2002; c) Mori, 2002; synonyms are given in brackets where relevant; * no taxonomic reference found; distribution: CR=Costa Rica, B=Brazil, FG=French Guayana, P=Peru, V=Venezuela; remarks: AG-rest.= ant-garden restricted, m=myrmecochorous, a=autogamous, n-a=not autogamous; f=preferentially in forest habitats, r=preferentially in riverine habitats, s=preferentially in secondary habitats, p=preferentially in plantations, EFN=with extrafloral nectaries; d=with domatia
references: 1: Ule, 1901-1906; 2: Prance, 1973; 3: Madison, 1979; 4: Kleinfeldt, 1986; 5: Belin-Depoux et al., 1987; 6: Belin-Depoux and Sarthou, 1988: 7: Davidson, 1988; 8: Belin-Depoux, 1991; 9: Cedeño et al., 1999; 10: Orivel and Dejean, 1999b

plant family	plant species	distribution	remarks	references
Araceae	*Anthurium affine* Schott (*A. solitarium* Schott)[a]	B	n-a	3, 4
Araceae	*Anthurium gracile* Lindl. (*A. scolpendrinum* Kunth) [a]	B, FG, P, V	AG-rest., m, f, s, p	1, 3, 4, 6, 7, 9,10
Araceae	*Anthurium scandens* Engler [a]	B	a	1, 4
Araceae	*Anthurium trinerve* Miq. [a]	V		9
Araceae	*Anthurium sp.nov.*	P	AG-rest.	7
Araceae	*Philodendron deflexum* Poepp. (*P. megalophyllum* Schott) [a]	P, V	AG-rest.	7, 9
Araceae	*Philodendron linnaei* Kunth [a]	FG		6, 8
Araceae	*Philodendron meliononi* Brongn. [a]	FG		6, 8
Araceae	*Philodendron myrmecophilum* Engler [a]	FG, P, B	f, EFN	1, 3, 4, 6, 8, 10
Araceae	*Philodendron ornatum* Schott[a]	FG	f	6, 8
Araceae	*Philodendron squamiferum* Poepp & Endl. [a]	FG	f	6, 8
Araceae	*Philodendron traunii* Engler [a]	FG, B	m, n-a, EFN	3, 4, 10
Araceae	*Rhektophyllum* sp.	FG		10
Bromeliaceae	*Aechmea brevicollis* L.B.Smith [a]	B	a	3, 4
Bromeliaceae	*Aechmea mertensii* Schult.f. [a]	FG, B	m, a, r, p	3, 4, 6, 8, 10
Bromeliaceae	*Aechmea spicata* Mart. [a]	P	n-a	1, 4
Bromeliacaea	*Aechmea tillandsioides* Baker[a]	V		9
Bromeliaceae	*Araeococcus micranthus* Brongn. [a]	FG		6, 8
Bromeliaceae	*Bromelia longifolia* Rudge. (*Streptocalyx longifolius* Baker) [a]	P	AG-rest.	7
Bromeliaceae	*Neoregelia sp.*	P	AG-rest.	9
Bromeliaceae	*Nidularium myrmecophilum* Ule [a]	P	m	1, 4
Bromeliaceae	*Streptocalyx angustifolius* Mez. [a]	FG, P, B	n-a	1, 3, 4, 10
Cactaceae	*Phyllocactus phyllanthus* Link (*Epiphyllum phyllanthus* Haw.) [a]	FG, B, P, V	a, AG-rest.	1, 3, 4, 6, 7, 8, 9
Clusiaceae	*Clusia sp.*	FG	s	6, 8, 10
Cyclanthaceae	*Asplundia sp.*	B	n-a	3, 4
Gesneriaceae	*Codonanthe calcarata* Hanst. [a]	FG, B, V	AG-rest., a, m, f, EFN	3, 4, 6, 8, 9, 10
Gesneriaceae	*Codonanthe crassifolia* Morton [a]	CR, B, V	AG-rest., a, m, p, EFN	4, 6, 8, 9

Gesneriaceae	*Codonanthe dissimulata* Moore (*Codonanthopsis dissimulata*) [a]	B, P	a, m	3, 4
Gesneriaceae	*Codonanthe formicarum* Fritsch [a]	P		1
Gesneriaceae	*Codonanthe uleana* Fritsch [a]	P, B	AG-rest., a, m, EFN	1, 3, 4, 7
Gesneriaceae	*Codonanthopsis dissimulata* [a]	B	a, m	3, 4
Gesneriaceae	*Codonanthopsis ulei* Mansf. [a]	B	n-a, m, EFN	3, 4
Lomariopsidaceae	*Elaphoglossum luridum* Christ.[b]	FG		6, 8
Moraceae	*Ficus amazonica* Miq. [a]	FG		6
Moraceae	*Ficus myrmecophila* Warb. [a]	FG, P, B	n-a	1, 3, 4, 6, 8
Moraceae	*Ficus paraensis* Miq. [a]	P	AG-rest.	7
Orchidaceae	*Epidendrum myrmecophorum* Barb. Rodr. [a]	FG		6, 8
Orchidaceae	*Epidendrum schomburgkii* Lindl. [a]	FG	p	6, 8, 10
Orchidaceae	*Vanilla planifolia* Andr. [a]	P	rare	7
Piperaceae	*Peperomia cf. elongata* H.B. & K. [a]	FG		6, 8
Piperaceae	*Peperomia macrostachya* Dietr. [a]	FG, B	a, m, f	3, 4, 6, 7, 8, 10
Piperaceae	*Peperomia nematostachya* Link [a]	P	n-a	1, 4
Piperaceae	*Verhuellia elegans* Miq. (*Peperomia serpens* Loud.) [a]	FG	f	6, 8
Polypodiaceae	*Polypodium ciliaris**	FG		6, 8
Solanaceae	*Ectozoma ulei* Damm. (*Markea ulei* Cuatrec.) [a]	P	domatia, AG-rest.	1, 4, 7
Solanaceae	*Juanulloa* sp.			
Solanaceae	*Markea camponoti* Ducke [c]	B		2, 4
Solanaceae	*Markea coccinea* Rich. [c]	FG		6, 8
Solanaceae	*Markea formicarum* Damm. [c]	FG, P, B	domatia	1, 2, 3, 4, 10
Solanaceae	*Markea sessiliflora* Ducke [c]	B	domatia	2, 4

12.13. Publications

Kaufmann, E., A. Weissflog, R. Hashim and U. Maschwitz, 2001. Ant gardens on the giant bamboo *Gigantochloa scortechinii* (Poaceae) in West-Malaysia. *Insectes soc. 48:* 125-133.

Malsch, A.K.F., E. Kaufmann, H.P. Heckroth, D.J. Williams, M. Maryati, and U. Maschwitz, 2001. First report on root mealy bug (Homoptera: Pseudococcidae) manipulation and sociobiology of *Pseudolasius* spp. (Hymenoptera: Formicidae). *Insectes soc. 48:* 333-341.

Kaufmann, E. and U. Maschwitz, 2002. The 'ant epiphyte puzzle' of tropical Asian rain forests. In: *XIV International Congress of IUSSI, The Golden Jubilee Proceedings*. Hokkaido University Press, Sapporo, Japan. p. 3

Hashim, R., S.H. Yek, E. Kaufmann, T. Akino, J. Billen and F. Ito (2002): Mimicry in an arboreal ant in Southeast Asia: *Camponotus* sp., a possible batesian mimic of *Crematogaster inflata*. In: *XIV International Congress of IUSSI, The Golden Jubilee Proceedings*. Hokkaido University Press, Sapporo, Japan. p. 196

Buschinger, A., U. Maschwitz and E. Kaufmann, 2002. Kein Kühlschrank? No problem! Wie *Crematogaster*-Ameisen in den Feuchttropen das Problem der Vorratshaltung lösen. *Ameisenschutz aktuell 16:* 1-5.

Kaufmann, E., A.K.F. Malsch, M. Erle and U. Maschwitz, in press. Compound nesting of *Strumigenys* sp. (Myrmicinae) and *Diacamma* sp. (Ponerinae), and other nesting symbioses of myrmicine and ponerine ants in Southeast Asia. *Insectes soc.*

Kaufmann, E., A.K.F. Malsch, D.J. Williams and U. Maschwitz, in press. *Pseudolasius* spp. and their trophobionts – Codispersal by colony-budding. *Sociobiology*

Kaufmann, E. and U. Maschwitz, submitted. Gardener ants and their tree gardens: How to understand the ant-epiphyte puzzle of Asian tropical rain forests. *Behav. Ecol. Sociobiol.*

Maschwitz, U., C. Go, E. Kaufmann and A. Buschinger, submitted. A unique strategy of host colony exploitation in a parasitic ant: Workers of *Polyrhachis lama* rear the brood of their colony in neighboring host nests. *Naturwissenschaften*

Weissflog, A., E. Kaufmann and U. Maschwitz, in prep. Ant gardens of *Camponotus* (*Myrmotarsus*) sp. (Hymenoptera: Formicidae: Formicinae) and *Hoya elliptica* (Asclepiadaceae) in Southeast Asia.

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