Domatia as most important adaptations in the evolution of myrmecophytes in the paleotropical tree genus *Macaranga* (*Euphorbiaceae*)

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Abstract: The paleotropical tree genus *Macaranga* (*Euphorbiaceae*) comprises all stages of interaction with ants, from facultative associations to obligate myrmecophytes. In SE.-Asia food availability does not seem to be the limiting factor for the development of a close relationship since all species provide food for ants in form of extrafloral nectar and/or food bodies. Only myrmecophytic *Macaranga* species offer nesting space for ants (domatia) inside internodes which become hollow due to degeneration of the pith. Non-myrmecophytic species have a solid stem with a compact and wet pith and many resin ducts. The stem interior of some transitional species remains solid, but the soft pith can be excavated. The role of different ant-attracting attributes for the development of obligate ant-plant interactions is discussed. In the genus *Macaranga*, the provision of nesting space seems to be the most important factor for the evolution of obligate myrmecophytism.

Many plant species in the tropics live in close relationship with ants. A wide range of plants produce food as carbohydrate rich secretions from extrafloral nectaries and/or from nutrient rich tissue as food bodies which attract ants. Many plants also provide cavities that consistently host ant nests. BEQUAERT (1922) and WHEELER (1942) reviewed the enormous variety of these plant chambers. The term "(myrmeco)domatia" is used for all structures that appear to be adaptations facilitating ant nesting (originally introduced by LUNDSTROEM 1887, in regard to acarodomatia on leaves). The associations of ants with plants vary from occassional and facultative relationships to very tight mutualistic systems which are specific and obligatory for all partners involved. That obligatory ant inhabitants can fulfil an important function for plants such as protection against herbivores and plant competitors has been demonstrated (reviews, e.g., BUCKLEY 1982, BEATTIE 1985, HUXLEY 1986, JOLIVET 1986, KEELER 1989, HÖLLDOBLER & WILSON 1990). Ants which come to the plants only for foraging, provide less advantages than those permanently present.

During the last years we have studied such a mutualistic ant-plant association in SE.-Asia, mainly on the Malay Peninsula: Here species of the paleotropical tree

genus *Macaranga* Thou. (*Euphorbiaceae*) live obligatorily together with a few ant species, mainly of the *Crematogaster borneensis*-group. The ants cultivate coccids inside the stem which are also restricted to this myrmecophytic system. The colonizing ants depend entirely on their host plants (Fiala & Maschwitz 1990). They protect their plant partners against herbivore damage and plant competition which is of great importance since the majority of the myrmecophytic *Macaranga* species occurs in habitats rich in fast growing vines (Fiala & al. 1989, 1991). *Macaranga* is the world's largest genus of pioneer trees with its centre of distribution in the Malesian region (Whitmore 1979). It can be regarded as the SE.-Asian analogue of *Cecropia* Loefl. (*Cecropiaceae*) from the American tropics (Fiala & al. 1991).

The genus *Macaranga* in Malaysia comprises the full range of species from non-myrmecophytes over intermediate forms to obligatory ant-inhabited species. This taxon is therefore especially suited for the study of the interspecific variation and the evolutionary development of myrmecophytism. What features led to the evolution of myrmecophytic plants, which often have obligate and species-specific associations? As we have pointed out elsewhere (Fiala & Maschwitz 1991, 1992), all non-myrmecophytic *Macaranga* spp. as well as the closely related genus *Mallotus* Lour. studied by us in Malaysia produce extrafloral nectaries and/or food bodies. Nonetheless only 23 of 52 *Macaranga* species in Malaysia (Peninsula and Borneo) are colonized by ants.

Here we compare presence and structure of cavities for nesting space in the genus *Macaranga* in Malaysia and assess their possible consequences for the evolution of obligatory interactions with their ant partners.

Material and methods

The general framework in which this study was conducted has been described elsewhere (Fiala & al. 1989; Fiala & Maschwitz 1990, 1991, 1992). The study was carried out during 1985–1990 covering a total of 16 months in various parts of the Malay Peninsula and Borneo (in a wide habitat spectrum from lowland swamp forest to mountainous regions). The stem structure of 35 *Macaranga* species was studied in the field (3–25 specimens of each species). We cut the stems of saplings of different sizes (10 cm to 1 m) and recorded cavites, pith structure, and presence of resin. Exemplarily transverse and longitudinal stem sections of *M. triloba, M. hosei,* and *M. tanarius* were studied under the microscope. For comparison we studied 5–10 specimens of species of the closely related genus *Mallotus* Lour. [*M. paniculatus* (Lam.) M. A., *M. macrostachyus* (Miq.) M. A., *M. leucodermis* Hk. fil.] and other common euphorbs:

Elateriospermum tapos Bl., *Endospermum diadenum* (Miq.) Airy Shaw, *Croton argyratus* Bl., *C. caudatus* Geisel, occurring in the same habitats. Presence of ants and the degree of their association with the plants were checked on all plants studied. In addition to the field investigations information on stem structure was obtained by studying the extensive material at the herbarium of the Forest Research Institute Malaysia, Kepong, Selangor (KEP). We also compiled information from original descriptions in the literature, especially for species not encountered in the field.

Identification of *Macaranga* and specific classification follow Whitmore (1967, 1973, 1975). Voucher specimens are deposited at the herbarium in Kepong, Malaysia (KEP) and in the collection of the first author.

Results

Myrmecophytic *Macaranga* species. In Malaysia 23 species can be regarded as obligate myrmecophytes (Table 1). 17 of these species offer hollow stems as nesting

sites for ants. Plants over > 1 m tall were usually colonized to more than 80%. Most young myrmecophytic *Macaranga* plants start being colonized by their obligate ant-partners when they are about 10 cm tall. At the stage the plants become inhabited by ants, usually only few secondary growth processes have taken place. In still unoccupied young stems all internodes from the second internode on may already be hollow because the thin-walled parenchymatic pith tissue has lost its cell contents and form, so that only dry flaky cell walls are left. In the region of the young shoot-apex, the epidermis and cortex are thin (about 0.5 mm) and the pith tissue is still turgid with cytoplasm contributing to the mechanical support of the internode. These top internodes initially remain uninhabited. Transverse section through the freshly colonized hollow internodes showed a rather thin cortical layer and vascular tissue hence forming a rather large cavity. The epidermis was still intact, the primary cortex consisted of 2–3 collenchyma layers, followed by about 6–9 layers of parenchyma. The vascular cylinder showed first secondary phloem and xylem elements, followed by degenerating parenchymatous pith tissue in the centre. Embedded in the cortical layer and pith parenchyma were resin vessels but no closed ring was formed, thus leaving spaces in between. There the ants chew entrance holes into the stem wall (Fig. 1). The resin channels are rather weakly developed in young plants, but become more obvious in older plants due to ramification of the ducts. Inside the stem often continuous connections between the internodes (Fig. 2) are made by biting through the nodal septa.

Non-myrmecophytic *Macaranga*. Most of the *Macaranga* species in Malaysia are not inhabited by ants (Table 1). Although there are always ants visiting the plants we did not find evidence for any species specific association or nesting of ants on these non-myrmecophytic *Macaranga*. Only myrmecophytic *Macaranga* were associated with one specific ant-partner whereas the non-myrmecophytic species were visited by a broad range of different ant species also found on other plant species in the vicinity (details FIALA & MASCHWITZ 1991). The stem morphology of these non-myrmecophytes differed considerably compared to ant-inhabited species. None possessed hollow stems (see Table 1). The structure of the stem was characterized by a rather thick cortex with a multi-layered collenchymatic cylinder, and a very thick pith tissue in the stem centre which varied specifically from rather spongy soft cells to very hard and compact ones. In larger plants very much secondary xylem with sclerenchymatic strains is produced and the stem is therefore strongly lignified. The most common feature also in young plants are the densely packed resin rings which secrete large amounts of a sticky gum-like fluid when injured (Fig. 3). Stems of some species, e.g., *Macaranga conifera* and *M. indica*, produce relatively little gum but have a very thick secondary xylem layer with many lignified xylem parenchyma cells. In *M. heynei*, for instance, younger stem parts are filled with pith containing resinous vessels whereas older parts are strongly lignified due to extensive secondary thickening processes (Fig. 4). In contrast to the myrmecophytic species the xylem tissue is much thicker and the pith remains compact. Young plants of *M. heynei* and *M. conifera*, however, often have very thin stems (< 5 mm) which also prevent ant-colonization.

Transitional species. At present we regard seven of the Malaysian *Macaranga* species as intermediate between the myrmecophytes treated above and the non-myrmecophytic species: *M. hosei*, *M. pearsonii*, *M. pruinosa*, *M. puberula*, *M.*

Table 1. Important stem structure characters of *Macaranga* species in Malaysia. Species according to WHITMORE (1975); all specimens were saplings up to 2 m. *M* Myrmecophyte, (*M*) transitional species, *N* non-myrmecophyte; *S* secondary habitats; *P* primary forests. Stem: *solid* centre filled with compact pith; *lignified* strong layer of hard xylem elements; *resin* many resin channels in cortex and pith parenchyma

Species	Association with ants	Stem structure	Main habitat
1. Sect. *Pachystemon* s. str.			
M. aetheadenia AIRY SHAW	M	hollow	P, S
M. beccariana MERR.	M	hollow	S, (P)
M. calcicola AIRY SHAW	M	hollow	?
M. constricta WHITMORE & AIRY SHAW	M	hollow	P, S
M. havilandii AIRY SHAW	M	hollow	P, (S)
M. hulletii KING ex HOOK. fil.	M	hollow	S, P
M. hypoleuca MUELL. ARG.	M	hollow	S, P
M. indistincta WHITMORE	M	hollow	P, (S)
M. kingii HOOK. FIL.	M	hollow	S, P
M. lamellata WHITMORE	M	hollow	P
M. motleyana MUELL. ARG. subsp. *griffithiana* (MUELL. ARG.) WHITMORE	M	hollow	S, (P)
M. petanostyla AIRY SHAW	M	hollow	P
M. trachyphylla AIRY SHAW	M	hollow	P, S
M. triloba (BL.) MUELL. ARG.	M	hollow	S, P
M. depressa MUELL. ARG.	N	solid	?
M. quadricornis RIDLEY	N	solid, resin	P, S
M. recurvata GAGE	N	solid, resin	S, P
2. Sect. *Pachystemon* s. lato			
M. caladiifolia BECC.	(M)	hollow, sometimes solid	S, P
M. puncticulata GAGE	(M)	hollow, sometimes solid	S, P
M. rostrata HEINE	(M)	solid; soft, dry pith	P, S
M. curtisii HK. FIL.	N	solid, strongly lignified	P, S
3. *pruinosa*-group			
M. hosei KING ex HK. fil.	(M)	solid; soft, dry pith can be excavated	S, P
M. pearsonii MERR.	(M)	solid; soft, dry pith can be excavated	S, (P)
M. pruinosa (MIQ.) MUELL. ARG.	(M)	solid; soft, dry pith can be excavated	S
M. puberula HEINE	(M)	solid; soft, dry pith can be excavated	P, S

Table 1 (continued)

Species	Association with ants	Stem structure	Main habitat
4. Sect. *Pseudo-Rottlera*			
M. andamanica KURZ	N	solid, lignified	P, (S)
M. baccaureifolia AIRY SHAW	N	solid, lignified	P
M. lowii KING ex HK. fil.	N	solid, lignified	P, (S)
M. setosa GAGE	N	solid, lignified	P
5. Sect. *Stachyella*			
M. amissa AIRY SHAW	N	solid, lignified	P, S
M. conifera (ZOLL.) M. A.	N	solid, lignified, thin stem	P, S
6. Sect. *Javanicae*			
M. costulata PAX & HOFFM.	N	solid, dry pith	S, (P)
M. heynei I. M. JOHNSTON	N	solid, lignified, thin stem	S
M. kinabaluensis AIRY SHAW	N	solid, dry pith	P, (S)
7. Sect. *Winklerianae*			
M. winkleri PAX & HOFFM.	M	hollow	S
M. winkleriella WHITMORE	M	hollow	?
Individually distinctive			
M. denticulata (BL.) M. A.	N	solid, lignified	S
M. diepenhorstii MIQ. (MUELL. ARG.)	N	solid, resin	S, (P)
M. gigantea (RCHB. fil. & ZOLL.) M. A.	N	solid, resin, very sticky	S, (P)
M. indica WIGHT	N	solid, resin, lignified	S, P
M. tanarius (L.) MUELL. ARG.	N	solid, resin	S
M. trichocarpa (RCHB. fil. & ZOLL.) M. A.	N	solid, resin	S

rostrata, *M. caladiifolia*, and *M. puncticulata*. The stem structure of *M. caladiifolia* and *M. puncticulata* remains unclear since all specimens found by us were hollow, even when not ant-inhabited. However, these species were as well recorded to be solid (WHITMORE 1967). The stem interior of the other intermediate species does not become hollow by itself but remains solid. However, the pith is soft and dry and the ants excavate it, thus forming internal cavities (Fig. 5). It takes up to five hours for a founding queen to chew her way into the interior and she runs a high risk of predation or parasitoid attack during this time. In these species only plants about 70 cm tall or larger provide sufficient nesting space due to thickening of the volume of the pith tissue, while younger ones can not be colonized. Before the colonization by their specific *Crematogaster* ant partner the young plants are, however, visited by a variety of ant species attracted by extrafloral nectaries. These nectaries are reduced on leaves which develop at the same plant size at which usually colonization becomes possible.
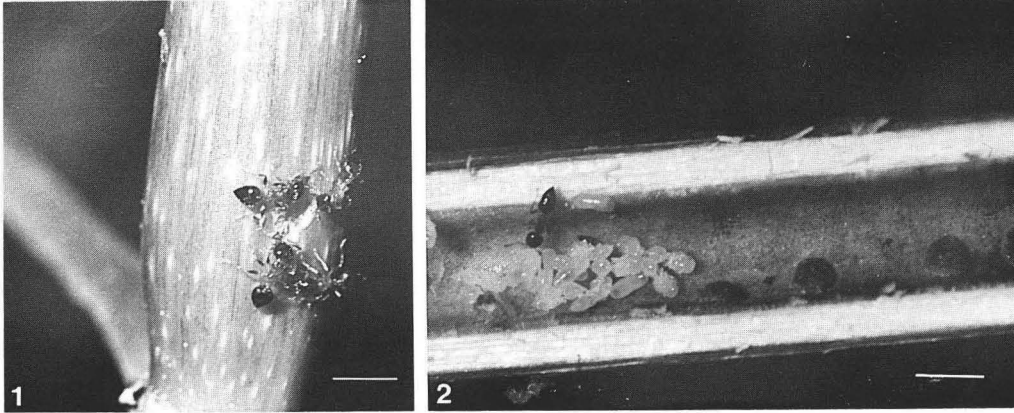
Fig. 1. *Crematogaster borneensis* workers chewing an entrance hole in a new internode of their *Macaranga triloba* host plant. Bar: 2.8 mm

Fig. 2. View into the stem interior of *Macaranga triloba* with ant brood and scale insects. The colonizing ants have connected the internodes by biting through the nodal septum. Bar: 3.2 mm
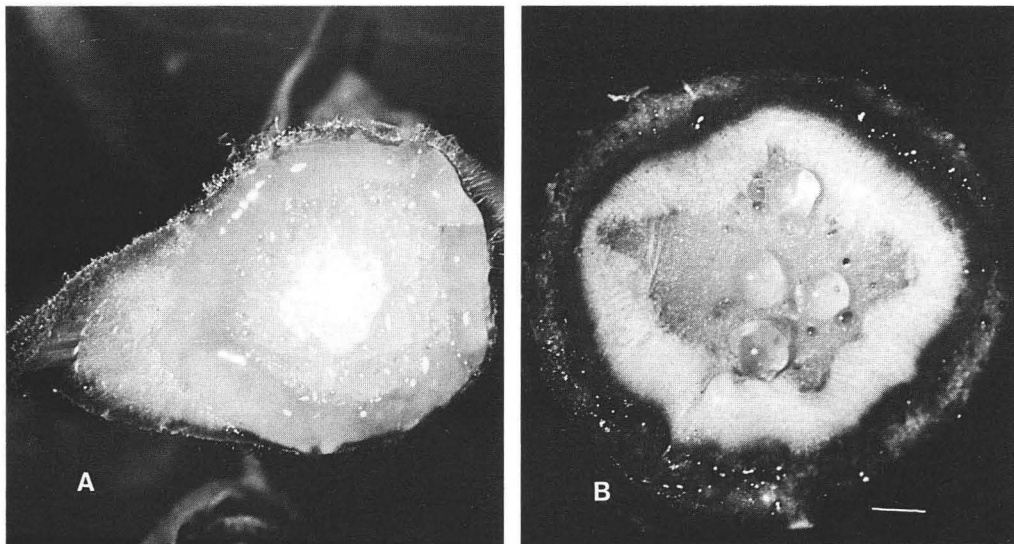

Fig. 3. Secretion of sticky fluid after stem injury (transverse section) of the stem of *a Macaranga gigantea* and *b M. diepenhorstii*. Bar: 2 mm

The percentage of ant-occupation in these transitional species is lower than in typical myrmecophytes (78–51%, cf. Fiala & al. 1991) and sometimes only parts of the plants are colonized.

Fig. 6 shows the main plant-attributes characteristic of the different levels of ant-association in the genus *Macaranga*.

Other *Euphorbiaceae*. Predispositions for myrmecophytism are present also in other *Euphorbiaceae* in Malaysia. For comparison we looked at three other euphorb
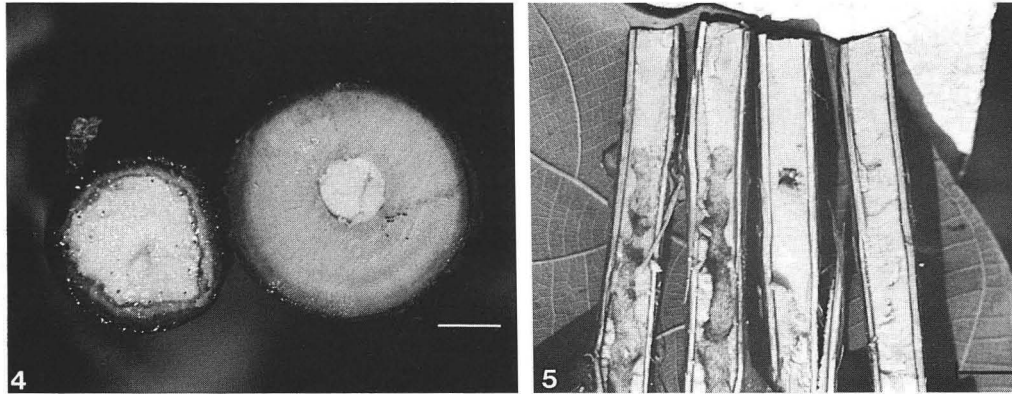
Fig. 4. Transverse section through stem of *Macaranga heynei*. Left side younger part, right older lignified stem part. Bar: 2 mm

Fig. 5. Longitudinal section through the stem of the transitional species *Macaranga pruinosa*. Uninhabited part of the stem filled with soft and dry pith (right side), ant-occupied parts of the stem excavated (left side). Bar: 3 cm
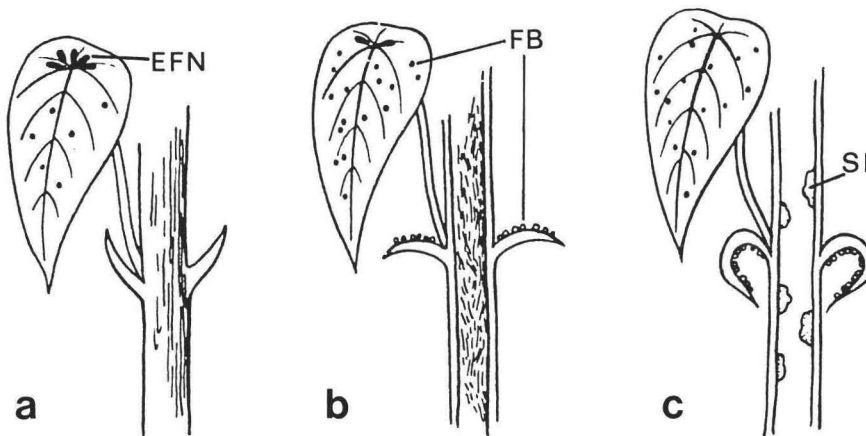

Fig. 6. Sketch of the steps in the development from unspecific interactions to obligate relationships with ants in the genus *Macaranga*. *a* **Non-myrmecophytes** with unspecific ant-associations. The plant produces extrafloral nectaries (EFN) and food bodies (FB) on the leaves. The stem is solid and filled with compact pith and resin ducts. *b* **Transitional forms.** Extrafloral nectaries are reduced, food bodies become concentrated on the adaxial side of stipules. The stem interior contains soft and dry pith, which can be excavated by ants. *c* **Obligate myrmecophytes.** Extrafloral nectaries are lacking, food bodies are produced mainly on abaxial side of the stipules. The stem is hollow and usually inhabited by ants and their scale insects (SI). (Schematic generalization of species, but based on *Macaranga tanarius, M. hosei*, and *M. hullettii*, resp.)

tree genera occurring in the same habitats as *Macaranga* which are facultatively associated with ants. The closely related genus *Mallotus* provides food for ants in form of extrafloral nectar and food bodies (FIALA & MASCHWITZ 1991, 1992).

However, no nesting takes place in the investigated species. The stem of all *Mallotus* species is hard and solid, and has only very little parenchymatic pith in the centre, thus being an effective barrier for colonization. A similar stem structure also occurs in *Croton agyratus* and *C. caudatus* which provides extrafloral nectar fed on by ants but no ant-colonization exists. Many ants visit the conspicuous extrafloral nectaries on the leaves of *Elateriospermum tapos*. These trees produce copious white, sticky latex which also prevents ant-colonization.

Another related genus is *Endospermum* from which two myrmecophytic and two facultatively ant-associated species have been recorded, none of which occur in Malaysia (SCHAEFFER 1971). These myrmecophytic species have a solid stem with a soft pith which is excavated by the associated *Camponotus quadriceps* ants. In Malaysia two species occur which are never inhabited by ants. The pith in the stem of these Malaysian species also consists of very soft thin-walled cells which could easily be excavated. The rather thin cortical layer without sclerenchymatic elements should not be a barrier for ants. Actually, sometimes ants were found nesting inside stem cavities perhaps excavated by stem boring caterpillars or beetles. However, no close relationship between *Endospermum* and ants has developed in Malaysia despite the provision of food in form of extrafloral nectar which is fed upon by various ant species.

Discussion

The significance of plant-attributes for ant-plant-interactions. Nesting space, especially in the tropics, is an important resource which is in short supply and thus very much competed for. Only part of the arboreal ant species is able to actively produce nesting space with the help of carton or silk (MASCHWITZ & al. 1985, 1991 a). The others are competing for the temporal available natural nesting space, mostly in dead wood before its rapid decomposition. WILSON (1959, 1987) regards nesting space as one of the most important regulative factors for colony size of ants in rain forests. Therefore, provision of permanent cavities should play a decisive role in the evolution of myrmecophytic systems.

Our studies on Malaysian ant-plant associations revealed different evolutionary levels of myrmecophytism: for instance, the numerous species of the genera *Myrmeconauclea* MERR. and *Nauclea* L. (*Rubiaceae*) provide stem domatia but no food. Many different ant species may use this nesting space in an opportunistic manner (MASCHWITZ & al. 1989). Some plants have developed closer and more specific but facultative associations with ants as it is the case in *Crypteronia griffithii* CLARKE (MASCHWITZ & al. 1991 b). On the other hand there also exist highly specific systems on an obligate mutualistic basis such as in the *Macaranga* association treated here, where nesting space and food are provided by the plant (FIALA & MASCHWITZ 1991, 1992; FIALA & al. 1991).

Even the not ant-inhabited *Macaranga* species produce extrafloral nectar and/ or food bodies which are collected by various ant species (FIALA & MASCHWITZ 1991, 1992). This could be regarded as a first step for a facultative association with ants which may already result in some protection for the plants (unpubl. results). However, no **obligate** and **specific** ant-plant association occurs in those *Macaranga* species which offer **only** food. Food provision by the plants certainly enhances attraction of the ants but ants can instead tend homopterans on plant species

offering no food. Therefore, another important factor for the evolution of myr-mecophytic relationships has to be taken into consideration: the availability of nesting space.

Importance of stem structure. Results presented here show that indeed stem morphology is an important factor in the obligatory ant-colonization of *Macaranga* plants. All non-myrmecophytic *Macaranga* species in Malaysia have solid stems, often with resin ducts being an effective barrier for ant colonization. In contrast, most myrmecophytic *Macaranga* species provide hollow stems as nesting sites. The transitional species are solid, but their soft pith can be excavated. Also other features like extrafloral nectaries and food bodies showed the intermediate position of these species (see Fig. 6) (FIALA & MASCHWITZ 1991, 1992). The positive protective effects of ant colonization as proven for the other myrmecophytic *Macaranga* were less clear-cut in these "transitionals", especially in *M. pruinosa*: usually only parts of the plants were colonized which was reflected in a higher amount of herbivore damage and vine growth in this species (FIALA & al. 1991). In this context it is interesting that *M. pruinosa* is not recorded to be ant-inhabited in Borneo and Sumatra. Also the transitional species *M. caladiifolia, M. puncticulata*, and *M. rostrata* are in some regions of Malaysia not colonized by ants (WHITMORE 1975, 1982).

Our results on *Macaranga*, that domatia are more important for the evolution of myrmecophytes than food sources, are supported by studies of McKEY (1989) in the leguminous plants. Most legume groups with extrafloral nectaries have not given rise to myrmecophytes, in his opinion due to the lack of provision of nesting space (*Acacia* is the only prominent exception). In general, many myrmecophytes have evolved in plant groups which do not offer any ant-attracting food (examples in JOLIVET 1986).

Predispositions for stem domatia are soft pith or even cavities in the stem, however, the plant also needs to be stable and resistent to herbivore damage, often achieved by resin production. Hollow stems or a soft pith are frequently found in quickly growing species, in the tropics mostly in secondary habitats. Indeed many myrmecophytic *Macaranga* species grow preferably in secondary habitats (Table 1) but just the two extremely light-demanding species have a solid stem with a compact pith and many resin ducts: *M. gigantea* and *M. tanarius*, the latter is probably the species with the highest growth rate of all Malaysian *Macaranga* (unpubl. work). Strong herbivore pressure may have prevented the development of hollow stems with only little resin in some *Macaranga* species. In contrast, the presence of hollow internodes is a characteristic feature of the neotropical counterpart *Cecropia*, even in the not ant-inhabited species. As far as known, *Cecropia monostachya* BERG is the only species with a solid stem filled with pith (BERG 1981).

Evolutionary considerations. Only few ant-species have developed the ability to bite into living plant material which is a crucial point of the pre-myrmecophytic systems. WARD (1991) pointed out for pseudomyrmecine ants, that a clue to the primary origin of ant-myrmecophyte associations lies in the tendency to occupy cavities in live plant parts, made by stem-boring insects. Once ants had acquired the ability of biting into living plant tissue, this could lead to the adoption of new host plants in quite different plant taxa. One example are myrmecophytic ant species of the genus *Cladomyrma* which colonize various plant genera in SE.-Asia (even

from different families; MASCHWITZ & al. 1989, 1991; AGOSTI 1991). For the ant-associates of *Macaranga*, host plant switching appears to be restricted within the genus.

DAVIDSON (1991) speculates that ant-plant mutualism can explain patterns of parapatric speciation among *Cecropia* spp. First aspects of species evolution in the genus *Macaranga* were discussed by WHITMORE (1969), who, however, did not consider the myrmecophytic aspects. The distribution of domatia only partly reflects taxonomic relatedness within the genus *Macaranga*. Although there are some sections with prevalence of domatia and its absence in others, some sections comprise species with and without preformed cavities (Table 1). The taxonomic relationships in *Macaranga* are still largely unknown and the genus needs thorough revision (WHITMORE, pers. comm.). To date, nothing is known whether these myrmecophytic systems have a monophyletic origin and whether speciation processes have been influenced by association with ants. Further investigations for instance with means of DNA-analysis (DNA-fingerprinting, PCR-analysis and sequencing) are under way to clarify the taxonomic relationships in the genus *Macaranga* and the role of myrmecophytism for speciation. This genus provides particular good opportunities to study speciation processes and thereby to gain insights in the ecology and significance of myrmecophytic associations in tropical systems.

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