

**CAPPARIS BUWALDAE JACOBS (CAPPARACEAE)
A NEW MYRMECOPHYTE FROM BORNEO**

U. MASCHWITZ¹, K. DUMPERT¹, J. MOOG¹, J.V. LAFRANKIE² & I.HJ. AZARAE³

SUMMARY

Capparis buwaldae, a climber of primary forests endemic to Borneo, is a myrmecophyte with stem domatia. The stems become hollow by pith degeneration and develop oval openings allowing ants to enter. These openings are localized at a strictly defined area above the insertion of the leaves and a pair of nodal thorny stipules. They gradually split open from the outside. The openings may develop into elevated chimney-like structures or close again by growth if not kept open by ants.

The plant may be inhabited by various opportunistically nesting arboreal ants including *Crematogaster*, *Monomorium*, and *Camponotus* species. Specialized myrmecophytic ants could not be found. Neither nectaries, nor food bodies, nor trophobiotic endophytic homopterans could be observed. In the Rijksherbarium, Leiden 65 other *Capparis* species and subspecies from the Indo-Australian region were examined for ant-plant characters. None of these species showed any myrmecophytic character.

INTRODUCTION

In latter years in Southeast Asia an increasing number of domatia-forming non-epiphytic ant-plants have been discovered in various families. Highly evolved systems came to light with specific partner ant species biting entrances into their domatia (Maschwitz et al., 1989, 1991; Moog & Maschwitz, 1994, and unpublished results), as well as more generalistic ant-plants whose domatia are opened by the plant itself through growth processes, giving access to a variety of opportunistically nesting arboricolous ants (Maschwitz et al., 1992, 1994a, 1994b, unpublished results). In the last five years at least 19 plant species from 10 genera in 8 angiosperm families proved to be new ant-plants. Therefore, the number of known Asian non-epiphytic ant-plant genera is nearly as large as that of the Neotropics (32 versus 39) which until now was thought to be by far the largest of the world (Davidson & McKey, 1993).

During an excursion through Sarawak (East Malaysia) we came upon a further new ant-plant which belongs to the second association type. For the first time we became attentive to its myrmecophytic character because the stem of the plant specimen was severely damaged by a rodent in a characteristic way which can frequently be observed in specific Asian ant-plants like *Macaranga* and *Neonauclea* (unpublished data). Recognizable by the traces of its teeth this animal (possibly a tree rat or squirrel) had torn up the hollow plant stem repeatedly in a section of half a metre. Similar traces of destruction could be observed in 5 other plant specimens.

- 1) Zoologisches Institut der J.W. Goethe-Universität, Siesmayerstrasse 70, D-60054 Frankfurt am Main, Germany.
- 2) Center for Tropical Forest Science, Institute of Education, Singapore.
- 3) University of Malaya, Department of Zoology, Kuala Lumpur, Malaysia.



Fig. 1. *Capparis buwaldae* Jacobs, habit of the upper part of the plant.

MATERIALS AND METHODS

Eight specimens of *Capparis buwaldae* were found in Lambir Hills National Park, an undisturbed mixed dipterocarp lowland forest near Miri about 100 m above sea level. They grew on a ridge in a dense and dark undergrowth of shrubs, tree saplings, and palms. In the Rijksherbarium (Leiden) specimens of *C. buwaldae* as well as other *Capparis* species from the Indo-Australian region were examined for possible ant-plant characters. Dried specimens of *C. buwaldae* have been deposited in the personal collection of J. Moog; later, they will be handed over to the Rijksherbarium at Leiden.

RESULTS

Capparis buwaldae (Capparaceae) is a climber 2–15 m long (Jacobs, 1960, 1976). The first specimen found by us, which will be described in more detail, was a deep-rooted, erect, woody, green-stemmed plant 1.5 m high, which was originally broken off at a height of 0.65 m (lower part) and had formed a new shoot 0.86 m high, with 21 leaves in the upper part and 3 small side branches. The leathery, short-stalked, lanceolate leaves (length = 18.2 ± 2.2 cm, width = 3.7 ± 0.5 cm) with a water draining tip (Fig. 1) were growing in a whorl. The leaves were sitting between two small thorny stipules which were slightly pointing downward. Instead of a leaf sometimes a peculiar thread-like green appendage was found, 0.2–1 cm long (Fig. 3a). About 3 mm above the insertion of leaves side branches had developed.

Ant-plant characters

The stem did not form any distinct internodal domatia swellings but was hollow as a whole. However, its upper region was rather wide. The cavity was developing by degeneration of the stem pith in the upper parts, i.e., the pith became fragmented into thin, lamellous, translucent, whitish discs (Fig. 2). The lowest and oldest parts of the stem, 5–6.5 mm in diameter, were solid. With increasing height and diameter

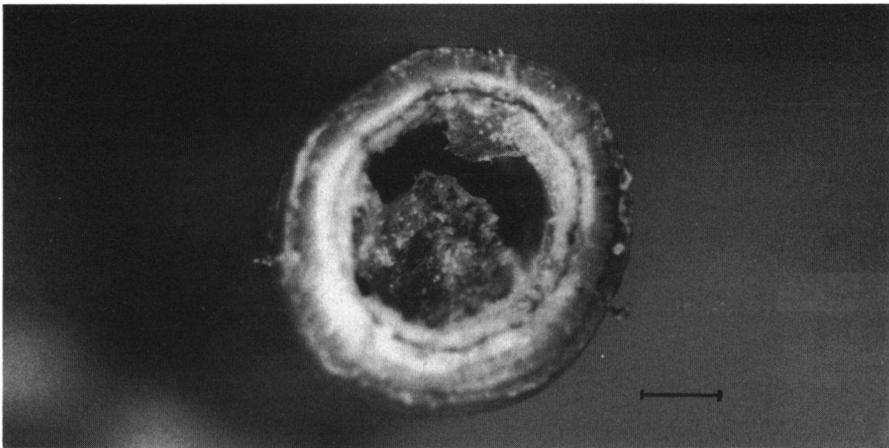


Fig. 2. Pith degeneration in a young shoot of *Capparis buwaldae* Jacobs. Scale bar = 1 mm.

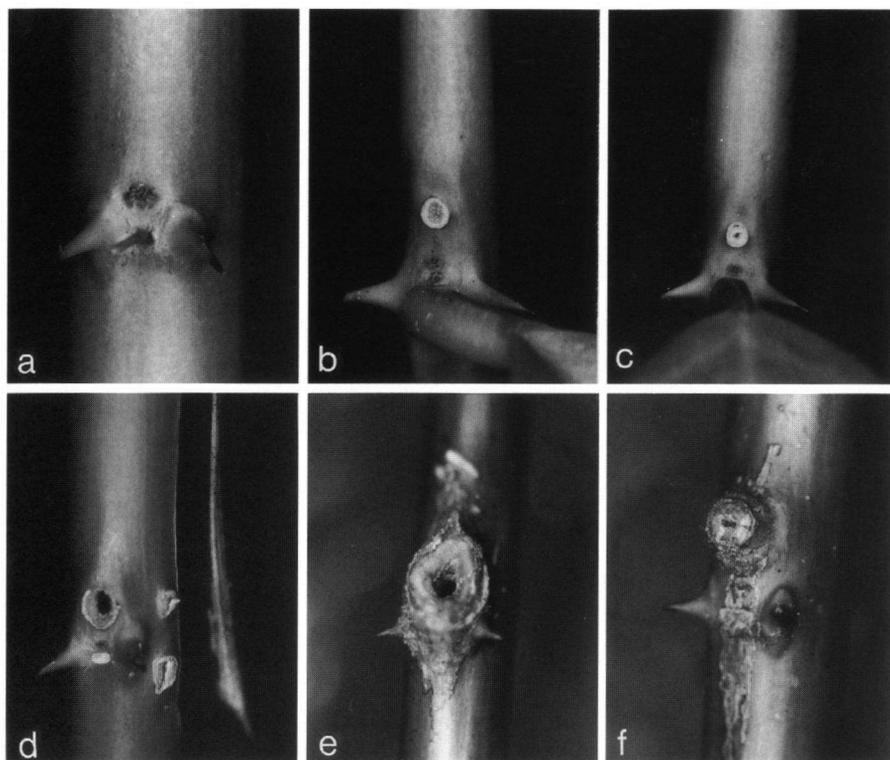


Fig. 3. Stages of stoma development in *Capparis buwaldae* Jacobs (from a to f). a. Stomaless node of a shoot; instead of a leaf a fathom-like green structure has developed between a pair of thorny stipules; b. still closed young stoma; c & d. developing stoma; e. elder stoma opening, kept open by ant inhabitants; f. unused stoma, closed again by callus growth.

of the stem the cavity was developing, measuring from 4 mm (stem diameter 11 mm) to 6.5 mm in width (stem diameter 10–11 mm in the upper stem region). In most hollow sections of the stem, wall openings (stomata) occurred. Their development could be observed best in the upper stem part (Fig. 3). The openings were located about 2–3 mm above the middle of the connection line of the two thorny stipules, i. e., at the same position where also the small side branches originated. In some cases neither an opening nor a branch had developed. The youngest still closed openings consisted of small green ring-shaped bulges on the green stem with a whitish centre (Fig. 3b). In this centre, beginning from the outer surface a tiny, oblong, slit-like groove (at first only visible with a hand lens) developed successively. Finally, the slit broke through into the interior and formed a small opening (Fig. 3c), which successively became larger (Fig. 3d). One such open oval stoma (1 mm long, 0.3 mm wide) could be observed in the upper leafy part of the new shoot. In the lower leafy part both still closed stomata and 3 fully open holes could be observed, the upper one was 1.2 by 0.85 mm in diameter, the middle stoma had a tiny but recogniz-

able hole and the lower one was 0.6 by 0.35 mm in diameter. As far as not destroyed by the predator very obvious stomata could be found also in the lower old part of the plant. They consisted of chimney-like elevations with thick crater-like bulges and a central hole (Fig. 3e). The largest elevation measured 10 mm in length, 9 mm in width, and 3 mm in height. Its hole measured 2 by 1 mm. A slightly smaller second stoma was open as well, while three others had closed again by plant growth (Fig. 3f). Possibly, the ants which had inhabited the stem prior to its partial destruction (and of which only nest remnants and unidentifiable parts were left) had kept open both holes.

Similar large stomata which were also partly closed by growth were found in the lower part of a second plant (0.95 m long). In its upper part the development of new stomata could be observed as described above.

The third plant, 1.3 m long, also had been partly destroyed at least three times. Here, too, large holes could be observed, partly at the normal sites above the thorns and partly at other sites, which apparently had been produced by gnawing of the predator and kept open by ants during subsequent regeneration of the stem. Judging from nest remains in the stem interior this plant had been occupied by ants, which had kept open the holes but later had disappeared. A young side shoot was thinner than the main stem (11 mm maximum) but hollow as well (5.5–7 mm outer diameter with hollow width 2.5–5 mm). Between the cavities of the main old and young shoot there was a short solid stem section. This shoot had never been inhabited by ants.

We could observe neither nectaries nor food bodies on the surfaces of leaves or stems.

Five further plants with a typical liana shape could be found during a second and third visit at the same site. The plants all showed the same typical ant-plant characters. They were climbing on trees or growing along the ground and were 6, 5, 3.5, 3, or 1.6 m long. All showed hollow internodes and the stems of four plants were partially torn open, presumably by a rodent, in the way described above.

Ant inhabitants

In the first plant, which appeared to have been initially inhabited by a colony of dolichoderine ants (*Tapinoma* sp.), small *Monomorium* workers were found. The second plant was colonized by a group of broodless workers of a large *Crematogaster* species, whose main nest with queen and brood probably was located elsewhere. In the third plant only ant colony remnants but no living ants were found. As already mentioned, the former ant inhabitants appeared to have been preyed upon by the predator (possibly a rodent). Though antless, this plant had produced new entrances at its young shoots. The fourth plant, 1.6 m long, was inhabited by a *Crematogaster* species as well. The nest entrances with a diameter ≥ 3 mm differed from the other openings by being protected with a 'carton' cover built by the ants. These 'carton' covers showed small round holes (diameter 1.5 mm), big enough to allow the ants to enter. The hollow stem interior was separated into several compartments by 'carton' walls. All internodes of a young side branch, 1.2 m long and with still unopened stomata, were hollow but not colonized by the ants.

Of all four plants with damaged stems one had been abandoned completely by its ants while the intact stem sections of the remaining three were inhabited by ants. One

was occupied by a colony of polymorphic *Crematogaster* and two by colonies of two *Camponotus* species, one of them belonging to the *saundersi* group, whose workers burst when gripped with the fingers.

All eight study plants lacked trophobiotic homoptera in the stem interior. None of the plant specimens showed any signs of colonization by a specific ant.

Herbarium material

In the Rijksherbarium at Leiden we could compare our plant samples with 10 *Capparis buwaldae* specimens collected in Borneo. In all aspects of their outer vegetative morphology, i.e., of stem, thorny stipules, and leaf structures, no differences to our plants could be detected. All other species of the region differ clearly from *Capparis buwaldae* in vegetative characters.

Only 4 of these 10 specimens of the Leiden herbarium were large enough in diameter to allow a meaningful investigation for ant-plant characters. One of these four plants showed stem structures which were similar to secondarily closed stomata, indicating a possible myrmecophytic character of this plant. However, its stem, as well as the stems of three other plants, were solid at the cutting site.

In the Leiden herbarium 65 other *Capparis* species and subspecies from the Indo-Australian region were examined for possible ant-plant characters. Twelve of these species were represented by 18 or more specimens each, a number which may be regarded sufficient to decide if a myrmecophytic character was present. None of the species checked showed any sign of ant-related structures such as domatia or pre-formed entrance holes: *C. callophylla* Blume (18 specimens), *C. cantoniensis* Lour. (45), *C. floribunda* Wight (24), *C. lanceolaris* DC. (41), *C. lucida* (Banks ex DC.) Benth. (19), *C. micracantha* DC. (121), *C. pubiflora* DC. (71), *C. pyrifolia* Lam. (44), *C. quiniflora* DC. (35), *C. sepiaria* L. (55), *C. zeylanica* L. (62), *C. zippeliana* Miq. (29).

DISCUSSION

Capparis buwaldae is the first myrmecophyte found in the Capparaceae. The ants gain access to the cavities in the stem through spontaneously formed short slit-like openings which become oval when enlarging. The small size and the compact design of the openings apparently does not compromise the stability of the stem. They soon close again when not used or strengthen their stability by growth when kept open by ants. Generally, stem stability appears an important factor in domatia evolution. Neglected till now, it has to be taken into account in future investigations and reflections.

The examination of herbarium material indicates that the formation of stomata is restricted to *C. buwaldae*, all the other 65 species checked are devoid of such structures (although for some species, including *C. buwaldae*, the sample sizes were small).

In Southeast Asia similar spontaneously formed stomata are known to occur in species of various plant families: *Myrmeconuclea strigosa* (Rubiaceae), several *Zanthoxylum* species (Rutaceae), *Ficus obscura* var. *borneensis* (Moraceae) and *Clerodend-*

drum fistulosum (Verbenaceae) (Maschwitz et al., 1989, 1992, 1994a, 1994b). All these plants are colonized by a variety of non-specific ants. Host specificity is not expected to be strongly developed since many different ants are able to colonize the stem if an entrance hole is provided by the host-plant. In contrast, ant-plants with (more or less) specialized ant tenants, for instance American *Cecropia*, *Triplaris*, African *Leonardoxa* and Asian *Macaranga*, form at most weak spots in the stem walls through which the colony-founding queens penetrate into the plant cavities. Only few ant species are able to tunnel entrances into living plant tissue and thus do not depend on herbivorous stem boring insects to establish protected permanent nest sites in living plant parts. Such traits in colony-founding ant queens, which lead to host specificity, cannot develop or will be lost if preformed stomata permit the colonization of the host-plant by opportunistically nesting non-specific ant species. In *C. buwaldae* we expect to find species of further ant genera as regular inhabitants of the hollow stems.

The ant species found in *C. buwaldae* did not cultivate homopteran trophobionts inside the stems. Other food sources for the ants like nectaries and food bodies could not be observed. The absence of any obvious food reward suggests that the ants have to leave their *Capparis* host to forage. Davidson & McKey (1993) discussed in *Myrmeconuclea* the possibility of nutrient augmentation by the ants. The storage of refuse and faeces in the domatia by the ants could concentrate nutrients which, if they could be resorbed, would enhance host fitness in nutrient-poor environments. At present, evidence for such a positive effect to *Myrmeconuclea* or *Capparis* by their inhabitants is lacking.

In South America the subtropical shrub *Capparis retusa* possesses nectaries and is often visited by nectarivorous ants. For example, one of these nectary visitors, *Camponotus blandus*, while not nesting in this *Capparis* species, nonetheless lowers the level of leaf damage inflicted by the leaf-cutting ant *Acromyrmex* (Farji Brener et al., 1992).

In some cases, myrmecophytism can be detrimental to the host-plant because of damage done by destructive vertebrate predators of ant brood. Damage to myrmecophytes by woodpeckers and mammals was often observed (Davidson & McKey, 1993; Maschwitz et al., 1994a). In *C. buwaldae* we recognized the same phenomenon presumably caused by a rodent. Six out of eight plants found (= 75%) showed damaged stem parts. Similar traces of destruction were observed in host-plants of the myrmecophytic ant genus *Cladomyrma*, i.e., in *Neonuclea*, *Drypetes*, and in *Saraca* (unpubl. results). Some predators seem to learn where to find the ant prey since most other host-plants in the vicinity suffered damage as well. But while the proportion of damaged plants in a population appears to be rather low, the impact of vertebrate damage on the maintenance of myrmecophytic associations is not easily assessed.

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