

The diversity of ant–plant interactions in the rainforest understorey tree, *Ryparosa* (Achariaceae): food bodies, domatia, prostomata, and hemipteran trophobionts

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Ant–plant relationships, with variability in both intimacy and the trophic structure of associations, are described for the Austro-Malesian rainforest tree genus *Ryparosa* (Achariaceae). The range of associations involves opportunistic interactions between plants and foraging ants, mediated by food bodies, and tighter associations in which ant colonies, tending hemipteran trophobionts, reside permanently in plant structures with different degrees of adaptation to house ants. Our study provides strong baseline data to suggest that *Ryparosa* could become a new model system for examining the evolutionary radiation of ant-related traits. To define the diversity of ant–plant associations in *Ryparosa*, we first present a review of ant–plant terminology and an outline of its use in this study. Field studies of ant interactions with food bodies in myrmecotrophic *R. kurrangii* from Australia and the association between myrmecoxenic *R. fasciculata* and two *Cladomyrma* plant–ant species on the Malay Peninsula provide detailed examples of ant–plant interactions. An examination of herbarium material revealed a diverse range of ant–plant associations in other *Ryparosa* taxa. All 27 species had evidence of food body production, seven species had evidence of stem inhabitation by ants, five species had specialized stem domatia, and the domatia of *R. amplifolia* featured prostomata. Variation in the specificity of *Ryparosa* ant–plant interactions is discussed in relation to known ant partners and other ant–plant associations. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 154, 353–371.

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INTRODUCTION

A PRELUDE: TAILORING TERMINOLOGY FOR THE TRANSITIONALS

Any current study on the association between plants and ants inevitably requires an outline of specific terminology to avoid misunderstandings. Historically, the theory behind plant–ant symbioses has been driven by authors with contrasting views on the mechanisms underlying the association and any perceived costs and benefits for each partner involved. Belt

(1874) and Müller (1874, 1876) were two of the first naturalists to formulate a coherent theory of myrmecophily, stating that plants attract ants by supplying food and/or suitable lodgings for the ants and, in return, the ants defend the plants against their enemies. Other naturalists of the time, including Darwin (1877), Trelease (1881), and Delpino (1886), observed similar interactions, and a theory of mutualistic symbiosis between plants and ants was established. Warburg (1892) proposed the replacement of the term ‘myrmecophilous’ (ant-loving) plants by the term ‘myrmecophytes’ (ant-plants), because the first implies that the plants have, in a sense, a biological interest in being visited by ants. In his definition, myrmecophyte was a more neutral term, denoting plants that form some sort of a steady and regular

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relationship with ants. Warburg (1892) further classified the myrmecophytes into plants offering food ('myrmecotrophic') or lodging ('myrmecodomic'), or both ('myrmecoxenic'). However, the existence of mutualism between ants and plants was widely disputed in the early literature (e.g. Wheeler, 1910; Holmgren, 1911; Bailey, 1923; Wheeler, 1942); von Ihering (1907) (paraphrasing Spruce, 1873, cited in Wallace, 1905: 65) concluded that plants 'have no more use of their ants than dogs do their fleas'.

In current usage, the term myrmecophyte includes Warburg's myrmecodomic and myrmecoxenic plants, whereas myrmecotrophic plants are generally called myrmecophiles; yet, the use of ant-plant terminology is not always consistent. For example, myrmecophily has been used to refer to a general association between ants and any other organism (e.g. plants and insects; Jolivet, 1996, 1998) or for pollination of flowers by ants (van der Pijl, 1955), and the plant features that constitute a domatium are still open to interpretation (e.g. Benson, 1985; Jolivet, 1996; Moog *et al.*, 2003). Likewise, myrmecodomic plants that take up nutrients from their ants (e.g. Janzen, 1974; Rickson, 1979; Huxley, 1982; Treseder, Davidson & Ehleringer, 1995) have also been described as myrmecotrophic (Beattie, 1985; Fonseca, 1994; Solano & Dejean, 2004), providing a different slant on the subject-object relationship of the term. In this study, the variability in the mechanisms underlying the associations between ants and plants required a more informative and focused set of descriptive terminology than the delineations in widespread use in current ant-plant literature. We also felt that the adoption of such terms would be valuable for establishing a better understanding of 'transitional' ant-plants and their place in the evolution of ant-plant interactions, as well as in the developing field of ant-plant sanctions. To avoid the implication of an evolutionary intermediary, the term transitional is used here, *sensu* Brouat & McKey (2000), in a morphological and ecological sense only.

Ant-plants, or myrmecophytes, are thus defined as plants which, during major parts of their life, are con-

tinuously inhabited by ants (Fig. 1). This practical though incomplete definition, however, remains burdened with current philosophical theories on the presence or absence of a mutualistic symbiosis. Although evidence for beneficial ant-plant associations is now accumulating, the existing evidence to assess the fitness consequences of particular associations is still often too meagre. In addition, recent studies have shown that, although some ant partners effectively reduce herbivory, they can also act as parasites that castrate their host (Yu & Pierce, 1998; Izzo & Vasconcelos, 2002; Moog, 2002). In order to avoid assigning the term myrmecophyte a dependence on an unknown outcome of the ant-plant association, the term is used here *sensu* Davidson & McKey (1993), in that it only describes plants regularly inhabited by ants, without implying that host plants actually benefit from the ant tenants. This also includes plants that, in the absence of known specialized structures, are nevertheless regularly inhabited by one or more plant-ant species (*sensu* Longino & Hanson, 1995; cf. Bequaert, 1922). It follows that plant-ants are not just ants inhabiting ant-plants; this would be a circular argument. Traits of plant-ants include: colony foundation by ant gynes in a particular host plant; a more or less strongly developed host specificity; host fidelity, defined here as the tendency of the ant colony to stay on the plant throughout the life of the colony; a high occupancy rate; and intraspecific competition for host plants. Quek *et al.* (2004: 555) introduced the term 'phytoecy' to denote 'the obligate lifelong inhabitation of live plant cavities' by ants. We prefer to use the term 'plant-ants' as defined here because the definition of 'phytoecious ants' by Quek *et al.* is ambiguous. It does not clearly state whether 'obligate' and 'lifelong' refer to the ants, the plants, or both. Furthermore, the definition does not exclude species of ants, such as some species of *Colobopsis*, *Crematogaster*, and *Gesomyrmex*, which obligately nest in live stems, but not necessarily in specific plant taxa; the occupancy rate of the latter can thus be very low. To avoid conflict with existing consensus, myrmecophilic plants are defined here as plants that, whilst providing direct food

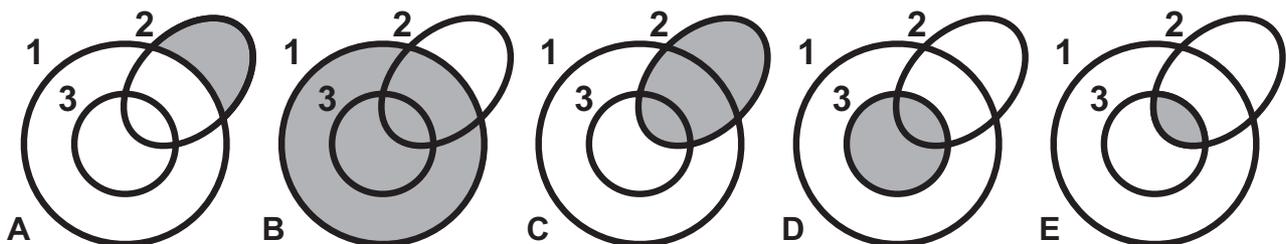


Figure 1. Euler diagrams for ant-plant terminology defined in this study. Conditions involved include ant habitation of the host plant (1), direct food rewards provided by the plant from specialized structures (2) and specialized domatia (3). A, Myrmecophilic; B, myrmecophytic; C, myrmecotrophic; D, myrmecodomic; E, myrmecoxenic.

resources that can be utilized by ants, are not regularly occupied by ant colonies (Fig. 1).

The establishment of nests in ant-plants and the structures with which they are associated are other contentious areas of ant-plant terminology. Lundström (1887) introduced the term 'domatia' to describe plant features that are intended to harbour mutualistic symbionts during an essential part of their development (cf. Jacobs, 1966). This original definition could be equally applied to domatia that are caulinary (e.g. *Cordia*; Yu & Pierce, 1998) or foliar (e.g. *Hirtella*; Izzo & Vasconcelos, 2002), constitutive (e.g. *Leonardoxa*; McKey, 1984) or induced (e.g. *Vochysia*; Blüthgen & Wesenberg, 2001), or occupied by ants (myrmecodomatia; e.g. Fiala *et al.*, 1999) or mites (acarodomatia; e.g. O'Dowd & Willson, 1991). In this study, we restrict the use of the term domatia to 'specialized structures' (i.e. those specifically adapted to house symbionts), rather than general plant features exploited by ants for nesting, and remove the requirement of occupancy by mutualistic symbionts. To differentiate between ant-plants with and without specialized features for harbouring symbionts, we use the term myrmecodomic to refer specifically to plants with domatia (Fig. 1). In reality, the degree of specialization of structures to house ants is often unclear (e.g. Huxley, 1986; Breteler & Nzabi, 1995; Moog *et al.*, 2003), and the application of this term will inevitably be influenced by the extent of knowledge on the developmental morphology of the host plant concerned. In addition to domatia, the other primary factor in ensuring a more reliable presence of ants on the host plant relates to the provision of food rewards. Therefore, the delineation between direct [e.g. food bodies (FBs), extra-floral (EF) nectar] and indirect (e.g. wound sap, hemipteran honeydew) food sources is also important when considering the potential for the host plant to control the flow of resources to its resident ants. Thus, we define myrmecotrophy as the provision of direct food resources by the plant from specialized structures (Fig. 1). As for Warburg's (1892) definitions, we similarly define myrmecoxeny as the combination of both myrmecodomic and myrmecotrophic traits in the same plant species (Fig. 1).

THE DIVERSITY OF ANT-PLANT INTERACTIONS

Early studies on ant-plant interactions tended to focus on systems with classical obligate symbioses, in which the adaptations involved and the benefits of the mutualisms for each partner were somewhat easier to define (e.g. Darwin, 1877; Janzen, 1967, 1969; Fiala *et al.*, 1989). However, there is now an increasing body of work on related members of plant lineages that vary in their ant-related traits, incorporating a range of

interactions from loosely facultative to tight obligate symbioses (e.g. Fiala *et al.*, 1999; McKey, 2000; Blattner *et al.*, 2001). The importance of understanding the place of these 'transitional' plant species in this continuum should not be underestimated, particularly with respect to the evolution of mechanisms that encourage a more reliable ant presence on the host plant (that is, lodging and food rewards). In systems such as *Leonardoxa* (McKey, 2000), *Macaranga* (Fiala *et al.*, 1999), and *Cecropia* (Yu & Davidson, 1997), variation in the intimacy of ant-plant associations can be attributed to evolutionarily modified features of one or both organisms involved, sometimes mediated by additional trophic levels. For example, *Cecropia* taxa display morphological variation in stem development, the presence of prostomata, and functionality of trichilia, and species geographically isolated from the ants they usually host (*Azteca* spp.) have lost many of their myrmecotrophic characteristics (Wheeler, 1942; Janzen, 1973; Rickson, 1977). However, the majority of plant genera in which there is a considerable radiation of ant-plant associations are found in the Neotropics (Davidson & McKey, 1993). In the Austro-Malesian region, *Macaranga* Thouars and *Neonauclea* Merr. are the only species-rich genera known to have considerable variation in their degree of association with co-occurring ant species (Risdale, 1989; Fiala *et al.*, 1999).

The Achariaceae (Flacourtiaceae *pro parte*; *sensu* Chase *et al.*, 2002) is a relatively small family of 30 genera (14 of which are monospecific) found across Asia, Africa, and America. Previously documented ant-plant interactions often consist of a range of unexplained observations detailed as side comments in studies of a different focus. Kohl (1909) reported *Buchnerodendron speciosum* Guerke as having hollow stem apices that supported *Crematogaster excisa* Mayr (identified by Forel, 1909 as *Crematogaster impressa* Mayr), but no evidence of regular ant occupation, plant food rewards, or associated hemipteran trophobionts was observed by Bequaert (1922), and both Kohl and Bequaert believed that *B. speciosum* was only accidentally occupied by ants. Likewise, *Caloncoba welwitschii* Gilg (formerly *Caloncoba laurentii* De Wild. & T. Durand) was also recorded as having hollow stems colonized by ants, although this was thought to be secondary colonization in tunnels made by stem-boring larvae (De Wildeman & Durand, 1899; Gilg, 1908). With respect to myrmecotrophic features, Rouppert (1926) listed *Hydnocarpus kurzii* (King) Warb. (formerly *Taraktogenos kurzii* Craib) as having FBs, based on observations from glasshouse plants, whereas it seems that EF nectaries are absent from the Achariaceae (Koptur, 1992). Detailed analyses of vegetative tissue anatomy are not known for any genus of Achariaceae, which makes it hard to draw

conclusions on how widespread ant-plant traits may be in the family.

Ryparosa Blume, a genus of rainforest trees comprising 27 species distributed from southern Myanmar and the Andaman Islands to New Guinea and Australia, is the genus of Achariaceae that is most frequently reported to have associations with ants. Schumann & Lauterbach (1901) and Mildbraed (1928) reported hollow stems and the presence of ants in *Ryparosa amplifolia* (K. Sch.) Mildbr. [syn. *R. javanica* (Blume) Kurz ex Koord. & Valetton *sensu* Sleumer, 1954; formerly *Gertrudia amplifolia* K. Sch.], and a number of current reviews still refer to the latter original synonym, creating some confusion (e.g. Hölldobler & Wilson, 1990; Jolivet, 1996). More recently, Jarvie & Stevens (1998) described swollen stem domatia in herbarium specimens of *R. porcata* P.F. Stevens and hollow stems without pith in *R. aff. hirsuta* J.J. Sm. and *R. fasciculata* King. Moog and collaborators (Moog *et al.*, 1997; Agosti, Moog & Maschwitz, 1999) identified two species of *Cladomyrma* plant-ants inhabiting *R. fasciculata*, and concluded that the relationship was mediated by large numbers of hemipteran trophobionts in the hollow stems (Heckroth *et al.*, 1998; Moog *et al.*, 2003). Although FBs were not previously known from *Ryparosa*, many early taxonomic papers described the presence of 'tubercles', 'verrucosities', or 'lenticels' on young stems in a range of *Ryparosa* taxa. The recent discovery of two distinct forms of FB in *R. kurrangii* B.L. Webber (Webber, Abaloz & Woodrow, 2007) prompted us to undertake a critical reassessment of the interactions with ants in this poorly known genus. Therefore, the aim of this research was to document the range of plant-ant associations in the genus *Ryparosa*. To achieve this, we focused on two species already being studied for other purposes (*R. kurrangii*, *R. fasciculata*), complemented by a range of material from herbarium collections. More specifically, the objectives were as follows: (1) to test the hypothesis that FB production leads to an increased ant presence in the myrmecotrophic *R. kurrangii*; (2) to quantify the observed nesting behaviour of *Cladomyrma* plant-ants and ant-plant-hemipteran interactions in the myrmecoxenic *R. fasciculata*; and (3) to conduct a detailed study of herbarium specimens to provide a baseline data set on other ant-plant traits in the genus.

MATERIAL AND METHODS

ANT-PLANT INTERACTIONS IN *RYPAROSA KURRANGII*

Ryparosa kurrangii is an understorey tree, endemic to the lowland tropical rainforests of the Daintree region in northern Queensland, Australia (Webber & Woodrow, 2006). Two distinct forms of FB have been

described in the species (Webber *et al.*, 2007). 'Type A' FBs, which correspond to Model III pearl bodies (*sensu* O'Dowd, 1982), are rich in lipids and carbohydrates and are produced on developing plant tissue. 'Type B' FBs are a unique form of lipid-rich multicellular FB that 'open' during development and are found exclusively on mature plant tissue (Webber *et al.*, 2007). *R. kurrangii* does not have hollow stems or other specialized structures which ants can inhabit (Webber, 2005), and nothing is known about ant visitation rates in natural populations. Field studies of *R. kurrangii* FBs were carried out at three separate locations in the Daintree lowlands region of north Queensland, Australia, using three separate methods: field exclusion, glasshouse-grown leaves introduced into the field, and seedling reintroduction trials. Initial leaf introduction trials were conducted at the Australian Canopy Crane site (16°06'S, 145°27'E). The surrounding forest is mesophyll vine forest (MVF, type 2a; *sensu* Tracey, 1982) and does not contain *R. kurrangii* populations in the immediate vicinity. Further Canopy Crane site descriptions can be found in Blüthgen & Reifenrath (2003). Field exclusion trials and further leaf introduction trials were conducted within an *R. kurrangii* population in the Cow Bay valley (Site A; 16°12'S, 145°25'E, 20 m a.s.l.) in MVF (type 2a; *sensu* Tracey, 1982). Seedling reintroduction trials were conducted on private property immediately adjacent to another population of *R. kurrangii* in the Cow Bay valley (Site B; 16°07'S, 145°24'E, 80 m a.s.l.) in complex mesophyll vine forest (CMVF, type 1a; *sensu* Tracey, 1982).

To study field-based FB production, a range of treatments were applied to exclude small invertebrates from leaves in the field. Five mature trees with new leaf growth were chosen, three trees on the edge of canopy gaps and two trees under a closed canopy of approximately 25–30 m. On each tree, three branches between 0.5 and 3.0 m above the ground were carefully examined to remove all signs of invertebrates. Onto two branches on each tree, a drawstring bag (35 × 25 cm) made of fine plastic netting (mesh diameter, 450 × 900 µm; Kathmandu Ltd., Melbourne, Australia) was placed over five to ten leaves at the end of each branch, incorporating a range of newly formed and mature leaves. One bag on each tree also had a coating of Tanglefoot pest barrier (The Tanglefoot Company, Grand Rapids, MI, USA) applied to the branch below the bag (applied onto electrical tape to avoid direct contact with the branch) to stop crawling invertebrates. On the third study branch on each tree, a coating of Tanglefoot was applied to isolate a similar number (five to ten) of leaves at the end of the branch. The treatments were applied on 20th June 2003 and the 15 branches were monitored for 6 months. Inspections were conducted

every 2 weeks with a hand lens to check for FB formation and herbivore damage, and to re-apply Tanlefoot barriers when necessary.

After very little FB production was observed in the field during the exclusion trials, two forms of field introduction of glasshouse-grown material (seedlings described in Webber *et al.*, 2007) were performed. Firstly, entire leaves covered at high density with 'Type B' FBs were air-freighted to the field sites from Melbourne. The lifespan of cut leaves was extended by immersing the petiole in a small vial of water. Two leaf introduction trials were conducted. Four leaves were placed on leaf litter at the Canopy Crane site at dusk on 8th April 2003 and examined for ant activity at dawn the next day. Ten leaves were attached to five mature trees (two leaves per tree) at the Site A population at a height of 0.5–1.5 m at dusk on 15th November 2003. The leaves were monitored at regular intervals (1–3 h, more frequently during heavy activity) for a 36-h period to check for the presence of animals. Secondly, eight seedlings that had been raised in glasshouse conditions, and that were covered in FBs, were re-planted into the existing *R. kurrangii* population at Site B. The seedlings were 40 months old at the time of reintroduction, approximately 80 cm in height, and had been raised under moderate (40% of full sun) or low (10% of full sun) light shade cloth in glasshouse conditions comparable to those described in Webber & Woodrow (2004). In the field, the seedlings were planted in either moderate light (canopy gap) or low light (understorey) environments in a full factorial design, taking into account glasshouse and field light conditions. Every effort was made to conceal soil and leaf litter disturbance caused by planting. Reintroduced seedlings were planted during the late afternoon of 29th March 2004. Regular observations (two to three times per day, more frequently during high activity) were made on animal activity for all seedlings and climatic conditions for 7 days. Identifications of invertebrates were performed on preserved specimens (lodged at the Australian National Insect Collection, ANIC, Canberra and the Tropical Ecosystems Research Centre, TERC, Darwin) or from macro photography when specimens could not be captured. Two weeks after the reintroduction of seedlings into the field, two leaves from each seedling were sampled for a detailed inspection.

ANT-PLANT INTERACTIONS IN *RYPAROSA FASCICULATA*

Ryparosa fasciculata is also an understorey tree, up to 20 m in height, endemic to southern Thailand and the northern half of peninsular Malaysia. It is an uncommon tree, growing in primary and old secondary forest from lowland regions to 900 m above sea level (Sleumer, 1954; J. Moog, pers. observ.). A field survey

of *R. fasciculata* plants was conducted at three main sites on the Malay Peninsula: Belum, Gerik, Perak (5°31'N, 101°25'E), Fraser's Hill, Raub, Pahang (3°43'N, 101°44'E), and Ulu Gombak, Selangor (3°19'N, 101°45'E). At each site, the following characters were studied: plant size and ant occupancy (either by *Cladomyrma* or other ant species; including the presence of colony foundations). Observations were made over a number of years, during daylight hours (between 08:00 and 18:00 h) and in both wet and dry seasons, on a number of *Cladomyrma* colonies occupying *R. fasciculata*, noting any distinctive worker behaviour. Plants of all sizes were examined to determine when ant colonization occurs and if it continues during the life of the host plant. For a subset of these plants, the characteristics of domatia (if present), ant colony size, number of entry holes, and nest chamber length (as a proportion of the total stem length) were measured. Ant collections were preserved in 75–80% ethanol and later identified in the laboratory, following the revision of *Cladomyrma* (Agosti *et al.*, 1999) or, for other ant taxa, the keys of Hölldobler & Wilson (1990) and Bolton (1994).

ANT-PLANT EVIDENCE FROM HERBARIUM SPECIMENS

A detailed examination of herbarium material, sourced from 15 herbaria with significant collections from Malesia (307 specimens identified as *Ryparosa*; details listed in Webber & Woodrow, 2006), formed the basis for our observations of any additional ant-plant features in the genus. Further observations were made on *Ryparosa* collections at Kew (K), The Natural History Museum (BM), and Leiden (L), encompassing all currently described species within the genus (27 species), as well as a number of new species that are yet to be formally described (B. L. Webber, unpubl. data). Between two and 60 specimens per species were available for examination. The herbarium material was examined for entry holes, hollow twigs, swollen stem sections, FBs, Type B FB scars, and any other morphological features possibly associated with ant-plant interactions. Entry holes of *Cladomyrma* ants are usually distinguishable from those made by other ant species or stemborers by their size, regular shape with clearly defined margins, and regular distribution along the twigs. In addition, herbarium specimen labels were checked for descriptions of ant occupation; however, most collectors failed to record any notes on this conspicuous trait. On a subset of herbarium material examined (where at least ten specimens were available for each species), evidence of intact FBs or scars left after the removal of FBs was quantified under magnification ($\times 20$ to $\times 40$). These specimens were classed as having 'conclusive evidence', 'probable evidence', or 'no evidence' of scars

of Type B FBs. In some cases, it was not possible to discriminate conclusively between extensive chewing that had removed large areas of the lower epidermis (generally indicative of heavy FB feeding) and FB scars. In these cases, the specimen was assigned to 'probable evidence'.

RESULTS

ANT-PLANT INTERACTIONS IN *RYPAROSA KURRANGII*

In the three methods of invertebrate exclusion used to study FB production in the field, no FBs were observed on any of the isolated tissue. This included new leaves produced on some of the branches only isolated with Tanglefoot. Minimal new leaf production was observed on bagged branches and some older leaves died whilst contained within the bags. The bags appeared to be quite successful at keeping out invertebrate insects, although, on one occasion, an unidentified phasmid (Orthoptera: Phasmatidae) was found in a non-Tanglefoot bag during routine inspections. In contrast, branches with only Tanglefoot barriers had a number of animals (unidentified slugs, snails, and nymphs of unidentified Auchenorrhyncha) on isolated leaves during random searches. At the conclusion of the experiment, a selection of isolated leaves was sampled and examined under magnification. Distinctive round scars, similar in size to the bases of Type B FBs, were found on the abaxial surface of a number of mature leaves from the unbagged Tanglefoot barrier branches (similar to those in Fig. 2). It was unlikely that these scars would have been missed during leaf inspections at the start of the trial, meaning that it was likely that FBs were formed but removed before being observed.

Initial leaf introduction trials confirmed that FBs were an attractive food source for animals. After placement on leaf litter for 12 h overnight, leaves bearing Type B FBs were covered in a high density (> 100 ants per leaf) of *Pheidole megacephala* (Fabricius) workers from two subcastes. Ants spent a considerable effort removing Type B FBs, and approximately half of the leaf FBs had been partially or fully removed. Some FBs were reduced to a small stub of brown tissue, whereas others had been entirely detached, leaving a flat brown circular scar on the leaf surface. The second leaf introduction trial involved attaching glasshouse leaves adjacent to new leaf flushes on the branches of mature trees in the field. Less than 3 h after the trial began, an *Austrosalomona* sp. nymph (Orthoptera: Tettigoniidae: Conocephalinae: Agraeciini) was observed feeding intensively on Type B FBs. In the following hour, the katydid stripped the leaf of approximately 80% (i.e. more than 200 from a total of c. 250) of its FBs, showing a preference for those more exposed on the lamina rather than midrib FBs. In the early hours of the morning of the first night, another Agraeciine (gen. et sp. nov., ANIC A-1 sp. 2; Orthoptera: Tettigoniidae: Conocephalinae) and an *Ornebius* sp. (Orthoptera: Mogoplistinae) were also observed consuming FBs for periods in excess of 1 h. Considerable numbers of FBs were removed during this period. No activity was observed during the following day; however, observation periods were only every 3 h. On the second night, two more *Austrosalomona* nymphs were observed feeding on Type B FBs on separate leaves placed on different trees. During the entire study, no eating of leaf blades was associated with the feeding of any orthopteran, and all leaf laminae remained intact. No ants were observed during the leaf introduction trials.

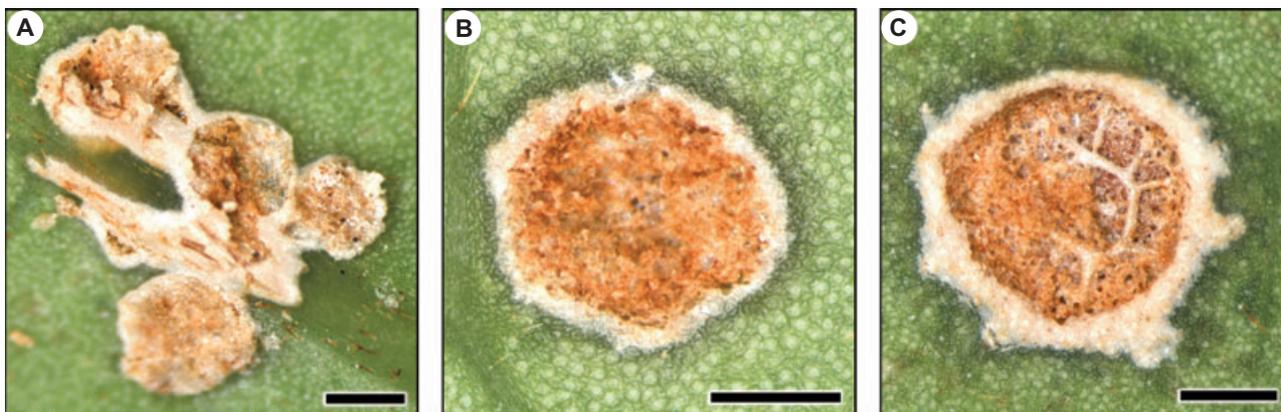


Figure 2. Food body scars remaining on the abaxial lamina of *Ryparosa kurrangii* leaves after removal of Type B food bodies by ants during field reintroduction trials. All food bodies had been at least partially harvested by foraging ants. The degree of food body removal and the resulting scar varied. Some scars had remnants of the food body remaining attached (A), other bodies were entirely removed at the level of the surrounding leaf lamina (B), and some scars resulted in substantial removal of the underlying mesophyll and exposure of leaf veins (C). Scale bars, 500 μ m.

Table 1. Ant species found harvesting on *Ryparosa kurrangii* food bodies in field trials of glasshouse-grown material

Subfamily	Taxon
Dolichoderinae	<i>Leptomyrmex unicolor</i> Emery
Formicinae	<i>Camponotus doryceus confusus</i> Emery; <i>Polyrhachis foreli</i> Kohout
Myrmicinae	<i>Pheidole megacephala</i> (Fabricius); <i>Pheidole</i> sp. A (Group F); <i>Pheidole</i> sp. B (<i>impressiceps</i> group); <i>Pheidole</i> sp. C (<i>longiceps</i> group); <i>Pheidologeton affinis</i> (Jerdon); <i>Tetramorium pacificum</i> Mayr; <i>Vombisidris renateae</i> (Taylor)

Pheidole megacephala was observed only during the leaf introduction trial, whereas all other ant species were observed during the seedling reintroduction trial.

Following the success of individual leaf introductions, entire *R. kurrangii* seedlings ($N = 8$) bearing FBs were reintroduced into gap and understorey locations in the field. Interactions of animals with the introduced plants were rather conspicuous, beginning soon after planting and lasting for the entire observation period. Although these results were not strictly quantified, four clear trends were documented. Firstly, the most common animals, by at least three orders of magnitude, to visit the plants were ants. During the observation period, workers of nine species were observed foraging on FBs present on the trunk and leaves (Table 1). In some cases, workers from multiple subcastes were involved in FB harvesting. All ant species present on plants were observed harvesting FBs, and no other animals were seen directly foraging on FBs. Other animals observed frequently (i.e. individuals present on more than five observation periods) on the seedlings during the trial were crickets (Orthoptera), spiders (Arachnida), and weevils (Coleoptera). Slugs (Gastropoda), cockroaches (Neoptera), and lepidopteran larvae were also present on the seedlings. No direct interactions between any animals on the seedlings were observed, although slugs were the only animals seen in close proximity to foraging ants. Across all seedlings ($N = 8$) for the entire study period, only two bouts of chewing herbivory ($< 3 \text{ cm}^2$ in total on separate seedlings) were noted on seedling leaf lamina tissue.

Secondly, overall ant abundance on *R. kurrangii* seedlings was highly variable. All plants were 'discovered' by ants within 5 h of planting. Ant activity on the seedlings peaked in the first 2 days after planting and then gradually decreased over the next 5 days. By the end of the trial, there was still a continual presence of ants on six of the eight seedlings, although these were spending more time patrolling the plant rather than harvesting FBs. The abundance of ants on the seedlings closely corresponded to the number of FBs remaining on the plants. Relative to the surrounding vegetation, ant abundance on the study seedlings was clearly higher throughout the trial. No distinct patterns were observed in abundance across ant species

between diurnal and nocturnal activity, between gap and understorey planting locations, or between seedlings raised in moderate and low light glasshouse conditions. During the study period, rain fell on five of the seven nights and three of the seven days and temperatures did not fall below $15 \text{ }^\circ\text{C}$. Within this narrow range of observation conditions, climatic parameters appeared to have no effect on foraging, although no observations were made during heavy rain.

Thirdly, the ant species foraging on *R. kurrangii* seedling FBs were temporally and spatially variable with no distinct patterns. The most common ant observed across seedlings, in terms of both density and temporal frequency, was *Tetramorium pacificum* Mayr (Myrmicinae). The species was documented removing FBs during the day and night, which was also the case for *Pheidole* sp. A (Group F; Myrmicinae), *Pheidole* sp. C (*impressiceps* group; Myrmicinae), *Leptomyrmex unicolor* Emery (Dolichoderinae), and *Pheidologeton affinis* (Jerdon) (Myrmicinae). In contrast, *Camponotus doryceus confusus* Emery (Formicinae), *Pheidole* sp. B (*longiceps* group), and *Vombisidris renateae* (Taylor) (Myrmicinae) were only observed at night, whereas *Polyrhachis foreli* Kohout (Formicinae) was only observed during the day. The number of individuals foraging per plant was frequently in excess of 20 for *T. pacificum*, *Pheidole* sp. A, *Pheidole* sp. B, and *Pheidologeton affinis*. In one notable feeding bout, well in excess of 500 *Pheidologeton affinis* individuals from two worker subcastes were harvesting FBs on one seedling (within 24 h of planting; Fig. 3A). Workers of the smaller subcaste of *Pheidologeton affinis* spent the majority of their time harvesting FBs, whereas the larger workers rarely harvested, and, instead, were observed patrolling the plant surfaces in a territorial manner (Fig. 3B). Other ant species were generally present at lower densities of up to ten individuals per seedling.

Lastly, the majority of FBs were removed by ants within the first 5 days. All ant species showed a preference for younger, softer FBs (Type A, unopened Type B), and these were preferentially harvested with relative ease. Considerable effort to remove older and

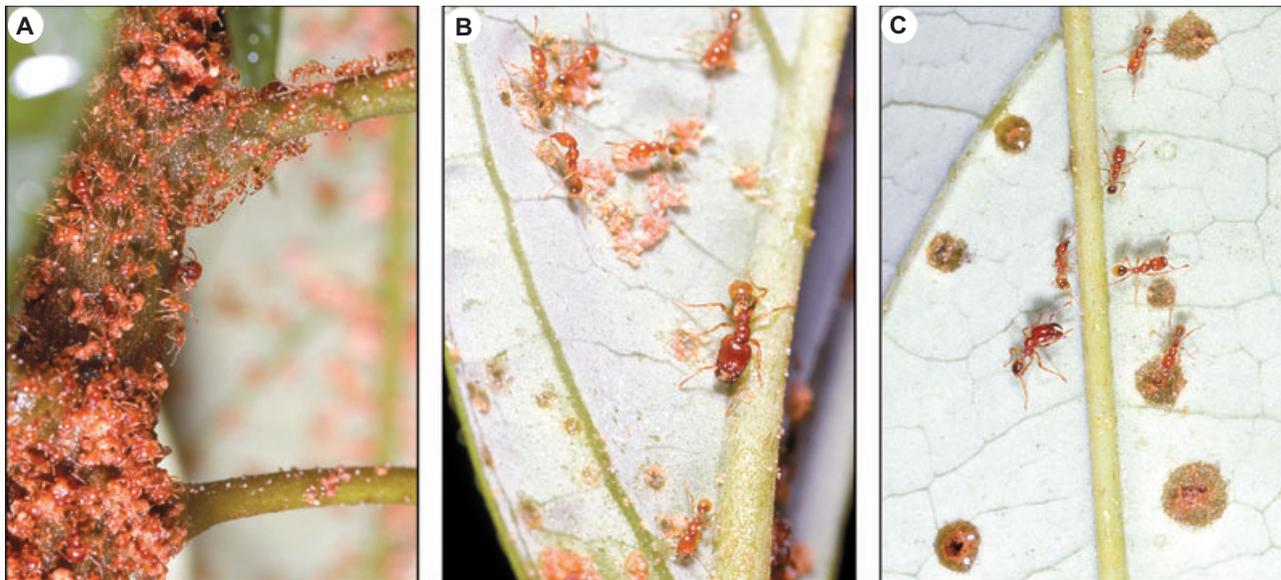


Figure 3. *Pheidologeton affinis* foraging in large numbers on *Ryparosa kurrangii* seedlings during field reintroduction trials. Ants were actively removing food bodies from stem (A) and foliar (B) tissue. Workers of two subcastes were present (B). After removal of unopened Type B food bodies, a wet circular scar remained on the leaf surface (C).

larger FBs was also observed. For example, some ants (e.g. *T. pacificum*) circled around opened Type B FBs, using their mandibles to work away at tissue underneath the FB collar, whilst pulling backwards to provide leverage. Smaller ant species removed portions of opened Type B FBs on the stem and leaves, yet fragments were often still as large as the ant carrying them. In all observed cases, ants left the plant carrying FB material shortly after successful detachment and presumably proceeded back to their nest. During one observation period, *T. pacificum* workers formed a constant trail away from one seedling, traceable for a distance of 1 m. Despite concerted efforts, tracking individual ants through the surrounding leaf litter was generally not successful beyond 0.5 m from the base of the seedling.

After FB removal by ants, leaves from reintroduced seedlings were left with distinctive scarring (Fig. 2). Evidence of Type A FB removal was barely noticeable, even under magnification. In contrast, unopened Type B FBs left a wet circular scar (Fig. 3C), and opened Type B FBs produced a similar scar with less surface liquid. When examined under magnification in the laboratory, it was clear that all Type B FBs had been at least partially harvested by foraging ants (Fig. 2). The degree of FB removal and the resulting scar varied. Some scars had remnants of the FB remaining attached (Fig. 2A), similar to the scar stubs observed in the leaf reintroduction trials. Other FBs were entirely removed at the level of the surrounding leaf lamina (Fig. 2B), whereas some scars showed substan-

tial removal of the underlying mesophyll and exposure of vascular tissue (Fig. 2C).

ANT-PLANT INTERACTIONS IN *RYPAROSA FASCICULATA*

Ants of the genus *Cladomyrma* (*Cladomyrma petalae* Agosti and *Cladomyrma nudidorsalis* Agosti, Moog & Maschwitz) were found to regularly inhabit the stems of *R. fasciculata*. Occasionally, other ant species, such as *Crematogaster* spp., *Tapinoma* sp., and *Camponotus* sp., were observed nesting on *R. fasciculata*, but they either lived in abandoned *Cladomyrma* tunnels or had built small carton nests around branches. Forty-seven *R. fasciculata* individuals were studied in the field (mean \pm SD tree height, 3.5 ± 2.89 m; range, 0.35–16 m), 91.5% of which ($N = 43$) were inhabited by *Cladomyrma* ants. The occupancy rate reached 100% for plants more than 1.4 m in height ($N = 34$).

Ryparosa fasciculata branchlets were slightly thickened at the nodes (Fig. 4A), the thickening probably being required for support of the large leaves (up to 55 cm in length). Although there was no strong swelling of the twigs, the primary diameter of the twigs of small saplings (0.4–1.0 m in height) was usually large enough to allow colony-founding *Cladomyrma* ants to colonize the plant through pith excavation (Fig. 4B). Usually, one entry hole was chewed into each internode, in plagiotropic shoots always on a lateral aspect (as opposed to abaxially or adaxially). The hollowed-out pith canal was large, representing a space of 2.0–3.9 mm in diameter (Fig. 4C). Colony-founding

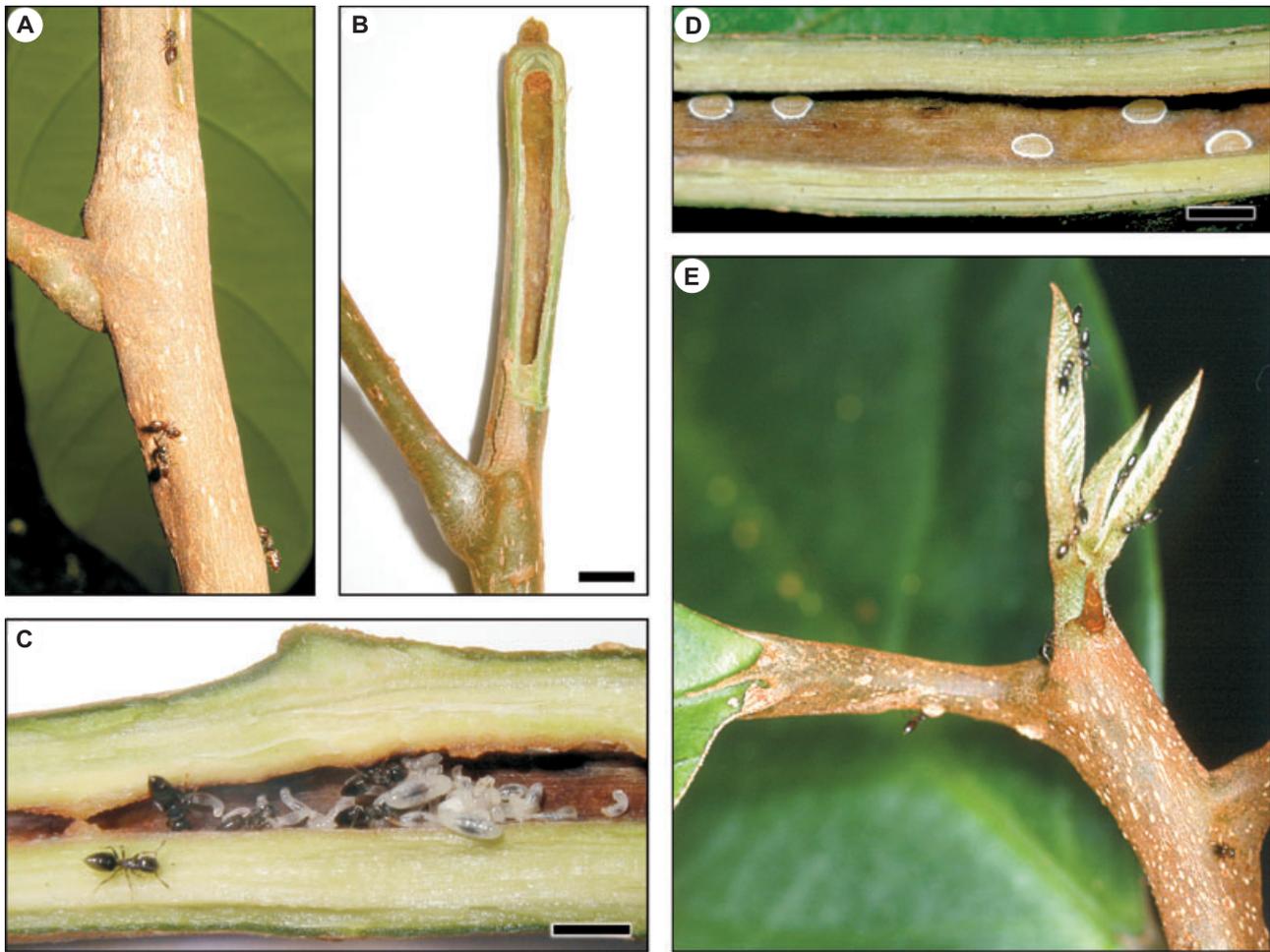


Figure 4. Field observations of ant-plant interactions in *Ryparosa fasciculata*. A, Shoot colonized by *Cladomyrma petalae* with slightly thickened nodes; B, shoot apex with colony founding chamber of *Cladomyrma* queen; C, dissected stem section with *Cladomyrma petalae* ants and brood; D, dissected stem with coccoid (*Paraputo* group; probably *Crenicoccus* sp.) trophobionts; E, *Cladomyrma* workers patrolling the young developing leaves on a colonized shoot tip. Scale bars: B, 5 mm; C, 3 mm; D, 2 mm.

Cladomyrma gynes were already observed in three saplings 0.35–0.4 m in height. As in other host plants of *Cladomyrma*, multiple colonizations of saplings by founding queens were common, but, eventually, a single, monogynous colony monopolized the entire host plant. The first emerging workers enlarged the initial founding chamber into neighbouring internodes. In plants with incipient colonies, the occupied stems were usually separated by sections of solid internodes with intact pith. However, in large plants with established colonies, the solid internodes had been chewed away and the nest formed a continuous, interconnected branched tunnel system throughout the entire host plant, showing no specific preference for orthotropic or plagiotropic branches (although there is no clear differentiation between these two branch categories in *R. fasciculata*). For example, the proportion of a

plant's total stem length hollowed out and occupied increased from 37% to 46% to 85% in trees of 1.15, 2.9 and 3.5 m in height, respectively. Colony size varied strongly according to plant size or portion of the plant occupied (Table 2). Established colonies of *Cladomyrma* reached a size of approximately 3000–5000 workers in trees greater than 5 m in height.

The stem interior not only provided a safe abode for the ant colony, but also served as the feeding substrate for trophobiotic coccoids that were tended by *Cladomyrma* ants. Hemipteran trophobionts entered the *Ryparosa*–*Cladomyrma* association during or shortly after the founding stage. A small sample of trophobionts collected from *R. fasciculata* stems have been so far identified as belonging to the Pseudococcidae [*Crenicoccus cladomyrmae* Williams, *Crenicoccus gullanae* Williams, *Maconellicoccus multipori*

Table 2. Tree height, queen number, ant colony size, number of entry holes, and associated hemipteran trophobionts for *Ryparosa fasciculata* individuals colonized by *Cladomyrma*

Tree height (cm)	Queens (<i>N</i>)	Workers (<i>N</i>)	Stem holes (<i>N</i>)	Colony coccoids (<i>N</i>)
35	1*	75	5	8
52	1	340	7	34
115	1†	134	12	27
235	1	1100	41	143
240	1	~2000	48	188
350	1‡	759	31	92
550	1§	860	29	85
580	1	3760	–	287
650	1¶	245	5	30

*The plant also contained five founding queens in separate chambers, four of which were dead (probably killed by the incipient colony).

†A small hollow twig was occupied by myrmicine ants that inhabited an abandoned *Cladomyrma* chamber; a founding chamber of *Cladomyrma* was empty.

‡Female alates were found.

§Only the crown was colonized; the bole was not hollowed.

¶The colony occupied only a side shoot of the crown. The crown and bole were hollowed out, but the former occupant *Cladomyrma* colony had died.

(Takahashi), and *Pseudococcus aurantiacus* Williams; Williams, 2004], and to the Coccidae [*Coccus macaranga* Morrison and *Coccus secretus* (Morrison); Heckroth *et al.*, 1998]. These coccoids were always restricted to the stem interior (Fig. 4D) and were never observed to be tended by *Cladomyrma* on the outer surface of the host plants. The sugary excreta of the coccoids (honeydew) presumably forms an essential part of the ants' diet, and the successful establishment of a *Cladomyrma* colony on its host appeared to be dependent on the early arrival of the coccoids in colony-founding chambers. The ratio of coccoids to worker ants in occupied *R. fasciculata* individuals was variable (Table 2), ranging from 1 : 5 to 1 : 13 (mean 1 : 9; *N* = 9), but may be dependent on factors such as the ontogeny of the ant colony, the identity of associated coccoid taxa, nymphal stages of the coccoids, or unquantified environmental variables within the study populations of *R. fasciculata*.

The spatial distribution of *Cladomyrma* workers on the surfaces of *R. fasciculata* was significantly biased towards young, immature plant parts (Fig. 4E). We were unable to find any evidence that this concentration of ant activity on young shoots and leaves was coupled with the provisioning of food rewards, such as FBs or EF nectar. For example, on no occasions were *Cladomyrma* workers observed harvesting plant structures easily identifiable as FBs. However, Type B FB scars were present on the young stems and abaxial leaf surfaces of the majority of plants under observation. *Cladomyrma nudidorsalis* and *Cladomyrma petalae* patrolled young leaves in a characteristic and stereotyped way. Patrolling workers walked con-

stantly, but slowly, over the entire leaf (somewhat more on the adaxial surface), appearing to survey or 'lick' the surface thoroughly, even though the leaf appeared clean to the naked eye. If larger particles, such as pith or organic fragments, were encountered, the ants actively discarded them from the plant.

ANT-PLANT EVIDENCE FROM HERBARIUM SPECIMENS

Based on a detailed examination of herbarium material, four distinct forms of ant inhabitation were observed in specimens from eight different *Ryparosa* taxa. These forms were as follows: (1) hollowed stems without swellings; (2) hollowed stems with moderately swollen shoot apices; (3) hollowed, moderately swollen stems with distinctly swollen shoot apices; (4) stem features such as observed in the latter with prostomata. These structures apparently open only superficially and do not reveal the underlying pith.

Firstly, *R. wrayi* King and *R. sp. nov. aff. calotricha* (*sensu* Webber & Woodrow, 2006; syn. *R. aff. hirsuta*, *sensu* Jarvie & Stevens, 1998) specimens were observed to have circular entry holes into non-swollen hollow stem internodes (Fig. 5A). *R. sp. nov. aff. calotricha* is a poorly known taxon from Borneo. Of the four collections of which we are aware, three had excavated stems (one with associated ant carton; Burley *et al.* 686) and entry holes typical of *Cladomyrma* colonization. It is thus possible that this taxon is regularly occupied by ants. Entry holes were only present in a minority of *R. wrayi* specimens examined (five of 40); however, the presence of unidentified ants was confirmed from one specimen (*Geesink et al.* 7200) and

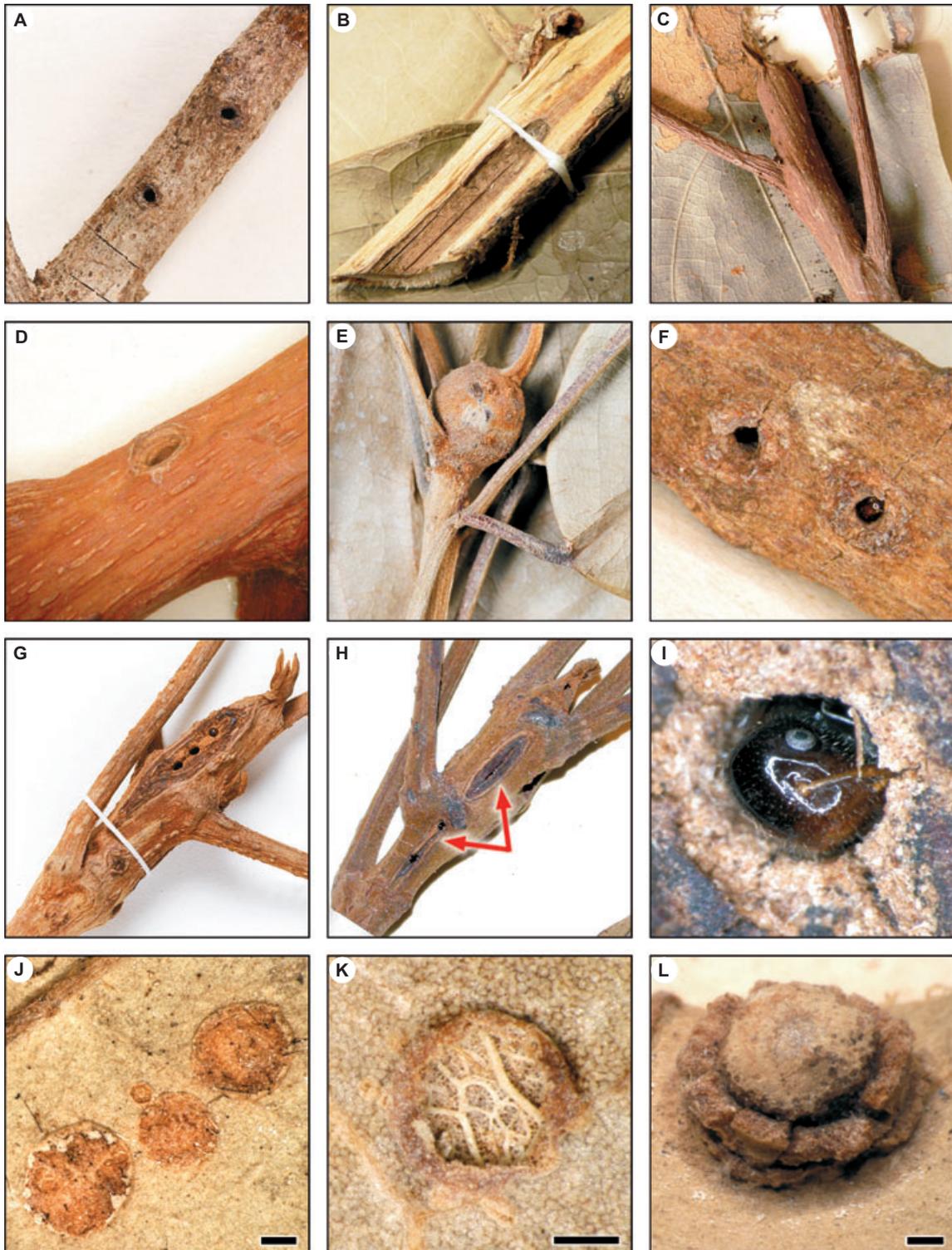


Figure 5. Ant-plant features of *Ryparosa* herbarium specimens. Entry holes (A) and excavated stems (B) in *R. wrayi* non-swollen internodes. Swollen shoot apex (C) and entry holes (D) in *R. fasciculata*. Swollen shoot apex (E) and internode with multiple entry holes and ant exoskeleton (lower hole; F) in *R. anterides*. Swollen shoot tip with entry holes (G) and slit-like prostomata (indicated by arrows; H) in *R. amplifolia*. Unidentified ant specimen in *R. amplifolia* domatia (I). Abaxial leaf lamina Type B food body scars from *R. anterides* (J) and *R. kurzii* (K). An intact Type B food body from *R. amplifolia* (L). Scale bar, 1 mm (J–L).

suggested in others by the blackened inner walls of hollow stems (e.g. *Kerr*, 16252; Fig. 5B). Most colonized stems had more than one entry hole per internode, and a lack of hollow stems not associated with entry holes suggests that hollow *R. wrayi* stems are excavated rather than forming naturally.

Secondly, *R. porcata*, *R. fasciculata*, and *R. scortechinii* King specimens were observed to have moderately swollen shoot apices and internodes with associated entry holes (Fig. 5C, D). It is likely that *R. fasciculata* and *R. scortechinii* (only separated by two traits that are now known to be ambiguous; B. L. Webber, unpubl. data) are the same species, and, as such, they will be treated together here. Domatia features in *R. fasciculata* herbarium specimens mirrored those previously described from field observations, and confirmed that the species is regularly inhabited by ants. In 80% of the collections assigned to *R. fasciculata* ($N = 15$), the stems were hollow and possessed typical entry holes of *Cladomyrma*. *R. fasciculata* was also the only species in which evidence of hemipteran trophobionts was observed. Although *R. porcata* is only known from a very limited number of specimens, our observations support the description of stem domatia and regular ant occupancy by Jarvie & Stevens (1998). Furthermore, ants extracted from the domatia of one specimen (*Ambrainsyah & Arbainsyah*, AA 1979) were identified as *Cladomyrma* sp. It was not clear whether the hollow stems of *R. porcata* resulted from pith degradation or excavation, as all stem material examined was occupied by ant domatia.

Thirdly, *R. calotricha* Mildbr. and *R. anterides* B.L. Webber were observed to have distinctly swollen shoot apices and moderately swollen stems, both with entry holes (c. 1.0–1.5 mm in diameter) into excavated stem sections (Fig. 5E, F). The majority of *R. anterides* specimens (13 of 18) had signs of ant colonization (entry holes, excavated stems), and one specimen (*Kostermans*, 21216) contained an unidentified ant (Fig. 5F). By contrast, only a minority of *R. calotricha* specimens (five of 48) had entry holes and stems with swollen shoot apices, although a significant proportion of the stem material collected appeared to be young tissue at the time of collection.

Lastly, *R. amplifolia* also had distinctly swollen shoot apices and moderately swollen stems (Fig. 5G). However, associated with the swollen shoot apices were elongated prostomata (up to 15 mm in length; Fig. 5H). These slit-like structures appeared to be the favoured sites for entry holes (Fig. 5G, I) and, although a number of slits opened superficially (Fig. 5H), these did not reveal the underlying pith, nor did they provide a gap sufficiently wide for stem entry such that they could be considered functional, self-opening slits. Multiple entry holes were often found on

one slit (c. 5 mm apart), but the size and distribution of entry holes were irregular between specimens, indicating that they were most probably caused by different ant species or by other stem-boring insects. Most specimen stem material was solid; however, without cutting the swollen internode apices, we were unable to provide evidence on whether or not *R. amplifolia* domatia become hollow naturally. Overall, the majority of *R. amplifolia* specimens (29 of 51) had evidence of ant occupation, and a *Camponotus* (probably *rubiginosus* species group) worker was found in one specimen (*Neth. Ind. For. Serv.*, bb25751). There were also three taxa, *R. maycockii* B.L. Webber, *R. multinervosa* Slooten, and *R. hirsuta* (*R. hirsuta* may be more closely aligned with the closely related genus *Eleutherandra* Slooten; B. L. Webber, unpubl. data), which seemed to consistently have hollow stems, most probably caused by the breakdown of pith. We were unable to find any associated evidence of ant occupancy in any of these taxa.

Given that specimen sheets and published literature variously referred to the presence of ‘tubercles’, ‘verrucosities’, or ‘lenticels’ on *Ryparosa* stems and leaves, herbarium specimens were also examined for FB scar evidence. Type B FB scars, similar to those observed from the field reintroduction trial (Fig. 2), were identified from the abaxial leaf laminas of specimens from all *Ryparosa* species (e.g. Fig. 5J, K). Scars were also observed on young stems, petioles, fruit epicarps, and adaxial leaf laminas. Not all specimens had conclusive evidence of FB scars, and from the subset of specimens in which this was quantified, there was considerable variation between taxa (Table 3). The three species with the lowest proportion of specimens having conclusive scarring evidence (*R. amplifolia*, *R. anterides*, *R. calotricha*) were also observed to have ants nesting in hollow swollen stems. Scar densities on the abaxial leaf lamina and young stems varied considerably between specimens, with no trend towards higher scar densities in any particular species. The highest density of FB scars was observed on the abaxial leaf surface towards the basal end of the midrib, whereas large intact Type B FBs were observed on three specimens of *R. amplifolia* (Fig. 5L). These FBs displayed the same ‘column and collar’ morphology (*sensu* Webber *et al.*, 2007) of Type B FBs observed in *R. kurrangii*, although they were considerably larger. In addition, small Type A FBs were found scattered amongst the hairs of fruit epicarps from multiple specimens of *R. kostermansii* Sleumer, *R. amplifolia*, *R. wrayi*, and *R. maculata* B.L. Webber.

DISCUSSION

Our results suggest that the genus *Ryparosa* is highly suitable for development as a new model system to

Table 3. Evidence of Type B food body scars on the leaves of a subset of *Ryparosa* herbarium specimens examined (where $N \geq 10$ for each species)

Taxon	<i>N</i>	Conclusive evidence (%)	Probable evidence (%)	No evidence (%)	Uncertain (%)
<i>R. amplifolia</i> (K. Sch.) Mildbr.*	51	41	12	37	10
<i>R. anterides</i> B.L. Webber*	15	53	20	27	0
<i>R. calotricha</i> Mildbr.†	44	48	14	36	2
<i>R. glauca</i> Ridl.	11	82	0	9	9
<i>R. javanica</i> (Blume) Kurz ex Koord. & Valetton	60	65	7	15	13
<i>R. kostermansii</i> Sleumer	14	93	0	7	0
<i>R. kurrangii</i> B.L. Webber	45	71	7	18	4
<i>R. maculata</i> B.L. Webber	10	80	0	20	0
<i>R. wrayi</i> King†	36	75	8	17	0

'Probable evidence' includes specimens in which it was not possible to discriminate between extensive chewing and unique food body scars. 'Uncertain' indicates that no examination was possible.

*Taxa with regular ant occupation.

†Taxa with occasional ant occupation.

study the evolutionary radiation of ant-related traits. Although detailed field studies are now required to expand upon our initial observations, the *Ryparosa* system may generate independent answers to questions regarding the evolution of protection mutualisms, and may provide a unique contrast to other established systems. Differences between *Ryparosa* species and their ant associations, on the one hand, and previously studied ant-plant systems, on the other, were found in several ant-related plant traits. A study of *Ryparosa* could yield new insights into the factors that influence the intimacy of a particular association, the evolution of ant-lodging structures and their appearance in plant ontogeny, and how different food rewards provided by plants for ants (directly through FBs or indirectly through trophobiont honeydew) shape the ant-plant association.

ANT-PLANT INTERACTIONS IN *RYPAROSA KURRANGII*

The distinct lack of FB presence throughout the field exclusion trial in *R. kurrangii* was somewhat disappointing, but may be explained by two mechanisms attributable to experimental design. The choice of very fine netting to protect FBs from flying insects dramatically reduced the amount of light available to the isolated leaves. Previous studies on other ant-plants have shown that FB production is significantly decreased with low light availability (Dale, 1901; Walter, 1921; Folgarait & Davidson, 1994). Thus, it may be that the reduced light levels inside the exclusion bags were too low for FB production. On the unbagged treatments that excluded ants with Tanglefoot, the lack of FBs but the presence of Type B FB scars suggest that FBs were produced but quickly con-

sumed. The consumption of FBs by flying insects was subsequently noted during leaf reintroduction trials, and has been reported in other ant-plants in the past (e.g. Letourneau, 1990; Jolivet, 1996; Dyer *et al.*, 1999). Therefore, the lack of accumulated FBs on leaves only protected by Tanglefoot was not unexpected. This has clear implications for studies that measure FB production by only implementing methods that exclude crawling invertebrates (e.g. Hatada *et al.*, 2002).

The introduction of single leaves to assess the interactions of invertebrates with FBs in the field allowed observations to be made on a short-term basis only. However, two notable observations were made during these studies. Firstly, the selective harvesting of FBs by orthopteran herbivores and the lack of any associated foliar herbivory suggest that FB tissue may be more palatable than mature (i.e. toughened) leaf tissue to browsing herbivores. Secondly, the documentation of introduced *Pheidole megacephala* workers in the middle of this environmentally sensitive region of National Park and World Heritage areas is a cause for concern. The devastating impact of exotic *Pheidole megacephala* colonies on other tropical ecosystems has been well documented (e.g. Hoffmann, 1998a; Vanderwoude, Lobry de Bruyn & House, 2000). Given that this appears to be a small outbreak and the first documentation of the species in this area, immediate action to control this tramp ant would be appropriate from an ecological as well as a financial viewpoint (Hoffmann, 1998b).

When glasshouse-grown *R. kurrangii* seedlings with large numbers of intact FBs were reintroduced, animal interactions in the field could be observed over a longer period. The resulting interactions between

the FBs and a range of ant species provided conclusive confirmation of the laboratory-based diagnosis of FB production in *R. kurrangii* (Webber *et al.*, 2007). In total, ten different ant species were identified removing FBs, including a wide range of arboreal and ground-nesting omnivorous ants (Table 1). By contrast to myrmecophytic plants that rarely have non-occupying ants present on the plant, myrmecotrophic species are typically associated with a wide range of ant taxa (O'Dowd, 1979; Whalen & Mackay, 1988; Fiala *et al.*, 1994). This diversity in associated ants is generally coupled with a correspondingly varied suite of defensive abilities, nesting behaviour, and foraging strategies. Although the life history of many Australian rainforest ant species remains poorly understood (Andersen & Majer, 2000), the majority of ants found attending *R. kurrangii* are known to nest on the ground but forage widely, including the lower parts of trees and shrubs (e.g. Kohout & Taylor, 1990). FBs on plant stems have been shown to encourage ground-dwelling ants to climb further up the plant (Fiala & Maschwitz, 1992; Fiala *et al.*, 1994), and stems were the primary access point for all ants observed. One exception to the ground-nesting rule was *Vombisidris renateae*, which is a rather rare ant known to nest and forage arboreally. Unfortunately, little else is known about its life history (Taylor, 1989; Bolton, 1991). Whether or not the ants foraging on FBs provide an effective defence against animal herbivores or fungal pathogens remains to be tested; however, significant patrolling and territorial behaviour by a number of taxa indicate that this may be likely.

ANT-PLANT INTERACTIONS IN *RYPAROSA FASCICULATA*

This study shows that an intimate symbiotic association between *Cladomyrma* ants and *R. fasciculata* is maintained from saplings to mature plants of more than 10 m in height (Fig. 4). The frequency of occupation is as high as in the most intimate ant-plant associations (e.g. *Leonardoxa-Petalomyrmex*, McKey, 1984; *Macaranga-Crematogaster*, Fiala *et al.*, 1989). Because the sample size of adult plants was low in this study, it is not yet known whether the observed occupancy rate is maintained in large reproductively mature trees. A decrease in the ant occupation rate with host size has been recorded, for example, in *Crypteronia griffithii* C.B. Clarke, a host of *Cladomyrma maschwitzi* Agosti (Moog, Drude & Maschwitz, 1998). Colony-founding *Cladomyrma* queens effectively find and recognize their uncommon host and, after landing on a suitable young stem, the queen sheds her wings and chews a founding chamber into the internode. Importantly, she does not rely on preformed 'weak spots' (prostomata) or naturally hollow stems to gain access into the host. However, a min-

imum primary diameter of the colonized internode is necessary to allow for the accommodation of founding queens and, because twig primary diameter increases over plant ontogeny (Brouat *et al.*, 1998), plants need to reach a certain size to become a host (Brouat & McKey, 2000, 2001). The slight but distinct stem swellings in *R. fasciculata* certainly appear to facilitate the early colonization of saplings by founding *Cladomyrma* queens, and can be considered true domatia because of this specific housing adaptation. Queens of *Cladomyrma nudidorsalis* and *Cladomyrma petalae* are of similar size (Agosti *et al.*, 1999), and there are no indications yet that the two ant species differ in their colonization ability of young saplings.

The early association of hemipteran trophobionts with *Cladomyrma* colonies on *R. fasciculata* is an important factor in long-term colonization success. *Cladomyrma* queens do not carry coccoids during their nuptial flight; therefore, the nymphal stages of coccoids either enter the founding chamber on their own accord through small secondary slits chewed by the queen, or are collected by the first emerging workers (Moog *et al.*, 2005). Some of the collected coccoid species, such as *Maconellicoccus multipori* and *Coccus secretus*, are known to have a broad host plant range; yet others, such as species of the recently described genus *Crenicoccus*, have been found only in association with *Cladomyrma* ants on a few host species (Williams, 2004). We suggest that the early arrival of honeydew-producing trophobionts is a key trait in the success of *Cladomyrma* host colonization. The acquisition of trophobionts during the initial stage of colony development can secure an essential part of the colony's diet, independent of direct food rewards produced by the host plant. Because trophobionts are also preyed upon by the ants (although this is not known from the *Ryparosa-Cladomyrma* system), the coccoids may also ensure a regular and predictable supply of protein. It remains to be tested how significant, if at all, plant FBs are in the diet of *Cladomyrma* colonies resident on *R. fasciculata*, and whether they even harvest such structures. Because of the rarity of field observations of FBs in *R. kurrangii* and other plant taxa (e.g. O'Dowd, 1982), the lack of observations on ant-FB interactions is not altogether unexpected.

Another conspicuous trait characterized in this study was the strong preference of *Cladomyrma* workers for patrolling young foliage and shoots of *R. fasciculata* (Fig. 4E). This spatial distribution of workers on the plant surface is common to all *Cladomyrma* species studied, irrespective of the host plant taxon (J. Moog, unpubl. data). Because the production of new leaves is linked to the production of ant housing structures, a potential ant-mediated protection of young leaves against herbivores is

facilitated. Although the effectiveness of resident ants in the protection of young leaves against animal herbivores was not tested, *Cladomyrma petalae* is known to significantly reduce young leaf herbivory in other host plants (*Saraca thaipingensis* and *Spatholobus bracteolatus*; J. Moog, unpubl. data). *Cladomyrma* workers were also observed to 'clean' the leaves of *R. fasciculata*, which may suggest an important role in protecting the plant against pathogens and epiphylls. Other studies have proposed such a role for similar behaviour in other ant-plant systems (de la Fuente & Marquis, 1999; Meunier *et al.*, 1999; Heil *et al.*, 2001). In addition, resident ants have been observed to exhibit pruning behaviour in experiments simulating encroachment of vegetation on their host plant (J. Moog, unpubl. data). Although *Cladomyrma* pruning behaviour appears to be subject to a considerable degree of variation (e.g. hardness or age of foreign plant parts touching the stem), *Cladomyrma* workers display an overall behaviour compatible with effective host tree defence.

ANT-PLANT INTERACTIONS IN *RYPAROSA*

It seems that *Ryparosa* can now be confidently added to the growing list of plant genera, such as *Macaranga*, *Leonardoxa*, and *Cecropia*, that have variable, sometimes specialized relationships with ants. The diversity in occupancy rates and lodging features provided by *Ryparosa* taxa may be the result of evolutionary pressures driven by ecologically relevant geographical variation and the corresponding distributions of potential ant partners. From this study, there are strong indications that *R. amplifolia*, *R. anterides*, and *R. porcata* could be considered as myrmecoxenic, based on evidence from herbarium specimens, and that *R. fasciculata* should be considered as myrmecoxenic from both field and herbarium observations. However, early collectors, who are responsible for the majority of *Ryparosa* material lodged in herbaria worldwide, often showed a bias against collecting colonized material because of the logistical complications caused by the associated ants (Stern & Eriksson, 1996). For the rest of the *Ryparosa* taxa with evidence of ant occupation, further field-based observations are required before firm conclusions can be drawn on issues such as colonization rates, primary ant partners, and any secondarily associated ant or hemipteran trophobiont taxa.

With respect to lodging features in *Ryparosa*, all species that showed evidence of colonization (with the possible exception of *R. amplifolia*; see below) appear to have solid stems in which the pith needs to be excavated, with varying degrees of further stem modification. The three taxa with what appears to be naturally degenerating pith, *R. multinervosa*, *R. maycockii*, and

R. hirsuta, showed no evidence of ant colonization. Although this may be partially a result of the limited material available for examination, the combination of naturally hollow stems and FB myrmecotrophy suggests that these taxa could be highly suited to ant inhabitation. Myrmecoxenic species that co-occur with *Cladomyrma* on Borneo and the Malay Peninsula, *R. fasciculata*, *R. porcata*, and *R. anterides*, appeared to be regularly colonized in distinctive stem swellings, which we interpret to be domatia. The infrequent colonization of *R. wrayi* and *R. sp. nov. aff. calotricha* does not appear to take place in any sort of specialized plant feature, and evidence of ant habitation may relate more to the exceptional colonizing ability of the co-occurring plant-ant, *Cladomyrma*.

Three key traits are thought to have resulted in *Cladomyrma* conserving the potential to colonize, over evolutionary time, new hosts possessing no myrmecophytic specializations. Firstly, they are able to gain access to living stems for colony foundation. *Cladomyrma* queens can chew through woody stems and hollow out live stems, and are not dependent on specialized stems with preformed entry holes (prostomata). *Cladomyrma* queens can effectively locate host plants and usually are the first colonizers. This priority of access secures the subsequent monopolization of the host. Secondly, *Cladomyrma* spp. exhibit a strong preference in patrolling activity on external plant surfaces, concentrating on young foliage and shoots, and thereby providing a potential benefit to their host. Thirdly, *Cladomyrma* acquires and maintains an association with (polyphagous) trophobionts, and hence can thrive in plants that provide no direct, specialized food reward. Taken together, these traits may select for the development of caulinary domatia. They may also explain why domatia appear in some *Ryparosa* species and not in others. As pointed out by Brouat & McKey (2000), the origin and timing of domatia onset are crucial factors in the evolution of ant-plant mutualisms. Within species of a lineage, ants may have initially colonized only plants at later stages of development, whose twigs had reached a minimum size. Brouat & McKey (2000) postulated that the early onset of domatia will be favoured by an increasing specialization of ants and plants that enhances both the probability of ant colony establishment and the ability of ants to confer protection.

Outside the distribution of *Cladomyrma*, the New Guinean endemic *R. amplifolia* develops distinctive stem swellings with prostomata. Given that the majority of herbarium specimen stem material was solid, domatia appear to be excavated in *R. amplifolia*. However, in other ant-plant taxa, short swollen stem sections can become naturally hollow with the remaining part of the internode being solid [e.g. Sulawesian and Sumatran *Neonauclea* ant-plants,

Razafimandimbison *et al.*, 2005; Bornean *Myrmeconuclea strigosa* (Korth.) Merr., Maschwitz *et al.*, 1989]. In Davidson & McKey (1993) (referring to Hölldobler & Wilson, 1990), *R. amplifolia* is listed as having naturally hollow stems, although the latter authors do not indicate how the hollow stems are formed. At present, the available evidence does not allow us to determine whether the domatia of *R. amplifolia* become hollow naturally or are excavated by ants or other stem-boring insects. Furthermore, it remains unclear whether this species is regularly colonized by a specialist plant-ant. Hölldobler & Wilson (1990) list *Camponotus* (subgenus *Colobopsis*) sp. dwelling in the hollow stems of *R. amplifolia* s.s., which appears to support the partial identification of ant material in *R. amplifolia* specimens in this study. Some *Colobopsis* species have been recorded from other Asian plants, especially from ant-plants in the genus *Macaranga* (Federle, Fiala & Maschwitz, 1998; Maschwitz, Fiala & Dumpert, 2004) and from an unidentified *Uncaria* (Rubiaceae) climber, whose status as an ant-plant is not clarified (Moog *et al.*, 2003). Although it may just be an artefact of selective specimen collecting, the low rates of colonization in *R. calotricha* specimens may reflect opportunistic colonization by *Camponotus* rather than true myrmecophytism, as the distributions of *R. calotricha* and *R. amplifolia* overlap in eastern New Guinea.

The examination of herbarium specimens for the distinctive Type B FB scars clearly showed that myrmecotrophy in the genus is not restricted to *R. kurrangii*. All *Ryparosa* taxa had evidence of Type B FB scars, and *R. amplifolia* specimens were also observed with large intact Type B FBs (Fig. 5). In the past, FB scars have been interpreted as lenticels and their density has been used to differentiate between taxa (Sleumer, 1954); it is likely that such conclusions would be inappropriate now. Interestingly, myrmecotrophic *Ryparosa* species had the lowest proportion of specimens with conclusive evidence of abaxial lamina FB scars (Table 3). This may suggest that FB production is decreased in these species, perhaps in response to food sources provided by hemipteran trophobionts. Decreasing FB production would appear at odds with ensuring maximum efficiency in ant patrolling. In the only species in which it has been confirmed that resident ants tend trophobionts, *R. fasciculata*, ample evidence of FB scars has been found on both field and herbarium material, but FBs have never been observed being harvested or aggregated in domatia by resident *Cladomyrma petalae* and *Cladomyrma nudidorsalis*. Alternatively, FB scars may be able to heal if harvesting occurs when the FBs are small. The likelihood of FB removal at an immature stage would be greatest in species with a resident ant colony (more

consistent patrolling), which may explain the decrease in scars on these specimens.

CONCLUSIONS

This study builds on fragments of information from the past 100 years that have alluded to ant-plant interactions in *Ryparosa*, but have failed to elucidate the suite of underlying mechanisms (Schumann & Lauterbach, 1901; Mildbraed, 1928; Heckroth *et al.*, 1998; Jarvie & Stevens, 1998). Here, we have presented clear baseline data that establish this genus as one of considerable diversity with respect to ant-plant features. Within the genus, there appears to be a considerable range of ant-plant traits: purely myrmecotrophic species (e.g. *R. kurrangii*), myrmecotrophic species that may also be myrmecophytic (e.g. *R. wrayi*), myrmecoxenic species (e.g. *R. anterides*), and myrmecoxenic species with prostomata (e.g. *R. amplifolia*) or associations with hemipteran trophobionts (e.g. *R. fasciculata*). Unfortunately, existing taxonomic uncertainties and the need for a generic revision, combined with very poor knowledge and limited collections of taxa distributed in more remote locations, mean that gaining a comprehensive understanding of *Ryparosa* ant-plant interactions may take time. However, with enlightened research combining the phylogenies of both partners in ant-plant interactions in mind (e.g. Chenuil & McKey, 1996; Quek *et al.*, 2004), the first logical step in developing the *Ryparosa* system may be to tackle the outstanding taxonomic issues as part of a wider phylogenetic treatment of associated ant-plant interactions.

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