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Philidris ants living inside *Dischidia* epiphytes from Thailand

Christian Peeters*[1] and Decha Wiwatwitaya[2]

[1]Laboratoire d'Ecologie, CNRS UMR 7625, Université Pierre et Marie Curie,
7 quai Saint Bernard, 75005 Paris, France

[2]Department of Forest Biology, Kasetsart University,
10900 Bangkok, Thailand

*Corresponding author's e-mail: cpeeters@snv.jussieu.fr

Abstract. The epiphyte *Dischidia major* has highly modified leaves ('pitchers') that provide lodging for various ants, especially *Philidris* (Dolichoderinae) but also *Cataulacus* and *Crematogaster* (Myrmicinae). In return, the plants can obtain extra nutrients but this depends on intimate contact between the branching adventitious roots growing within inhabited pitchers and the organic debris brought in by the ants. *D. major* pitchers were sampled in two very different habitats in Thailand: coastal heathland in the South, and the canopy of a 30 m-high *Dipterocarpus alatus* in the North-East. We recognized only one species of *Philidris* in these two locations. Up to a few hundreds of workers and many brood were found in each pitcher. Several dealate queens were all mated and egg-laying. Workers are polymorphic in size and morphometric analysis showed that large individuals have disproportionally big heads. Importantly, *Philidris* th01 divided each pitcher into compartments by building walls around the roots; this increases surface area for their brood but this selfish behaviour also matches the epiphyte's trophic interests. The entrances of adjacent pitchers were often enclosed by soil runways, connecting separate pitchers into one extensive nest. This external accumulation of substrate may also benefit the epiphyte. *Philidris* th01 occurs in different habitats throughout Thailand, including disturbed vegetation. Some nests were found away from *D. major*, indicating that this ant-plant mutualism is not obligate.

Keywords: mutualism, symbiosis, myrmecophyte, ant-plant, domatia, polygyny, worker polymorphism, *Crematogaster*

INTRODUCTION

A striking testimony to the success of arboreal ants is the evolution of intimate interactions with plants. Many ant-plant mutualisms have been described, with several degrees of sophistication (Beattie 1985, Moog *et al*. 2003). Generally, the ant partners are provided with housing and/or food. In return, the plants are protected because the ants deter herbivorous insects. Additional trophic benefits for plants concern only a minority of mutualisms (e.g. Bazile *et al*. 2012). This seems particularly important for epiphytes that often face severe nutritional constraints. A diversity of epiphytes are known to house ants, and this privileged relationship was recognized long ago (Bequaert 1922). *Dischidia major* (Vahl) Merr. (junior synonym is *D. rafflesiana*) is a succulent creeper (Asclepiadaceae) with two kinds of leaves growing off a central stem. Small coin-like regular leaves contrast with pouched leaves called 'pitchers' with the latter kind often predominating (Fig. 1). Adventitious roots grow at the leaf joints to attach the stem to the host plant,

Fig. 1. Cluster of pitcher leaves of *Dischidia major* growing on a tree trunk.

Table 1. Demographics of *Philidris* th01 inhabiting five clusters of *Dischidia* pitchers collected from separate trees in Songkla province. All pitchers in a cluster were opened. Queens were all dealate. Many workers escaped and are not included in the counts.

Pitchers	No. queens	No. workers	No. pupae	No. larvae	eggs
A1	0	46	473	19	0
A2+3	1	444	647	139	#
A5	0	84	89	613	0
A7	0	75	372	69	0
cluster A (details above): 7 pitchers & soil runway; 5 inhabited and 2 vacant *					
cluster B: 24 pitchers, no soil runway 3 pitchers inhabited: 1 queen, workers, pupae and larvae 3 pitchers vacant* but roots + soil. All others are completely empty					
cluster C: 14 pitchers 7 pitchers inhabited: 4 had single queen + brood. A few males in 5 pitchers 6 pitchers vacant* but roots + soil; 1 small pitcher empty					
cluster E: 14 pitchers 2 pitchers inhabited: 1 & 3 queens, few workers and brood (including eggs) 12 pitchers vacant* but roots + soil					
cluster X: one pitcher contained 6 queens and sexual larvae					

* vacant pitchers may contain a few workers but no brood
\# not checked

but one root grows into the pitcher cavity through an opening at the base. This root proliferates inside pitchers that are inhabited by ants, usually *Philidris* (subfamily Dolichoderinae). Most pitchers contain ant-deposited debris, leading Janzen (1974) and Huxley (1980) to predict that the plants assimilate some of it. This was confirmed by Treseder *et al*. (1995) who traced the movement of carbon and nitrogen isotopes from ants to plants; 29% of the host nitrogen originates from ant debris. Moreover, stomata located inside the pitchers can absorb ant-respired carbon dioxide, providing 39% of the carbon in occupied host plants. In general, the quality of ‘domatia’, i.e. cavities produced by the plant to house ants, is highly variable between plant species (Moog *et al*. 2003); the pitchers of *Dischidia major* must rank among the best because they are completely enclosed with an easily defendable small entrance.

In Thailand we sampled two populations (850 km apart) of *Philidris* nesting in *D. major*. We recognized only one species, referred to as *Philidris* th01. In southern Thailand, Kaufmann & Maschwitz (2006) studied *Philidris* sp$_{\mathrm{KfmA}}$85 nesting in *D. major*, while *P. myrmecodiae* (= *Iridomyrmex myrmecodiae;* Shattuck 1992, 1994) was studied in Sarawak (Janzen 1974) and northern Thailand (Kerr 1912). Although this mutualism is well described, we know little about the colony and physical attributes of *Philidris*; Tschinkel (2010) has emphasized that ‘bottom-up’ data are essential to understand the ontogeny, life history and evolution of ants. We counted and measured the inhabitants of pitchers, and used morphometrics to analyse worker polymorphism and queen-worker differences. We dissected queen ovaries and determined that colonies are polygynous. We describe the partitions built by *Philidris* inside the pitchers and discuss how this self-interested behaviour maximizes trophic benefits for the host plant.

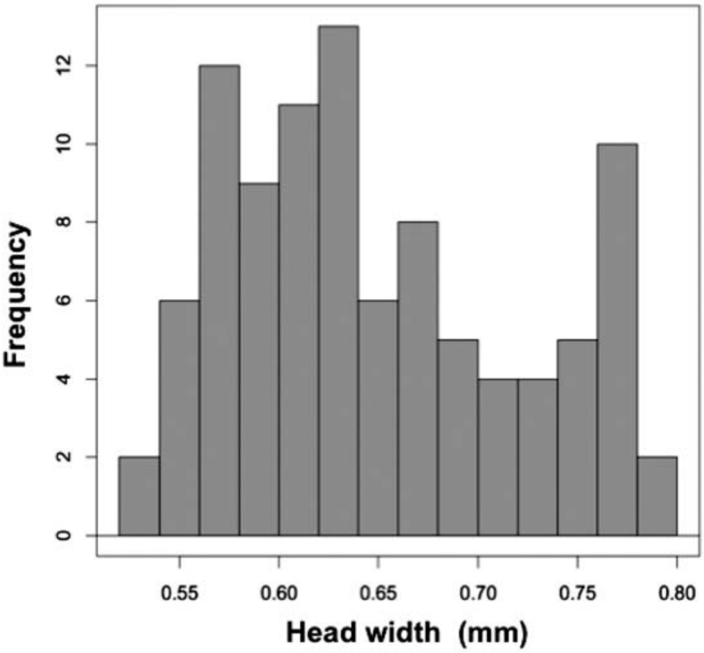
Fig. 2. Workers and dealate queen of *Philidris* th01 showing strong size dimorphism. Callows are very lightly pigmented.

MATERIAL AND METHODS

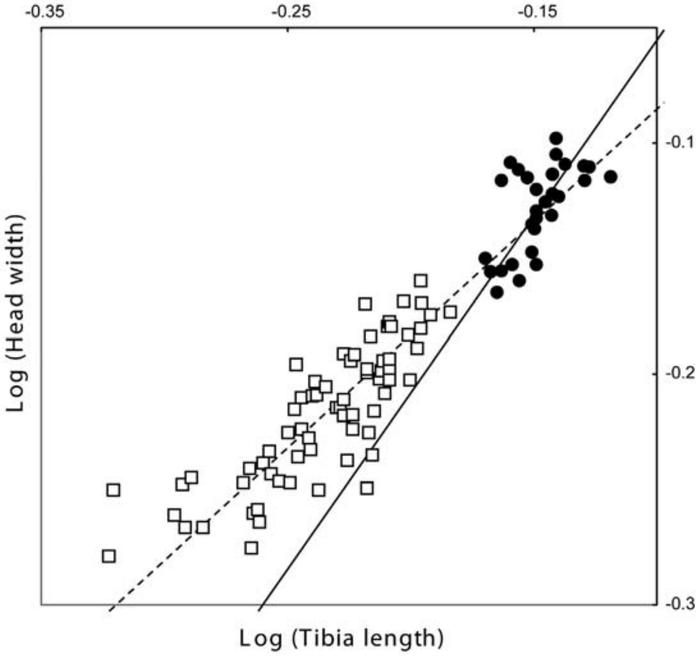
In January and November 2007, we collected pitchers of *Dischidia major* in the Faculty of Forestry Station, Kasetsart University, near Sakaerat (Nakhon Ratchasima province). Using binoculars, we checked for the presence of *Dischidia* in the crown of a 30 m high *Dipterocarpus* tree. An assistant climbed an adjacent tree and dislodged the epiphytes using a long bamboo pole. Clusters of pitchers thus fell to the ground where we retrieved them in one bag. Since the epiphytes were cut randomly, we lack information on the spatial relationship between clusters, as well as exact contents (ants can move between pitchers during transit). A few of these nests were maintained for months in Paris, using plaster nests with a glass roof that allowed behavioural observations. Temperature (25°C) and the humidity of the plaster of Paris nest were controlled. Ants were fed with crickets, Bhatkar's diet (Bhatkar & Whitcomb 1970) and honeywater. A few queens were individually marked with paint. When plants of *D. major* were purchased from nurseries in Germany, the ants readily moved in.

In December 2011 we collected in two localities in Songkla province (Southern Thailand): a forest in Ton-Nga-Chang (700 m elevation, Hat Yai district) and a coastal heathland in Cha-Na district. Here, *D. major* grows on small trees at a height of 1 – 2 m. Accordingly we could photograph and then isolate four clusters of pitchers in separate plastic bags. To prevent ant relocations among pitchers, these were kept in a fridge (4°C) before being cut open for examination of contents.

Variations in the shape of individuals result from both size differences and allometry (i.e. differential growth rates across body parts). A random sample of 97 workers (one colony from Sakaerat) was photographed and measured (head width, posterior tibia length and thorax dimensions) with Image J (http://rsb.info.nih.gov/



(a)



(b)

Fig. 3. Measurements of 97 workers from the same colony of *Philidris* th01 in Sakaerat: (a) size frequency distribution of head width, showing bimodality; (b) length of head relative to tibia. The slopes of the regression lines correspond to the allometry coefficients: 1 for small workers (isometry;white points and dotted line) and 1.5 for large workers (allometry, black points and solid line). Slopes are significantly different (SMA regression; p = 0.005).

ij). Following Molet *et al*. (2007), we calculated thorax volume as a mean of two volumes: lateral area multiplied by dorsal width and dorsal area multiplied by lateral height. To assess differences between large and small individuals, we computed growth rules between several traits (Peeters & Molet 2010a). Thorax volume was also calculated for queens (n = 12) to describe size dimorphism relative to workers, as well as other species; such measures are useful for comparative studies of colony-founding ability in ants.

We dissected 12 dealate queens under a stereomicroscope, and examined ovaries and spermatheca. To elucidate the nature of debris present inside the pitchers, the inner partitions were examined by scanning electron microscopy. Voucher specimens have been deposited in Kasetsart Ant Museum (AMK) in Bangkok, Australian National Insect Collection (ANIC) in Canberra, and California Academy of Sciences (CAS) in San Francisco, USA. Sakaerat specimens in CAS that have been imaged are CASENT0906672 (worker), CASENT0906673 (worker), CASENT0906674 (dealate queen); Songkla specimens are CASENT0906669 (worker), CASENT0906670 (dealate queen), CASENT0906671 (male) - see http://www.antweb.org//specimenImages.do?name=casentxxxxxxx.

RESULTS

Polygyny and worker polymorphism

We recognized only one morphospecies (*Philidris* th01) in both locations. Pitchers of *Dischidia major* collected in Songkla province contained up to 444 *Philidris* workers as well as brood (Table 1). Some pitchers included mostly larvae, others mostly pupae. Adult males and sexual larvae also occurred. A maximum of six dealate queens were collected together in the same pitcher.

Trophallaxis among workers, queens and larvae was frequent. We never observed any antagonism among queens. All dealated queens were mated (n = 12), with about 20 ovarioles in each ovary and many yolky oocytes. Their spermatheca is kidney-shaped and it was always full of sperm. As seen in Fig. 2, queens are much bigger than workers, with large bulbous compound eyes comprising 300 – 350 ommatidia, compared with the smaller eyes of workers (50 – 60 ommatidia). Queens also have three prominent ocelli on top of the head. Thorax volume of queens was 28 times greater than that of workers.

For each of three separate traits (head width, tibia length, thorax volume), the frequency distribution of *Philidris* th01 workers (n = 97) was bimodal (see Fig. 3a for head width). Growth rules based on three pairs of measures (head-tibia, head-thorax, thorax-tibia) indicated that small individuals are isometric (body parts have the same length ratios in different-sized workers), whereas large individuals are allometric (body parts have different ratios in different-sized workers) with modified head shapes (Fig. 3b). Our assessment is compatible with Shattuck's (1992) general diagnosis of *Philidris* workers: "polymorphic, majors with ocelli (occasionally monomorphic)", except that we did not find traces of ocelli in large workers from Thailand.

Structure of ant nests inside pitchers

Many of the pitchers were inhabited (Table 1), and ant presence was associated with both extensive root development and a variable quantity of debris (Fig. 4). Some pitchers had clearly never been inhabited, with tiny or unbranched internal roots. Other pitchers lacked workers and brood even though there were highly branched roots and debris (Table 1); the ants had probably moved out of these to settle in adjacent pitchers. Pitchers offer a large empty space, much of which is unavailable to the ants unless they structure it. *Philidris* build partitions by using the internal roots as framework (Fig. 5). They bring debris from outside as construction material. The strong cementing of the partitions allowed two tiny strips to be examined by SEM, although this was not very conclusive, showing mostly plant tissues and no pieces of insect exoskeleton (Fig. 6).

In several clusters, soil runways had been built between the bases of adjacent pitchers (Fig. 7). Runways built by ants looked distinct from the more solid tubes built by termites (usually mud mixed with saliva and faeces).

Fig. 4. Vacant and inhabited pitchers of *D. major*, cut away to reveal presence or absence of roots and debris.

Other inhabitants of the pitchers

Both in Ton-Nga-Chang and Cha-Na, some pitchers were inhabited by *Crematogaster rogenhoferi* (workers, larvae and pupae). Plant fibres were woven together around the internal adventitious roots, and this construction was very distinct from *Philidris* partitions. *Crematogaster* was equally able to build runways between pitchers by weaving fibres. There were large carton nests of *C. rogenhoferi* on neighbouring trees (away from pitchers), hence it is possible that the colonies in pitchers were newly founded. Indeed, one dealate queen and many eggs were collected in one of four adjacent pitchers, which is clear evidence of an incipient colony. *Cataulacus granulatus* was also found in some pitchers (few workers, larvae and winged gynes), but the root was short and unbranched, and there was no debris. In Sakaerat, several pitchers growing in the canopy of *Dipterocarpus* were inhabited by *Dolichoderus thoracicus*.

In *Philidris* colonies from Sakaerat, many workers carried one large reddish oribatid mite (Order Oribatulidae) attached on the tarsi of one hind leg (sometimes both legs). In Songkla, the same mite was also riding on the ants' tarsi, and some were found hiding in the debris in pitchers (including vacant ones). We found no other myrmecophiles, no scale insects on the inner leaf surfaces and no obvious fungi growing on debris.

Distribution in Thailand

Philidris is widely distributed across different bioclimatic regions in Thailand, and it often occurs in secondary forests, including rubber plantations. Examination of specimens deposited in the Kasetsart Ant Museum indicates the following provinces of origin: Kanchanaburi (mixed deciduous forest and teak plantation), Narathiwat (along trail in rainforest), Pattani, Chumphon (mangrove and rubber plantation), Kanchanaburi (mixed deciduous forest and disturbed vegetation), Chiang Mai (Doi Ang Khang 1300m elevation, roadside and plantation, Doi Chiang Dow 300 m mixed deciduous forest), Chanthaburi (along trail in rainforest), Nakhonratchasima (Khao Yai NP, edge of hill evergreen forest), Trad (mangrove forest). Despite extensive size polymorphism among nestmate workers, *Philidris* is morphologically invariant in Thailand and appears to be just one species. In the South, Kaufmann (2002) reported one species of *Philidris* ($\mathrm{sp}_{\mathrm{KfmA}}$85) nesting in *D. major*, but we have been unable to examine these specimens.

In Sakaerat, some *Philidris* nests were found away from *Dischidia*, in the rotting bark of small trees (3 – 5m high), or in decaying branches or stumps close to ground. Free-living *Philidris* construct their shelters in a manner similar to pitcher-inhabiting colonies. Kaufmann (2002) described extensive carton nests of *Philidris* $\mathrm{sp}_{\mathrm{KfmA}}$37 on stems or branches.

DISCUSSION

Reproductive strategy

Established colonies of *Philidris* th01 are clearly polygynous, but we speculate that they start off with a single foundress (see Peeters & Molet (2010b) for a review of strategies of colonial reproduction). The presence of inhabited *Dischidia* pitchers isolated in the 30 m high crown of *Dipterocarpus* attests to the flying and searching ability of *Philidris* foundresses. Independent foundation in ants is difficult to study in the field (small time window during the year), but aspects of queen morphology indicate that foundressess have sufficient metabolic reserves to raise the first worker brood without foraging outside (i.e. claustral foundation): (1) overall size dimorphism relative to workers is striking (Fig. 2), and the large difference in thorax volume (28x) indicates the presence of large wing muscles that can be resorbed to feed the first larvae; (2) the first thorax segment (pronotum) is small, revealing that neck muscles are much reduced, hence queens do not forage (Keller *et al*. 2014). A foundress that succeeds in finding an empty pitcher can presumably produce her first workers in relative safety. Given high queen fecundity (many ovarioles), a colony can quickly grow in size and expand into adjacent pitchers. In Sarawak, Janzen (1974) reported each of 14 colonies of *P. myrmecodiae* to have a single physogastric (i.e. abdomen is stretched out to accommodate highly developed ovaries) queen, and these may have

Fig. 5. Inner partitions built by *Philidris* th01 ants with debris, using roots as a frame.

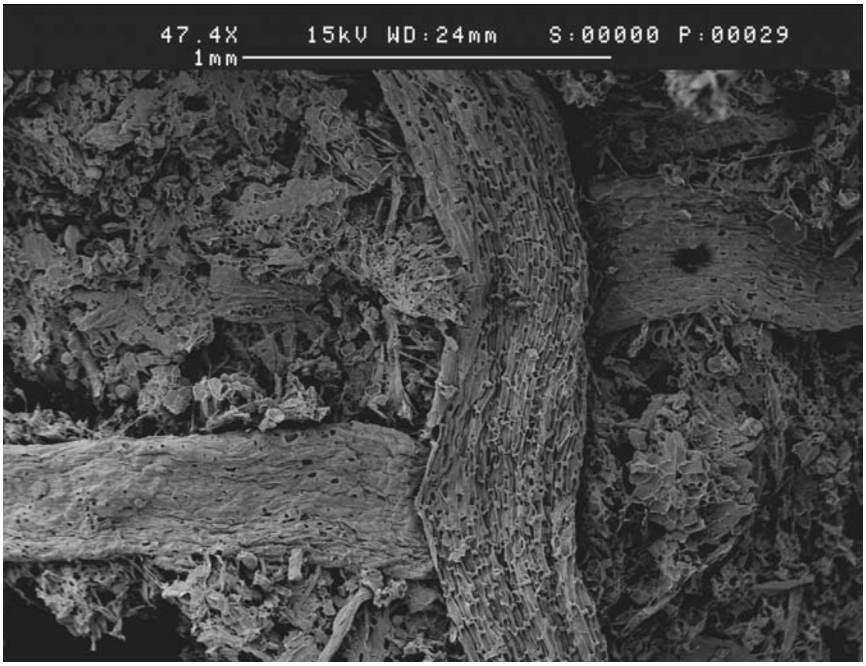


Fig. 6. Scanning electron micrograph of a partition built inside a *Dischidia* pitcher by *Philidris*. Plant material is criss-crossed by the epiphyte roots.

been the original foundresses. In *Philidris* th01, secondary polygyny could result from accepting young queens, possibly daughters of the original foundress that mate close to the nest. In the obligate symbiosis between *Crematogaster* and *Macaranga,* Feldhaar *et al*. (2000) interpreted secondary polygyny to be an adaptation to extend the life span of colonies, enabling them to use resources of the host plant continuously. Kaufmann (2002) described monogyny in *Philidris* sp$_{\text{KfmA}}$37. Another species of *Philidris* nesting in a different epiphyte (*Hydnophytum* in Papua New Guinea) was reported to be monogynous (Maeyama & Matsumoto 2000). If polygyny is indeed secondary in *Philidris* th01, future studies must attempt to distinguish between new and old colonies.

Benefits of ant-plant mutualism

We documented that inhabited pitchers are often packed with workers and brood. The quantity of larvae and pupae was particularly striking, filling up all vacant spaces among the network of roots and partitions. Pitchers become spatially divided into many compartments as a result of the ants' building behaviour, and this allows for optimal use of the entire volume. Debris are brought from outside to build walls, which causes extensive root growth and branching, and in turn more roots may encourage the ants to continue building. Roots are used as a frame for the partitions, thus creating intimate contact appropriate for absorption. Tiny root hairs were seen developing wherever roots entered in contact with any substrate (see also Janzen 1974). Kerr's (1912) observations of "clay mixed with bits of wood and other vegetable matter" are not contradicted by our SEM data. *Philidris* scavenge on dead or dying arthropods, and also obtain honeydew from various homopterans outside the pitchers (Kaufmann & Maschwitz 2006). Thus it is not surprising that insect exoskeletons can be present in the ants' debris, even though we found very few, unlike Janzen (1974) who stated that *P. myrmecodiae* differs in behaviour from other arboreal ants that throw their refuse out of the entrance. The benefits for the two partners in this mutualism are clear: ants get a safe and spacious home that is easily defended (one small entrance) against other ants. The epiphyte is able to use ant-deposited debris, in addition to faeces and discarded food, as a nitrogen source, although this trophic benefit depends on the self-interested building activity of the ants. In contrast, other myrmecophytes that chase herbivorous insects or remove encroaching vegetation behave specifically to help the plant.

In addition to internal partitions, the ants also build soil runways that connect the entrances of neighbouring pitchers, which can sometimes be extensive (Fig. 7). This accumulation of substrate is also likely to benefit the epiphyte, e.g. short-term water storage for the adventitious roots clinging to the stem. Runways seem to be a general characteristic of *Philidris* nests, including species that are not associated with *D. major* (e.g. Kaufmann 2002). Runways strongly suggest frequent movement of workers and brood between pitchers. Accordingly it is semantic whether a nest corresponds to a single pitcher or one cluster of pitchers, and 'polydomy' must be used with caution. We assume that adjacent pitchers are all part of the same colony but we did not investigate whether there can be other clusters belonging to the same colony on the same tree. Total colony size remained unknown. Kaufmann (2002) states that a colony of *Philidris* sp$_{\text{KfmA}}$37 can reach 18000 workers (based on an estimate of 7 workers/cm^3, obtained from counting workers and brood in six nests).

Asclepiads generally contain poisonous latex which protects against most herbivores. Although Janzen (1974) dismissed protection by the ants, we observed that upon the slightest disturbance a large number of ants streamed out with open mandibles (Fig. 7). A large patrolling force seems advantageous to defend the plant host as well as to gather resources. Moreover, the large workers with proportionally larger heads (i.e. more powerful mandible muscles) can be especially efficient.

Pitchers inhabited by *Crematogaster* ants lacked accumulations of debris. Their partitions are built with vegetable carton, and it is unknown if they can be exploited by the plant roots. It is possible that different ant species compete over pitchers. Beccari (1884) found *D. major* in Java to be inhabited by *Dolichoderus thoracicus* (=*bituberculatus*) or *Crematogaster*

Fig. 7. Soil runways built by the ants to connect the entrances of adjacent pitchers. The central stem of *Dischidia* can no longer be seen.

brevis. Similar to our observations in Songkla, Kerr (1912) collected *Cataulacus granulatus* inside *Dischidia* pitchers in northern Thailand.

Philidris **th01 is an opportunist**

Dischidia major appears widely distributed across SE Asia (Rintz 1980, Weir & Kiew 1986). We collected it in strikingly different microhabitats in Thailand, coastal heathland and high canopy, both exposed locations. Generally, a limiting factor on epiphyte growth is nutrient deficiency. It is possible that mutualism with ants gives *Dischidia* a competitive advantage over other epiphytes in nutrient-poor microhabitats. In other *Dischidia* species that lack pitcher leaves, some roots penetrate *Crematogaster* nests (in cavities inside living branches) by following tunnels used by ants, and 'scavenge' their waste material (Weir & Kiew 1986).

Philidris th01 is distributed throughout Thailand (except the drier eastern part), including disturbed habitats and plantations. Its opportunistic nature is confirmed by the presence of occasional nests in decaying wood or bark near the ground, i.e. away from *Dischidia*. In Sarawak, *P. myrmecodiae* also nests in other epiphytes (*Hydnophytum* and *Myrmecodia*; Janzen 1974). Kaufmann (2002) studied other species of *Philidris* that build carton nests connected by runways, away from *Dischidia*.

Many ant-plants provide trophic rewards (specialized food bodies, or extrafloral nectar) for ants. *Philidris* th01 does not depend on its epiphyte for food, and this may explain the lack of an obligate relationship. Its nesting behaviour resembles that of congeneric species not involved with ant-house epiphytes. Similarly, comparisons with related *Dischidia* species are useful to understand the evolution of this well-matched ant-plant mutualism.

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