

HOYA MITRATA KERR (ASCLEPIADACEAE): A NEW MYRMECOTROPHIC EPIPHYTE FROM SOUTHEAST ASIA WITH A UNIQUE MULTILEAVED DOMATIUM

Andreas Weissflog¹, Joachim Moog¹, Walter Federle², Michael Werner¹, Rosli Hashim³ & Ulrich Maschwitz¹

¹ Zoologisches Institut, J. W. Goethe-Universität, Siesmayerstrasse 70, D-60054 Frankfurt, Germany

² Zoologie II, Biozentrum, Am Hubland, D-97074 Würzburg, Germany

³ Institute of Biological Science, University of Malaya, 50603 Kuala Lumpur, Malaysia

Key words: *Hoya mitrata*, *epiphytes*, *ants*, *myrmecodomatia*, *myrmecotrophy*, *southeast Asia*.

INTRODUCTION

The perhumid tropical areas of the Australasian region show a unique diversity in myrmecotrophic epiphytes (reviews in Bequaert 1922 and Jolivet 1996). A variety of plant structures apparently adapted to harbor ant colonies (myrmecodomatia) are found in different plant families, e.g., fleshy tubers derived from the hypocotyl in *Hydnophytum* and *Myrmecodia* (Rubiaceae) and rhizomes in the fern *Lecanopteris* (Polypodiaceae). In addition there are several myrmecophytic species of the Asclepiadaceae genus *Dischidia* which provide nesting space for ants either under convex-orbicular leaves attached to the plant surface as found, e.g. in the species *D. imbricata*, or inside complex leaf-pitchers as found in *D. major* (= *D. rafflesiana* Treub 1883) and *D. complex* (Rintz 1980).

In epiphyte-ant associations, the principal benefit for the plant seems to be nutritional. Myrmecotrophy, the feeding of plants by ants, has been convincingly demonstrated in several ant-house epiphytes (Janzen 1974, Rickson 1979, Beattie 1985, Benzing 1991). Particularly ants of the genus *Philidris* (Dolichoderinae) are reported as dominant and regular associates of myrmecotrophic epiphytes in the Australasian region. These ants typically place large quantities of debris and insect remains into the plants which absorb their decomposition products (Treseder *et al.* 1995).

The vegetative characters of epiphytes in the genus *Hoya* (Asclepiadaceae) are very similar to those

of *Dischidia*. However, myrmecophytic specialization seems to be rare in this genus and, with the exception of *H. imbricata*, *Hoya* species were not included in reviews of myrmecotrophic epiphytes (Davidson & Epstein 1989, Jolivet 1996).

During field trips in primary mixed dipterocarp forests in Sarawak (Miri), Malaysia (4°20'N, 113°50'E) and Thailand (Klong Thom, 7°40'N, 99°60'E), we came upon a conspicuous *Hoya* species with multileaved structures which turned out to be ant domatia. Here we report (1) the structure of a new domatium type (2), the ant species inhabiting these structures, and (3) other known myrmecodomatia in the genus *Hoya*.

RESULTS

The plant. Using Rintz's (1978) key for the Malayan *Hoya* species we identified the plant as *Hoya mitrata* Kerr. It was described by Kerr (1940) based on a single specimen from Thailand. Special domatia structures were not reported by him. This rare species is also found in the lowlands and forested hills of the Malay Peninsula, Sumatra and Borneo (Rintz 1978).

Hoya mitrata is an epiphytic twining climber with dimorphic foliage. As in all members of *Hoya* the fleshy stiff leaves are arranged mainly in an opposite and decussate position. Type 1 leaves are elongated, have a broad obovate shape and are apically mucronate with an apical tip and a cuneate-cordate base. The veins are prominent on the lower surface and easily visible on the upper surface (Figs. 1A, 2B). Type 2 leaves are elongated and lanceolate in shape

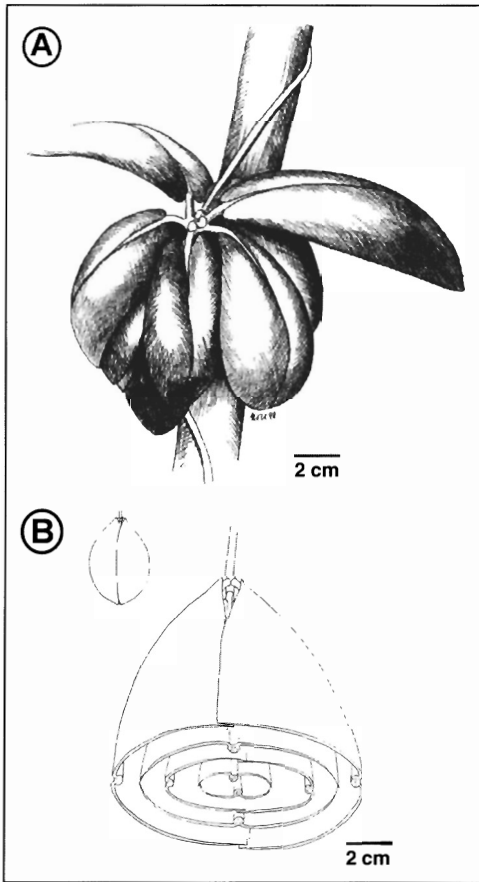


FIG. 1. (A) Arrangement of type 1 leaves in a typical domatium of *Hoya mitrata*. The cluster consists of 10 leaves (length = 9.3 ± 3.4 cm, width = 4.5 ± 1.0 cm). Three more leaves have already fallen off and only the leaf scars remain. (B) Schematic illustration of a domatium. The arrangement of the vault-like leaves in clusters results in several interconnecting chambers of different sizes which are easily entered by ants. Dotted line indicates position of cross section.

(Fig. 2 A). The midrib is prominent on the lower side while forming a groove on the upper side. Leaf type 2 is stiffer than the type 1 leaf as well as glossier and darker green in color.

The largest *H. mitrata* specimen we collected had 54 type 1 and 12 type 2 leaves. It was c. 6 m long and grew in the crown of a small tree (> 9 m). Twis-

ting internodes around the stem and branches of the host tree fasten the *Hoya* to the phorophyte. Type 1 leaves typically form clusters as a consequence of extremely stunted internodes (length < 1 cm compared to 9–16 cm for normal internodes, $n = 31$). The clustered leaves have a vaulted shape. Tightly joined together in whorls or in opposite pairs, they form the ovoid domatium structures (Fig. 1). The tip and margins of the first domatium leaf are appressed to the host tree surface, thus forming a chamber beneath the bark and the underside of the vaulted leaf. The next leaves of the cluster have their margins tightly appressed to the surfaces of the older leaves below, thus covering them partly like a roof tile and forming further cavities. All leaf tips of the cluster point downwards. Consequently, a rainproof multichambered cavity is created.

The result is a multilayered domatium structure with interconnecting chambers of different sizes (Fig. 1 B). Nodal and internodal roots borne on the stem filled the dark, humid chambers. They remained comparatively short (< 2 cm) if no ants occupied the cavity but reached a length of up to 15 cm and developed many branchlets and dense root hairs if organic material was provided by ants nesting inside. The undersides of all leaves forming the domatium were conspicuously purple in color, as were the upper sides of the inner leaves if covered by the outer ones. In contrast, the remaining leaves (type 2) on the long shoots were green. The length of the leaf clusters in five plants varied between 12 and 32 cm. The size of slits between overlapping leaves in unoccupied domatia was between 1 and 2 cm. Table 1 lists domatium sizes of 9 different plant specimens.

Ant inhabitants. At the collection sites in dense lowland dipterocarp forests, eight out of nine plants were inhabited by ants. They belonged to the genera *Crematogaster*, *Pheidole*, *Polyrhachis*, *Camponotus*, and *Tenomyrmex* (Table 1).

Crematogaster sp. A, *Camponotus* sp. and the silk-weaving *Polyrhachis* sp. used the domatia merely as shelters since for these species no ant brood was found. The other ants found to be nesting within the domatia are of special interest, for they partly filled the spaces between the leaves and also closed gaps and edges with carton structures consisting of chewed-up plant fibers, soil, insect fragments and other small particles. This nutrient-rich material was infiltrated extensively by the *Hoya* roots.

One ant species (*Pheidole* sp.) was found to tend scale insects on the host tree surface, another one

(*Crematogaster* sp. B) on the *Hoya* leaves. In one domatium of plant no. 3 (Table 1) colonies of two different ant species shared the nesting space. *Crematogaster* sp. B occupied the inner cavities formed by the host tree surface and the *Hoya* leaves, while *Technomyrmex* sp. inhabited the remaining space between overlapping leaves. On plant no. 5 (Table 1), besides *Crematogaster* sp. D a few workers of a parabiotic *Camponotus* sp. were found inside the same domatium.

DISCUSSION

The plant. Structural characteristics of the leaf clusters, e.g., the closed-off shape, the downward position of the entrances preventing accumulation of organic matter, as well as their multichambered and rainproof interior, indicate their domatium character. It is unlikely that the observed structure formed by modified leaves and a shortened stem axis (reduced elongation of internodes) functions as a mechanical protection for flower and leaf buds since (1) the flowers occur only on long-shoots (Thorut 1992, A. Weissflog, pers. observation) and (2) the young non-clustered leaves develop on the shoots outside of the cluster.

Kerr (1912) and Janzen (1974) reported the augmentation of roots in *Dischidia major* if the domatium was filled with debris and concluded that in this way the plant was fed by the ants. More recently Treseder *et al.* (1995), using stable isotope analysis, calculated that in *Dischidia major* in Sarawak 29% of the plant nitrogen is derived from debris deposited in the leaf cavities by ants. The massive root development into the ant carton material within the *H. mirrata* leaf cluster cavities strongly indicates that the nest material serves as a source of nutrients. Since the *H. mirrata* leaf clusters store materials (such as plant particles, insect remains and debris) which can be expected to be rich in nutrients, and also provide a protected nesting site for the ant colony, it is by definition a myrmecotrophic domatium (Beattie 1989, Benzing 1991).

Southeast Asian ant-epiphytes are mostly defined as well developed cases of plant-ant mutualism based on trophic relationships rather than protection (Janzen 1974, Rickson 1979). Because of the small number of *H. mirrata* specimens we could not investigate the effect of ant inhabitants on herbivores. However, particular carton-building ants collect epiphyllae and other microscopic particles from leaves

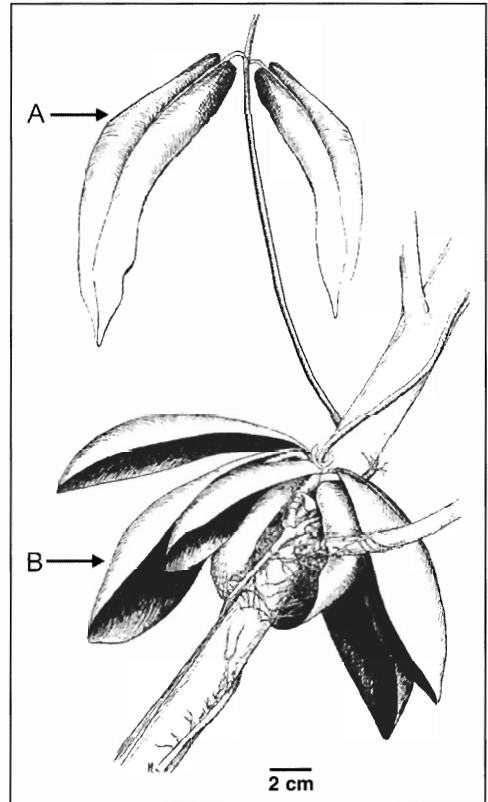


FIG. 2. The myrmecotrophic epiphyte *Hoya mirrata*. (A) Lanceolate leaves (leaf type 2). (B) Vault-like leaves (leaf type 1) forming the ovoid domatium structure. The leaves have been partially moved aside to show the roots filling the domatium.

and utilize them to build and maintain nest structures (Weissflog *et al.*, in prep.). In that way they may clean the photosynthetic surface of the epiphyte leaves.

The complex multichambered leaf structure is very unusual among the various myrmecotrophic domatia in epiphytes, which normally consist of one defined plant part, e. g., a modified hypocotyl, rhizome or leaf. Rather similar domatia structures are known only from the Neotropical Bromeliaceae genus *Tillandsia*, formed by a rosette-like inflation of the leaf bases, e.g., *T. bulbosa* (Huxley 1980).

In the entire epiphytic genus *Hoya* (consisting of about 200 species, Jolivet 1996) only a few further myrmecophytic species are known. The domatia

TABLE 1. Domatium size [maximum length (l) and width (w)] and number of nine *Hoya mitrata* specimens and their ant inhabitants. The plants were collected in Sarawak (nos. 1-5) and South Thailand (nos. 6-9).

Plant no	Length of plant	Size of domatia (l x w) [cm]	No. of domatia	Ant species	No. of ant individuals	Trophobionts
1	6 m	13 x 6 15 x 6 18 x 7 21 x 10	4	<i>Pheidole</i> sp.	> 200 + brood	+ ¹
2	0,3 m	25 x 17	1	<i>Crematogaster</i> sp. A	> 50	-
3	5 m	32 x 18 15 x 8	2	<i>Polyrhachis</i> sp. <i>Crematogaster</i> sp. B	12 > 1000 + brood	- + ²
4	1,2 m	16 x 9	1	<i>Technomyrmex</i> sp. <i>Crematogaster</i> sp. C	> 50 + brood > 100	- -
5	1,3 m	30 x 17	1	-	-	-
6	3,5 m	15 x 7 17 x 9 16 x 6 12 x 6	4	<i>Crematogaster</i> sp. D	> 100 + brood	-
7	5,5 m	22 x 12 15 x 8 19 x 10 15 x 7	4	<i>Crematogaster</i> sp. D <i>Camponotus</i> sp.	> 300 + brood few workers (Parabiosis)	- -
8	2 m	10 x 6	1	<i>Crematogaster</i> sp. ?	> 100 + brood	-
9	3 m	24 x 12 16 x 9 17 x 7 16 x 8	4	<i>Crematogaster</i> sp. E	> 100 + brood	-

¹ scale insects on the phorophyte, ² scale insects on the *Hoya*

of *H. imbricata* (Merrill 1946) and *H. maxima* (Schlechter & Warburg 1906/1907), found in the Philippines and New Guinea, are similar to myrmecophytic *Dischidia* species with circular convex domatia leaves tightly appressed to the bark of the phorophyte. During our literature study we came across an additional *Hoya* species that is similar to *Dischidia*, which has remained unnoticed in the literature on myrmecophytes. In addition to its normal oblong leaves, the Philippine *H. darwinii* (Loher 1910) possesses hollow spherical domatia leaves of golf-ball size divided into multiple separated cavities filled by roots. Their structure is similar to the chambered pitcher leaves of *Dischidia* complex (Rintz 1980). It should be mentioned that the inner domatium surface of all myrmecophytic species of *Hoya* (including *H. mitrata*) and *Dischidia* (Huxley 1980)

possess a deep purple coloration. In addition to some role in plant physiology such a dark leaf coloration may function as light protection, thus making it an acceptable ant nest-site (Janzen 1974). While the genus *Dischidia* is very rich in myrmecophytes (almost one third of the Australasian species are known to be myrmecophytic, Huxley 1980) only very few myrmecophytes with leaf domatia (< 2 %) have evolved in the genus *Hoya*.

The ant inhabitants. Anderson (1963) first drew attention to the tight arrangement of leaves in pseudo-whorls. Both he and C.H. Thorut (1992), a *Hoya*-collecting horticulturist, mentioned the occasional occurrence of ants in these structures without giving any information on their species identity or nesting methods.

Our findings indicate that the association of *H. mitrata* with ants seems to be non-specific. The contribution of the ants to the nutrition of their host plant is probably highly variable depending on the ant species involved, especially their different abilities to modify and close the domatia chambers with carton material. The benefit to the ants is a sturdy, rain-protected and long-lived nest site, a resource often in limiting supply for arboreal ants (Wilson 1959).

Interestingly, the typical Australasian myrmecotrophic epiphytes, like the numerous species of *Myrmecodia*, *Dischidia*, etc., are inhabited by specialized members of the ant genus *Philidris* (Dolichoderinae) if growing in open conditions (Huxley 1978, 1980; Beattie 1985, Maeyama *et al.* 1997). This seems not to be the case with *H. mitrata*, which was discovered by us at only two sites in dense mixed dipterocarp forests without potentially specific ant partners. It may therefore be the case that habitat characteristics rather than species-specificity determine which ant species colonize such ant-house plants (see also Yu & Davidson 1997).

ACKNOWLEDGMENTS

We thank the Economic Planning Unit (EPU, Malaysia) for research permission and the Deutsche Forschungsgemeinschaft (DFG) for financial support (Ma 373/ 17-5; SPP "Mechanismen der Aufrechterhaltung tropischer Diversität"). We are grateful to Winfried Noll for the drawings of *Hoya mitrata*. Christine M. Burton (Porterdale) from the *Hoya* Society International and Ted Green (Kaaawa, Hawaii) provided useful information about *Hoya*-related literature.

REFERENCES

- Anderson, J.A.R. 1963. The flora of the peat swamp forests of Sarawak and Brunei, including a catalogue of all recorded species of flowering plants, ferns and fern allies. *Gardens Bulletin Singapore* 20 (Ser. 3. Part 2.): 131–228.
- Beattie, A.J. 1985. The evolutionary ecology of ant-plant mutualism. Cambridge, UK.
- Beattie, A. 1989. Myrmecotrophy: plants fed by ants. *TREE* 4: 172–176.
- Benzing, D.H. 1991. Myrmecotrophy: origins, operation, and importance. Pp. 353–373 in Huxley C.R., & D.F. Cutler (eds.). *Ant plant interactions*. Oxford, UK.
- Bequaert, J. 1922. Ants in their diverse relations to the plant world. *Bull. Am. Mus. Nat. Hist.* 45: 333–584.
- Davidson, D.W., & W.W. Epstein. 1989. Epiphytic associations with ants. Pp. 200–233 in Lüttge, U. (ed.). *Vascular plants as epiphytes: evolution and ecophysiology*. New York.
- Huxley, C.R. 1978. The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships between their morphology, ant occupants, physiology and ecology. *New Phytol.* 80: 231–268.
- Huxley, C.R. 1980. Symbiosis between ants and epiphytes. *Biol. Rev. Camb. Phil. Soc.* 55: 321–340.
- Janzen, D.H. 1974. Epiphytic myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. *Biotropica* 6: 237–259.
- Jolivet, P. 1996. Ants and plants. An example of coevolution. Leiden.
- Kerr, A. 1912. Notes on *Dischidia rafflesiana*, Wall., and *Dischidia nummularia*, Br. *Scient. Proc. Royal Dublin Society XIII*: 291–318.
- Kerr, A. 1940. *Hoya mitrata* Kerr. *Asclepiadaceae*. *Tribus Marsdenieae*. *Hookers Icones Plantarum* 35: tabula 3406.
- Loher, H. 1910. New or noteworthy plants. *Hoya darwinii*. *Gardeners Chronicle* 47, 3 rd. Series: 66.
- Maeyama, T., Terayama, M., & T. Matsumoto. 1997. Comparative studies of various symbiotic relationships between rubiacerous epiphytic myrmecophytes and their inhabitant ant species (Hymenoptera: Formicidae). *Sociobiology* 30: 169–174.
- Merrill, E.D. 1946. *Plant life of the Pacific World*. New York.
- Rickson, F.R. 1979. Absorption of animal tissue breakdown products into a plant stem – the feeding of a plant by ants. *Amer. J. Bot.* 66: 87–90.
- Rintz, R.E. 1978. The Peninsular Malaysian species of *Hoya* (Asclepiadaceae). *Malayan Nature Journal* 30: 467–522.
- Rintz, R.E. 1980. The Peninsular Malaysian species of *Dischidia* (Asclepiadaceae). *Blumea* 26: 81–126.
- Schlechter, R., & O. Warburg. 1906/1907. *Asclepiadaceae novae Asiae australis et orientalis*. II. Pp. 339–347 in Fedde, F (ed.). *Repertorium novarum specierum regni vegetabilis*. Berlin-Wilmersdorf.
- Thorut, C. 1992. *Hoya mitrata* Kerr, and other Thailand Hoyas. *The Hoyan* 13: 70.
- Treseder, K.K., Davidson, D.W., & J.R. Ehleringer. 1995. Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. *Nature* 375: 137–139.
- Treub, M. 1883. Sur les urnes du *Dischidia rafflesiana* Wall. *Ann. Jard. Bot. Buitenzorg* 3: 13–34.
- Wilson, E.O. 1959. Some ecological characteristics of ants in New Guinea rain forests. *Ecology* 40: 437–447.
- Yu, W.D., & D.W. Davidson. 1997. Experimental studies of species-specificity in *Cecropia*-ant relationships. *Ecological Monographs* 67: 273–294.

Accepted 17 August 1999.