

**CLERODENDRUM FISTULOSUM (VERBENACEAE),
AN UNSPECIFIC MYRMECOPHYTE FROM BORNEO
WITH SPONTANEOUSLY OPENING DOMATIA**

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SUMMARY

Clerodendrum fistulosum Becc. is a true myrmecophyte as it offers nesting space for ants in hollow internodes. In contrast to previous reports our investigations proved that these domatia open by themselves, thus providing cavities for a variety of different ant species. In Sarawak, Malaysia, we did not find an obligate relationship between *C. fistulosum* and a specific ant-partner. For comparison, studies on herbarium material of other *Clerodendrum* species were carried out: a further species, *C. deflexum* from the Malay Peninsula and Sumatra presumably also is myrmecophytic.

INTRODUCTION

The genus *Clerodendrum* comprises about 400 species, mostly paleotropical or subtropical. Some species have hollow internodes and are inhabited by ants (8 species in Africa, 3 in Asia, Schnell & Beaufort, 1966; Jolivet, 1986). Many also have extrafloral nectaries [Rao & Ramaya (1992) list 15 species].

Clerodendrum fistulosum Becc. has early been described as an ant-plant due to its domatia and especially to having ants inside (Beccari, 1884). (The term domatia is used for all plant chambers that appear to be adaptations facilitating ant nesting.) Beccari found it in Sarawak to be associated with a specific and obligatory partner ant, *Camponotus (Colobopsis) clerodendri* Emery. It has been reported until recently that the searching queens of this species bite entrance holes into a swollen hollow internode during colony foundation (e.g., Huxley, 1986; Jolivet, 1986). However, the discoverer of this ant-plant, Beccari himself, doubted whether ants were responsible for the very regular openings and speculated that they were developed naturally. Obviously his opinion was incorrectly translated from the original Italian version and this error was maintained.

In Sarawak we found a series of these plants and were able to study them in the field. In addition, we were able to cultivate four plants in the greenhouse in Germany and grow two specimens from seed. In contrast to previous reports we could observe that entrance holes develop by themselves. As the myrmecophytic status of this ant-plant apparently was misunderstood by several authors we briefly report our findings on biology and ecology of this plant-ant system.

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During a stay in Sarawak in 1992 fifteen specimens of *Clerodendrum fistu.* were found in a low, undisturbed kerangas (heath) forest on poor sandstone near Kuching (2° 20' N, 110° 25' E, 100 m a.s.l.; for habitat description, see Brunig, 1965). The plants and their partner ants were thoroughly checked in the field. Ant voucher specimens are deposited in the collection of the first author. The presence of glucose in gland secretions was tested with Dextrostix (Merck).

For observation of details of domatia formation and seedling growth four plants and two seeds, respectively, were cultivated in the greenhouse in Germany. For comparative studies herbarium specimens of *Clerodendrum* spp. were checked at the Forest Research Institute Malaysia (FRIM, Kepong, Peninsular Malaysia).

RESULTS

General description of the plant

Clerodendrum fistulosum is a small shrub. The 15 plants investigated in the field ranged from 4 to 131 cm in height and their stems were unbranched. The largest plant, with 10 internodes, carried a panicle of green-yellow buds sitting in green red-tipped calyces. In the greenhouse one specimen, only 15 cm high, already developed its white flowers. In the field one plant of 65 cm height bore 5 blackish blue drupes with a thin bright wax-cover. While most plants possessed several leaf-pairs, this specimen had shed all its leaves. It was colonized by *Crematogaster* ants. In older plants the decussate leaves were situated directly at the top of the internodes (Fig. 1). The first eight leaves of small saplings grew in spirals (greenhouse observation).

Domatia

In *C. fistulosum* in the field the inflated and hollow internodes varied from 1.5 to 18 cm in length ($\bar{x} = 7.2 \text{ cm} \pm 5.3$, $n = 28$). They were club-shaped and rounded, rather flattened in cross section ($\bar{x} = 1.02 \text{ cm} \pm 0.13$; $n = 9$). As soon as they were fully elongated, they became lignified and stiff. Many of the internodes possessed one hole or a pair of holes on the broader side of the internode just beneath the insertion of the leaf petioles (Fig. 1). From 32 internodes checked in the field, 11 had two open holes, 14 had one open hole, two fully grown internodes had no holes at all, and in 5 internodes without ants one or both holes apparently had closed again. As we could observe both in the field and in the greenhouse, the holes did not develop synchronously. As we could conclude from detailed observation of the distribution of ants within the internodes and direct observation of growing plants in the field as well as the in the greenhouse the holes develop *spontaneously* through growth processes of the plants *independently of the presence of ants* (Fig. 2). We found open internodes which apparently had never been inhabited by ants and were still not colonized. All stages of openings were present. Only after development of fully opened holes a part of the domatia became inhabited. The holes arose as slit-like structure which later became rounded [slits: $\bar{x} = 2.5 (\pm 0.7) \times 1.7 \text{ mm} (\pm 0.5)$; rounded holes: diameter $\bar{x} = 1.2 \pm 0.5 \text{ mm}$, $n = 21$]. All plants in the greenhouse developed domatia openings in the course of two years (8 holes in 5 plants); 11 slits did not fully open.

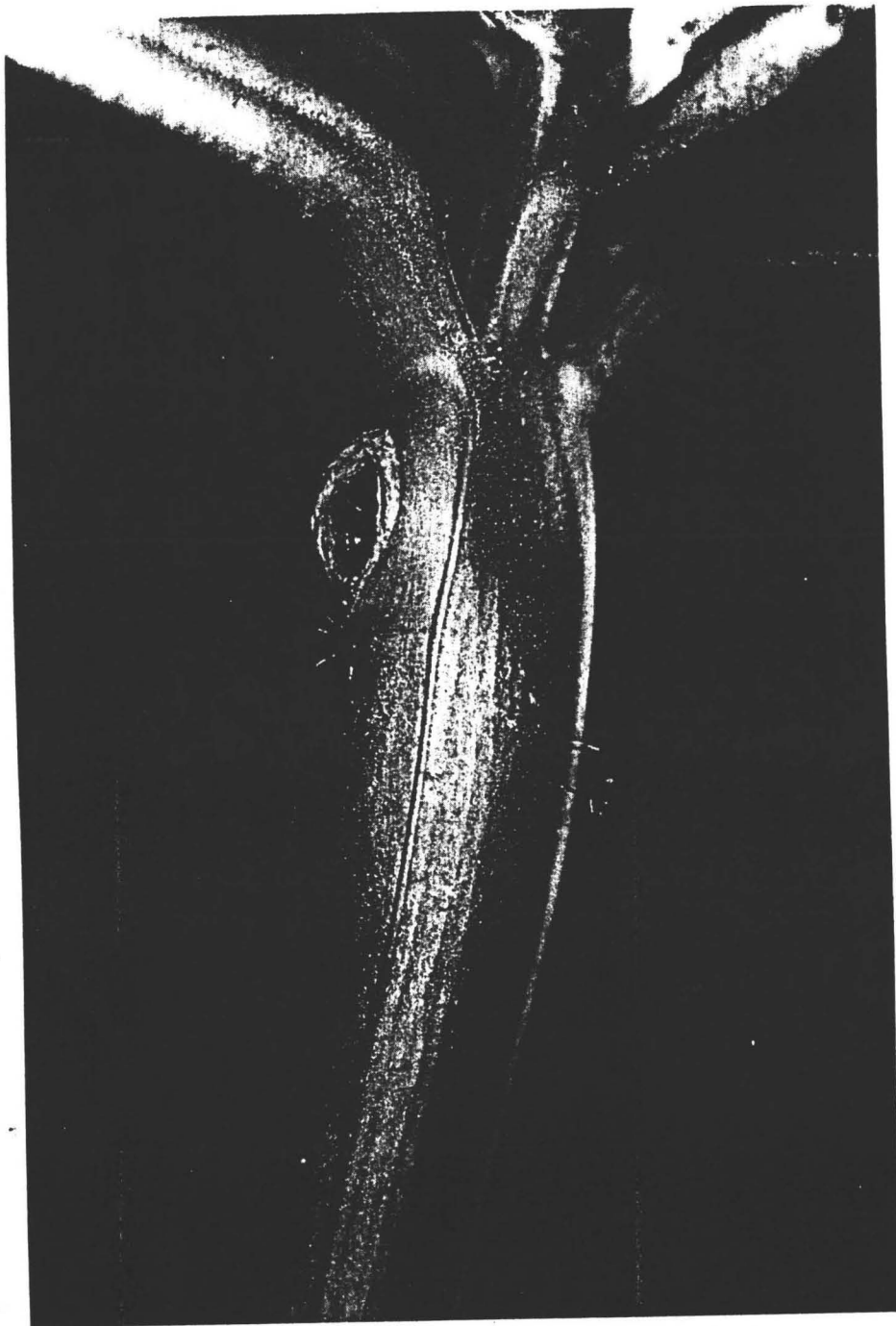


Fig. 1. Upper part of an ant-inhabited *Clerodendrum fistulosum* shrub. One *Crematogaster* ant is entering the domatium entrance, another one is climbing into the flower bud panicle.



Fig. 2. Domatium entrance slit at the upper end of an internode which did not fully open (see arrow; greenhouse plant; sizes are given in the text).

Ant inhabitants

Ten of the fifteen specimens of *C. fistulosum* studied in the field were inhabited by ants. Each of these was occupied by only one ant colony. A further plant had no live ants but the internodes were still partly filled with detritus and ant remains. We observed five ant species of four genera (of subfamilies Formicinae, Dolichoderinae and Myrmicinae) living in the internodes: *Camponotus* sp. (1 colony), *Iridomyrmex* sp. (2 colonies), *Technomyrmex* sp. (1 colony), and two *Crematogaster* spp. (each with 2 colonies). The *Camponotus* sp. we found did *not* belong to the subgenus *Colobopsis* as described by Beccari.

A plant grown from seed in the greenhouse developed its first inflated internode at a height of 3 cm. At this developmental stage the leaves are not yet decussate but still spirally arranged. The first entrance slits developed more than a year later.

Nectaries

The lower leaf surface of *C. fistulosum* is covered with numerous nectaries (Fig. 3). The nectaries are c. 0.5 mm in cross section; they develop as green and roundish dots on the reddish underside of the young leaves. These dot glands produced a secretion with a glucose concentration of more than 2.5 g/l (maximum reading of the Dextrostix test). When access to the plants was allowed in the greenhouse the nectaries were visited by tiny ants of the genus *Plagiolepis* (Formicinae). The first nectaries appeared on the fourth leaf (1 cm long) on the one-month-old seedling (c. 1 cm high). On leaf number 7 ten nectaries were counted. Large leaves of the greenhouse plants possessed up to 60 nectaries mostly along the main nerves.

Apparently, the inner base of the bud-carrying calyces produced extranuptial nectar. Many workers of a *Crematogaster* sp. constantly visited these ring-like, slightly domed structures around the insertion of the long corollae. Special food-bodies as often occur on myrmecophytes have not been observed in *C. fistulosum*.

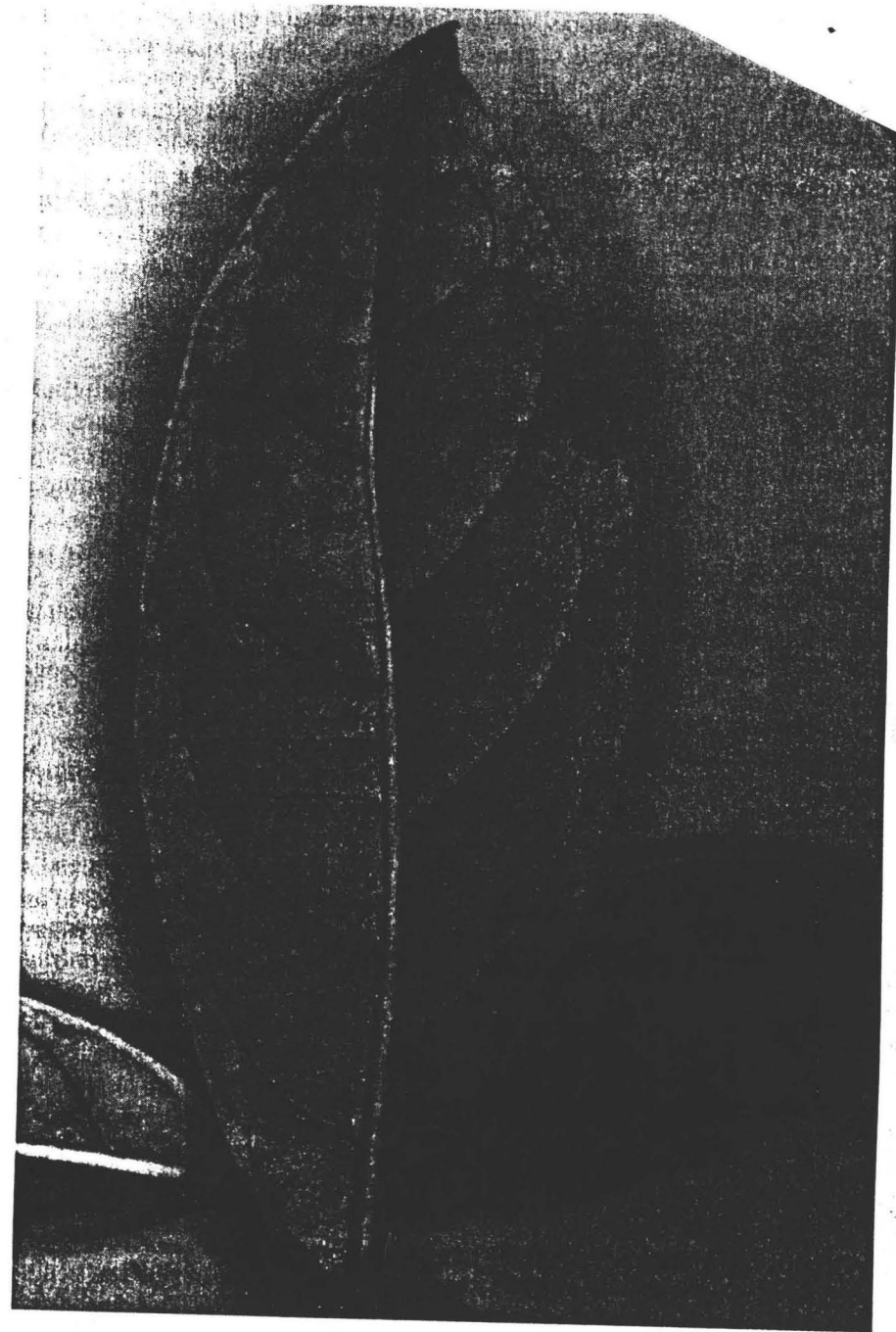


Fig. 3. Lower leaf surface of *Clerodendrum fistulosum*. The numerous dots near the midrib are extrafloral nectaries.

We did not find any homopterans within the internodes or on the surface of the plants. In two internodes small cockroaches were found. On some plants large wounds were conspicuous which had, however, already healed. Apparently, some animal, probably a rodent or a bird, had opened the domatia to get access to the ant colonies. In other areas of Sarawak we have seen similar wounds at the domatia of other myrmecophytes like *Neonauclea* and *Macaranga* species. In Kalimantan we observed a woodpecker picking into and widening the entrance holes of *Macaranga hypoleuca*. In Sekinchan, West Malaysia, we found scars of rodent teeth on a stem of *Macaranga pruinosa*.

DISCUSSION

Like other species of the genus *Clerodendrum*, *C. fistulosum* possesses extrafloral nectaries (Jolivet, 1986; Padma Rao & Ramayya, 1992). Apparently an unspecific nutritional attraction of ants is a good predisposition for further steps in the evolution of myrmecophytism. However, as we have discussed for the SE Asian myrmecophytic genus *Macaranga*, the presence of extrafloral nectaries does not seem to be an essential feature in the evolution of myrmecophytes. The offer of nesting space is of great importance for the development of obligate and specific relationships with ants (Fiala & Maschwitz, 1991, 1992a, b). Also in *C. fistulosum* only the additional development of domatia makes this species a true myrmecophyte. A combination of both these ant-related characters can be found in many myrmecophytes (Jolivet, 1986). In *C. fistulosum* extrafloral nectar is produced by the sapling long before the domatia occur (more than six months in the greenhouse). This order in the development of ant rewards seems to be due to plant size constraints at first view. Perhaps time of development and also quantity and quality of such rewards should be thoroughly considered also under cost-benefit-aspects (as discussed by Davidson & Fisher, 1991). In certain *Macaranga* species, for instance strategies of plant defence and ant rewards can change drastically during life time of a tree (Fiala et al., 1994).

As was mentioned in the introduction, *C. fistulosum* is reported to be a myrmecophyte associated with one specific ant partner: *Camponotus (Colobopsis) clerodendri*. In contrast we did not find an obligate specific relationship between *C. fistulosum* and a specific ant-partner. The ant queens are thought to get access to the hollow internodes by biting holes through the domatia walls at preformed praestomatal sites beneath the paired leaf petioles (Huxley, 1986; Jolivet, 1986). Also, the workers are reported to force their entrance into the hollow chambers by biting through the thin-walled parenchyma at the upper end of the internodes (Blatter, 1928). According to our observations already small plants less than 10 cm in length can produce internodal domatia which soon become lignified. Our investigations proved that the domatia open by growth and degeneration processes of the plant stem itself. The resulting holes are very regular in shape and develop directly beneath the leaf petioles. They remain open for a long time even when not inhabited by ants. This demonstrates that the plant offers nesting space for opportunistic ant species nesting in plant hollows from the very beginning. As might be expected many of these cavities are used by a variety of different ants out of several subfamilies for nesting (as described for *Myrmeconuclea strigosa*, Rubiaceae, by Maschwitz et al., 1989). A *Colobopsis* spe-

cies was not found at all at in *C. fistulosum* at our investigation site. Such unspecific ant colonization might hinder colonization by a specific ant-partner (as in *Leonardoxa africana*, Leguminosae, where the specific ant-partner *Petalomyrmex phylax*, is excluded by *Cataulacus mckeyi*; McKey, 1984). Moreover, the small usually unbranched shrubs do not represent a good nesting opportunity for a myrmecophytic ant with large colonies, like a *Colobopsis* sp.

In the same habitat we found another myrmecophyte, viz. *Macaranga caladiifolia*, containing among other ant species two *Colobopsis* spp. indicating that arboreal ants of that subgenus were common there. However, the ant fauna composition of *M. caladiifolia* was nevertheless rather similar to that of *C. fistulosum*, *Crematogaster* and *Camponotus* being the most abundant ants.

From SE Asia two more true myrmecophytic (i.e. domatia-bearing) *Clerodendrum* taxa are reported: *C. phyllomega* Steud. var. *myrmecophilum* (Ridley) Moldenke and *C. breviflorum* Ridley, both small shrubs. The former species occurs in Borneo and Sumatra, the latter is endemic to the Malay Peninsula (Ng, 1978).

Jolivet (1985) reported *Clerodendrum fallax* Lindley from Java as inhabited by a number of different ant species which seem to intrude by leaf scars. In the Cape Verde Archipelago, where this species was introduced, it is also inhabited by ants. In Jolivet's opinion in this species the evolution towards myrmecophytism is less perfect as in the above mentioned Southeast Asian species since the internodes are not inflated.

We had no opportunity to see specimens of these latter mentioned species. However, in herbarium specimens of other *Clerodendrum*s we did not detect any domatia on the following species: *C. hispidum* Hend., *C. inerme* (L.) Gaertn., *C. nutans* Jack, *C. paniculatum* L., *C. ridleyi* King & Gamble, *C. serratum* Spreng., *C. umbratile* King & Gamble, *C. villosum* Blume. One further species, however, displays myrmecophytic characters: *C. deflexum* Wall. var. *bracteatum* Ridley. It is common throughout the Malay Peninsula and Sumatra (Ng, 1978). It possesses hollow and partly inflated internodes. The openings, however, are not paired and not situated at a fixed point of the internode as in *C. fistulosum*. We suppose that also this species is a true myrmecophyte associated with unspecific ants nesting in living wood.

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