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New and Little-known Myrmecophytic Associations from Bornean Rain Forests

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Abstract: The woody climber *Millettia niuewenhuisii* (Fabaceae) and the shrub *Myrmeconauclea strigosa* (Rubiaceae) in Sabah, Borneo are associated with ants. The hollow stems of *Millettia nieuwenhuisii* are regularly inhabited by an aggressive *Cladomyrma* sp., which keeps pseudococcids inside the stem. On *Myrmeconauclea strigosa* the ants live in hollow internodal swellings near the end of the branches. In this plant many different ant species use the nesting space in an opportunistic manner.

INTRODUCTION

During field study in Sabah (NE Borneo) in January 1989 we came across two plants which were inhabited by ants. One was a large woody climber, *Millettia nieuwenhuisii* (Fabaceae). The other was the shrub *Myrmeconauclea strigosa (Rubiaceae)* (Fig. 1), which Merrill (1920) mentioned to be associated with ants. Since little is known as yet about the ant-inhabitants of these myrmecophytes we studied the relationship in detail. Data characteristic for the associations are presented.

RESULTS

Millettia nieuwenhuisii J.J. Smith (Leguminosae)

We found a specimen of this large woody climber in lowland primary forest at Poring in Kinabalu State Park (Figure 2). The leaves of this liana are pinnate, with 2–5 pairs of opposite leaflets and one terminal leaflet. The pink, papilionaceous flowers are arranged in paniculate inflorescences. The pith of all younger branches near the ground as well as in the crown region

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Figure 1. *Myrmeconauclea strigosa* growing in the inundation zone of a small river

was excavated and inhabited by ants: a small blackish-brown *Cladomyrma* species with dimorphic workers connected by some intermediate forms typical of the genus. Inside the hollow stem we found brood and alate females as well as many pseudococcids, often sited in depressions of the stem walls. After disturbance (e.g. shaking) small as well as large workers came out of the numerous nest entrances and attacked by biting and releasing formic acid and other weak smelling substances which were produced by glands of the gaster.

The ants continued to attack up to one hour after the end of the disturber's contact with the plant if they could find a good place to bite while wandering over him. This persistent and long lasting fighting behaviour, which is also typical for other ants living on Asiatic myrmecophytes, makes

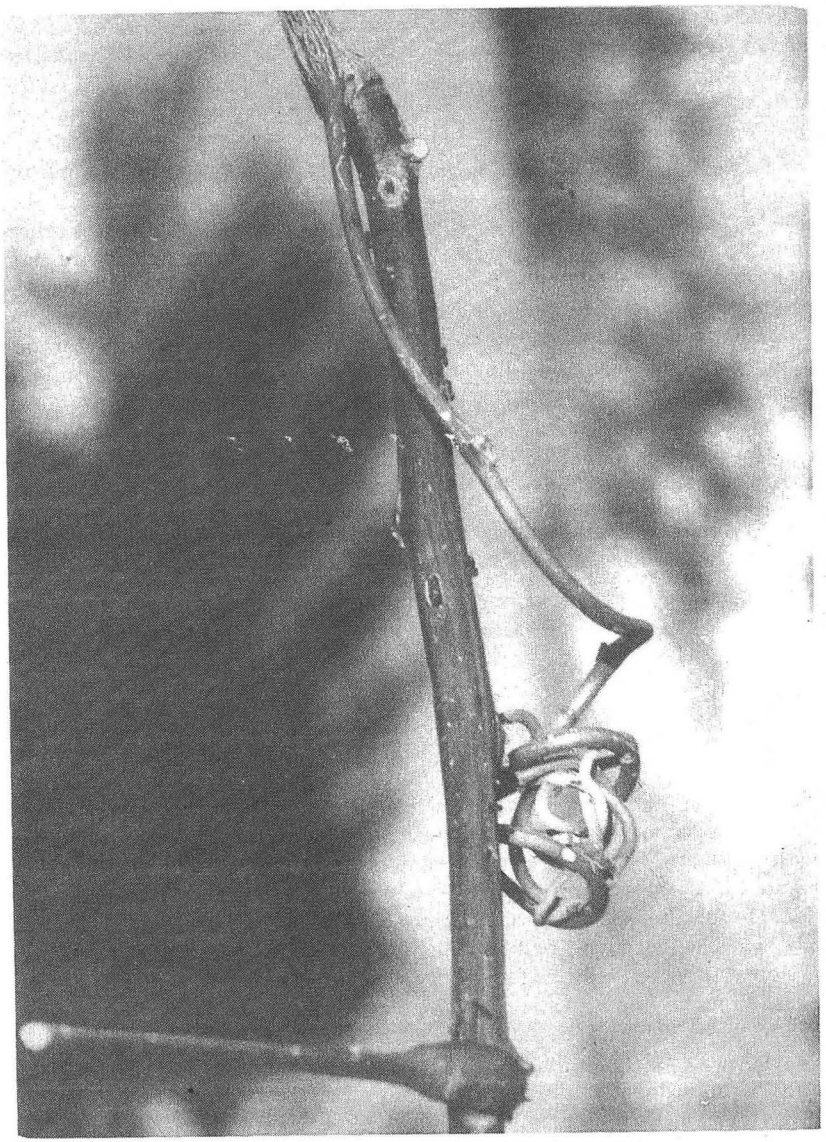

Figure 2. Branch of *Millettia nieuwenhuisii* inhabited by *Cladomyrma* ants

Cladomyrma an unpleasant opponent and contributes to its efficiency as a protective partner of the system.

Unlike the bites of other small camponotines, the skin where the *Cladomyrma* ant had bitten remained red and itchy for days. Obviously the

ant secretes skin irritating substances in addition to formic acid.

A few kilometres away we found one more specimen of *Millettia nieuwenhuisii* also inhabited by *Cladomyrma* sp.. An investigation of all 29 *Millettia nieuwenhuisii* specimens with vegetative twigs in the Herbarium of the Forest Research Centre at Sepilok, Sandakan, produced further evidence for a possible obligatory association. 26 of these specimens originating from different parts of Sabah and Sarawak had entrance holes on the stems of the same appearance and density as those found on the living plants. All other Bornean *Millettia* species examined at Sepilok are trees which are not associated with ants and do not have hollow stems. These include *M. atropurpurea, M. hemsleyana* and *M. vasta.*

Millettia species from Peninsular Malaysia examined in the Herbarium of the Forest Research Institute Malaysia, Kepong, have solid stems and no entrance holes, either for the tree species *Millettia atropurpurea, M. albiflora, M. hemsleyana* and *M. gallifragans* or the climbers *M. dasyphylla, M. maingayi* and *M. sericea.*

We did not check whether these plants had extrafloral nectaries such as the trees *Saraca thaipingensis* (Caesalpiniaceae) and *Cryperonia griffithii* (Crypteroniaceae) have and which are also inhabited by *Cladomyrma* (Maschwitz *et al.*, in press).

Myrmeconauclea strigosa (Korth.) Merrill (Rubiaceae)

We found *Myrmeconauclea strigosa* in Garinono (near Sandakan, Sabah). The small shrubs with a maximum height of 2.10 m grew on the bank of a small river in the inundation zone (Figure 1): a habitat typical for this species (Merrill 1920). Stipules and young stems are densely hairy, the leaves simple and opposite. The whitish-yellow flowers are arranged in solitary heads terminal on unbranched flowering axes. The *M. strigosa* shrubs were richly branched and had numerous hollow internodal domatia distally (Figure 3). These were on average 36 mm (+ 6.43) long and 7.6 mm (+1.1) wide. On the top was a longish entrance slit 0.7–1 cm long and 0.5–2 mm wide. The cavities were partly inhabited by ants. The swellings and the slits developed spontaneously and gradually without the presence of ants. In the field we found all intermediate developmental stages on plants without ants (Figure 4a). This also occurred in plants kept in the greenhouse. The swellings seem to become hollow by gradual degeneration of the pith and the entrances are evidently formed by splitting along the stem wall in the course of development. These entrances gradually close again in older swellings by secondary thickening of the stem.

Later the domatia slowly disappear so they can no longer be recognized on stems 1.5 cm or more in diameter. A small number of swellings failed in their development, i.e. despite the swelling of the stem no entrance was formed (7% of n = 50), or the swelling opened for almost its entire

Figure 3. Internodal swellings in the branches of *Myrmeconauclea strigosa*

length (5%) (Figure 4b). We could find neither extrafloral nectaries nor food bodies on the plants.

Table 1 gives an overview of the ant inhabitants of 11 twigs of different shrubs. They were inhabited by different ant species from three subfamilies. A total of 23% of the 198 domatia suitable for colonization had ants living in them. In some hollow swellings we found sediment of mud from a flood a few days previously. Regular flooding in this habitat probably affects the percentage of occupation.

Of the open domatia 3.5% contained dead queens, 20% of the inhabited swellings had colonizing females and 80% were occupied by workers and brood partly with queens. These branches were inhabited by ants of nine species in three subfamilies: 2 species of *Camponotus (Colobopsis),* 1 *Nylanderia* sp. (Camponotinae), 1 *Tetraponera* sp. (Pseudo-

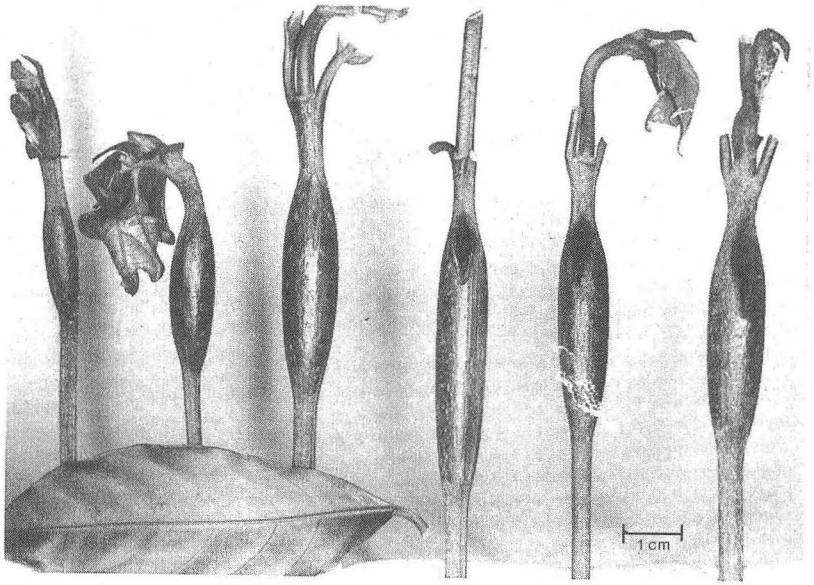

Figure 4a. *Myrmeconauclea strigosa.* Intermediate stages in the development of internodal swellings and open slits (entry sites)

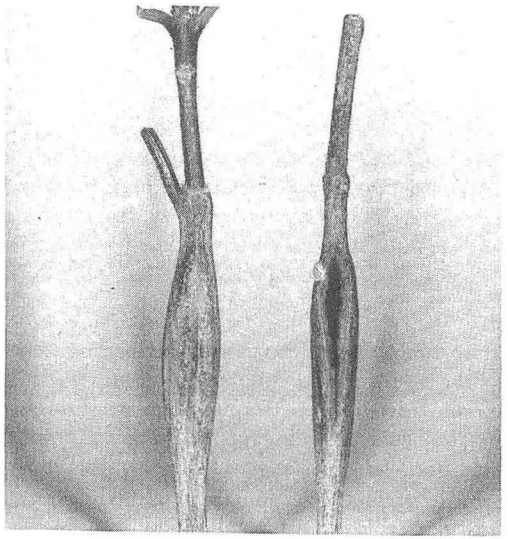

Figure 4b. Abnormalities in the development of entrance slits on *Myrmeconauclea strigosa.* Left: mature domatium without entrance, right: domatium with too long an entrance

Table 1. Occupation rates and contents of dissected swellings from 11 branches of *Myrmeconauclea strigosa*

(PO = Ponerinae, M = Myrmicinae, PS = Pseudomyrmecinae, C = Camponotinae)

Number of domatia						Number of	
with open entrance	percentage occupation	with pseudo-coccids	with colonizing queens	with workers (partly with queens)	with dead queen	ant species	subfamilies present
13	38	1	2	2	–	3	2(PS, M)
16	31	–	1	2	–	3	1(M)
9	33	–	–	3	1	1	1(M)
13	23	–	–	3	–	2	1(M)
19	21	1	2	2	1	3	2(M, PO)
35	26	–	2	7	1	2	2(M, PO)
24	25	–	1	5	1	4	2(M, C)
14	7	–	–	1	–	1	1(M)
9	11	1	–	1	1	1	1(M)
17	18	–	–	3	–	1	1(M)
15	20	–	1	2	1	2	2(M, PO)

myrmecinae), 1 *Monomorium* sp., 1 *Tetramorium* sp. and 3 *Crematogaster* spp. (Myrmicinae). In two cavities we found workers of *Cerapachys* (Ponerinae) which are known as ant-hunters (Wilson 1971). They probably visited the plant to prey on the other ants. One twig contained 4 species, two twigs 3 species each, four twigs 2 each and four twigs housed 1 species. The biggest branch with the most swellings was almost completely colonized by a large colony of *Colobopsis* sp., in addition only two colonizing females of a *Crematogaster* species (still without any brood) were present. Pseudococcids were found only in a few domatia, mostly in those without ants.

DISCUSSION

Relatively few plant species have been added to the list of the ant-plants of the tropics since the studies of Bequaert (1922) and Wheeler (1942). Bequaert listed 109 myrmecophytes for the Indo-Malayan region compared to 116 in America and 42 in Africa. Benson (1984) reported 150 ant-plants for Asia. Our studies in Malaysia have already yielded four new myrmecophytes in a relatively short time (Maschwitz *et. al.*, in press), so we are certain that further investigations will reveal still more myrmecophytic plants in SE Asia.

There are two basic types of associations: 1. Nutrient symbioses which have been described primarily for ant-associated epiphytes which seem to

dominate in SE-Asia and Australia (Janzen 1974, Huxley 1978). Actually, the typical ant-epiphytes like *Myrmecodia* and *Hydnophytum* are restricted to the Asian and Australian tropics. 2. Symbioses providing the plant with protection against vine-growth and herbivores. These relationships have been studied mainly in the neotropics and tropical Africa (e.g. Janzen 1967, 1969, 1972; McKey 1984; review Beattie 1985). In SE Asia our investigations of the association of *Macaranga* with ants showed it is equivalent to the systems on the other continents (Fiala *et al.* 1989).

Nauclea s.l. belongs to the family Rubiaceae which comprises several myrmecophytic forms worldwide, e.g. *Myrmecodia, Hydnophytum, Nauclea* (Malesia), *Duroia* (America), *Cuviera, Gardenia, Uncaria* (Africa) (Schnell 1970). The myrmecophytic species of *Nauclea s.l.* (cited in Haviland 1987 and Jolivet 1986) have been transferred to two new genera: thus Merrill (1920) transferred *N. strigosa* to *Myrmeconauclea*. However, he did not elaborate on its ant-association. The other *Nauclea* species have been transferred to *Neonauclea* (see Ridsdale 1978). Ridsdale (1989) gives an overview of the ant-inhabited chambers (myrmedomes) in *Neonauclea* and lists 17 species which have been recorded with myrmedomes. Their occurrence is restricted to Sumatra (2 species), Borneo (8), Celebes (6) and to the southern Philippines (1). Nothing is known about their ant inhabitants.

The provision of chambers, which are used by ants as nest sites, plays an important role in the evolution of myrmecophytic systems. Nesting space is especially important in the tropics, because there are few permanent cavities available due to the rapid decomposition of all dead wood. Brown (1960) speculated that the lack of suitable nest sites was a prominent factor for the relative scarcity of arboreal ants in Australia and Melanesia. Almost any plant which has natural cavities such as hollow stems may be used for nesting.

The associations with ants fall into two groups: the regular, highly specific systems on an obligate mutualistic basis, in which food is often provided for the ants; and the unspecific facultative associations involving a variety of ant species. Such casual relationships comprise the majority of the systems.

Millettia nieuwenhuisii is specifically associated with a *Cladomyrma* species. *Cladomyrma* is an ant genus with a myrmecophytic way of life (Maschwitz *et al.*, in press). All three species found in Peninsular Malaysia live in close association with woody plants. *Cladomyrma* is not a cryptic genus as assumed by Wheeler (1910) but is an active and dominant colonizer of trees and climbers. It is a typical plant-colonizing form as is indicated by the short mandibles of queens and workers of all species, which facilitates biting entrance holes into the woody parts of the young stems.

The *Myrmeconauclea* plants described here clearly belong to the category of facultative associations as many different ant species use the nesting space in an opportunistic manner. All evidence indicates that *M. strigosa* unspecifically offers nesting sites but no food. The plants continuously provide new chambers (which later degenerate) in their most vulnerable growing regions. The nesting space is opportunistically accepted by various colonizing queens. The occupation of one plant by a single population of a mature *Camponotus* colony, which produced sexuals, indicates competitive fights in the course of colony development. (The 2 females of *Crematogaster* found on this plants had probably just arrived and had not yet been discovered by *Camponotus* workers). The dominating *Camponotus* colony appeared to be competitively superior.

Schemske (1983) argued the more complex the reward offered by the plant the greater is the degree of specialization of its ants, a view supported by observations by Davidson *et al.* (1989) on neotropical myrmecophytes. Their investigations showed that the occurrence of one ant species significantly reduced the likelihood of occupancy by other ants. However, the species composition was different on small and large myrmecophytic plants with domatia. These studies also suggest that a variety of ants compete for plants and that the more specialized inhabitants are competitively superior. Numerous factors may additionally contribute to a large stochastic component in colony establishment, e.g. proximity of nest trees releasing new queens and timing of queen production.

Myrmeconauclea strigosa typically grows on the banks of rivers, where the shrubs are sometimes submerged for short periods. This may be a factor in the stability of the ant association: the flooding may prevent the development of more stable and permanent relationships. Interestingly, in the Amazon basin ant-inhabited trees are also common in seasonally flooded forest (Buscalioni & Huber 1900). Schnell (1970) reports in addition at least five other myrmecophytes occurring in inundation zones along riversides in Africa and America. Benson (1985) suggested that plants in seasonally flooded areas compensate the reduced foraging activity of ants by providing permanent domatia.

The scarce presence of ants in such a habitat would explain why a plant like *Myrmeconauclea strigosa* has developed nesting chambers.

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