

THE TUBEROUS EPIPHYTES OF THE RUBIACEAE 1: A NEW SUBTRIBE - THE HYDNOPHYTINAE

C.R. HUXLEY¹ & M.H.P. JEBB^{1 2}

SUMMARY

The morphology and ant-association of the five genera *Hydnophytum* Jack, *Myrmecodia* Jack, *Anthorrhiza* Huxley & Jebb, *Squamellaria* Becc. and *Myrmephytum* Becc. are described. On the basis of shared character states in tuber cavity development and inflorescence structure these five genera are united as a subtribe, the Hydnophytinae.

CONTENTS

	page
Introduction	1
The genera	3
Comparative morphology	5
Tuber	5
Roots and spines	9
Stems	10
Leaves and stipules	10
Inflorescence and bracts	11
Flowers	12
Fruit and pyrenes	14
Distribution and ecology	15
Distribution	15
Ecology	15
Ant-association	15
The recognition of a subtribe Hydnophytinae	16
Rationale of the subtribe	16
Position in the Psychotrieae	16
Hydnophytinae	17
Table of comparison of the genera	18
Key to the genera	19
Acknowledgements	19
References	19

INTRODUCTION

The tuberous epiphytes of the Rubiaceae have long been a subject of interest because of their complex chambered tubers which are often inhabited by ants. The tubers are derived from the hypocotyl which swells, and phellogens arise within the

1) Department of Plant Sciences, Oxford University, South Parks Road, Oxford, OX1 3RB, U.K.

2) Now at Christensen Research Institute, P.O. Box 305, Madang, Papua New Guinea.

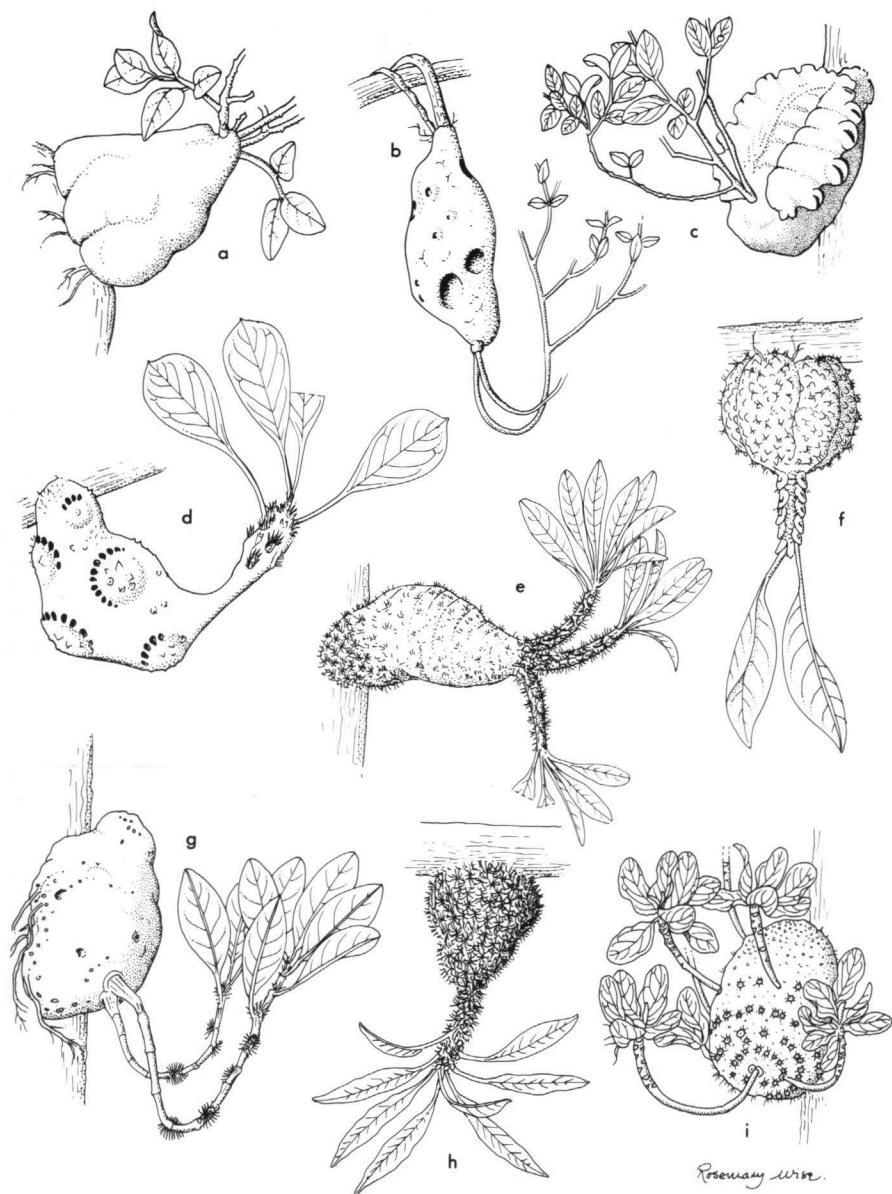


Fig. 1. External form of the Hydnohytinae. a. *Hydnophytum moseleyanum* Becc.; b. *H. myrtifolium* Merr. & Perry; c. *H. guppyanum* Becc.; d. *Myrmecodia tuberosa* Jack; e. *M. brassii* Merr. & Perry; f. *M. platyrea* Becc.; g. *Anthorrhiza recurispina* Huxley & Jebb; h. *A. caerulea* Huxley & Jebb; i. *Squamellaria major* A.C. Smith. Drawn by Rosemary Wise.

parenchyma cutting out volumes of tissue which die, leaving cavities. Ants usually occupy these cavities and through their debris provide the plant with a source of macronutrients (Huxley, 1978). The five genera with these tubers have undergone considerable specialization and speciation (Huxley, 1981; Jebb, 1985).

Rumphius first described these plants in 1750, but Linnaeus did not take up the work and Jack (1823) gave the names to the two main genera: *Hydnophytum* and *Myrmecodia*. Odoardo Beccari (1884–86) described a further three genera: *Myrmephytum*, *Myrmedoma*, and *Squamellaria*, although he had no details of the tubers in the latter genus. Since Beccari's work, species have been added piecemeal except for Valetton's effort to make a comprehensive survey, but he died while this was in progress (see Huxley, 1976, 1978, 1981). A new genus *Anthorrhiza* has now been described (Huxley & Jebb, 1990, 1991a) which is defined on inflorescence, floral, and tuber cavity characters, but variable in its vegetative appearance. *Myrmedoma* has now been sunk into *Myrmephytum* on account of its floral and inflorescence similarities (Huxley & Jebb, 1991b).

It is now apparent that the tuber and cavities of all these genera are almost certainly homologous; coupled with similarities in inflorescence structure, floral characters, and chorological evidence, this suggests that these genera have had a single origin. The group is also homogeneous in its vegetative morphology, ecology, and distribution (figs. 1 & 2). We therefore propose that these genera are united as a subtribe, the Hydnophytinae.

Our studies of the Hydnophytinae have covered the ecology, morphology, taxonomy, tubers and ant-interactions of *Myrmecodia*, *Hydnophytum*, *Anthorrhiza*, and *Squamellaria* (Huxley, 1976, 1978, 1981; Jebb, 1985). *Myrmephytum* (including *Myrmedoma*) has been examined taxonomically in the light of these other genera, but only one species was available for morphological study. Revisions of the genera are published in this volume or are in preparation.

During the late 19th century, studies and speculations were made on the formation of the tubers and the role of the ants (Treub, 1883, 1888; Beccari, 1884–86; Karsten, 1895). Miehe (1911a & b) made detailed studies of the ant-association demonstrating absorption by certain of the cavity surfaces. Interest then focused on 'physiological' explanations for the tubers (Spanner, 1939), until Janzen's ecological study of the plants and their ants (1974). Isotope tracer studies have now shown that nutrients brought by the ants, can be absorbed by the plants (Huxley, 1978).

THE GENERA

Hydnophytum, with some 50 species, is the largest genus in the group, and some species share underived character states with much of the Psychotrieae. In *Hydnophytum* several shrubby stems arise from the tuber apex (fig. 1a–c). The tuber is rounded and most species lack spines. The tuber cavities of this genus show the greatest range of form of all the genera in the Hydnophytinae (fig. 3a–c), but they are not as complex as in *Myrmecodia* and *Squamellaria* (fig. 4). In four species the inflorescence is sympodial and terminal, and falls shortly after flowering and fruiting (fig. 5a), which is the common condition in the Psychotrieae. In the remaining species the inflorescence is delayed and does not appear terminally, but arises in one axil

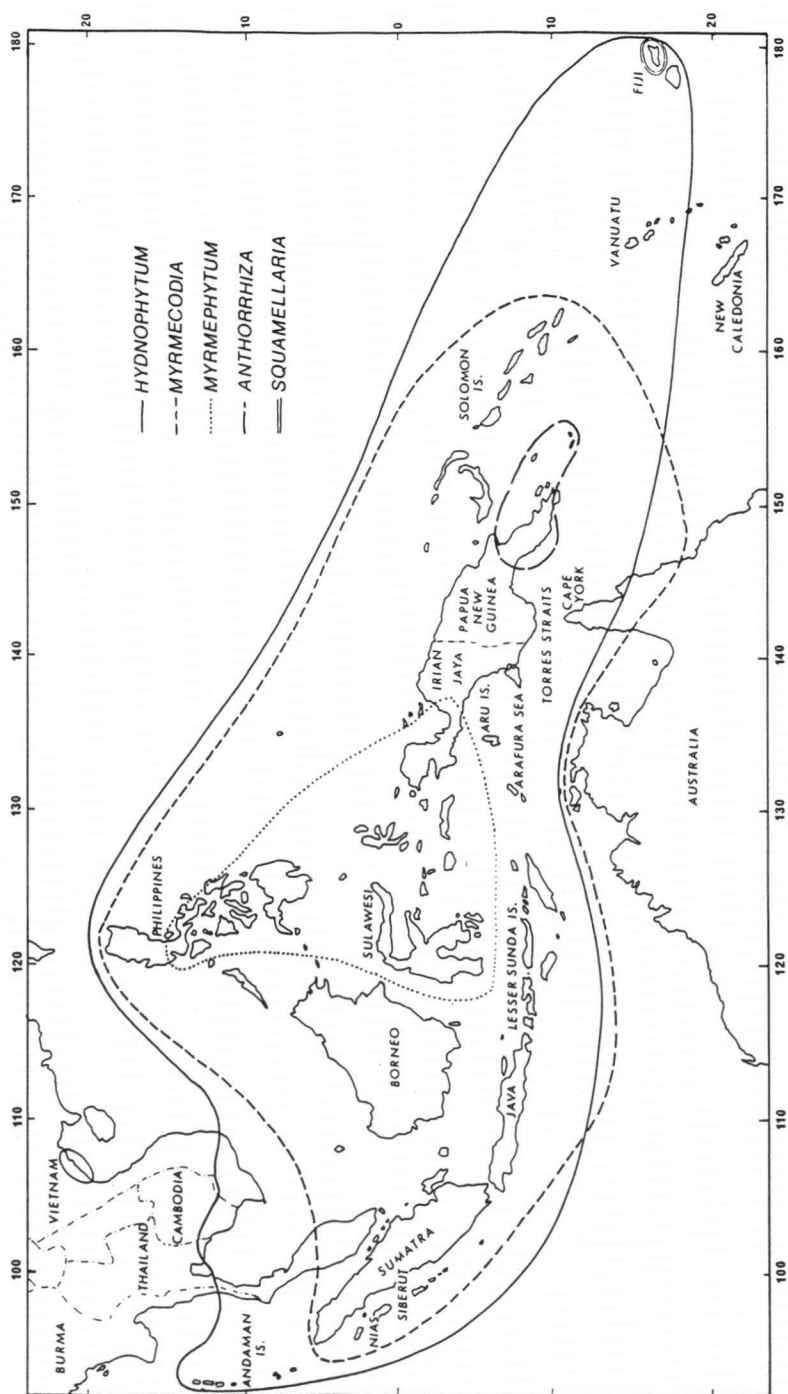


Fig. 2. Distribution of the five genera of the Hydnohytinae.

at each node and is paired, one part lying to each side of the leaf axil (fig. 5b). In several species the inflorescence is pedunculate, while in the remainder it is sessile, generally long lived, and occasionally covered by persistent bracts.

Myrmecodia has fewer species (c. 25), but occupies a similar range to *Hydnophytum* (fig. 2). In *Myrmecodia* the stems are few in number, thick with short internodes, and rarely branched (fig. 1d–f). Both stem and tubers bear spines. The tuber cavities of *Myrmecodia* are sharply differentiated into smooth and absorptive chambers. In *Myrmecodia* the inflorescence is always paired, and sunken in alveoli either side of the leaf axil (fig. 5d). The partial inflorescences are larger than those of *Hydnophytum*, often exceeding one centimeter in diameter. These inflorescences continue to produce flowers throughout the life of the plant. The genus *Anthorrhiza* comprises eight species, and exhibits a range of vegetative morphological variety which encompasses that seen in both *Myrmecodia* and *Hydnophytum* (fig. 1g, h). This situation obscures the formerly clear cut morphological distinction between the spiny, pachycaulous *Myrmecodia* and the non-spiny, leptocaulous *Hydnophytum*. In *Anthorrhiza* the single, large, axillary inflorescence lies more or less central to the leaf axil (fig. 5d).

With the exception of *Myrmephytum* (including *Myrmedoma*) all the genera have 4-merous flowers. *Myrmephytum* has 6-merous, blue flowers, and the inflorescence is solitary and bract enclosed (Huxley & Jebb, 1991b). Much like *Anthorrhiza*, *Myrmephytum* demonstrates a range of vegetative morphology, which is explicable in ecological and evolutionary terms. These two small genera inhabit non-overlapping areas within the range of *Hydnophytum* and *Myrmecodia* (fig. 2).

Squamellaria consists of three species with elongated stems and sparsely spined tubers (fig. 1i) (Jebb, 1991). The inflorescence is solitary and slightly displaced laterally in the leaf axil. Stems arise laterally as well as apically on the tuber of *Squamellaria*. The genus was originally recognised by Beccari on the strength of floral characters, especially the squamules inside the corolla tube and the capitate, fringed stigma (1886). The tubers of this genus have a different cavity structure, which has greatly strengthened the generic distinction. *Squamellaria* is geographically isolated, in Fiji, lying outside the range of *Myrmecodia*, and demonstrates several parallels to *Myrmecodia*, *Myrmephytum*, and *Anthorrhiza* in New Guinea.

COMPARATIVE MORPHOLOGY

TUBER

External features

The tuber is formed by the hypocotyl of the seedling which swells, even in the absence of ants (Forbes, 1880; Treub, 1883). In small species typical tubers may be 8 × 15 cm but in most cases the tuber continues to grow and may reach 50 cm across in some *Hydnophytum* species. In only one species (*H. normale* Becc.) is the tuber reported to be facultatively absent (Beccari, 1884–86), although this is doubtful. The exact nature of this absence is uncertain; for example stems of *Hydnophytum* can take root by layering or through cuttings, and then do not form a tuber.

The shape of the tubers results from the way in which new cavities are added. In *Hydnophytum* growth is usually all over the surface or lateral, and the tubers are

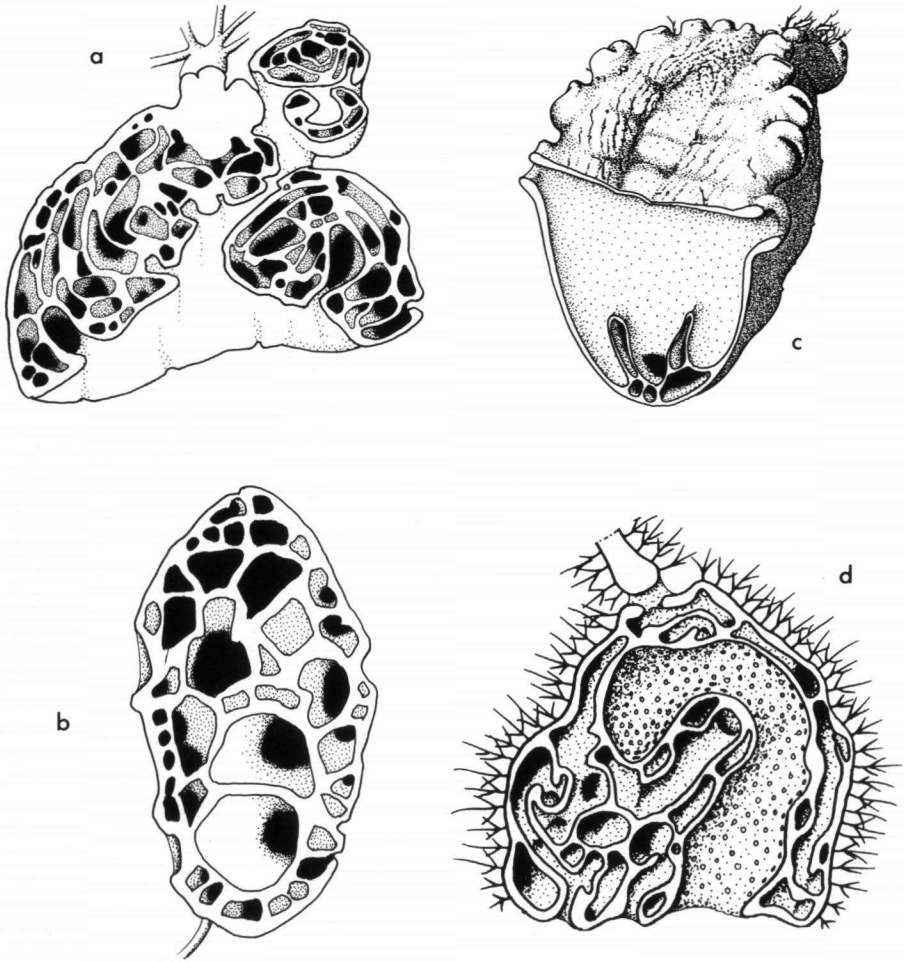


Fig. 3. Tuber cavity structure in *Hydrophytum* and *Anthorrhiza*. a. *H. moseleyanum*; b. *H. myrtifolium*; c. *H. guppyanum*; d. *Anthorrhiza caerulea*. Drawn by Rosemary Wise.

globose, flattened or clasping (fig. 1a). In some species growth is apical, producing elongated tubers (fig. 1b, c). In *Myrmecodia* apical growth produces a more regular ovoid, cylindrical tuber (fig. 1d, f). Rarely there is a distinct lower and upper portion (fig. 1e). In *Anthorrhiza* the tubers vary from conical and globose to flattened (fig. 1g, h). *Squamellaria* has relatively large obovoid to cylindrical tubers which are bilaterally symmetrical (fig. 1i).

The colour of the tuber surface varies between species from dark brown through fawn to grey. Young areas of the tuber may be greenish. The flesh of the tuber is normally buff or green, but is magenta in several species of *Hydrophytum* and *Myrmecodia*. Longitudinal ridges are common in *Myrmecodia* (fig. 1f), but absent from

the other genera. *Squamellaria* tubers are 'hooped', being swollen between the rings of entrance holes. The tuber surface in some *Hydnophytum* and *Anthorrhiza* species is often areolate, while in the remaining genera it is generally smooth. In some species of *Myrmecodia* small (1–2 mm) swellings similar in structure to the internal warts (see below) are sometimes present externally (Spanner, 1938). In *Squamellaria* rather larger (3–4 mm) swellings are present which, at least in *S. major* A.C. Smith, are associated with fungal hyphae (Jebb, 1985). These swellings have not been investigated anatomically.

Formation of the tuber cavities

The tuber cavities are made by phellogens, meristematic layers which arise de novo in the parenchyma of the swollen hypocotyl and enclose volumes of parenchyma. In some *Myrmecodiae* and *Hydnophyta* the phellogens sometimes cut through vascular bundles. Following suberization of a single layer of cell walls, the enclosed tissue dies and shrivels (Treub, 1883, 1888; Huxley, 1978). This process is similar in all five genera, and may be unique to this group of plants. The first cavity is initially a simple hook shape in all the genera, except some members of *Myrmecodia* where the apex is bifid. During subsequent growth of the tuber the first cavity expands only slightly, except in *Anthorrhiza* where it grows considerably (fig. 3d), and to a lesser extent in some species of *Hydnophytum* and *Myrmephytum*. The first cavity always has a single basal opening to the outside. This hole is initially covered by the epidermis of the tuber which is usually torn open, either as the tuber grows or by ants or other invertebrates.

The cavity system develops by further discrete phellogens each forming a new cavity. Their position and structure is often complex and highly characteristic but is difficult to examine because each cavity is formed among existing ones. Later cavities may have none, one, few or many entrance holes to the outside. These holes are scattered or may be arranged in arcs, rings, or two parallel rows along the tuber (fig. 1c).

Later cavities may or may not connect with existing cavities, though not with the initial cavity. Interconnections with other cavities are formed in a similar way to entrance holes, with the new phellogen fusing to the earlier cavity's wall. In certain species of *Myrmecodia* and *Anthorrhiza*, cavities may open at the base of the stem (figs. 3d, 4a), and in some *Myrmecodiae* form within the stem.

Smaller holes to the outside, referred to as pores, too small to admit an ant, are also found in many species of *Myrmecodia* (fig. 4b) and in some *Myrmephyta*. They are located in small groups or rings over particular areas of the cavities (see below).

Warts are small (c. 1 mm diameter) pale protrusions on certain of the cavity surfaces. Although described as lenticel-like they do not have air spaces between the small cytoplasm-filled cells (Huxley, 1978). The pale surface of the wart is unsuberized and almost certainly highly absorptive. Warts are probably adapted from root tips, in *Hydnophytum guppyanum* Becc. and *H. kajewskii* Merr. & Perry they appear like tiny roots (Beccari, 1884–86). The initial cavity is usually warted, as are some blind-ended extremities of later cavities. Cavity walls without warts are referred to as smooth. As a rule the cavity walls of superficial cavities are more darkly pigmented than deeper-lying cavities.

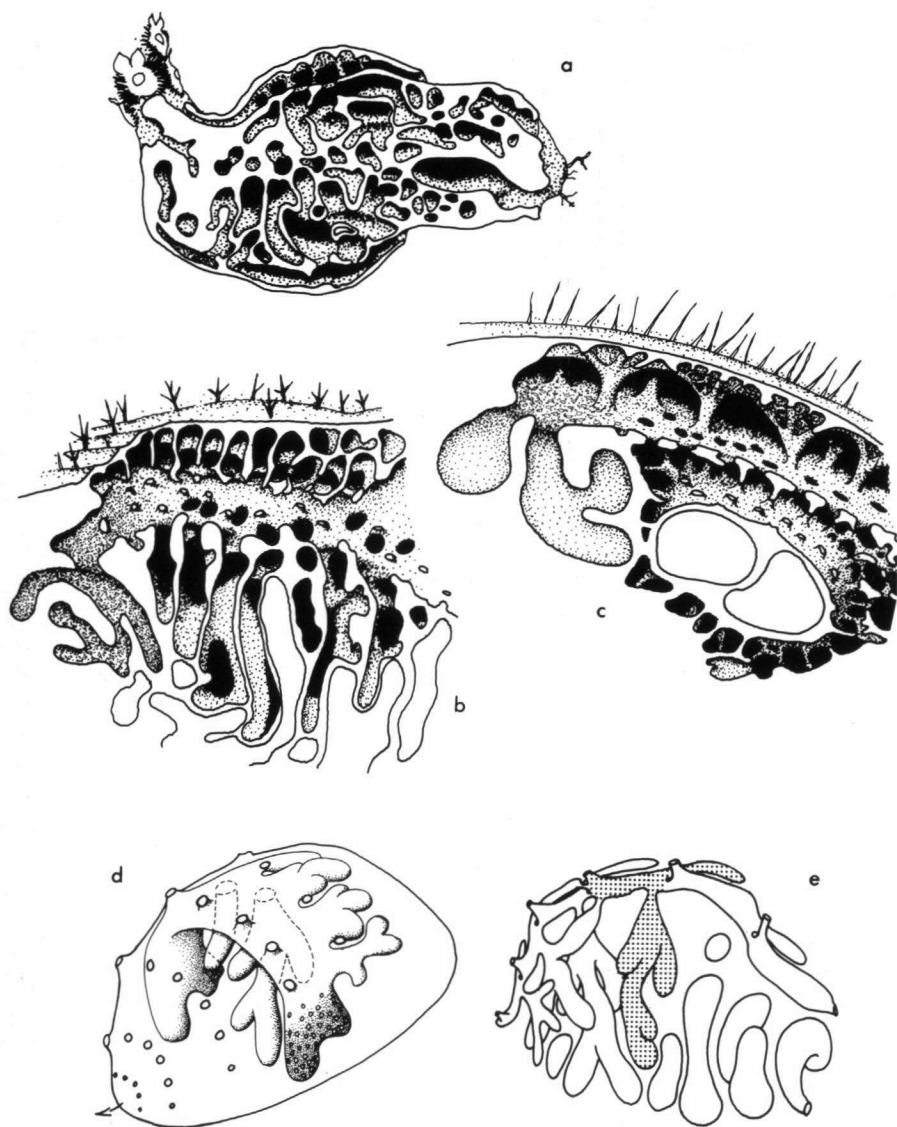


Fig. 4. Tuber cavity structure in *Myrmecodia* and *Squamellaria*. a. *M. tuberosa*; b. *M. platytyrea*; c. *M. schlechteri*; d & e. *Squamellaria imberbis*. Drawn by Rosemary Wise.

Structure and position of the cavities

The structure of the cavities and the position in which they are added are important characters at specific and generic level and in understanding the whole group. Broadly there are two kinds of arrangement of the cavities: a) cavities of two major types: some produced early, which are for the most part warded, and later cavities

which are smooth, or only slightly warted; and b) all the cavities (after early development) are essentially the same (repeat cavities) and are internally differentiated into chambers with distinct shapes and presence or absence of warts. The two-cavity type and the repeat-cavity type appear to be two morphological solutions to the problem of maintaining a balance of the functionally distinct warted and smooth-walled surfaces as the tuber develops. In *Anthorrhiza* the two cavity-type system is developed and the early warted cavities are able to expand not only in size but also in complexity, becoming branched (fig. 3d). In *Myrmecodia* and *Squamellaria* the repeat cavities are differentiated into chambers with distinct shapes and surface characteristics, these cavities are added at the apex of the tuber (fig. 4). In the only species of *Myrmephytum* studied a combination occurs, the first cavities grow while later cavities form repeat units incorporating both warted and smooth chambers. In *Hydnophytum* some species have two-cavity types, while in others repeat cavity units are added either laterally (fig. 3a) or apically (fig. 3b). The different types of arrangement are not sharply distinguished in *Hydnophytum*, and the repeat cavities are not as complex as those of *Myrmecodia* and *Squamellaria*.

ROOTS AND SPINES

Roots

The radical is soon joined by two to four other roots arising from around the base of the swollen hypocotyl. These roots grow and attach the plant to its host tree. Sometimes a mature plant is blown loose and may hang suspended from its host by roots up to a meter long. Roots are only very rarely produced within the cavities. The roots of other epiphytes (e.g. *Dischidia* species, Asclepiadaceae) often enter the cavities, and may be mistaken for those of the rubiaceous ant-plant (Janzen, 1974; pers. obs.).

Spines

Spines are present in all five genera. They have a vascular structure which indicates they are modified adventitious roots, newly grown spines have root caps (Treub, 1883), and there is also a gradation from spines to roots. Spines are most common on the tubers, especially around the entrance holes. They are also common around the inflorescence, and densely clothe the stems in many species of *Myrmecodia*.

Spines sometimes occur in unexpected places: in the spiny species of *Anthorrhiza* and *Myrmecodia* leaf scars occasionally give rise to spines. In *Anthorrhiza* spines have been found on torn and eaten surfaces of the leaves. The spines may be simple, varying from weak to very stout, or branched. Branching may be irregular, or stellate in *Myrmecodia*, *Myrmephytum*, *Anthorrhiza* and one species of *Hydnophytum*. Colour varies from black to golden or silvery.

Spines are only rarely present in *Hydnophytum*, and in *Squamellaria* they are simple and flexible. Sometimes short adventitious roots may be present around the inflorescence of *Hydnophytum* species.

Spines are usually present on the tuber and stem of *Myrmecodia*. They vary from simple or root-like to repeatedly branched or regularly stellate or club-shaped. On the stem they are often well developed round the alveoli and clypeoli; while on the tuber they are most developed round the entrance holes, and on the ridges.

In *Anthorrhiza* there is a range from complete absence of spines to dense, stellate spines. When spines are present on both stem and tuber, those on the stem are longer and more branched than those on the tuber. In *Anthorrhiza*, but not in the other genera, spines sometimes arise within the inflorescences on ridges of tissue between the flower bearing patches. They also arise on longitudinal ridges along the stems. The spines of *Myrmephytum* are denser on the tuber than on the stem, and vary from simple to irregularly stellate.

STEMS

The stems of the five genera are subherbaceous to woody, and reach between 10 and 100 cm in length. The first few nodes are sterile, and after the stem becomes fertile the internodes are shorter and fatter.

In *Hydnophytum* there are few to many, often freely branched, stems, while in *Myrmecodia* one or a few little or unbranched stems are present, the stem is very thick and the fertile internodes are greatly reduced in length. In several species of *Myrmecodia* there is a shield-shaped boss from which each leaf arises, these clypeoli may be spine fringed and hide the stem entirely (fig. 4a). In a few species cavities are present, making four tunnels along the stem which open at the alveoli and often interconnect. In *Anthorrhiza* and *Myrmephytum*, both *Hydnophytum*-like and *Myrmecodia*-like stems are found. In *Squamellaria* stems are present at the apex and laterally on the tuber, either singly or in clusters. In *S. major* one stem arises between each ring of entrance holes, and the internodes are thickened and contracted towards the stem apices. The vascular tissue in *Hydnophytum* stems forms a cylinder, while in *Myrmecodia* it is present as four broad strands. In *Myrmephytum arfakianum* (Becc.) Huxley & Jebb the highly condensed stem does not begin to elongate and flower until the tuber has reached a substantial size.

LEAVES AND STIPULES

Leaves

The entire leaves are typically leathery, being sometimes rather fleshy in *Hydnophytum*, and usually larger and thinner in *Myrmecodia*. At high altitudes *Hydnophytum* and some species of *Anthorrhiza* tend to lack ants and have small, sclerophyllous leaves (fig. 1b); while *Myrmecodia* and species of *Anthorrhiza* with ants have long, narrow leaves (fig. 1e, h). The midrib and petiole are usually green but may be almost white or maroon coloured in *Myrmecodia*. Some species of all the genera except *Hydnophytum* have undulate leaf margins.

Stipules

The stipules of all genera form a square-based pyramid covering the next pair of leaves. As these leaves extend and the stem swells, the stipules split in a characteristic way. In *Hydnophytum* and *Squamellaria* they split opposite the petioles, leaving two triangular pieces across the nodes. These stipules soon fall. In *Myrmecodia* the stipules split opposite and between the petioles, and usually persist as pairs of triangular projections in each leaf axil. In some species they are prominent and persistent on the clypeoli (fig. 5d). In *Anthorrhiza* the stipules are caducous to persistent, and

split irregularly opposite the petiole, while in *Myrmephytum* they are small and inconspicuous.

INFLORESCENCE AND BRACTS

Inflorescence

Once flowering has started an inflorescence occurs in one leaf axil at each node ('pseudoaxillary', Robbrecht, 1988). The inflorescences usually continue to flower over a long period, only the very basal ones on a stem being without flowers. The inflorescence is pedunculate or sessile, paired or solitary. However, in two species

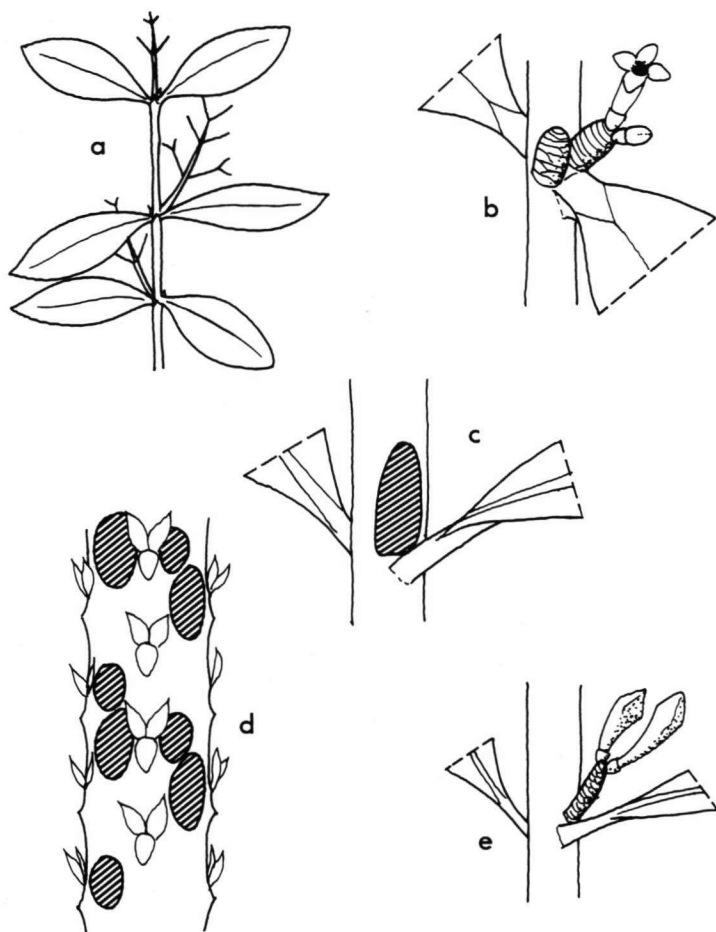


Fig. 5. Diagrams of the inflorescence insertion in the Hydnophytinae. a. *Hydnophytum guppyanum*; b. *H. moseleyanum*; c. *Anthorrhiza echinella* Huxley & Jebb; d. *Myrmecodia tuberosa*; e. *Squamellaria imberbis* (A. Gray) Becc.

of *Hydnophytum* (*H. guppyanum* and *H. kajewskii*) the distichously branched panicle appears terminally and is later overtopped by the stem which is thus sympodial. In *Hydnophytum* a series of inflorescence forms are present, which can be interpreted broadly as a progressive loss of the peduncle (fig. 5a, b). The solitary, distichous panicle of *H. kajewskii* is often pseudodichotomous by loss of the main axis, which may be terminated by a functional or aborted flower. In several species (e.g. *H. albertisii* Becc.) a paired structure is present which has the appearance of the two branches of a *H. guppyanum* inflorescence, as though by loss of the basal section of the peduncle. The flower bearing branches are reduced, the sessile flowers becoming closely packed. In the majority of *Hydnophytum* species the inflorescence appears as a pair of fertile mounds (fig. 5b).

In the two species of *Hydnophytum* from Fiji only a solitary mound is present, at the side of each axil, and a single flower may appear apically between the stipules. This arrangement is similar to the solitary and laterally displaced inflorescence of *Squamellaria* (fig. 5e).

In *Myrmecodia* the inflorescence is paired and usually sunken into alveoli. One inflorescence is often larger than its pair and displaced along the stem (fig. 5d). The stem is sometimes so condensed that there appears to be a continuous mass of inflorescences and their arrangement is obscured by spines which arise round but not within the alveoli, or by prominent bracts or bract hairs.

In *Anthorrhiza* the inflorescence is a single bract or spine covered area, which is nearly central to the leaf axil, but slightly displaced (fig. 5c), as is confirmed by examining the vascular supply. The inflorescence is composed of peduncular patches — areas of fertile tissue which are separated by non-fertile tissue, which may or may not protrude as walls bearing numerous spines. This non-fertile tissue is interpreted as stem-tissue by Jebb (1985). Branches of the main stem arise from within the inflorescence, being surrounded on all sides by fertile, flower producing tissue.

In *Myrmephytum* the sessile inflorescence is solitary and comprises a highly condensed, dichotomously branched, flower bearing area. In one species the products of the first dichotomy become slightly separated and the inflorescence may appear paired.

Bracts

Further work is required on the bracts, the following is a provisional statement. Each flower is contained in a single (paired in *Myrmephytum*) papery or leathery bract which splits along one edge. In *Anthorrhiza* later flower buds arise from within earlier bracts, and are contained, along with the current flower, inside the bracts. Almost all species have a large or small number of hairs within the bracts, attached at the lower edge. In some species of *Hydnophytum*, *Myrmecodia*, and *Anthorrhiza* the inconspicuous papery bracts are rapidly lost, but the bract hairs may be numerous and persist, surrounding the flower, and filling the inflorescence with a dense cushion. In other species and in *Myrmephytum* the bracts are large and leathery, while the bract hairs are short and less conspicuous.

In *Squamellaria* the bracts are scarcely visible. In *Myrmephytum* the inflorescence is surrounded by two prominent triangular bracts which are leathery to fleshy. Later flowers are contained within pairs of bracts within the initial pair. Later formed bracts are often less robust and more hairy.

FLOWERS

Heterostyly

Heterostyly is common in *Hydnophytum*, *Myrmecodia* and *Anthorrhiza* and is also found in *Myrmephytum*. In *Myrmecodia* heterostyly is often not well defined and may be breaking down, some species appear to be cleistogamous with the pollen germinating in the unopened flower. *Squamellaria* is homostylous, with a capitate stigma. Two Fijian species of *Hydnophytum* have dimorphic flowers, with pistillate flowers having sterile anthers. Smith (1988) interpreted this as polygamodioecism, with plants bearing either staminate or pistillate flowers or both staminate and hermaphrodite flowers. Extensive field studies by M.H.P.J., however, revealed that in these species, although the pistillate flowers do have sterile anthers, those flowers with fertile anthers have a style much shorter than the corolla tube. Moreover, although the stigma is borne above the anthers, the style is plucked from the disc during growth of the corolla tube, effectively neutering the ovules (Jebb, 1985). Both flower types have been found in the same inflorescence.

Perianth

The flowers are 4-merous except in *Myrmephytum* which is 6-merous. The tubular calyx is thin and scarious, truncate to shallowly 4-lobed, rarely reaching more than 2 mm. The corolla is white, rarely blue, or tipped with red or green. The corolla is 10–20(–50) mm long in *Hydnophytum*, *Myrmecodia* and *Anthorrhiza*. It is divided into lobes for one quarter to one half of its length. The lobe tips are thick and in *Myrmecodia* may project downwards internally forming a hook, uncus. More rarely the lobe tips are free and spreading in the bud. The corolla is typically white, but blue in *Myrmephytum* and one species of *Anthorrhiza*. Except in *Squamellaria* there is usually a ring of hairs somewhere in the corolla tube; it may be broad or narrow and its position varies with that of the anthers and stigma.

The flowers of *Squamellaria* are comparatively large, ranging from 20 to 40 mm in length. They are minutely pubescent without. The corolla is white, but some species have red or green markings on the lobes. The tube may be quadrangular or inflated, and is slightly recurved. *Squamellaria* is characterised by the presence of 4 fringed plates (scales or squamellae) at the base of the corolla tube opposite the lobes. These plates resemble minute water fonts, being attached to the corolla wall along their lower edge and sides. Like the ring of hairs inside the corolla of the other genera, these fringed plates occlude the lumen of the corolla.

Anthers and pollen

The anthers are typically white or yellowish, sometimes with blue flecks, but may be dark blue. The pollen shows interesting generic patterns in the group. Most *Hydnophytum* pollen is very uniform, it is small, 60–100(–130) μm diameter, tricolpate and with a fine pattern of perforations in the pollen wall, vesicles are absent. However, the two species from Fiji have large (110–130 μm), 4- (3–5)-colpate pollen with a large reticulation, and the colpi with a distinct margo. This pollen is very similar to that of *Squamellaria*.

In *Myrmecodia* the pollen is (1-) 2- or 3-porate; one, two, or three protoplasmic vesicles often protrude through the apertures and in some species the pollen wall covers only a small part of the grain. This must have implications for pollination, as such pollen could probably not survive long in the open and may depend on self-pollination (cf. other exine-less rain forest pollen, Robbrecht, 1988).

Anthorrhiza has triporate pollen, occasionally with thickened borders to the pores. Reticulation is fine to medium. Protruding vesicles may be large.

In *Squamellaria* the pollen grains are relatively large (110–160 μm), with an open reticulation of the outer wall (meshes wide, diameter 6–30 μm). There are four colpi, rarely three or five), almost extending the total height of the grain, sometimes partly occluded by projections from the borders of the colpus. The reticulation is very large. The pollen of *Myrmephytum* is 3- (or 4-) colpate, 70–160 μm diameter, with variable reticulation.

Disc and gynoecium

A prominent ring-shaped disc is present between the base of the corolla and style. It appears to secrete nectar especially after the corolla has fallen. The disc is often prominent on the mature fruit.

The stigma varies in position from low in the tube to exserted; it is lobed, with as many lobes as there are locules, except in *Squamellaria* and the Fijian *Hydnophytum* where it is capitate. In *Squamellaria* the stigma is fringed below, and positioned just above the anthers.

The locules are uniovular. There are 2 (4) locules in *Hydnophytum*, 4–8(–10) in *Myrmecodia*, 4–8 in *Myrmephytum*, 2–8 in *Anthorrhiza* and 4 in *Squamellaria*.

THE FRUIT AND PYRENES

Fruit

The fruit is a rounded or elongate drupe, except in one species of *Squamellaria* in which it is leathery and square in cross section. The remains of the calyx and the disc are more or less conspicuous at the apex.

The developing fruit is greenish, becoming red, orange, yellow, or white when ripe. In *Myrmecodia* the fruit develops within the alveolus and at maturity the base of the fruit elongates pushing the upper part with the pyrenes out into an exposed position. A juicy thread of flesh is attached to the base of each pyrene. In some species the development of the fruit appears to be delayed after fertilization.

Pyrenes

The pyrenes are obovate and flattened where they abut another pyrene: being semicircular in cross section if there are two pyrenes; triangular if there are three, and progressively more narrowly triangular if more than three. The apex of the pyrenes may be apiculate along the adaxial line or have shoulders or horns at the apex where they abut the neighbouring pyrenes. The horny endocarp is straw coloured to dark brown and splits irregularly at the base on germination. The endosperm is non-ruminate.

DISTRIBUTION AND ECOLOGY

DISTRIBUTION

These genera are found in the tropical Far East (fig. 2), with the highest diversity in New Guinea. There is a further small diversification in Fiji which parallels that in other groups such as *Mucuna* Adans. (Fabaceae, Mimosoideae) and the genus *Kingiodendron* Harms (Fabaceae, Caesalpinioideae) (B. Verdcourt, pers. comm.).

The three small genera occur in different parts of the range of *Hydnophytum*. *Anthorrhiza* and *Myrmecophytum* overlap with both *Hydnophytum* and *Myrmecodia*, while *Squamellaria* is found outside the range of *Myrmecodia*.

Lowland areas are generally covered by a few widespread, variable species of *Myrmecodia* and *Hydnophytum* which are most abundant in open forests. The greatest number of species occurs in the montane areas of New Guinea. It is common to find *Hydnophytum* together with one of the other genera at a given locality, but unusual to find more than one species of any of the genera.

ECOLOGY

Hydnophytum and *Myrmecodia* are most common in seasonal, open forests. *Melaleuca* savanna in western Papua New Guinea has abundant ant-epiphytes of these genera and from other families. Mangroves and trees such as *Casuarina*, in open agricultural areas are also favoured. In closed lowland rain forest members of Hydnophytinae are present in low numbers. Montane forest is again favoured and some species grow terrestrially above the tree line. Some species of all the genera are locally abundant in areas with low-nutrient soils. This occurs at Bako in Borneo (Janzen, 1974), and in various areas in New Guinea, e.g. on Normanby Island, and around the Anggi Gigi Lakes in the Vogelkop.

The Hydnophytinae mostly colonize branches rather than trunks and some have clear preferences for different positions in the canopy. Some trees are more frequent hosts than others.

ANT-ASSOCIATION

A number of species of *Hydnophytum* and at least one of *Anthorrhiza* are not normally associated with ants, but all the other species of the five genera are usually inhabited by one of three species of *Iridomyrmex* (Dolichoderinae) (Huxley, 1978). In species without ants there is often some water present in the tuber as well as invertebrates and biological detritus. Frogs and their eggs have been found in montane species of *Hydnophytum* (Jebb, 1985).

Among ant inhabited plants, those near human habitation and along roads are quite often occupied by other ants, and in Australia the cosmopolitan tramp ant, *Pheidole megacephala*, may be replacing *Iridomyrmex* extensively. In Papua New Guinea *Myrmecodia* is more consistently inhabited by *Iridomyrmex* than is *Hydnophytum* (Huxley, 1976). In lowland areas and open forest up to 1000 m *Iridomyrmex corda-*

tus (Fr. Smith) is the usual symbiont but it is replaced by *I. scrutator* in rain forest and at higher altitude (Huxley, 1976). Jebb (1985) found that two species of the *I. scrutator* group are involved.

Other organisms are also associated with the Hydnophytinae. Lycaenid butterflies, leaf-miner moths, Homoptera and fungi (Huxley, 1976, 1978). Most regular of these is a fungus, *Arthrocladium* (Moniliales), which grows on the surface of the warted chambers. It is almost always present in *Myrmecodia* with *Iridomyrmex cordatus* but less common in *Hydnophytum* or in plants with *I. scrutator*. An unidentified fungus is also apparently parasitic in the tissue of the smooth chambers of *Myrmecodia tuberosa*.

THE RECOGNITION OF A SUBTRIBE HYDNOPHYTINAE

RATIONALE OF THE SUBTRIBE

It has become overwhelmingly apparent that the five genera (*Hydnophytum*, *Myrmecodia*, *Anthorrhiza*, *Myrmephytum*, and *Squamellaria*) are closely related. Their tubers and cavities, although widely different in mature shape, initiate and are developed by a similar mechanism. The tuber is formed by the hypocotyl of the seedling, which swells even in the absence of ants. Phellogens arise *de novo* in the parenchyma cutting through vascular bundles and enclosing volumes of parenchyma and vascular tissue which then die and shrivel leaving hollow cavities. Putative absorptive sites, warts, arise in certain areas of some of the cavities in all the genera. The genera also show similarities in stem, spine, inflorescence, flower, and fruit characters described above. This makes it almost certain that these genera are monophyletic. Hence it is desirable to recognize a taxon comprising these five genera. We have chosen to adopt a name, the Hydnophytinae, at the subtribe level.

The Hydnophytinae are also linked chorologically (fig. 2). The two main genera have a similar distribution, while two minor genera occupy discrete areas within the main range, and *Squamellaria* falls within the range of *Hydnophytum* but outside that of *Myrmecodia*. This correlates with the greater specialization for association with ants shown by all the genera relative to *Hydnophytum*.

POSITION IN THE PSYCHOTRIAE

Schumann (1891) placed the tuberous Rubiaceae (*Myrmecodia*, *Hydnophytum*, *Myrmephytum* and *Myrmedoma*) in the tribe Psychotrieae where they continue to appear quite natural (Darwin, 1976; Robbrecht, 1988). The delimitation of the Psychotrieae is not problematic except for the delimitation against the Morindeae (Robbrecht, 1988). The Psychotrieae has not previously been classified into subtribes. With the Hydnophytinae divided off, the resulting group, the Psychotriinae, will probably require future subdivision after study of the whole tribe.

Psychotria L. itself appears to be the genus most closely related to the Hydnophytinae. Of the genera in the Malesian area (Backer & Bakhuizen, 1963) *Psychotria* has the appropriate terminal inflorescence which soon becomes lateral; the main axis of this inflorescence carries pairs of opposite branches, which are branched again. *Psy-*

chotria has white, heterostylous, and often 4-merous flowers, and a 2-celled ovary. These features are all present in some members of *Hydnophytum*, which is probably 'primitive' within the Hydnophytinae.

HYDNOPHYTINAE Huxley & Jebb, Bull. Jard. Bot. Nat. Belg. 60 (1990) 420–421

Differs from the other Psychotrieae in the swollen hypocotyl forming a tuber which is divided by a series of phellogens into complex cavities. Type genus: *Hydnophytum* Jack.

Other genera included: *Myrmecodia* Jack, *Myrmephytum* Becc. (including *Myrmedomia* Becc.), *Squamellaria* Becc., and *Anthorrhiza* Huxley & Jebb.

Shrubby epiphytes, some species occasionally terrestrial on nutrient poor soil or at high altitude. Hypocotyl forming a succulent tuber. *Tuber* 10–100 cm long, conical, cylindrical, rounded, or flattened. The surface smooth, lobed, longitudinally ridged, or 'hooped'; often with spines derived from adventitious roots. Cavities in the tuber formed by a series of phellogens. Cavities sometimes warted, and variously differentiated into chambers, opening to the outside by entrance holes 0.3–3 cm in diameter, and sometimes by pores c. 0.1 cm in diameter.

Stems 10–100 cm, woody to succulent, one to several from the tuber apex, sometimes elsewhere on the tuber in *Squamellaria*. Branching frequent to absent. The internodes condensed or not, typically longer and narrower when sterile; once flowering starts almost all the nodes are fertile. Simple, branched, or stellate spines often present on the stem, especially around the inflorescence. *Leaves* usually leathery, sometimes stiff or fleshy. Stipules extending right round the stem when young, splitting opposite, or opposite and between the petioles when mature, deciduous or persistent.

Inflorescence usually appearing laterally in the axil of one of each pair of leaves, but in two species of *Hydnophytum* initially terminal, becoming lateral, the stem being sympodial. The inflorescence forms a branched panicle with opposite branches through a paired pseudodichotomous structure with the axes terminated by a functional or aborted flower and the lateral branches highly condensed, to paired or single mounds, or sessile areas or paired, sunken peduncular patches (fig. 5). Bracts paired or single, prominent thick and leathery to scale-like, or apparently absent. Hairs along the basal inner margin of the bracts septate, flat, dry, chestnut to rufous brown, sometimes forming a dense cushion-like mass.

Flowers 4- or 6-merous, sometimes heterostylous. Calyx short, truncate, notched, rarely dentate or lobed. Corolla white (turquoise, green, red); lobes often uncinatate. A ring (4 bundles) of hairs is usually present within the tube, rarely exserted. In *Squamellaria* hairs absent but 4 small fringed plates (squamules or scales) present. Pollen 3- (1–5-)colpate, colpate or porate, often with protoplasmic vesicles, reticulation fine to coarse, 60–163 μm . Stigma capitate or 2–10-fid. Disc prominent. Ovary 2–10-locular; locules uni-ovular. Fruit a fleshy (rarely dry), translucent or opaque drupe, white, yellow, or red in colour. Calyx and disc usually persistent and prominent on the fruit. Pyrenes 2–10, with a fleshy thread at the basal end, broadest above the middle, apex blunt or apiculate, base tapered. Opening by irregular splits from the base on germination. Endosperm non-ruminate.

Table — Comparison of characteristic features of the five genera of the Hydnoephytinae.

	<i>Hydnophyllum</i>	<i>Myrmecodia</i>	<i>Anhorhiza</i>	<i>Myrmephytum</i>	<i>Squamellaria</i>
Tuber	cylindrical, spherical, or flattened	cylindrical or spherical	spherical to conical or flattened	spherical to conical	spherical to ovoid
Cavity types	one or two types	repeat cavities	two types	two types	repeat cavities
Cavity addition	apical or lateral	apical	peripheral	apical and peripheral	apical
Stems	apical, several; not condensed; branched	apical, one to few; rarely condensed; rarely branched	apical; condensed or not; branched or not	apical; condensed or not; little branched	apical and lateral; not condensed; rarely branched
Leaves	xeromorphic	usually mesomorphic	mesomorphic or xeromorphic	mesomorphic or xeromorphic	mesomorphic or xeromorphic
Spines	rare on tuber or around inflorescence	always present, especially on tuber and around inflorescence	present or absent	present or absent, never on stem (?)	rare
Inflorescence	paired or solitary, displaced; pedunculate or sessile	paired; sunken	solitary, ± central to axil; sessile to sunken	solitary; sessile	solitary, displaced to side of axil; on mounds sessile
Bracts	rarely prominent	prominent or not	prominent or not	prominent or minute	minute
Flower	4-merous	4-merous	4-merous	6-merous	4-merous
Corolla lobes	white; not uncinatate; ring of hairs	white; uncinatate; ring of hairs	white, blue; not uncinatate; hairs rare	white or blue; ± uncinatate; hairs ±	white; not uncinatate; hairs absent; squamules
Style	bilid (capitate)	4-8-fid	2-8-fid	6-fid	capitate, fringed
Pyrenes	2 (4)	4-8 (10)	2-8	? 4-8	4

KEY TO THE GENERA OF THE HYDNOPHYTINAE

- 1a. Flower 6-merous, bracts or bract hairs conspicuous **Myrmephytum**
- b. Flower 4-merous, bracts and bract hairs conspicuous or not 2
- 2a. Inflorescence solitary, \pm central or laterally displaced in the leaf axil 3
- b. Inflorescence paired, side by side, sometimes displaced along the stem 5
- 3a. Inflorescence \pm central to leaf axil, sessile to sunken, large, 0.5–4 cm across; stem branches and spines sometimes conspicuous, arising among the peduncular patches **Anthorrhiza**
- b. Inflorescence not central to leaf axil, pedunculate to sessile, rarely terminal, less than 0.5 cm broad at the base. Spines absent from the inflorescence, but adventitious roots sometimes present 4
- 4a. Tuber with rings of entrance holes, concentric about the tuber axis. Corolla with fringed plates at the base of the tube **Squamellaria**
- b. Entrance holes scattered over the tuber surface or in two lines along the sides of the tuber. Corolla glabrous or with a ring of hairs within the tube. **Hydnophytum**
- 5a. Inflorescence sunken. Tuber and stem with spines or adventitious roots especially around holes and inflorescences. Stems one to few, thick, branching sparse or absent; vascular tissue in 4 bundles. Leaves never less than 5 cm long. Pyrenes 4–10 **Myrmecodia**
- b. Inflorescence pedunculate to sessile. Tuber and stem without spines, occasionally with adventitious roots. Stems one to many, slender, \pm freely branching; vascular tissue forming a cylinder. Leaves 0.3–30 cm. Pyrenes 2–4 **Hydnophytum**

ACKNOWLEDGEMENTS

We would like to thank our supervisor, F. White, for his continuous support; Dr. E. Robbrecht, Dr. B. Verdcourt, and Dr. A.C. Smith for taxonomic assistance; all the institutions cited for loan of material; and all the very many people, especially the Papua New Guineans, who have made this work possible.

REFERENCES

- BACKER, C.A., & R.C. BAKHUIZEN VAN DEN BRINK. 1963. Flora of Java. Noordhoff, Groningen.
- BECCARI, O. 1884–86. *Piante Ospitatrici, Malesia 2*. Istituto Sordo-Muti, Genoa.
- DARWIN, S.P. 1976. The subfamilial, tribal and subtribal nomenclature of the Rubiaceae. *Taxon* 25: 595–610.
- FORBES, H.O. 1880. Notes from Java. *Nature* 22: 148.
- HUXLEY, C.R. 1976. The ant-plants Hydnophytum and Myrmecodia (Family: Rubiaceae) of Papua New Guinea, and the ants which inhabit them. M.Sc. Thesis, University of Papua New Guinea.
- HUXLEY, C.R. 1978. The ant-plants Myrmecodia and Hydnophytum (Rubiaceae), and the relationships between their morphology and occupants, physiology and ecology. *New Phytol.* 80: 231–268.
- HUXLEY, C.R. 1981. Evolution and taxonomy of myrmecophytes with particular reference to Myrmecodia and Hydnophytum (Rubiaceae). D.Phil. Thesis, University of Oxford.
- HUXLEY, C.R., & M.H.P. JEBB. 1990. New taxa in the myrmecophilous Psychotrieae (Rubiaceae). *Bull. Jard. Bot. Nat. Belg.* 60: 420–421.

- HUXLEY, C.R., & M.H.P. JEBB. 1991a. The tuberous epiphytes of the Rubiaceae 2: The new genus *Anthorrhiza*. *Blumea* 36 (1991) 21–41 (this issue).
- HUXLEY, C.R., & M.H.P. JEBB. 1991b. The tuberous epiphytes of the Rubiaceae 3: A revision of *Myrmephytum* to include *Myrmedoma*. *Blumea* 36 (1991) 43–52 (this issue).
- JACK, W. 1823. Account of the *Lansium* and some other genera of Malayan plants. *Trans. Linn. Soc. Lond.* 14: 122–125.
- JANZEN, D.H. 1974. Epiphytic myrmecophytes in Sarawak: mutualism through feeding of plants by ants. *Biotropica* 6: 237–259.
- JEBB, M.H.P. 1985. Taxonomy and tuber morphology of the rubiaceous ant-plants. D.Phil. Thesis, University of Oxford.
- JEBB, M.H.P. 1991. The tuberous epiphytes of the Rubiaceae 4: A revision of *Squamellaria*. *Blumea* 36 (1991) 53–61 (this issue).
- KARSTEN, G. 1895. Morphologische und biologische Untersuchungen über einige Epiphytenformen der Molukken. *Ann. Jard. Bot. Buitenzorg* 12: 185–195.
- MIEHE, H. 1911a. Untersuchungen über die javanischer Myrmecodia. In *Javanische Studien* 2. Abh. Math.-Phys. Cl. Königl. Sächs. Ges. Wiss. 32: 312–361.
- MIEHE, H. 1911b. Über die javanische Myrmecodia und die Beziehung zu ihren Ameisen. *Biol. Centralbl.* 31: 733–738.
- ROBBRECHT, E. 1988. Tropical woody Rubiaceae. National Botanic Garden of Belgium; Meise.
- SCHUMANN, K. 1891. Rubiaceae. In: A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien* IV, 4: 1–156.
- SMITH, A.C. 1988. *Flora Vitiensis Nova* 4: 240–245. Pacific Tropical Botanic Garden, Hawaii.
- SPANNER, L. 1938. Ein Beitrag zur Morphologie einiger Myrmecodien. *Beih. Bot. Zentralbl.* 58: 267–290.
- SPANNER, L. 1939. Untersuchungen über den Wärme- und Wasser-Haushalt von Myrmecodia und *Hydnophytum*. *Jahrb. Wiss. Bot.* 88: 243–283.
- TREUB, M. 1883. Sur le *Myrmecodia echinata* Gaudich. *Ann. Jard. Bot. Buitenzorg* 3: 129–159.
- TREUB, M. 1888. Nouvelles recherches sur le *Myrmecodia* de Java. *Ann. Jard. Bot. Buitenzorg* 7: 191–212.