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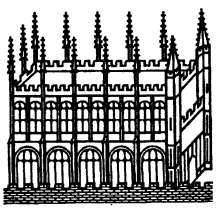

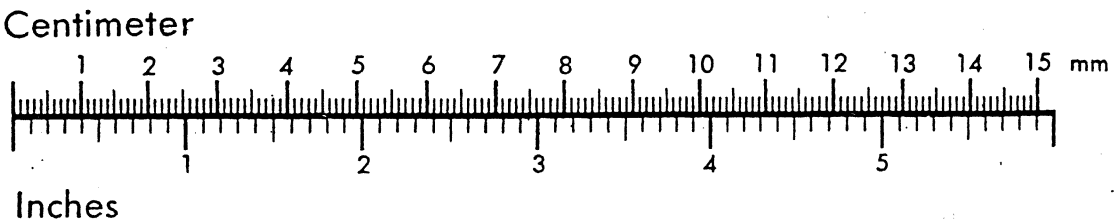

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Evolution and Taxonomy

of

Myrmecophytes

with particular reference to

Myrmecodia and Hydnophytum

(Rubiaceae)



By

Camilla R. Huxley - Lambrick

A thesis submitted for the degree of

Doctor of Philosophy

at

Oxford University

Wolfson College

Hilary Term 1981

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Abstract of D. Phil. thesis:

'The evolution and taxonomy of myrmecophytes with particular reference to Myrmecodia and Hydnophytum (Rubiaceae).'

By Camilla R. Huxley-Lambrick, Wolfson College, Oxford; February 1981.

Those epiphytes which are inhabited by ants are reviewed; they comprise nine genera in four families. All are tropical and most are from the Far East. They probably all gain mineral nutrients from material brought by the ants. This contrasts with myrmecophytic trees and shrubs which are defended against insect herbivores by ants collecting food produced by the plant.

Five of the nine genera of ant-epiphytes belong to the Rubiaceae; two of these, Hydnophytum and Myrmecodia are highly diversified and specialized. They are found throughout the tropical Far East in a range of habitats, but are most abundant in open canopies. Ants (Iridomymex cordatus and I. cf. scrutator) occupy cavities in the enlarged hypocotyl.

The 'tuber' cavities and other unusual morphological features are elaborated in Myrmecodia. For instance, spines of different types are derived from adventitious roots; internodes are condensed and covered by outgrowths at each leaf-base; stipules are enlarged and differ in their splitting. The inflorescence rachis is progressively reduced in Hydnophytum, and the flowers sunk in the stem in Myrmecodia. These structural changes possibly benefit the ants, but may have reduced the frequency of cross-pollination, though some heterostyly is present. The morphology of the satellite genera (Myrmephytum, Anthorhiza and Squamellaria) shows some parallels with that of Myrmecodia.

The five genera are united as a subtribe - the Hydnophytinae. Detailed taxonomic treatment of Myrmecodia and the satellite genera, but not Hydnophytum, is given. Myrmecodia is reduced from 43 to 18 species. One is a variable, widespread, lowland species which is divided into informal categories. One is polytypic with three subspecies, four are variable, but not divided, and the rest are monotypic, geographically restricted, mostly montane species. The pattern of variation is often reticulate, and a hierarchy or infrageneric grouping was not identified.

Myrmecodia and the satellite genera appear to have evolved independently from Hydnophytum-like ancestors. Structures probably advantageous to the ants have arisen repeatedly, but may also have led to inbreeding and taxonomic difficulty. The more sophisticated symbiosis in Myrmecodia may be reflected by the more mesomorphic nature of that genus, and is a prime example of coevolution between higher plants and animals.

I. Introduction

1. STATEMENT OF THE PROBLEM
2. MATERIALS AND METHODS
3. GENERAL TAXONOMIC CONSIDERATIONS
4. PLAN OF THE THESIS

1. STATEMENT OF THE PROBLEM

The diversity of flowering plants amazes the observer still; not only by the seemingly endless different combinations of characters, but because we understand neither the selective pressures and genetic material which have brought about the diversity, nor the mechanisms by which speciation occurs. If the pattern of variation in a group of plants is analysed, as is done in this thesis, it is common to find that certain characters are gained or lost repeatedly, and that after the aquisition of a given feature, radiation in others may follow. This is to be expected given the similar genetic material and potential for mutation of the parent stock. Under comparable environmental conditions in different areas this gives rise to frequent parallel and convergent evolution. The resulting pattern of variation is a reticulate network in which the closeness of relationship of different forms and the sequence of the various developments is often hard to unravel.

Even when the variation in a group of plants is known, the selective forces which may have led to it remain obscure. Not only can we not guess what forms might arise in a genus, we cannot even estimate what conditions were necessary for the evolution of known species. It is interesting that this problem is more acute in plants than in animals. In an animal the characters which are used to identify it are usually either clearly adaptive to its environment or they enable members of the species to recognize one another. In a plant though, characters used for identification often appear unrelated to its environment. For instance leaf-shape, venation, indumentum, ovary position and stamen number may serve to identify a plant; but another plant, differing in all these characters may occupy the same habitat, perhaps even sharing the same pollination and dispersal mechanisms. Thus many of the characters traditionally used to establish a taxonomic hierachy may give only a limited indication of the action of natural selection. It is however precisely the influence of natural selection on evolution which is of great interest.

Add to this problem, the rudimentary state of our knowledge of the mechanisms of speciation. Polyploidy, geographical isolation and selection for incompatibility mechanisms all play their part. It is not clear, though, under what conditions the different mechanisms may occur, or what their relative importance is.

This thesis is a study of the diversity of a group of plants in which a new mode of nutrition has arisen, and the plants have subsequently undergone considerable evolution. This new form of nutrition is a result of symbiosis with ants. These ants live inside the plants and leave there waste material which then forms a source of mineral nutrients and possibly organic nitrogen compounds. The plants have structures which absorb these compounds. This type of symbiosis has evolved at least five times in four different plant families and appears to have enabled the plants to become successful epiphytes. In one of the families, the Rubiaceae, these 'ant-epiphytes' have diversified to fill a wide range of habitats over a large geographical area. Some of these plants have also become more specialized in their association with ants. One in particular of the genera, Myrmecodia, has modifications of the stem and of the chambers which are used by the ants. This genus is also the one which is most consistently occupied by ants (Huxley, 1978).

The thesis is devoted mainly to this genus, Myrmecodia, which occurs throughout the eastern archipelago from Indochina to Australia. The genus has required considerable taxonomic revision as it was last treated monographically a century ago (Beccari, 1884-6). Since then names have been added piecemeal, without regard for the group as a whole.

The morphology of the genus is remarkable for a number of most unusual structures particularly the outgrowths along the stem (clypeoli) and the stellate spines. Various of these features are possibly of benefit to the ants and no other function is apparent. It is therefore especially interesting to trace the course of development of these features in the genus. This task however has not been easy; neither myself nor previous authors have found a

satisfactory system of subgeneric division of the genus, nor is a progressive sequence readily discernible between the different forms.

Ecologically Myrmecodia is quite catholic, occurring in most forest types from sea-level to above the tree-line. The response of the genus to altitude is particularly surprising as the leaves remain large and mesomorphic; whereas in the related genus Hydnophytum they become small and leathery at high altitude.

Comparison with the other ant-associated epiphytes from the Rubiaceae and from other families reveals illuminating parallels and differences (see Chapter II). The other genera and families in which analagous symbioses are found are Dischidia (Asclepiadaceae), Tillandsia (Bromeliaceae), and Lecanopteris and Solenopteris (both in the Polypodiaceae). Many of the structures and variations found in these genera are comparable to those found in the Rubiaceae.

The patterns of variation and adaptation of these plants is examined in order to gain some understanding of the evolution which has taken place. In particular the nature of the influence of the ants, if any, on the evolution of the plants is considered and speculative hypotheses are put forward.

This study was stimulated by ecological and physiological investigations of the ant-plants which I made in Papua New Guinea during 1974-1976. That work was presented for a Master's degree at the University of Papua New Guinea and later published (Huxley, 1978). The major findings were that the plants are able to absorb nutrients fed to the ants, and that two species of the ant genus Iridomyrmex occur in these ant-plants in different habitats. In order to consider the great diversity of plants encountered and to evaluate the role of the symbiosis in that diversity an adequate taxonomic base was required; this is not available in the literature. I also wished to compare the species I had seen with the total range in the group and to obtain an overall view of the evolution in these symbiotic plants.

I have therefore begun a monographic study based on herbarium material. The interesting questions about the

interaction and evolution of species can only really be answered by field studies of the ecology and reproductive biology of the plants, in combination with studies of cytology and physiology. Such investigations must however follow questions raised by broad, descriptive accounts such as the one presented here. It is hoped that this work will form both an inspiration and a foundation for others.

2. MATERIALS AND METHODS

This study is based on herbarium material, both that which I collected (c. 140 numbers in the University of Papua New Guinea series), and material loaned from Arnold Arboretum, Bogor, Brisbane, British Museum, Geneva, Grey Herbarium, Kew, Lae, Leiden, Paris, Vienna, and Wroclaw. I also visited the herbaria at Berlin, Brussels, Paris and Florence. At an earlier stage I had visited Lae, Brisbane, Canberra (CANB and CBG), Melbourne, Atherton (QRS), Singapore, Bogor, Kuala Lumpur and Kepong.

In addition to dead material there are several living plants at Oxford and elsewhere, which have been used in morphological studies.

The nature of the material available has often rendered the taxonomic treatment less complete than desired. Being succulent and filled with biting ants, these plants and especially the tubers, are not easy to collect or to preserve. Collection of an adequate specimen usually requires the whole plant to be destroyed, so for conservation reasons as well, only few duplicates are made. The flowers are not easy to see, and collectors overlooking them often leave the plants.

Characters used include features of the tubers, stems, leaves, spines and floral characters. The flowers are few and difficult of access so information about them is particularly sparse. Floral characters are also confused by the presence of heterostyly.

Owing to the small number of specimens available, statistical methods of comparison of specimens and taxa

have not been used. In order to aid the assessment of variation in several characters simultaneously, extensive use has been made of leaf silhouettes and ideograms drawn onto maps showing the localities. Decisions based on several features have then been simplified and variation in a few characters is illustrated here in order to show the nature of the discontinuities which have, and have not, been recognized at different taxonomic levels.

The leaf silhouettes were prepared from tracings, usually of the largest typical leaf (White, 1962). Where there is considerable variation within one specimen two leaves are shown either overlapping (as in Fig. 14) or connected by lines (as in Fig. 19). Most of the tracings are straight, this was done by ruling a line on the tracing paper first and keeping this on the midrib while tracing. This was not done in Figs. 14 and 21.

3. GENERAL TAXONOMIC CONSIDERATIONS

Being primarily a student of evolution and ecology rather than of taxonomy, I would like to make some comments on the problems of taxonomy as seen from a general biological stand-point.

In the basic task of producing a nomenclature of morphological units, a taxonomist tries to create approximations to 'biological' species. He should also, however, form a classification which is useful for students of phylogeny and ecology and for people with a general or economic interest in the group. It is for this reason that not only aspects of the breeding systems but also phylogeny, ecology and general considerations may influence a taxonomy. For instance if there are reasons for believing that a morphologically uniform taxon is polyphyletic a taxonomist will tend to divide it. Likewise, if two variants have distinct ecological requirements this will lend weight to an argument for splitting them. Also, if a morphological variant is of value to, say, a timber interest, it would seem sensible to name it. Similarly, in the face of the numerous microspecies of

apomicts, it may be convenient to designate rather artificial groups of microspecies.

I suspect that to search conscientiously for 'natural' genera, 'biological' species, and neatly replacing subspecies is a wild goose chase - one might seek for ever for things that do not exist. To admit that there are no absolute rules of procedure is, however, to open the way for arbitrary variation in taxonomic treatment which makes comparison between different groups difficult. An illustration of this is given by two recent examples. Among the highland rhododendrons of New Guinea Sleumer (1966 and 1973) recognizes 162 species; while in Allophyllus L. 255 species have been reduced to one species extending from Africa to Hawaii (Leenhouts, 1967). It is indeed often true that populations in mountainous areas become isolated and tend to speciate, while in the lowlands gradual variation from place to place may lead to vast continua. It is this enormous range in the size and the nature of species which is of great interest to the student of speciation, and he must compare the behaviour of species in different families which have been treated by different taxonomists. Inevitably one needs to compare the species proposed by different authors, and this is often difficult.

Part of the solution to the problem of variation between authors has been to propose arbitrary numbers of correlated character differences which should occur between taxa at a given rank (e.g. Hedberg's rule, White, 1971). This can be difficult to apply, especially when dealing with variable characters which involve a range of shape and size. Another arbitrary rule is that when more than a certain percent of the individuals fall within defined categories they should be regarded as subspecies; but if the proportion of intermediates is higher, it should be regarded as a continuum. However, what is perhaps more important than the method used, is that the data are presented in such a way that the decisions made can be independently assessed without going back to the original material. To this end adequate methods of visual presentation of the data are important. In this work

extensive use has been made of the pictorialized distribution map. In this way the nature of the taxa I recognize can be seen and compared with taxa in other families.

4. PLAN OF THE THESIS

This thesis is divided into two parts, of which the first comprises general chapters, while the second is a taxonomic conspectus of the ant-epiphytes of the Rubiaceae.

Chapter II is a comparative review of ant-associated epiphytes of all families. It discusses the nature of the symbiosis in each case and the structure of the plant chambers which are inhabited by ants. The chapter was written as a separate paper (Huxley, 1980).

An account of previous taxonomic work on the group is given in Chapter III. The morphological characters of the ant-plants, particularly those which are unusual or are associated with the ants, are described in Chapter IV. Chapter V describes the distribution of the ant-plants and the climate and vegetation of the habitats which they utilize. Then in Chapters VI and VII follow discussions of the delimitation of the species and genera involved. Conclusions regarding the taxonomic status of the groups recognized and their implications are outlined in Chapter VIII. Finally, in Chapter IX, possible lines of evolution are traced and speculated upon.

The second part of the thesis, Chapters X to XVI, constitutes a conspectus of the taxonomy of the five ant-associated epiphytic genera of the Rubiaceae. While it is my long term intention to revise the whole group, time only permitted a detailed study of the medium-sized genus Myrmecodia and the three small satellite genera, Myrmephytum, Anthorhiza and Squamellaria. The largest genus, Hydnophytum, was not tackled, but a key to the major species and species groups is given so as to illustrate the main features of the genus. An annotated list of specific epithets in the genus is also given.

A : GENERAL CHAPTERS

II. Symbiosis between ants and epiphytes

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1. INTRODUCTION

2. DIVERSITY AND ORIGINS

3. STRUCTURE OF THE NESTING SITES

   a) Rubiaceous ant-epiphytes

   b) Dischidia

   c) Fern ant-epiphytes

   d) Tillandsia

4. BENEFIT TO THE PLANTS

   a) Rubiaceous ant-epiphytes

   b) Dischidia

   c) Fern ant-epiphytes

   d) Tillandsia

5. BENEFIT TO THE ANTS

   a) Iridomyrmex cordatus

   b) Iridomyrmex cf. scrutator (det. R. Taylor)

   c) Azteca traili Forel

   d) Crematogaster spp.

6. ECOLOGY

   a) Rubiaceous ant-epiphytes

   b) Dischidia

   c) Fern ant-epiphytes

   d) Tillandsia

7. DISCUSSION

   a) Structure and function in the ant-epiphytes

   b) Ant-epiphytes contrasted with ant-associated trees

   c) Ecological success of the ant-epiphytes

8. SUMMARY

9. ACKNOWLEDGEMENTS

1. INTRODUCTION

When one thinks of mutually beneficial interactions between higher plants and animals, the examples which come to mind are pollination and seed dispersal. In both these cases the static plant obtains some form of transport, either of its gametes or dispersal units. A great number of plants, from alpine herbs to rainforest trees, take advantage for these functions of a huge variety of animals, from slugs to bats. The plants usually provide some form of 'reward' for the animal, for instance nectar or a sweet fruit. Also a vast array of more or less specific and elaborate mechanisms have evolved for attracting the animals.

Compared with pollination and dispersal by animals, other mutualisms between plants and animals are relatively scarce, especially outside the tropics. Moreover, although their role is quite varied, only one group of animals is involved - the ants. Symbiotic associations between plants and ants fall into two broad categories: those in which the role of the ants is defensive, and those in which it is nutritive.

The plants which are defended by ants form by far the larger and better known group. This kind of mutualism was first recognized in the bull's horn acacia by Belt (1874). Ants of the genus Pseudomyrmex hollow out and inhabit the swollen thorns of these trees. The plant also produces protein-rich bodies at the tip of each leaflet. The ants forage over the whole tree to collect these 'Beltian Bodies' and in the process they encounter and attack insect pests of the host tree (Janzen, 1966). Several ant-tree symbioses have now been studied and can be seen to conform to a general pattern. The tree produces nest chambers in thorns, hollow stems or leaf-pouches, and also either food-bodies or extrafloral nectar. The ants perform various defensive activities - attacking insect or mammalian herbivores, chewing at plant competitors or removing epiphyllae (plants which grow on other plants' leaves) and fungal spores from the leaf surfaces (Bequaert, 1922; Janzen, 1967; 1968).

Less well understood are the numerous trees, shrubs and herbs which produce extra-floral nectar but no nest sites. Ants visit to feed on the nectar and have sometimes been found to be protecting the plant (Bentley, 1977). These associations are less specific and much less permanent than if a nest site is present, but they have the advantage for the plant that they need only be seasonal. Nectar or any other reward is only produced at the time when protection is most required. Thus functional nectaries are usually associated with growing tips, young foliage and developing flowers.

The second category of plants which harbour ants are those in which the role of the ants is nutritive. These plants come from a range of families in both dicotyledons and monocotyledons but they are all epiphytic. They produce a hollow structure in the stem or leaf in which ants nest, but the provision of nectar or food-bodies is less conspicuous and common. Unlike the ants which are symbiotic with trees, the ants which inhabit these epiphytes are not very aggressive and tend to be scavengers which bring a certain amount of material back to the plant. It has long been supposed that the plants, which are equipped with apparently absorbtive structures, are able to absorb nutrients from this material. Recently studies with radio-isotopes have confirmed that some at least of these plants do absorb nutrients from inside the chambers.

Another form of symbiosis between ants and epiphytes is seen in the ant-gardens of Central and South America. These consist of arboreal ant nests on which grow numerous epiphytes. The ants (Azteca spp.) are said to collect and plant seeds of these epiphytes on their nests and the roots and stems form a support for the growing nest. The plants gain not only seed dispersal but also a suitable place to grow with their roots surrounded by the fibre of the ant nest (Ule, 1902, 1906)*. The ant-gardens form a rather distinct type of association and are not discussed in detail here.

In this paper I review the varied nesting structures and the food produced by epiphytes which harbour ants. The

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* See an important paper by Kleinfeldt (1978).

behaviour of the ants is described in relation to the plant structures, and the possible benefits to both plants and ants are considered. The adaptations of the ant-epiphytes are contrasted with those of trees which are associated with ants and the differences are related to the different behaviour and role of the ants. Finally the ecological consequences of the symbioses are compared.

2. DIVERSITY AND ORIGINS

Ant-associated epiphytes are found in a wide range of families in the dicotyledons, monocotyledons and ferns (Table 1). This phylogenetic diversity is matched by the variety of plant organs which are modified as chambers and occupied by ants; examples are leaves, leaf-bases, hypocotyls and rhizomes. In some cases a chain of intermediates connects the ant-associated species to unspecialized members of the genus or family. In other cases there are no intermediates and one has no picture of how the symbiosis arose.

The majority of ant-epiphytes belong to two genera from the Far East, Myrmecodia and Hydnophytum in the tribe Psychotrieae of the Rubiaceae. In these genera, and also in the three satellite genera, Myrmedoma*, Myrmephytum and Squamellaria, the ants occupy cavities which arise in tubers derived from the hypocotyl. These fleshy tubers were probably storage organs in origin, though no species exist which have the tubers without cavities. It has been suggested that the initial function of the cavities was to collect rain-water. If this was so, however, the entrances to the chambers would have had to be wide and upward pointing and ants would have been deterred by the flooding.

While the Rubiaceae as a whole are rather poor in epiphytes, the other groups containing ant-epiphytes are predominantly epiphytic and usually show some transitional species. For instance, the Old World genus of climbing epiphytes Dischidia (Asclepiadaceae) is largely non-myrmecophytic, with biconvex or flat leaves. Several species, however, have domed leaves with the edges pressed against the host tree. Adventitious roots from the stem grow under these leaves and ants also nest there. Other species of Dischidia

*Note that this chapter follows published taxonomy in recognizing Myrmedoma but not Anthorhiza.

Table 1

Genera of epiphytes which are regularly or irregularly associated with ants.

Epiphyte	+A	±A	-A	Geographical distribution	Chambered structure
Rubiaceae					
Hydnophytum Jack	40	6	0	S.E.Asia, Malesia* Pacific	Hypocotyl
Myrmecodia Jack	25	0	0	S.E.Asia, Malesia	Hypocotyl
Myrmedoma Becc. †	2	0	0	Malesia	Hypocotyl
Myrmephytum Becc.	3	0	0	Malesia	Hypocotyl
Squamellaria Becc.	3	0	0	Fiji	Hypocotyl
Asclepiadaceae					
Dischidia R. Br.	25	4	50	S.E.Asia, Malesia Pacific	Whole leaf
Polypodiaceae					
Lecanopteris Reinw.	9	0	0	S.E.Asia, Malesia	Rhizome
Solenopteris Copel.	4	0	0	Tropical America	Rhizome branches
Polypodium L.	0	1	500	Cosmopolitan	Rhizome
Bromeliaceae					
Tillandsia L.	4	2	400	Tropical America	Leaf-bases
Wittmackia Mez	0	1	2	Tropical America	Leaf-bases
Aechmea Ruiz et Pav.	0	1	150	Tropical America	Leaf-bases
Melastomaceae					
Pachycentria Blume	0	4	12	S.E.Asia, Malesia	Root
Orchidaceae					
Schomburgkia Lindl.	0	2	12	Tropical America	Pseudobulb
Diacrium Benth.	0	1	4	Tropical America	Pseudobulb
Solanaceae					
Marckea Rich.	0	1	5	Tropical America	Root

The approximate number of species, their distribution and the plant structure which is modified as a chamber are also shown. +A = number of species regularly associated with ants. ±A = number of species irregularly associated with ants, or with apparently suitable hollow structures. -A = number of species not associated with ants.

* Malesia comprises Malaysia, the Philippines, Indonesia and Papua New Guinea.

† Note that this Chapter follows the published taxonomy recognizing Myrmedoma but not Anthorhiza.

have increasingly complex leaf-pitchers which are entered by adventitious roots and are inhabited by ants. The domed and enclosed leaf-shapes must also help to reduce transpiration as the majority of the stomata are on the lower and inner leaf surface.

The diversity of ant-epiphytes in the New World is much less than in the Old World. This is reflected in the two genera of ant-occupied ferns, both in the family Polypodiaceae. The neotropical genus Solenopteris contains only four species, all of which are rather rare, while the Old World Lecanopteris comprises nine species, one of which is very common and widespread. In both genera the fleshy central parenchyma of the rhizome breaks down leaving cavities which are then used by ants.

The only other New World epiphytes with well-developed structures inhabited by ants are in the Bromeliaceae. This family contains many epiphytes in which a rosette of chanelled leaves catch rain-water and funnel it into a 'tank' formed by the closely appressed leaf-bases. Detritus is also caught in these reservoirs and the plant absorbs both water and nutrients through complex peltate hairs on the leaf surface. In the genus Tillandsia (Bromeliaceae) three different growth habits are found: typical 'tank' epiphytes; 'atmospheric' species, e.g. Spanish Moss (T. usnoides), which absorb atmospheric water through hairs on the small, linear leaves; and myrmecophytic species in which the leaves are tightly constricted above the expanded leaf-bases forming a 'bulb'. Water does not enter these 'bulbs' and ants nest in the cavities between the leaf-bases. The distinctions between these three types however are not sharp.

Specialized cavities which are regularly inhabited by ants are formed by members of all the foregoing nine genera (Myrmecodia, Hydnophytum, Myrmedoma, Myrmephytum, Squamellaria, Dischidia, Solenopteris, Lecanopteris and Tillandsia). Besides these there are numerous epiphytes which, though often infested by ants, do not have modifications which could be advantageous only in the presence of ants. For instance the large hollow pseudobulbs of a neotropical orchid (Schomburgkia tibicinis Batem.) are sometimes occupied by ants (Ames & Correll, 1953; D.H. Benzing, pers.

comm.). Storage tubers on the roots of Pachycentria spp. (Melastomaceae) are also sometimes hollow and ant-occupied (Beccari, 1884-6). Almost nothing is known of the specificity or importance of these associations, and they are not discussed here beyond the list in Table 1.

The diversity of ants which inhabit ant-epiphytes is much lower than that of the plants involved. In relatively dry, lowland areas of the Far East the ant-epiphytes (Myrmecodia, Hydnophytum, Dischidia and Lecanopteris) are usually occupied by the ant Iridomyrmex cordatus (Fr. Smith), = I. myrmecodiae Emery, in the subfamily Dolichoderinae. In wetter lowland areas and at higher altitudes in Papua New Guinea this ant is replaced by a second species of Iridomyrmex. The New World fern, Solenopteris, is inhabited by a species of Azteca which also forms ant-gardens (Gómez, 1977). Myrmecophytic species of Tillandsia are reported to be inhabited by various ants, mainly species of Crematogaster (Benzing, 1970). Existing data suggest that there is generally some specificity but the associations are not obligatory for either epiphyte or ant.

3. STRUCTURE OF THE NESTING SITES

a) Rubiaceous ant-epiphytes

In Myrmecodia, Hydnophytum and their allies the hypocotyl of the young seedling swells to form a tuber. Cavities arise in this tuber by an active process of cell division and differentiation. This occurs even when ants are absent, as was shown by Forbes (1880) and Treub (1883b, 1888). The final shape and complexity of the chambers is very varied in different species and reflects different degrees of association with ants and the various climatic conditions under which these plants live.

The cavities are made by a succession of separate meristems (phellogens) which arise de novo in the parenchyma of the swollen hypocotyl. The cells of the inner layer created by the meristem mostly become suberized and the enclosed tissue dies and shrivels up, leaving a cavity (Treub, 1883b). The meristems cross existing vascular bundles and create shapes which are unrelated to the tuber surface.

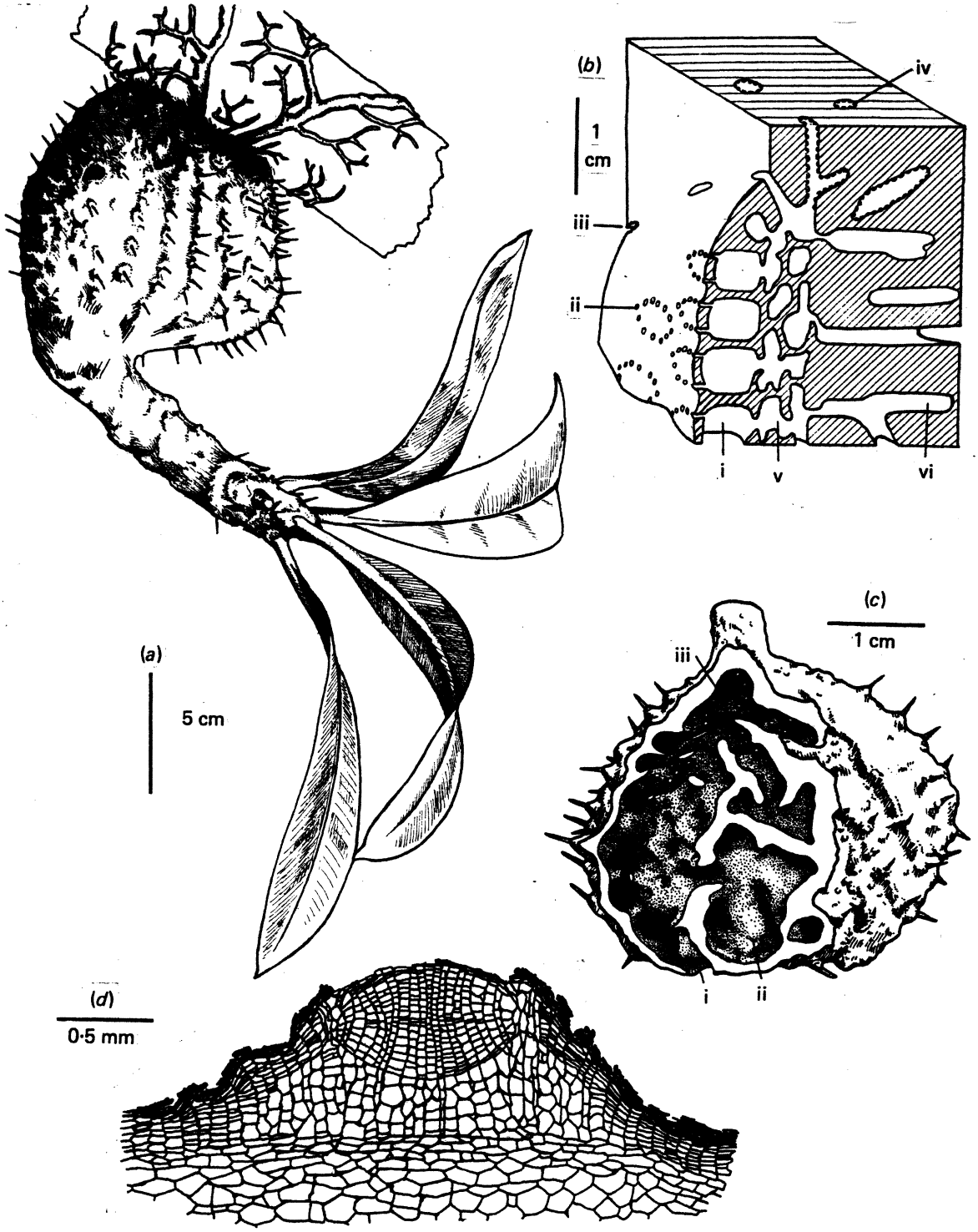


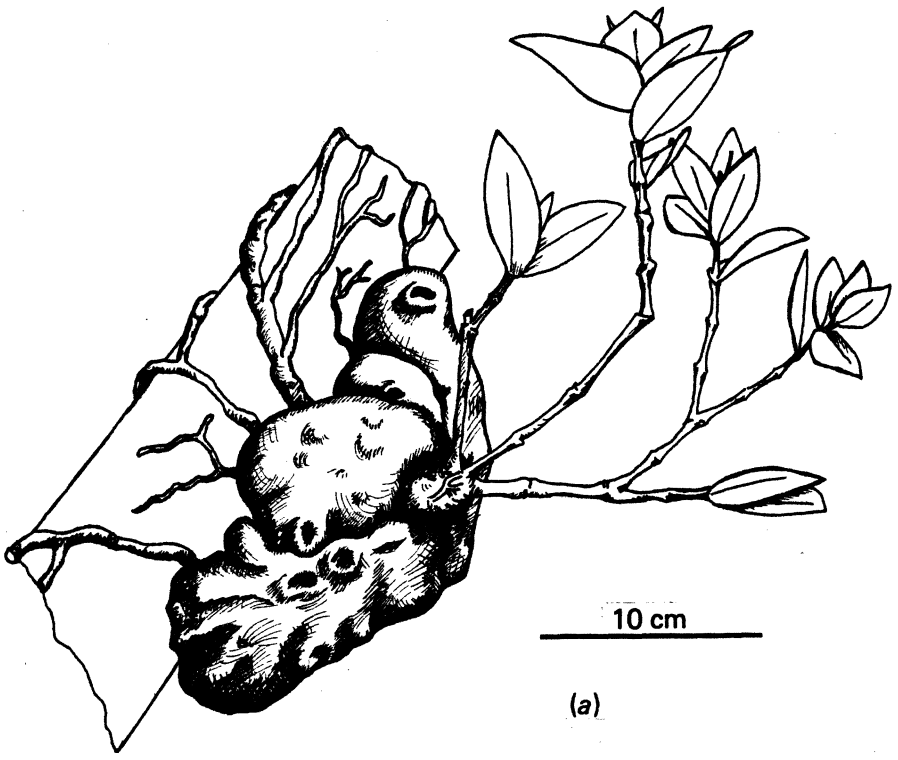
Fig. 1. (a) Myrmecodia tuberosa Jack, whole young plant. (b) Diagrammatic block section of tuber of a species of Myrmecodia with complex internal structure (from Manus, Papua New Guinea, UPNG 3437); (i) One 'cell' of honeycomb; (ii) pores in ring at the top of a 'cell'; (iii) entrance hole at periphery of honeycombed area; (iv) warted tunnel; (v) smooth, dark tunnel in open network area; (vi) smooth, shelf-like, straw-coloured tunnel. (c) Tuber of young plant of M. tuberosa cut away to show the cavity formed by the third phellogen; (i) Entrance hole; (ii) inner smooth chamber; (iii) dark brown, warted tunnels. (d) Longitudinal section of a wart, showing cell outlines only. [b) After Huxley (1978) reproduced with permission from New Phytologist.]

While the first cavity is hook-shaped, later cavities may be differentiated into chambers with distinct shapes and types of internal surface. The surfaces may be more or less strongly suberized and may or may not have warts. These are small, white, lenticular structures (Fig. 1d) which were first described by Treub who thought their function was gaseous exchange. Later Miehe (1911a, b) showed that these warts absorb both water and stains. Spanner (1938) reported similar structures on the outer surface of Myrmecodia tubers but their function is not clear.

In Hydnophytum the warted and smooth areas are not sharply differentiated; the warts are mostly developed at the extremities of blind-ending tunnels. The cavity formed by each meristem is fairly simple in shape, rarely interconnecting with itself or other cavities, and only forming a few openings to the outside (Fig. 2b).

In species of Hydnophytum growing in mountainous areas, where ants are less frequent and often absent from the plants, the cavities in a tuber have markedly different shapes and sizes. The central tunnels may reach 10 cm in diameter while those on the periphery are less than one cm across (Huxley, 1978). Moreover, warts are almost absent from the cavities of these species. It is probable that these cavities have some function other than harbouring ants, but this has not been studied.

Each new cavity in Myrmecodia comprises different types of chamber. Fig. 1c shows a young plant cut away to show the third cavity with an outer chamber which is dark and warted especially in its tunnel-like projections in the upper part of the plant, and an inner chamber which has smooth, straw-coloured walls. In the later cavities of more specialized species of Myrmecodia (Fig. 1b) the straw-coloured areas are shelf-like and just under the tuber surface there are honeycomb-like 'cells' with smooth, dark brown walls. A ring of holes used by the ants for access surrounds each honeycombed area, and rings of pores are found at the tip of each 'cell' of the honeycomb. These pores are too small for the ants to go through and may serve to ventilate the cavities.



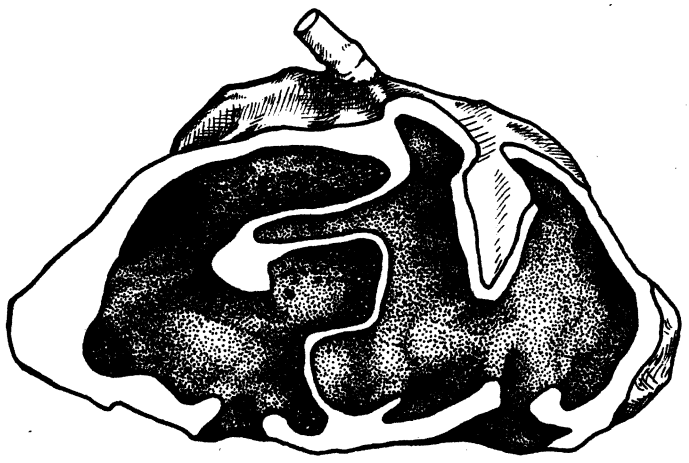


Fig. 2. (a) Hydnophytum cf. papuanum Becc., whole young plant. (b) Tuber of younger plant of same species cut away to show two cavities each with a single entrance hole. The one on the left with considerable development of warts at the extremities.

Tubers of the satellite genera Myrmephytum and Squamellaria contain cavities which are similar to those of typical Hydnophytum, and those of Myrmedoma are similar to those of Myrmecodia (Beccari, 1884-6). In both Myrmecodia and Hydnophytum the proportion of tissue to cavity in the tubers varies greatly between species, increasing in those which occupy habitats subject to greater water shortage (Huxley, 1978). This suggests that the tuber tissue stores water and would support the view that the initial function of the swollen hypocotyl was water storage.

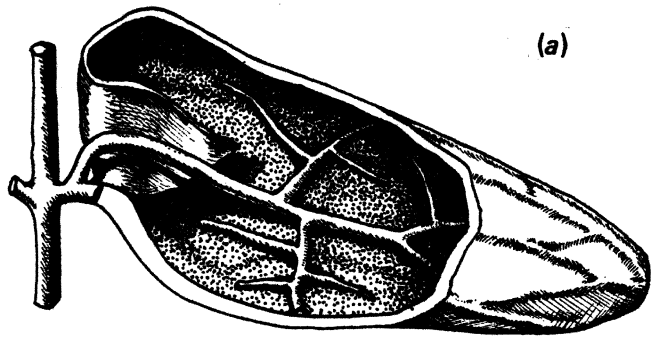
b) Dischidia

There are three groups of species of Dischidia which show increasing modification for occupation by ants (Fig. 3). Firstly, there are the species in which the leaves are domed with their edges pressed tightly against the bark of the host tree, e.g. D. collyris Wall. Secondly, there are species with some leaves modified as cylindrical, flask-like structures, e.g. D. rafflesiana Wall (Fig. 3a). Finally, there are species in which the flask-like leaves have a second small chamber within the first one, e.g. D. complex Griffith (Fig. 3 b) (Beccari, 1884-6; Pearson, 1902).

The flask leaves are evolved from the domed ones by expansion of the centre of the lamina and the constriction and turning in of the edge of the leaf (Treub, 1883a; Scott & Sargant, 1893; Thistleton-Dyer, 1902). The tip of the leaf goes quite far into the flask, forming an entrance tunnel (Fig. 3a). In the double flasks the tip of the leaf is rolled back on itself again (Fig. 3b). The inner chamber is almost divided in two by a median constriction of the wall (Pearson, 1902).

Adventitious roots arise near each node and enter the space beneath the domed leaves and enter the flask leaves, but do not penetrate into the inner chambers of the double flasks. These roots remain little developed unless debris is present; then they proliferate and fill the flasks (Treub, 1883a; Scott & Sargant, 1893; Groom, 1893; Janzen, 1974).

Other features of the flasks include the deep purple colour of the inner surfaces (Griffith, 1846; Scott & Sargant, 1893); the more frequent stomata (Plate 1) on



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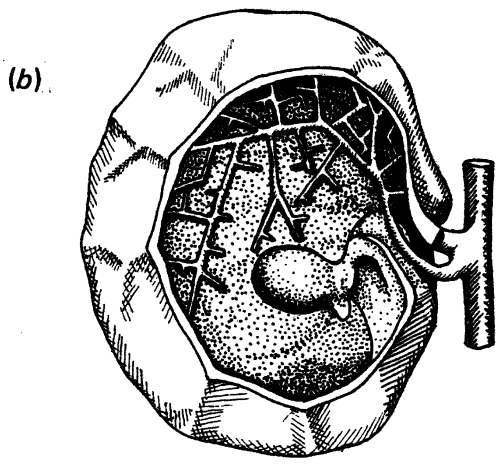


Fig. 3. (a) Dischidia rafflesiana, semi-diagrammatic representation of a flask-leaf cut open to show inturned leaf tip and adventitious root. (d) Dischidia cf. pectenoides, semi-diagrammatic representation of flask-leaf cut open to show leaf tip curled back on itself to form an inner second chamber. [(b) after Pearson, 1902.]

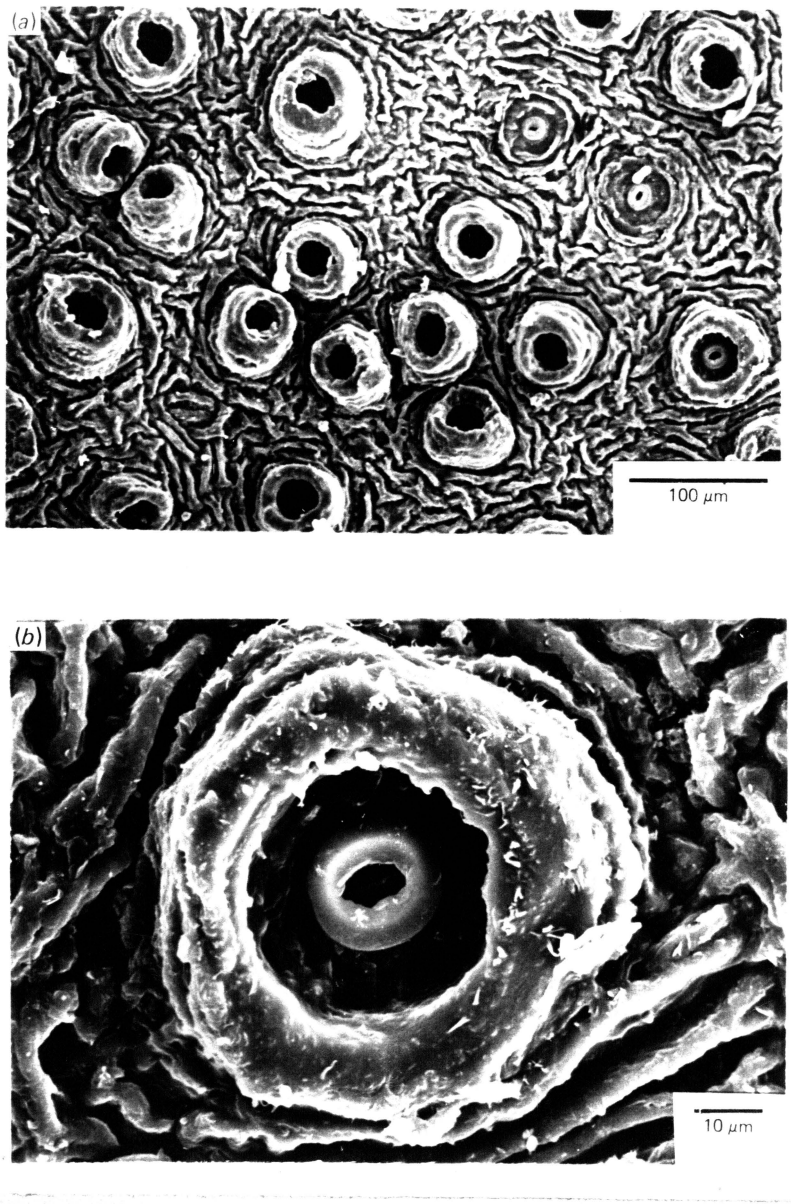


Plate 1. Stomata on inner surface of flask leaves of Dischidia rafflesiana. (a) General view, two stomata have lost the doughnut shaped cuticular ring, this occurs commonly in older flasks. (b) Close up of single stoma. [Scanning eletron micrographs courtesy of Dr. R. Mepham; specimen from Port Moresby, Papua New Guinea.]

the inner relative to the outer leaf surfaces first noted by Griffith (1846); and the presence of various plant structures which may act as food for the ants. These features are discussed later.

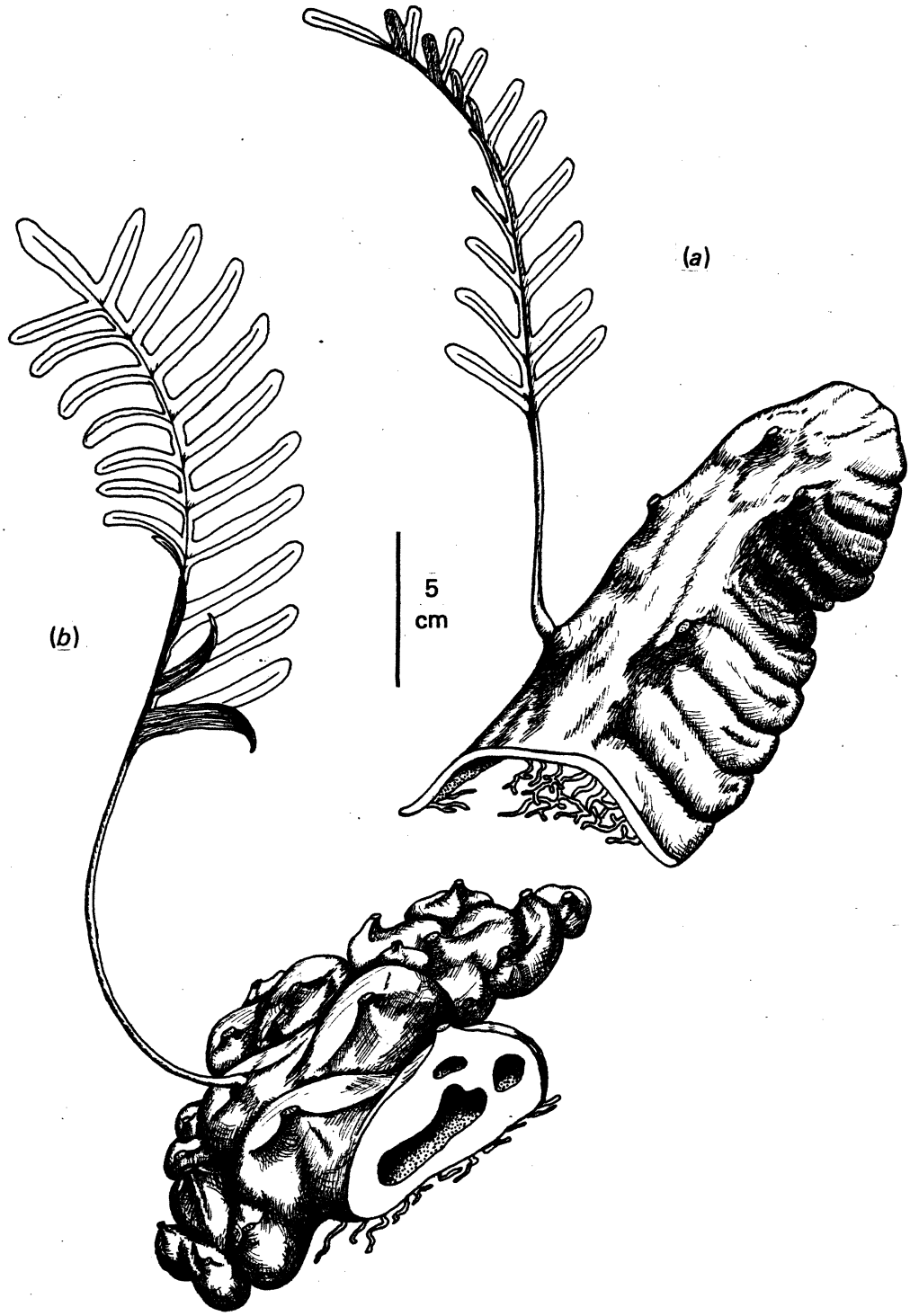
c) Fern ant-epiphytes

In the fern Lecanopteris the main rhizome becomes hollow, leaving an elongate chamber with regular, short side-branches under each leaf-base. These side-branches are extended at the tip into as many as three blind-ending lobes in some species (Fig. 4b) (Yapp, 1902; Jermy & Walker, 1975). Pores opening to the outside are formed at the ends of lobes or lateral branches of the rhizome of L. spinosa Jermy & Walker. In Solenopteris the rhizome forms short, more or less spherical, side branches with lobes corresponding to four fronds and branches which are never developed. The lower surfaces of these spherical side-branches invaginate, forming an entrance tunnel, and the internal parenchyma of the rhizome breaks down leaving partitions (Fig. 5b). Ants are normally responsible for opening the end of the invagination and removing the sugary parenchyma (Senn, 1910; Rauh, 1955; Hagemann, 1969; Wagner, 1972).

The inner surfaces of the chambers of Lecanopteris are sculptured but lack obvious sites for absorption (Yapp, 1902). In Solenopteris, adventitious roots arise from the inner end of the entrance tunnel and grow into the tuber. In both genera the tissue lining the cavities becomes pigmented and in some species of Lecanopteris the outer epidermis also becomes almost black (Jermy & Walker, 1975).

Lecanopteris mirabilis (C.Chr.) Ching differs from the other species in that the rhizome is solid but flattened and arched, so that it encloses a spece against the host trunk (Fig. 4a). Roots develop in this space as they do under the domed leaves of Dischidia species (Karsten, 1895). One of the epiphytes which is only irregularly associated with ants is a fern, Polypodium schomburgkianum Kunze, which has a similar broad flattened rhizome under which ants sometimes nest (Spruce, 1908).

Fig. 4. (a) Lecanopteris mirabilis arched rhizome with single frond, showing adventitious roots in cavity beneath rhizome. (b) Lecanopteris carnosa, rhizome cut to show chambers, only a single frond shown.



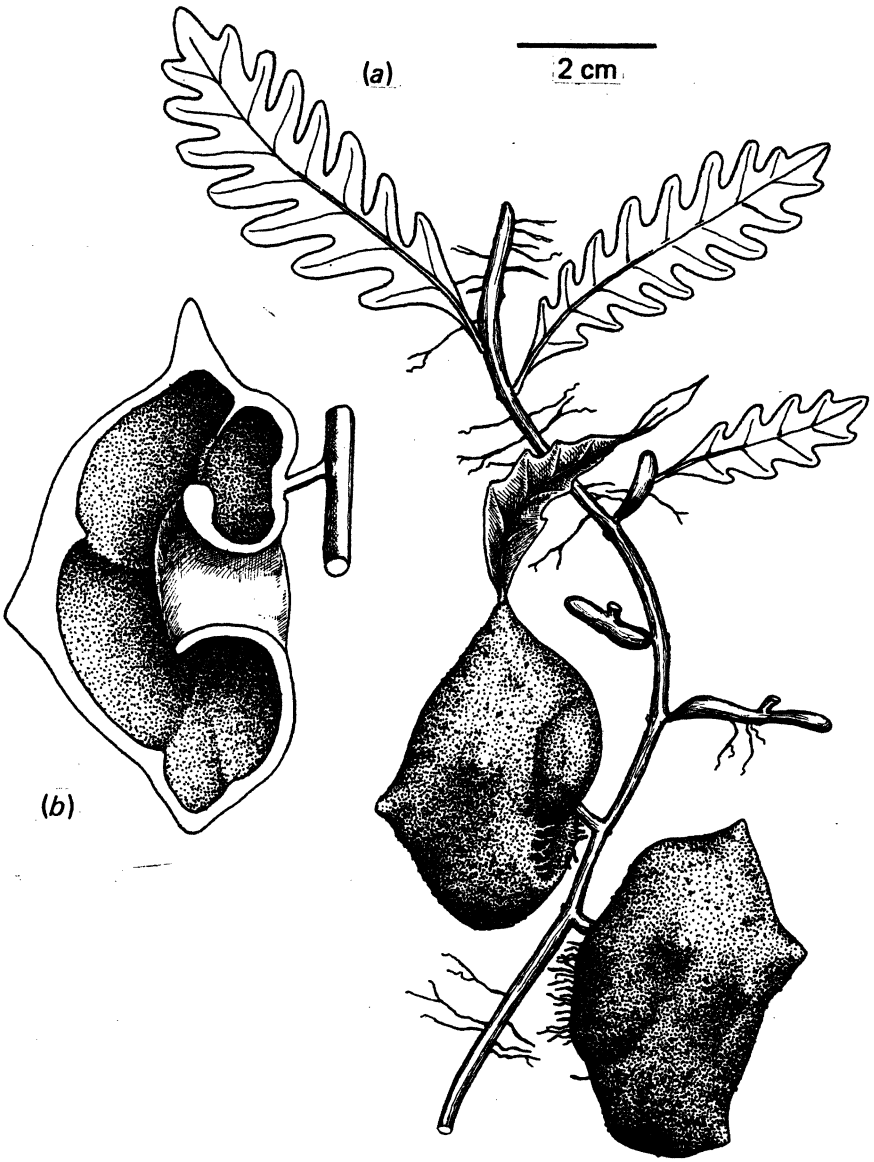


Fig. 5. Solenopteris sp. (a) Diagrammatic representation of whole plant. (b) Single rhizome branch cut away to show internal structure, adventitious roots which arise from the entrance tunnel are not shown. [After Rauh, 1955.]

d) Tillandsia

In many of the 'tank' Bromeliads the leaves are somewhat constricted above the reservoir, this tends to reduce evaporation and spillage. In the myrmecophytic species of Tillandsia the leaves are tightly constricted and water does not enter the spaces between the leaf-bases at all (Fig. 6). Moreover the leaf-blades are rolled so that water is not channelled along them. Another modification is that the lower corners of the leaf-blades are not appressed to each other, thus ants can enter the spaces between the leaf-bases from below and move from one space to another.

Complex, peltate trichomes (hairs) are abundant on both surfaces of the leaf-bases of the myrmecophytic Tillandsia butzii Mez and T. caput-medusae E. Morren (Benzing, 1970). These trichomes are similar to others which can absorb minerals (Benzing et al., 1976, 1978). As in the Dischidia the inner surfaces of the cavities are darker purple in myrmecophytic than non-myrmecophytic species.

4. BENEFIT TO THE PLANTS

a) Rubiaceous ant-epiphytes

Miehe (1911a) showed that the warted cavities of Myrmecodia and Hydnophytum absorb water rapidly while the smooth ones do not; moreover, stains placed on the cavity surfaces are absorbed only by the warts. This and observations on the behaviour of the ants led him to the conclusion that the plants gain a source of essential nutrients from faecal material and debris brought in by the ants. He also found a fungus growing on the warted cavity surfaces which he thought was eaten by the ants and might also secrete enzymes which would solubilize organic material in the cavities. Recent studies confirm that a fungus, Arthrocladium caudatum Papendorf, is usually present on the warted cavity walls of Myrmecodia spp. occupied by Iridomyrmex cordatus (Huxley, 1978). Other micro-organisms such as nematodes and mites are frequently present, but the role, if any, of the fungus or other organisms has not been investigated.

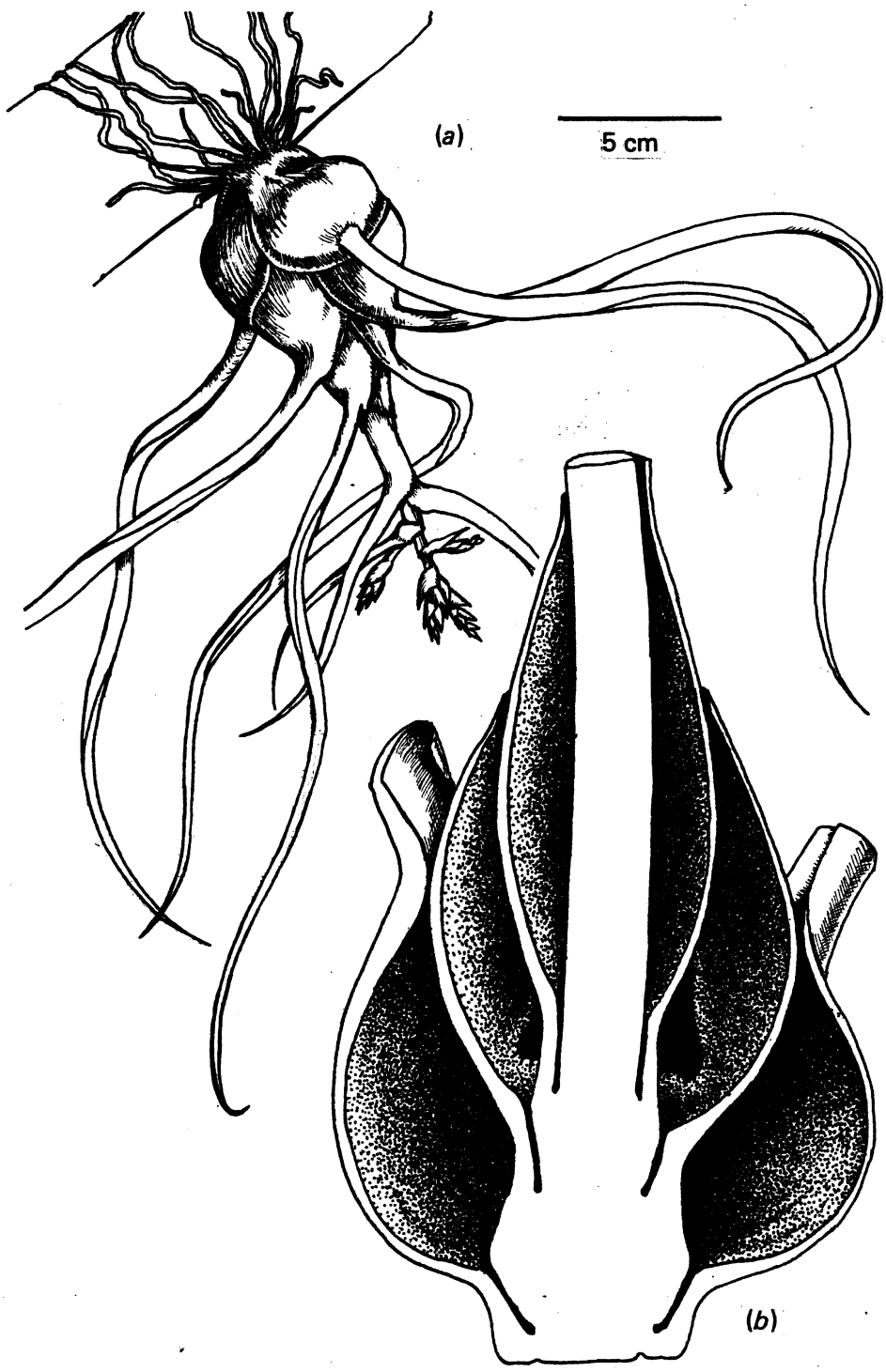


Fig. 6. Tillandsia bulbosa (a) Whole, flowering plant. (b) Longitudinal section of base of plant to show inflated leaf-bases, with the lower corners not appressed.

Measurements of growth of both Myrmecodia and Hydnophytum suggested that the ants have a beneficial effect on the survival and growth of the plants (Huxley, 1978). Radioisotope tracers showed that both organic and inorganic compounds can be absorbed by the plants from warted surfaces (Huxley, 1978). Rickson (1978) showed that tracer in fly larvae fed to the ants is eventually absorbed by the plants. He suggested that the ants 'sequester' more food than they need in such a way that some of it remains for the plant.

Other possible benefits to the plant include protection, which may occur, since the leaves are not usually grossly attacked though they are often eaten by leaf miners (Huxley, 1978). The ants may also be dispersal agents, as they incorporate seeds of ant-epiphytes into their runways made of 'carton' - a mass of vegetable fragments stuck together.

b) Dischidia

Only circumstantial evidence is available for the function of the flask leaves of Dischidia. The presence of considerable amounts of organic debris and the abundant development of roots in the older flasks strongly suggest that the plant absorbs essential nutrients from the contents of the flasks. Ants (Iridomyrmex cordatus) are usually found in the flasks and use the young leaves for their brood; they bring plant and animal fragments and soil into the older flasks (Groom, 1893; Scott & Sargant, 1893; Janzen, 1974). The adventitious roots proliferate only when debris is present. The ants also construct carton runways over the external roots and along the stems. Seeds are collected for their oil-bodies, and again incorporated into the carton (Docters van Leeuwen, 1913; Leeuwen-Reijnvaan, 1913).

Another major benefit to the plant must arise from the abundance of stomata on the inner but not the outer surfaces of the flasks (Griffith, 1846). Levels of carbon dioxide and humidity in the flasks are presumably kept high by the ants and their brood and by the roots and micro-organisims in the debris. Thus the plants could be obtaining carbon dioxide with minimal loss of water through transpiration, though this has not been demonstrated. The cuticular collars (Plate 1) may prevent debris from blocking these stomata.

c) Fern ant-epiphytes

Evidence for benefit to the fern Lecanopteris is even more scanty; Janzen (1974) has found that Iridomyrmex cordatus brings debris into the rhizomes of L. sinuosa (Wall.) Copel., and the highly indented inner surface of the cavities can absorb water (Yapp, 1902). It appears that the ants feed on the spores and sporangial tissue and may therefore be responsible for dispersing the plants (Docters van Leeuwen, 1929). It was found by Jermy & Walker (1975) that L. mirabilis is particularly susceptible to attack by slugs and they suggested the ants may provide protection.

Gómez (1974) found that the ants Azteca and other invertebrates bring debris into the tubers of Solenopteris brunei (Wercklé) Wagner . When the tuber dies it shrinks, becomes permeable to water and acts as a nutrient-rich sponge surrounding a mass of roots.

d) Tillandsia

Analyses of debris from the cavities in the leaf-bases of myrmecophytic Tillandsia have shown that substantial quantities of nitrogenous compounds are present, and it has also been shown that the leaf-bases are able to absorb and translocate calcium. The bioassay for availability of this nitrogen was however negative, perhaps because the seedlings of Aechmea (Bromeliaceae) used were unable to take up nitrogen in the form present (Benzing, 1970). Further experiments are needed to confirm the transfer of nutrients to the plants via the ants and also to investigate whether the ants show any pattern of use of the chambers for their brood and for waste material.

5. BENEFIT TO THE ANTS

No studies have been made of the significance of the ant-epiphytes to their occupants, but it is clear that there are two major benefits: an arboreal nesting site and a source of food.

a) Iridomyrmex cordatus

Janzen (1974) identified the ant symbiont at Bako, Borneo, as I. myrmecodiae Emery which is confined to ant-epiphytes. R. Taylor (C.S.I.R.O., Canberra) does not dis-

tinguish I. myrmecodiae from the widespread ant of open environments, I. cordatus, which nests in a variety of sites (Dahl, 1901). Trees in open habitats tend not to accumulate dead branches and plant litter, it is therefore in these habitats that ant-epiphytes are likely to be important in enabling ants to occupy the crowns of trees. It is possible that the spines of Myrmecodia protect the ants from bird and lizard predators. I. cordatus normally moves about under carton runways, and on the tuber and stem of Myrmecodia the carton is supported by the spines. It may be significant that the inflorescence of Myrmecodia is well protected by shield-like outgrowths and adventitious roots, and by bracts in Myrmedoma and Myrmephytum.

In some Myrmecodia the honeycombing and pores probably moderate the temperature regime in the tubers (Miehe, 1911a), as similar structures in termite nests do.

Iridomyrmex cordatus may obtain food from various of its hosts, e.g. the oily seeds of Dischidia (Docters van Leeuwen, 1929); foliar appendages of Dischidia (Treub, 1883a; Beccari, 1884-6; Scott & Sargant, 1893; Pearson, 1902); nectar of Myrmecodia and Hydnophytum (Huxley, 1978); and sporangial tissue of Lecanopteris (Docters van Leeuwen, 1929; Guttenberg, 1935; Jermy & Walker, 1975).

b) Iridomyrmex cf. scrutator (det. R. Taylor)

This was the commonest ant found in Myrmecodia and Hydnophytum in the lowland and montane rain forests of Papua New Guinea, where it appears to replace I. cordatus (Huxley, 1976, 1978). It also brings debris into the warted chambers of the ant-epiphytes but nothing is known of its other nesting and feeding habits. Other species of Iridomyrmex are reported from ant-epiphytes in Fiji (Mann, 1921) and the Solomon Islands (Mann, 1919).

c) Azteca traili Forel

Solenopteris brunei in Costa Rica is occupied by an ant closely resembling Azteca traili found in a fern (probably S. bifrons (Hook.) Copeland) in Peru by Ule (Gómez, 1977). This ant also forms ant-gardens (Ule, 1906).*

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* See also Madison (1979).

Gómez (1974) observed that Solenopteris on nectariferous trees is more often occupied by Azteca than when it is growing on other trees. This suggests that a nesting site is most useful to Azteca when another food source is available, even though the ants also feed on the sugary parenchyma of the fern tubers.

d) Crematogaster spp.

Benzing (1970) found a number of different ants occupying Tillandsia butzii and T. caput-medusae. Many of his sites, however, were roadside areas, and my experience in New Guinea suggested that a wide variety of ants enter ant-plants under such disturbed conditions. Crematogaster was the most frequent occupant of Tillandsia spp. though it is not known how many species were involved. The myrmecophytic species of Tillandsia do not apparently produce anything used by the ants as a food, but field observations on the ants are needed.

6. ECOLOGY

a) Rubiaceous ant-epiphytes

Both Myrmecodia and Hydnophytum are medium-sized genera distributed throughout the Malesian region and extending into Indo-China, Australia and Fiji. At their centre of diversity, in New Guinea, they occupy a wide range of habitats from mangrove swamp to upper montane forest and they even grow terrestrially associated with Nepenthes (pitcher-plants) in herbaceous vegetation above the tree-line (Lam, 1924). Both genera are most abundant in coastal and riverine trees, lowland savanna (except Eucalyptus savanna) and secondary montane forest. Though less abundant they are present throughout the lowland and montane evergreen forests, but are notably absent from semideciduous and deciduous forest in the south east (Huxley, 1978). This pattern contrasts with the general distribution of vascular epiphytes which are most abundant in the rain forests and less frequent in discontinuous canopies, but, like the ant-epiphytes, are rare in semideciduous and deciduous forests.

At two sites toward the limit of their range ant-epiphytes, especially Hydnophytum, are abundant on areas

of poor sandy soil covered by a stunted rather open woodland largely of myrtaceous trees. In both areas, at Bako in Borneo and Gunung Jerai on the Malay Peninsula, ant-epiphytes are very rare in the surrounding forest on better soil. It is also noteworthy that the inhabitant ants, Iridomyrmex cordatus, appear to be feeding mostly off scale insects (Janzen, 1974; Huxley, 1978).

b) Dischidia

Dischidia occurs throughout the range of the rubiaceous ant-epiphytes, but is confined to the lowlands. D. collyris with domed leaves typically grows in rain forest, while D. rafflesiana and D. nummularia, with biconvex leaves are usually found in open canopies, for instance in coastal or riverine forest (Karsten, 1895). D. rafflesiana is often prominent on dead trees, a habitat with particularly high insolation and low humidity. D. nummularia frequently grows with D. rafflesiana and the roots of both often enter the chambers of the rubiaceous ant-epiphytes.

c) Fern ant-epiphytes

Lecanopteris sinuosa is a common and widespread species growing best in open or man-made environments. Other species of the genus occupy a range of habitats, L. carnosa (Reinw.) Bl. and L. spinosa being montane.

Solenopteris brunei is an uncommon plant of the evergreen moist forest of pre-montane and montane Costa Rica (Gómez, 1974) and Panama and has recently been found in lowland rain forest in the western foothills of the Andes, south Colombia (Hagemann, 1969). S. bifrons grows in the rain forests of Peru, Ecuador and Colombia, and the less known S. tuberosum and S. bismarckii Rauh in Ecuador and Peru respectively. Solenopteris species are by no means always occupied by ants, and Gómez (1974) observed that ant occupation is most common on nectariferous trees. Only once did he find S. brunei in secondary forest.

d) Tillandsia

The myrmecophytic species of Tillandsia appear to occupy habitats intermediate between the moist conditions required

by 'tank' species and the very exposed habitats colonized by 'atmospheric' species. For instance they were found in an area of cloud forest in northern Colombia (Sugden & Robins, 1979). They are also found in relatively isolated trees and secondary forest (Benzing, 1970)..

7. DISCUSSION

a) Structure and function in the ant-epiphytes

There are some interesting parallels of structure between the cavities of different ant-epiphytes despite their varied evolutionary and morphological origins. The significance of these parallels is considered in terms of the symbiotic role of the ants.

The most important parallel is the presence of absorptive organs, though of very different origin and anatomy, in the cavities. In Dischidia and Solenopteris there are adventitious roots, while in Myrmecodia, Hydnophytum and their allies there are warts on the cavity surfaces. In Tillandsia there are absorptive hairs and in Lecanopteris the general inner surface of the rhizome can absorb water.

As well as the presence of absorptive structures, it is significant that these structures cover only part of the cavities or are present for only part of the life-span of a cavity. For example in Hydnophytum, and even more in Myrmecodia, each separate cavity possesses both smooth and warted chambers. In Dischidia and Solenopteris the cavities are initially empty or contain only a few roots, and only later become filled by roots. In these two genera, and not in any of the others, the plant produces a succession of new ant-chambers which eventually die while the plant continues to grow. The absorptive structures are clearly essential for the plants to obtain nutrients from the debris, and the differentiation in space or time of absorptive and non-absorptive sites enables the behaviour of the ants to be usefully directed. This discriminatory behaviour does occur; at least, when Iridomyrmex cordatus was fed with radioactive honey more activity was found in the warted than in the smooth areas in Myrmecodia.

One of the noticeable characteristics shared by many of the ant-epiphytes is the dark colour of the inner surface of the ant-chambers. In Dischidia and Tillandsia the appropriate

leaf surfaces are deep purple only in the myrmecophytic species. In Myrmecodia the outer honeycombed chambers are much darker brown than the inner, smooth, shelf-like ones. In some species of Lecanopteris the outer epidermis becomes almost black as well as the inner surface. The significance of this pigmentation is presumably that ants require dark places in which to nest (Janzen, 1974).

A final similarity is that the ant-chambers often have narrow, tunnel-like entrances which are horizontally orientated with the opening appressed to the host tree. This is found in the rubiaceous ant-epiphytes, and in Dischidia and Solenopteris. Indeed, the domatia of Dischidia and Solenopteris are remarkably similar as the entrance tunnel is formed by an inturned lip which resembles that of a traditional school ink-pot and probably has the same effect of preventing the contents from falling out. The narrow, horizontal entrance tunnels would also reduce the amount of light entering the cavities and the tendency of the chambers to collect rain-water which would damage the ant colony.

The existence of these parallels between the ant-chambers of different ant-epiphytes reflects the similarity of the role and requirements of the ants. In all the cases for which there is evidence it appears that the activity of the ants, in bringing plant and animal remains and leaving faecal material in the chambers, provides the plants with a source of nutrients.

b) Ant-epiphytes contrasted with ant-associated trees

The nature of the ant-chambers and of the food taken by the ants differs in ant-associated epiphytes from that found in ant-associated trees. The ant-chambers of the trees Acacia, Barteria and Cecropia consist of hollowed out stems or stipules. They are simple, undifferentiated structures except for the presence in some species of localized thin areas in the wall through which the ants gain access to the cavities, e.g. Barteria (Janzen, 1972). In all the ant-associated trees the ants have to chew out an entrance and remove the pith.

Food-bodies on ant-associated trees are typically numerous appendages distributed over the foliage; examples are the Beltian bodies on the tips of the leaflets of the

compound leaves of Acacia and the Müllerian bodies on pads at the leaf-bases of Cecropia. The foraging ants are thus attracted over the whole of the tree, and the plant, in effect, controls the distribution of its body-guard, for instance directing the ants over the young shoots that are most vulnerable to attack by herbivores. In Bateria, however, the ants gain most of their food from scale insects and fungi within the hollow stems. The ant-epiphytes produce relatively little food for the ants and it is often on protected parts of the plant. For instance in Solenopteris and Dischidia the food is within the cavities, while in Myrmecodia the inflorescences where the ants may feed are sunken in the stem and covered by shield-like outgrowths or adventitious roots. In two of the satellite genera and some species of Hydnophytum the sessile flowers are surrounded by large bracts. The sporangia on the fronds of Lecanopteris are eaten by ants, and it has been suggested on other grounds that these plants may be protected by the ants. In general, however, it appears that the food is only a secondary incentive to ants to occupy ant-epiphytes rather than being an integral part of the symbiotic process as in the ant-associated trees.

c) Ecological success of the ant-epiphytes

There are various features of the ecology of the ant-epiphytes which reflect the influence and success of the symbiosis. Most spectacular of these is the unexpected abundance of Hydnophytum and Dischidia on trees in two areas of poor soils. The myrtaceous trees at these sites form an open canopy with few other epiphytes. The general abundance of Old World ant-epiphytes in open and secondary habitats suggests that the influence of the ants is considerable. In these environments the availability of nutrients from run-off water and accumulated plant litter is relatively low. Hydnophytum and Myrmecodia occupy a particularly wide range of habitats suggesting that the symbiosis is especially successful in these genera.

Another example of the success of these plants is the abundance of Dischidia rafflesiana on dead trees where they must suffer extreme insolation and low humidity. Their survival here is almost certainly a result of the position of

many of the functional stomata within the pitcher where there is a supply of carbon dioxide from the ants and their brood, and from any decaying debris. Transpirational water loss from these leaves is therefore likely to be minimal.

It is, however, mainly in the Far East that ant-epiphytes flourish to this extent. In the New World the few species of Solenopteris are rare and local. The myrmecophytic species of Tillandsia are more common and may achieve abundance in areas where the rainfall is too low for the 'tanks' of typical bromeliads to be very useful. The relative scarcity of ant-epiphytes in the neotropics may possibly be a partial result of competition from the immensely successful 'tank' bromeliads and the ant-garden epiphytes. It is interesting to note that the other major group of vascular epiphytes, the orchids, are also dependent on a symbiosis at least for their early nutrition; in this case the symbiosis is a mycorrhizal association with fungi.

8. SUMMARY

(1) Plants from nine genera of epiphytes are regularly occupied by ants: Myrmecodia, Hydnophytum, Myrmedoma, Myrmephytum, and Squamellaria (Rubiaceae); Dischidia (Asclepiadaceae); Lecanopteris and Solenopteris (Polypodiaceae); and Tillandsia (Bromeliaceae). The first seven of these are inhabited mainly by Iridomyrmex spp. (Dolichoderinae); Solenopteris by Azteca sp; and Tillandsia spp. by Crematogaster spp. and other ants.

(2) The ants nest in cavities formed in the tubers derived from the hypocotyl (in the Rubiaceae); in the leaves (Dischidia); in the rhizome (the ferns); or in the leaf-bases (Tillandsia).

(3) The plants gain nutrients via the ants as indicated by the following:-

a) Possibly absorptive sites occupy localized areas within the hollow structures.

b) The ants keep their brood in the nonabsorptive areas and deposit organic remains in the absorptive areas.

c) Studies with radioactive tracers have shown that Myrmecodia and Tillandsia can absorb nutrients from the cavities.

(4) The ants gain a habitation but little or no food from their hosts.
(5) In contrast to ant-epiphytes, ant-trees produce food-bodies on the foliage which attract the ants to visit, and thus protect, all parts of the plant.
(6) Ecologically the symbiosis removes a major constraint on the distribution of epiphytes and enables these plants to diversify and colonize otherwise unfavourable habitats.

9. ACKNOWLEDGEMENTS

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III. Taxonomic history of the Rubiaceous ant-epiphytes

1. INTRODUCTION

2. PRE-LINNEAN TO THE FIRST VALID PUBLICATION

3. CONFUSION 1824-1872

4. FROM THE 'GENERA PLANTARUM' (1873) TO BECCARI (1884-1886)

5. AFTER BECCARI TO VALETON (1927)

6. AFTER VALETON

7. CONCLUSION

1. INTRODUCTION

This chapter describes some of the difficulties which surround the classification and nomenclature of the group. Early problems were caused by the loss of types and the rarity of duplicates. This was exacerbated by the lack of availablity of specimens to most of the taxonomists of this group during this century. This resulted in various misidentifications and the repeated naming of taxa.

2. PRE-LINNEAN TO THE FIRST VALID PUBLICATION

The first person to describe the ant-plants was Georg Rumphius who was working for the Dutch East India Company at Amboina in the Moluccas. His classic work 'Herbarium Amboinense' was prepared during the latter half of the seventeenth century, delayed by the joint ravages of fire and blindness, and not published until 1750. Rumphius' names for the ant-plants, Nidus formicarum niger (now Hydnophytum formicarum) and Nidus formicarum ruber (now Myrmecodia tuberosa), and are therefore pre-linnean. Linneaus, although aware of the work, did not incorporate it into his system.

Joseph Banks on the first voyage of the'Endeavour'found ant-plants in Queensland. Solander (ms) described the plant as Epidendroides tetrandra but his manuscript and illustration were not published, and the discovery of this plant remained unrecognized till long after J.D. Hooker had described it as Myrmecodia beccarii (Beaglehole, 1962).

The third encounter with ant-plants was also tragic; William Jack's specimens were lost by fire and his descriptions of Hydnophytum and Myrmecodia were published after his premature death. Jack (1823) described Myrmecodia tuberosa from Pulo Nias Is. off Sumatra, and identified it with Rumphius' Nidus formicarum ruber. He described Hydnophytum formicarum from Sumatra and identified it with Nidus formicarum niger. No specimens of ant-plants associated with these three authors are known to have existed or to exist today.

3. CONFUSION 1824-1872

Two years after Jack's publication Sprengel (1825) transferred both species from their genera in the Rubiaceae to Lasiostoma Schreber in the Loganiaceae. They were however returned to their proper position by Blume (1826-1827, Vide Stafleu and Cowan, 1976: 236). Blume also collected a specimen of Myrmecodia from western Java,which he placed tentatively in M. tuberosa Jack, but noted that it had a spiny tuber, a feature mentioned by neither Rumphius nor Jack. He also found Hydnophytum in

western Java and described it as a new species H. montanum. This species he said had short petioled, oblong leaves, while H. formicarum had subsessile ovate leaves. Since, however, Jack described H. formicarum as having short petioled, elliptic-ovate leaves, the distinction was somewhat tenuous. Later J.D. Hooker (1881) sank H. montanum into H. formicarum Jack.

Gaudichaud (1830) described collections made in the Moluccas on Freycinet's voyage of the 'Uranie'. He wrote without reference to Sprengel or Blume. The Myrmecodia he described as Mirmecodia [sic] echinata, but since he identified the plant with M. tuberosa Jack the name is nomenclaturally superfluous and hence illegitimate (Act. 63: 58 Int. Code of Bot. Nomen, 1972). He also sank the genus Hydnophytum into Mirmecodia and published the name M. inermis which comprised H. formicarum Jack and his new collection from the Moluccas.

A.P. de Candolle (1830) re-separated the genera, but unfortunately used the name M. inermis Gaudich. to indicate a spineless species of Myrmecodia which he identified with M. tuberosa Jack and Nidus formicarum ruber of Rumphius. He created a new species M. armata to include Blume's collection from Java (M. tuberosa Jack, according to Blume) and also Gaudichaud's M. echinata. Since Gaudichaud's name was superfluous, M. armata DC is correct. De Candolle followed Blume in recognizing H. formicarum Jack and H. montanum Blume.

For a while there was peace; Henschel (1833) followed Jack, and Don (1834) and Dietrich (1839) followed de Candolle. Richard (1834) mentioned M. hispida, but apparently meant M. echinata. Then Bentham made an error in thinking he had found numerous seeds in a fruit of what is in fact a species of Hydnophytum with two pyrenes. He revived Lasiostoma as a genus in the Rubiaceae and described two species in it (1843). These were later placed in Hydnophytum by Beccari (1885); they are H. oblongum (Benth.) Becc. and H. loranthifolium (Benth.) Becc. from New Ireland and New Guinea respectively.

Hasskarl (1844) and Korthals (1851) followed de Candolle without alterations. Miquel (1855) recognized Blume's two species of Hydnophytum but he transferred the pre-Linnean name Nidus formicarum niger from H. formicarum Jack to H. montanum Blume, he also observed that these two species are scarcely to

be distinguished. In Myrmecodia he removed de Candolle's superfluous name M. inermis, using M. tuberosa Jack instead. He retained the name M. echinata Gaudich. to include Blume's collection from Java and Gaudichaud's from the Moluccas, ignoring de Candolle's name M. armata for these two collections. In his account of Sumatran plants (1861) Miquel followed Blume.

In 1858 Asa Gray presented an account of Seemann's collections from Fiji to the American Academy of Arts and Sciences, though this was not published until 1860. He described two new species, one was Hydnophytum longiflorum and the other Myrmecodia imberbis which was later transferred by Beccari to a new genus Squamellaria. Gray was rather confused by the existing literature and said sadly "There is no small obscurity about the one or two old species of this genus and respecting the distinction between it and Hydnophytum which the Dutch botanists ought to clear up". Seemann, apparently unaware of Gray's description, published in 1861 the name M. vitiensis, but as Gray (1862) pointed out this was the same plant that he had called H. longiflorum.

More confusion was still to arise. Miquel (1869) named a new species H. ovatum based on collections by Teysmann and de Vriese from Ternate. He discussed the similarity between H. formicarum Jack and H. montanum Blume and concluded they were not distinct. He confused later writers by referring to H. ellipticum Blume which appears to be an error for H. montanum Another red herring was his H. lanceolatum collected by Zippelius and referred by him to Cephaelis laevigatum; Beccari (1886) removed it from the ant-plant genera. Miquel also mentioned another incomplete collection of Zippelius from ?New Guinea which Beccari (1885) called H. zippelianum.

The next report was of ant-plants collected by Nares from Cape York, Australia. Baron von Mueller (1871) referred to them as H. formicarum and M. armata.

4. FROM THE 'GENERA PLANTARUM' (1873) TO BECCARI (1884-1886)

Bentham and Hooker in their 'Genera Plantarum' (1873) succeeded in clarifying the distinction between Hydnophytum and Myrmecodia noting the stem and tuber characters as well as floral ones. They also recognized that

'M. inermis' A. Gray (meaning M. imberbis A. Gray) belongs to a distinct genus, but did not describe it.

In 1874 Beccari entered the arena with a description of Myrmecodia selebica which he later transferred (1884) to a new genus Myrmephytum Becc. Von Mueller in 1875 listed D'Albertis'collections from southern Papua, assigning them to H. formicarum and Myrmecodia echinata. In 1877 Kurz found Hydnophytum on the Andaman Islands and identified it as H. formicarum Jack.

Baillon in his 'Histoire des Plantes' (1880) suggested that Hydnophytum be sunk into Myrmecodia again and that the two should be regarded as a section of the non-myrmecophytic genus Uragoga L. He also mentioned Lasiostoma Bentham of which he saw the specimens but found no flowers. No-one seems to have followed Baillon's ideas. In 1880 Britten mentioned M. glabra from Borneo, but this was probably a mistake for M. inermis.

J.D. Hooker in 1881 took the step of sinking H.montanum Blume into H. formicarum Jack. Horne in the same year listed two species of Hydnophytum he had collected in Fiji, though descriptions were not published till 1883 by Baker who realized that one of these species, H. wilsonii, was not a typical Hydnophytum; indeed Beccari transferred it to Squamellaria in 1886. Franz Antoine gave a history of the taxonomy of the group in a paper mainly on the morphology of these plants (1882).

Odoardo Beccari published his monumental study of ant-associated plants as the second part of his three-volume work 'Malesia' between 1884 and 1886. This volume is subtitled 'Piante Ospitatrici; ossia piante formicarie della Malesia e della Papuasia descritte ed illustrate da O. Beccari.' It deals extensively with other ant-associated plants, namely Myristica, Endospermum, Macaranga, Clerodendron, Acacia, Cecropia, Korthalsia, Calamus, Nepenthes, Pachycentria, Pogonanthera, Lecanopteris, Dischidia and Cordia, he also mentions Schomburgkia and Kibara. By far the greatest part of the work however concerns the Rubiaceae. His revision of Myrmecodia and Hydnophytum was based on extensive knowledge of the plants in the field and he was familiar with the type material in Europe. He added sixteen species to the existing two

of Myrmecodia and twenty-nine to the six of Hydnophytum. One species from each genus he removed to form the new genus Squamellaria Becc. (M. imberbis A. Gray and H.? wilsonii Horne ex. J.G. Baker). He did not believe Squamellaria to be ant-associated as there was then no evidence of its having tubers. He also transferred his previously described Myrmecodia selebica to a new satellite genus Myrmephytum. This, along with his other new genus, Myrmedoma, has a six-merous corolla and large bracts, but they differ in vegetative characters, resembling respectively Hydnophytum and Myrmecodia. Beccari also recorded the different species of ants present in the ant-plants and discussed their relationship with the plants.

5. AFTER BECCARI TO VALETON (1927)

After Beccari there was a phase of piece-meal description of new species. J.D. Hooker (1886) honoured Beccari's work by naming Myrmecodia beccarii, a distinctive species from mangrove vegetation in Australia. This was the plant which had been seen but not published by Banks and Solander. Schumann in 1888 also honoured Beccari, this time with a species of Hydnophytum, but found that he had made an error and moved the species to Psychotria in 1889.

Northeastern New Guinea had become a German colony and new exploration led to new finds. Warburg (1891, 1894) named three species of Hydnophytum , one of Myrmecodia and one of Myrmedoma, and Schumann (1898) added two species of Myrmecodia from the Bismarck Archipelago. Hooker (1892) named a new species of Hydnophytum from the British colony of Papua. In a careless moment Drake (1895) described a specimen of Scyphiphora hydrophyllacea (Rubiaceae) as H. costatum, this was spotted by Pitard in 1924.

Schumann and Lauterbach created a new species of Hydnophytum in 1905 and Rechinger two more in 1913. Then German activity ceased but American authors began in earnest; Merrill (1907; 1908; 1913; 1915) and Elmer (1911; 1913; 1934) described a total of eight species of Hydnophytum and four of Myrmecodia in the Philippines. Almost all of these will have to be sunk.

Valeton had already named several species of ant-plants from New Guinea (1911; 1912a; 1912b) when he undertook the Rubiaceae for Lauterbach's 'Flora

von Papuasien'. But he was an elderly and ailing man; he saw neither the material at Florence (Beccari's) nor at Kew, and he left undescribed names in his key, and names on specimens. Unfortunately many of the collections he described were not only fragmentary, but were later lost in Berlin. Thus his account of Myrmecodia consists of a key to species in New Guinea followed by descriptions of seven new species, of which fragments of three and photographs of two are all that survive. His sixteen new species of Hydnophytum fared a little better.

6. AFTER VALETON

In the same year that Valeton's work appeared Moore described three species collected by Brass on one of the many and important Archbold Expeditions. These three species of Hydnophytum were however all very close to species previously described by Hooker and Beccari, which Moore did not apparently examine.

In 1940 Fosberg described a new species of Hydnophytum from the Solomon Islands, and in 1942 Bremekamp published H. inerme (Gaudich.) Bremek. as a new combination for H. gaudichaudii Beccari. But the Gaudichaud specimen which was the type for H. gaudichaudii Becc. was not the type for M. inermis Gaudich. since this species included H. formicarum Jack.

In 1945 Merrill and Perry published seven species of Myrmecodia and fifteen of Hydnophytum from the Brass collections. Like Valeton they did not see existing types and thus missed a number of relationships and identities with earlier species. Many of the collections came from areas not explored before and little since, the variability and range of these species was therefore probably often underestimated.

Finally in 1967 A.C. Smith studying the flora of Fiji found a distinct species of Squamellaria and called it S. major.

7. CONCLUSION

The taxonomic history of the group shows little synthesis or understanding; Beccari was the only author stimulated by an interest in the unique symbiosis

of these plants. This led him to study the plants at first-hand over much of their range and to examine all the available types. His treatment is the only one which covers the group throughout its distribution, discusses subgeneric grouping, attempts to define the variation of what I interpret as the ochlospecies H. formicarum, and which considers heterostyly and the association with ants. Valeton, and Merrill and Perry only had first-hand knowledge of the commonest species; this, together with their limited acquaintance with existing collections, led to their work being little more than a listing of new collections.

IV. Morphology and anatomy

1. INTRODUCTION

2. THE TUBER

a) Morphology of the tuber and chambers

b) Spines on the tuber and stem

3. THE STEM

a) Number and branching

b) Clypeoli and cavities

4. THE ROOTS

5. THE LEAVES

a) The lamina

b) The petiole

c) The stipules

6. THE INFLORESCENCE

a) Position and branching

b) Bracts

c) Heterostyly

d) Calyx and corolla

e) Anthers and pollen

f) Pistil and ovary

g) Fruit and pyrenes

1. INTRODUCTION

The rubiaceous ant-plants have a number of morphological features which are highly unusual and therefore require more description than normal. The most striking of these features is the huge, swollen and modified hypocotyl, referred to here as a 'tuber', with its numerous, complex phelogens[1]. Scarcely less remarkable are the spines derived from adventitious roots and the shield-like structures, clypeoli, at the base of each petiole in some species of Myrmecodia. Also in Myrmecodia the inflorescence normally arises in depressions in the stem,

referred to as alveoli. Our knowledge of these structures is imperfect and more needs to be known of their phenotypic variability and taxonomic value.

2. THE TUBER

a) Morphology of the tuber and chambers

The process of development of the tuber and its chambers is described in Chapter II and discussed in more detail by Treub (1883b) and Huxley (1976 and 1978). Further study of this aspect of the chambers requires fresh material, and has not been attempted here. The configuration of the cavities is rarely clear from herbarium specimens, and characteristics, such as whether separate cavities interconnect and whether the cavities have both basal entrance holes and entrance holes over the tuber surface, are unknown for many species. Serial sectioning of whole tubers is the only satisfactory way to determine the cavity morphology and a series of plants of differing ages is a great advantage. This process has only been carried out by myself for Myrmecodia tuberosa 'muelleri' from Hombrom Bluff, Central Province, Papua New Guinea, and Hydnophytum cf. moseleyanum from the same locality.

The cavities of Hydnophytum are relatively simple in shape (Fig. 2 b), as they have rather few openings to the outside, and the branches of a single cavity rarely interconnect with each other or with other cavities. Moreover each cavity, though branched and with warts towards the tips of the branches, does not form distinct types of chamber with particular structures as is found in Myrmecodia. Later cavities arise peripherally to earlier ones, each having at least one opening at the base of the plant and usually one to several scattered over the tuber surface.

In some montane specimens two distinct types of cavity occur in the tuber. There are large central cavities which form a spiral ascending through the tuber; these are 2 - 12 cm in diameter and have a large basal opening. Just beneath the surface of the tuber there are numerous smaller, tunnel-like cavities each of which has one or two openings to the tuber surface. Only a few specimens like this have been dissected (UPNG 5931 and UPNG 5932; Huxley, 1978), and it is not clear how widespread the phenomenon is. The lowland species H. guppyanum

has similarly distinctive cavities, the central chambers being much larger than peripheral ones.

I have not seen a specimen which definitely lacks a tuber, however, this has been reported three times for Hydnophytum. Beccari collected a specimen with no tuber on Japen Island, Irian Jaya, and described it as H. normale (Beccari, 1885; 131). Unfortunately the specimen at Florence is cut off above the base of the stem. Valeton (1927; 139) identified three Ledermann collections (7180, 12296 and 8542) as H. normale but these collections were lost in Berlin. Brass reported that the tuber is faculatatively absent, especially in young plants, in H. albertisii (Merrill and Perry, 1945: 24).

In Myrmecodia the cavities of the tubers are sometimes remarkably complex; as described in Chapter II of each of the later cavities is differentiated into chambers with different shapes, colours, anatomy and presence or absence of warts. The most distinctive of these features, and the one which can be seen most readily in herbarium specimens, is the honeycombing (Fig. 1b). This feature, however, may not always be visible in preserved specimens and is not always strongly developed. There is some evidence that in certain species the presence or absence of honeycombing is variable.

Honeycombing is usually associated with pores, these are openings from the cavities to the outside which are less than 1 mm in diameter. In some species (e.g. in M. tuberosa 'manusensis' and M. albertisii ssp. dentrecastensis) they form neat little rings at the tip of each 'cell' of the honeycomb (Fig. 1b). In other species the pores are more scattered. Areas of honeycombing with pores are usually surrounded by more or less complete rings of entrance holes. In M. tuberosa 'versteegii' the entrance holes are closely set and the area enclosed appears almost detached and is raised above the general tuber surface (Fig. 25).

In both Hydnophytum and Myrmecodia there is a range in the proportion of tissue to cavity in the tuber. Available evidence suggests the proportion of tissue is higher in species subject to water shortage (Huxley, 1978).

The range of forms in the tubers of the satellite genera falls within that of the two major genera. In Myrmephytum the tuber may resemble that of lowland

Hydnophytum or of Myrmecodia with moderately developed honeycombing. The tubers of Anthorhiza and Squamellaria have not been dissected, but probably resemble those of Hydnophytum.

b) Spines on the tuber and stem

The spines which occur on the tubers and stems of the ant-plants are derived from adventitious roots. This is indicated by the presence of intermediate states, particularly where a part of the tuber or stem is covered by humus the spines develop as short adventitious roots. Rather thin root-like spines developed on plants of H. cf. moseleyanum grown in a shade house where the conditions are more uniformly humid than in the open (Huxley, 1976). The anatomy of the spines shows a central core of vascular tissue similar to that of the roots in basic structure, but with reduced phloem and cortex (Treub, 1883a; Spanner, 1938).

In Hydnophytum fully developed spines are not formed. The tuber sometimes has a few adventitious roots which stand out perpendicular from the surface. On the stem there may be short, sinuate roots around the inflorescence.

In Myrmecodia spines, or at least adventitious roots on the stem, are rarely absent. They vary in form and size from simple to repeatedly branched (Fig. 7). When simple they may be long, fine and chestnut brown (as in M. archboldiana, Fig. 7b) or short, stout and black (as in M. pteroaspida, Fig. 7a), or many other combinations. In the ochlospecies M. tuberosa a range of spines is found from nearly absent through simple, branched, club-like to richly branched (Fig. 7e, f and g). Freely branched, rather fine spines are found in M. albertisii and M. pendula (Fig. 7h, i, m and o).

Regularly stellate spines occur in M. wauensis (Fig. 7p). It is possible that they are derived from either branched spines or from simple spines clustered on mounds as in M. archboldiana (Fig. 7 d).

The spines of the tuber and stem of a plant are generally similar, but this is not always so. In M. erinacea the arrangement of simple spines around the alveoli and usually branched spines on the stem surface and on the tuber is a diagnostic taxonomic character (Fig. 7j, k and l; and Fig. 33).

Fig. 7. Spines of ant-plants. All x 2.

a) Myrmecodia pteroaspida, spines on mounds or ridges on tuber.

b, c and d) M. archboldiana, spines isolated or clustered on tuber.

e) M. tuberosa 'muelleri ', on stem and tuber.

f) M. tuberosa 'versteegii', especially large example of spine on edge of raised area on tuber.

g) M. tuberosa 'pulvinata', club-like spines on tuber.

h and i) M. albertisii ssp. albertisii, on tuber.

j, k and l) M. erinacea: j) on stem around alveoli; k) on general surface of stem; l) on tuber.

m, n and o) M. pendula: m) on stem; n and o) on tuber.

p, q and r) M. wauensis: p) on tuber; q and r) on stem.

s) Anthorhiza clemensii ssp. louisiadensis, on stem.

t) A. clemensii ssp. clemensii, on stem.

u and v) Myrmephytum selebicum: u) on stem; v) on tuber.

w) Myrmephytum arfakianum, on tuber.

x) Myrmephytum species 3., on tuber.

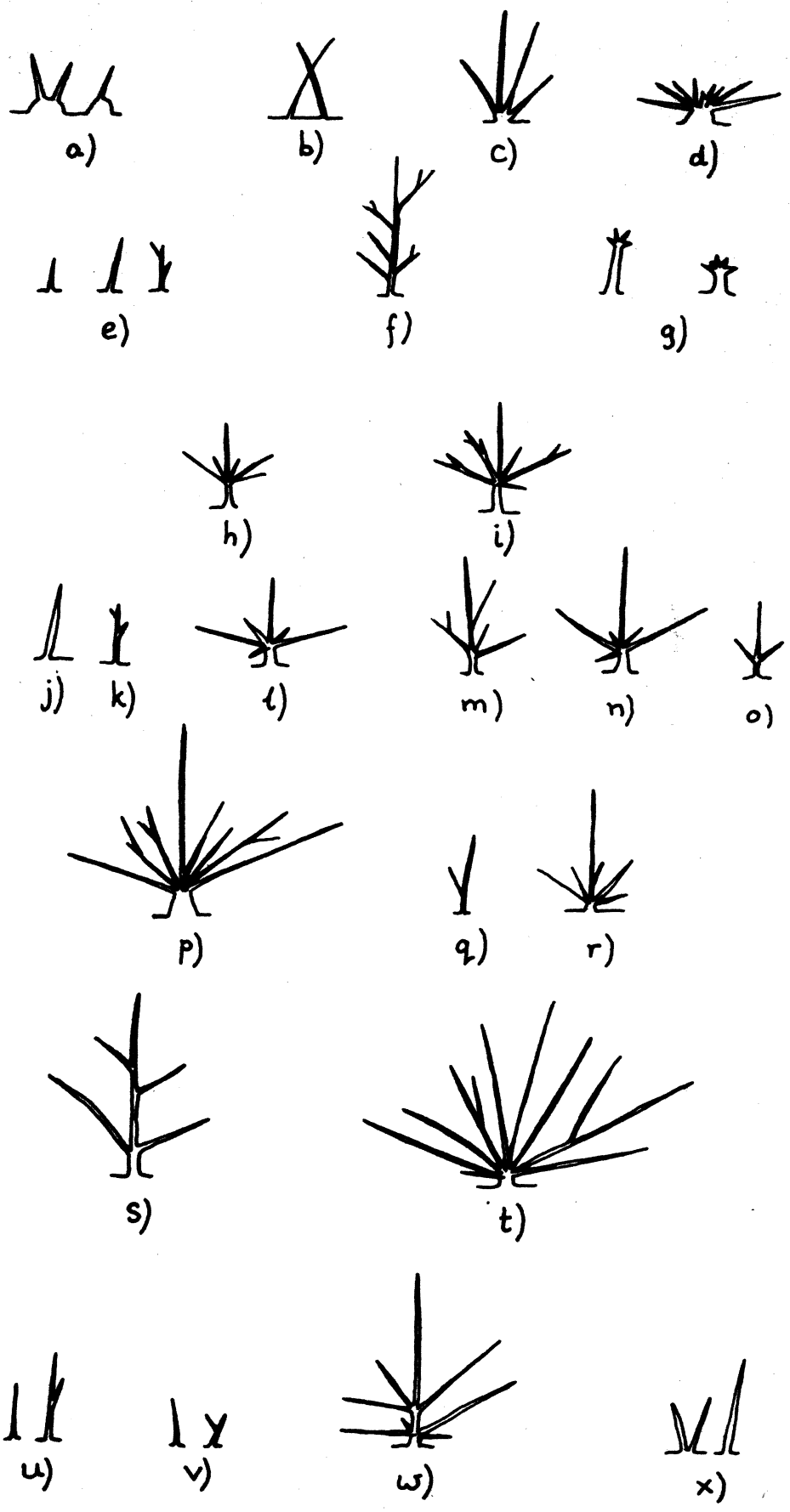


Fig. 7.

The position of the spines is also often characteristic. On the tuber they may be largely restricted to the ridges or they may be most abundant around the entrance holes, as in M. tuberosa 'versteegii'. On the stem the spines may be confined to the rims of the alveoli or clypeoli, or scattered.

In two species (e.g. M. lamii) different parts of the tuber bear different types of spine. The lower part of the tuber has clusters of short, thick, simple spines and the apical part has long, fine spines (see Chapter XVI 5 c).

In Myrmephytum branched spines are usually present. These are rather sparse and weakly developed in M. selebicum (Fig. 7 u and v) and M. beccarii, but rather dense and richly branched in M. arfakianum (Fig. 7 w). Spines are almost absent from the stem in M. arfakianum which is densely covered in bracts.

Anthorhiza is unique in having spines among the flowers in the inflorescence, and in parallel lines along the stem (Plate 9). The spines are large and freely or stellately branched (Fig. 7 s and t).

Squamellaria, like Hydnophytum, lacks spines. I have not seen specimens of the tubers, but photographs and notes do not suggest any spines. No spines or adventitious roots are found on the stems.

3. THE STEM

a) Number and branching

The stems of ant-plants rival the tubers in the interest of the characters they show. There is variation not only in the gross morphology from long, narrow, freely branched stems, to short, thick, unbranched ones, but also in the modifications of the stem surface, armature and vascularization.

In Hydnophytum several stems usually arise from a mound at the apex of the tuber (Fig. 2 a). The stems are branched, and may form a stiff, shrubby, upward growth or a pendent, more flexible structure. The branching is normally by one axillary bud developing at node; if both buds develop the terminal bud is usually lost.

The stem varies from terete to quadrangular (with the corners opposite and between the leaves) and is slightly winged in H. tetrapterum.

The vascular tissue in Hydnophytum stems forms a complete cylinder in the internodes , with a hollow centre. The cortex is quite narrow.

In some montane specimens swellings occur along the stem with small hollows like those of the tuber (UPNG 3484). It is not, however, clear whether this is a characteristic of particular species, or a freakish development under certain conditions.

In Myrmecodia the number of stems arising from the tuber is typically one or two, though it may be more, as in M. lamii, where the numerous, unbranched stems give the plant the appearance of a sea-anenome (Fig. 41) (Lam, 1924; Huxley, 1978). Branching of the stems is generally reduced and is quite absent in several species, especially the clypeolate ones. Branching can be fairly free, as in M. beccarii (Fig. 30), but the arrangement of the branches is obscured by the thick stems.

In all species of Myrmecodia (except M. hydnostipula, Fig. 43) the internodes are markedly condensed and the stems thicker than is usual in Hydnophytum. The vascular tissue in the internodes of Myrmecodia exists in four separate strands. This may be the result of the shortening of the internodes or may indicate a neotenous state which has enabled the other modifications of the stem to occur.

In Myrmephytum the same change from long internodes with branching to condensed internodes without branching, is found as occurs between Hydnophytum and Myrmecodia. The stem of Anthorhiza is quite broad (1.5 cm) but is branched and hollow with long internodes and cylindrical vascular tissue, as in Hydnophytum. As in its spine and tuber characteristics, Squamellaria does not differ from Hydnophytum in its stems.

b) Clypeoli and cavities

In Myrmecodia, but not in any of the other genera, the stem is a remarkable and highly modified structure. This is partly a result of the reduction of the internodes and the sinking of the inflorescences into pits, alveoli, in the stem. There is, however, another modification; in about a third of the species of Myrmecodia, at the base of each petiole, there is a fleshy, shield-like structure - a clypeolus (Fig. 8). Stipules form a rim

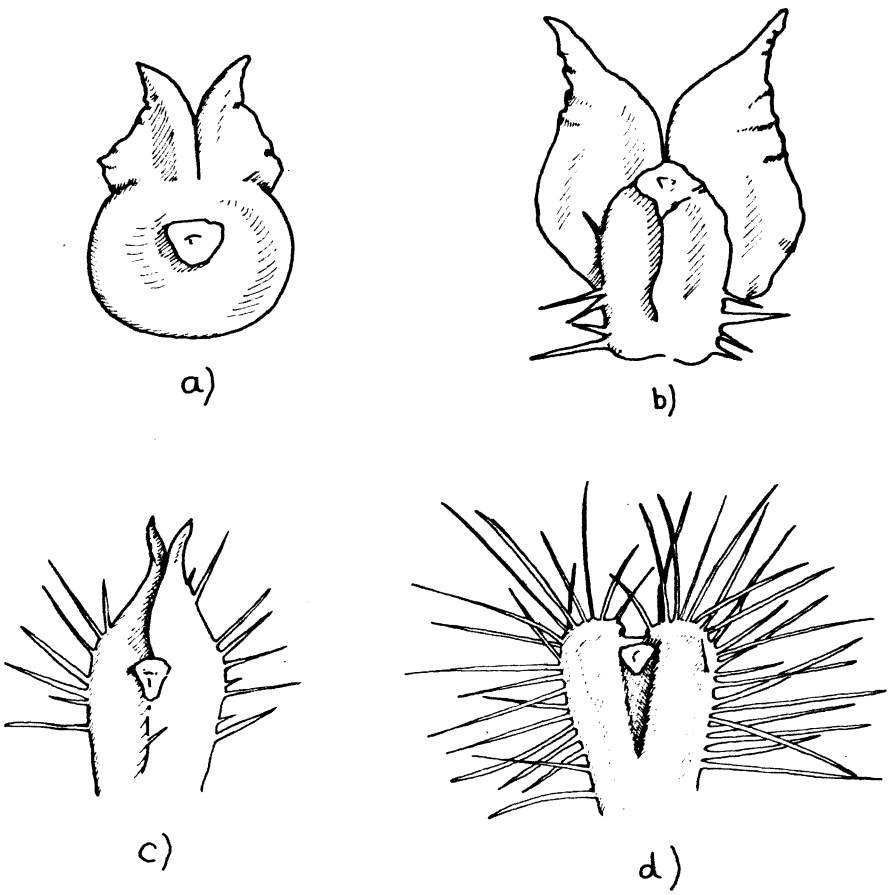


Fig. 8. Clypeoli of Myrmecodia. All x 2.

a) M. oblongata; b) M. pteroaspida; c) M. species 4 'wisselensis'; d) M. archboldiana.

along the apical edge of the clypeolus and the sides are either armed with simple spines or winged. The clypeoli are not always fully developed; in M. longissima and M. oblongata they appear as rounded bosses at the base of the petiole, and in M. tuberosa all states from none to conspicuous clypeoli are present. The spreading spines of neighbouring clypeoli normally interweave, thus covering the channels between them. In one species, M. melanacantha, the cavities of the tuber connect by tunnels through the stem with the alveoli.

4. THE ROOTS

The roots which hold the tubers to the host tree or ground have not been studied and are not used as taxonomic characters. However, it is useful to mention that in two species (M. angustifolia and M. archboldiana) the tuber does not remain tightly attached to the branch but is suspended by 20 - 50 cm of root. Spanner (1938) made some studies of root structure.

5. THE LEAVES

a) The lamina

There is considerable variation in the size, texture and shape of the lamina in ant-plants.

Lowland rainforest species of both Myrmecodia and Hydnophytum tend to have quite large (c. 25 x 8 cm) elliptical leaves. In Hydnophytum these are leathery, but in Myrmecodia are thin and mesomorphic. Spanner (1938) found that Hydnophytum leaves tend to have fewer stomata and thicker cuticle than those of Myrmecodia.

The leaf-shape and size associated with montane species differs markedly in the two genera. Hydnophytum has small, tough to brittle leaves. These may be almost orbicular (c. 0.4 x 0.3 cm) as in H. vitis-idaea, to linear (to 4 x 0.2 cm) as in H. minutifolium. Myrmecodia on the other hand, tends at high altitude to have long, narrow leaves; for instance M. archboldiana has leaves c. 30 x 3.5 cm, and M.wauensis c. 26 x 5 cm.

In seasonally dry and coastal areas Hydnophytum often has thick, fleshy leaves, e.g. H. moseleyanum. A similar development occurs only once in Myrmecodia, in the Australian M. beccarii. In the Psychotrieae as a whole

this is an unusual feature.

The variation in the leaves of the satellite genera falls within that of the two major genera.

b) The petiole

The petiole varies in length, is triangular in section and is rather stout except in the small, thin-leaved species. It is usually shorter in Hydnophytum than in Myrmecodia, the lamina being often almost sessile. In Hydnophytum the blade may be cordate at the base (in H. ovatum) and is never decurrent; conversely in Myrmecodia it is sometimes decurrent, but never cordate.

The vascularization of the petiole varies between examples of the two major genera and may provide a useful character if studied further.

c) The stipules

The stipules of the ant-plants show a wide range of both size and texture, and, more interestingly, in the manner in which they separate.

In Hydnophytum the stipules are usually not more than 0.5 cm long, papery and soon caducous. In the bud they form a pyramidal shape with the corners running towards and between the petioles (Fig. 9 a). As the new pair of leaves emerges the stipules split along the corners opposite the petioles (Fig. 9 b). The remaining triangular pieces usually shrivel and fall.

In Myrmecodia the stipules often reach 1 cm in length and are more leathery and persistent. They also start as pyramidal structures (Fig. 9 c) and divide initially partly opposite the petioles (Fig. 9 d) and then completely divide between them (Fig. 9 e). Different species of Myrmecodia vary in the degree of splitting opposite the petioles, and in the final shape of the stipules. In two species the stipules form a conspicuous wing along the apical rim of the clypeoli (M. lamii and M. pteroaspida). Due to the condensation of the internodes the stipules overlap the clypeoli of the next petiole along the stem and, as a result, the surface of the stem is completely covered.

In M. hydnostipula and a little known variant (Myrmecodia species 2) the stipules resemble those of Hydnophytum in splitting opposite the petioles (Fig. 43). The stipules of the satellite genera follow those of Hydnophytum

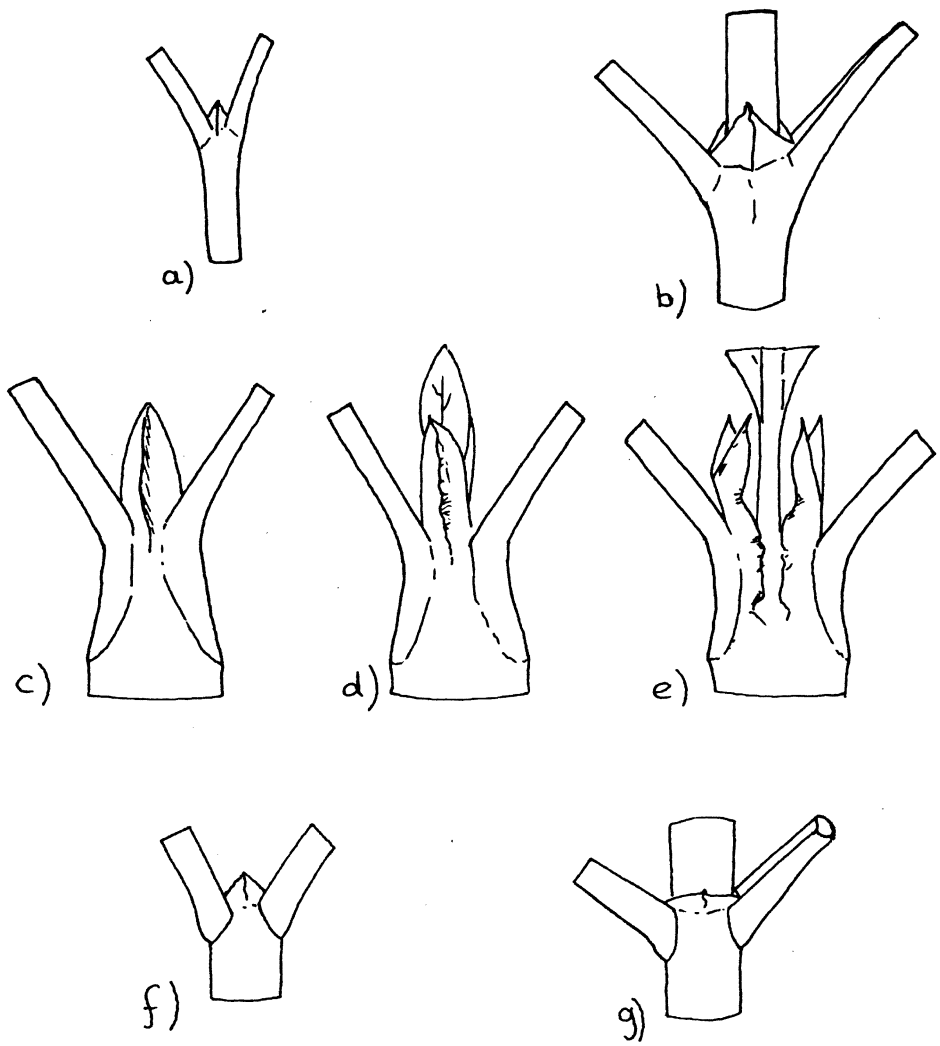


Fig. 9. Stipules of the Hydnophytinae. All x 2.

a and b) Hydnophytum cf. keiense; a) Stipules forming a pyramidal cover over the apical bud; b) Stipules split opposite the petioles.

c, d and e) Myrmecodia tuberosa 'muelleri'; c) Stipules forming a pyramidal cover; d) Stipules initially splitting part of their length opposite the petioles; e) Stipules finally splitting between the petioles.

f and g) Myrmephytum beccarii; f) Stipules forming a cover; g) Stipules split opposite the petioles.

(Fig. 9 f and g).

6. THE INFLORESCENCE

a) Position and branching

The inflorescence is often a useful character in the Rubiaceae (Petit, 1964). There is much variation in the position and in the pattern of branching. Reduction of the inflorescence to sessile, clustered flowers occurs repeatedly, e.g. in Nauclea (Naucleae) and parts of Psychotria.

In the Hydnophytinae the inflorescence is axillary with only one exception; this is Hydnophytum guppyanum et aff. in which the inflorescence is sometimes terminal (Fig. 10 a). The usual situation is that at each node an inflorescence arises in the axil of one only of the pair of leaves. Once flowering has commenced in the young plant an inflorescence is usually found at each node, except where branching occurs.

The position of the inflorescence normally spirals up the stem (Treub, 1883b; Beccari, 1884). In Hydnophytum and Squamellaria the regular spiral is not infrequently broken. The spiral is clockwise.

In H.guppyanum a solitary peduncle arises in the leaf axil, and is central to it. This contrasts with the situation in the rest of the genus, where the inflorescence either arises on two peduncles or is solitary but placed on one side of the axil. Before discussing this further, however, it is necessary to consider the branching pattern in H. guppyanum which is quite variable (Fig. 10 b). The basic pattern is opposite and decussate, terminating in a solitary flower and two lateral branches; the terminal flower may be missing. Sometimes this termination occurs at the first node, in which case the inflorescence is apparently dichotomous. The lateral branches may branch at first in an opposite decussate way but after the second division are pseudodichotomous. The ultimate segments of the inflorescence rachis are usually condensed or fascicled so that the flowers are close to one another. All the flowers are sessile.

In species of Hydnophytum with pedunculate flowers, other than H. guppyanum, two peduncles arise in one leaf axil, and follow a pseudodichotomous pattern (Fig. 10 c and d). It is as though the first segment of the peduncle of a

Fig. 10. Inflorescences of Hydnophytum.

a) Terminal inflorescence of H. guppyanum (BSIP 13194);

b) Lateral opposite decussate inflorescence with dichotomous final branching, H. guppyanum (Brass 4321);

c) Apparently paired, dichotomously branched inflorescence in H. radicans vel. aff. (NGF 19033);

d) Apparently paired, dichotomous branched inflorescence with the final branches rather long with close packed flowers; H. albertisii (Brass 7017);

e) Inflorescence reduced to a pair of short branches with close packed flowers, H. ovatum (Schlechter 19636);

f) Inflorescence consisting of a single short branch placed to one side of the leaf axil, H. tenuiflorum (Smith 455).

All x 1.

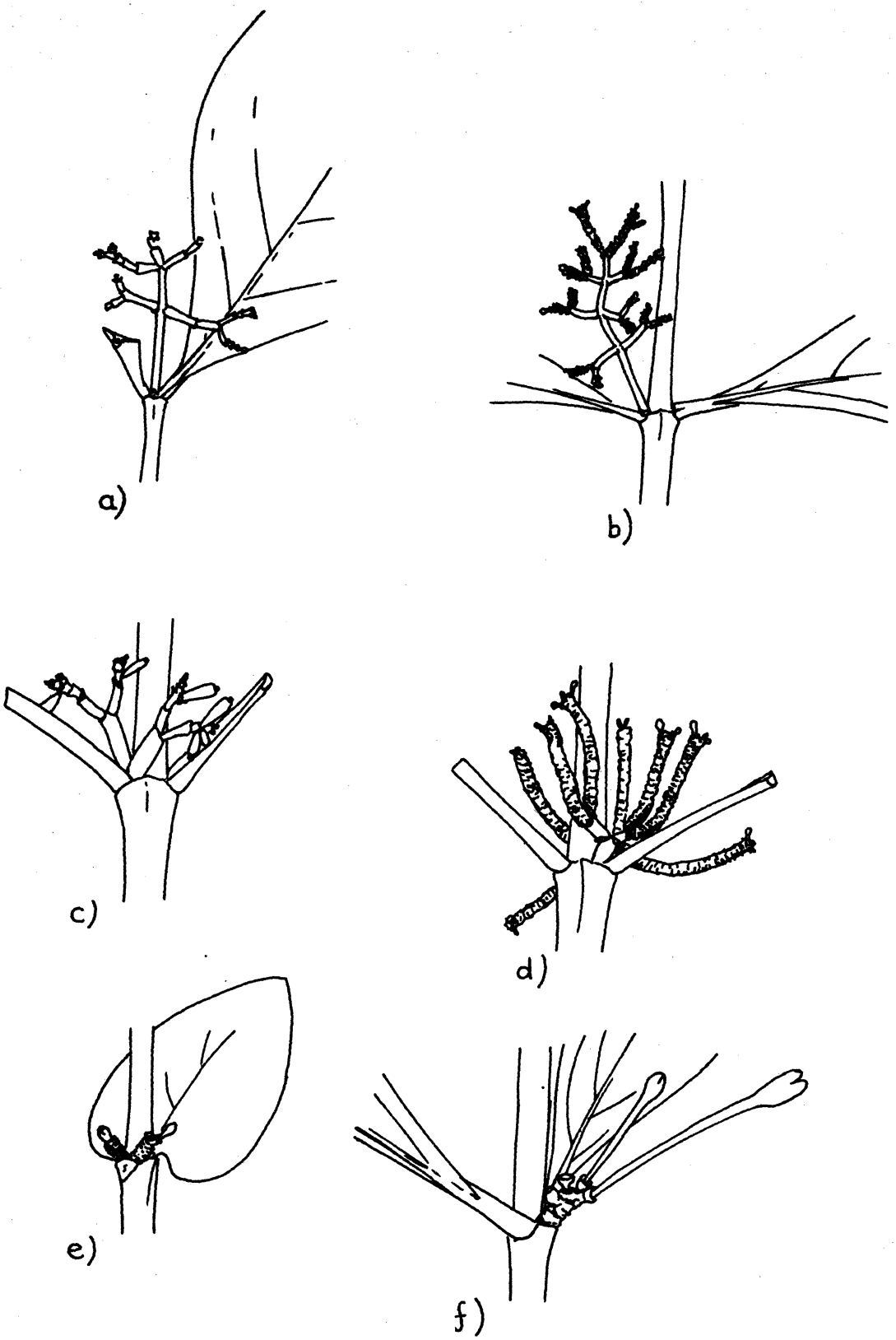


Fig. 10.

pseudodichotomous inflorescence of H. guppyanum were reduced to zero and the two lateral branches placed in the axil (Fig. 10 c). The inflorescence rachis is condensed after the first or second node (Fig. 10 d). In young individuals and other species the inflorescence rachis is not branched and flowers are borne close together from the base of the rachis.

By further reduction of the inflorescence rachis, the paired inflorescences come to be simply on mounds, or sessile, or even slightly sunken into the stem. Inflorescences on mounds are found in H. formicarum, H. moseleyanum, H. ovatum (Fig. 10 e) and many other species.

Finally there are species in which the inflorescence is solitary and placed to one side of the leaf-axil. This is found in H. grandiflorum and H.tenuiflorum (Fig. 10 f). It appears as if one of a pair of inflorescences in other species has been lost.

In Myrmecodia the inflorescence is sunken into the base of alveoli in the stem. The alveoli are paired at each leaf-axil, one arises to each side of it. The buds mature slowly and reach anthesis gradually, so that flowers may be found all along a stem.

In Myrmephytum the inflorescences are sessile. They may be clearly discrete or form a mass which completely conceals the stem. In Anthorhiza the inflorescence is again sessile in axillary areas, but is unique in being interspersed with spines (Plate 9). The inflorescence of Squamellaria is solitary and sessile or on slight mounds, resembling those of H. grandiflorum.

b) Bracts

The bracts vary from insignificant to conspicuous in each of the three genera Hydnophytum, Myrmecodia and Myrmephytum. In Squamellaria and Anthorhiza they are always slight. Enlargement and elaboration of the bracts is not uncommon in the Rubiaceae.

In Hydnophytum the bracts are usually inconspicuous. In pedunculate species they form papery rims at each node, and where the rachis is condensed they form short rims between each flower. In at least three unnamed species the bracts are rather conspicuous. In one of these the bracts are thin and shiny and form dense chestnut-brown, hairy cushions (Docters van Leeuwen 9566).

In Myrmecodia where the alveoli are deep or covered by clypeoli or spines, the bracts are often very small. However, where the alveoli are less well protected, the thin, chestnut-brown bracts often form dense masses which fill,or extend, cushion-like, out of the alveoli e.g. in M. tuberosa 'pulvinata'. These bracts have numerous hairs formed by single, double at the base, files of cells on their abaxial surface.

In Myrmephytum outer bracts are large and thick, either leathery, or almost fleshy; they surround each inflorescence. Thinner bracts are interspersed through the inflorescence, these are hairy.

c) Heterostyly

Heterostyly is common in the Psychotrieae, but unfortunately the number of flowers available for disection here was so low, that in most cases its presence or absence could not be determined with any certainty. Four species of Myrmecodia are probably heterostylous e.g. M. albertisii (Fig. 31). Two species are variable in the presence or absence of hairs in the corolla tube. In two other species (M. erinacea, Fig. 33, and M. melanacantha) three different arrangements of the anthers, stigma and hairs are known. It is possible that in some species, especially those in which the corolla remains closed, heterostyly is breaking down. The heterostyly affects pollen structure, see below,and also the stigma, though this has not been documented. The extent of heterostyly in Hydnophytum and the satellite genera is not clear.

d) Calyx and corolla

The calyx is rather constant in the ant-plants, being chestnut-brown, tubular and truncate with only rarely slight teeth around the margin. It varies somewhat in thickness and in length (from 1 to 6 mm), and in one species is hairy. Raphide bundles are usually visible, especially at the base of the calyx.

The corolla is typical of the Rubiaceae being tubular with as many valvate lobes as stamens. It is usually white though in two species the colour is a rather grey greenish-blue (M. wauensis and M. erinacea) and is reported to be orange-red in one collection (M. species 3 'rouffaerensis') and pink in another.

The corolla tube is usually cylindrical widening somewhat at the ring of hairs, which is usually at the mouth of the tube in Hydnophytum but at any height in Myrmecodia. In some species of Myrmecodia and Myrmephytum the corolla widens gradually giving a conical shape (e.g. Fig. 40).

The lobes of the corolla have hooks, unci, at the tip. In the four genera other than Myrmecodia this is quite a small feature, but in Myrmecodia these hooks are larger and their lower edges may remain together closing the mouth of the tube at anthesis when the tips of the lobes have diverged. These hooks are referred to as unci, the lobes being uncinate.

In one part of Hydnophytum (H. grandiflorum et aff) the tube reaches 20 - 40 mm (Fig. 10 f), and in Squamellaria the corolla is also over 20 mm long.

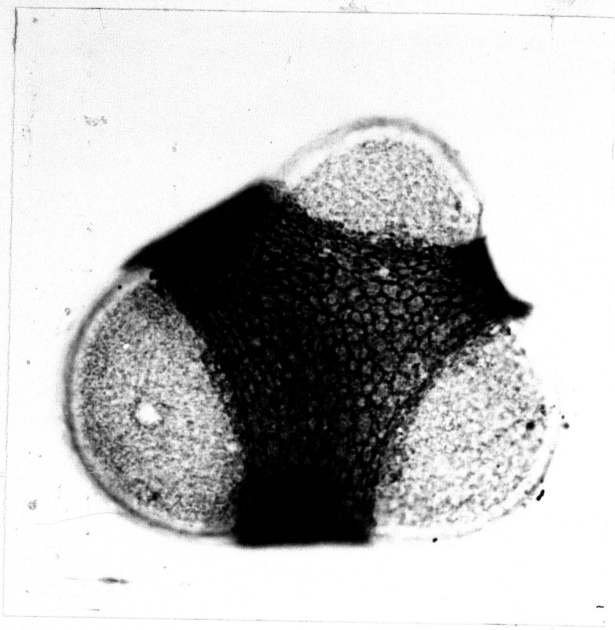
e) Anthers and pollen

The anthers are usually exserted at the mouth of the corolla tube in Hydnophytum, but lie at different levels within the tube in Myrmecodia. The free filaments are usually shorter than the anthers. The anther walls in Myrmecodia are sometimes more or less dark blue.

The pollen is of considerable interest because it shows great variation both between and within genera and species. This was discovered independently by Dr. E. Robbrecht in Brussels. In Myrmecodia it is unusual in normally having one, two or three or more protoplasmic vesicles. These vesicles may parallel those found in the Cousareae (Verdcourt, 1958). There may be as many vesicles as pores, or a smaller number.

The apertures may be round or more or less colpate, and their edges, where the vesicles break through, may be ragged or neat or more or less thickened (Plates 2 - 6). The surface of the exine shows a reticulate pattern which varies considerably. It may be almost smooth, with small pits, (Plate 3 a), referred to as fine reticulation, through a moderately open mesh (e.g. Plate 5 b), medium reticulation; to an open network as seen in Myrmecodia archboldiana (Plate 4 b), (coarse reticulation). In M.tuberosa'salomonensis' the bars forming the reticulation fail to join up (Plate 2 d).

Pollen characters are useful in defining some taxa. For instance the massive aperture borders in M. erinacea (Plate 5 c), and the triporate pollen



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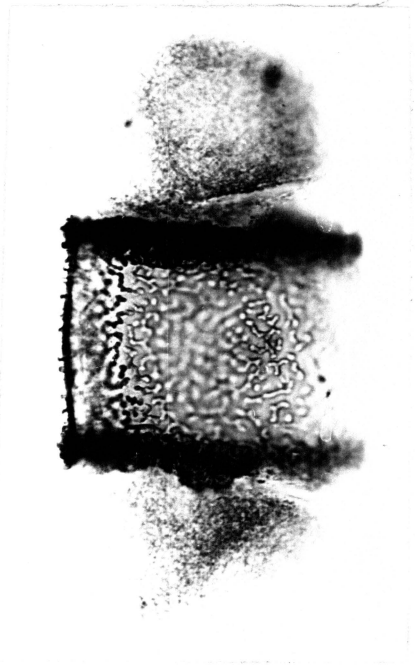

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Plate 2. Pollen of the ochlospecies Myrmecodia tuberosa.
a) M. tuberosa 'muelleri ' (UPNG 3432); b) M. tuberosa 'oninensis' (Wentholt 128); c) M. tuberosa 'pulvinata' (UPNG 5904); d) M. tuberosa 'salomonensis' (Brass 2585). Magnification x 547; Wodehouse preparation.

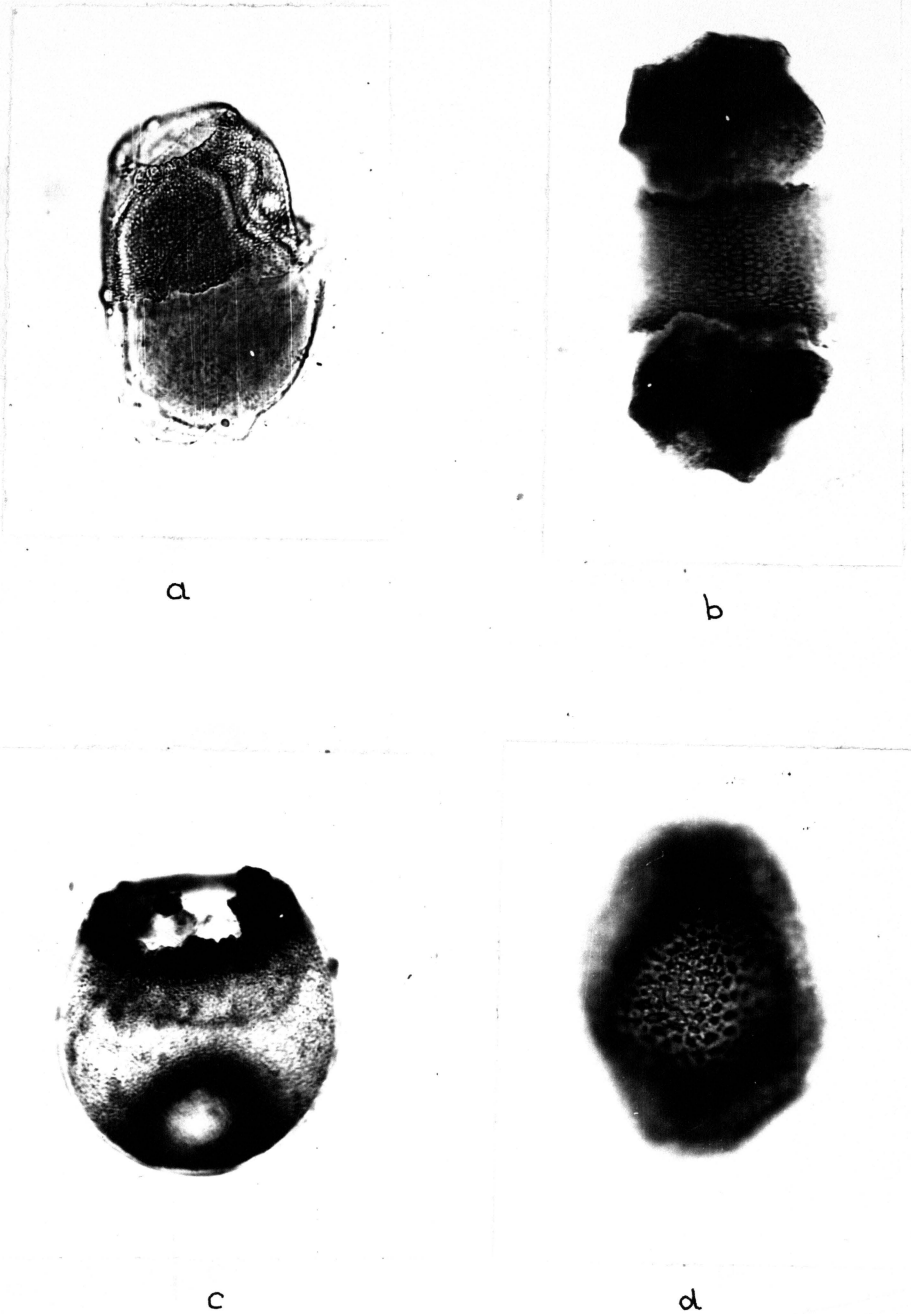
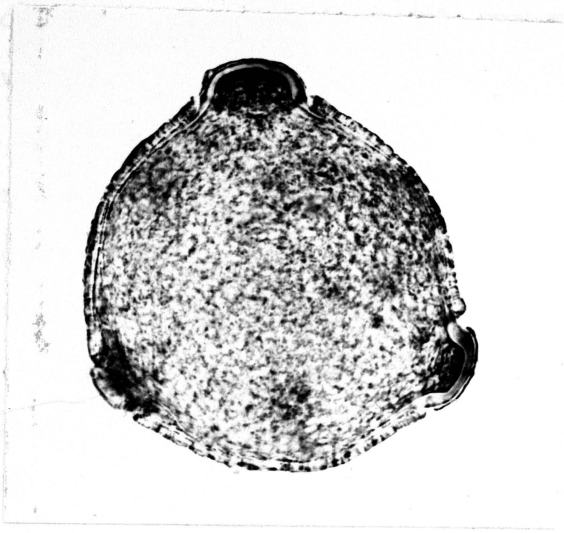


Plate 3. Pollen from heterostylous species of Myrmecodia.
a and b) M. albertisii ssp. albertisii; a) Pollen from longistyle flower (Brass 8580 (A)); b) from brevistyle flower (Brass 7599). c and d) M. sterrophylla; c) longistyle flower (Pulle 781); d) brevistyle flower (Eyma 4930). Magnification x 547; Wodehouse preparation.



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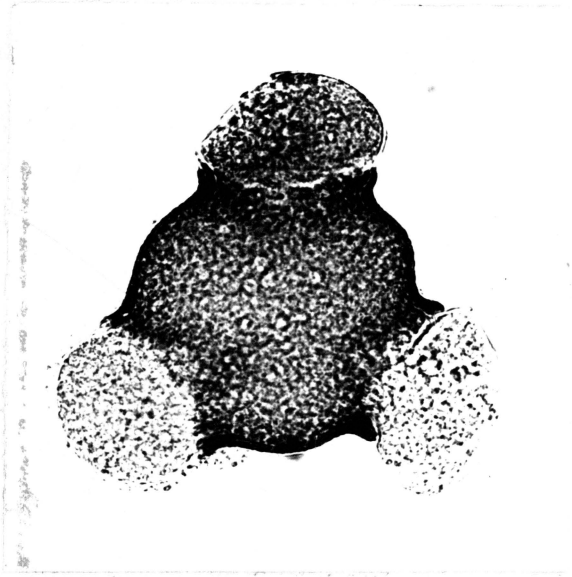

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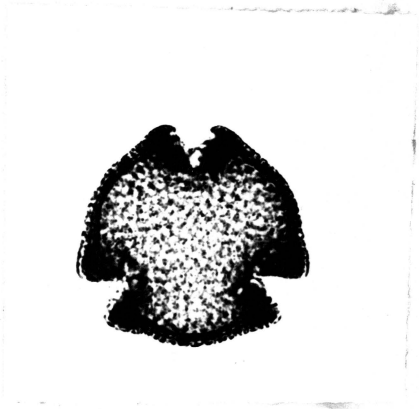

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Plate 4. Pollen of various triporate species of Myrmecodia. a) M. hydnostipula (LAE 55709); b) M. archboldiana (Brass 11216); c and d) M. wauensis (UPNG 3410), c) with vesicles, d) not fully developed or infertile. Magnification x 547; Wodehouse preparation.

of M. wauensis (Plate 4 c and d). In other cases interpretation of the data has been more difficult because of the variability of the pollen. The grains from one anther often vary in vesicle number, though it has been found for one cultivated plant of M. platytyrea that a series of flowers of different ages had a constant proportion of grains with the different numbers of vesicles. Pollen from different populations of the same flower type of a given taxon can vary quite widely, particularly in the size of the reticulation. The most important source of variation is however that associated with heterostyly. This affects the size of the pollen grain, the openess of the reticulation and the number of vesicles (Plate 3). Insufficient flowers have been available for the changes to be fully investigated. In both M. albertisii ssp. albertisii and M. sterrophylla the pollen from longistyle flowers has finer reticulation than that from brevistyle flowers. In M. albertisii the grains from brevistyle flowers are also larger, this parallels a difference observed in Mapouria by Bremekamp (1963).

In Hydnophytum the pollen from the few species investigated was triporate with no or very small vesicles and with no thickening of the aperture borders. The pollen is also characteristically much smaller than that of Myrmecodia (Plate 7 a). The exine reticulation varies from fine to medium and in H. guppyanum is ornamented (Plate 7 b). The species from Fiji (H. grandiflorum) shows a remarkable similarity to Squamellaria (Plate 7, c and d). In both the pollen is 4-colpate and large. The reticulation is very coarse and deep with a characteristic lobed and bobbly appearance.

In Myrmephytum the grains are more or less colporate and in M. arfakianum are particularly large and the reticulation is extremely open (Plate 6d). Anthorhiza has triporate pollen grains, with slight vesicles, no borders and medium reticulation.

Pollen was examined using the Wodehouse preparation (Wodehouse, 1935) which does not involve removal of the protoplasm in order to leave the vesicles intact. This does not provide so much information about the pollen wall as staining procedures after acetolysis.

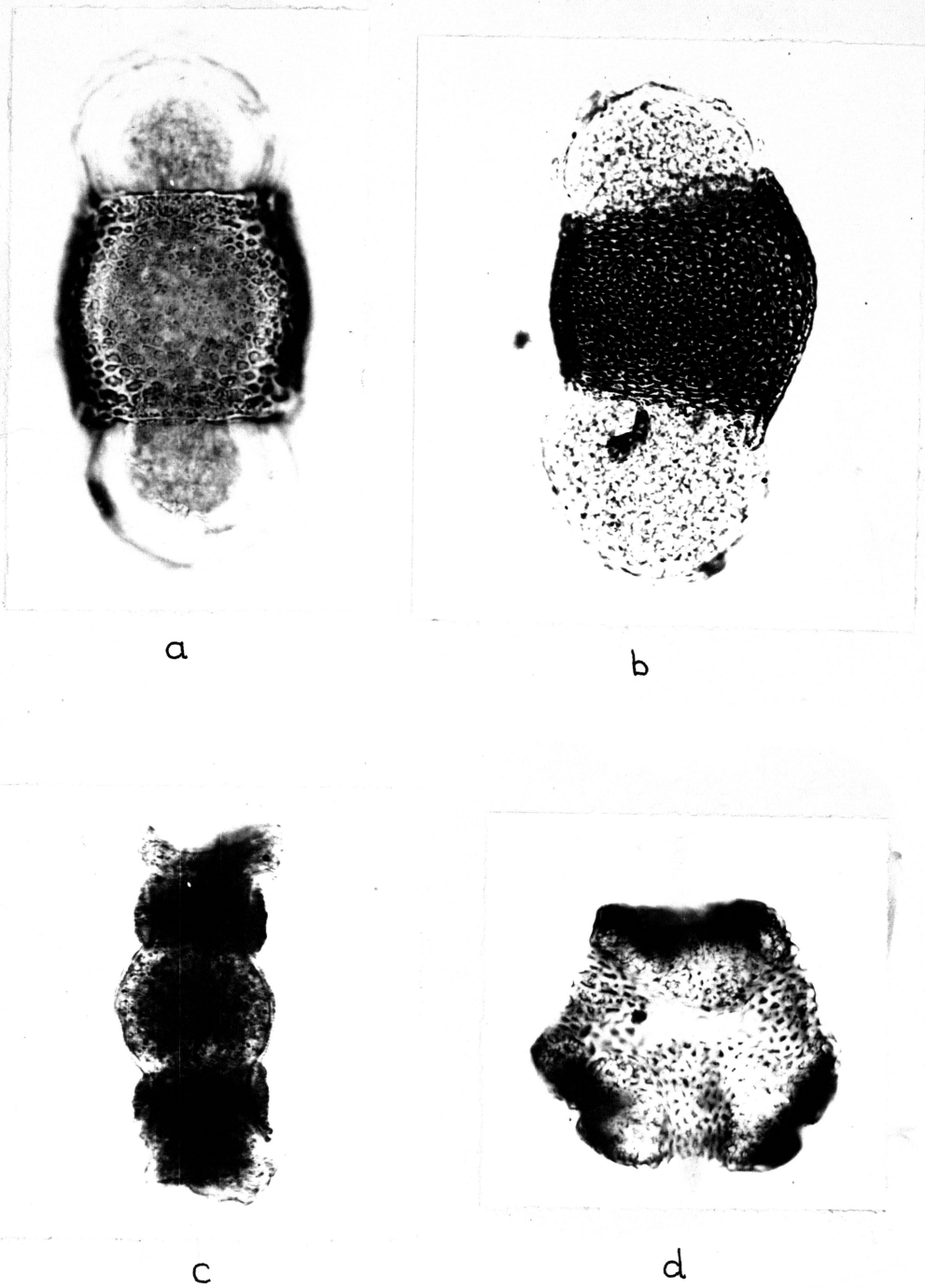
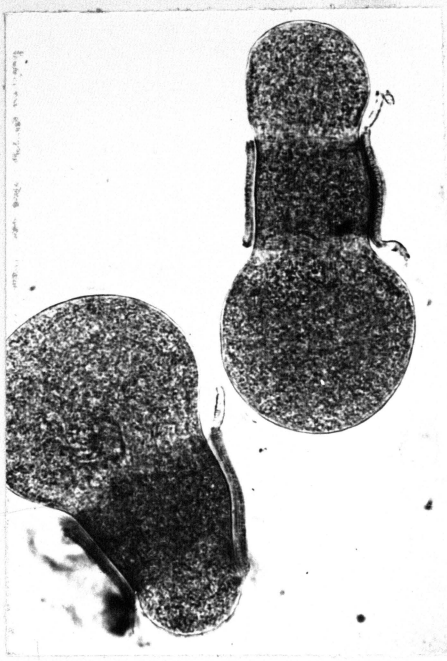


Plate 5. Pollen of various species of Myrmecodia.

a) M. melanacantha (UPNG 5939); b) M. pteroaspida (UPNG 3461); c) M. erinacea (van Royen 3079); d) M. species 2, 'mamberamoensis' (van Leeuwen 9540). Magnification x 547; Wodehouse preparation.



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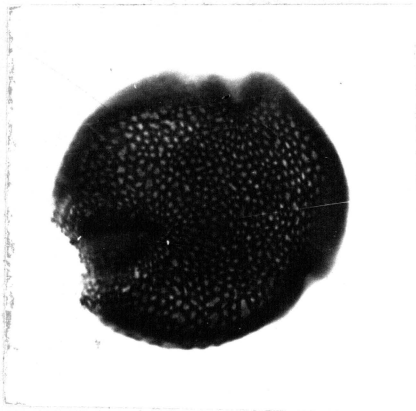

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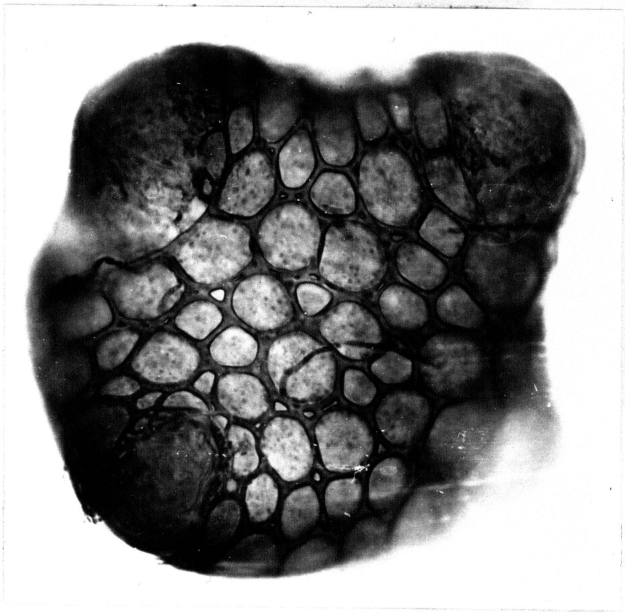

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Plate 6. Pollen of various species of Myrmecodia and Myrmephytum.

a) Myrmecodia pendula (UPNG 5922);

b) Myrmecodia beccarii (UPNG 3439);

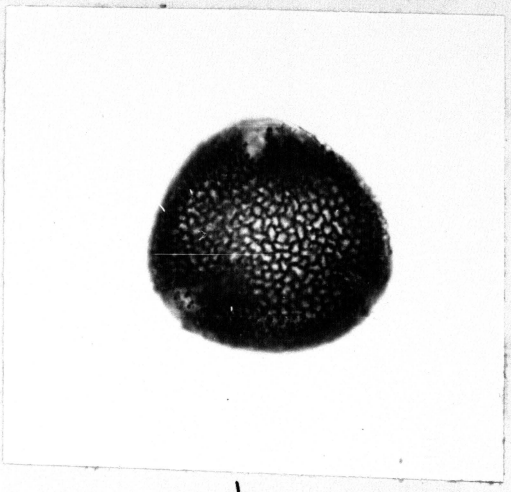
c) Myrmephytum beccarii (Sulit 21513);

d) Myrmephytum arfakianum (Kanehira and Hatusima 13714).

Magnification x 547; Wodehouse preparation.



a



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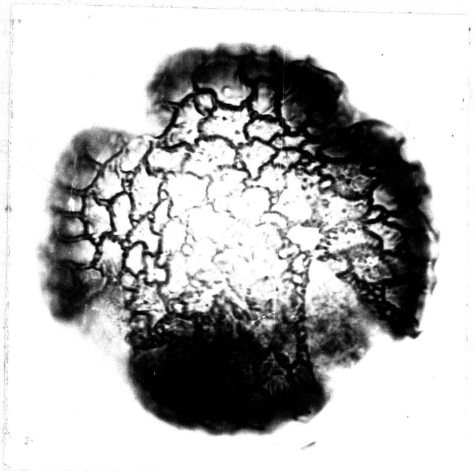


c



d

Plate 7. Pollen of Hydnophytum and Squamellaria.

a) Hydnophytum hellwigii (NGF 8776);

b) H. guppyanum (Schodde 3741);

c) H. grandiflorum (Smith 7603);

d) Squamellaria wilsonii (Smith 1787).

Magnification x 547; Wodehouse preparation, except d) which was acetolysed by Dr. E. Robbrecht.

f) Pistil and ovary

In all genera except Squamellaria the stigma is lobed to the same number as the number of locules. The lobes are usually 1-3 mm long, slightly spreading at anthesis and somewhat papillate. The stigma may vary according to the style length in heterostylous flowers.

In Squamellaria the stigma is capitate with a circular flange above and below (Beccari, 1884-6). It is not known whether this acts as a receptaculum pollinis as in other parts of the Psychotrieae.

The ovary is 2-10 locular, with one ovule per locule.

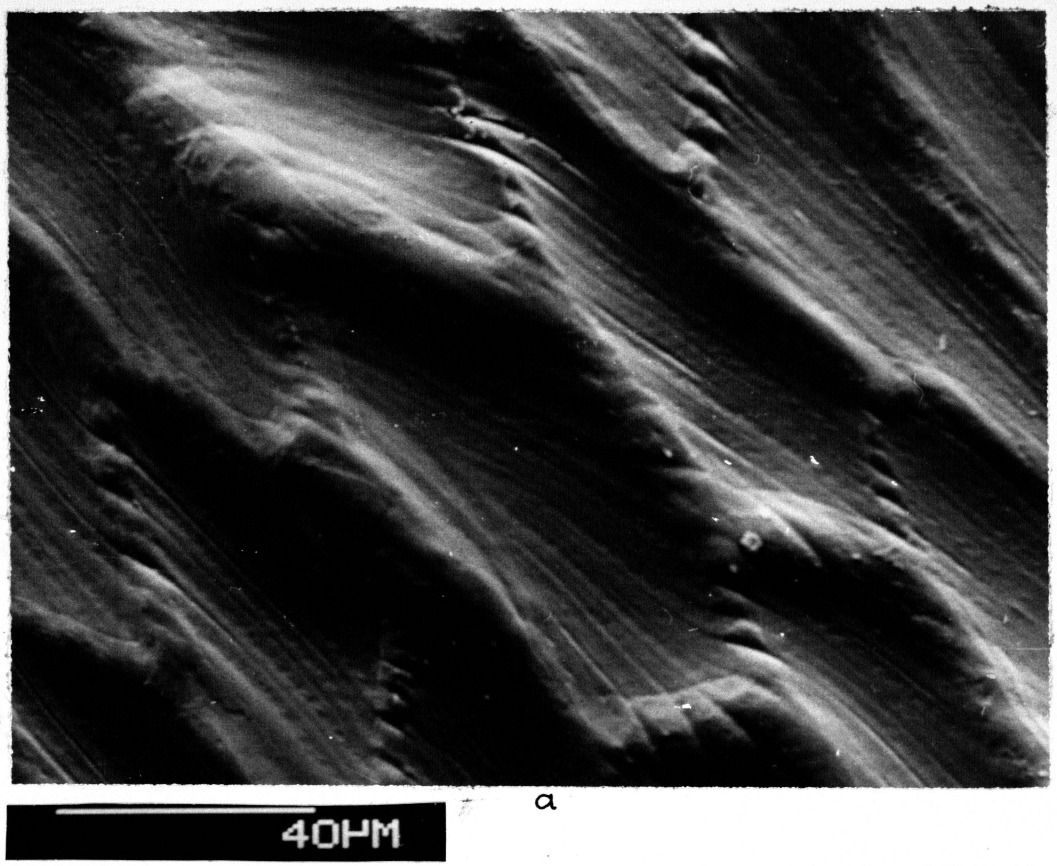
g) Fruit and pyrenes

The fruit is a fleshy, somewhat translucent drupe, coloured white, yellow, orange or, most commonly, red. The flesh is sweet and slightly sticky; there are chalazal threads at the base of each pyrene. The calyx forms a papery rim at the apex of the fruit.

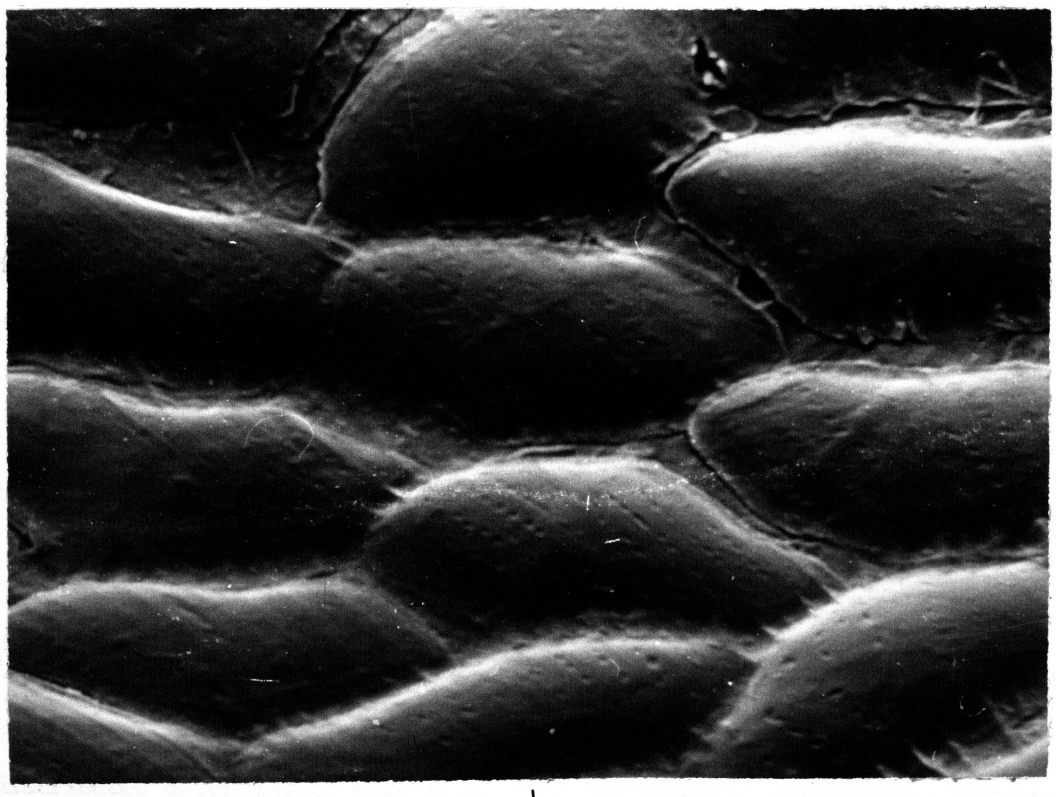
The pyrenes have a tough, springy coat which dehisces from the base by a few, somewhat irregular splits. In a variant of Myrmecodia tuberosa from Sulawesi and in Squamellaria the apex of the seeds is horned.

The embryo is straight or curved and the endosperm surface is smooth.

The scanning electron microscope was used to examine the pyrene and seed-coat of Myrmecodia to see whether any taxonomic characters were available. The outer surface of the pyrene is very rough and composed of broken cells. The inner surface of the pyrene forms a distinctive pattern (Plate 8 a) partly mirroring the seed-coat within (Plate 8 b). Several species were examined:- M. beccarii, M. platytyrea, M. pteroaspida. M. wauensis and M. tuberosa 'muelleri' and 'versteegii'. Insufficient variation was found however to indicate that the characters would be useful in taxonomic work.



a



b

Plate 8. Pyrene and seed coat of Myrmecodia beccarii.

a) Inner surface of pyrene; b) outer surface of seed coat.

V. Distribution and ecology

1. INTRODUCTION

a) General

b) Climate

c) Floristics

2. VEGETATION TYPES

3. DISTRIBUTION OF THE GENERA

4. DISTRIBUTION OF THE SPECIES

a) General

b) Distribution and ecology of Myrmecodia in New Guinea

c) Distribution of species of Myrmecodia in Australia

1. INTRODUCTION

a) General

A study of the distribution and ecology of a group of plants reveals the different roles played by the morphological taxa and their relative success. Parallels of morphology in comparable environments may suggest a functional role of that morphology. Parallels of structure in totally different environments will point to different interpretations. The pattern of sympatry and vicariousness will suggest how far different morphological forms are able to avoid competition.

The distribution of plant genera and species is a result of complex interaction of the physiological, dispersal and evolutionary potential of a taxon with the physical and biotic environment through time. Within broad geographical boundaries defined by climatic and physical barriers, taxa are distributed according to more local soil and climatic conditions. For an epiphyte, the existing vegetation is apt to be more important than it is for more dominant life-forms. Not least, though often difficult to assess, the distribution of animals and fungi will influence the distribution of a plant taxon. In a group of plants which is symbiotic with ants, the distribution

of these ants is also likely to be of importance to the distribution of the plants.

The distribution of the rubiaceous ant-plants is centred on Malesia, and extends nearly 20° north and south of the equator and from the Andaman Islands off Burma in the west to the Fijian Islands in the east (Fig. 11). This area includes parts of the two continental plates and one oceanic plate; the Australian plate to the south, the Asian plate to the north west and the Pacific plate to the north east. Running across the area is a line of volcanoes and uplift which marks the boundary between the Pacific and the other two plates.

The greatest diversity of ant-plants is found in New Guinea which is a relatively recently raised edge of the Australian plate, where it meets the Pacific plate. New Guinea is thought to have existed as several separate islands during the Tertiary Period, and is only relatively recent as a complete land mass. During the Quarternary Period there was a land-bridge across the Arafura Sea and Torres Straits to Australia (Walker and Flenley, 1979).

b) The climate

Since the land-masses comprising Malesia are relatively small and broken up, the air streams are normally moist and so the climate is usually rather wet without strong seasonality. Over New Guinea south easterly winds during the northern summer alternate with north westerlies during the northern winter. The pattern of wet and dry seasons which this brings depends on the intervening mountain ranges. As shown in Fig.12 , overlay 1, only in a small part of southern New Guinea does evapotranspiration exceed precipitation for any appreciable length of time. The season of most rain is reversed on the two sides of the island.

Temperature also varies more with topography than season. Mean monthly temperatures vary little, but there is a 5.8°C drop in temperature for every 1000 m rise in altitude (Walker and Flenley, 1979).

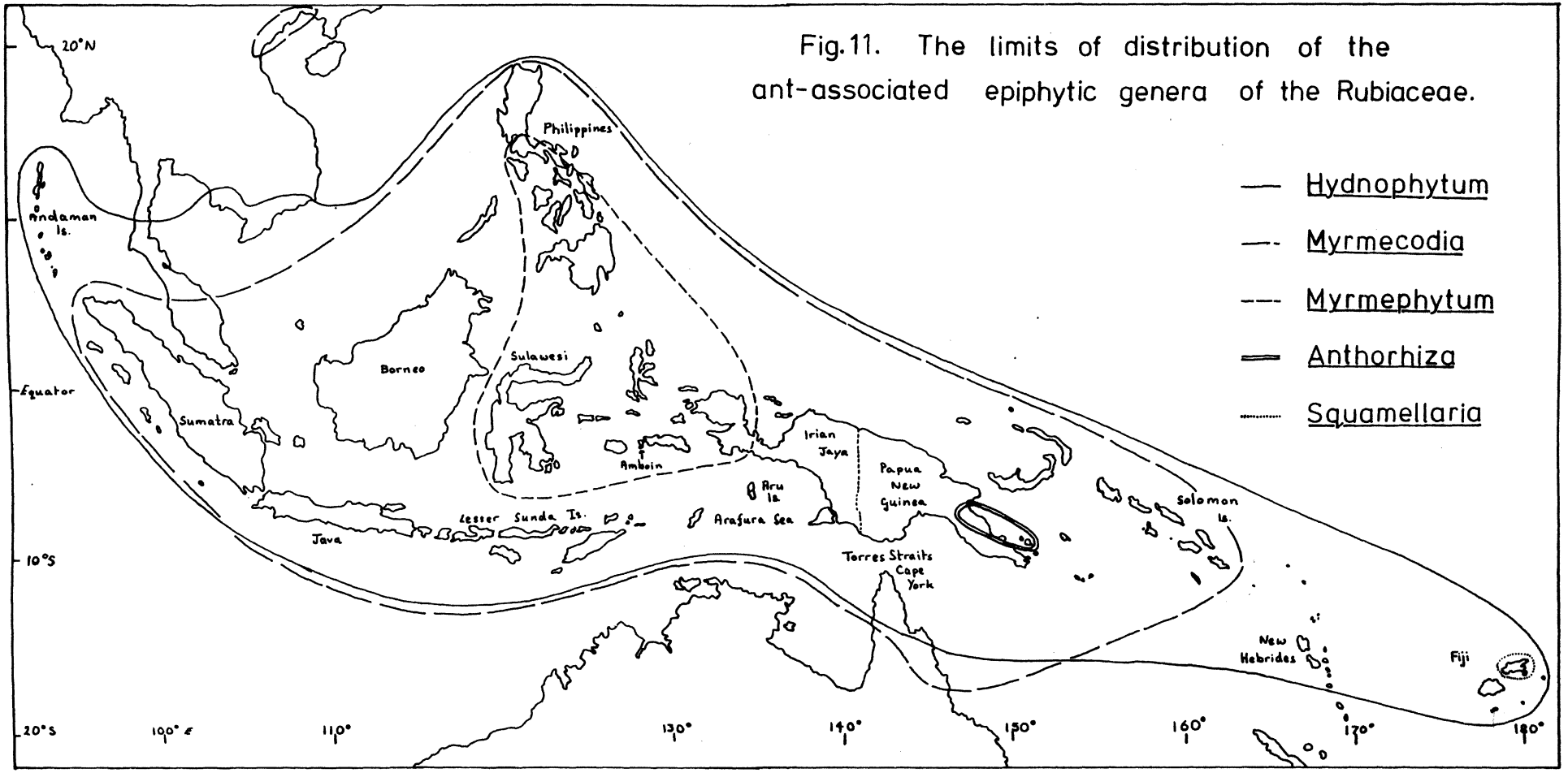


Fig.11. The limits of distribution of the ant-associated epiphytic genera of the Rubiaceae.

Fig.11.

Cloud cover is an important factor controlling vegetation types, especially the boundary between lower and upper montane forest (Walker and Flenley, 1979). It is also of particular importance for epiphytes.

c) Floristics

In its geological history and its fauna New Guinea appears as an extension of Australia; but floristically New Guinea has twice as many plant genera centred in countries to the north and west rather than in countries to the south and east (Balgooy, 1976). At the level of family there is no endemism in New Guinea, but 7% of the genera are strictly endemic and a further 7% are strongly centred in New Guinea (Balgooy, 1976). Good (1960) has estimated that the New Guinea angiosperms comprise 9000 species of which 90% are endemic.

2. VEGETATION TYPES

A wide range of vegetation types are found in the area occupied by ant-plants and a majority of them are inhabited by at least one species of these plants. The following list is not exhaustive and refers mainly to vegetation types visited by the author in Papua New Guinea. The classification of vegetation types follows approximately that of Paijmans (1976).

Coastal: strand flora - herbaceous - ant-plants absent.

beach scrub and woodland - ant-plants were not seen in this semi-deciduous woodland.

mangrove - ant-plants often present, throughout their range.

mixed littoral forest - ant-plants present, especially on Callophyllum, in areas without a marked dry season.

Lowland: swamp forest - not known.

lowland rainforest - ant-plants usually present at low frequency.

semi-deciduous woodland - ant-plants were not found in this vegetation type.

savanna - ant-plants often abundant, though rare on Eucalyptus.

Fig. 12. Map of New Guinea, northern Australia and the Solomon Islands showing altitude and the main rivers.

Overlay 1. (in pocket inside back cover). Rainfall and temperature in New Guinea and adjacent areas. Isohyets in Papua New Guinea after 'Maps of Papua New Guinea' Office of Forests, Port Moresby. Isohyets in Irian Jaya and Australia after the Times Atlas (1973).

Rainfall and temperature diagrams (Walter and Lieth, 1967) show annual march of monthly means of rainfall (upper line except rarely) and temperature (usually lower line), on a scale of $10^{o}C$ = 20 mm; the ordinate shows 0 - $50^{o}C$ and 0 - 100 mm. Times when the temperature line overtops the rainfall line are strictly arid (open stipules), times when the rainfall line overtops the temperature line are humid (dense stipules). Monthly mean rainfall exceeding 100 mm is shown at a scale reduced 10 times, and coloured black. Further details are given in Walter and Lieth (1967). The numbered localities shown here correspond to the following diagrams in that work:-

1 = 2.7. 45; 2 = 2.7. 46; 3 = 2.7 47; 4 = 2.7. 48; 5 = 2.7. 49; 6 = 2.7. 50; 7 = 2.7. 51; 8 = 2.7. 52; 9 = 2.7. 137; 10 = 2.7. 157; 11 = 2.7. 78; 12 = 2.7. 77; 13 = 2.7. 107; 14 = 6. 66; 20 = 6. 77; 21 = 6. 71; 22 = 6. 73; 23 = 6. 1; 24 = 7.2. 42; 25 = 7.2. 43; 26 = 7.2. 44; 27 = 7.2. 45; 28 = 7.2. 46; 29 = 7.2. 48.

Locality 10 is Port Moresby.

Overlay 2. (in pocket of inside back cover). Distribution of montane species of Myrmecodia.

a = M. angustifolia; ar = M. archboldiana; b = M. brassii; h = M. hydnostipula; la = M. lamii; lo = M. longissima; m = M. melanacantha; o = M. oblongata; pn = M. pendens; pl = M. pendula; pt = M. pteroaspida; s = M. sterrophylla; w = M. wauensis.

Overlay 3. (in pocket inside back cover). Distribution of lowland species of Myrmecodia, excepting M. tuberosa and M. beccarii.

a = M. albertisii; e = M. erinacea; p = M. platytyrea.

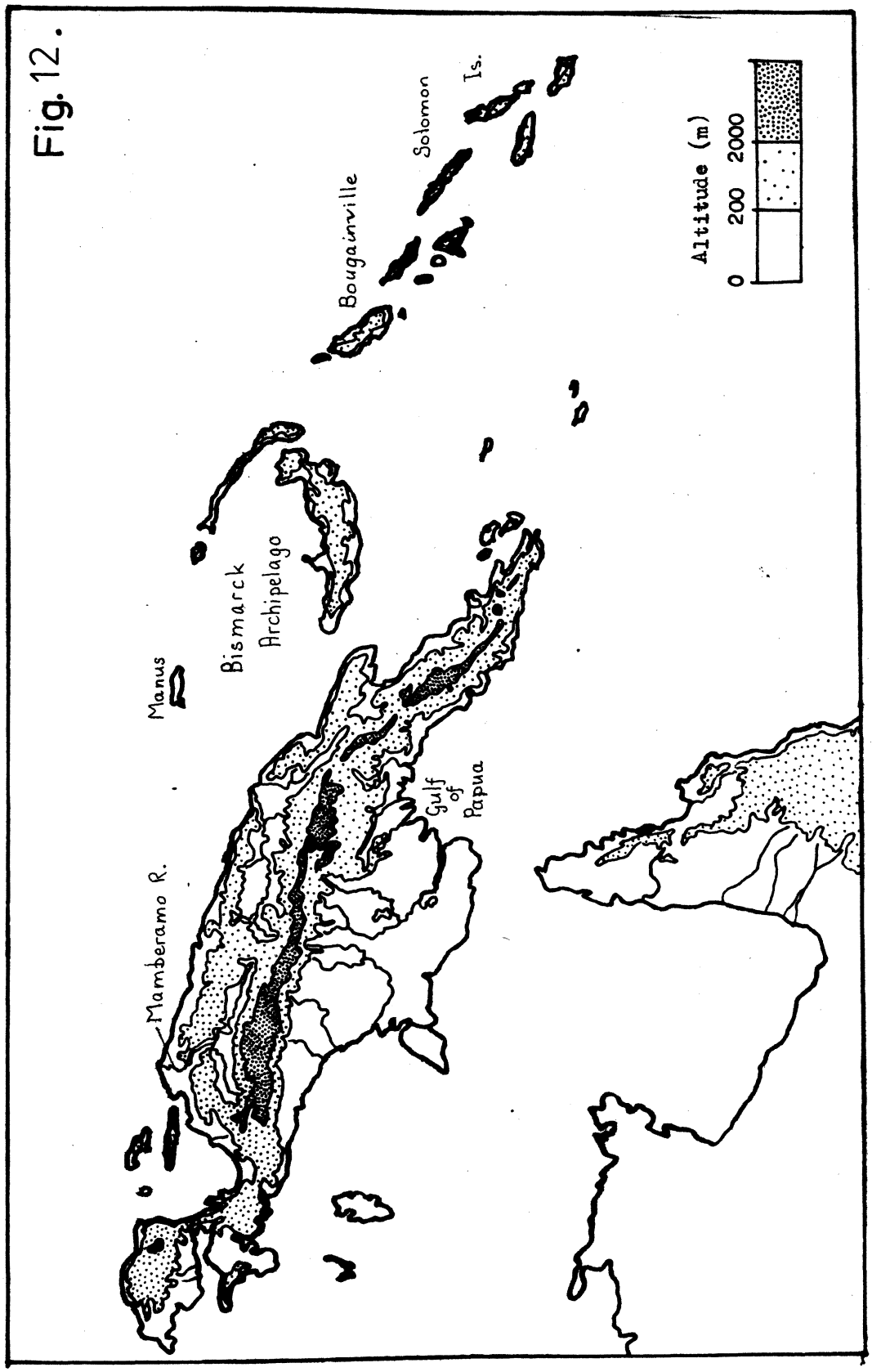


Fig. 12.
Bougainville
Solomon Is.
Altitude (m)
0 200 2000
Bismarck Archipelago
Manus
Gulf of Papua
Mamberamo R.

Fig. 12.

trees in open agricultural or riverine situations - ant-plants often present.

herbaceous vegetation - ant-plants rarely terrestrial in rocky areas.

Montane: lower montane mixed forest - ant-plants usually present at low frequency.

Castanopsis forest - ant-plants sometimes abundant.

Nothofagus and upper montane forest - ant-plants often present.

mossy forest - ant-plants sometimes abundant.

open agricultural areas - ant-plants often abundant.

Above the tree line: ant-plants abundant in some areas in Irian Jaya.

An interesting feature of the distribution of ant-plants in different vegetation types is found on two poor-soil localities where ant-plants are abundant (See Chapter II 6).

3. DISTRIBUTION OF THE GENERA

As shown in Fig. 11 Hydnophytum and Myrmecodia are both widespread and cover almost the same geographical area. The satellite genera are relatively restricted. They do not overlap one another, but are distributed across the centre and east of the area occupied by the two major genera. Myrmephytum and Anthorhiza occur in areas where both the major genera are present, while Squamellaria is confined to Fiji where Myrmecodia is absent.

4. DISTRIBUTION OF THE SPECIES

a) General

Two thirds of the type localities of described species of Hydnophytum are in New Guinea. A ninth are in the Philippines, but this is probably an over estimate due to avid splitters working in this area. A similar pattern is shown by Myrmecodia and is now emphasised as all the Myrmecodia north and west of New Guinea are regarded as part of a single ochlospecies. Thus the overwhelming majority of the species of the Hydnophytinae are in and confined to New Guinea.

b) Distribution and ecology of Myrmecodia in New Guinea

The distribution of each species of Myrmecodia has been plotted onto two maps shown in Fig.12 , overlays 2&3. This reveals two main types of distribution. Firstly, there are widespread, lowland species extending all round New Guinea (M. tuberosa and M. platytrea) or round part of the coast with extensions inland (M. albertisii and M. erinacea). Secondly there are more restricted species which are found at higher altitudes. There are two main concentrations of these species; one in Irian Jaya on the Carstenz mountains and the other along the main range in central and eastern Papua New Guinea. It is however likely that the paucity of species between these two concentrations is at least partly due to undercollecting along the political border.

In various areas of New Guinea several species of Myrmecodia occur sympatrically. In large parts of lowland New Guinea M.tuberosa and M. platytrea are sympatric. For instance they often grow together in the same tree in Melaleuca/Casuarina/Eucalyptus savanna at 600 m, near Port Moresby. Under these circumstances they are occupied by the same species of ant, and there is no evidence that they are using different parts of the physical environment. Comparison of levels of attack by the leaf-miner (Cangetta aurantaica) showed that M. tuberosa 'muelleri' suffered more than M.platytrea (Huxley, 1978). In Western Province these two species are joined by M. albertisii, which has similar leaf characteristics to the other two species.

The highest concentration of species however, occurs in Irian Jaya, at both low and high altitudes in the upper reaches of the Mamberamo River, Fig.12 , overlay 2. Within this area there is a wide range of habitats available and it may be that these species are parapatric rather than sympatric. The local montane species in Papua New Guinea tend not to be sympatric.

c) Distribution of species of Myrmecodia in Australia

The distribution of the three species of Myrmecodia in Australia is shown in Fig. 13. In this area the three species are rarely sympatric, but tend to be geographically and ecologically isolated. M. beccari is a mangrove and coastal species which occurs south of the others. M. tuberosa 'muelleri' occurs

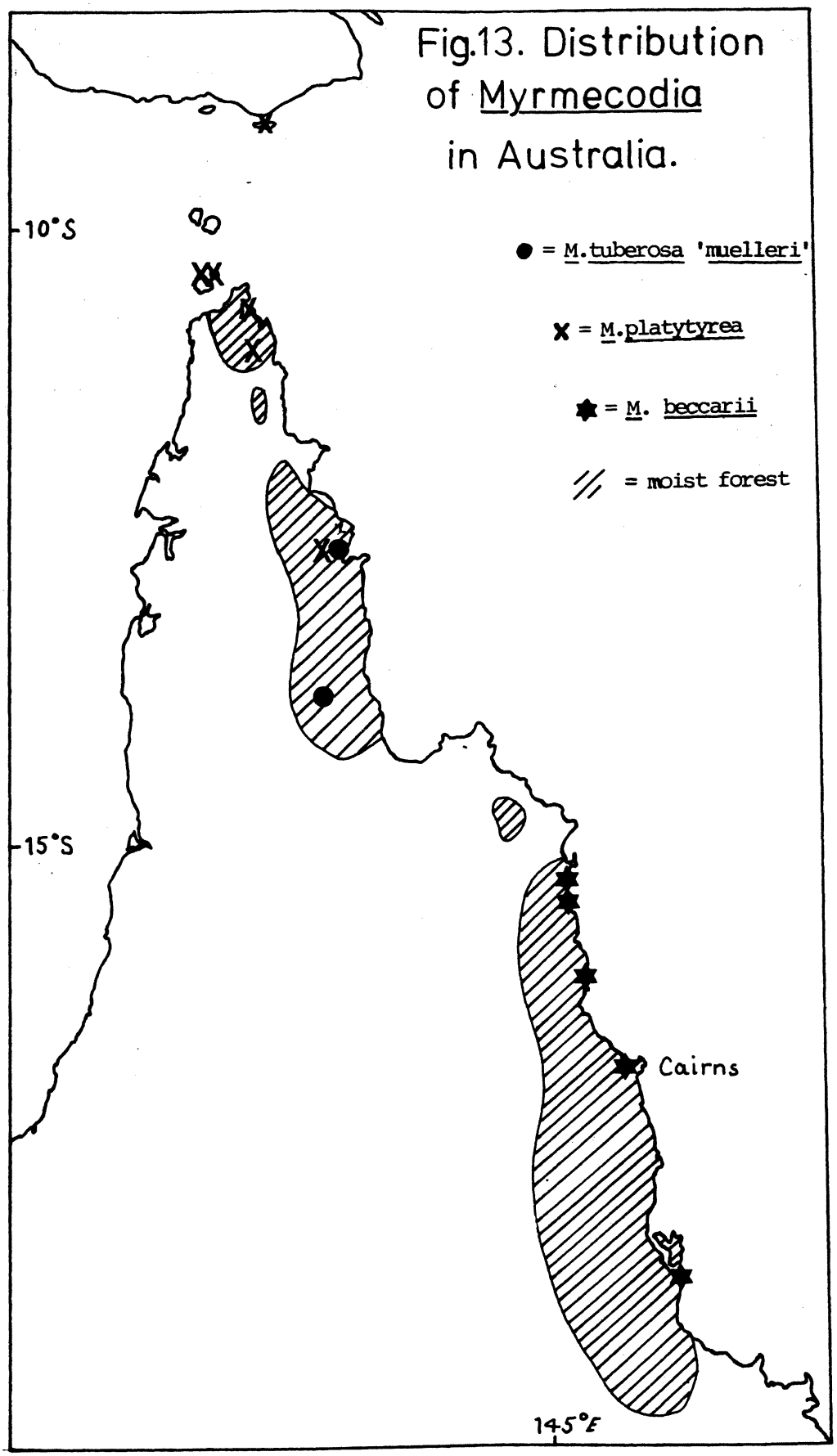


Fig.13. Distribution of Myrmecodia in Australia.
10°S
15°S
● = M.tuberosa 'muelleri'
✕ = M.platytyrea
★ = M. beccarii
// = moist forest
Cairns
145°E

Fig.13.

in rainforest areas midway up Cape York, while M. platytyrea occurs in the savanna areas of northern Cape York and the Torres Straits Islands.

VI. Delimitation of the species and infra-specific taxa

1. INTRODUCTION

2. THE OCHLOSPECIES MYRMECODIA TUBEROSA AND ITS SATELLITE

   a) General

   b) M. tuberosa north and west of New Guinea

   c) M. tuberosa on mainland New Guinea

   d) M. tuberosa on the islands east of New Guinea

3. POLYTYPIC AND VARIABLE SPECIES OF MYRMECODIA

   a) Introduction

   b) M. albertisii and its satellite M. angustifolia

   c) M. erinacea

   d) M. melanacantha

4. GROUPS OF CLOSELY RELATED SPECIES OF MYRMECODIA

   a) M. platytyrea / M. pendens / M. sterrophylla

   b) M. archboldiana / M. brassii

   c) M. longissima / M. oblongata

5. TAXONOMICALLY ISOLATED SPECIES OF MYRMECODIA

   a) M. pendula

   b) M. wauensis

   c) M. lamii

   d) M. pteroaspida

   e) M. hydnostipula

6. DELIMITATION OF THE SPECIES OF HYDNOPHYTUM

7. DELIMITATION OF THE SPECIES IN THE SATELLITE GENERA

   a) The species of Myrmephytum

   b) The subspecies of Anthorhiza

   c) The species of Squamellaria

1. INTRODUCTION

Delimitation of the species of Myrmecodia has not been a straight-forward task. This is the result of many factors; as indicated in Chapter I, collection and preservation of these plants is not easy and so duplicates are few and tubers and flowers are often missing. A considerable number of early collections have been entirely lost. Almost nothing is known of the phenotypic variability of the characters, but there are indications that the development of the spines for instance may be affected by humidity.

At one stage in the work I thought it would be possible to subdivide the genus on the basis of the clypeoli and the branching of the spines. These characters are not, however, correlated with pollen and other floral characters. Since natural groupings have not been identified, the species are arranged here according to the nature of their variation and their degree of similarity to their inferred relatives. The most variable species is described first; then the other variable species, then groups of closely related species, and finally taxonomically isolated species.

2. THE OCHLOSPECIES MYRMECODIA TUBEROSA AND ITS SATELLITE

a) General

The plants which are here treated as one species, M. tuberosa, were formerly divided into 21 species. They cover an area from Indochina to Australia. Examination of the specimens has shown that we are dealing with a continuum comprising considerable morphological variation. The variation though, does not fall into a pattern of ecogeographically replacing units. This species is therefore an example of an ochlospecies (White, 1962).

One of the patterns that occurs frequently in ochlospecies is that a variant from one area is matched by specimens from a quite distant region, which appear likely to have arisen independently from the same basic stock. An example of this is found in Sumatra and Sulawesi. Some of the specimens from these two widely disjunct areas resemble each other closely in clypeolus and leaf characters. On Siberut Island, off Sumatra, this variant

forms a small, isolated population (Fig. 14a) while in Sulawesi it forms part of a continuum with a wide range of leaf shapes (Fig. 14b), see also Chapter XVI 2b. A similar case involves the large leaved specimen from an island off Peninsular Malaysia (Fig. 14c), which is more similar to collections from the Solomon Islands than any others. In view of these wide disjunctions, and the variability of the species elsewhere, it appears that these are probably cases of polytopic evolution. In this type of situation it is impossible to construct a series of taxa which can be keyed out morphologically and are monophyletic.

Another pattern which occurs in ochlospecies, and which makes them intractable, is when there is a continuum of variations in which forms which might be named account for less than 80% of the collections. This kind of situation is found in M. tuberosa 'muelleri' in New Guinea.

In this thesis formal subspecific or varietal names are not proposed as the true status of the variants is not clear. Some of the variants may later be found to be sufficiently sharply defined to require formal definition. Others are continuous with each other, with broad areas of overlap, or are polytopic. Field studies of each variant are needed before their relationships can be understood. In the meantime, informal 'nicknames' are given to the different variants. These mostly follow previous specific epithets, but two new names are added for forms which have not previously been recognized. This informal treatment is similar to that used by Duvignaud and Brenan (1966) for Cryptosepalum moraviense.

b) M. tuberosa north and west of New Guinea

North and west of New Guinea M. tuberosa varies considerably, but without obvious pattern, in clypeolus, spine and leaf characters (Fig. 14). Time did not permit analysis of floral characters and also a certain amount of the relevant herbarium material has not been seen (e.g. that from Manilla), therefore, the present treatment is provisional, though it is unlikely that the picture will be substantially changed by further work. The material from this area is here all referred to as M. tuberosa 'tuberosa'. Some of the variants within this area are however rather distinct and it is possible

Fig. 14. Myrmecodia tuberosa 'tuberosa'. Map showing localities and leaf silhouettes of a representative sample of collections of M. tuberosa 'tuberosa'.

Variants mentioned in the text are marked as follows:-

a = variant on Siberut Is.

b = variant on north eastern Sulawesi

c = variant on Anamba Is.

l = variant on Lesser Sunda Is.

Type localities are marked as follows:-

T ap = M. apoensis

T ar = M. armata

T g = M. goramensis

T k = M. kandariensis

T m = M. menadensis

T r = M. rumphii

T si = M. sibuyanensis

T so = M. sorsogonensis

T u = M. urdanetensis

Imprecise localities are marked by a cross.

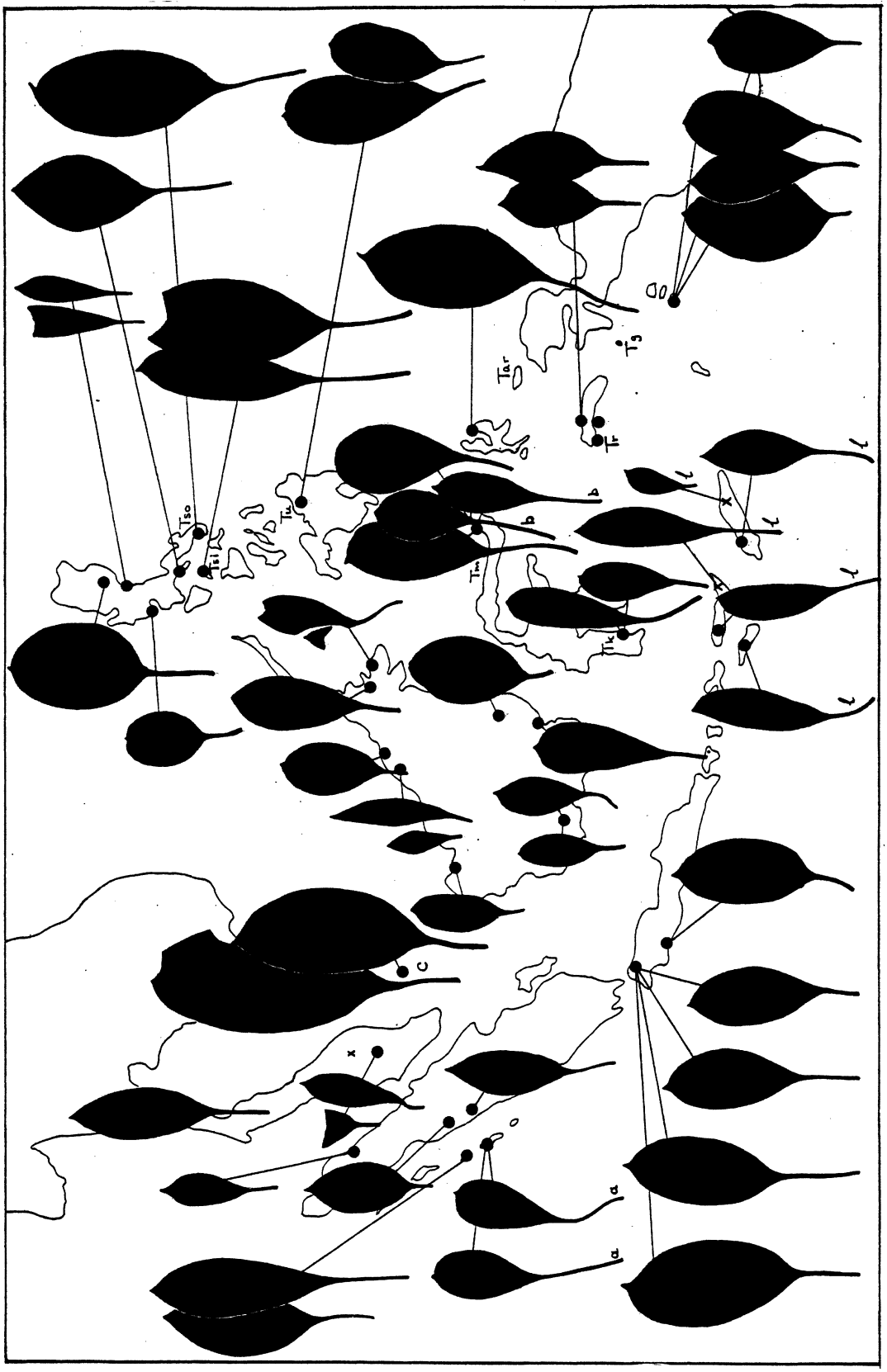


Fig. 14.

that further study may show that they deserve taxonomic recognition. For instance, the clypeolate form with slender, obovate leaves from Siberut Island off Sumatra, and the form with narrowly elliptic leaves from the Lesser Sunda Islands (Fig. 14 l).

c) M. tuberosa on mainland New Guinea

Within New Guinea the variation was examined and a simplification of the analysis showing the characters which gave the best correlation is shown in Fig. 15. The spines and degree of development of the bracts are variable, but do not correlate well with each other or with other characters.

Vegetation patterns in New Guinea are not simple; large changes in rainfall and seasonality may occur over short distances. It is therefore difficult to ascertain how far a morphological change is correlated with environmental changes. It is also true that where such correlation does occur one would expect the pattern of replacement to be complex.

There are several examples of parallel, polytopic evolution within the species. These involve characters of leaf-shape and size and development of the clypeoli. Unfortunately, insufficient is known of the environments of the areas they come from to indicate whether parallel forms occupy comparable habitats.

The clearest morphological correlation is between spathulate leaves and raised areas on the tubers surrounded by entrance holes (Fig. 15). This variant, M. tuberosa 'versteegii', is ecologically restricted to rainforest. Another variant with a clear ecological preference is M. tuberosa 'oninensis' which is found in the coastal savannas of southwest New Guinea. It is characterized by rather long, slender petioles, narrow laminae and silvery grey tubers (Fig. 26, Chapter XVI 2e).

Six other species belonging to this complex were formerly recognized on mainland New Guinea. However, their delimitation is not sharp and only two named variants are maintained here. M. tuberosa 'pulvinata' is distinguished by its club like spines, well-developed bracts and broadly elliptical leaves. Flowers from three plants all have an unusual arrangement of the

Fig. 15. Myrmecodia tuberosa in New Guinea and the Solomon Islands. Map showing leaf silhouettes and ideographs at the localities of the collections. The different variants are marked as follows:-

D = M. tuberosa 'dahlii'

Ma = M. tuberosa 'manusensis'

Mu = M. tuberosa 'muelleri'

O = M. tuberosa 'oninensis'

P = M. tuberosa 'pulvinata'

S = M. tuberosa 'salomonensis'

V = M. tuberosa 'versteegii'

One specimen shown is a type, it is marked T.

The ideographs show variation in the following characters:-

○ = Bracts not conspicuous

◑ = Bracts filling alveoli

● = Bracts forming cushions extending outside the alveoli

ȣ = Raised areas on the tubers surrounded by arcs of entrance holes.

○ = Spines absent or sparse

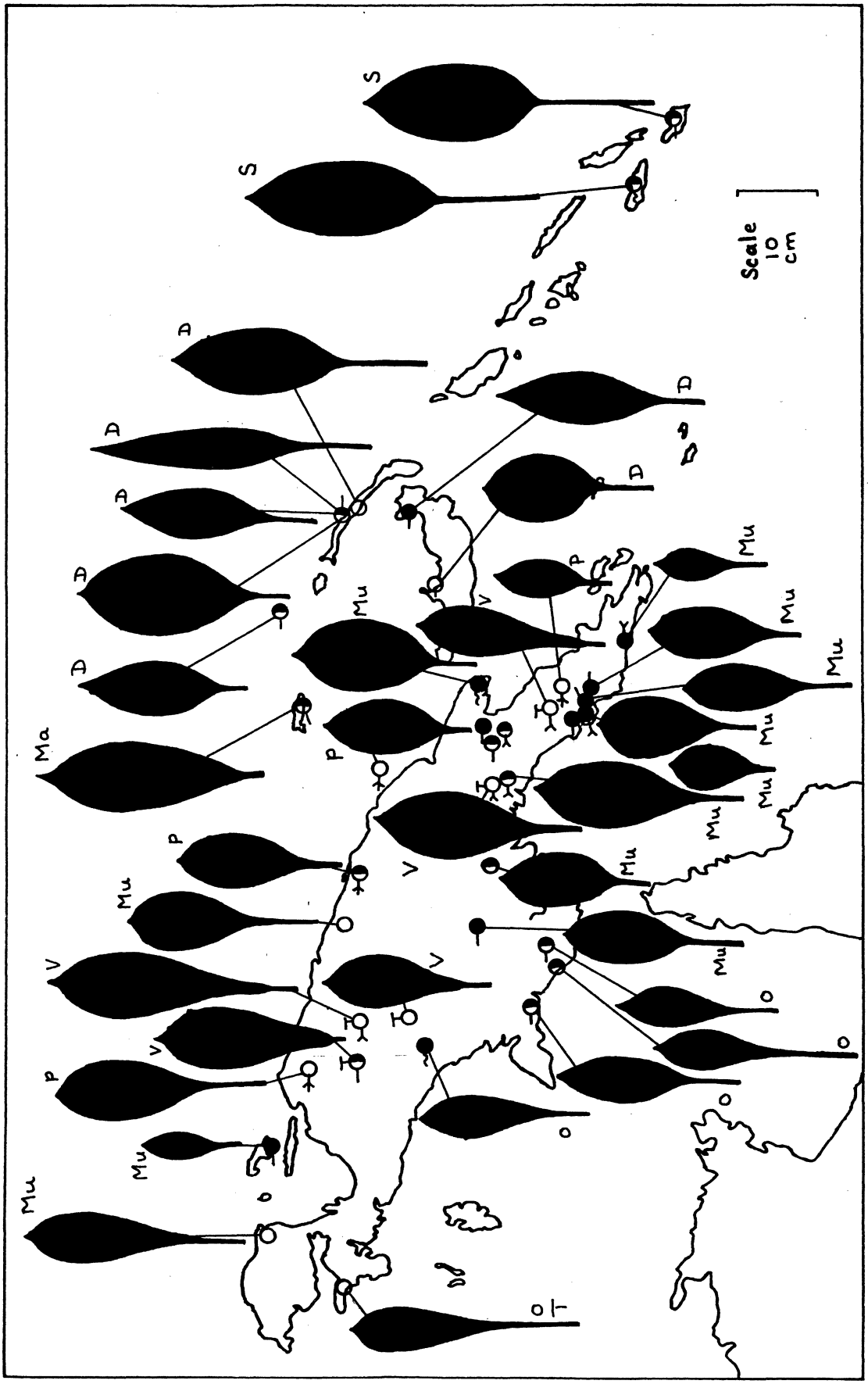
—○ = Spines mostly simple

≻○ = Spines mostly branched

✦○ = Spines mostly club-like

∿○ = Spines mostly sinuate.

(The spine symbols are shown at different angles where the ideographs are too close for them to be in the usual position).


S
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V
V
V
V
O
O
O
O
O
O
O
Scale
10
cm

Fig. 15.

ring of hairs, anthers and stigma all being placed close together at the base of the corolla tube. The pollen is also consistent (Fig. 27).

The remaining material of M. tuberosa also sometimes has the bracts filling the alveoli and is also variable in respect of its spine branching and size, honeycombing and flower and pollen characters (see Chapter XVI 2d). The name M.paucispina referrred to a rainforest form with few spines and rather large leaves. M. bullosa had pronounced honeycombing and weak spines. These and other combinations are not however consistent and the whole is referred to here by the name M. tuberosa 'muelleri'. This variant extends round large parts of mainland New Guinea and also into northern Cape York, Australia.

d) M. tuberosa on the islands east of New Guinea

East of mainland New Guinea, M. tuberosa extends through the Bismarck Archipelago into the Solomon Islands. Three moderately distinct forms occupy different island areas. In New Britain and New Ireland there is a form with moderate sized (usually less than 25 cm) leathery leaves, no clypeoli and usually one stem (M. tuberosa 'dahlii'). On Bougainville and the Solomon Islands there are plants with larger (to 36 cm) leathery leaves and rather distinct clypeoli (M. tuberosa 'salomonensis', Fig. 28). Finally on Manus Island there is a form with broadly obovate, thin leaves, short petioles, indistinct clypeoli and several stems (M. tuberosa 'manusensis', Fig. 29). The last two variants both have two vesiculate pollen with large reticulation, but in M. tuberosa 'salomonensis' the reticulation is broken (Plate 2d), this is a unique character. The morphological separation between M. tuberosa 'dahlii' and M. tuberosa 'salomonensis' is not sharp in eastern New Ireland (Fig. 15).

The variants on islands east of New Guinea appear to be geographically rather than ecologically defined.

The satellite of M. tuberosa, M. beccarii, differs in its small, fleshy leaves, freely branched stems and massive, fleshy tuber, as well as in floral characters (Fig. 30). There are no morphologically intermediate specimens, M. beccarii occupies an area outside the ecological and geographical range of

M. tuberosa (Fig. 13). Its thick leaves and fleshy tuber adapt it for the highly seasonal rainfall and probably high salt levels in its mangrove environment (Fig.12 , overlay 1).

3. POLYTYPIC AND VARIABLE SPECIES OF MYRMECODIA

There are five moderately variable species of Myrmecodia, of which two are lowland, two montane and one extends from lowland savanna to montane forest. This last (M. albertisii) is also the only one which shows geographic disjunctions and complete morphological separation between the forms, and is therefore divided into subspecies. In the other four species which are rather variable, clear-cut geographical replacement by the different variants is lacking, so subspecies are not recognized. Two of these four species are closely related to each other and are therefore considered in the next section (these are M. platytyrea and M. pendens).

b) M. albertisii and its satellite M. angustifolia

As shown ir Fig. 16 a, k and d there are three discrete populations of M. albertisii which do not overlap in their range of leaf-shape, though they do form an almost continuous series. The stoutness of the spines and the shape of the tubers also differ between the three populations which therefore form satisfactory subspecies. Floral and pollen characters in M. albertisii ssp. albertisii vary according to whether they are long or short styled (Plate 3a and b). Floral variation in the other subspecies falls within that of M. albertisii ssp. albertisii.

The ecological conditions occupied by the three subspecies differ markedly. The type subspecies is found in the low lying Melaleuca savannas of western Papua New Guinea, subspecies koiariensis occupies rather dry mid-montane forest of the Central Province in the rainshadow of the Owen Stanley Range. Between these two areas, inland of the Gulf of Papua, lies an expanse of rainforest. The final subspecies (dentrecastensis) is found in the upper montane forests of the D'Entrecasteaux Islands east of New Guinea. These three subspecies show a gradation in leaf shape from large and broadly elliptic in the type, through smaller, more narrowly elliptic, to narrowly lanceolate in the upper montane

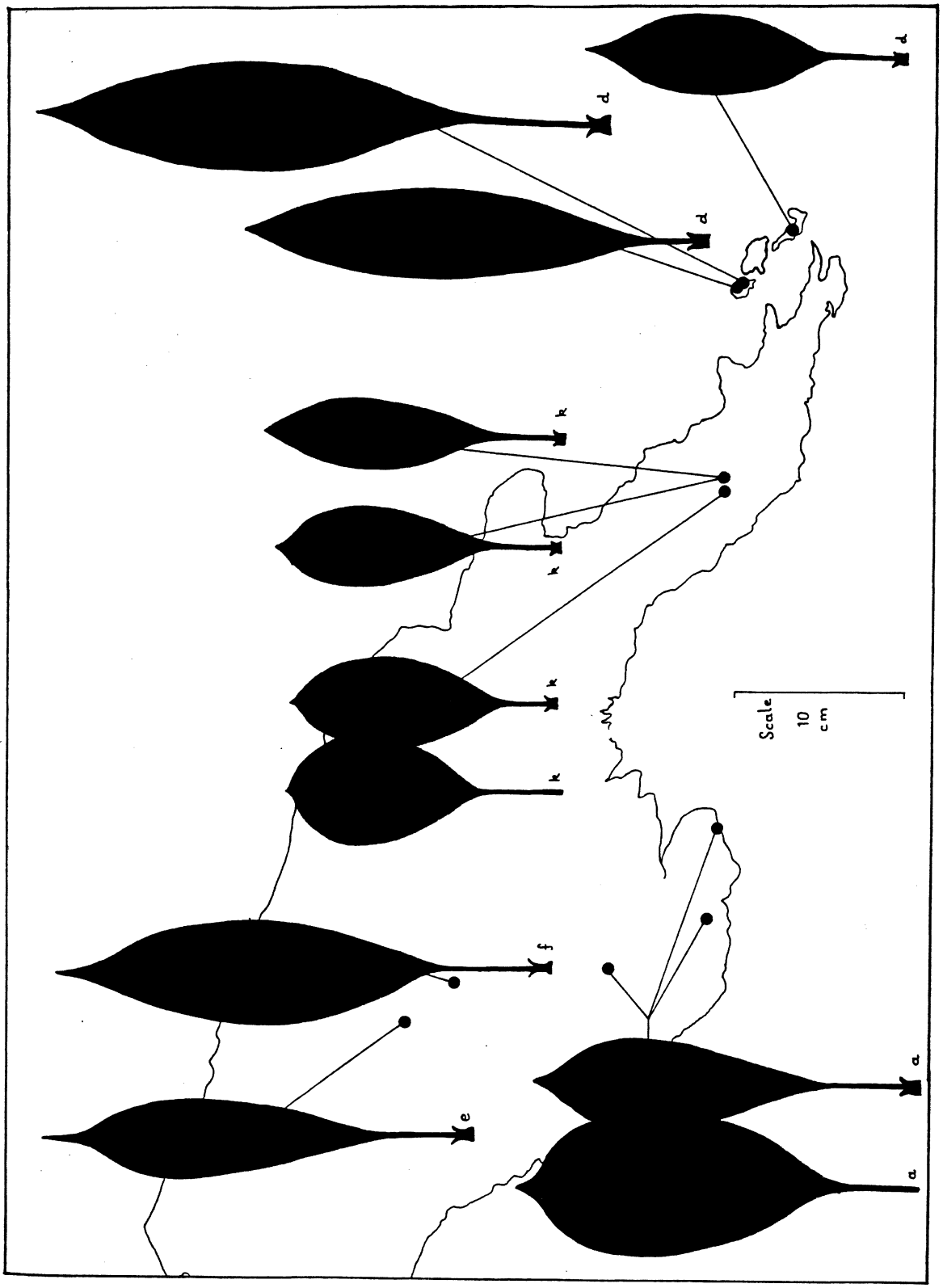


Fig. 16. Myrmecodia albertisii. Map showing localities and leaf and stipule silhouettes of the three subspecies and possibly related variants. The three subspecies are:- a = M. albertisii ssp. albertisii; two leaves showing the range of variation from the three known localities; k = M. albertisii ssp. koiariensis; d = M. albertisii ssp. dentrecastensis. The two possibly related collections which share similar spine and stem characters are e = Kalkman 4268 and f = NGF 31855.

Fig. 16.

subspecies (Fig. 16). This is a trend in leaf shape paralleled repeatedly in the genus.

The species M. angustifolia is known only from fragmentary specimens, but is regarded as a satellite of M. albertisii as it shares the stem and spine characters. It differs in its linear leaves and is widely allopatric (Fig. 32).

Two other collections possibly belong in this group (Fig. 16 e and f). They both have narrowly acuminate leaves, narrow stipules and stouter spines; the floral characters differ somewhat. These collections are geographically and ecologically isolated and their final status has not been decided (see Chapter XVI 3 a i).

c) Myrmecodia erinacea

This is a quite widespread species in lowland Irian Jaya. It is defined by a unique combination of simple spines round the aveoli and often branched spines elsewhere on the stem, and by its bordered pollen (Fig. 33; Plate 5c). It is however variable in leaf-shape, tuber size and in the spines on the tuber. Four earlier species are united here (Fig. 17). Beccari recognized three species (M. alata, M. aruensis, and M. erinacea) which are morphologically and geographically isolated. More recent collections, especially those from inland sites, suggest that we are dealing with a plant which is phenotypically variable or in which the pattern of replacement of the variants is complex. Three different flower types have been observed (Fig. 33) but it is not known whether these forms are associated with the different leaf shapes, replace one another, or possibly form a tristylous system. These collections are regarded here as forming a species, it is possible however, that further work may suggest that they are a group of related species, or that infraspecific variants should be recognized.

M. erinacea is an exception to the rule that is the montane forms which have long, narrow leaves, as both narrow and broader leaved forms occur at low altitude, sometimes in the same locality.

d) M. melanacantha

This is a highland taxon from a relatively restricted part of Papua New

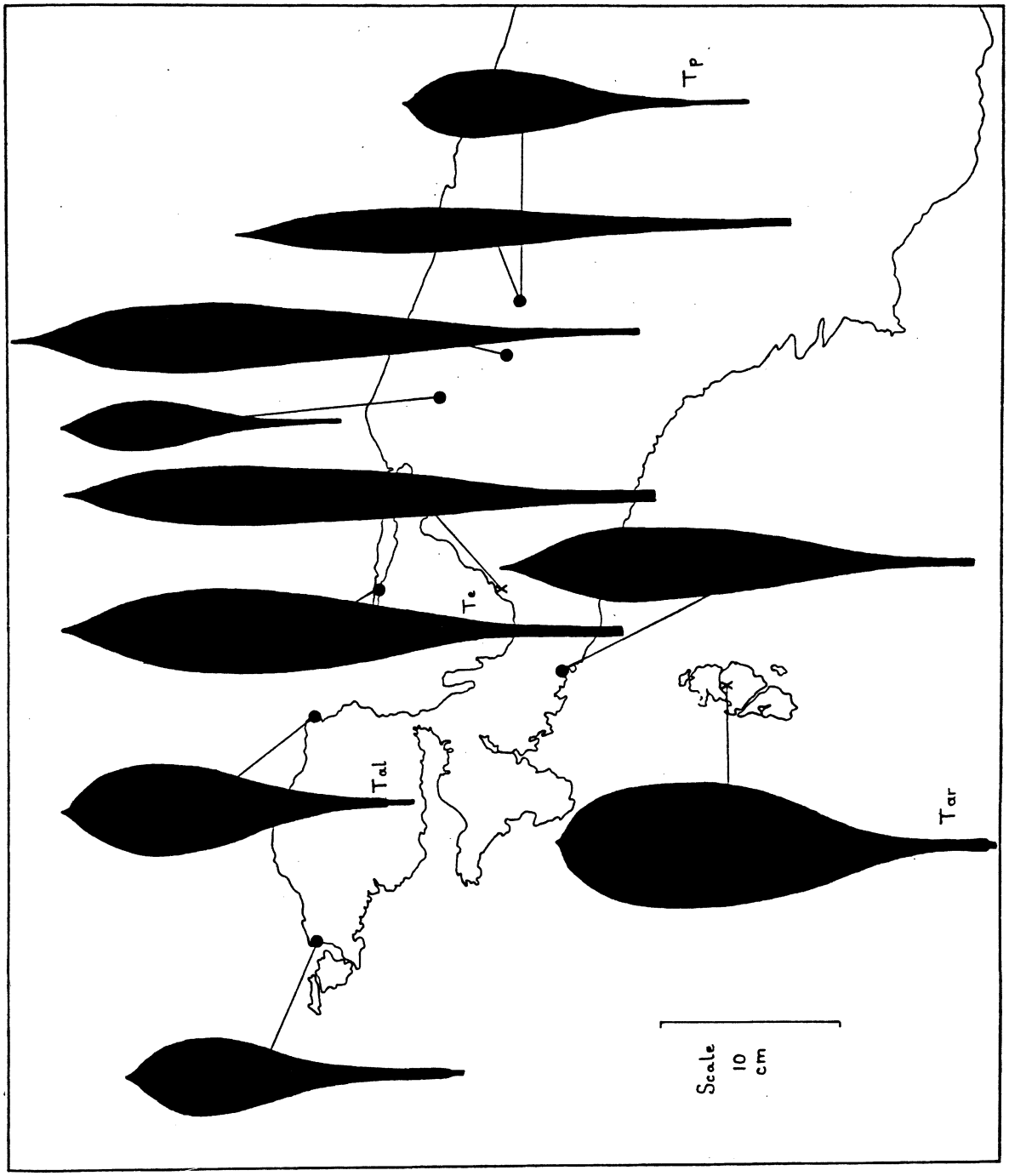


Fig. 17. Myrmecodia erinacea. Map showing localities and leaf silhouettes of all specimens of M.erinacea. The type specimens are as follows: T al = type of M.alata Becc.; T ar = type of M. aruensis Becc.; T e = type of M. erinacea Becc.; T p = type of M. prolifera Merr. and Perry. Imprecise localities are marked by a cross.

Fig. 17.

Guinea. Like the last species, it is clearly defined by stem and spine characters. In this case the alveoli have swollen rims bearing massive, simple black spines, and there are tunnels connecting the alveoli to one another and to the tuber chambers (Chapter XVI. 3c). Again the leaves vary considerably and without following a geographical pattern, Fig. 18.

4. GROUPS OF SPECIES IN MYRMECODIA

Within the genus there are a number of pairs or small groups of species which can be seen to be related to each other. In some cases further collecting may lead to some of these taxa being sunk, but there is insufficient evidence for this at present.

a) M. platytyrea/M. pendens/M. sterrophylla

This group represents a large number of plants extending over the whole of New Guinea, from lowland savanna to upper montane forest. It is united by the presence of well defined clypeoli bordered with simple spines. It comprises one widespread lowland species, one quite widespread mid-montane species, and one local montane species. The lowland species, M. platytyrea, occurs throughout New Guinea; it is found in both rainforest and savanna and is rather variable (Fig. 34, Chapter XVI 4a). Beccari (1884: 115-116) divided it into two species, but the characters he used, leaf and clypeolus shape do not give good separation (Fig. 19). There are nevertheless differences between savanna and rainforest plants, especially in the tubers.

While M. platytyrea has broadly elliptic leaves similar to those of many variants of M. tuberosa, its two montane relatives have narrowly oblanceolate to linnear leaves. Unfortunately these two species are known from only a few specimens. M.pendens occurs in two isolated localities in Papua New Guinea (Fig. 35). It is distinguished by the narrowly oblanceolate leaves, white petioles and midribs and white ridges on the tuber. The second montane species, M. sterrophylla, shares the long narrow leaves, though they differ in shape and texture. It is found in the western part of New Guinea, where it comes quite close to some M. platytyrea in leaf-shape (Fig. 19).

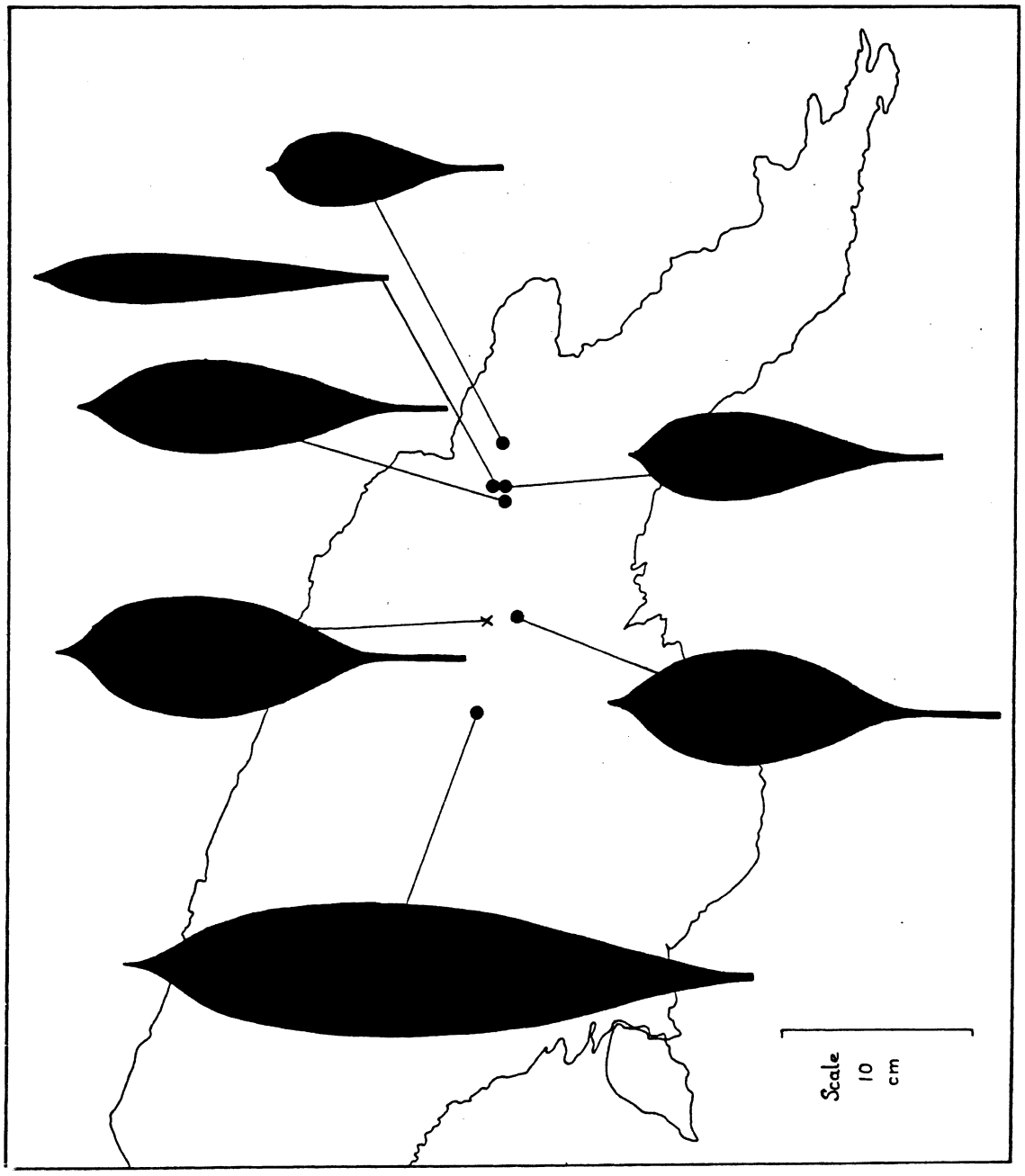


Fig. 18. Myrmecodia melanacantha. Map showing localities and leaf silhouettes of most of the specimens of M. melanacantha sp. nov. Imprecise localities are marked by a cross.

Fig. 18.

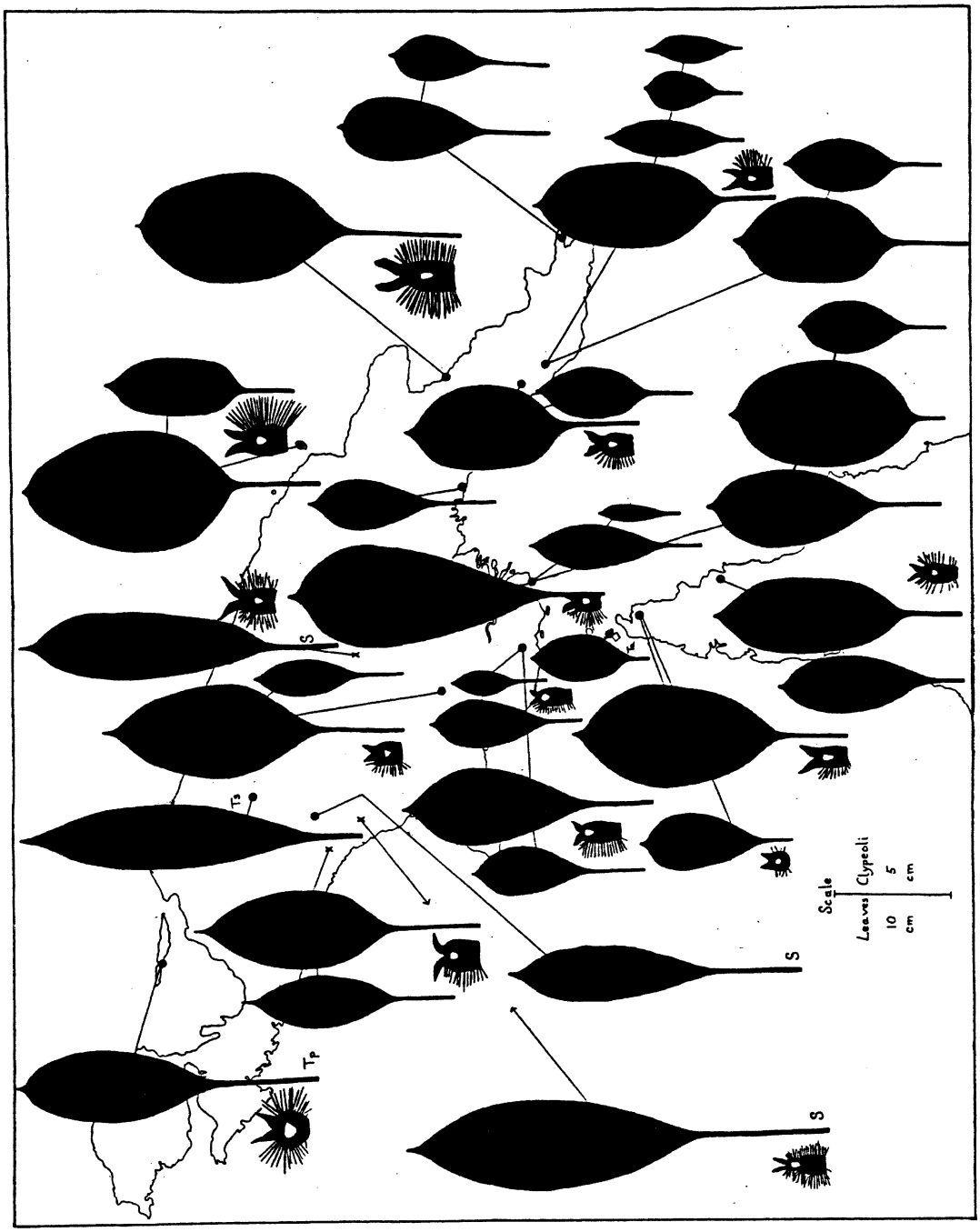


Fig. 19. Myrmecodia platytyrea and M. sterrophylla. Map showing localities and leaf and clypeoli silhouettes of most specimens of the two species. All silhouettes belong to M. platytyrea unless marked S, in which case they belong to M. sterrophylla. Largest and smallest leaves are shown where there is a significant difference in shape. Types are shown as follows: Ta = type of M. antoinii Becc.; Tp = type of M. platytyrea Becc.; Ts = type of M. sterrophylla Merr. and Perry. Imprecise localities are marked by a cross.

Fig. 19.

b) M. archboldiana/M. brassii

This pair of species is also clypeolate, but differs from the last group in floral characters. As shown in Fig. 20 these two species are rather local, sympatric species from the highlands of Irian Jaya. The solitary collection of M. brassii appears close to M. archboldiana in the light of recent collections (especially Hope ANU 16059, Fig. 20h). Examination of the floral characters of M. brassii, not possible with the present limited material, and ecological information, is necessary before these two species can be fully understood (Figs. 36 and 37).

c) M. longissima/M. oblongata

These two species are known from very few specimens. They differ conspicuously in leaf-shape, but the stem and clypeoli suggest they are closely related (Fig. 38).

5. TAXONOMICALLY ISOLATED SPECIES OF MYRMECODIA

These are species which do not have apparent affinities with other taxa; some are morphologically rather distinctive. All five are montane.

a) M. pendula

This quite widespread and well represented species is found in the mid-montane agricultural valley of central Papua New Guinea, often growing in Casuarina and Castanopsis. Its branched spines, tubers and floral characters suggest a possible relationship with M. albertisii, but the leaf shape is quite different (Fig. 39). It is interesting for being remarkably uniform over its entire range (Fig. 21).

b) M. wauensis

Known from several collections in a restricted area, this montane species is highly distinctive morphologically. The stellate spines, bordered pores of the pollen grains, blue flowers and narrowly lanceolate crinkled leaves (Fig. 40) might suggest an affinity with M. erinacea. The simple spines round the alveoli in the latter species leave the significance of this resemblance uncertain. They are also widely disjunct.

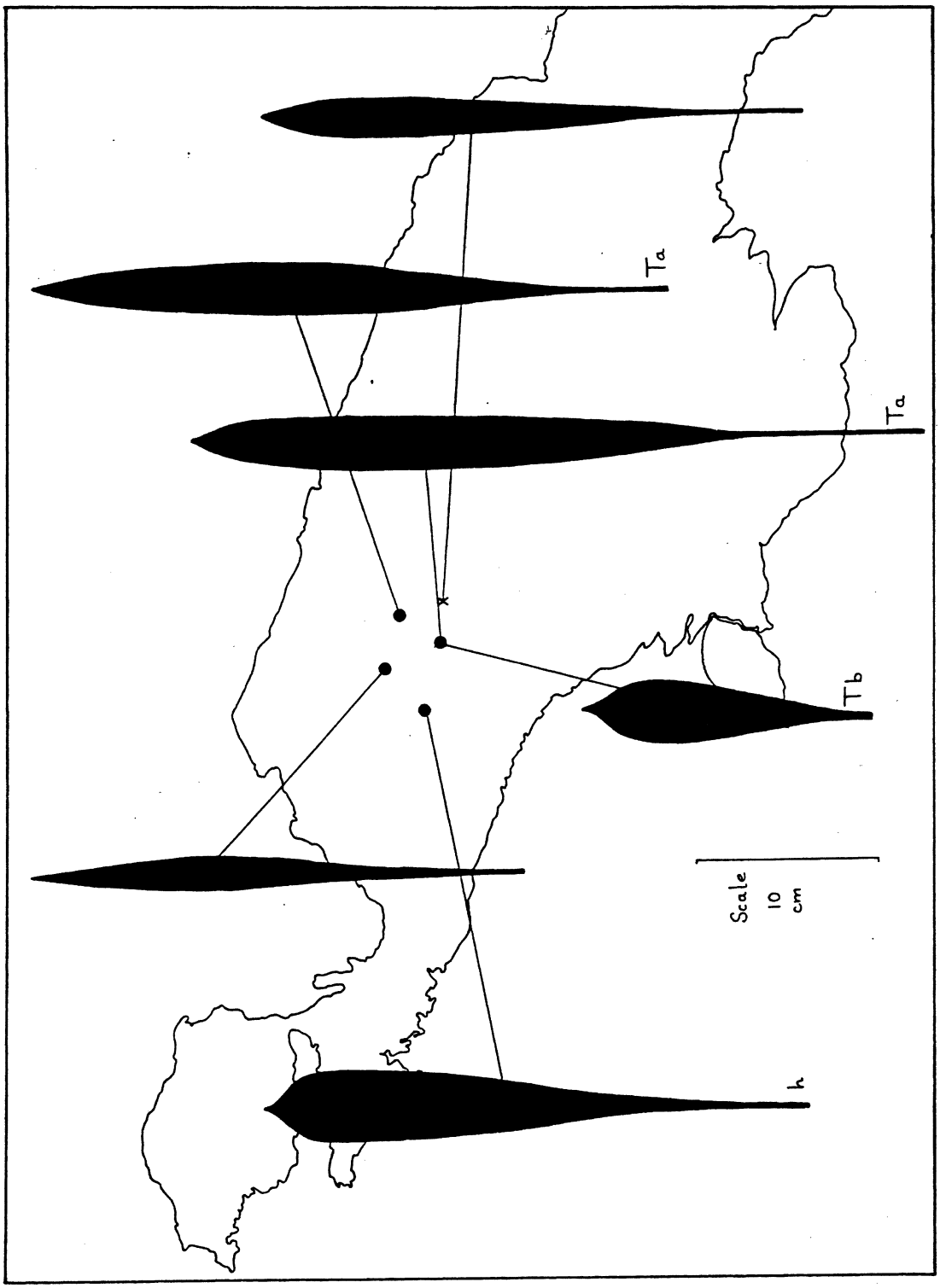


Fig. 20. Myrmecodia archboldiana and M. brassii. Map showing all localities and leaf silhouettes for these two species. Imprecise localities are marked by a cross. Types are as follows: Ta = type of M. archboldiana Merr.& Perry; Tb = type of M. brassii Merr. & Perry; h = Hope ANU 16059.

Fig. 20.

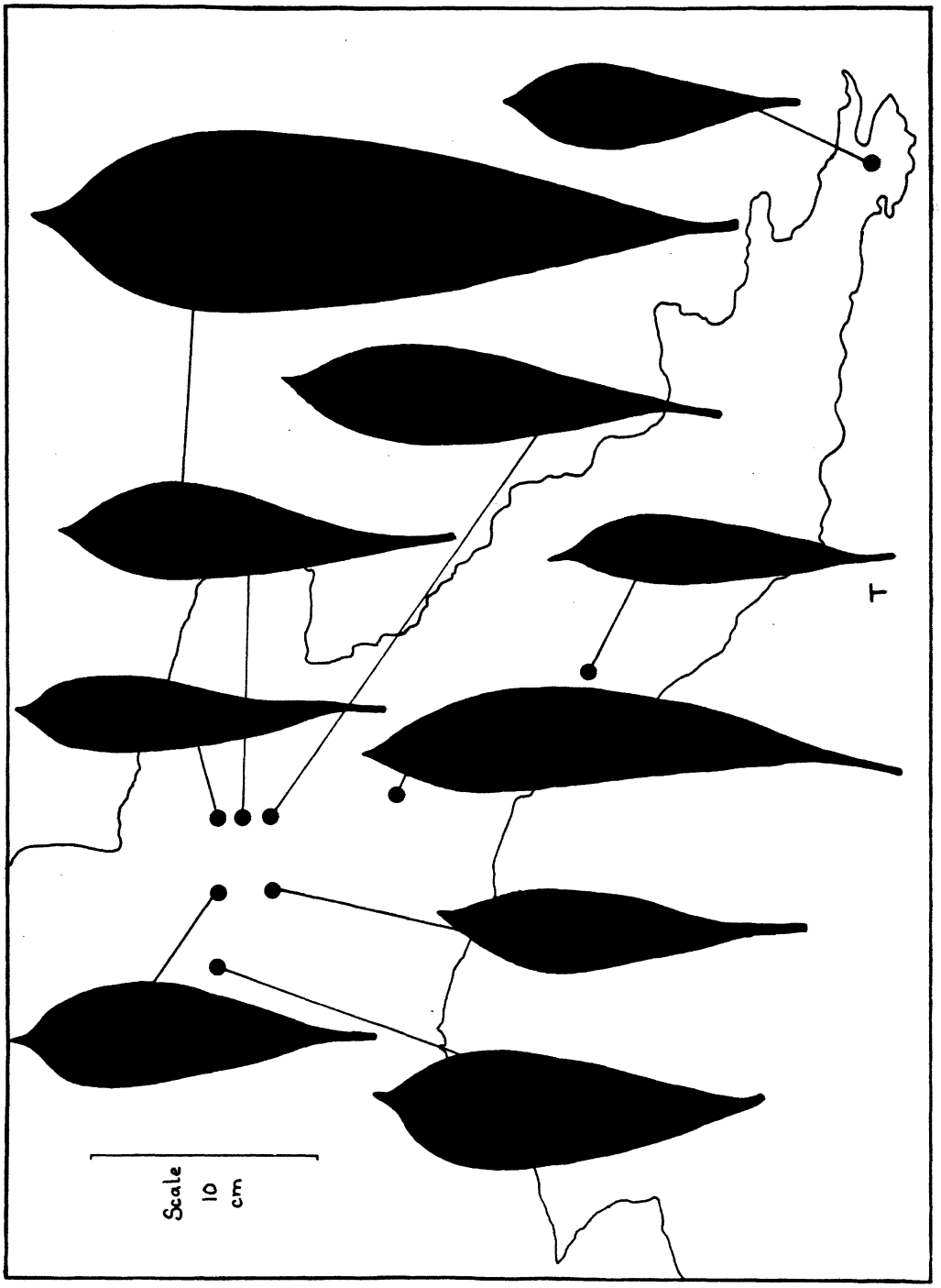


Fig. 21. Myrmecodia pendula. Map showing localities and leaf silhouettes of most collections. T = type specimen .

Fig. 21.

c) M. lamii

This large striking plant is distinguished by the broadly winged clypeoli and numerous stems (Fig. 41). Floral characters suggest a possible relationship with the sympatric and also clypeolate M. archboldiana.

d) M. pteroaspida

The two collections of this species resemble the previous one in the broadly winged clypeoli, but floral differences, notably the 2-vesiculate pollen, and the different spines on the tubers of M. lamii indicate an unrelated convergence (Fig. 42).

e) M. hydnostipula

This species is known from only two collections at one locality, which look superficially dissimlar due to different degrees of development of the branched spines. The stipules which do not split between the petioles, the bilobed stigma and 3-porate pollen with fine reticulation, are all characters resembling Hydnophytum. So this species appears to some extent to be intermediate between the two genera. Its affinities within Myrmecodia are not clear.

6. DELIMITATION OF SPECIES OF HYDNOPHYTUM

As time did not permit a detailed study of this genus only a few remarks are made here.

Beccari recognized subgenera in Hydnophytum based on the inflorescence. This remains one of the most interesting and conspicuous modifications in the genus. The delimitation is rarely sharp, however, as the degree of condensation of the peduncle and inflorescence rachis appears to vary with the age and vigour of the stem. H. guppyanum (and its close relatives H. kajewskii and H. dahlii) are distinctive in the solitary state of the inflorescence and its branching (see Chapter IV 6a).

Then there are plants with paired, pedunculate and sometimes branched inflorescences. Although many names have been applied to this group, it may comprise a single variable taxon. These forms mostly have rather broadly elliptic leaves and occur in rainforest.

All the other species have the inflorescence rachis reduced to a mound.

In most species the inflorescence is paired; they include the very variable H. formicarum, which is found mainly in lowland areas throughout Malaysia, Indonesia and the Philippines. Around the coasts of New Guinea, there are several variable, fleshy-leaved species. In montane New Guinea there are again numerous small leaved forms which do not appear to fall readily into species. Finally there is a group of species in Fiji with solitary inflorescences on mounds (H. grandiflorum et aff.). This group also has long, narrow corolla tubes and capitate stigmas.

Besides these rather broad groupings there are several more local species which are sharply defined. For instance, in the Bismarck Archipelago and eastern Papua New Guinea there is a lowland species with slender stems and small thin ovate leaves (H. hellwigii) which occurs sympatrically with other species. There is a coastal species characterised by its leathery, cordate leaves (H. ovatum), and an inland species with winged stems (H. tetrapterum). Also three rather distinct taxa are marked by strong development of the bracts. Most important of these is a group of collections from the D'Entrecasteaux Islands, but they have not been named yet.

7. DELIMITATION OF SPECIES IN THE SATELLITE GENERA

a) The species of Myrmephytum

The two species of Myrmephytum from the Philippines and Sulawesi are only known to be clearly distinguished on leaf characters. They are not sympatric and possibly should be regarded as subspecies. The species from New Guinea is distinguished by its shortened internodes, larger lamina, longer petioles and denser spines (Fig. 22).

b) The subspecies of Anthorhiza

Although only one species of this genus is recognized here, it includes two geographically separated populations which differ in the presence or absence of spines on the tuber, the frequency of secondary branching on the stem spines (Fig. 7s,t), the shape of the leaves, the number of lateral nerves and the length of petiole (Fig. 23). Floral differences are obscured by the small number of flowers available and the presence of heterostyly.

c) The species of Squamellaria

In this genus leaf characters of size and shape distinguish the three species. Only one of the species is also characterised by venation and minor floral features. These species are sympatric, or occupy adjacent islands in a restricted area. It is possible that they should be regarded as subspecific variants (Fig. 24).

VIII. Delimitation and relationships of the genera

1. INTRODUCTION

2. CHARACTERS DISTINGUISHING THE GENERA

a) Characters separating Hydnophytum from Myrmecodia

b) Characters separating Myrmephytum

c) Characters separating Anthorhiza

d) Characters separating Squamellaria

3. FREQUENCY AND IMPORTANCE OF CHARACTERS USED TO DELIMIT THE GENERA

4. PARALLELISM BETWEEN THE GENERA

5. SUPRA-GENERIC RELATIONSHIPS

a) Position in the Rubiaceae

b) Coherence of the genera as a subtribe, the Hydnophytinae

c) Links with other Psychotrieae

1. INTRODUCTION

In this chapter evidence is presented for the recognition of five genera of rubiaceous ant-epiphytes:- Hydnophytum, Myrmecodia, Myrmephytum, Anthorhiza and Squamellaria. The unique characters found in these genera and the reticulate nature of the variation between them suggests that they should be united as a subtribe of the Psychotrieae - the Hydnophytinae.

2. CHARACTERS DISTINGUISHING THE GENERA

a) Characters separating Hydnophytum from Myrmecodia

Myrmecodia is distinguished from Hydnophytum by numerous characters both vegetative and floral, though all the characters break down in some cases. In Hydnophytum the tuber is usually flattened along its axis, and is unridged, whereas in Myrmecodia the tuber is normally elongate and ridged (an exception is M. hydnostipula). The cavities are not usually differentiated into chambers in Hydnophytum, but the central and peripheral cavities may be distinctive. The latter does not occur in Myrmecodia. The high degree of differentiation of the

cavities in some species of Myrmecodia and the associated characters such as pores and arcs of entrance holes are restricted to that genus.

Well-developed spines are absent from Hydnophytum, though erect adventitious root may be found over the tuber surface in some species under humid conditions. Spines are almost always present on Myrmecodia tubers, though some individuals of M. tuberosa from New Guinea and Moluccas are an exception.

The internodes of the stems of Hydnophytum are not reduced as is typical of Myrmecodia. The inflorescence of Hydnophytum is normally pedunculate and only rarely, and then only slightly, sunk into the stem, whereas in Myrmecodia it is always sunk and the ovaries are often initially embedded in the stem tissue at the base of the alveoli. The corolla is usually distinctive, for in Hydnophytum the lobes have only minute unci at the tips, and at anthesis bend back, leaving the anthers and stigma exserted. In Myrmecodia the unci are longer and often remain closed at anthesis; the ring of hairs may be inserted between the anthers or elsewhere in the corolla tube. The ovary is almost always 2-locular in Hydnophytum (except H. simplex) and the stigma likewise divided; while in Myrmecodia the ovary is usually more than 2-locular. In some species of Hydnophytum the corolla tube is long and narrow; probably adapted for moth pollination. In Myrmecodia the most interesting variations on the usual theme are the open, conical, blue flowers of M. wauensis. The pollen differs between the genera being typically larger, vesiculate and variable in the number of pores in Myrmecodia

b) Characters separating Myrmephytum

Myrmephytum is distinguished from the other genera by its 6-merous corolla and stamens, and the greater development of the bracts than is found elsewhere. In the other genera the corolla is always 4-merous, though the bracts are also somewhat enlarged in at least three species of Hydnophytum (particularly in six Brass collections from the D'Entrecasteaux Islands).

Myrmephytum was described as two genera by Beccari - Myrmephytum and Myrmedoma, which are separated on the basis of tuber, stem and leaf characters. These are characters which distinguish Myrmecodia from Hydnophytum; Myrmephytum resembled Hydnophytum vegetatively and Myrmedoma resembled Myrmecodia. There

are, however, no correlated floral differences, and since there are vegetative intermediates, the two are probably more closely related to each other than to either of the two major genera. Myrmedoma is therefore treated here as part of Myrmephytum.

c) Characters separating Anthorhiza

This genus is characterised by the branched spines which occur among the flowers. Otherwise it shares with Myrmecodia the presence of stellate branched spines on the tuber, and with Hydnophytum several characters of the stem, leaf and stipule. Thus its inclusion in either genus would extend the range of that genus and blur the distinction between them. The unique character of the spines among the flowers and the presence of many features typical of Hydnophytum indicate that this genus is not an intermediate, but a separate line of evolution from Hydnophytum.

d) Characters separating Squamellaria

Beccari distinguished Squamellaria on the following characters: capitate, rimmed stigma; squamules in the corolla tube; the curved embryo and seed shape. To these A.C. Smith added the colpate pollen (Smith, pers.comm;1967). One species of Hydnophytum from the same geographical area (H. tenuiflorum) shares these pollen and stigma characters, so this generic distinction requires further study (Plate 7 c and d).

3. FREQUENCY AND IMPORTANCE OF CHARACTERS USED TO DELIMIT THE GENERA

It is interesting to note which characters are repeatedly significant in distinguishing the genera, as this may give an indication of adaptive radiation following the adoption of the symbiosis with the ants. Table 2 shows an analysis of whether or not characters of the tuber, stem, leaves and inflorescence distinguish each pair of genera. The conclusion is that floral characters are most often important and leaf characters least often.

4. PARALLELISM BETWEEN THE GENERA

Parallelism is not infrequent between the genera. It appears that the floral development in Myrmephytum has been followed by vegetative developments

		Tuber	Stem	Leaves	Inflorescence
Hydnophytum	Myrmecodia	✓	✓	✓	✓
Hydnophytum	Myrmephytum	✓̸	✓̸	X	✓
Hydnophytum	Anthorhiza	✓̸	X	X	✓
Hydnophytum	Squamellaria	X	X	X	✓
Myrmecodia	Myrmephytum	X	X	X	✓
Myrmecodia	Anthorhiza	✓̸	✓	✓̸	X
Myrmecodia	Squamellaria	✓	✓	✓̸	✓
Myrmephytum	Anthorhiza	X	X	X	✓
Myrmephytum	Squamellaria	✓̸	✓̸	✓̸	✓
Anthorhiza	Squamellaria	X	✓̸	✓̸	✓
	Total ✓'s	2	3	1	9

Table 2. Characters which distinguish the genera. ✓ indicates that the two genera can almost always be distinguished by characters of the given structure. ✓̸ indicates that they can sometimes be distinguished on characters of that structure, and X that they can rarely be distinguished by characters of that structure.

which parallel differences between Hydnophytum and Myrmecodia. The branched spines which are found in Myrmecodia, Myrmephytum and Anthorhiza probably evolved independently, and as they are all derived from adventitious roots, they are homologous. These three genera also have features which protect the inflorescence; but these arise from different structures and are therefore analogous, not homologous.

Where modifications are homologous it may indicate that a character can arise readily by mutation and/or that there is a selection pressure for it. Where parallel developments occur which are analogous rather than homologous, the same mutation cannot be responsible and one must suggest that a similar selective pressure has been working.

5. SUPRA-GENERIC RELATIONSHIPS

a) Position in the Rubiaceae

The presence of raphides and albuminous seeds places the ant-plant genera in the subfamily Rubioideae (Verdcourt, 1958; Bremekamp, 1966). Within this subfamily Hydnophytum is a typical member of the tribe Psychotrieae, as it is a 'shrub' with solitary, erect ovules in the two locules; the fruit is a succulent drupe, the pyrenes have a rather thin coat and the pollen is 3-porate. The inflorescence is, however, almost always axillary; this is exceptional in the Psychotrieae, where it is normally terminal or only apparently axillary.

b) Coherence of the ant-plants as a subtribe, the Hydnophytinae

The main reason for regarding the ant-plants as closely related and monophyletic is the presence of the chambered 'tuber' derived from the hypocotyl - this feature is found in no other plant. The formation of the tuber in the seedling is similar in those species of Hydnophytum and Myrmecodia which have been observed. The similarity of the basic pattern of the cavities, their anatomy and that of their warts, also suggest the tuber has evolved only once. The formation of the tuber in the satellite genera has not been studied, but the final form of the tuber lies within the range found in the two major genera.

The tuber is rarely, if ever, lacking; this is reported from two species, neither of which appears to be primitive according to the inflorescence. It is

therefore likely that in these cases the tuber is being secondarily lost.

Other characters which unite the genera are the adventitious roots which occur in all the ant-plants and become spine-like in three of the five genera. This character is not found elsewhere in the Psychotrieae, and is rare in the Plant Kingdom as a whole. A condensation of the inflorescences similar to that in Hydnophytum is found in other parts of the Rubiaceae. Various unique modifications in Myrmecodia might suggest that this genus is quite distinct from the other ant-plant genera, but they are all connected by a series of intermediates. The flowers, and particularly the fruits and pyrenes, are relatively uniform in the ant-plants. The coherence of the genera is also indicated by the presence of intermediate species which link them. For instance one species of Hydnophytum from Fiji has pollen identical to that of Squamellaria. Also there is one species and one little known variant which are intermediate in stipule and stem characters between Hydnophytum and Myrmecodia.

The parallel evolution between the genera and the reticulate pattern of variation indicate that they are a closely related group. A new subtribe, the Hydnophytinae, is therefore proposed here to include the five genera discussed above. Definitions of the subtribe and genera are given in the Taxonomic Conspectus.

c) Links with other Psychotrieae

Psychotria itself may be the genus closest to the Hydnophytinae; it shares with Hydnophytum the 2-locular ovary and 3-porate pollen without vesicles or bordered pores. In Psychotria the inflorescence is terminal, or when apparently lateral, is solitary and arises in one axil only of each leaf pair of leaves. In one species of Hydnophytum (H. guppyanum) the inflorescence is occasionally terminal but usually axillary, being solitary and central, in one axil at each node. In other species of Hydnophytum the inflorescence diverges further from Psychotria, being axillary in one axil, but is paired or if solitary is not central to the axil. The branching of the inflorescence also shows a link between Psychotria and H. guppyanum. In Psychotria the usual branching is opposite and decussate and the typical form in Hydnophytum is pseudodichotomous. It is interesting that a little known species, Psychotria dipteropoda, has axillary inflorescences.

VIII. Taxonomic conclusions and pointers for further work

Myrmecodia has proved to be remarkably complex, especially in the lowland areas. Specimens which at first appear quite distinct, were frequently later seen to be connected by intermediates to one or other of the large variable species. This suggests that proliferation of the different forms has taken place recently and that there has been relatively little extinction to eliminate the intermediates. Indeed it appears likely that evolution is still rapidly progressing in the genus.

One of the features which causes taxonomic difficulty is the common occurrence of parallel and convergent evolution. This has led to a reticulate pattern of variation in which it is often difficult to suggest a sequence in which different evolutionary steps have occurred, or to set up a natural, hierarchical, infra-generic classification.

Most of the taxa described here are based upon stem and spine characters, though the pictorialized distribution maps make use of the more labile leaf-shape. Floral characters have been difficult to make full use of because of the small number of flowers and the presence of heterostyly. Further investigation of these characters would be useful. The task of correlating morphological changes with variation in the environment has also been difficult. This is partly because information on rainfall and evapotranspiration rates is very sparse, and also because the steep terrain leads to rapid changes in climatic and edaphic conditions.

It has been found most convenient to analyse the genus provisionally into the following categories:-

One ochlospecies and a closely related satellite (M. tuberosa and M. beccarii);

One polytypic species comprising three ecogeographically replacing subspecies, and a related satellite (M. albertisii and

M. angustifolia);

Two morphologically distinctive but variable species without close relatives (M. erinacea and M. melanacantha);

Two clypeolate, variable species related to one another and to a smaller species (M. platytyrea, M. pendens and M. sterrophylla);

Two pairs of probably related, small species (M. archboldiana/M. brassii and M. longissima/M. oblongata);

Five taxonomically isolated species, which are all montane and mostly restricted in range (M. pendula, M. wauensis, M. lamii, M. pteroaspida and M. hydnostipula).

It is interesting that the other genera of the subtribe behave somewhat differently: Hydnophytum appears to have several complexes which will probably come to be seen as ochlospecies and relatively few distinctive and restricted species. The satellite genera include no ochlospecies and are generally less diverse.

The taxonomic difficulty of the group may stem not only from the current progress of evolution, but also from the particular mode of speciation. In Myrmecodia it appears likely that increasing protection of the ants and of their access to the inflorescences may have reduced the access for pollinators. It would be interesting to know whether heterostylous systems are breaking down here, as occurs in many species which achieve long distance dispersal (Baker, 1959). It may be that enforced self-pollination is leading to proliferation of local variants. Field studies are required to illuminate this problem.

IX. Evolutionary interpretations

1. SUGGESTED PHYLOGENY OF THE HYDNOPHYTINAE

2. INTERPRETATION OF CHARACTERS SEPARATING MYRMECODIA FROM HYDNOPHYTUM

3. EVOLUTION IN THE SATELLITE GENERA

4. COMPARISON WITH THE NON-RUBIACEOUS ANT-EPIPHYTES

5. EPILOGUE

1. SUGGESTED PHYLOGENY OF THE HYDNOPHYTINAE

I would like to consider the course of evolution in the Hydnophytinae, and to evaluate the part, if any, played in it by the symbiosis with ants.

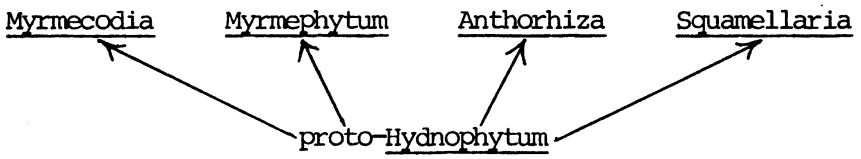
Hydnophytum is probably 'primitive' in the subtribe because of characters which it alone shares with other members of the tribe Psychotrieae. The other four genera are believed to be derived from Hydnophytum-like ancestors, since they share the chambered tuber but possess modifications both of it and of the stem and inflorescence.

Two of the satellite genera (Myrmephytum and Anthorhiza) have characters typical of both the major genera as well as having unique features. As they share different characters with Myrmecodia it is unreasonable to suppose that they are derived from a single stock intermediate between Hydnophytum and Myrmecodia. This implies that the structures these genera have in common with Myrmecodia have been acquired independently more than once. Examples of these structures are the modification of adventitious roots into branched spines and the reduction in length of the internodes.

Although some of the floral characters of the third satellite genus, Squamellaria, resemble states found in Myrmecodia, the pollen, stigma and vegetative characters are very similar to those of Hydnophytum, suggesting an independent evolution. Thus Squamellaria probably also represents an independent development from a Hydnophytum-like stock.

The pattern of characters distinguishing the genera therefore suggests that each of the other four genera has been derived independently from a

Hydnophytum-like ancestor:-



2. INTERPRETATION OF CHARACTERS SEPARATING MYRMECODIA FROM HYDNOPHYTUM

The differences between Hydnophytum and Myrmecodia are the most interesting in the group because these two genera occur sympatrically over a wide area. Both genera occupy a similar range of habitats, and the characters separating them, modification of the tuber, stem, spines, corolla and locule number, appear unconnected with the regional environment. This suggests that some feature enables them to use different niches in the same habitat.

The tubers of these two genera are quite distinctive, the cavities in Hydnophytum being simpler. In several species of Myrmecodia there are honeycombed areas with numerous pores to the outside. Measurements of the temperature of tubers without honeycombing has shown that the interior is somewhat insulated (Spanner, 1939). Honeycombing would be likely to increase an insulating effect, but this has not been investigated. It is noteworthy that the honeycombing resembles the shape of superficial tunnels in certain termite nests where it is associated with ventilation (M. Jebb, pers. comm.; Frisch, 1975). While it appears probable that insulation is of limited importance to the plant, it might have considerable effect on juvenile ants developing inside the tuber. One may therefore suggest that the honeycombing and pores in Myrmecodia is an adaptation beneficial to the ants.

Modifications of the tuber in Hydnophytum are rather different. In H. guppyanum, which is 'primitive' with respect to its inflorescence structure, the tuber has large central, and smaller peripheral chambers. Most lowland species have more evenly sized chambers, but the high altitude species again have a great disparity of size, which makes them apparently less suitable for ants. It is possible that both for H. guppyanum and the high altitude species,

functions other than harbouring ants may predominate. These cavities have been found containing other invertebrates and water. So, in both the typical form of the tuber and adaptations of it, Myrmecodia appears to be more suited for symbiosis with ants than Hydnophytum.

The ridges common on Myrmecodia tubers call to mind similar structures in cacti and succulents. These ridges allow changes in volume and thus in water content of the tuber tissue. Myrmecodia again seems to have a more adaptable tuber structure in this way.

The condensation of the inflorescence in Hydnophytum and its sinking into alveoli in Myrmecodia would tend to protect the inflorescence. The bizarre clypeoli and spines of the stem of Myrmecodia appear to have the same effect. The corolla at anthesis and the ripe fruit are both elongated relative to those of most species of Hydnophytum, presumably so as to reach beyond the spines, clypeoli and stipules. It would be reasonable to suppose that these structures protect the inflorescence from herbivores; due to its isolation from the Asian fauna, New Guinea is poor in vertebrate herbivores. Some potential herbivores are present, such as species of mouse, marsupial possums and tree-kangaroos, but I am not aware of records of these animals eating ant-plants. North of the Wallace Line numerous apes and monkeys are present, and it has recently been found that Myrmecodia leaves form a substantial part of the diet of gibbons in Sumatra (T. Whitten, pers. comm.).

Besides protection of the plants from herbivores, however, another explanation is possible. Although ants have not been seen visiting the flowers at anthesis, and are not implicated in pollination, they do visit the inflorescences and apparently take nectar from the receptacle after the corolla has fallen. Now these ants normally build a covering of vegetable matter over the runways, presumably for protection from bird and lizard predators (Janzen, 1974). Where these runways cross an ant-plant, the spines are incorporated and help support the carton. Branched and stellate spines are particularly effective in this way. The interlocking spines and stipules on the clypeoli, and tunnels through the stem in one species, provide cover for ants visiting the inflorescences. It is notable that other groups of plants associated with ants

often tend to have spines or long, stiff, scattered hairs (Spruce, 1908). An example is the fern Leconopteris spinosa, but plants other than epiphytes often show this feature e.g. Diospyros conocarpa Guerke and K. Schum. and Hirtella sp. (F. White, pers. comm.). In conclusion, I would suggest that some of the tuber and stem characters which distinguish Myrmecodia from Hydnophytum are connected with the ant-symbiosis, and are beneficial to the ants.

The leaves of Myrmecodia differ generally from those of Hydnophytum in being larger and thinner with more numerous stomata and thinner cuticles. These features might be expected to suit the genus to more mesic conditions, but in fact Myrmecodia is found growing in seasonally dry areas alongside Hydnophytum. The relative xeromorphy of Hydnophytum may be analogous to that of many plants of moist but nutrient poor environments (Grubb, 1977). This implies that some aspect of the physiology of Myrmecodia, either with regard to its access to water or to nutrients, enables it to behave as a mesophyte. The difference between the genera which might be associated with this mesophytism is the more highly sophisticated symbiosis with ants which is apparently found in Myrmecodia. It is possible that an improved nutrient supply via the ants allows Myrmecodia to be more mesophytic.

The form of the leaves of the two genera at high altitudes is also characteristically different. In Hydnophytum the leaves tend to become small and leathery or brittle, whereas leaves of Myrmecodia become long and narrow, but remain mesophytic. This may reflect a similar difference in nutritional status between the two genera. There is some evidence that Myrmecodia is occupied by ants at high altitudes while Hydnophytum is not (Lam, 1924).

In only one species of Myrmecodia do the leaves show a clear adaptation to habitat. This is the species which grows in mangrove and swamp savanna trees under conditions of lower and more seasonal rain-fall than any other species; it has rather small, thick, fleshy leaves.

The interpretation of changes in floral characters betweeen Hydnophytum and Myrmecodia is again, necessarily, speculative. The condensation of the inflorescence and proliferation of protective structures is likely to have affected adversely access for pollinators to flowers of Myrmecodia. There

are some hints that Myrmecodia may be often self-pollinated:- no pollinators have been seen; the corolla may fall without opening; and there is a high rate of seed set. Heterostyly, which occurs in some species of Myrmecodia would tend to promote outbreeding. The evidence for heterostyly is, however, slight and equivocal, and it is not known how common it is in Hydnophytum as compared with Myrmecodia. If self-pollination is frequent in Myrmecodia this would increase the tendency towards numerous and local variants.

In conclusion, it appears that the two sympatric genera are divided by the sophistication of their association with ants, the degree to which they are mesophytic, and possibly by pollination mechanisms. One might hypothesise that Myrmecodia has evolved a closer association with ants; the resulting improvement in nutrient supply enables mesomorphic species of Myrmecodia to occupy the same environments as species of Hydnophytum with small, thick leaves. A change in pollination mechanism would have allowed the genetic isolation necessary for this evolutionary change.

3. EVOLUTION IN THE SATELLITE GENERA

In this section, both the characters which distinguish the satellite genera and developments within these genera, are considered and compared with the situation in Hydnophytum and Myrmecodia.

Myrmephytum is characterized by its 6-merous flowers and prominent bracts. These features may be related to pollination mechanisms, but no information is available. The bracts appear to protect the inflorescence in a similar way to the spines etc. of Myrmecodia. Indeed the flowers are not always exerted beyond the bracts and are thus even more protected. The two major species of Myrmephytum show the vegetative characteristics respectively of Hydnophytum and of Myrmecodia. It is therefore probable that comparable selective forces acting on material of similar mutational capacity have produced parallel evolution.

As implied by Beccari, it is also possible that the two species were derived respectively from Hydnophytum-like and Myrmecodia-like ancestors. In this case, the 6-merous flowers and large bracts are assumed to have arisen

together on two independent occasions. This seems less likely than the combination arising once and being followed by modifications paralleled elsewhere. The large size of the pollen of Myrmephytum presents the possibility that polyploidy is involved.

Anthorhiza again has conspicuous protection of the inflorescence, this time by adventitious roots, not around, but among the flowers. It also has unique rows of spines along the stems which facilitate the building of carton runways between the tuber and the inflorescence, and thus again protect the ants. In view of the recurrence of such protection, by analogous and homologous structures, it is likely that it is of selective advantage. It would be most interesting therefore to know whether the plants require pollinators whether the ants gain substantial amounts of nutrient from the inflorescences, and also whether they gain significant protection from the spines, clypeoli and bracts of these plants.

Diversification within Anthorhiza is only at the subspecific level and only involves leaf-shape and spines on the tuber. If this genus is derived from something like Hydnophytum, then one would suggest that the subspecies lacking spines on the tuber gave rise to the one with them. In which case the development again parallels that found in Myrmephytum and between Hydnophytum and Myrmecodia. It is worth mentioning that Anthorhiza lacks floral differentiation from Myrmecodia, and is the least diversified of the genera. This might suggest that a change in pollinator has been necessary for widespread sympatry and speciation of genera in this subtribe.

Squamellaria is distinguished by floral characters; vegetatively it resembles Hydnophytum, and grows sympatrically with it. A change in pollinator is therefore likely to have been the major pressure behind the evolution of this genus. Again no studies of pollinators have yet been made.

The main distinction between species of Squamellaria lies in minor leaf-shape and floral characters. There is no available evidence of a difference in habitat preference between the species, and they occur in a very restricted area.

4. COMPARISON WITH THE NON-RUBIACEOUS ANT-EPIPHYTES

Speciation in the non-rubiaceous ant-epiphytes has been much less than in Hydnophytum and Myrmecodia. The largest of these genera is Dischidia (Asclepiadaceae), in which about 25 ant-harbouring species have been described, though this number is almost certainly too high. This is the only other genus in which qualitative elaboration of the chambers is found. There are three distinct types of leaf-flask of increasing complexity (see Chapter II). The most complex type resembles Myrmecodia in having separate and quite distinct absorptive and non-absorptive chambers.

In different species of the fern genus Lecanopteris there is an increase in the number and branching of the tunnels available to ants. The other ant-harbouring epiphytes show even less diversification; these are Tillandsia (Bromeliaceae) and Solenopteris (Polypodiaceae). These two genera, unlike the others, are neotropical. As pointed out in Chapter II, associations between ants and epiphytes in the neotropics are abundant in the form of ant-gardens - ball-shaped ant nests in which many epiphytes are rooted. A recent study of the ant-garden Gesneriad Codonanthe has shown that this association is truly symbiotic (Kleinfeldt, 1978). The ants gain a food source and support for their nests while the plants gain seed dispersal and a humus matrix for their roots. The advantages gained in this symbiosis are thus similar, though not identical to those in the Far Eastern ant-harbouring epiphytes. Whether any comparable structural modifications and speciation have occurred in the ant-garden plants has not been investigated.

5. EPILOGUE

Finally I would like to draw attention to the Hydnophytinae as a prime example of coevolution resulting in mutual benefit between plants and animals. Here as nowhere else in the higher plants there has been repeated evolution at the generic and specific level of characters which are best interpreted as beneficial to a symbiont. The current and rapid evolution which is of such great interest is however also the source of the intractable taxonomic difficulty of the group.

B : TAXONOMIC CONSPECTUS

X. Introduction and the position of the ant-plants in the Rubiaceae.

1. INTRODUCTION TO THE TAXONOMIC CONSPECTUS
2. THE SUBTRIBE HYDNOPHYTINAE

1. INTRODUCTION TO THE TAXONOMIC CONSPECTUS

In this conspectus four tasks are attempted:

a) Definition of a new subtribe comprising the ant-plant genera,

b) Definition of the constituent genera,

c) A skeleton treatment of Hydnophytum to illustrate the extent of the genus,

d) A more detailed treatment of the remaining four genera - Myrmecodia, Myrmephytum, Anthorhiza, and Squamellaria.

Note that many of the species given a more detailed treatment are known only from a few collections; further work is therefore likely to result in some changes of status.

Formal provision for publication of the taxa discussed here is not carried out, for instance selection of new type specimens and giving Latin descriptions. This is because further material from New Guinea and various herbaria should be seen before final decisions are reached. Details of existing types (holo-, syn-, etc.) are also not shown as they have not been ascertained in all cases. Herbarium listings are not exhaustive and refer to material seen by the author unless marked 'not seen'.

Some of the characters important in this group are unfamiliar, explanations and illustrations will be found in Chapter IV. The illustrations in this chapter are semi-diagrammatic; they were initiated for each taxon as a working tool, but only a selection are shown here. The leaf outlines are tracings from the largest typical leaf. The scales of the drawings are standardized unless indicated otherwise. Leaves are at x 1; whole plants x a sixth; spines and clypeoli x 2; flowers and pyrenes x 10; pollen x 160.

In the text the dimension of the pollen is the diameter of the grain without the vesicles. The number in brackets after the word 'flowers', indicates the number of flowers of that taxon dissected.

2. THE SUBTRIBE HYDNOPHYTINAE

Family	:	Rubiaceae
Subfamily	:	Rubioideae
Tribe	:	Psychotrieae
Subtribe	:	Hydnophytinae subtrib. nov.

Usually epiphytic. Hypocotyl forming a 'tuber' (rarely absent) chambered by phellogens which arise de novo in the parenchyma. The length and branching of the stems sometimes reduced. Simple or branched spines derived from adventitious roots often present on the stem and tuber. Stipules inter- and intra-petiolar; either caducous and splitting opposite the petioles, or more persistent and splitting between the petioles. Inflorescence in one axil at each node (rarely terminal), peduncles paired (solitary), or flowers sessile or sunken in alveoli. Pedicels absent. Corolla and anthers 4 (6) -merous. A ring of hairs usually present within the corolla tube. Pollen 3 (1-5) porate, colporate, or colpate, sometimes with protoplasmic vesicles. Stigma lobed (capitate). Ovary with 2-10 uniovular locules. Fruit a fleshy, translucent drupe.

The Hydnophytinae comprises five genera:- Hydnophytum, Myrmecodia, Myrmephytum, Anthorhiza and Squamellaria.

XI. The genera

1. SYNOPTIC KEY TO THE GENRA
2. *HYDNOPHYTUM* JACK
3. *MYRMECODIA* JACK
4. *MYRMEPHYTUM* BECC.
5. *ANTHORHIZA* GEN. NOV.
6. *SQUAMELLARIA* BECC.

1. SYNOPTIC KEY TO THE GENERA

1. Corolla 6-fid. Spines present. Internodes condensed or not, clypeoli absent. Inflorescence sessile, bracts large, leathery . . . . . MYRMEPHYTUM

1. Corolla 4-fid. Bracts usually small, rarely leathery :

2. Internodes condensed. Spines present. Clypeoli sometimes present. Stipules splitting between the petioles. Flowers usually sunken in alveoli. Bracts occasionally hairy and conspicuous. Ovules 4-10 . . . . MYRMECODIA

2. Internodes not condensed. Spines present or absent. Clypeoli absent. Stipules splitting opposite the petioles. Inflorescence pedunculate or condensed or sessile. Ovules 2-6 :

3. Stigma capitate. Spines absent. Inflorescence sessile. Pollen 4 (3-5) colpate. Embryo curved. Pyrenes horned . . . . . SQUAMELLARIA

3. Stigma 2-4 fid. Spines present or absent. Inflorescence sessile or pedunculate. Pollen 3 porate or colporate. Embryo straight. Pyrenes not horned :

4. Inflorescence pedunculate, condensed or sessile. Spines never intermixed with flowers, only rarely present, and then root-like. Bracts sometimes conspicuous. Leaves small to large . . . . . HYDNOPHYTUM

4. Inflorescence sessile, surrounded by and intermixed with large, branched spines. Bracts inconspicuous. Leaves large . . ANTHORHIZA.

2. HYDNOPHYTUM JACK

[Nidus formicarum niger Rumphius, Herbarium Amboinense :119, tab.55 (1750).]

Hydnophytum Jack, Trans. Linn. Soc. Lond. 14:124 (1823); Blume, Bijd. Fl. Ned. Ind. :955 (1826); de Candolle, A.P., Prod. 4:450 (Sept. 1830); Bentham & Hooker, Gen. Plant. 2:132 (1873); Beccari, Malesia 2:120 (1884); Valeton, Bot. Jahrb. 61:127 (1927); Merrill & Perry, J. Arn. Arb. 26:14 (1945).

- Type species: H.formicarum Jack.

Lasiostoma sensu Sprengel non Schreber, Syst. Veg. :422 (1825), pro parte quoad L.formicarum (Jack) Sprengel tantum.

Myrmecodia [Mirmecodia] sensu Gaudich., in Freycinet, Voyage autour du Monde :472, Pl.95 (March 1830), pro parte quoad M.inermis Gaudich. tantum.

Lasiostoma Benth., Lond. J. Bot. 2:224 (1843).

- Type species: L.loranthifolia Benth.

Tuber rarely absent, facultative, or with swellings along the stem; usually wider than tall, unridged, occasionally with erect adventitious roots. Chambers simple in shape. Stem (1), several, branched, internodes several times longer than wide. Leaves usually leathery. Petioles short. Stipules predominantly interpetiolar, caducous. Inflorescence

solitary or paired. Inflorescence rachis pseudodichotomous or opposite decussate with ultimate branches condensed; or entirely condensed; or peduncle reduced, or rachis also reduced to a mound, or absent. Bracts and bracteoles usually less than 0.5cm. Corolla white, 4-lobed, lobes spreading at anthesis; ring or bundles of hairs usually at base of lobes. Anthers more or less exserted. Pollen usually 3-porate, 30-60 μm, reticulation fine (medium); rarely 4-colpate, 102 μm, reticulation coarse. Stigma 2(4) lobed. Ovules 2(4).

3. MYRMECODIA JACK

[Nidus formicarum ruber Rumphius, Herbarium Amboinense : 119, tab.55 (1750).]

Myrmecodia Jack, Trans. Linn. Soc. Lond. 14:122 (1823); Blume, Bijd. Fl. Ned. Ind. : 1001 (1826-1827); Gaudichaud, in Freycinet, Voyage autour du Monde :472, Pl.96 (March 1830), pro parte excl. M.inerme Gaudich. tantum; de Candolle, A.P., Prod. 4:450 (Sept.1830); Bentham & Hooker, Gen. Plant. 2:132 (1873); Beccari, Malesia 2:95 (1884); Valeton, Bot. Jahrb. 61:144 (1927); Merrill & Perrry, J. Arn. Arb. 26:26 (1945).

- Type species: M.tuberosa Jack.

Lasiostoma sensu Sprengel non Schreber, Syst. Veg. :422 (1825), pro parte quoad L.tuberosum (Jack) Sprengel tantum.

Tuber often ridged and longer than wide. Spines (absent), simple, branched or stellate. Chambers often complex with arcs of entrance holes surrounding swollen honeycombed areas with pores. Stems solitary or few, little or unbranched. Internodes about as long as wide. Clypeoli often present. Leaves: stipules splitting between the petioles and partly splitting opposite them, often persistent. Inflorescence sunken in alveoli. Bracts inconspicuous or with hairs forming a dense mass. Corolla white or blue, 4-lobed; lobes uncinate, not usually spreading at anthesis; the tube with a ring of hairs at varying levels. Anthers usually enclosed. Pollen 2-4 (1-5) porate or colporate; apertures sometimes bordered; vesicles usually present; reticulation fine to coarse. Stigma lobed, as many as ovules. Ovules 2-10.

4. MYRMEPHYTUM BECC.

Myrmephytum Becc., Malesia 2:92, tabs.8 & 9 (1884).

- Type species: M.selebicum (Becc.) Becc.

Myrmedoma Becc., Malesia 2:94, tab.10 (1884).

- Type species: Myrmedoma arfakiana Becc., syn. nov.

Tuber more or less spherical. Chambers with or without honeycombing. Spines simple or branched. Stems either few, branched, with internodes not condensed; or solitary, unbranched, with condensed internodes. Sometimes with a few spines. Leaves leathery. Stipules splitting irregularly between the petioles. Inflorescence sessile, surrounded by triangular bracts which are leathery to fleshy, and interspersed with papery, hairy bracts. Corolla 6-lobed, blue, usually with a ring of hairs. Anthers 6, at the apex of tube. Pollen 3(-4) colporate, 70-160 µm; reticulation medium to coarse. Ovules 6-8.

Note: Myrmephytum selebicum was first described as a member of Myrmecodia (Beccari, 1874).

5. ANTHORHIZA GEN. NOV.

FIG.23.

Tuber bearing scattered entrance holes and rather weak, stellate spines. Stems 1-few, rarely branched. Internodes not condensed. Leaves large (15-25 cm) leathery. Stipules splitting opposite the petioles, caducous. Inflorescence sessile, surrounded by and intermixed with rather weak stellate spines. Bracts not conspicuous. Corolla white, 4-merous, lobes shortly uncinate, spreading at anthesis. Pollen 3-porate. Stigma 4-5 lobed. Ovules 4-6.

6. SQUAMELLARIA BECC.

Squamellaria Becc., Malesia 2:228, tab.46 (1886); Smith, Contrib. U.S. Nat. Herb. 37:90 (1967).

- Type species: S.imberbis (A.Gray) Becc.

Tuber, stem, and leaves as in Hydnophytum. Inflorescence sessile or on mounds or fascicled on a rachis which arises off centre of the leaf axil. Bracts inconspicuous. Corolla white, 4-merous, 20-45 mm; lobes 4-9 mm; tube with 4 groups of squamules near the base. Anthers at apex of tube. Pollen 4 (3-5) colpate, 115-190 µm; reticulation coarse, formed by narrow, rather deep walls. Stigma just above anthers, capitate, with a tubular fringe pointing downwards, and a rim upwards. Ovules 4. Pyrenes hooked, embryo curved.

Note: Of the three species of Squamellaria, one was initially placed in Hydnophytum (Horne, 1881; Baker, 1883), and one in Myrmecodia (Gray, 1860).

XII. Hydnophytum

1. INTRODUCTION

2. ARTIFICIAL KEY TO THE MAIN SPECIES AND SPECIES GROUPS IN HYDNOPHYTUM

3. ANNOTATED LIST OF SPECIFIC NAMES IN HYDNOPHYTUM

1. INTRODUCTION

Time has not permitted a detailed study of Hydnophytum; however a large proportion of the existing material has been seen in order that a picture of the whole of the Hydnophytinae could be built up. As Hydnophytum is probably both the largest and the most primitive genus in the subtribe, it is vital that it should be considered. Two summaries of my brief observations are presented here - a key and a list of specific epithets.

2. ARTIFICIAL KEY TO THE MAIN SPECIES AND SPECIES GROUPS IN HYDNOPHYTUM

The key is artificial and leads only to the major species and species groups, and is intended as a guide to the main divisions in the genus. It is not comprehensive and uses only characters available in a preliminary study. I do, however, expect that other correlating characters will be found which will confirm that these are the major taxa in the genus.

1.Inflorescence at least sometimes distinctly pedunculate:

2.Peduncle solitary in leaf axil, rarely terminal . . H.guppyanum et aff.

2.Peduncles paired in axils, never terminal . H.radicans et aff.

1.Inflorescence not pedunculate, rachis mostly condensed or reduced to a mound or absent:

3.Inflorescence rachis 0.5-4.0 cm long . H.keiense et aff.

3.Inflorescence rachis reduced to a mound or absent:

4.Corolla (10-) 20-30 mm long; Fiji Is. . . . . H.grandiflorum et aff.

4.Corolla to 15 mm:

5.Leaves hairy, more or less orbicular . . H.microphyllum

5.Leaves glabrous, shape various:

6. Leaves usually smaller than 3x1 cm, thin; lowland plant:

7.Leaves more than 4 times as long as broad . H.parvifolium

7.Leaves less than 4 times as long as braod . H.hellwigii

6.Leaves larger, or small, but then leathery and plant montane:

8.Leaves usually more than 3cm long, leathery or fleshy, lowland plant:

9.Bracts usually less than 4mm, not conspicuous:

10.Leaves oblong:

11.Stems terete; throughout Malaysia, Indonesia and the Philippines . . . H.formicarum et aff.

11.Stems quadrangular; New Guinea . H.tetrapterum

10.Leaves not oblong, various:

12.Leaves orbicular, cordate . . H.ovatum

12.Leaves elliptic, lanceolate or spathulate:

13.Leaves fleshy, less than 4 times as long as broad, more or less ovate, apex acute, base cuneate. Petiole c. 0.5cm:

14.Leaves usually less than 7cm long; often coastal . . *H.moselyanum* et aff.

14.Leaves usually more than 7cm; usually inland . . . *H.crassifolium* et aff.

13.Leaves not as above:

15.Leaves more than 4 times as long as broad:

16.Leaves falcate . . *H.falcatum*

16.Leaves straight . . *H.agatifolium*

15.Leaves not as above . . various species

9.Bracts usually more than 4mm long . . at least 3 distinct, unnamed species

8.Leaves often less than 3cm long, leathery or brittle; plant montane:

17.Leaves narrowly lanceolate to linnear . *H.minutifolium*

17.Leaves ovate to orbicular:

18.Leaves often less than 1 cm long . *H.vitis-idaea*, *H.buxifolium* and other species

18.Leaves usually less than 1 cm . . . . . *H.archboldianum* and *H.alboviride*.

3. ANNOTATED LIST OF SPECIFIC NAMES IN HYDNOPHYTUM

This alphabetical list of published species gives their existing synonomy, the protologue and important taxonomic references, the type locality and collectors name and number. The herbaria at which duplicates of the type are known to exist are shown, though no exhaustive search has been made. Probable affinities between species are also noted.

Not listed are a number of Valeton names which exist only in keys; some names which have been used in error; manuscript names, mainly of Valeton; and species names which have subsequently been transferred to other genera.

1. H.agatifolium Valeton, Nova Guinea 8:774 (1912). - Type: Irian Jaya, Djayapura, Gjellerup 137 (BO, L).
2. H.albense Valeton, Bot. Jahrb. 61:128 (1927); Merrill & Perry, J. Arn. Arb. 26: (1945). - Type: Papua New Guinea, Albo, S of Astrolabe Bay, Schlechter 16164 (B†). Similar to H.radicans.
3. H.albertisii Becc., Malesia 2:124 (1884), 136 (1885). - Type: Papua New Guinea, Fly River, d'Albertis sn 1877 (FI). Similar to H.keiense, H.amplifolium and H.subnormale.

4. H.alboviride Merr. & Perry, J. Arn. Arb. 26:21 (1945). - Type: Irian Jaya, 18km SW of Bernhard Camp, Brass 12683 & 12682. ? cf. H.archboldianum.

5. H.amboinense Becc., Malesia 2:138 (1885). - Type: Amboin, Beccari 5530 (FI, K). cf. H.formicarum.

6. H.amplifolium S.Moore, Journal of Botany 65:270 (1927). -Type: Papua New Guinea, Vailala R., Upoia, Brass 1151 (A, BRI). cf. H.albertisii.

7. H.andamanense Becc., Malesia 2:138 (1884). - Type: Andaman Is., Kurz (CAL). cf. H.formicarum.

8. H.angustifolium Merr., Philippine Journal of Science 3:162 (1908). - Type: Philippines, Mindanao, Lake Lanao, Camp Keithley, Clemens sn (?). cf. H.formicarum.

9. H.archboldianum Merr. & Perry, J. Arn. Arb. 26:16 (1945). - Type: Irian Jaya, Lake Habbema, Brass 9506 (A, L).

10. H.brachycladum Merr., Philippine Journal of Science 10: 142 (1915). - Type: Philippines, Mindoro, Calapan, Mangubat BS 924. cf. H.formicarum.

11. H.bracteatum Valeton, Nova Guinea 8:506 (1911). - Type: Irian Jaya, Noord R., Nepenthes Hugel, Versteeg 1765 (BO, L).

12. H.brassii S.Moore, Journal of Botany 65:271 (1927). - Type: Papua New Guinea, Gulf Prov., Kerua, Brass 1200 (A, BRI, K). cf. H.papuanum.

13. H.buxifolium Merr. & Perry, J. Arn. Arb. 26:22 (1945). - Type: Irian Jaya, Idenburg R., 18km SW of Bernhard Camp, Brass 12681 (A).

14. H.camporum S.Moore, Journal of Botany 65:271 (1927). - Type: Papua New Guinea, Central Prov., Bisiatabu, Brass 605 (A, BRI). cf. H.crassifolium.

15. H.capitatum Valeton, Bot. Jahrb. 61:129 (1927). - Type: Papua New Guinea, Wobbe, Schlechter 16489 (B†).

16. H.confertifolium Merr. & Perry, J. Arn. Arb. 26:20 (1945). - Type: Irian Jaya, Idenburg R., 18km SW of Bernhard Camp, Brass 12680 (A, L).

17. H.contortum Merr. & Perry, J. Arn. Arb. 26:17 (1945). - Type: Papua New Guinea, Oriomo R., Wuroi, Brass 5849 (A, BO, BRI).

18. H.cordifolium Valeton, Bot. Jahrb. 61:129 (1927). - Type: Papua New Guinea, Dischore, Schlechter 19636 (G, K). cf. H.ovatum.

19. H.coriaceum Becc., Malesia 2:158 (1885). - Type: Sarawak, Beccari 661 (FI). ?cf. H.formicarum.

20. H.crassifolium Becc., Malesia 2:124 (1884); tom.cit. :148 (1885). - Type: Aru Is., Giabu-lengan, Beccari sn (FI, K). ?cf. H.papuanum.

21. H.cuneatum Valeton, Bot. Jahrb. 61:133 (1927). - Type: Papua New Guinea, Hauptlager Malu, Ledermann 6556 & Ledermann 10428 (L).

22. H.decipiens Merr. & Perry, J. Arn. Arb. 26:20 (1945). - Type: Irian Jaya, Idenburg R., 18km SW of Bernhard Camp, Brass 12684 (A, BRI).

23. H.dipteropodum (Lauterb. & Schumann) Valeton, Psychotria dipteropoda Schumann & Lauterb., Flora von deutsch Schutzgebiete in der Südsee :576 (1901). Valeton, Bot. Jahrb. 61:130 (1927). - Type: Papua New Guinea, Astrolabe Bay, Lauterbach 2066.

24. H.dolichophyllum Valeton, Bot. Jahrb. 61:130 (1927). - Type: Papua New Guinea, Sepik R., Lordberg, Ledermann 9889 & 12723 (L).

25. H.ellipticum Merr. & Perry, J. Arn. Arb. 26:19 (1945). - Type: Irian Jaya, Idenburg R., 15km SW of Bernhard Camp, Brass 12111 (A).

26. H.forbesii J.D.Hook. Bot. Mag. t.7218 (1892). - Type: Papua New Guinea, Forbes sn (K). cf. H.moseleyanum.

27. H.formicarum Jack, Trans. Linn. Soc. 14:124 (1823). For synonomy see Chapter XI 1.- Type: Sumatra, Jack sn (†).

28. H.grandiflorum Becc., Malesia 2:126 (1884); tom.cit. 171 (1885). - Type: Fiji Is., Ovalau, Horne cf. H.longiflorum, H.horneanum, H.tenuiflorum and H.wilkinsonii.

29. H.grandifolium Valeton, Nova Guinea 8:773 (1912). - Type: Irian Jaya, Djayapura, Gjellerup 226 (BO, L).

30. H.guppyanum Becc., Malesia 2: 129, 133 (1885). - Type: Solomon Is., Shortland Is., Guppy 140 (FI, K). cf. H.hahlii, H.kajewskii and H.longipes.

31. H.hahlii Rech., Fedde: Repertorium specierum novarum regni vegetabilis 11:186 (1913). - Type: Bougainville Is., Djup, Rechinger 3552 (W), 4018 (W) & 4445 (W). cf. H.guppyanum.

32. H.hellwigii Warb. Bot. Jahrb. 18:209 (1894). - Type: Papua New Guinea, Morobe, Finschafen, Hellwig 469 (B†).

33. H.heterophyllum Merr. & Perry, J. Arn. Arb. 26:15 (1945). - Type: Irian Jaya, Idenburg R., 6km SW of Bernhard Camp, Brass 12857 (A).

34. H.horneanum Becc., Malesia 2:125 (1884); tom.cit. 168 (1885). - Type: Fiji Is., Horne 282 (K). cf. H.grandiflorum.

35. H.inerme (Gaudich.) Bremek., Blumea 5:245 (1942).- Type- Irian Jaya, Rawak, Gaudichaud sn (G, P). = H.gaudichaudii Becc. Malesia 2:139 (1885), type as above. = M.inermis Gaudich., in Freycinet, Voyage autour du Monde :472, type as above.

36. H.intermedium Elmer, Leafl. Philipp. Bot. 3:1039 (1911). - Type: Philippines, Mindanao, Davao Distr., Todaya, Mt. Apo, Elmer 10782 (L). cf. H.formicarum.

37. H.kajewskii Merr. & Perry, J. Arn. Arb. 26:25 (1945). - Type: Papua New Guinea, Bougainville, Kupei Gold Field, Kajewski 1716 (A, BM, BO, G, P). cf. H.guppyanum.

38. H.keiense Becc., Malesia 2:131 (1884). - Type: Moluccas, Kei Is., Beccari (FI, K). cf. H.albertisii.

39. H.kelelense Valeton, Bot. Jahrb. 61:134 (1927). - Type: Papua New Guinea, Kelel, Schlechter 16237 (B†). cf. H.radicans.

40. H.kochii Valeton, Nova Guinea 8:507 (1911). - Type: Irian Jaya, Etna Bay, Koch 26 (BO, L).

41. H.laurifolium Warb., Bot. Jahrb. 18:209 (1894). - Type: Irian Jaya, McCluer Gulf, Sigar, Naumann sn 17.6.1875 (B†).

42. H.lauterbachii Valeton, Nova Guinea 8:505 (1911). - Type: Irian Jaya, Noord R., Nepenthes Hugel, Versteeg 1226 (BO, K, L) & 1776 (BO, L).

43. H.ledermannii Valeton, Bot. Jahrb. 61:134 (1927). - Type: Papua New Guinea, Sepik R., Felspitze, Ledermann 12925 (B†).

44. H.leytense Merr., Philippine Journal of Science 8:390 (1913). - Type: Philippines, Leyte, Ormoc-Binahaan, Wenzel 45 (G).

45. H.linearifolium Valeton, Bot. Jahrb. 61:135 (1927). - Type: Papua New Guinea, Sepik Prov., April R., Lager 18, Ledermann 9700 (B , L).

46. H.longiflorum A.Gray, Proc. Am. Acad. 4:42 (1860). Myrmecodia vitiensis Seemann, Bonplandia 9:256 (1861). - Type: Fiji Is., Kadavu, Seemann 216 (G, GH, K, P). cf. H.grandiflorum.

47. H.longipes Merr. & Perry, J. Arn. Arb. 26:23 (1945). - Type: Bougainville, Kieta, Kajewski 1571 (A, BRI). cf. H.guppyanum.

48. H.longistylum Becc., Malesia 2:152 (1885). - Type: Solomon Is., Faro Is., Guppy 183 (FI, K). cf. H.crassifolium.

49. H.loranthifolium (Benth.) Becc., Malesia 2:146 (1885). Lasiostoma loranthifolia Benth., Lond. J. Bot. 2: (1843). - Type: New Guinea, Hinds sn 1841 (K). cf. H.crassifolium.

50. H.lucidulum Valeton, Bot. Jahrb. 61:137 (1927). - Type: Papua New Guinea, Dischore, Schlechter 19628 (BM, G, K, L) & nr. Gobi, Waria, Schlechter 19855 (G, K).

51. H.macrophyllum Warb., Bot. Jahrb. 13:441 (1891). - Type: Papua New Guinea, Morobe Prov., Finschafen, Warburg 21449 (B†).

52. H.magnifolium Merr. & Perry, J. Arn. Arb. 26:15 (1945). - Type: Irian Jaya, Idenburg R., Bernhard Camp, Brass 13768 (A) & Brass 14130 (A, L).

53. H.membranaceum Merr., Philippine Journal of Science 10:143 (1915). - Type: Philipines, Mindoro, Camanligue, Merritt For. Bur. 3720 (?). cf. H.formicarum.

54. H.microphyllum Becc., Malesia 2:174 (1885). - Type: Irian Jaya, Vogelkop, Wa-Sampson, Beccari 5528 (FI).

55. H.mindanaensis Elmer, Leafl. Philipp. Bot. 3:1039 (1911). - Type: Philippines, Mindano, Davao Distr., Todaya, Elmer 10874 (FI, L). cf. H.formicarum.

56. H.mindorense Merr., Philippine Journal of Science 10:143 (1915). - Type: Philippines, Mindoro, Alag R., Merrill 6182.

57. H.montis-kani Valeton, Bot. Jahrb. 61:138 (1927). - Type: Papua New Guinea, Kani Mts., Schlechter 17056 (K). cf. H.radicans.

58. H.moseleyanum Becc., Malesia 2:150 (1885). - Type: Papua New Guinea, Manus Is., Moseley sn 3.1875 (K). cf. H.forbesii.

59. H.myrtifolium Merr. & Perry, J. Arn. Arb. 26:19 (1945). - Type: Papua New Guinea, E Mt.Tafa, Brass 4093 (A, BO, BRI, K, L).

60. H.nigresens Merr. & Perry, J. Arn. Arb. 26:16 (1945). - Type: Papua New Guinea, Western Prov., 3km below junction with Black R., Brass 7171 (A, BM, BRI).

61. H.nitidum Merr. Philippine Journal of Science 2:307 (1907). - Type: Philippines, Mindoro, Mt. Halcon, Merrill 6181. ? cf. H.formicarum.

62. H.normale Becc., Malesia 2:123 (1884); tom.cit. 130 (1885). - Type: Irian Jaya, Japen Is., Ansus, Beccari sn (FI). ? cf. H.radicans.

63. H.oblongum (Benth.) Becc., Malesia 2:124 (1884). Lasiostoma oblonga Benth. Lond. J. Bot. 2:225 (1843). - Type: Papua New Guinea, New Ireland, Barclay sn (K). cf. H.crassifolium.

64. H.orbiculatum Elmer, Leafl. Philipp. Bot. 5:1860 (1913). - Type: Philipines, Mindanao, Bulusan, Irosin, Elmer 15583 (BO, BM, FI, G, GH, L, P, W). cf. H.formicarum.

65. H.ovatum Miq., Ann. Mus. Bot. Lugd.-Bat. 4:257 (1869). Beccari, Malesia 2:143 (1885). - Type: Moluccas, Ternate, Teysmann & de Vriese sn (L). ? cf. H.cordifolium.

66. H.papuanum Becc., Malesia 2:124 (1884); tom.cit. 147 (1885). - Type: Irian Jaya, Soron, Beccari P.P. 186 (FI, K). cf. H.brassii.

67. H.parvifolium Valeton, Bot. Jahrb. 61:140 (1927). - Type: Papua New Guinea, nr. Waria, Pema, Schlechter 19405 (G, K, L) & Schlechter 17416 (G).

68. H.petiolatum Becc., Malesia 2:124 (1884); tom.cit. 144 (1885). - Type: Irian Jaya, Soron, Beccari P.P. 187 (FI, K).

69. H.philippinense Becc., Malesia 2: 125 (1884); tom.cit. 149 (1885). - Type: Philippines, Malanipa, Zamboanga, Moseley sn 1-2:1875 (K). ? cf. H.formicarum.

70. H.punamense Lauterb., in Schumann & Lauterbach, Die Flora der deutsche Schutzgebiete in der Südsee :401 (1901). - Type: Papua New Guinea, New Ireland, Punam, Schlechter 14671 (WRSL). Schlechter 14671 belongs to H.hellwigii; the name is often applied to specimens with leaves c. 1.5 x 0.2 cm, which probably belong to H.parvifolium.

71. H.radicans Becc., Malesia 2:123 (1884); tom.cit. 132 (1885). - Type: Irian Jaya, Vogelkop, Andai, Beccari P.P. 793 (FI). cf. H.albense, H.kelelensis, H.montis-kani, and H.simplex.

72. H.ramispinum Merr. & Perry, J. Arn. Arb. 26:22 (1945). - Type: Irian Jaya, Idenburg R., 6km SW of Bernhard Camp, Brass 12858 (A, L).

73. H.robustum Rech., Fedde: repertorium specierum novarum regni vegetabilis 11:186 (1913). - Type: Papua New Guinea, New Britain, Gazelle Pen., Toma, Rechinger 3751 (W) & 4970 (W).

74. H.selebicum Becc., Malesia 2:125 (1884); tom.cit. 157 (1885). - Type: Sulawesi, Kandari, Beccari (FI). cf. H.formicarum.

75. H.simplex Becc., Malesia 2:123 (1884); tom.cit. 129 (1885). - Type: Aru Is., Vokan, Beccari sn (FI). cf. H.radicans.

76. H.spathulatum Valeton, Icones Bogoriense t. 340 (1912). - Type: Moluccas, Batjan, Smith sn 2.9.1900 (BO).

77. H.stenophyllum Valeton, Bot. Jahrb. 61:140 (1927). - - Type: Papua New Guinea, Finisterre Mts., Schlechter 18173 (K).

78. H.stewartii Fosb., Lloydia 3:123 (1940). - Type: Solomon Is., Guadalcanal, Kau Kau Bay, Stewart sn 23:5:1933. cf. H.crassifolium.

79. H.subfalcifolium Valeton, Bot. Jahrb. 61:141 (1927). - Type: Papua New Guinea, Toricelli Mts., Axur, Schlechter 20119; & road from Ramu to coast, Schlechter 14202 (BM, BO, K, WRSL).

80. H.subnormale Schumann, Schumann & Lauterbach, Nachträge, Flora der deutsche Schutzgebiete in der Südsee :400 (1905). - Type: Papua New Guinea, Sattelberg, Nyman 725. cf. H.albertisii.

81. H.subrotundum Valeton, Bot. Jahrb. 61:142 (1927). - Type: Papua New Guinea, road from Ramu to coast, Schlechter 14177 (WRSL).

82. H.subsessile Valeton, Bot. Jahrb. 61:142 (1927). - Type: Papua New Guinea, Bismarck Mts., Lauterbach 3164 (WRSL).

83. H.sumatranum Becc., Malesia 2:124 (1884); tom.cit. 137 (1885). - Type: Sumatra, Padang Prov., Ajer Manicor, Beccari sn (FI). cf. H.formicarum.

84. H.tenuiflorum Becc., Malesia 2:169 (1885). - Type: Fiji, Viti Levu, Graeffe 1573 (K) & Graeffe 1555. cf. H.grandiflorum.

85. H.tetrapterum Becc., Malesia 2:126 (1884); tom.cit. 173 (1885). - Type: Irian Jaya, Vogelkop, Wa-Sampson, Beccari sn (FI). A distinctive species.

86. H.tortuosum Becc., Malesia 2:124 (1884); tom.cit. 141 (1885). - Type: Irian Jaya, Vogelkop, Soron, Beccari P.P. 185 (FI, K).

87. H.virgatum Valeton, Bot. Jahrb. 61:143 (1927). - Type: Papua New Guinea, Schraderberg, Ledermann 11849 (B†).

88. H.vitis-idaea Merr. & Perry, J. Arn. Arb. 26:21 (1945). - Type: Irian Jaya, Idenburg R., 15km SW of Bernhard Camp, Brass 12046 (A, BM, BRI, K, L).

89. H.wilkinsonii Horne ex Baker J.G., Horne, A Year in Fiji :263 (1881); Baker J.G., J. Linn. Soc. 20:365 (1883); Beccari, Malesia 2:170 (1885). - Type: Fiji, Vanua Levu, Bua, Horne 1078 (K). cf. H.grandiflorum.

90. H.zippelianum Becc., Malesia 2:174 (1885). - Type: New Guinea, Zippelius ?sn (L).

XIII. Myrmephytum

1. KEY TO THE SPECIES

2. MYRMEPHYTUM SELEBICUM (BECC.) BECC.

3. MYRMEPHYTUM BECCARII ELMER

4. MYRMEPHYTUM ARFAKIANUM (BECC.) COMB. NOV.

5. LITTLE KNOWN SPECIES

1. KEY TO THE SPECIES

1. Spines on tuber dense, well-developed, freely branched. Stems 1, internodes condensed. Inflorescences covering the stem . . . . M.arfakianum

1. Spines on tuber sparse and weak, unbranched. Stems 1 to few. Internodes not strongly condensed. Inflorescences clearly discrete, though sometimes overlapping:

   2. Petiole short, less than 1 cm . . M.selebicum

   2. Petiole long, more than 2 cm . . M.beccarii.

2. MYRMEPHYTUM SELEBICUM (BECC.) BECC., Malesia 2:93, tabs.8 & 9 (1884). FIG. 22. - Type: Sulawesi, Beccari sn, 11.1873 (BM, FI, K).

Myrmecodia selebica Becc., Nuov. Giorn. Bot. Ital. 6:195 (1874). - Type: as above.

Tuber: spines rather slender, simple or occasionally branched. Stems 1-2, rarely branched. Internodes 1-5 cm long x 0.5 - 1.5

MYRMEPHYTUM

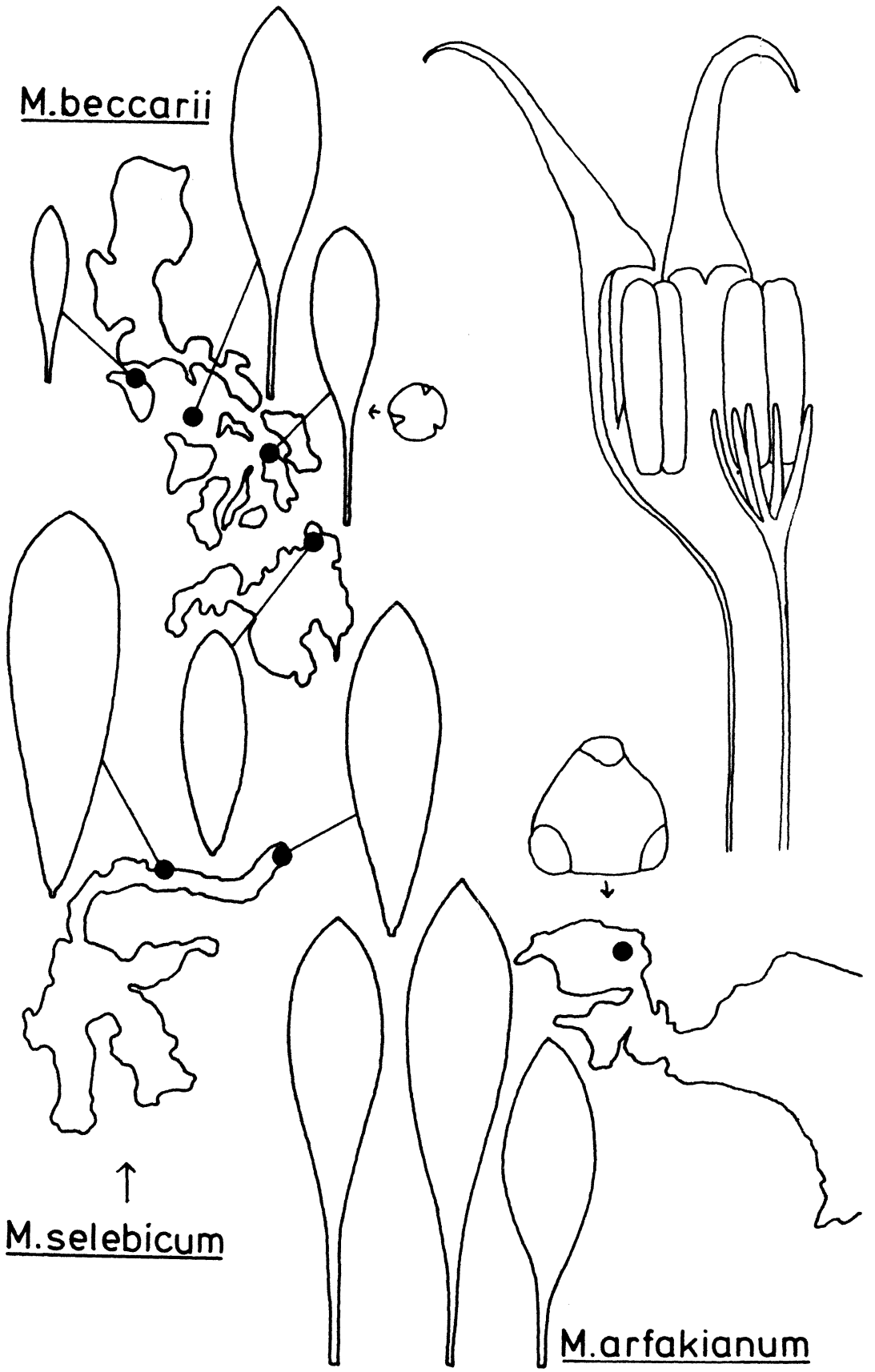


Fig. 22.

cm across, sometimes with a few simple spines. Leaves 11x3 - 22x6 cm. Lamina broadest above the middle; apex rounded; base tapering gradually. Petiole 0.2-0.5 cm. Lateral nerves 6-9. Inflorescence: flowers surrounded by and interspersed with bracts. Outer bracts to 2 cm long, 1 cm wide at base, acutely tapered, thick and leathery. Inner bracts shorter, thinner and rufous hairy. Corolla lobes acuminate; tube with a dense ring of hairs at the base. Stamens at the apex of tube. Pollen unknown.

Ecology 0-300 m.

Distribution The Philippines and Sulawesi.

Philippines: NE 08° 125° Mindanao, Butuan, Agusan Prov., Florida SO. San Mateo BO, Mendoza PNH 42302 (L).

Sulawesi: NE 01°28' 125°13' nr. Bituangus, Jones sn, 3:8:1977. 01°10' 121°50' Bool Prov., Palele, Koorders 18622 (BO). 01°23' 125°05' Kema, Beccari sn, 11:1873 (type). SE 02°45' 121°35' Tourveti Meer, Kjellberg 2295 (BO).

Discussion The specimen from the Philippines differs in its longer narrower internodes and thinner smaller leaves, its flowers have not been seen.

3. MYRMEPHYTUM BECCARII ELMER, Leafl. Philipp. Bot. 3:1037 (1911). FIG. 22. - Type: Philippines, Elmer 11467a (A, BM, BO, FI, G, K, L, P, W, WRSL).

Tuber: spines root-like, weak and simple or absent, c.0.5 cm. Stem 1-few, little branched. Leaves 10x2.5 - 22x5 cm. Lamina broadest above the middle; apex rounded; base gradually tapered. Petiole 3-5 cm. Inflorescence discrete to

contiguous. Bracts to 1.5 cm, as in M.selebicum. Corolla blue, 12 mm; lobes acuminate; tube with a ring of hairs near base. Anthers at apex of tube. Pollen 3-colporate, 70-85 µm; reticulation medium (Plate 6c).

Ecology Montane.

Distribution Philippines.

NE 13°20' 121°20' Mindora, Calapan, Mangubat BS 925 (K). 12° 122° Sibuyan, Capiz, Magallanes, Mt. Gitting Gitting, Elmer 11467a (type). 11°124° Biliran Is., Mt. Surio, Sulit PNH 21513 (L).

Discussion The specimen collected by Mangubat differs in its smaller leaves, freely branched stem and shorter, bluntly acute bracts. This species is closely related to M.selebicum.

4. MYRMEPHYTUM ARFAKIANUM (BECC.) COMB. NOV.

Myrmedoma arfakiana Becc., Malesia 2:94, tab.10 (1884).

FIG. 22. - Type: Irian Jaya, Beccari 5499 (FI).

Tuber densely covered with stellate spines with long, 1.0-1.5 cm, central branches and shorter, 0.5-1.0 cm laterals. Honeycombing well-developed. Stem solitary, unbranched, 1.5-2.0 cm across. Leaves 12x3.8 - 26x6 cm, glossy above, dull below, undulate. Lamina elliptic; apex acute; base tapered to and decurrent along the petiole. Lateral nerves 10-13. Petiole 2-3 cm, triangular.

Inflorescence a dense mass covering the stem. Bracts narrowly acuminate, 1.2-2.0 cm long, drying black, with a scarious margin, rufous hairy within. Corolla blue, widening sharply 3mm below apex of tube, hairs absent. Stamens at tube apex.

Pollen 3-4 colporate, 100-160 µm; reticulations very coarse (Plate 6d). Stigma lobed, at anthers.

Ecology At 1600-2500 m, terrestrial or epiphytic in scrubby vegetation, locally abundant (Gibbs, 1917).

Distribution Irian Jaya.

SE 01°20' 133°50' Vogelkop, Anggi Lakes, above Testega, Mt. Kobreimot, Sleumer & Vink BW 14163 (L, LAE); Angi Gita Lake, Mt. Tembruk, Sleumer & Vink BW 15411 (L, LAE); Angi Gita Lake, Kostermans 2406 (BO, L); Angi, Kanehira & Hatusima 13714 (A, BO). Locality uncertain: Arfak Mts., Gjellerup 1178 (L); Arfak Mts., Hatam, Beccari 5499 (type).

5. LITTLE KNOWN SPECIES

a) **Myrmedoma naumannii** Warb., Bot. Jahb. 18:111 (1894).- Type: Irian Jaya, MacCluer Gulf, Sigar, Naumann (B†, L photo). The leaves and arrangement of the inflorescence resemble those of M.selebicum more than those of Myrmephytum from New Guinea.

b) **Myrmephytum species 1.** Kanehira & Hatusima 12302 (BO) is distinguished by its lamina c. 44x4 cm and lateral nerves c. 16. This duplicate bears the legend Myrmedoma longissima, but no publication has been traced. Irian Jaya, Dalman, Nabire.

c) **Myrmephytum species 2.** van Royen 3417 (A, K, L). has long internodes with discrete, but elongate inflorescences which are clasped by two broadly triangular bracts with wide, 2.4cm, bases. Stems to 50 cm long. Irian Jaya, Vogelkop, E of Sorong, Mlasoen Hill.

d) **Myrmephytum species 3.** van Royen & Sleumer 8088 (K, L) has stout, simple, black spines to 1.2 cm long (Fig.7x). The inflorescences are overlapping. The leaves are narrowly elliptic; apex acute. Irian Jaya, Vogelkop, Nettoti Ra., Wekari R. Camp.

XIV. Anthorhiza

1. ANTHORHIZA CLEMENSII SP. NOV.

FIG. 23. Plate 9.

Tuber rounded, unridged. Chambers 0.6-5.0 cm diameter. Stems c. 80x0.9 cm. Internodes (2-) 4-8 cm long. A few irregularly stellate spines, smaller than those associated with the inflorescence or tuber are found in lines along the stem. Leaves: midrib prominent, triangular below; lateral nerves not prominent, but clearly visible. Inflorescence elongate elliptic, spines 1.5-2.5 cm long. Flowers(7) heterostylous. Corolla 15-20 mm; lobes c. 4mm. In longistylous flowers anthers at ring of hairs above middle of tube (Fig.23). Pollen unknown. Stigma above anthers. In brevistyle flowers a ring of hairs near base of tube, anthers at apex. Pollen 3-porate, 60-70 µm; vesicles small; apertures not bordered; reticulation fine to medium. Stigma mid way up tube (or at apex).

Distribution Papua New Guinea, Morobe Province and the Louisiade Islands.

Discussion The species falls into two morphologically and geographically distinct subspecies.

subspecies clemensii subsp. nov.

Spines on the stem and tuber regularly stellate. Leaf blade 20x7 - 28x8 (25x6.5) cm, lateral nerves 11-18, petiole 1-3 cm.

Ecology 0-1000 m.

Anthorhiza

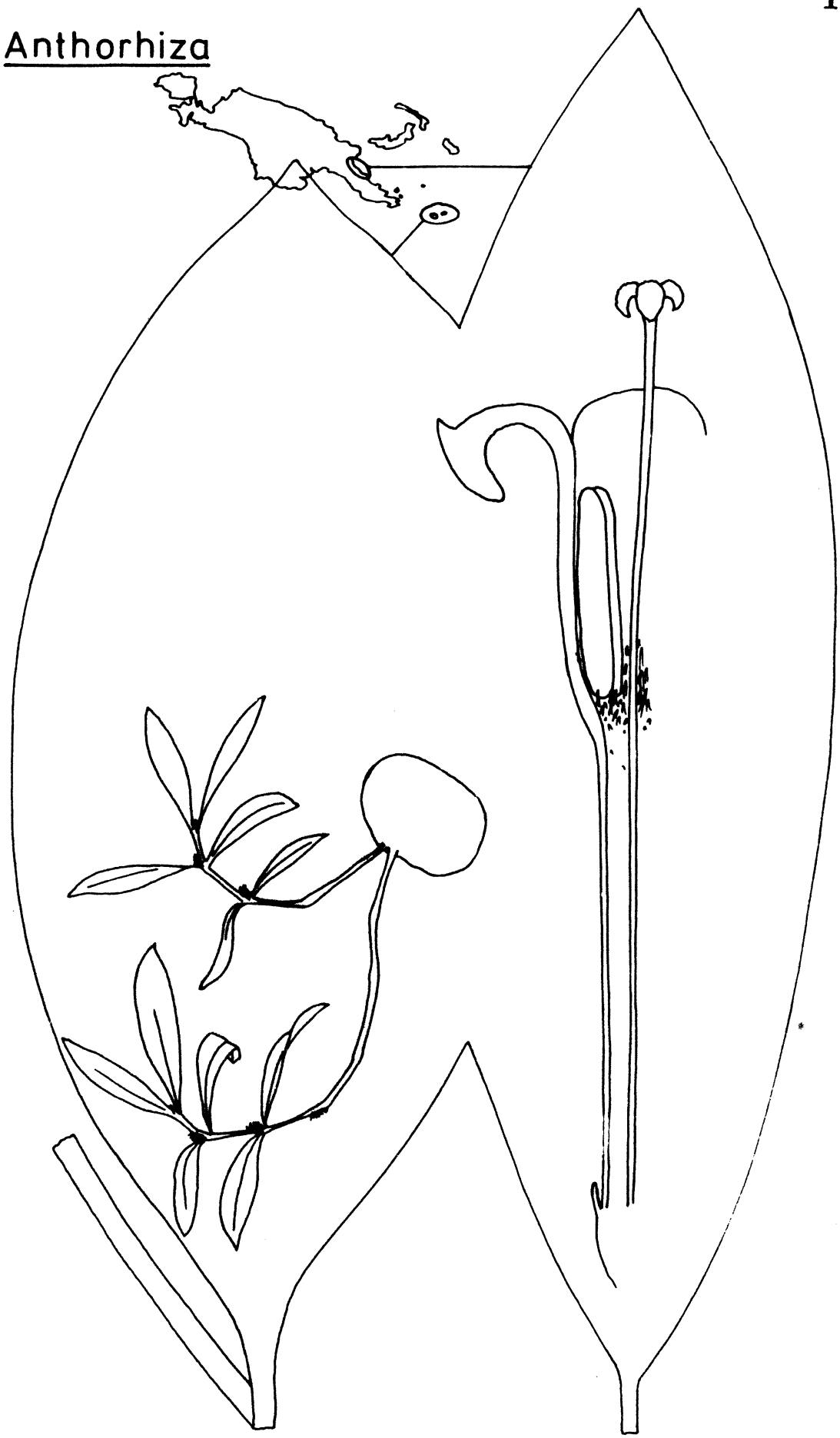


Fig. 23.

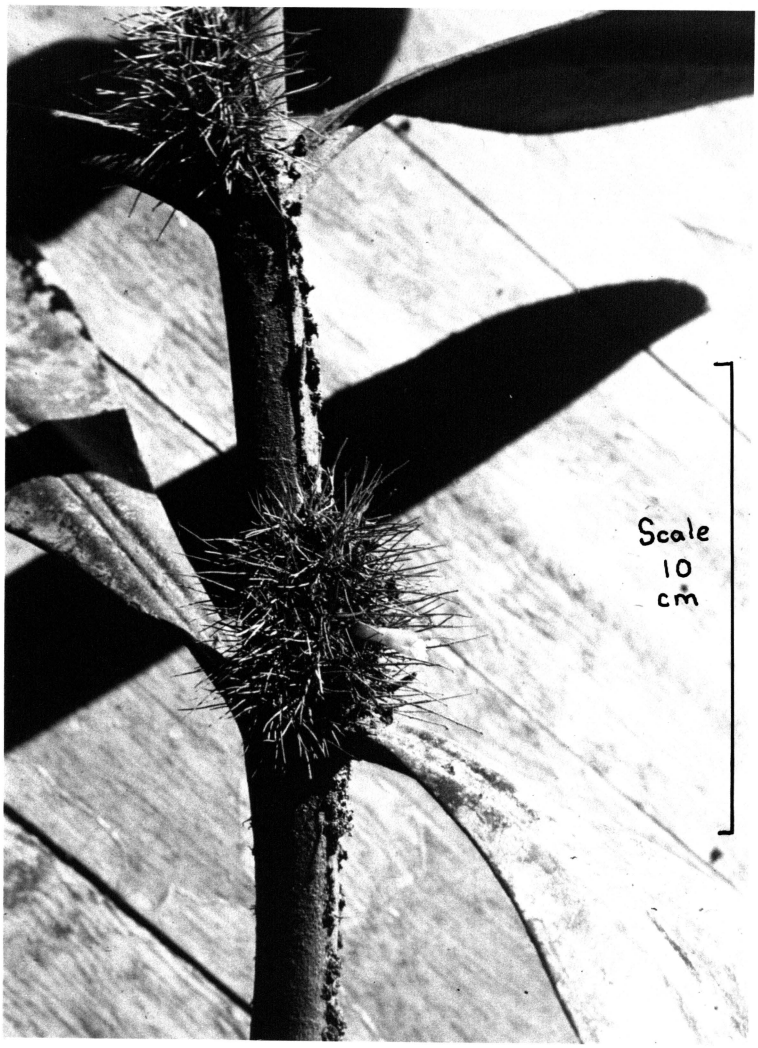


Plate 9. Anthorhiza clemensii ssp. clemensii. Close-up of stem showing two inflorescences and one flower. Lines of rudimentary spines along the stem are being used by the ants to support their carton runways.

Distribution Morobe Province. SE 06°33' 147°47' Qwembung, Clemens 1266 (A, G, L). 06°54' 146°38' Wau-Bulolo Rd., Perakles Pass. UPNG 3463. 07°25' 147°10' Buso, NGF 39094 (LAE) & NGF 45103 (BRI, LAE). Lasanga Is, NGF 44188 (A, BRI, K, L, LAE). Fly Is., c. 80 km S of Salamoa, UPNG 5950.

subspecies louisiadensis subsp. nov.

Spines absent from tuber, irregularly stellate on stem. Lamina 15x9 -22x10 cm; lateral nerves 9-12; petiole 4-9 cm.

Ecology 0 to 250 m.

Distribution Louisiade Archipelago.

SE 11°30' 153°26' Sudest Is., Mt. Riu, W slopes, Brass 27967 (A, K, L). Locality uncertain: 11° 154° Rossel Is., Ableti, Brass 28346 (A, BO, K).

XV. Squamellaria

1. KEY TO THE SPECIES

2. SQUAMELLARIA IMBERBIS (A.GRAY) BECC.

3. SQUAMELLARIA WILSONII (HORNE EX J.G.BAKER) BECC.

4. SQUAMELLARIA MAJOR A.C.SMITH

1. KEY TO THE SPECIES

1. Leaves more than 10x3 cm, apex rounded, apiculate. Lateral nerves arched, anastomosing. Calyx thick, opaque when dry . . . S.major

1. Leaves less than 10x3 cm, apex acute. Lateral nerves not arched or anastomosing. Calyx thin, translucent when dry:

2. Leaves to 7x3 cm. Petiole to 0.5cm. Upper part of corolla puberulent without . . . . S.imberbis

2. Leaves to 14x3 cm. Petiole to 3.5cm. Corolla glabrous without . . . . . S.wilsonii.

2. SQUAMELLARIA IMBERBIS (A.GRAY) BECC., Malesia 2:228, tab.46,1-12 (1886); Parham, Plants of the Fiji Islands :209 (1964). FIG. 24. - Type: Fiji, Seemann sn (K, P).

Myrmecodia imberbis A.Gray, Proc. Am. Acad. 4:42 (1860); Seemann, Flora Vitiensis :132 (1866); Bentham & Hooker, Gen. Plant. 21:132 (1873). - Type as above.

Tuber c. 25cm across. Stem 0.3-0.4 cm diameter. Leaves 4.5x1.8 - 7x3 cm. Apex of lamina acute, base cuneate. Petiole 0.3-0.5 cm. Lateral nerves 4-6. Inflorescence: calyx translucent when dry. Corolla lobes c. 9mm, lobes and upper part of tube puberulent without.

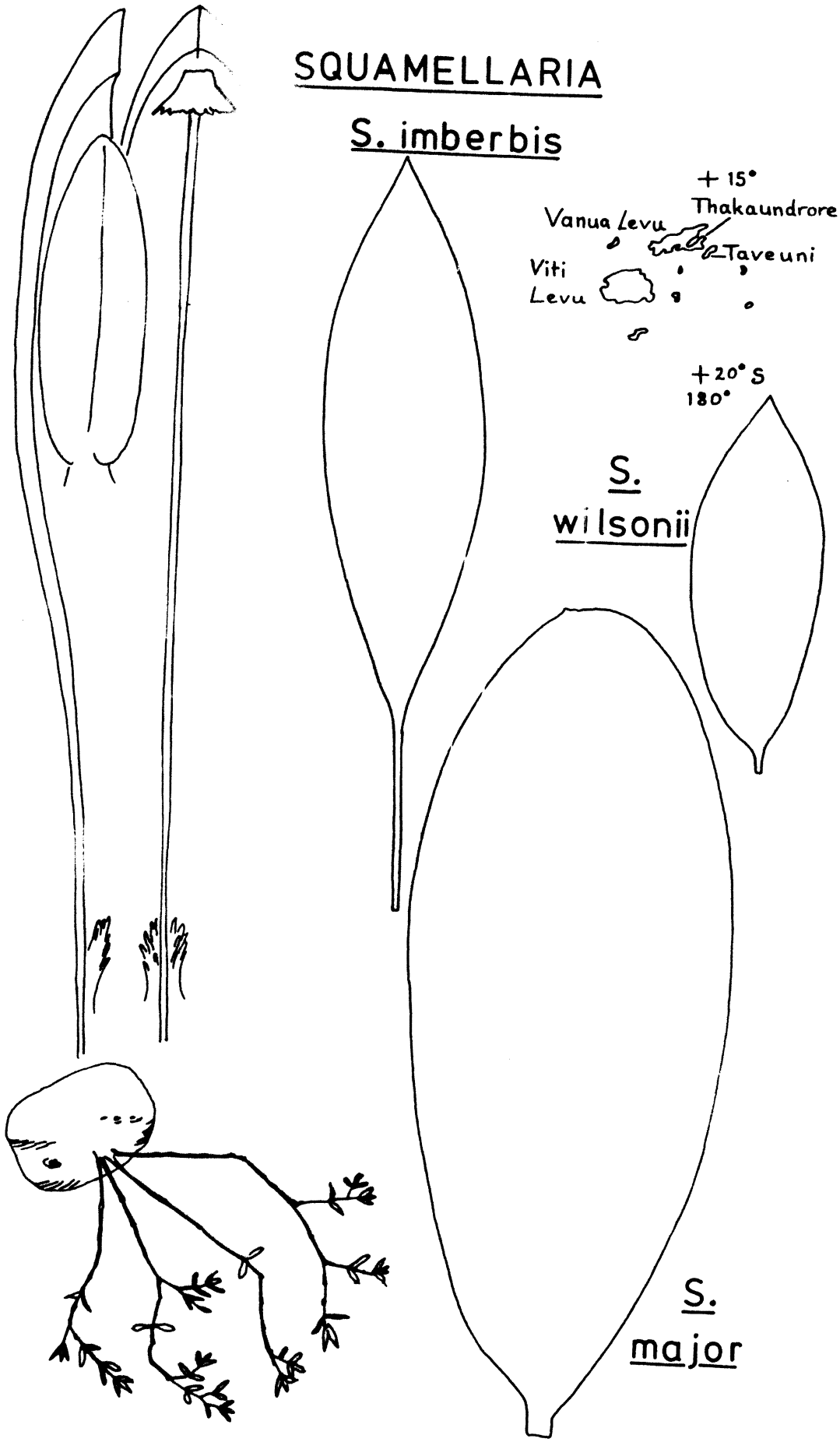

SQUAMELLARIA
S. imberbis
+ 15°
Thakaundrore
Vanua Levu
Taveuni
Viti
Levu
+ 20° S
180°
S.
wilsonii
S.
major

Fig. 24.

Ecology In dense forest at 300-400 m.

Distribution Fiji.

SE 16°30' 179°19' Vanua Levu, Thakaundrore, Yanawai R. Region, Mt. Kasi, Smith 1787 (BISH not seen, GH, K, P). Locality uncertain: Vanua Levu, Smith 564 (?BISH not seen); Seemann sn (type).

Discussion This species is rather similar to the next and they may represent subspecific variants since one is found on Vanua Levu and the other only on the neighbouring island.

3. SQUAMELLARIA WILSONII (HORNE EX J.G.BAKER) BECC., Malesia 2:229, tab.46,13-21 (1886); Smith, Contrib. U.S. Nat. Herb. 37:91 (1967). FIG.24. - Type: Fiji, Horne 1139 (K). Hydnophytum wilsoni Horne, A Year in Fiji :263 (1881); Baker, J. Linn. Soc. Bot. 20:365 (1883). - Type: as above.

Stem 0.3-0.5 cm diameter. Leaves 7x2 - 14x3.8 cm. Lamina narrowly elliptic, apex acute, base cuneate. Petiole 2-3.5 cm. Midrib rounded, prominent below, yellowish above; lateral nerves 5-7. Stipules to 0.2cm. Inflorescence: calyx translucent. Corolla glabrous without. Pollen 170-190 µm (Plate 7d).

Ecology Montane forest at 300-900 m.

Distribution Fiji, Taveuni.

SE 16°48' 179°58' western slope between Somosomo and Wairiki, Smith 750 (BO, GH, P). 16°50' 179°59' slopes of

Manuku, E of Wairiki, Smith 8191 (GH, L, P) & Smith 8326 (K, L, P). Locality uncertain: Qacavulo Est., Smith et al Fl. Fiji 16935 (BRI); Forest Creek Est., Horne 1139 (type).

Discussion see previous species.

4. SQUAMELLARIA MAJOR A.C.SMITH, Contrib. U.S. Nat. Herb. 37:90 (1967). FIG.24. - Type: Fiji, Smith 8323 (US not seen, BISH not seen, K, L).

Tuber to 40cm long. Stem 0.4-0.8 cm diameter; internodes c. 1.5cm. Leaves 11x3.5 - 17x6.5 cm. Lamina undulate, narrowly obovate, apex rounded and apiculate, base rounded, rapidly decurrent to petiole which is 0.3-0.5 cm long. Nerves prominent above and below; midrib sometimes apparently bifurcating towards the leaf apex; lateral nerves 5-7, arched and anastomosing. Stipules 0.3-0.4 cm. Inflorescence: calyx thick, leathery, not translucent when dry. Corolla sparsely hairy on outer surface of lobes. Pollen 115-130/um.

Ecology Dense forest at 300-600 m.

Distribution Fiji, Taveuni.

SE 16°50' 179°59' slopes of Mt. Manuka, E of Wariki, Smith 8323 (type).

Discussion All the leaves seen appear slightly diseased along some of the nerves, this may have influenced the leaf shape and the nerves.

XVI. *Myrmecodia*

1. INTRODUCTION

2. THE OCHLOSPECIES *MYRMECODIA TUBEROSA* AND ITS SATELLITE

   a) *M.tuberosa* Jack
   b) *M.tuberosa* 'tuberosa'
   c) *M.tuberosa* 'versteegii'
   d) *M.tuberosa* 'muelleri'
   e) *M.tuberosa* 'oninensis'
   f) *M.tuberosa* 'pulvinata'
   g) *M.tuberosa* 'dahlii'
   h) *M.tuberosa* 'salomonensis'
   i) *M.tuberosa* 'manusensis'
   j) The satellite *M.beccarii*

3. POLYTYPIC AND VARIABLE SPECIES

   a) *M.albertisii* and its satellite *M.angustifolia*
   b) *M.erinacea*
   c) *M.melanacantha*

4. GROUPS OF CLOSELY RELATED SPECIES

   a) *M.platytyrea* / *M.pendens* / *M.sterrophylla*
   b) *M.archboldiana* / *M.brassii*
   c) *M.longissima* / *M.oblongata*

5. TAXONOMICALLY ISOLATED SPECIES

   a) *M.pendula*
   b) *M.wauensis*
   c) *M.lamii*
   d) *M.pteroaspida*
   e) *M.hydnostipula*

6. UNCERTAIN AND LITTLE KNOWN SPECIES

   a) *M.decasperma*
   b) *M.lanceolata*
   c) *M.longifolia*
   d) *M.longispina*
   e) *M.schlechteri*
   f) *M.species 1 'angi-gita'*
   g) *M.species 2 'mamberamoensis'*
   h) *M.species 3 'rouffaerensis'*
   i) *M.species 4 'wisselensis'*

1. INTRODUCTION

Delimitation of the species in Myrmecodia is rarely sharp, only a few of the well-collected species are indisputable in their limits. Many species are restricted in range, and more extensive species often vary considerably, especially in leaf characters.

Subgeneric groupings are not clear in Myrmecodia, so the species are arranged here according to the type of species; first the most variable, then those which fall into groups and finally those which are clear-cut and isolated. This gives a picture of the constituents of the genus without suggesting evolutionary patterns.

No herbaria are quoted for the UPNG (University of Papua New Guinea) numbers, after publication they will be distributed to UPNG, L, K, FHO, CANB and BO.

2. THE OCHLOSPECIES MYRMECODIA TUBEROSA AND ITS SATELLITE

The concept of M.tuberosa is extended here to include a whole variable continuum from Indochina and the Philippines to Australia and the Solomon Islands. The species does not fall readily into discrete, replacing units and should therefore be regarded as an ochlospecies. The material from north and west of New Guinea has not been examined in detail and is referred to as M.tuberosa 'tuberosa'. In New Guinea the pattern has been examined in more detail, and descriptions of the main variants are given; these largely

follow existing specific epithets. These units are not sufficiently discrete to name as subspecies and are therefore given informal 'nicknames'. The reasons for this nomenclature are given in Chapter VI 2.

a) **Myrmecodia tuberosa Jack**

[Nidus formicarum ruber Rumphius, Herbarium Amboinense :119, tab. 55 (1750).]

M.tuberosa Jack, Trans. Linn. Soc. Lond. 14:123 (1823); Blume, Bijd. Fl. Ned. Ind. :1001 (1826); Beccari, Malesia 2:99, tabs. 13-14 (1884); Merrill & Perry, J. Arn. Arb. 26:26 (1945). - Type: Sumatra, Jack sn (†).

Lasiostoma tuberosum (Jack) Sprengel, Syst. Veg. 1:422 (1825). - Type: as above.

M.echinata Gaudich., in Freycinet, Voyage autour du Monde :472 (1830). - Type: as above.

M.inermis non Gaudich. DC, Prod. 4:450 (1830) - Type: as above.

M.armata DC, Prod. 4:450 (1830). - Type: Moluccas, Gaudichaud sn (G, P), syn. nov.

M.hispida sphalm. Richard, Mem. Soc. Nat. Hist. Paris 5:224 (1834).

- Type: as above.

M.kandariensis Becc., Malesia 2:100, tab.15 (1884) - Type: Sulawesi, Beccari 5516 (FI), syn.nov.

M.muelleri Becc., Malesia 2:102, tab.16 (1884); von Mueller, Papuan Plants :90 (1875). - Type: Papua New Guinea, D'Albertis 5904 (FI), syn.nov.

M.pulvinata Becc., Malesia 2:103, tab.17 (1884). - Type: Irian Jaya, Beccari P.P. 769 (FI), syn. nov.

M.bullosa Becc., Malesia 2:108, tabs.20 & 26 (1884). - Type: Irian Jaya, Beccari P.P. 184 (FI), syn. nov.

M.oninensis Becc., Malesia 2:110, tab.21 (1884). - Type: Irian Jaya, Beccari P.P. 51 (FI), syn. nov.

M.jobiensis Becc., Malesia 2:111, tab.22 (1884). - Type: Irian Jaya, Beccari 5507 (FI), syn. nov.

M.rumphii Becc., Malesia 2:117, tab.12,1-6 (1884). - Type: Seram, Beccari 5510 (FI), syn. nov.

M.goramensis Becc., Malesia 2:118, tab. 24 (1884). - Type: Moluccas, Beccari 5508 (FI), syn. nov.

M.salomonensis Becc., Malesia 2:175, tab.53,1 (1885). - Type: Solomon Islands, Guppy 141 (FI, K), syn. nov.

M.menadensis Becc., Malesia 2:176, tab.53, 2-7 (1885). - Type: Sulawesi, Teysmann sn (CAL not seen, FI), syn. nov.

M.vivipara Warb., Bot. Jahrb. 18:209 (1894). - Type: Papua New Guinea, Hellwig 357 (B†), syn. nov.

M.dahlii Schumann, Notiz. Bot. Gart. Berlin 2:153 (1898). - Type: Papua New Guinea, Dahl sn (B), syn.nov.

M.pentasperma Schumann, Notiz. Bot. Gart. Berlin 2:154 (1898). - Type: Papua New Guinea, Dahl sn (B), syn.nov.

M.apoensis Elmer, Leafl. Philipp. Bot. 3:1040 (1911). - Type: Philippines, Elmer 11261 (?PNH not seen), syn.nov.

M.sibuyanensis Elmer, Leafl. Philipp. Bot. 3:1041 (1911). - Type: Philippines, Elmer 12336 (BM, BO, FI, G, K, L, ?PNH not seen, W, WRSL), syn. nov.

M.urdanetensis Elmer, Leafl. Philipp. Bot. 5:1876 (1913). - Type: Philippines, Elmer 14083 (?PNH not seen), syn. nov.

M.paucispina Valeton, Bot. Jahrb. 61:150 (1927). -Type: Papua New Guinea, Schlechter 14178 (B†, L photo, WRSL rubbing), syn. nov.

M.peekelii Valeton, Bot. Jahrb. 61:147 (1927). - Type: Papua New Guinea, Peekel 468 (B†), syn. nov.

M.sorsogonensis Elmer, Leafl. Philipp. Bot. 9:3253 (1934). - Type: Philippines, Elmer 15964 (BM, BO, FI, G, K, L, P, ?PNH not seen), syn. nov.

Tuber 12x6 - 40x15 cm, shapes various. Ridges, entrance holes over the surface and pores present or absent. Spines present or absent, usually simple, sometimes branched or club-like. Stems one to few, branched or unbranched. Clypeoli present or absent. Alveoli present, sometimes densely filled with cushion-like masses of bract hairs. Leaves 10x3 - 47x14 cm, leathery or thin. Lamina elliptic, oblanceolate or spathulate; apex acute or acuminate; base abruptly to gradually tapered. Midrib prominent below, whitish or green. Petiole 2-13 cm. Stipules 0.5-1.5 cm, triangular. Inflorescence: bracts variable, to 8 mm, hairy. Calyx 0.5-3 mm. Flowers heterostylous. Corolla white, c. 11 mm. Ring of hairs, anthers and stigma varying in relative position. Pollen 2-4 porate; apertures bordered or not; vesicles 1-3 (-4); reticulation fine to coarse. Stigma 4-6 lobed. Ovules

4-6. Fruit orange-red to pink, c. 7 mm long.

b) **M.tuberosa 'tuberosa'**

M.tuberosa Jack, Trans. Linn. Soc. Lond. 14:123 (1823); Blume, Bijd. Fl. Ned. Ind. :1001 (1826); Beccari, Malesia 2:99, tabs. 13-14 (1884); - Type: Sumatra, Jack sn (†).

Lasiostoma tuberosum (Jack) Sprengel, Syst. Veg. 1:422 (1825). - Type: as above

M.echinata Gaudich., in Freycinet, Voyage autour du Monde :472 (1830). - Type: as above.

M.inermis non Gaudich. DC, Prod. 4:450 (1830) - Type: as above.

M.armata DC, Prod. 4:450 (1830). - Type: Moluccas, Gaudichaud sn (G, P).

M.hispida sphalm. Richard, Mem. Soc. Nat. Hist. Paris 5:224 (1834). - Type: as above.

M.kandariensis Becc., Malesia 2:100, tab.15 (1884). - Type: Sulawesi, Beccari 5516 (FI), syn.nov.

M.rumphii Becc., Malesia 2:117, tab. 12, 1-6 (1884). - Type: Seram, Beccari 5510 (FI), syn. nov.

M.goramensis Becc., Malesia 2:118, tab. 24 (1884). - Type: Moluccas, Beccari 5508 (FI), syn. nov.

M.menadensis Becc., Malesia 2:176, tab. 53, 2-7 (1885). - Type: Sulawesi, Teysmann sn (BO, CAL not seen, FI, L), syn. nov.

M.apoensis Elmer, Leafl. Philipp. Bot. 3:1040 (1911). - Type: Philippines, Elmer 11261 (?PNH not seen), syn.nov.

M.sibuyanensis Elmer, Leafl. Philipp. Bot. 3:1041 (1911). - Type: Philippines, Elmer 12336 (BM, BO, FI, G, K, L, ?PNH not seen, W, WRSL), syn. nov.

M.urdanetensis Elmer, Leafl. Philipp. Bot. 5:1876 (1913) - Type: Philippines, Elmer 14083 (?PNH not seen), syn. nov.

M.sorsogonensis Elmer, Leafl. Philipp. Bot. 9:3253 (1934). - Type: Philippines, Elmer 15964 (BM, BO, FI, G, K, L, P, ?PNH not seen), syn. nov.

Tuber as for the species except spines not club-like. Stem often clypeolate (this character is rare in other variants). Leaves as for the species, but not spathulate. Inflorescence as for the species. Pyrenes sometimes horned.

Ecology varied.

Distribution Indochina, the Philippines, Malaysia and Indonesia excluding Irian Jaya.

Vietnam: Annam, Blao, nr. Haut Douai, Poilane 23550 (P).

Philippines: NE 16° 121° Luzon, Mt. Province, Pugu, Banue, Ifuga, Conklin & Buwaya PNH 78749 (A, K, L). 16° 121° Luzon, Prov. Nueva Vizcaya, nr. Dupax, Mcgregor BS 11312 (BM). 15°121° Luzon, Sierra Madre, Jacobs 7977 (K, L). 14°120° Luzon, Bataan Prov., Lamao R., Mt. Mariveles, Whitford 1144 (K). 13°122° Quezon, Hinabaan, Guinayangan, Mendoza PNH 97950 (L). 12° 122° Sibuyan, Giting Giting, Elmer 12336 (type of M.sibuyanensis). 12° 124° Luzon, Bulusan, Elmer 15964 (type of M.sorsogonensis). 8° 125° Mindanao, Butuan, Fenix BS 15892 (A). 8° 125° Agusan, Cabadbaran, Mt. Urdaneta, Elmer 14083 (type of M.urdanetensis). 6° 125°

Mindanao, Davao, Todaya, Mt. Apo, Elmer 11261 (type of M.apoensis).

Peninsula Malaysia and Singapore: NE 05° 102° Kelantan, Kampong Kubang, Haniff 10217 (BM, BRI, SING). 05° 103° Sungai Ayer Maras Jenaja, Henderson SFN 20450 (BO). 04° 100° Perak, Taiping, Simpang, Krian Rd., Haniff SFN 13288 (SING). 04° 101° Kelantan, Gua, Panjung Ulu, UNESCO Limestone Exped. Fl. Malaya 668 (SING). 04° 102° Pahang, S Sat, Ulu Tembeling, Henderson SFN 21973 (SING). 03-04° 102° Pahang, Sungai Tohan, Holttum SFN 20827 (BO, SING). 03° 103° Pahang, Kuantan, Telok, Sisik, Henderson sn, 1929 (SING). 01° 103° Singapore, Sungai Jurong, Ridley 3854 (SING) & Ridley 81061 (SING). 01° 103° Singapore, Bukit Timah, Ridley sn, 6:1886 (SING). 01° 103° Pulau Pisang, Burkill & Kiah 667 (SING). Locality uncertain: Pahang Kwala, Ridley 1462 (BM). Pahang, Davison sn, 1886 (SING).

Sumatra: NE 03° 98° Residentie S.O.K., Tingi Radja, Joehems 7 (BO). SE 00° 98° Batoe Is., Raap 637 (BO). 00° 99° West coast, G. Taloe, Bunnemeijer 184 (BO). 00° 100° E of Pajakumbuh, R. Tjampo, Taram, Meyer 6745 (L). 01° 98-99° Siberut, Iboet 63 (BO, L), Boden-Kloss 12299 (BO, K) & Witten sn, 1978-9 (BO).

Borneo: NE 05° 117° Pangkalang Weslerafd, Dunselman 153 (BO). 05°118° Sq Susuk, N of Sanghuliang, Kostermans 6198 (BO). 04°114° Brunei, Tutong Distr., van Niel 4330 (L). 04° 114° Baram, Haviland & Hose sn, 2:1894 (K). 04°114° Baram, Lobok Pasir, Anderson 9873 (L, SING). 03° 113-114° Dulit Ridge, Richards 2163 (K). 01°110° Telok Asam, Bako Nat. Pk., Purseglove 489 (A, K, L). 00°116° W Kutei, Kelindjan R., nr.

Melan, Kostermans 9619 (BO). SE 01° 116° Sq Wain Region, N of Balipapan, Kostermans 21578 (BO). 02° 112° 10km W of Sampit, Buwalda 7834a (BO, L). Locality uncertain: Danau Pentoelah, Polak 1933 (BO, L).

Sulawesi: NE 01° 124° Menado. Teysmann 5308 (type of M.menadensis). 01° 124° Tomohon, Koorders 18621 (BO). 01° 124° Menado, Bloembergen 4070 (L). SE 04° 120° Bone, Nengo, van der Pijl 773 (BO). Locality uncertain: Kandar, Beccari 5516 (type of M.kandariensis).

Moluccas: NE 02°128° Morotai, Kostermans 9681 (BO). 02° 128° Morotai, Lam 3660 (BO). SE Rawak, Waigeo, Gaudichaud sn, sd (type of M.armata). 03°126° Buru Is., D'Urville 97 (P). 02°129° Seram, Tg Parigi b. Wahai, Kornassi 229 (BO, L). 02-3°129° W Seram, Batoe Lhinia, Eyma 2463 (BO). 02-03°128° W Seram, Salahoetoe, Biv.III, Eyma 3100 (BO). 02-03°128° W Seram, Hatoe Walkone, Eyma 2572 (BO). 02-03°129° Seram, Eyma 2979 (BO). 03°129° S Seram, Rohua Village, UPNG 3451. 03° 128° Amboin, Soya di Atas, Wiljes-Hissink 27 (A, L). 03°128° Amboin, van der Pijl 779 (BO). 04°131° Goram, Beccari sn 4:1872 (type of M.goramensis). 06°134° Aru Is., Trangan, Ngaibor, Buwalda 5401 (BO, L) & Buwalda 5313 (BO).

Java: SE 06°106° Bantam, Tjitoiak & Moentjang, NW of Tjitvedjah, Anon 844. 06°106° Batavia Residentie, G. Liiang, Kp. Karangtengah, van Steenis 2444 (BO). 06°106° by Buitenzorg, G. Pantjar, Koorders 40362 (BO) & Hochreutiner 1851 (G). 06°106° Leuwiliang, G. Sodang, Bakhuizen van den Brink 5291 (BO) & 77g (BO). 06°106° Bantam, Backer 1844 (BO). 06°106° Salak, Buitenzorg, Lecomte & Finet sn, 1.1912 (P).

07° 107° Nangela, van Leeuwen 12054 (L). Locality uncertain: G. Tjipaelih, by Tjiampba, Tjipaleuh, Bakhuizen van den Brink 4210 (BO). Tjibjoeroeg, Tjidadap by Tjiberber, Residentie Guiangan, Bakhuizen van den Brink 7018 (BO). Blume 22 (L).

Lesser Sunda Islands: SE 08° 120° Flores, Kae Valley, Puangkeko Crk., Schmutze 3084 (L). 08°120° Flores, Mt. Mandusawa to Rana Ka, Schmutze 3390 (L). 08°119-122° Flores, Tempat, Pong Nggeok, Verheijen 2348 (L). 09°124° Timor, Naepesu-Mutis, Schmutze 2322 (L). Locality uncertain: Sumba, Verheijen 4091 (L). Portugese Timor, Fuiloro, van Steenis 18331 (L). Timor, Bioba-Oi Poela, Bloembergen 3419 (L).

Discussion M.tuberosa 'tuberosa' includes some rather distinct variants. For instance on Siberut and Sulawesi there are clypeolate forms with long petioles and narrowly obovate, acuminate laminae. Plants from the Lesser Sunda Islands tend to have rather long narrow leaves, as does one plant from Borneo. The pattern is particularly complex in the Moluccas where both leaf-shape and texture, and armature vary considerably (Fig.14).

c) **M.tuberosa 'versteegii'**

FIG. 25.

Tuber cylindrical with rings or arcs of entrance holes surrounding raised areas usually with more entrance holes; pores absent. Spines absent to dense, usually branched, often clustered round the entrance holes. Stems: alveoli deep, with thickened rims. Spines absent or few. Leaves 22x7 - 30x11 cm. Lamina spathulate; apex acuminate. Petiole c.2 cm. Inflorescence: flowers (3). Corolla tube with ring of hairs c. half way up. Anthers at apex of corolla tube. Pollen 2-porate, 1-vesiculate; reticulation medium.

Ecology In rainforest at 50-580 m.

Distribution Inland areas of New Guinea.

Irian Jaya: SE 03°32' 139°14' Bernhard Camp, Brass 13829 (A, BO, L). 04°45' 138°48' Van Weels camp, Versteeg 1177 (BO). Locality uncertain: Rouffaer River, van Leeuwen 10361 (A, BO, K, L).

Papua New Guinea: SE 08°31' 147°00' Central Prov., Mafulu, Brass 5496 (A, BO, BRI). Locality uncertain: Gulf Prov., Purari R., Wabo Crk., UPNG 3479.

Discussion This variant is distinguished by its spathulate leaves and the raised areas on the tubers surrounded by and covered with entrance holes (Fig. 15). The latter condition is approached in rainforest forms of M.tuberosa 'muelleri'.

Myrmecodia tuberosa 'versteegii'

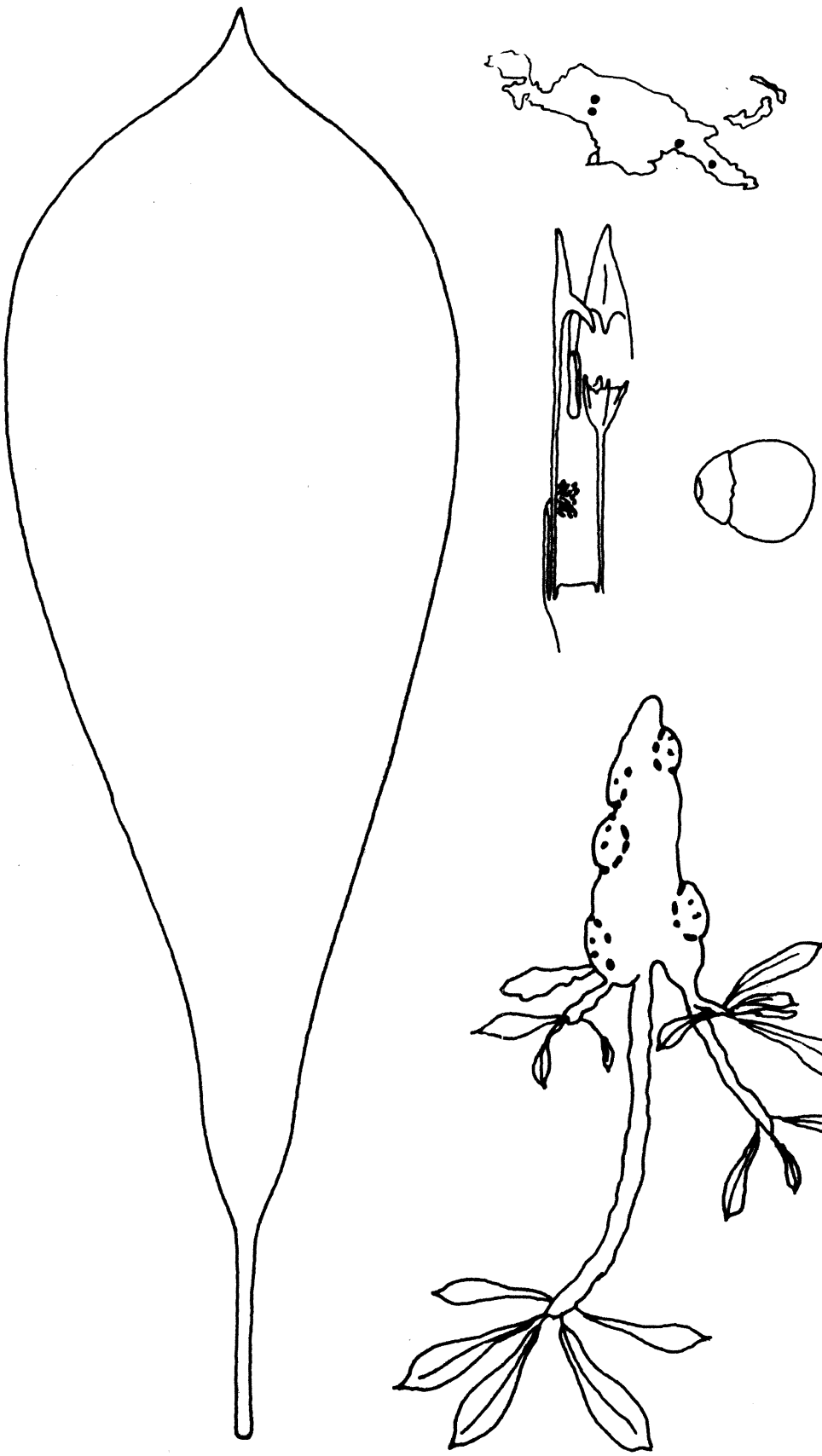


Fig. 25.

d) **M.tuberosa 'muelleri'**

M.muelleri Becc., Malesia 2:102, tab.16 (1884); von Mueller, Papuan Plants :90 (1875). - Type: Papua New Guinea, D'Albertis 5904 (FI), syn. nov.

M.bullosa Becc., Malesia 2:108, tabs.20 & 26 (1884). - Type: Irian Jaya, Beccari P.P. 184 (FI), syn. nov.

M.jobiensis Becc., Malesia 2:111, tab.22 (1884). - Type: Irian Jaya, Beccari 5507 (FI), syn. nov.

M.vivipara Warb., Bot. Jahrb. 18:210 (1894). - Type: Papua New Guinea, Hellwig 375 (B†), syn. nov.

M.paucispina Valeton, Bot. Jahrb. 61:150 (1927). - Type: Papua New Guinea, Schlechter 14178 (B†, L photo, WRSL rubbing), syn. nov.

Tuber rounded to irregular. Honeycombing not usually well-developed. Spines usually simple, short and stout. Stem 1-few, branched. At least the younger alveoli filled with cushion-like masses of protruding bracts. Spines usually few or absent. Leaves 10x3 - 22x7 cm, leathery. Lamina obovate to oblanceolate; apex acute to shortly acuminate. Petiole 2-6 cm. Inflorescence: bracts hairy, sometimes forming dense masses. Flowers (5). Corolla 10 mm, lobes 4 mm. Ring of hairs near base of tube. Anthers at apex of tube; filaments 1-2 mm. Pollen 1-3 vesiculate, apertures not bordered, reticulation fine to coarse (Plate 2a). Pyrenes 4-7.

Ecology Coastal trees, savanna and rainforest, extending to 1000m.

Distribution New Guinea and Australia.

Irian Jaya: SE 00°53' 131°15' Sorong, Beccari P.P.(type of M.bullosa). 01°08' 136°05' Biak, Oregon Trail, Brongersma sn, 15:2:1952 (L). 01°35' 135°42' Ansus, Jappen Is., Beccari 5507 (type of M.jobiensis). 05°01' 138°39' Bivak Eiland, Pulle 31 (L).

Papua New Guinea: SE 03°12' 141°21' W Sepik, Kilifas Village, NGF 48201 (K, L, LAE). 05°41' 141°43' Western Prov., Palmer R. 3km below Black R. junction, Brass 6936 (A). 06°30' 147°46' Morobe, Sattelberg, Clemens 281 (BR, L). 06°31' 143° 10' 20km SW of Lake Kutubu, Waro, Jacobs 9234 (L). 06°36' 147'51' Finschafen, Hellwig 375 (type of M.vivipara). 06°40' 146°47'Morobe, 20km SW of Lae, Hartley 9782 (A). 06°54' 146° 38' Morobe, Perakles Pass, UPNG 3462. 07°20' 146°50' Morobe, c. 6 km E of Kaisenik, UPNG 5946. 09°01' 146°57' Central Prov., Kanosia, Carr 11517 (A, K, L, SIN). 09°15' 147°13' Central Prov. 4km SE of Brown R., UPNG 3477. 09°22' 147°22' Central Prov., Hombrom Bluff, UPNG 3432, UPNG 3434 & UPNG 5944. 09°25' 147°22' Central Prov., entrance to Varirata Nat. Pk., UPNG 5943. 09°23' 147°17' Central Prov., Ilimo Fm., UPNG 3414. 09°26' 147°36' Central Prov., Musgrave R., UPNG 3427. 10°10' 148°24' Kubiano, Cape Rodney, UPNG 3474. Locality uncertain: On route from Ramu to coast, Schlechter 14178 (type of M.paucispina). Morobe Prov., Lae, 3ml Agricultural Stn., Floyd 5392 (LAE).

Australia: SE 12°40' 143°20' Cape York, Iron Range, Brass 19305 (A, G, K, L) & Dunlop 1707 (CBG). 12°45' 143°15' Cook Distr., Tozers Gap, Gittins 1072 (BRI). 13°50' 143°10' McIlwraith Ra. 11km NE of Coen, Wrigley N.Q. 1655 (CBG). Locality uncertain: Cape York, Jones 2501 (BRI).

Discussion M.tuberosa 'muelleri' comprises a range of variation from small-leaved plants with dense cushions along the stem and short, simple spines on the tubers, to large-leaved forms in which the alveoli often become empty in older plants and the spines are frequently branched. These two variants show some ecogeographic separation, the small-leaved form being found in coastal vegetation and lowland savanna, especially along the south coast of Papua New Guinea and in Australia, while the larger leaved form is found in gallery and rainforest. There is much overlap, however, and the character correlations break down, so that only one form is recognized here. If two were named the large-leaved variant would be M.tuberosa 'paucispina' (Fig.15, Chapter VI 2).

e) **M.tuberosa 'oninensis'**

M.oninensis Becc., Malesia 2:110, tab.21 (1884). FIG.26. - Type: Irian Jaya, Beccari P.P. 51 (FI), syn. nov.

Tuber: spines short and simple. Stem pale grey. Alveoli more or less rimmed by short, simple or root-like spines; usually filled by somewhat hairy bracts. Leaves 16x3.5 - 25x5 cm, rather thin. Lamina apex acuminate. Petiole 3-9 cm. Inflorescence: flowers (3), heterostylous. Longistyle flowers with a ring of hairs a third the way up the tube; anthers just above the hairs. Pollen one vesiculate; apertures bordered; reticulation fine. Stigma at apex of tube. Brevistyle flowers with a ring of hairs a third of the way up the tube. Anthers at apex of tube. Pollen 1-2(-3) vesiculate; apertures unbordered; reticualation medium (Plate 2b). Stigma 6-lobed, just above the ring of hairs.

Myrmecodia tuberosa 'oninensis'

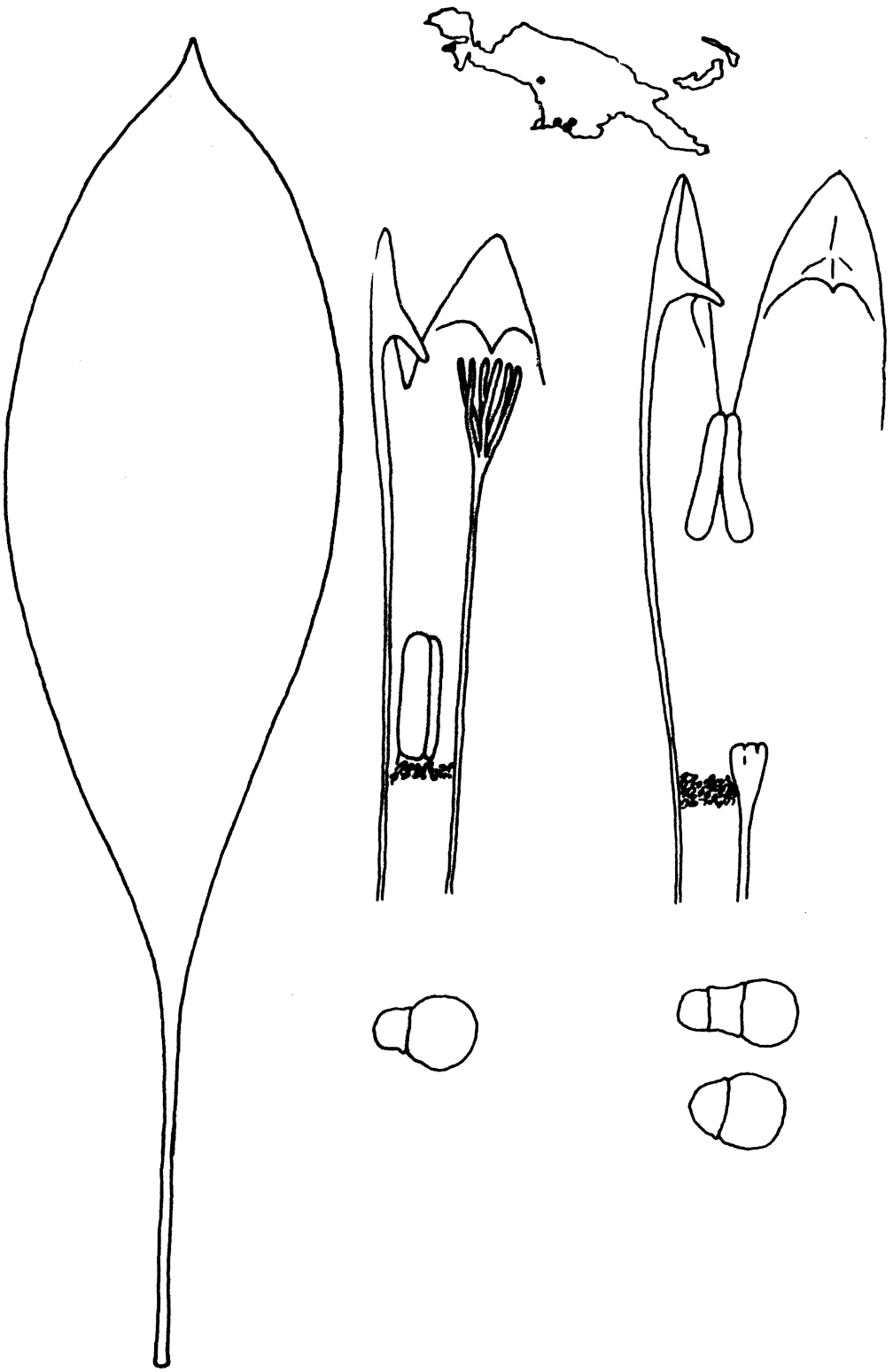


Fig. 26.

Ecology In Acacia-Melaleuca woodland at low altitudes.

Distribution Western Province of Papua New Guinea and southern Irian Jaya.

Irian Jaya: SE 08°06' 139°46' Merauke, Okaba, Branderhorst 85 (BO). 08°15' 140°44' Merauke, Mopa, van Royen 4551 (L). Locality uncertain: Onin, Kulo Kadi, Beccari 51 (type).

Papua New Guinea: Locality unknown: Western Prov., WLL 1312 (UPNG).

Discussion This variant is distinguished by the combination of narrow leaf-blades, long petioles, rather grey stems, weak spines and bordered pollen. A somewhat similar combination of characters occurs in New Ireland. The leaves of M.tuberosa 'oninensis' are, however, much smaller and the two variants are widely disjunct (Fig.15).

f) **M.tuberosa 'pulvinata'**

M.pulvinata Becc., Malesia 2:103, tab. 17 (1884). FIG. 27. - Type: Irian Jaya, Beccari P.P. 769 (FI), syn.nov.

Tuber conical to spherical; ridges more or less prominent. Spines club-like, on the ridges. Stem usually solitary, unbranched. Alveoli usually densely filled with bract hairs. Leaves 15x6 - 28x8 cm. Lamina obovate; apex acuminate; base decurrent. Petiole 1.5-5 cm. Inflorescence: flowers (3). Corolla 12mm, unci 3-4 mm. A narrow ring of hairs a third of the way up the tube. Anthers just above the hairs. Pollen one-vesiculate; apertures unbordered; reticulation fine (Plate 2c). Stigma at the same level as the anthers. Ovule number unknown.

Myrmecodia tuberosa 'pulvinata'

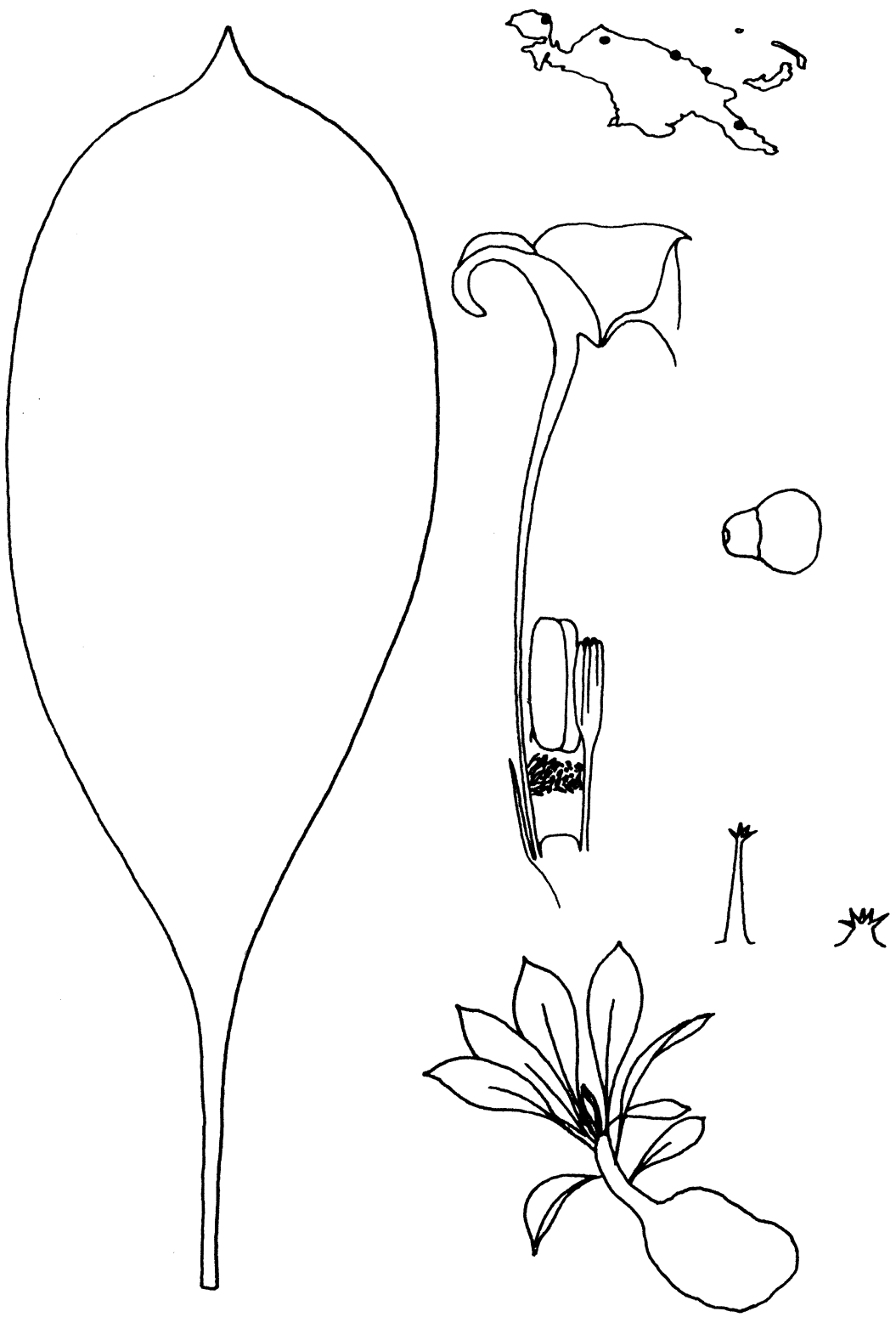


Fig. 27.

Ecology At 100-400m in more or less disturbed rainforest.

Distribution North coast of New Guinea.

Irian Jaya: SE 00°53' 134°05' Manokwari, Gibbs 6197. 00°55' 134°00' Fak Fak, Andai, Beccari P.P. 769 (type). 02°20' 138°00' Mamberamo R., Albatros Bivak, van Leeuwen 9642 (A, BO, K, L).

Papua New Guinea: 03° 143° 8km SE of Wewak, UPNG5904. 04° 145° Karkar Is., UPNG 5928. 08°50' 147°45'Kokoda, Millar TNG 23536 (LAE). 08°53' 147°44', Central Prov., Kokoda, Carr sn, 8:4:1936 (L).

Discussion This variant grades into M.tuberosa 'muelleri' which occasionally has club spines and similar leaves. They do, however, occupy ecogeographically distinct (Fig.15) areas and the flowers differ.

g) **M.tuberosa 'dahlii'**

M.dahlii Schumann, Notiz. Bot. Gart. Berlin 2:153 (1898). - Type: Papua New Guinea, Dahl sn, sd (B), syn. nov.

M.pentasperma Schumann, Notiz. Bot. Gart. Berlin 2: 154 (1898). - Type: Papua New Guinea, Dahl sn, sd (B), syn. nov.

M.peekelii Valeton, Bot. Jahrb. 61:147 (1927). - Type: Papua New Guinea, Peekel 468 (B†), syn. nov.

Tuber conical to cylindrical; ridges, entrance holes, pores, honeycombing and simple or root-like spines absent to conspicuous. Stem one to few, rarely branched. Leaves: Lamina lanceolate, sometimes narrowly so, rarely oblong or broadly ovate; apex acute or acuminate. Inflorescence: bracts hairy, not extending beyond alveoli. Flowers (4) heterostylous. In

brevistylous flowers a ring of hairs half way up the tube. Anthers at tube apex. Pollen 1- (2) vesiculate; apertures not bordered; reticulation fine. Stigma at anthers. In longistylous flowers a ring of hairs near base of tube. Anthers at tube apex. Pollen 2-vesiculate; apertures not bordered; reticulation coarse. Stigma above anthers. Pyrenes 4-6.

Ecology Coastal to 900m, often in rather open disturbed areas, eg plantations. Sometimes on limestone.

Distribution New Britain and New Ireland, Papua New Guinea.

New Ireland: SE 01°40' 150° 00' Kavieng Subdistr., Emira Is., Mussan, NGF 40467 (L). 02°22' 150°12' Lavongai (New Hanover), Cape Entrance, N. coast, LAE 65398 (A, L, LAE). 02°40' 150°56' 10km S of Kavieng on coast road, UPNG 3440. 03°07' 151°42' Konos on E coast, c. 4km inland, UPNG 3443, UPNG 3446, UPNG 3447 & UPNG 3448. 03°07' 151°43' Konos on E coast, coastal, UPNG 3442. 03°20' 151°50' Lelet plateau, Limbim Village, UPNG 5947, UPNG 5948. Locality uncertain: Paremecho Village, NW coast, UPNG 5949. Namatanai subdistr., Daufu R. basin, Coode sn, 31:1:1970 (LAE). Namatanai, Peekel 468 (type of M.peekelii).

New Britain: SE 04°13' 151°50' Gazelle Peninsula, Massava, Schlechter 13732 (L drawings). 04°15' 152°08' Gazelle Peninsula, Simpsonhafen, Rechinger 3987 (WRSL). 04° 20' 151°40' Gazelle Peninsula, road from Rabaul to Keravat, UPNG 3416. 04°23' 152°10' Gazelle Peninsula, nr. Toma, Rechinger 3642 (WRSL). 04°56' 151°26' Hoskins subdistr., crater rim of North Son, LAE 58513 (A, L). 05°01' 150°08' W side of central

Peninsula of Lake Dakataua, Willaumez Pen., 5km S of Cape Hollmann, LAE 66565 (LAE). 05°20' 150°30' W New Britain, 16km N of Kimbe, UPNG 3466. 05°30' 150°28' W New Britain, nr. Hoskins, UPNG 3449. Locality uncertain: Gazelle Peninsula, Ralum, Dahl sn (type of M.dahlii) & Dahl sn (type of M.pentasperma).

Discussion The specimens from the Bismarck Archipelago are variable with little correlation in such characters as leaf-shape, alveoli, spines and chambers of the tuber, ovule number and corolla structure. M.tuberosa 'muelleri', the most similar mainland variant, differs in its relatively wide, short petioled leaves and often densely filled alveoli.

At the eastern end of the range two collections of M.tuberosa 'dahlii' resemble M.tuberosa'oninensis' in their long narrow leaves, silvery white stems and often glabrous tubers. Other collections resemble M.tuberosa 'salomonensis' in flower, pollen and leaf characters (Fig.15, Chapter VI 3).

h) **M.tuberosa 'salomonensis'**

M.salomonensis Becc., Malesia 2:175, tab.53,1 (1885); Merrill & Perry, J. Arn. Arb. 26:31 (1945) descr. ampl. FIG.28. - Type: Solomon Islands, Guppy 141 (FI, K).

Tuber cylindrical, to 45x16cm. Spines absent or simple, weak to root-like, small, to 0.6 cm. Ridges slight, over non-honeycombed areas. Honeycombing well-developed with mounds bearing pores over each cell of the honeycomb. Stem usually solitary and unbranched. Clypeoli more or less well-developed. Spines as on tuber. Leaves 22x6.5 - 36x9 (-47x14)cm. Lamina elliptic; apex acuminate, or, less often, acute; base rather abruptly cuneate.

Myrmecodia tuberosa 'salomonensis'

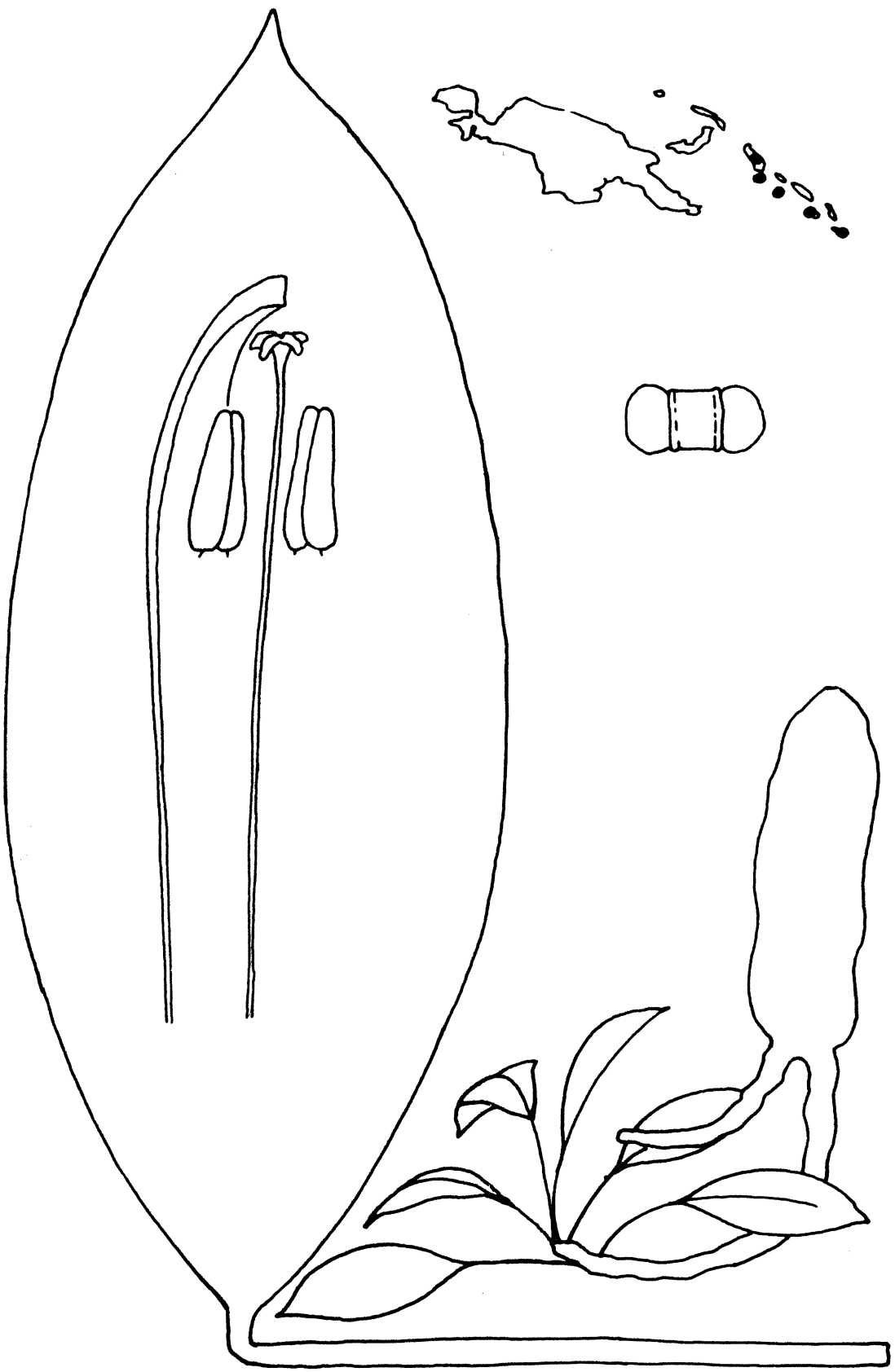


Fig. 28.

Lateral nerves c. 10. Petiole 5-13 cm. Stipules 1.3-2.0 (-3.0)cm. Inflorescence: bracts not conspicuous. Flowers (3). Calyx 1.0-1.5mm. Corolla 14mm; lobes 4-5mm; unci less than 1mm. A ring of hairs at the base of the tube is reported by Merrill & Perry but not seen again. Anthers at apex of tube. Pollen 2-vesiculate; apertures sometimes bordered; reticulation coarse, sometimes forming a broken network (Plate 2d).

Ecology Coastal and inland to 500m, mainly along rivers.

Distribution Bougainville and the Solomon Islands.

Bougainville: SE 04°30' 154°15' Nissan Is., Nachman 554 (LAE). 06°10' 155°20' Taki Village, SE of Toiumonapu Plantation, NGF 16410 (A, BO, BRI, K, L). 06°15' 155° 37' Kieta, Rechinger sn, 1905 (W).

Solomon Islands: SE 07°05' 155°45' Shortland Is., Guppy 141 (type). 08°20' 157°30' New Georgia, Waterhouse 162 (K). 09°20' 159°50' Guadalcanal, 8km along Umsami R., Hunt 2169 (BRI, L, P). 09°29' 159°59' Guadalcanal, Mt. Mambulu sumit, BSIP 7938 (K, L, SIN). 09°30' 160°00' Guadalcanal, Pendelton 448 (A). 10°27' 161°52' San Christobal, Waimamura, Brass 2585 (A, BRI, L). 10°29' 162°01' San Christobal, Warahito R. 10km inland, Whitmore RSS 6186 (A, K, L, P).

Discussion Though distinguished by its long petioles, large laminae, rather distinct clypeoli, massive, honeycombed tubers and pollen, this variant is not sharply differentiated from the variable populations in New Ireland. The tuber and pollen is similar to that of M.tuberosa 'manusensis'.

i) **M.tuberosa 'manusensis'**

FIG. 29.

Tuber cylindrical, reaching c.30x10 cm. Honeycombed areas raised and surrounded by entrance holes. Pores in rings on mounds over each of the honeycomb cells. Spines absent. Stems several, unbranched. Clypeoli present, rimmed by rather irregular, weak, simple spines. Leaves 18x8 - 28x9 cm, thin, wavey along the edges.Lamina apex acuminate, broadest above the middle, tapering evenly to the base. Petiole 1-2cm. Inflorescence: flowers (1). Corolla 12mm. A ring of hairs a quarter of the way up the tube. Anthers at apex of tube. Pollen 2-vesiculate; apertures not bordered; reticulation coarse. Stigma at anthers. Pyrenes 7.

Ecology On trees in mangrove swamps.

Distribution Manus Island, Papua New Guinea.

SE 02°01' 147°16' half way between Lorengau and airport, UPNG 3437. 02°10' 146'45' Metaphor Village, S coast, 21km W of Pelikawa, LAE 59269 (LAE). Locality uncertain: Sands 2927 (K).

Discussion This variant is distinct in its broadly oblanceolate, rather thin leaves with short petioles. Stem, tuber and floral characters suggest links with M.tuberosa 'salomonensis' and to a lesser extent M.tuberosa 'dahlii'.

j) **The satellite M.beccarii**

M.beccarii J.D. Hook., Bot. Mag. t.6883 (1886). FIG.30. - Type: Australia, Veitch sn, 1884 (FI, K).

Tuber irregularly cylindrical to 20x12 cm, pale grey. Spines simple, stout, to 0.4cm, bourne on mounds. Pores and entrance

Myrmecodia tuberosa 'manusensis'

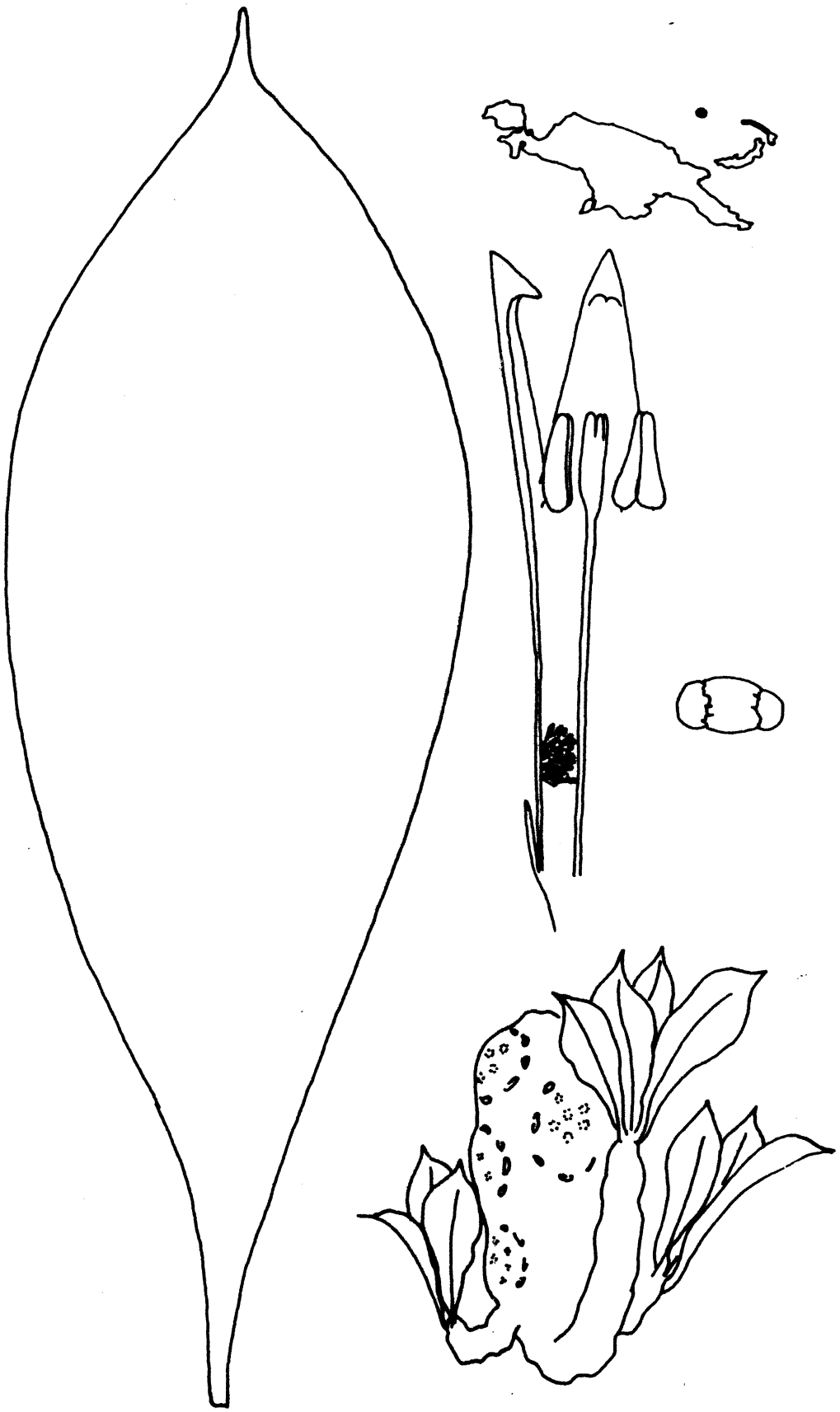


Fig. 29.

Myrmecodia beccarii

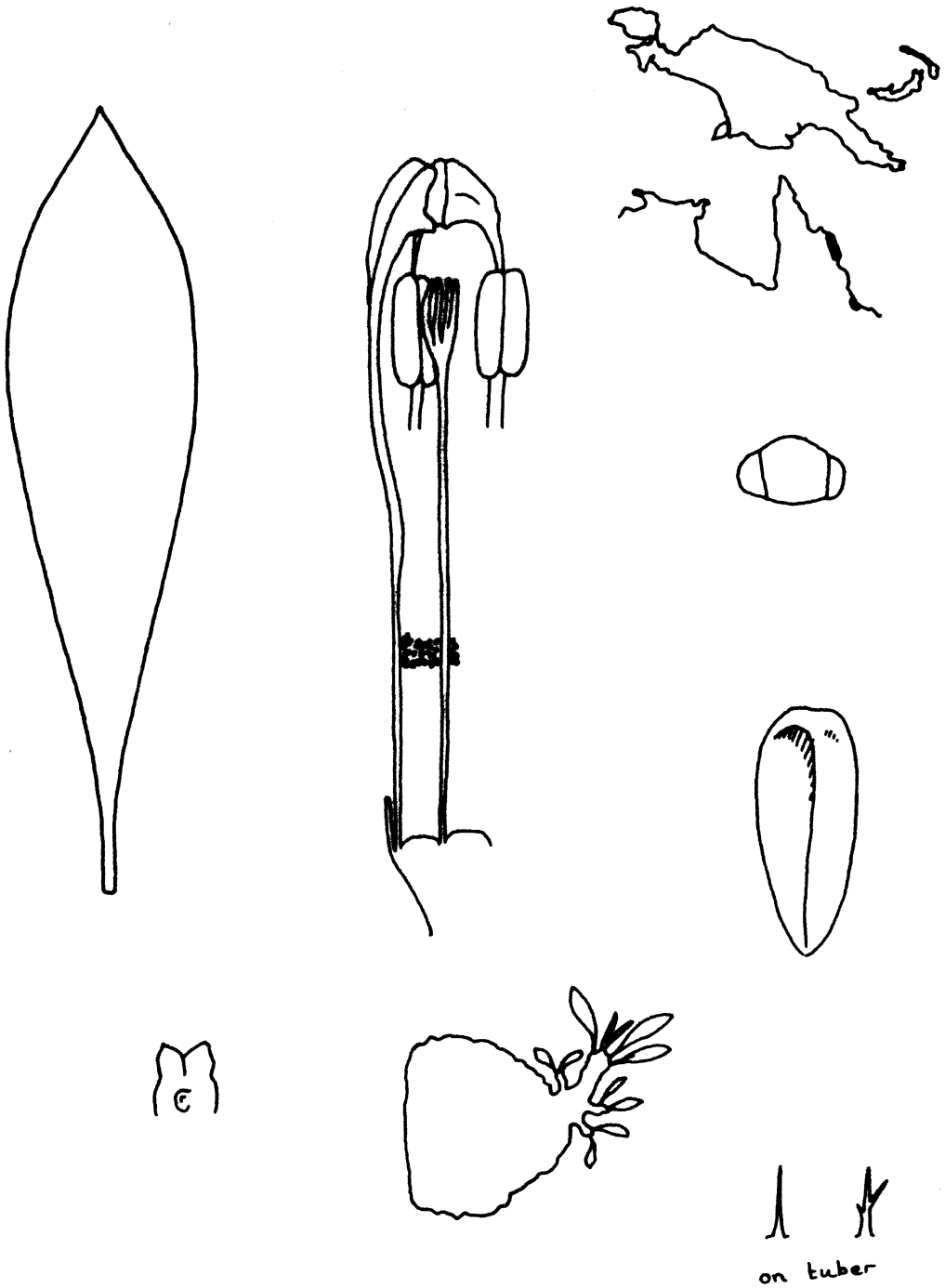


Fig. 30.

holes absent. Chambers rarely more than 1cm across, tissue between chambers broad 0.5-1.5 cm. Stems several, freely branched, pale grey, to 10x2.5 cm. Alveoli more or less round, with broad, fleshy rims. Spines sometimes present, scattered, simple or root-like. Leaves 9x2 - 12x3.5 cm, fleshy, pale green. Lamina elliptic; apex acute; base tapering gradually. Petiole 1-2cm, rounded in cross-section. Stipules triangular, 0.3 cm long, soon caducous. Inflorescence: bracts to 0.4cm, straw-coloured. Flowers (2). Calyx 1mm. Corolla white, 11mm; lobes 3mm. A ring of hairs just below the middle of the tube. Anthers at the mouth of the tube, blueish. Pollen 2-porate, 2-vesiculate; reticulation medium (Plate 6b). Stigma of 4 narrow lobes, at level of anthers. Fruit pink. Pyrenes 4.

Ecology On mangrove trees and in coastal Melaleuca savanna.

Distribution Australia, north east coast.

SE 15°20' 145°10' Cooktown, French sn (QRS). 15°25' 145°72' Endeavour R., Volck 4561 (BRI). 15°30' 145°10' 5km from Pt. Archer towards Cooktown, Wrigley NQ 1311 (CBG). 16°10' 145°20' Bailey's Crk., N of Daintree R., Wrigley NQ 939 (CBG). 16°50' 145°40' Cairns Inlet, Wah Day Crk., Flecker & Pearson NQ 2103 (BRI). 16°50' 145°0' Cairns Inlet, Cairns, UPNG 3492, UPNG 3493 & Anon NQ 82 (BRI). 18°30' 146°10' Forest beach, east of Ingham, Anon sn (CBG). Locality unknown: Gulf of Carpenteria (?), Veitch sn (type).

Discussion This species is distinctive in its small fleshy leaves and richly branched stems. It most closely resembles M.tuberosa 'muelleri' though there are no intermediates, and the populations are geographically isolated (Fig.13).

3. POLYTYPIC AND VARIABLE SPECIES

Although five species of Myrmecodia are considered to be polytypic or variable, two of these are treated in the next section as they are both related to one another and to other species.

a) **Myrmecodia albertisii and its satellite M.angustifolia**

i) **Myrmecodia albertisii** Becc., Malesia 2:112, tab.11 (1884); Valeton, Bot. Jahrb. 61:145 (1927); Merrill & Perry, J. Arn. Arb. 26:31 (1945). - Type: Papua New Guinea, D'Albertis sn, 1877 (FI).

Tuber conical to cylindrical, to 50x23 cm. Ridges sometimes present, slight. Spines sparse to dense, irregularly branched, stout and short, 0.4cm, to weak and long, 1.0cm. Honeycombing, pores and entrance holes present. Stem solitary, sometimes branched. Spines dense, as on tuber. Clypeoli absent. Alveoli indistinct, empty to densely filled with hairy bracts. Leaves 13x3 - 33x9, or - 32x6.5 cm. Lamina broadly to narrowly elliptic or oblanceolate. Midrib prominent below. Petiole 3-8 cm. Stipules to 1.2 cm, triangular. Inflorescence: flowers heterostylous, at least in part of the range. Corolla white, with a ring of hairs. Pollen heteromorphous (Plate 3). Fruit orange-red. Pyrenes 4-6.

Ecology Swamp savanna to mossy forest at 1600m.

Distribution Southern Papua New Guinea.

Discussion This taxon is extended here to include not only the type form from western Papua New Guinea, but also collections from Central Province and from the D'Entrecasteaux Islands off

the eastern tip of the mainland. Plants from these three disjunct areas are recognized as subspecies (Fig.16, Chapter VI 3).

Two other collections are provisionally regarded as geographically isolated variants of M.albertisii. One (Kalkman 4268 (A, L, LAE) from Irian Jaya, Star Mts., Sibil Valley, SE 04°55' 140°37') is distinguished by its long, narrowly acuminate leaf-tip, pale blue corolla and bi-lobed stigma (Fig.16e). It was found in Araucaria/Nothofagus forest at 1200-1300 m. The other (NGF 31855 (A, BRI, K, L) from Papua New Guinea, Western Prov., Ingembit Village, SE 05°38' 141°00') has acuminate leaves and long, narrow stipules, the corolla is similar to brevistyle M.albertisii ssp. albertisii (Fig.16f). Habitat - rainforest at 160m.

M.pendula may be a related species, but it differs in leaf-shape, petiole length and stem branching.

subspecies albertisii

FIG.31.

Tuber conical, pale grey. Spines dense, usually short and stout. Stem usually unbranched. Alveoli densely filled by hairy bracts. Leaves 15x4.0 - 34x9 cm, leathery. Lamina oblanceolate to elliptic; apex acuminate; base cuneate. Petiole 3-7cm. Inflorescence: flowers (3) heterostylous. Corolla lobes 2mm. In brevistylous flowers a ring of hairs near the base of the tube. Anthers at the apex of the tube. Pollen 2-vesiculate; reticulation coarse (Plate 3b). Stigma broadly 4-lobed, just above ring of hairs. In longistyle flowers a ring of hairs just below the middle of the tube. Anthers among hairs. Pollen 1-vesiculate; reticulation fine (Plate 3a). Stigma narrowly 6-lobed, above apex of corolla tube. Pyrenes 6.

Myrmecodia albertisii ssp. albertisii

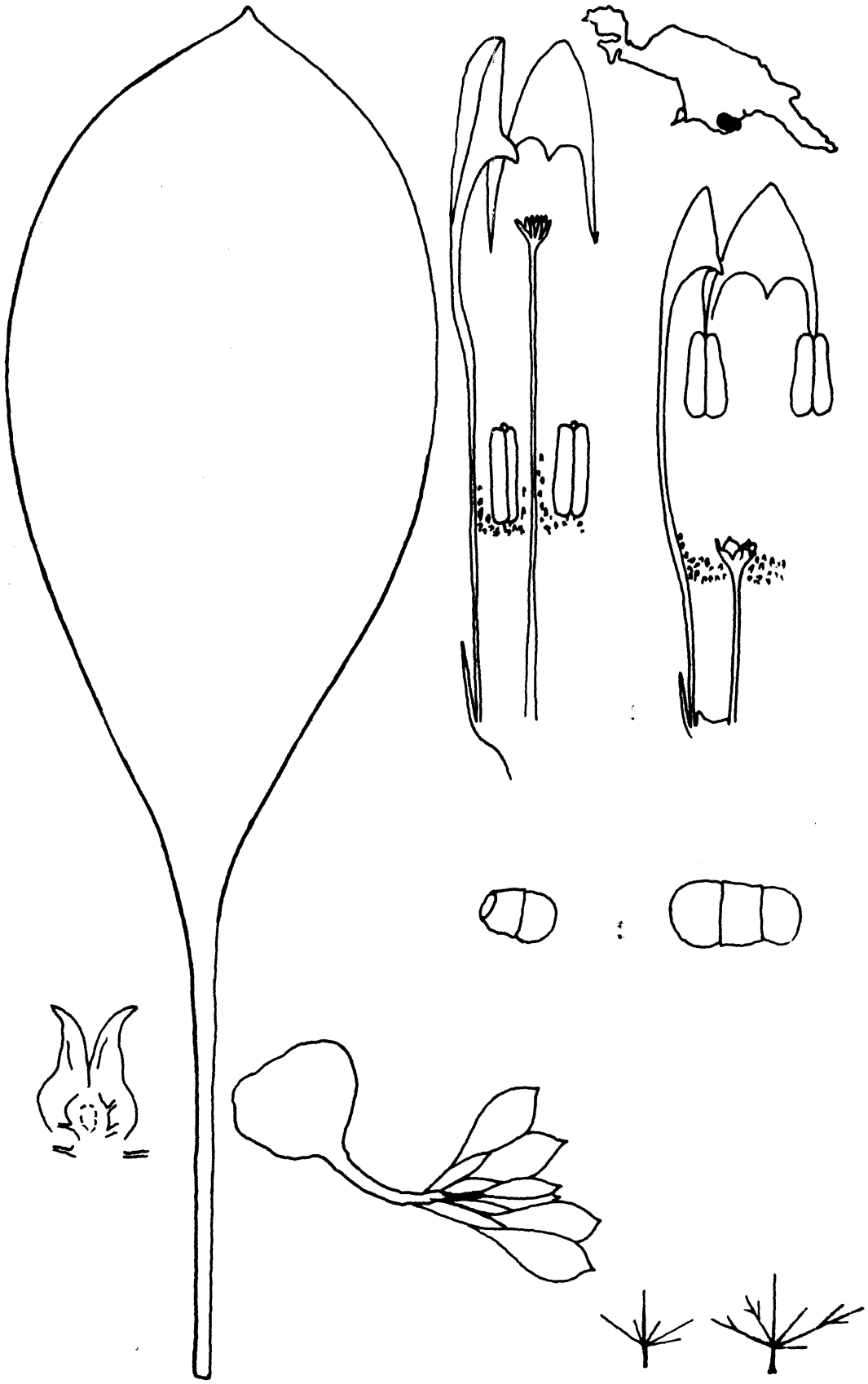


Fig. 31.

Ecology In lakeside trees and savanna of Tristania, Acacia and Xanthostemon.

Distribution Western Province of Papua New Guinea.

SE 07°33' 141°15' Lake Daviumbu, Brass 7599 (A, BM, BO, BRI, L). 08°50' 141°54' Tarara, Wassi Kusa R., Brass 8580 (A, BM, BO, BRI, L). 09°00' 143°10' Wuroi, Oriomo R., Brass 5848 (A, BO, BRI). Locality uncertain: Fly R., D'Albertis sn, 1877 (type). Western Prov., UPNG 5924.

subspecies koiariensis subsp. nov.

Tuber conical to cylindrical, 14x7.5 cm. Spines stout. Stem unbranched. Leaves 12x3 - 17x6.5 cm. Lamina elliptic; apex broadly acute; base cuneate. Petiole 3-5 (-6) cm. Stipules 0.5-0.8 cm. Inflorescence: bud only (2). Pollen one vesiculate; reticulation fine.

Ecology In secondary or dry sclerophyll forest at 1200-1900 m.

Distribution Central Province.

SE 09°05' 147°38' Boridi, Carr 14659 pro parte (K, L, LAE). 09°09' 147°40' N facing slope of mountain between Efogi and Launumu, LAE 60555 (A, L, LAE). 09°09' 147'41' nr. Lanumu, LAE 52469 (A, L, LAE).

Discussion The morphological characters and geographical distribution of ssp. koiarianesis are intermediate between the other two subspecies (Fig.16, Chapter VI 3a).

The duplicate of Carr 14659 at A belongs to M.wauensis, which is distinguished by its longer, fine spines, obconical corolla and triporate pollen.

subspecies dentrecastensis subsp. nov.

Tuber reaching 41x13 cm, cylindrical. Spines weaker and mostly longer than in the other subspecies, c.0.8 cm. Stem unbranched, to 16cm. Leaves 13x3.5 - 32x6.2 cm. Lamina narrowly elliptic; apex acute; base gradually tapered. Petiole 4.5-8 cm. Stipules 1.2 cm. Inflorescence: flowers (3). Corolla 10 mm; lobes 3.5 mm. Ring of hairs a third to half the way up the tube. Anthers at apex of tube. Pollen 1- (2)-vesiculate; reticulation fine. Stigma broadly 4-lobed, between the anthers and the ring of hairs. Pyrenes 4.

Ecology Mossy forest 820-1600 m.

Distribution D'Entrecasteaux Islands, east of New Guinea.

SE 09°19' 150°15' Goodenough Is., NE slopes of Mt. Oriadamawaia, UPNG 3499. 09°21' 150'16' Goodenough Is., E slopes, Brass 24889 (A, L). Locality uncertain: Normanby Is., Mt. Pabinama, Brass 25657 (A, L).

Discussion The collections from the two islands differ in leaf size, but are clearly consubspecific, Fig. 16d.

ii) **Myrmecodia angustifolia** Valeton, Bot. Jahrb. 61:144, in key (1927). FIG. 32. - Types: Irian Jaya, Pulle 471 (L) & Pulle 566 (L).

Tuber 10x4.5 cm, oblong, drying blackish, hanging by up to 50 cm of root. Spines dense, stellate branched, on ridges, to 0.7cm long. Pores and entrance holes not visible beneath dense spines. Chambers to 2 cm diameter; walls c.3mm. Stem solitary, unbranched, 10x1 cm. Clypeoli indistinct. Alveoli with cushion-like masses of bract hairs. Spines dense, simple, irregularly or stellate branched, on margins of alveoli and clypeoli. Leaves to 22x1.1 cm, leathery. Lamina tapering gradually at both ends. Midrib prominent below; lateral nerves obscure, 6-9. Petiole to 3cm, triangular, red. Stipules c. 0.6cm, united at the base only, forming a slight wing on the clypeoli. Inflorescence unknown.

Ecology Forest from 300 to 1600m, abundant in higher part of range (Lam, 1924, 1945).

Distribution Irian Jaya.

SE 03°20' 138°20' hill nr. Doormantop, Lam 1536 (BO). Locality uncertain: Mamberamo R., Perameles Bivak, Pulle 471 (type) and Pulle 566 (type).

Discussion Lam 1536 differs from the Pulle specimens in the white petioles and finer, irregularly rather than stellately branched spines. The Lam specimen is, however, immature. The floral characters suggest a relationship with M.albertisii.

Myrmecodia angustifolia

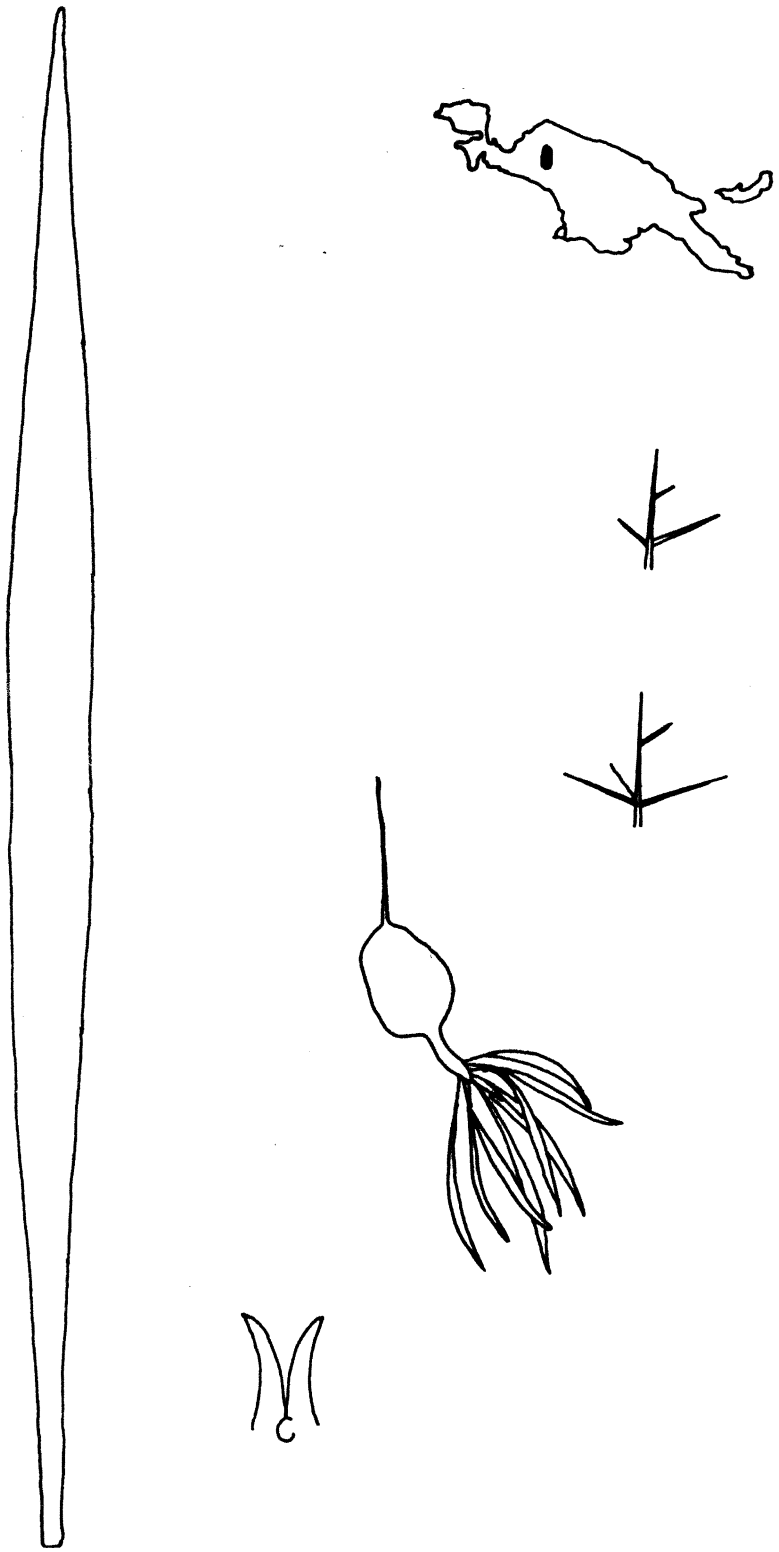


Fig. 32.

b) **Myrmecodia erinacea** Becc., Malesia 2:105, tab.12,7-11 (1884); Valeton, Nova Guinea 8:514 (1911); Valeton, Bot. Jahrb. 61:145 (1927); Merrill & Perry, J. Arn. Arb. 26:29 (1945). FIG.33. - Type: Irian Jaya, Beccari sn, 12:4:1875 (BM, FI, K).

M.alata Becc., Malesia 2:106, tabs.18 & 25 (1884). - Type: Irian Jaya, Beccari P.P. 758 (BM, FI), syn. nov.

M.aruensis Becc., Malesia 2:108, tab.19,1 (1884); Valeton, Bot. Jahrb. 61:145 (1927). - Type: Aru Is., Beccari sn, 3:1873 (FI), syn. nov.

M.prolifera Merr. & Perry, J. Arn. Arb. 26:30 (1945). - Type: Irian Jaya, Brass 13935 (A, BM, BO, BRI, L), syn. nov.

Tuber to 15x7cm, cylindrical. Spines (simple) slightly branched or stellate, to 0.7cm. Swollen areas with pores and honeycombing usually present; entrance holes few. Stem 1(-3), unbranched. Alveoli oval. Spines on alveoli rims, simple, dense; spines on stem surface few, sometimes branched. Leaves 15x4 - 28x7 cm, lamina spathulate, acuminate; or linear 25x2.5 - 35x3.5 cm. Midrib white, lateral nerves 10-25. Leaf margin sometimes recurved or crinkled. Petiole to 3 cm, white. Inflorescence: bracts obscure. Flowers (4), ? tristylous. Corolla greenish-blue; a ring of hairs half way up the tube. Stamens at apex of tube, or among the hairs. Pollen 2 (-3) vesiculate; apertures very broadly bordered (Plate 5c). Stigma 2-4 lobed, at or above anthers. Fruit yellow. Pyrenes 4.

Ecology In mangrove, swamp and river-plain forest, and on Quercus in Dillenia forest at 50m.

Myrmecodia erinacea

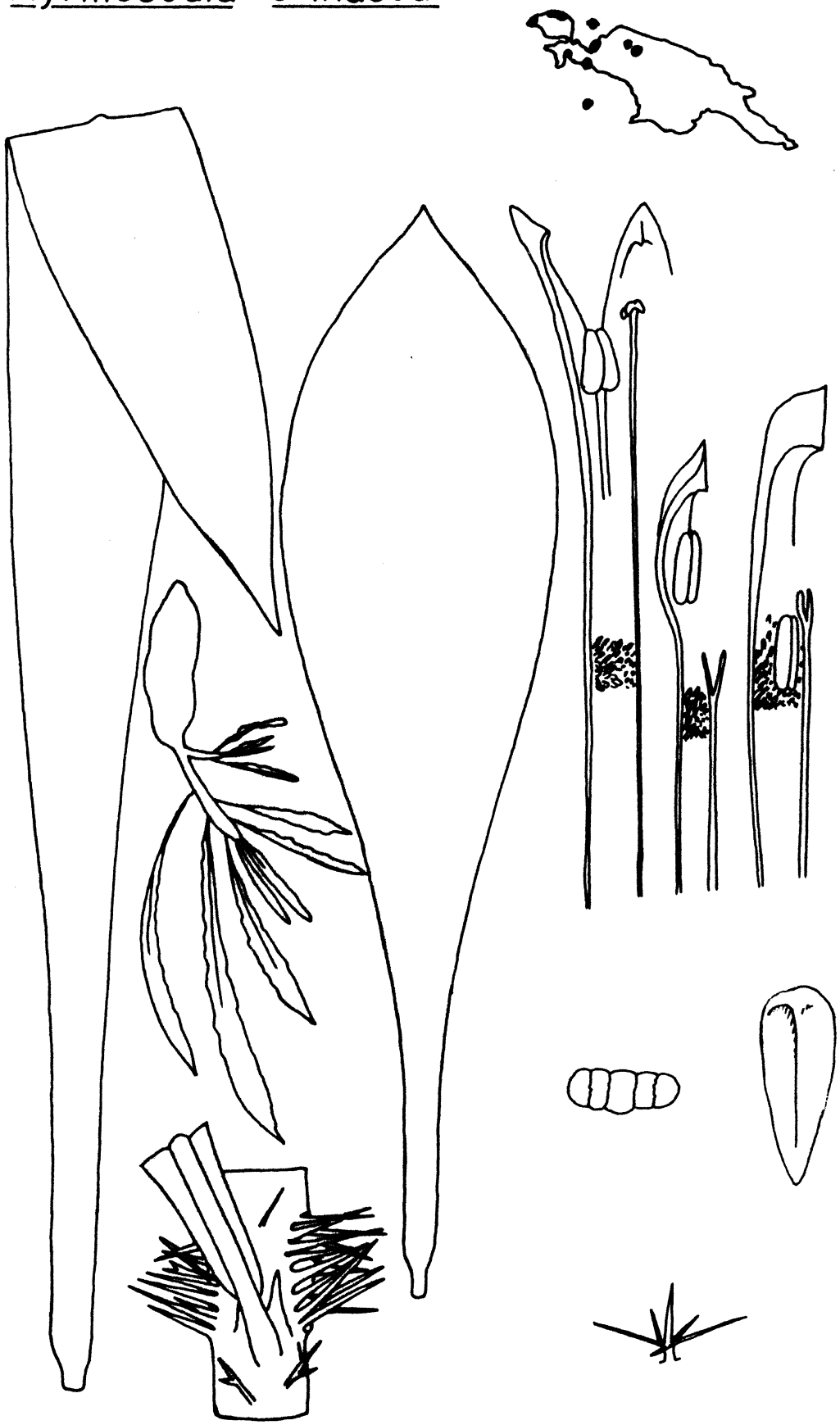


Fig. 33.

Distribution Irian Jaya.

SE 00°53' 131°15' Sorong, Mlasoen Hill, van Royen 3079 (L). 00°55' 134°00' Andai, Beccari P.P. 758 (type of M.alata). 01°44' 135°49' Japen Is., Ansus, Beccari sn, 12:4:1875 (type of M.erinacea). 02°20' 138°00' Mamberamo R., Albatros Bivak, van Leeuwen 9539 (BO, L). 03°17' 138°35' Mamberamo R., Prauwen Bivak, Lam 1095 (L). 03°29' 139°14' Idenburg R., Bernhard Camp, Brass 13934 (A, L), & Brass 13935 (type of M.prolifera). 03°50' 134°40' Etna Bay, Koch 706 (BO, L). Locality uncertain: E coast of Geelvink Bay, Manipawei, Janowsky 17 (BO, L). Aru Is., Giabu-Lengan, Beccari sn, 3:1873 (type of M.aruensis).

Discussion This taxon is distinguished by its unique stem and pollen characters. There is considerable variation in leaf shape and size, and floral characters, which formed the basis for the three former species (Fig.17, Chapter VI 3b). Further material has lead to the breakdown of character correlations and shown that the pattern is more continuous than was thought. A single species is therefore recognized here.

c) **Myrmecodia melanacantha** sp. nov.

Tuber irregularly cylindrical, to 30x15 cm, with ridges to 2cm apart. Surface usually smooth, greyish-green when young, grey when mature, partly rough with lenticel-like structures, drying brown. Spines simple, stout, black, usually on ridges, or singly on mounds between the ridges; 0.4-1.0 cm. Stem solitary, unbranched; 1.5-3.5 cm across. Clypeoli absent. Alveoli rounded with prominent, swollen, black rims. Spines simple, stout, black, 0.8-1.6 cm, with broad rounded bases, especially dense on alveoli rims. Tunnels within the stems connect the alveoli to the tuber chambers. Leaves 12x4.5 - 19x6 (- 31x6) cm. Lamina

elliptic; apex acuminate; base gradually tapered; or narrowly oblanceolate, tapered almost to the base of the petiole. Midrib reddish. Petiole (0.5-) 2-3.5 cm, usually reddish-brown. Stipules 1-2 cm. Inflorescence: bracts short, hairy. Flowers (1). Calyx 0.5mm. Corolla 16mm; lobes c. 5mm, unci 1mm. A ring of hairs 3mm from base of tube. Anthers at apex of tube. Pollen 2-vesiculate; reticulation coarse (Plate 5a). Stigma obscurely lobed, just below unci. Fruit red. Pyrenes 8.

Ecology Montane forest, 2000-2600 m; terrestrial or in open, secondary, or undisturbed forest.

Distribution Papua New Guinea.

SE 05°46' 142°45' Koruba subdistr., 3km S of Guala Mission, Mt. Alubudua, UPNG 5918. 05°59' 145°30' Madang Prov., Mt. Otto, Schlechter 18682 pro parte (K). 06°01' 145°26' Goroka Trout Farm, UPNG 5939. 06°03' 145°15' Kassam Pass, UPNG 3458. 06°07' 145°00' Chimbu Prov., Kundiawa, Sinasina, c. 1.5km SW Koge Mission, Hide 239 (LAE). 06°08' 145°51' c.20km N of Kainantu, Sayers 46 (K). 06°10-20' 143°50-59' Ialibu subdistr., SE Mt. Giluwe, nr. Onim, UPNG 3476. Locality uncertain: Alipe Manya, Kepaka, Upper Kaguel, Bowers 463 (K, LAE), Bowers 584 (LAE), and Bowers 888 (LAE).

Discussion This species is characterized by the swollen alveoli rims bearing stout, black spines, and tunnels within the stem. It is somewhat variable in leaf-shape (Fig.18). Schlechter 18682 is a mixed collection probably comprising three species: duplicates of it are the types for M.decasperma and M.longispina but both are lost (see UNCERTAIN AND LITTLE KNOWN SPECIES). Both descriptions for these two species indicate branched spines which the duplicate at Kew does not have.

4. GROUPS OF CLOSELY RELATED SPECIES

a) M.platytyrea/M.pendens/M.sterropylla

i) **Myrmecodia platytyrea** Becc., Malesia 2:115, tab.23,1-3 (1884); Valeton, Nova Guinea 8:513 (1911). FIG.34. - Type: Irian Jaya, Beccari 5902 (FI).

M.antoinii Becc., Malesia 2:116, tab.19,2-4 (1884); Hooker, J.D., Bot. Mag. tab.7517 (1897). - Type: Torres Straits, Antoine sn (K), syn. nov.

Tuber globose to cylindrical, to 20cm long. Spines simple, stout, on ridges or mounds, 0.3-0.6 cm. Surface grey or brown. Honeycombing present with pores and entrance holes. Flesh sometimes red. Stem solitary, unbranched. Clypeoli well-developed, 1x0.6 - 2x1.3 cm, grey or brown. Spines rimming clypeoli in a single row, rather broad, stout, simple, (0.3-) 0.5-1.3 cm. Leaves 12x4 - 30x9.5 cm. Lamina elliptic or oblanceolate; apex acuminate (acute); base abruptly cuneate. Petiole 2-9 cm, reddish. Stipules 0.5-1.2 cm, broadly to narrowly triangular, united for about half their length. Inflorescence: bracts short. Corolla white, 16mm; lobes 5mm, unci 1.5mm. A ring of hairs half way up the tube. Anthers at apex of tube. Pollen 1-2 vesiculate; apertures not bordered; reticulation small. Stigma 4-lobed, at anthers. Fruit red. Pyrenes 8.

Ecology Commonest in savanna areas of southern Papua New Guinea, but also in gallery and other evergreen forest in lowland areas.

Myrmecodia platytyrea

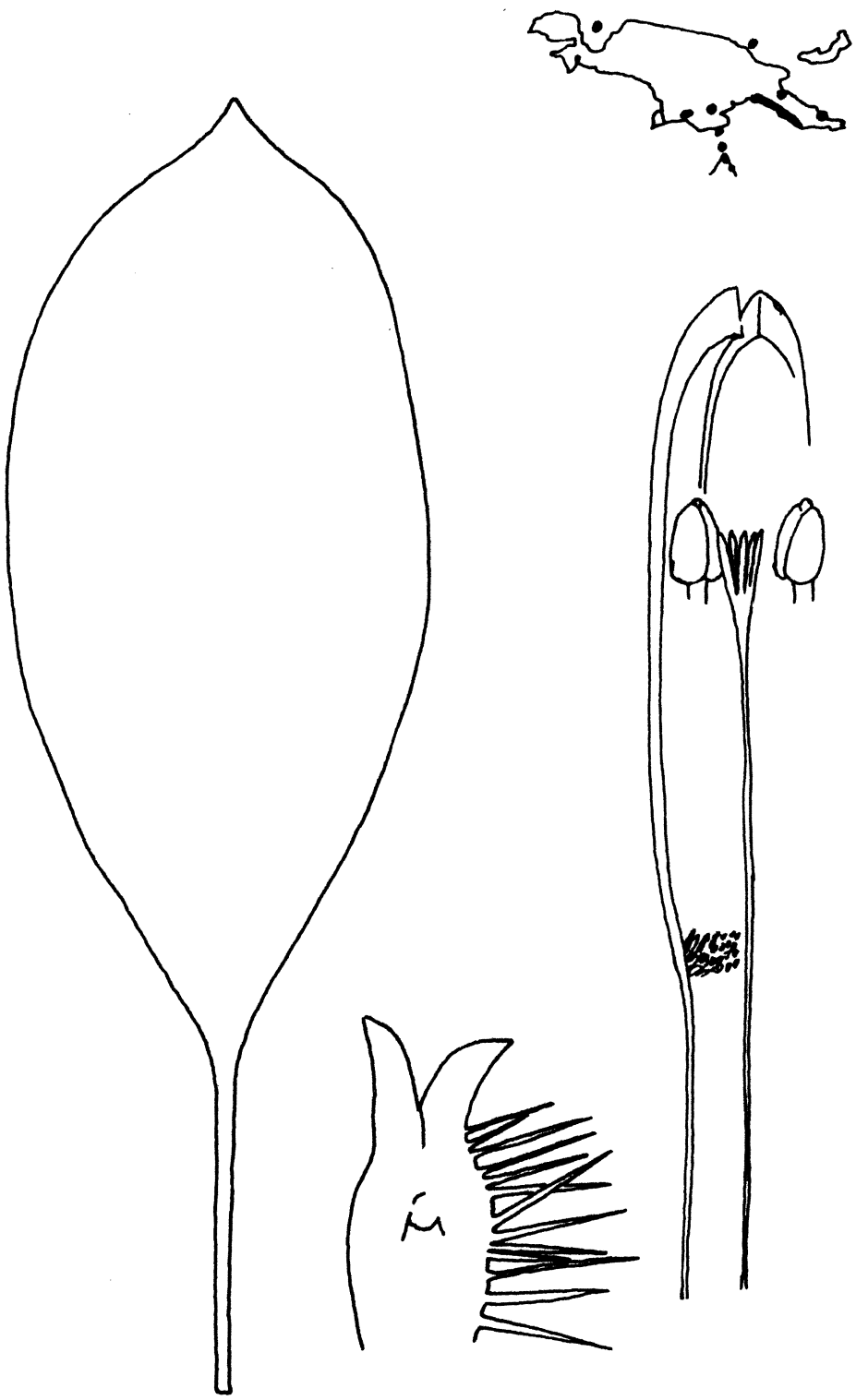


Fig. 34.

Distribution New Guinea and Cape York, Australia.

Irian Jaya: SE 01°35' 135°42' Japen Is., Ansus, Beccari 5902 (type of M.platytyrea). 07°13' 141°03' Merauke, Lake Wam, van Royen 4764 (BO, K, L, LAE). Locality uncertain: Nepenthes Hugel, Versteeg 1299 (BO, L).

Papua New Guinea: SE 04°30' 145°50' Madang Prov., Karkar Is, UPNG 5929. 07°25' 147°10' Morobe Prov., opposite Lasanga Is., Jacobs 9588 (L). 07°49' 145°05' Gulf Prov., Maipenairu, UPNG 5921. 08°50' 141°54' Western Prov., Tarara, Wasi Kussa R., Brass 8670 (A, BO, BRI, L). 08°50' 147°00' Central Prov., Kuriva, UPNG 3428. 09°05' 143°10' Western Prov., Daru Is., Brass 6447 (A, BM, BO, L) & LAE 51701 (L). 09°22' 147°20' Central Prov., Hombrom Bluff, UPNG 3433, UPNG 5941, & UPNG 5942. 09°44' 149°57' Milne Bay Prov., Cape Vogel, Arorara R., Brass 21953 (A).

Australia: SE 09°30' 142°40' Torres Straits, Saibai Is., Stocker 1334 (QRS). 10°35' 142°15' Torres Straits, Horn Is., Cameron 2134 (QRS). 10°37' 142°10' Torres Straits, Thursday Is., Antoine sn (type of M.antoinii). 10°40' 142°30' Newcastle Bay, 3km S of Somerset, Brass 18725 (A). 11°01' 142°30' Bamaga, 27km SW of Cape York., Smith 12668 (BRI). 12°40' 143°20' Iron Range, UPNG 3491. Locality uncertain: Scrubby Crk., Cook Distr., Whitehouse sn (BRI). Bamara, Cape York, Jones 2501 (BRI).

Discussion Beccari distinguished M.antoinii of Western Province and Australia by its smaller leaves, 9x4 cm rather than 20x5 cm, and shorter petioles. These characters, however, do not hold, though there are differences in tuber and lamina characters between plants of dry savanna and those of more equable areas. There is too much overlap for separate taxa to be recognized at this stage. The variation in leaf and clypeolus

shape in this species and M.sterrophylla is shown in Fig.19.

ii) **Myrmecodia pendens** Merr. & Perry, J. Arn. Arb. 26:32 (1945). FIG. 35. - Type: Papua New Guinea, Brass 5401 pro parte (A).

Tuber cylindrical, 17x8 cm, shiny dark brown with white edged ridges. Spines numerous, mainly on the ridges, simple, straight, stiff, finely tapered, 0.5-0.8 (-1.5) cm. Central chambers transversely flattened, honeycombing and pores present; entrance holes not seen. Stem solitary, unbranched to c. 11x1.7 cm; leaves clustered at apex. Clypeoli distinct, the upper part winged by an extension of the stipules, the lower part densely rimmed by stiff simple, slender or rather broad spines, c.1.2 cm long. Alveoli indistinct, rimmed with similar spines. Leaves 15x2 - 35x3.5 cm, dark green and glossy above. Lamina narrowly lanceolate; apex acute, to slightly acuminate; base gradually tapered. Midrib sharply keeled below; lateral nerves clearly visible, 9-13. Petiole 0.5-2.0 cm. Petiole and midrib whitish. Stipules 1-2 cm, narrowly tapered at apex. Inflorescence: flowers (2). Calyx 0.7 mm. Corolla white, 13mm; lobes 3mm; unci 0.5mm. A ring of hairs 3-4 mm from the base of tube. Anthers at apex of tube. Pollen 2-vesiculate; apertures not bordered; reticulation coarse. Stigma 4-fid, above anthers. Pyrenes 4.

Ecology Edge of upper mixed forest, oak forest, and Nothofagus forest, 1200-1645 m.

Distribution Papua New Guinea.

SE 08°18' 146°58' Central Prov., 2km N of Taipini, UPNG 5938. 08°33' 147°00' Central Prov., Mafulu, Brass 5401 pro parte

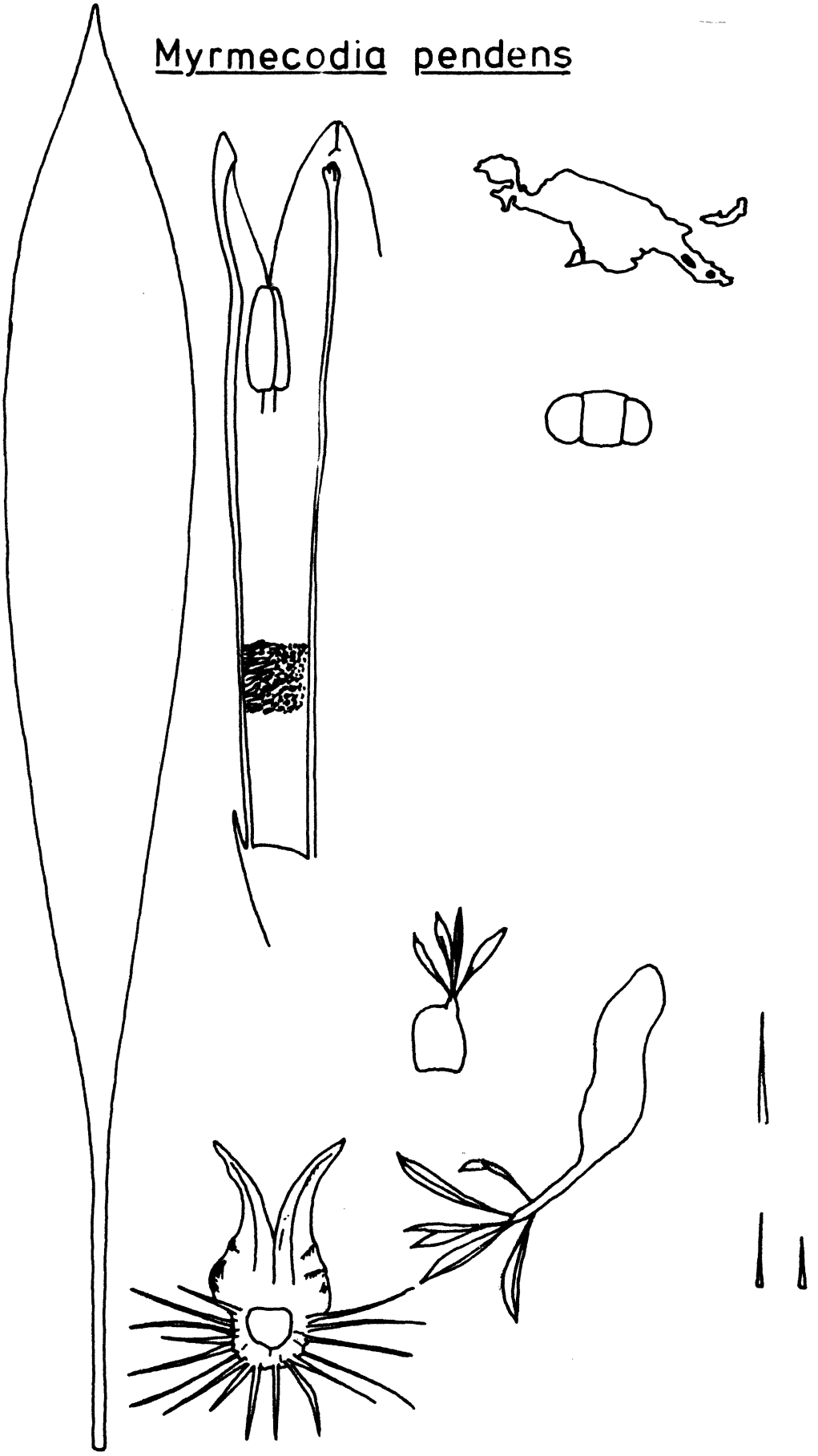


Fig. 35.

(type). 09°45' 149°04' Milne Bay Prov., Mayu R., Mt. Suckling, LAE 55708 (A, BRI, CANB, K, L, LAE). Locality uncertain: Milne Bay Prov., nr. Agaun, UPNG 3465.

Discussion This species is rather uniform in leaf-shape, which is more narrowly oblanceolate than in M.sterrophylla.

iii) **Myrmecodia sterrophylla** Merr. & Perry, J. Arn. Arb. 26:28 (1945). - Type: Irian Jaya, Brass 12138 (A).

Tuber cylindrical, ridged. Spines simple, fine, black at the base and reddish brown at the tip, 0.5-1.3 cm long, on the ridges. Surface partly smooth, partly covered in lenticel-like structures. Stem solitary, unbranched. Clypeoli to 1.5x1.2 cm. Spines simple, slender (stout), rimming the clypeoli in a dense mass, 0.3-1.0 cm long. Leaves 19x3.5 - 30x8.5 cm, thick. Lamina narrowly elliptic; apex acute or acuminate; base cuneate. Midrib prominent, rounded below; lateral nerves 9-12, usually more visible from above than below when dry. Petiole 2-6 (-10) cm, rounded below. Stipules to 1.9 cm, narrowly triangular. Inflorescence: bracts inconspicuous, hairy. Flowers (3) heterostylous. Calyx 2-3 mm. Corolla white. Brevistyle flowers: a ring of hairs a half to a third the way up the tube. Anthers towards or at apex of tube. Pollen 2-porate, 2-vesiculate; apertures not bordered; reticulation coarse (Plate 3d). Stigma half way up the tube. Longistyle flowers: a 4mm broad band of short, 0.1mm, hairs in the upper half of the tube. Anthers at apex of tube. Pollen 2-porate; apertures bordered; reticulation fine (Plate 3c). Stigma ?5-lobed, just above anthers. Fruit red. Pyrenes 6 (-8).

Ecology Epiphytic or terrestrial, at 1800m.

Distribution Central New Guinea.

Irian Jaya: SE 03°35' 139°08' 15km SW of Bernhard Camp, Brass 12138 (type). 04°40' 138°40' Hellwig Gebirg Zuid, Pulle 781 (L). Locality uncertain: Wissel Lake region, Div. Omstreken van Post, Enz (Environs Station), Eyma 4930 (A, BO, K, L).

Papua New Guinea: SE 05° 141° Upper Ok Tedi, UPNG 3490.

Discussion This taxon is distinguished from M.platytyrea by its fine spines, tuber surface and leaf-shape; and from M.archboldiana by leaf-shape, spine and pollen characters. Its few localities are widely scattered (Fig.19). The Pulle specimen bears the manuscript name 'M.stupenda' Valeton which was never published, but suggests that Valeton intended to recognize the species.

b) **M.archboldiana / M.brassii**

i) **Myrmecodia archboldiana** Merr. & Perry, J. Arn. Arb. 26:29 (1945). Fig.36. - Types: Irian Jaya, Brass 11216 (A, BO, BRI, L) & Brass 12047 (A, BO, L).

Tuber c.30x16 cm, drying dark brown. Spines 0.6-1.2 (-1.8) cm, simple, clustered on ridges or on mounds, pale brown, narrow and finely tapered but stiff. Pores sometimes present. Entrance holes not seen. Chambers rather large, sometimes honeycombed. Stem solitary, to 20x1.2 cm. Clypeoli distinct, shape variable (Fig.8). Spines dense on the rims and sometimes on the clypeoli surfaces, as on tuber or longer. Leaves 25x3 - 35x4 cm. Lamina broadest at the middle or towards the apex; tapering gradually at the base. Inflorescence: flowers (3) all different: corolla white; Brass 11216 corolla glabrous; anthers at base of lobes; stigma bifid, just above lobes. Brass 12047 (A) corolla glabrous; anthers at base of lobes; stigma lobing not clear, 1mm

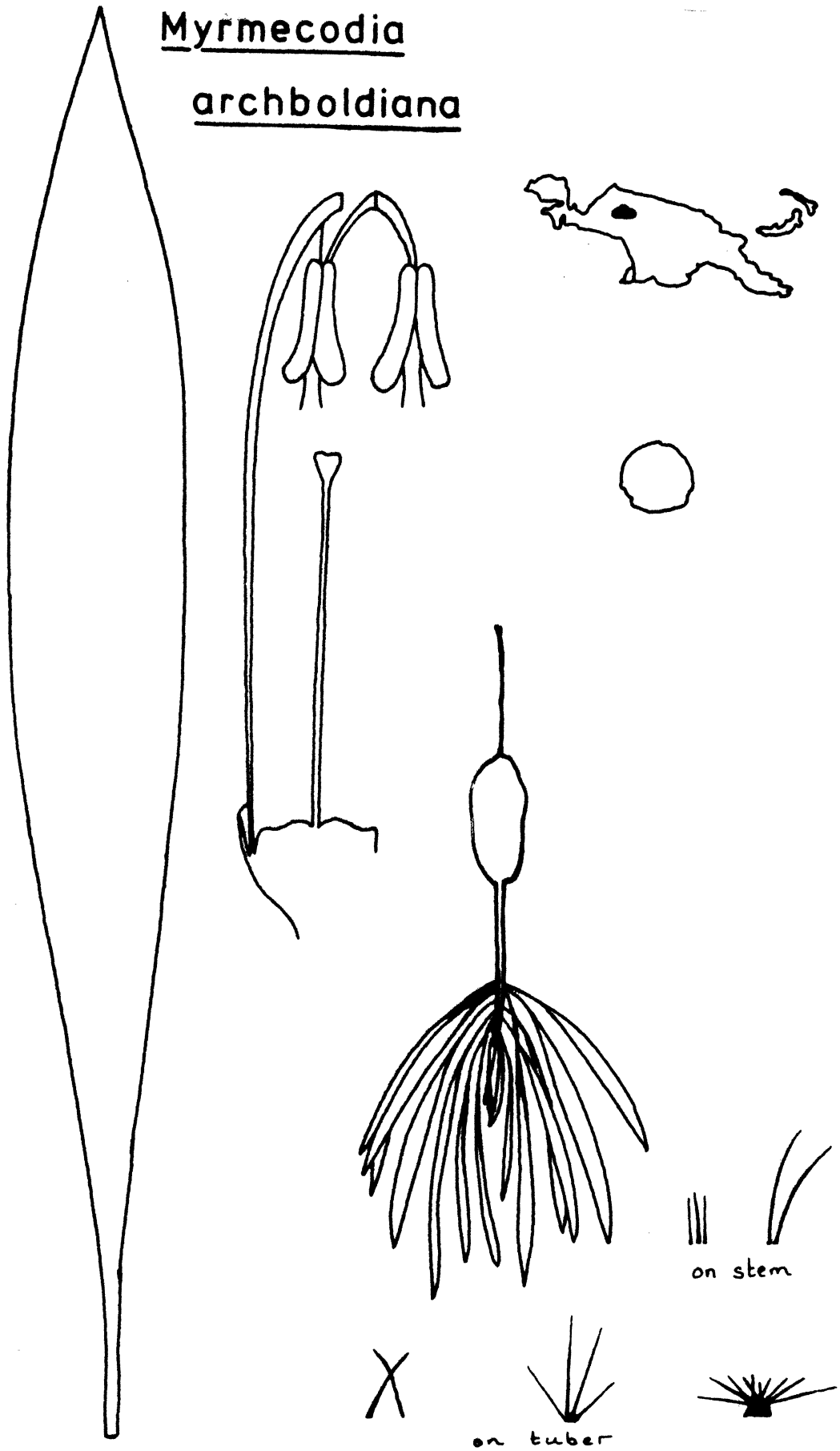


Fig. 36.

below anthers. Lam 1517 corolla with a ring of hairs just below middle of tube; anthers just above hairs; stigma bifid, at apex of tube. Pollen of all 3 flower types uniform; spherical to triangular, 3-porate, sometimes slightly 3-vesiculate; apertures unbordered; reticulation medium (Plate 4b). Ovules 2-4.

Ecology 1800-3600 m, in a variety of forest types - primary oak forest, secondary forest, mossy forest, and open stunted forest (Lam, 1924).

Distribution Irian Jaya.

SE 03°20' 138°20' hill nr. Doormantop, Lam 1517 (L). 03°30' 139°00' 15km SW of Bernhard Camp, Idenburg R., Brass 12047 (type). 03°50' 137°50' Kemabu Plateau, 15km N of Carstenz Mts., Hope ANU 16059 (L). Locality uncertain: Baliem Valley, above Wellesey, Kostermanns & Soengeng 752 (BO, L).

Discussion The inclusion of the Hope and Kostermans & Soengeng collections increases the variation in this species, especially in its floral characters (Fig.20). M.brassii is distinguished by its shorter, almost sessile, leaves, the fat, stubby, clustered spines on part of the tuber and the flower structure.

ii) **Myrmecodia brassii** Merr. & Perry, J. Arn. Arb. 26:28 (1945). FIG.37. - Type: Irian Jaya, Brass 9446 (A, BM, BRI, L).

Tuber irregularly cylindrical, often curved downwards. Upper part of tuber ridged, drying shiny black; spines simple, rather fine, curved, to 1.4 cm, on ridges and in clusters between them. Lower part of tuber not ridged, surface drying dark brown, warted, rough; spines broad, short, to 0.8cm, in neat clusters, which are not on mounds. Stems several, unbranched, 17x2.2 cm, variously curved, or hanging down. Clypeoli to 1.2x0.7 cm. Alveoli present. Spines simple, rather fine, usually curved, densely inserted on margins of clypeoli. Leaves to 1.5x3.6 cm, thick, leathery, slightly recurved along the margins. Lamina broadest above the middle, tapering gradually at the base. Midrib sharply prominent below; lateral nerves c.9, obscure above. Petiole triangular, 1cm.Stipules c. 0.8cm, divided almost to the base. Inflorescence: bracts hairy. Calyx 3mm. Corolla 12mm; lobes 4mm. A ring of hairs midway up the tube. Anthers at and above the hairs. Pollen not seen. Stigma 4-6 lobed, at the anthers. Pyrenes 4-6.

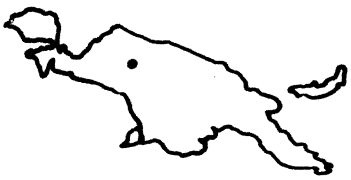
Ecology Epiphytic, seldom terrestrial, in upper montane forest at 3225m. Often associated with M.lamii.

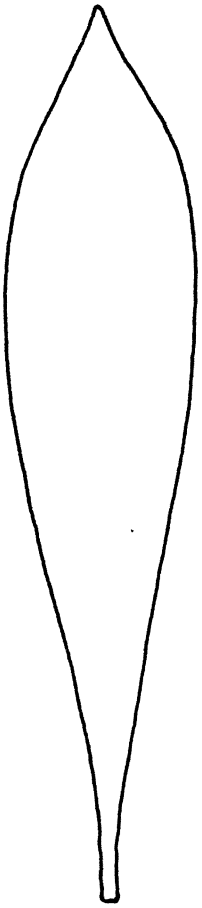
Distribution Irian Jaya.

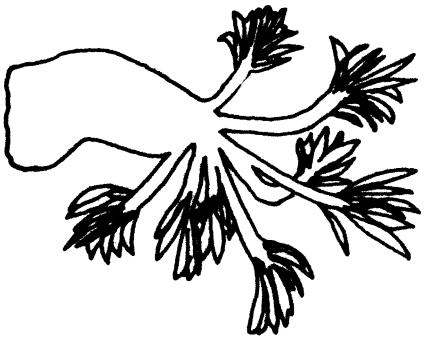
SE 04°09' 138°40' Lake Habbema, Brass 9446 (type).

Discussion see M.archboldiana and M.lamii.

Myrmecodia brassii







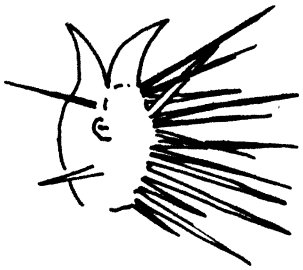


Fig. 37.

c) **Myrmecodia longissima and M.oblongata**

i) **Myrmecodia longissima** Valeton, Bot. Jahrb. 61:148 (1927).

FIG.38. - Type: Papua New Guinea, Ledermann 12623 (B†).

Tuber irregularly cylindrical, grey, ridged to 40x20 cm. Spines scattered on ridges, simple, c. 0.8cm, rarely mixed with shorter, branched spines. Stem solitary, unbranched, c. 15x1.8 cm. Clypeoli c. 1.5cm across; upper part winged, lower part rounded, jutting out from the stem. Spines few to several, mainly simple. Leaves 40x1.5 - 60x3.5 cm. Lamina apex acute (acuminate). Midrib whitish, or purple-brown, prominent below. Inflorescence: bracts forming dense cushions, hairy. Flowers (2) heterostylous. Corolla 15mm, white (pink). In brevistyle flowers a ring of hairs at the base of tube. Anthers at tube apex. Pollen unknown. Style short. In longistyle flowers corolla lobes 6mm, a ring of hairs at the apex of tube. Anthers at the hairs. Pollen 2-porate; apertures slightly bordered; reticulation medium. Stigma 4-lobed, 3mm above the anthers.

Ecology Rainforest at 70-1500 m.

Distribution New Guinea.

Irian Jaya: Locality uncertain: Djayapura Distr., hill nr. Tablasoefoe, van Royen & Sleumer 6484 (L).

Papua New Guinea: 04°30' 142°40' Sepik Prov., Ambunti subdistr., eastern ridge of Sumset (Mt. Huntstein), Hoogland & Craven 10920 (LAE). Locality uncertain: Sepik R., Station Felspitze, Ledermann 12623 (type).

Discussion The similarity of the stem spines, clypeoli, and bracts leave no doubt that these specimens represent a good taxon, though the leaf width varies somewhat. This species is probably related to M.oblongata, see under that species.

Myrmecodia longissima

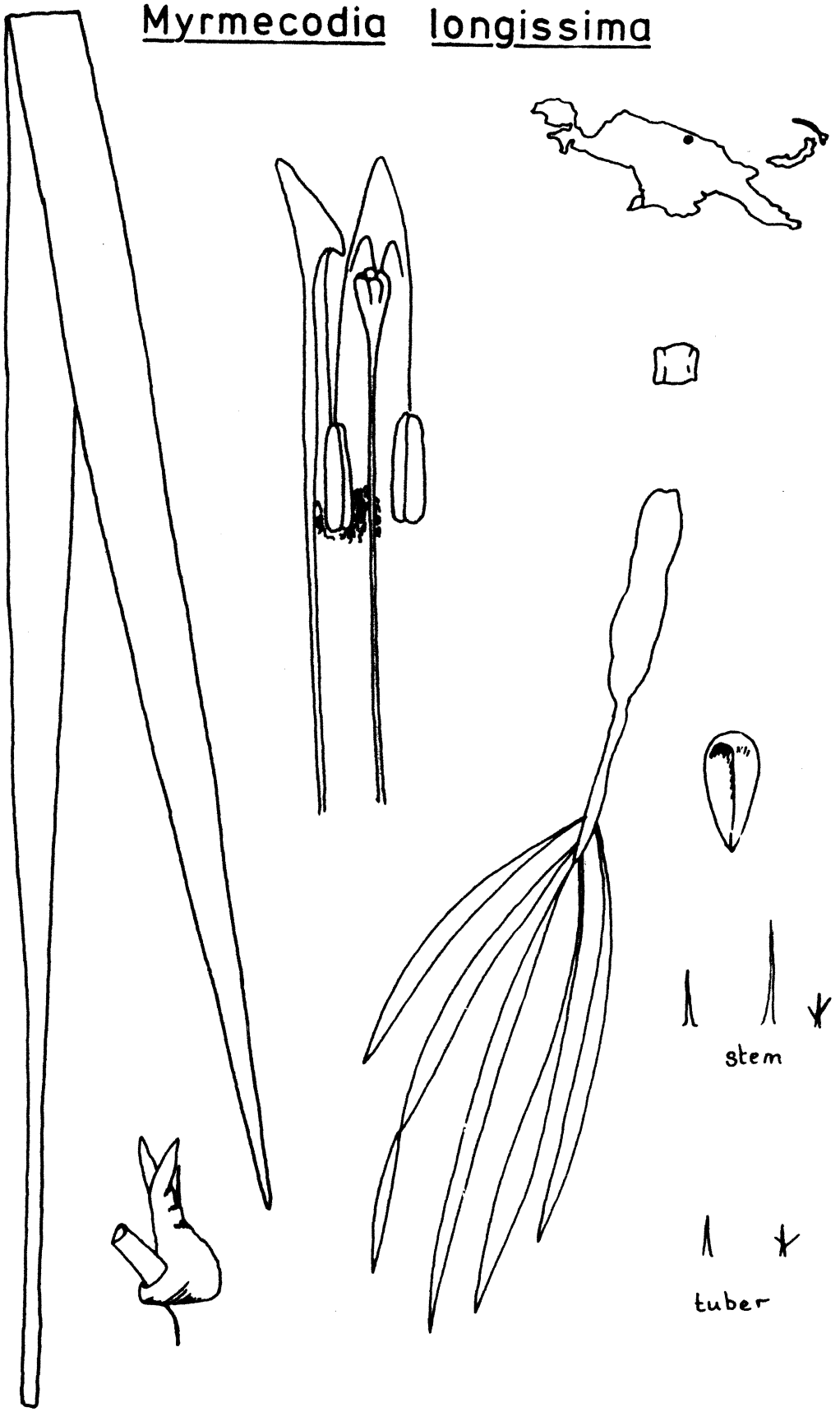


Fig. 38.

ii) **Myrmecodia oblongata** Valeton, Bot. Jahrb. 61:149 (1927).

- Type: Papua New Guinea, Ledermann 11225 (B†, L photo).

Tuber without ridges. Spines mostly simple, fine, short, quite dense. Pores over honeycombed areas. Stem 16x2.5 cm, unbranched. Clypeoli more or less circular, 2.3 cm across, without spines (Fig.8). Alveoli irregularly rimmed by simple (branched), rather weak spines, 0.6-1.5 cm long. Leaves 22x4.7 cm. Lamina narrowly oblong; apex somewhat abruptly acuminate; base cuneate. Midrib rounded below; lateral nerves conspicuous, c. 25. Petiole c. 2.5 cm. Stipules 1.7 cm. Inflorescence: bracts hairy. Calyx 1mm. Corolla 10mm; lobes 4mm. A ring of hairs midway up the tube. Anthers at and above hairs. Pollen unknown. Stigma 4-lobed, above anthers. Pyrenes 4.

Ecology at 1400m.

Distribution Papua New Guinea.

SE 04°30' 142°40' Sepik Prov., Huntsteinspitze, Ledermann 11225 (type).

Discussion Although found in the same locality as M.longissima and sharing its stem characters, this taxon is maintained, at least until further collections are made, on the basis of its much shorter and broader leaves.

5. TAXONOMICALLY ISOLATED SPECIES

a) **Myrmecodia pendula** Merr. & Perry, J. Arn. Arb. 26:32 (1945). FIG.39. - Type: Papua New Guinea, Brass 5401 pro parte (BO, BRI, NY).

Tuber 20x11 cm, cylindrical, more or less ridged, drying brown. Spines rather weak, few to dense, 0.5-0.8 (-1.1)cm, irregularly or more or less stellate branched. Honeycombing and pores present. Stem solitary, often branched, to 15x1.4 cm, leaves clustered at apex. Alveoli elongate. Clypeoli indistinct. Spines rimming alveoli and clypeoli, as on tuber. Leaves 13x3 - 16x4.5 (- 31x8) cm. Lamina oblanceolate; apex acute to acuminate; base gradually tapered. Midrib prominent below; lateral nerves 6-11. Petiole 0.5-2.0 cm. Stipules 0.6-1.0 cm, broadly triangular. Inflorescence: bracts hairy, filling the alveoli. Flowers (3). Calyx 1.2 mm. Corolla 8-9 mm. A ring of hairs a third the way up the tube. Anthers half way up the tube. Pollen 2-porate, 1-2 vesiculate; apertures not rimmed; reticulation fine (Plate 6a). Stigma 4-6 lobed, at anthers. Fruit orange-red. Pyrenes 4-6.

Ecology 1200-2300m, in upper edge of mixed forest, Castanopsis forest and isolated trees in agricultural areas.

Distribution Papua New Guinea.

SE 06°01' 144°59' Chimbu Prov., nr. Kundiawa at beginning of road to Kegelsugul, UPNG 5922. 06°01' 145°55' Eastern Highlands, 20km N of Kainantu, Sayers 63 (K). 06°05' 145°25' Eastern Highlands, Goroka, NGF 15912 (BRI, L) & UPNG 3456. 06°14' 145°59' Eastern Highlands, Kassam Pass, Undoe Bridge, UPNG 3454. 06°22' 145°58' Eastern Highlands, Yanku, off road to

Myrmecodia pendula

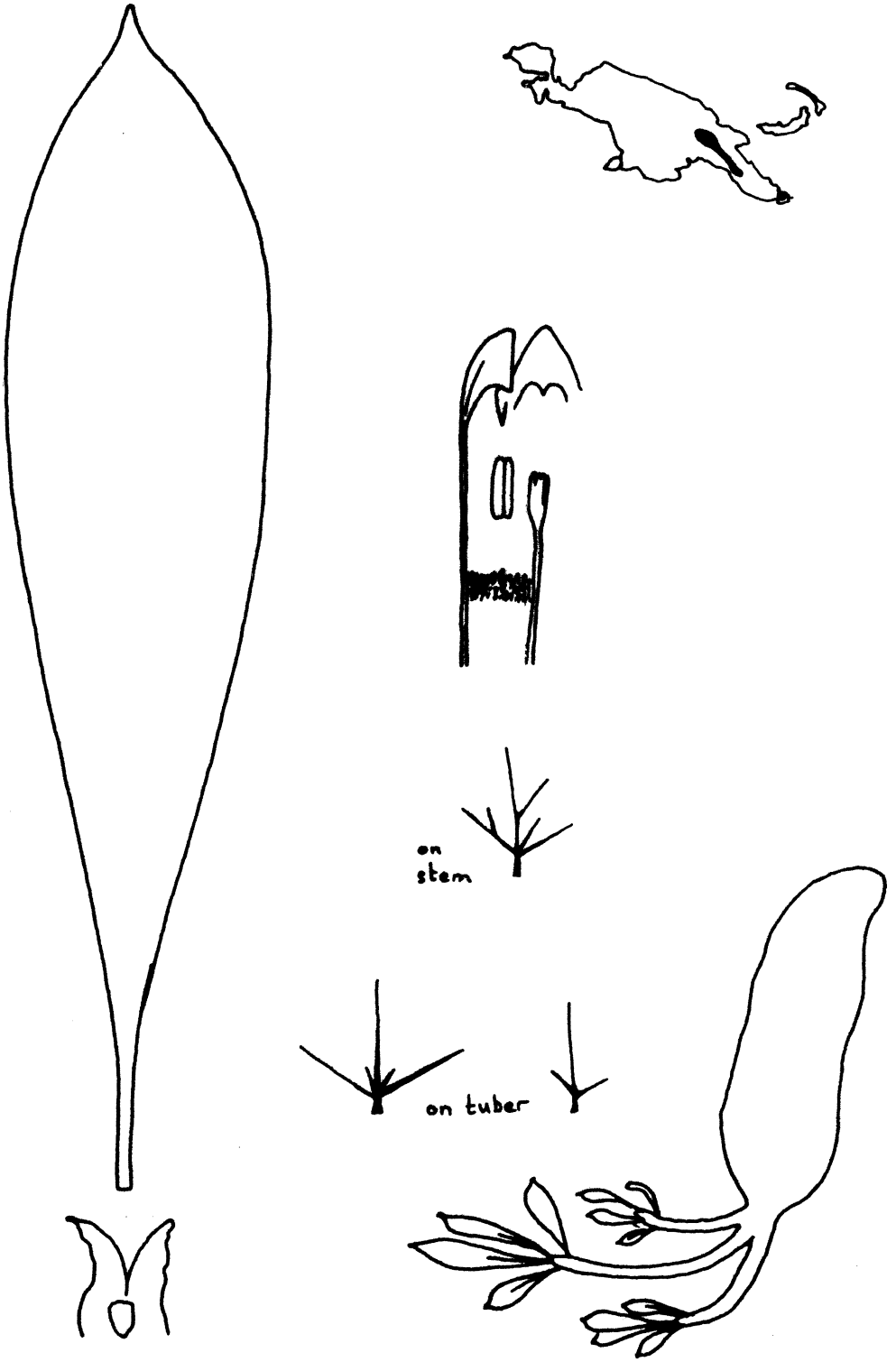


Fig. 39.

Ukarumpa, UPNG 3455. 06°30' 145°32' Eastern Highlands, nr. Okapa, UPNG 3459. 07°10' 146°00' Morobe Prov., Menyamya, NGF 35885 (L). 08°33' 147°00' Central Prov., Mafulu, Brass 5401 pro parte (type). 10°22' 150°15' Milne Bay Prov., N Sagarai Valley, NGF 16894 (A, BRI).

Discussion This species is relatively homogeneous as shown in Fig.21. The plant from Milne Bay is geographically isolated, but clearly belongs here. This species is possibly related to or even conspecific with M.schlechteri and or M.longispina of which the types are lost (see UNCERTAIN AND LITTLE KNOWN SPECIES). Until collections are made from the type localities they are left as uncertain.

b) **Myrmecodia wauensis** sp. nov.

FIG.40.

Tuber conical, 16x15 cm, shiny blackish-brown, not ridged. Spines stellate, dense, central branch 1-2 cm, side branches 0.5-1.0 cm; spine branches finely tapered, straight and stiff, sometimes branched again. Pores and entrance holes absent. Chambers to 4 cm across, walls thin, c. 0.2 cm across. Stem solitary, unbranched, to 40x1.5 cm. Spines dense, larger than on the tuber, stellate and branches often branched again. Alveoli elliptic with raised walls rimmed with spines. Stem sometimes dorsiventral, the alveoli all apparently on the upper side of the stem, the lower side only sparsely spiny. Stems often completely concealed by spines. Leaves 24x4.5 - 31x5 cm, leathery, dark glossy green above, matt below, margin usually crinkled. Lamina broadest at or above the middle, tapering gradually. Midrib prominent, rounded, whitish below; lateral

Myrmecodia wauensis

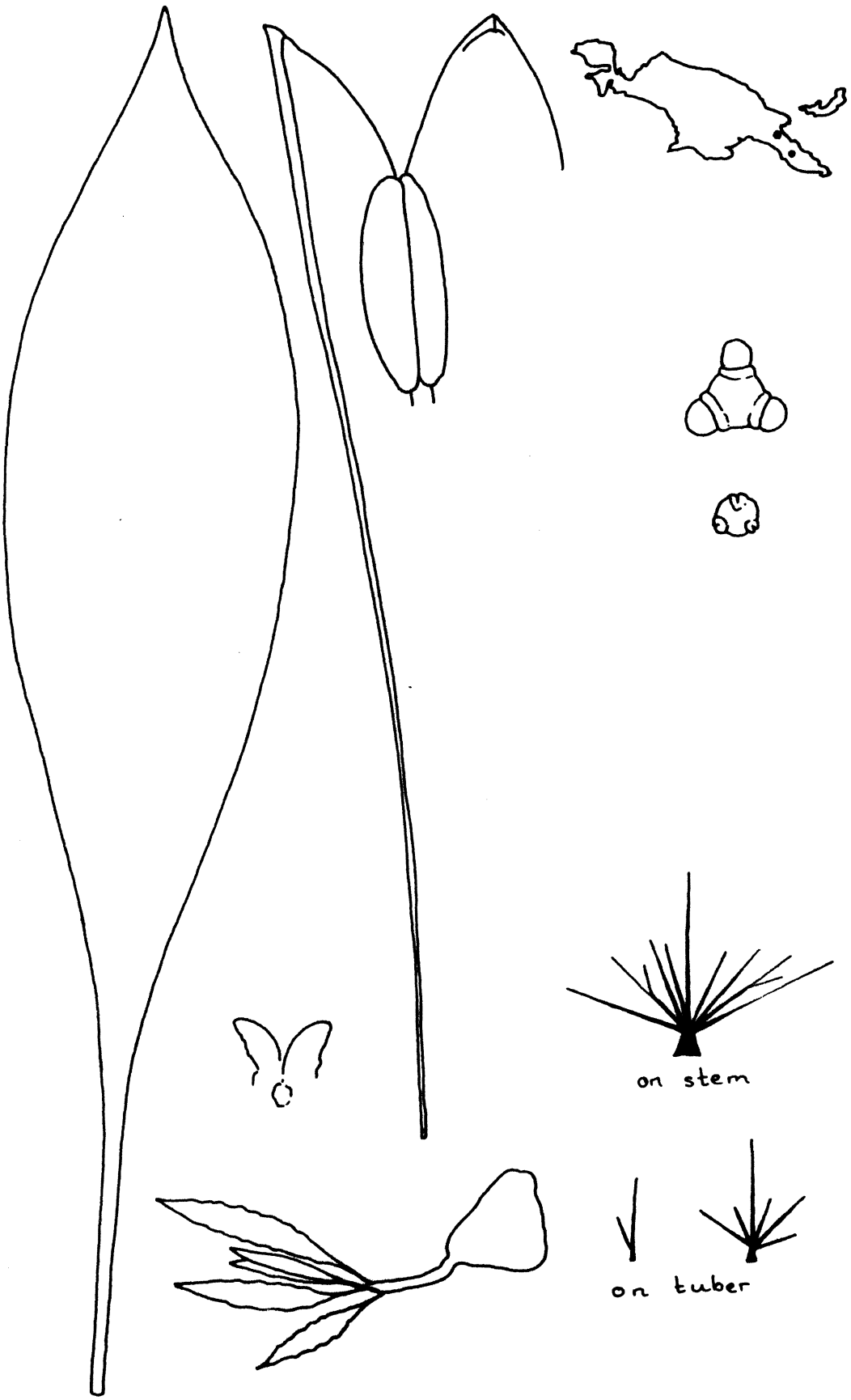


Fig. 40.

nerves c.12. Petiole winged, c.2cm, white. Stipules to 0.7 cm, triangular, divided to base. Inflorescence: bracts to 5 mm. Corolla pale turquoise, to 20mm, obconical, lobes 5mm, tube glabrous. Anthers at tube apex. Pollen 3-porate, 3-vesiculate; apertures slightly bordered; reticulation medium (Plate 4,c&d). Stigma 7 lobed, above anthers. Fruit orange. Pyrenes 7.

Ecology Lower to mid montane forest, especially Nothofagus, 1800-2000 m.

Distribution Papua New Guinea.

SE 07°19' 146°40' Morobe Prov., Wau, Mt. Kaindi, 200m below turning to Eddie Crk., UPNG 3408 & UPNG 3498. 07°20' 146°52' Morobe Prov., 16km SE of Kaisenik, UPNG 3410. 07°20' 146°45' Morobe Prov., Kaisenik logging road, LAE 62284A (LAE). 09°05' 147°38' Central Prov., Boridi, Carr 14659 pro parte (A).

Discussion Possibly conspecific with M.decasperma, see UNCERTAIN AND LITTLE KNOWN SPECIES , M.wauensis shares the narrowly oblanceolate leaves and dense spines of that species, but the leaves are longer in M.wauensis, no simple spines are present, the stipules are not connate and only 7 pyrenes per fruit have been found.

This species can be confused with M.albertisii ssp. koiariensis (to which the rest of the mixed collection Carr 14659 belongs) as the leaf-shape and spine branching are superficially similar. The corolla and pollen of M.wauensis are, however, quite different.

c) **Myrmecodia lamii** Merr. & Perry, J. Arn. Arb. 26:27 (1945). FIG.41. -Type: Irian Jaya, Brass 9445 (A, BM, BO, BRI, G, K, L).

Tuber often terrestrial, standing erect, to 70x45 cm, when epiphytic usually smaller and projecting horizontally. Basal part of tuber glabrous except for a few small groups of short thick spines; apical part with simple, weak, longer spines to 2cm, clustered on ridges or mounds. Entrance holes and pores not seen. Chambers to 2 cm diameter, walls 0.2-0.3 cm. Stems numerous, unbranched, reaching 100 x 1.5-2.5 cm. Alveoli shallow, hidden by the prominent, winged clypeoli. Clypeoli with groups of weak, simple spines, to 1.5 cm. Leaves to 22x5 cm, leathery, clustered at apex of stem. Lamina oblanceolate; apex acute or acuminate, base gradually tapered. Midrib prominent, rounded below; lateral nerves c. 11. Petiole pale green, 0.5-4.0 cm. Stiplues triangular, c.1.1x0.7cm, with a glossy, wide (0.5 cm), wing around the clypeolus, drying blackish. Inflorescence: bracts present, hairy. Corolla white or pale blue, 12mm; lobes 4mm; tube glabrous. Anthers in upper part of tube. Pollen 3-porate; vesicles absent; apertures not bordered; reticulation coarse. Stigma 4 lobed, just above anthers. Pyrenes 4.

Ecology Epiphytic in medium or stunted forest, or terrestrial, especially above the tree-line, 1900-3580 m. Often associated with M.brassii when epiphytic (Lam, 1924).

Distribution Irian Jaya.

SE 03°30' 138°26' Doormantop, Lam 1804 (BO, L). 03°59' 138°46' 18km NE of Lake Habbema, 2200 Camp, Brass 11554 (A, BO,

Myrmecodia lamii

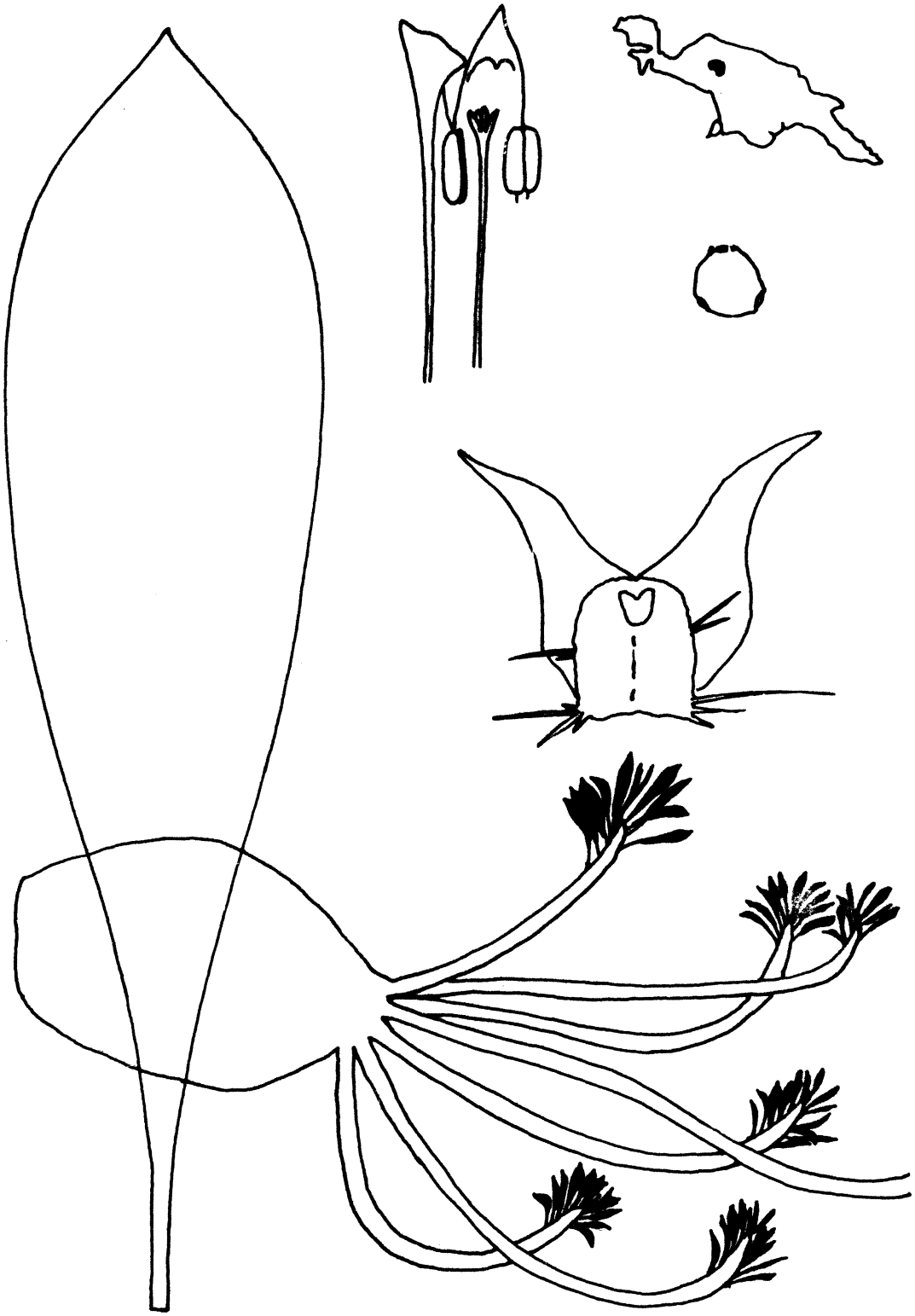


Fig. 41.

L). 04°01' 138°43' 9km NE of Lake Habbema, 2800m Camp, Brass 10689 (A, BO, BRI, L). 04°03' 138°41' Lake Habbema, 3225m Camp. Brass 9445 (type). 04°20' 138°40' Wichmansberg, Pulle 1058 (L).

Discussion This species is characterised by its broadly winged clypeoli and long, fine spines on the upper part of the tuber. The pollen and corolla suggest affinity with M.archboldiana or M.wauensis. The spine characters resemble those of M.brassii. Although the winged clypeoli are reminiscent of M.pteroaspida, the floral characters are quite different. Contrary to Merrill & Perry (1945) this species was first collected by Pulle, his specimen at L carries the legend M.acrophila det. Valeton, but the name was not published.

d) **Myrmecodia pteroaspida** sp. nov.

FIG.42.

Tuber 18x10 cm, irregularly cylindrical, grey. Ridges prominent. Spines stout, simple, black, conical, to 0.5 cm. Pores irregularly present on swollen areas. Entrance holes few. Stem 1 or 2, unbranched, 13x2 cm. Clypeoli 1.8x1.5 cm; upper part winged by glossy grey extensions of the stipules; lower part matt brown. Spines on the edges and rarely the median ridge of the clypeoli, similar to those on the tuber. Leaves to 12.5x4.5 cm, somewhat leathery, bright green. Lamina spathulate; apex acuminate. Midrib prominent below. Petiole winged to base. Stipules 1.5 cm, triangular. Inflorescence sunken in stem. Bracts inconspicuous, hairy. Calyx 5mm. Corolla white, 11mm. A ring of hairs near base of tube. Anthers blue, at apex of tube. Pollen 1-2 vesiculate; apertures unbordered; reticulation medium

Myrmecodia pteroaspida

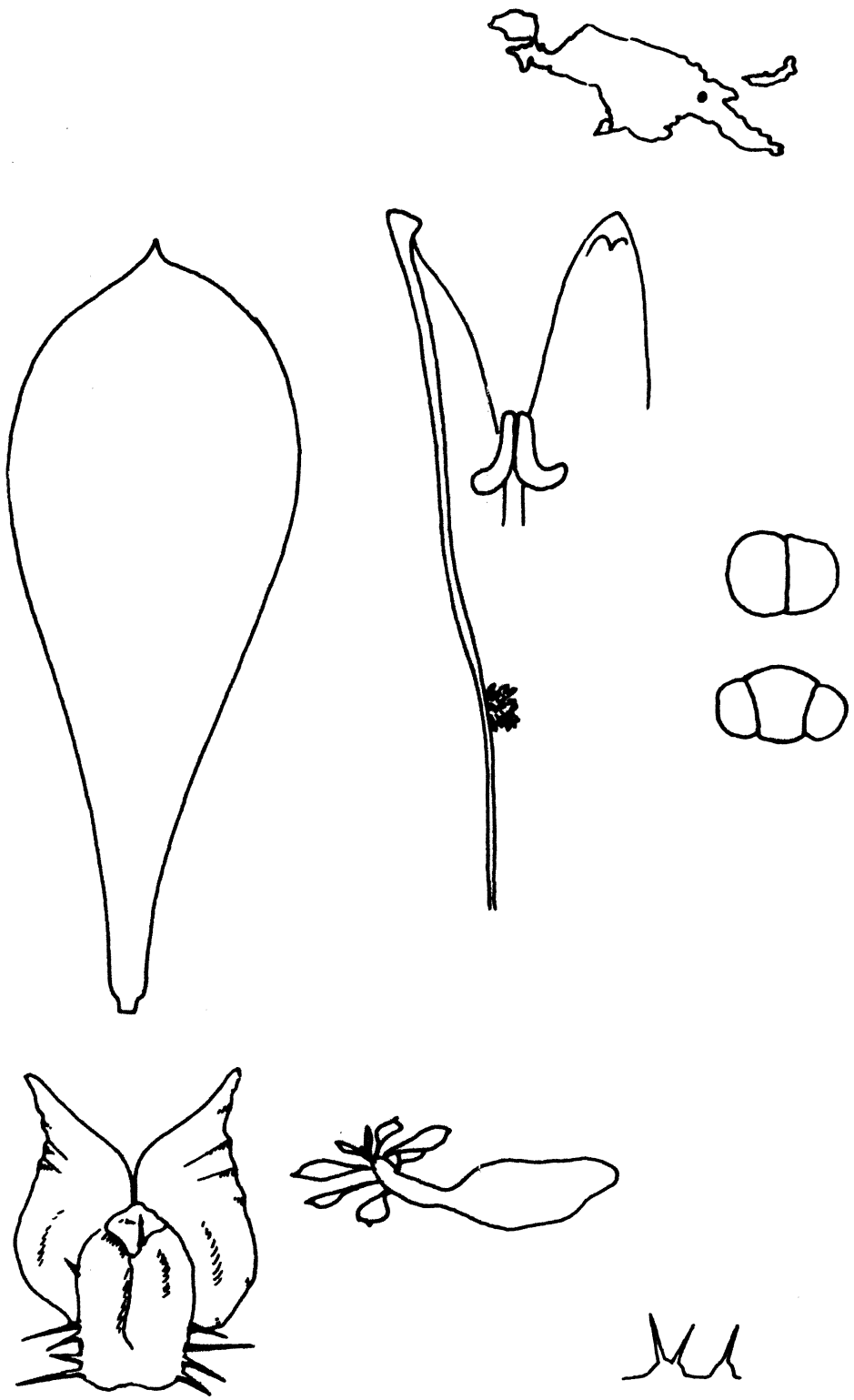


Fig. 42.

(Plate 5b). Stigma 5- ?6 lobed, below anthers. Pyrenes 5-6.

Ecology In secondary forest in a largely agricultural area, 1600m.

Distribution Papua New Guinea.

SE 06°30' 145°32' Eastern Highlands, nr. Okapa, c.45km S of Goroka, UPNG 3460 & UPNG 3461.

Discussion This species resembles M.lamii in its winged clypeoli, but differs in many respects, see under that species. The stout black spines are similar to those of M.melanacantha.

e) **Myrmecodia hydnostipula** sp. nov.

FIG.43.

Tuber much broader than tall, 5x14 cm, surface drying dark brown. Spines variable from sparse, rather weak and simple to dense, stout and more or less stellate branched; blackish brown, usually less than 0.7 cm. Stem 1 or 2, to 27x0.9 cm, branched, curving upwards. Spines sparse on surface, simple or branched. Alveoli elliptic, more or less densely rimmed with branched or root-like spines to 1cm. Leaves c. 8x2.5 cm, thick, somewhat fleshy. Midrib rounded below; lateral nerves obscure, c.4. Petiole c.0.6 cm, triangular. Stipules, remaining united between the petioles, splitting apart opposite the petioles (Fig.43). Inflorescence: bracts hairy. Calyx 1mm. Corolla white, 14mm; lobes 2mm. A ring of hairs half way up the tube. Anthers between hairs and tube apex. Pollen 3-porate, 3 slight vesicles, apertures not bordered; reticulation fine (Plate 4a). Stigma

Myrmecodia hydnostipula

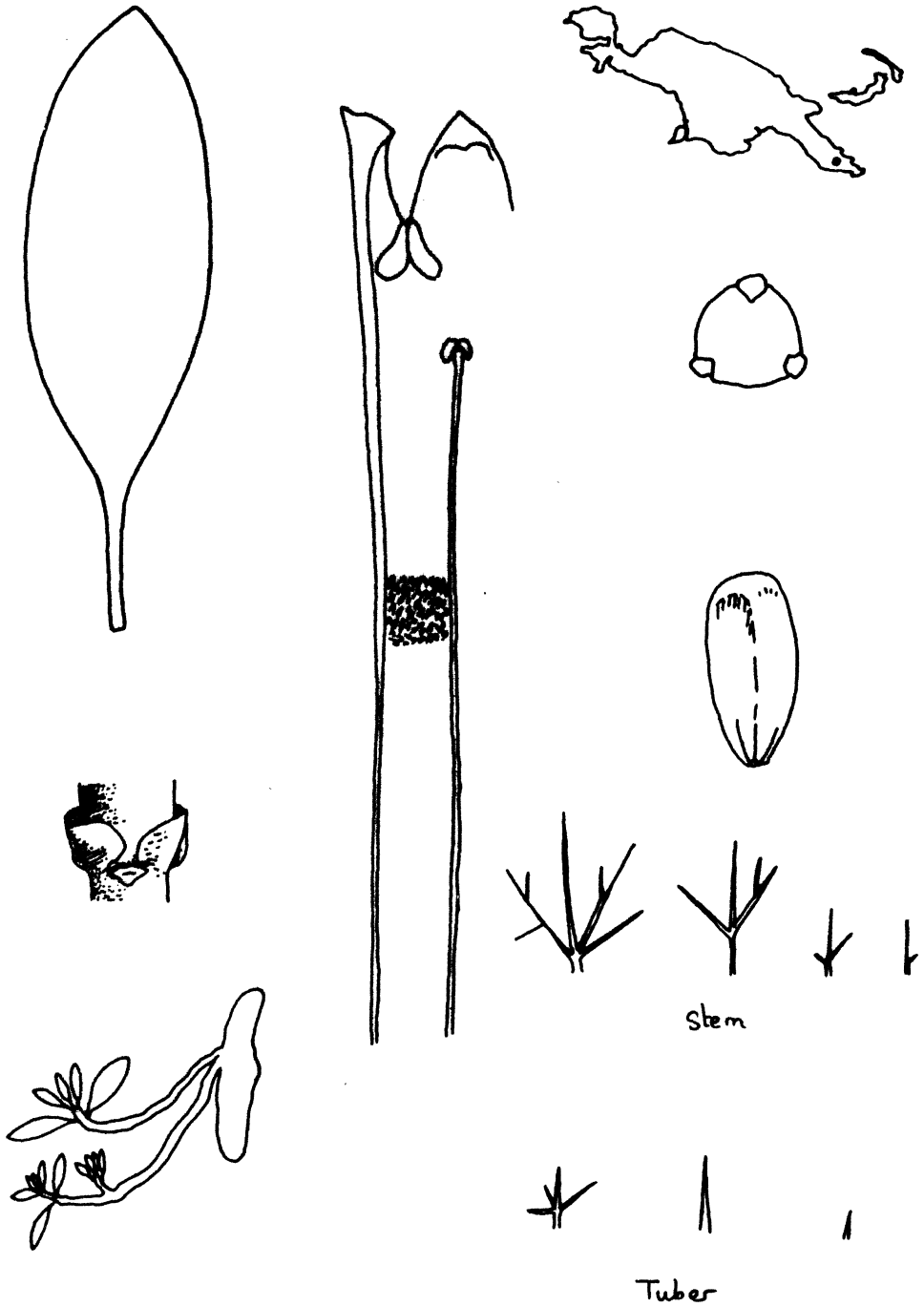


Fig. 43.

bilobed, just below anthers. Fruit orange. Pyrenes 3.

Ecology Montane forest, 1600-2000 m.

Distribution Papua New Guinea.

SE 09°45' 149°04' Milne Bay Prov., Mt. Suckling, Mayu R., LAE 55709 (L, LAE) & LAE 55690 (L, LAE).

Discussion The persistent interpetiolar connection of the stipules is similar to that in Hydnophytum. The pollen also has similarities to that of Hydnophytum. The very different degree of development of the spines in the two collections makes them appear superficially rather different.

6. UNCERTAIN AND LITTLE KNOWN SPECIES

a) **Myrmecodia decasperma** Valeton, Bot. Jahrb. 61:145 (1927). - Type: Papua New Guinea, Bismarck Mts., Schlechter 18682 pro parte (B†). The type has not been found, nor the type locality re-collected. The description suggests a relationship with M.wauensis, but simple spines have not been found in that species, and there are only 7 pyrenes per fruit.

b) **Myrmecodia lanceolata** Valeton, Nova Guinea 8:510 (1911). - Types: Versteeg 1046 (L) & Versteeg 1246 (L). These two collections do not appear to be conspecific and their relationships are not clear.

c) **Myrmecodia longifolia** Valeton, Nova Guinea 8:509 (1911). - Type: Irian Jaya, Noord Fluss, nr. foot of Geluks Hugel, Bivak Alkmaar, Versteeg 1522 (BO, L). This taxon might be conspecific with M.pendens as the tuber and stem characters are similar; differences in flower structure may be due to heterostyly. The petiole is longer and the leaf more rapidly tapered in M.longifolia.

d) **Myrmecodia longispina** Valeton, Bot. Jarhb. 61:145 (1927). - Type: Papua New Guinea, Bismarck Mts., Schlechter 18682 pro parte (B†). Both this and the following species are probably related to M.pendula, but have not been united with that species in the absence of collections from the type localities.

e) **Myrmecodia schlechteri** Valeton, Bot. Jahrb. 61:146 (1927). - Type: Papua New Guinea, Kani Mts., Schlechter 17033 (B†) & Schlechter 17275 (B†). See M.longispina.

f) **Myrmecodia species 1 'angi-gita'** Irian Jaya, Vogelkop, Arfak, Angi-gita Lake, Kostermans 2500 (BO). The leaf-shape and spine characters of this collection do not suggest affinities with any other species.

g) **Myrmecodia species 2 'mamberamoensis'** Irian Jaya, Mamberamo R., opposite Albatros Bivak, van Leeuwen 9540 (A, L) & Rouffaer R., van Leeuwen 10134 (A, BO, K, L) & ? Japen Is., Barclay sn (BM). The two van Leeuwen specimens are unique in their Hydnophytum-like tubers; stems without spines; leaves to 40x10cm; flowers with bi-lobed stigmas; and pollen 3-4 porate; apertures bordered; reticulation coarse (Plate 5d). The Barclay specimen is similar though the tuber is unknown and the pollen aprertures not bordered.

h) **Myrmecodia species 3 'rouffaerensis'** Irian Jaya, hills nr. Rouffaer R., van Leeuwen 10126 (BO, K, L). This collection is unique in its orange-red flowers with papillate lobes; it is also unusual in its tough, leathery leaves. The stem and spine characters do not suggest affinities.

i) **Myrmecodia species 4 ' wisselensis'** Irian Jaya, Maiari Is. in Wissel Lake, Eyma 4514 (BO, K, L). Although resembling M.archboldiana in its clypeoli (Fig.8) and spines, the leaves of this collection only reach 16cm, the stipules are much narrower and the pollen apertures are bordered. M.sterrophylla occurs in the same area but differs in other characters.

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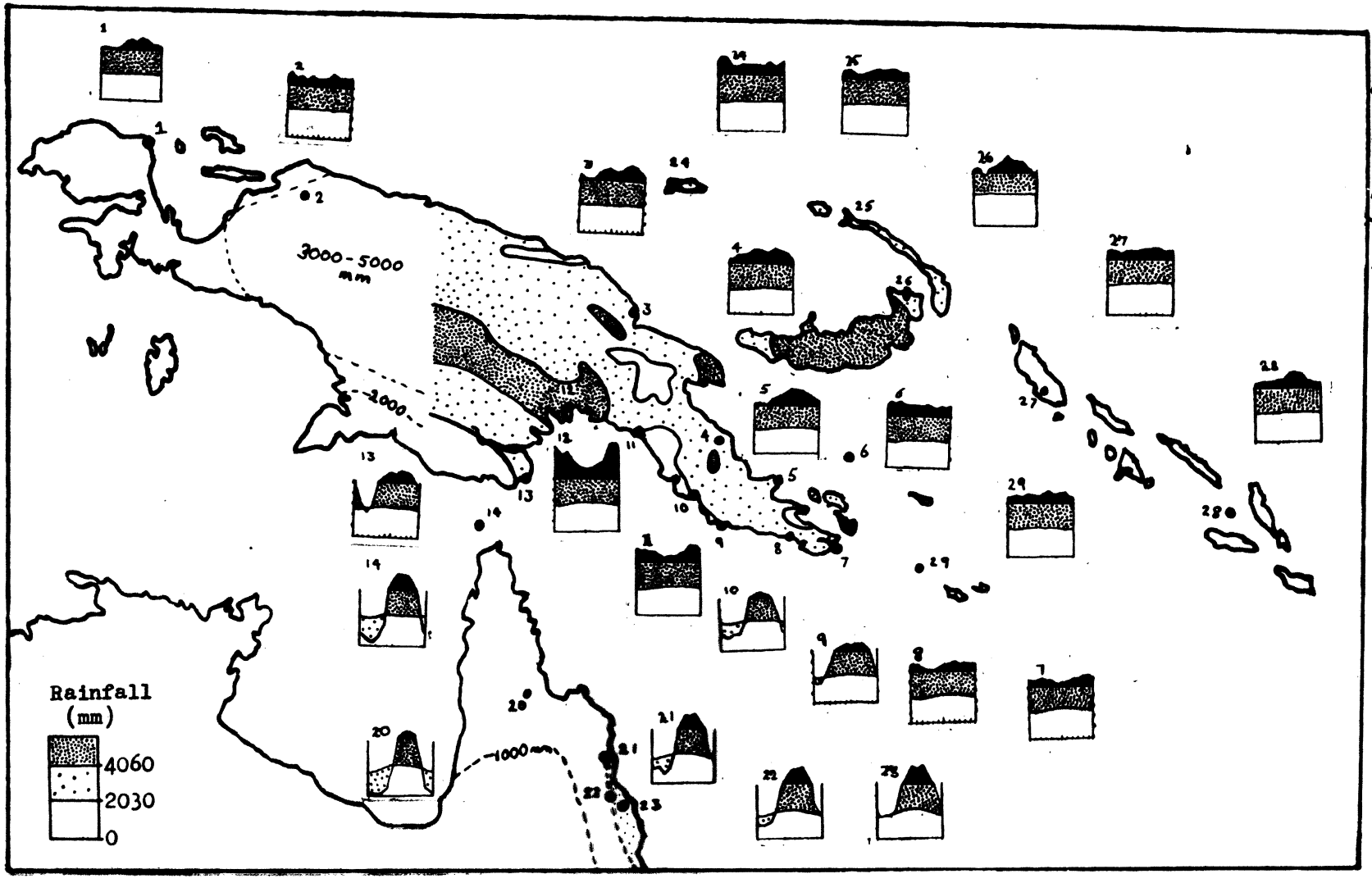
Overlays



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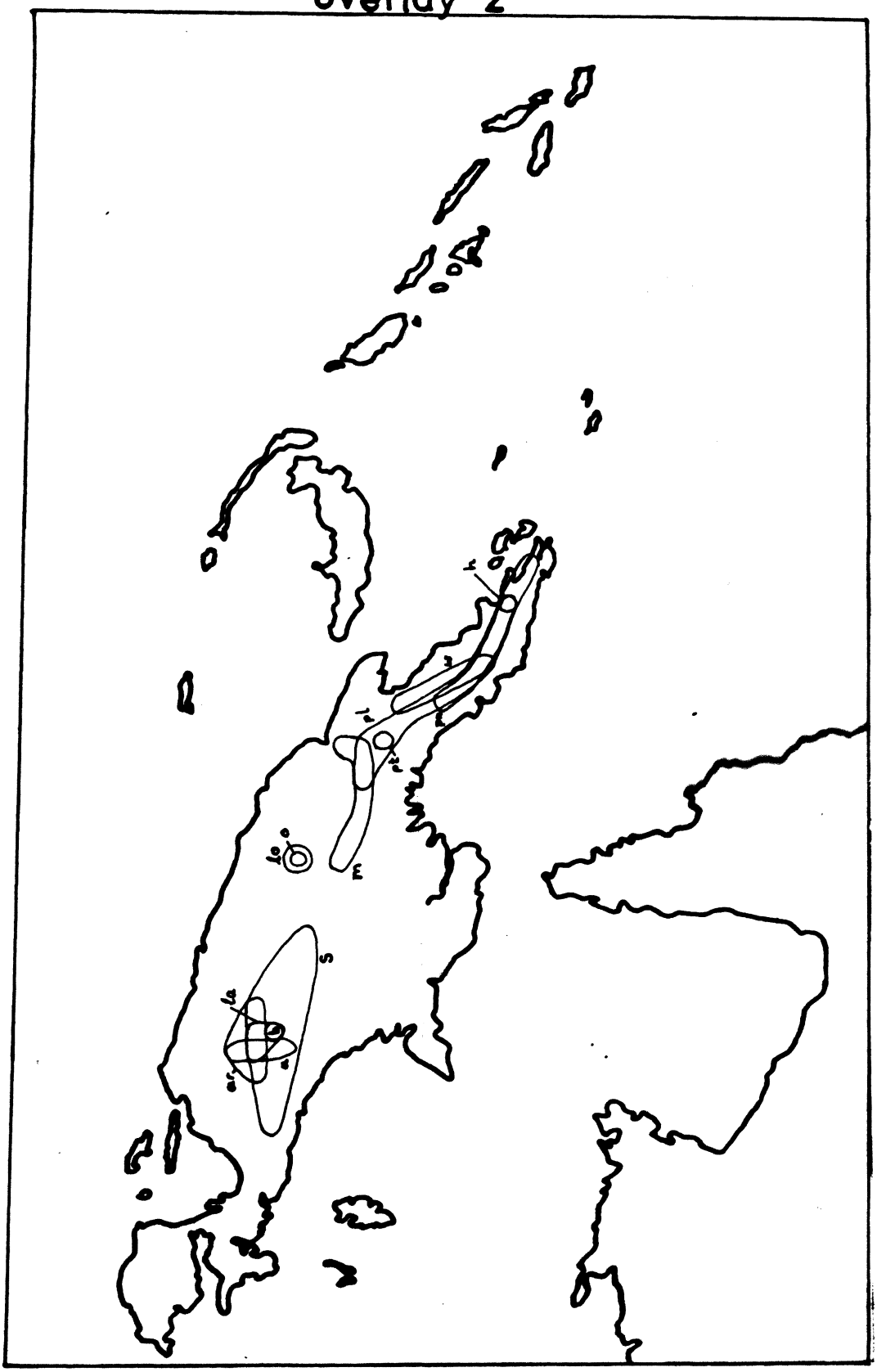

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