

THE TUBEROUS EPIPHYTES OF THE RUBIACEAE 5: A REVISION OF MYRMECODIA

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SUMMARY

Myrmecodia Jack, a tuberous epiphytic genus of the Psychotrieae, Hydnophytinae, is revised to contain 26 species. A key and listing of all specimens are included.

INTRODUCTION

Of the five genera of tuberous epiphytes of Hydnophytinae (Rubiaceae) (Huxley & Jebb, 1991a) *Myrmecodia* is the most closely associated with ants. The genus comprises some 26 species from Malesia and surrounding areas. All the species have a chambered tuber which is normally occupied by ants. The plants can be cultivated readily without the ants, and form apparently normal, chambered tubers.

Myrmecodia has a greater variety of complex tubers than the related genera. These have been described in the course of our work (Huxley, 1976, 1981; Jebb, 1985). The genus falls into a pattern of groups of species according to the tuber structure (Huxley & Jebb, unpubl.).

All specimens cited have been seen unless stated otherwise. The figure in brackets after *Flower* in the descriptions is the number of flowers dissected. Where known the latitude and longitude of each locality is given as closely as determined.

DISTRIBUTION AND ECOLOGY

Myrmecodia is distributed from Peninsular Malaysia, through the Philippines, Sumatra, Borneo, Java, New Guinea, Cape York to the Solomon Islands. This distribution is only slightly more restricted than that of *Hydnophytum* (see figure in Huxley & Jebb, 1991a). The greatest diversity of *Myrmecodia* species is found on the island of New Guinea, where the highland species are local in extent. In the lowlands there are a few widespread species which are very variable. *Myrmecodia tuberosa* is described as an ochlo species, and informal names are given to the main variants. No key is given to these variants since many character combinations recur in different parts of the range and are only defined geographically.

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Ecologically, *Myrmecodia* is distributed from mangrove and coastal trees to high altitudes, 2400 m. It is most abundant in savanna vegetation, for instance in *Melaleuca* in Western Province of Papua New Guinea. *Myrmecodia* is rare in lowland rain forest, but frequent in montane forest and often abundant in open agricultural areas at c. 600 m. *Myrmecodia* is epiphytic on a wide range of trees, being common on *Melaleuca*, *Casuarina*, *Castanopsis*, and *Nothofagus*, but is rare on trees with a smooth or non-absorbent, flaking bark, such as *Eucalyptus*. *Myrmecodia* also grows terrestrially in low nutrient, treeless areas (e.g. *M. sterrophylla* at Ok Tedi) and above the tree line (e.g. *M. lamii* in Irian Jaya).

The symbiosis between *Myrmecodia* and ants is closer in this genus than in any of the other genera of the Hydnophytinae. Plants in the wild are almost invariably inhabited by ants and more consistently by three species of the genus *Iridomyrmex* than are the other Hydnophytinae (Huxley, 1978). Moreover, two species of fungus are regularly found in the tubers of *Myrmecodia* when they are inhabited by the open environment symbiont, *I. cordatus*. One of these fungi is *Arthrocladium* sp. which is found in the warted cavities, and the other is an unidentified monilialine fungus which grows inside the cells of the smooth walled chambers (Huxley, 1978). *Myrmecodia* has not been found harbouring geckos, frogs or the wide range of invertebrates found in *Hydnophytum* tubers. This greater specificity of the symbiosis is probably correlated with the greater complexity of the tuber cavities in *Myrmecodia*.

The symbiosis with ants may also have affected other features of *Myrmecodia*, the mesophytic leaves may reflect improved nutrient status due to ants, relative to *Hydnophytum* which often has sclerophytic and small leaves. The ants may have interfered with the pollination mechanism as well, heterostyly is often incomplete with the stigma at the anthers, the anthers sometimes dehiscent while the corolla is closed, and the pollen with large vesicles unprotected by sporopollenin, and ill-fitted to insect dispersal.

MORPHOLOGY

Tuber

The tuber of *Myrmecodia* is typically spheroidal when young, becoming ellipsoid, either shortly so or elongate, when mature. Rarely the tuber is branched with stems arising at two or more apices. The tubers are almost always spiney, the root-derived spines often being most frequent along ridges or around the holes into the cavities. The spines vary from being short, stout, and simple, through long, stellate or irregularly branched. The tuber surface is usually smooth, but, especially in *M. tuberosa*, may have protrusions which look like lenticels but are anatomically similar to the warts found on certain of the cavity walls.

The tuber has a system of cavities, the formation of which is described in Huxley (1978) and Huxley & Jebb (1991a). After the initial rather simple cavities which are added laterally, later cavities are added apically and are differentiated into smooth-walled chambers and warted ones. The form and interconnection of these chambers is highly characteristic and has been used to develop an informal classification of the genus (Jebb, 1985, 1991, and unpubl.). Each later cavity is composed of three types of chamber: superficial, inner smooth, and warted chambers. The superficial chamber usually lies beneath a raised area of the tuber surface (Fig. 2b) which has pores (holes

usually 0.5–1.5 mm diameter) to the outside. In some species (e.g. *M. tuberosa*) the later cavities open by larger holes to the outside, these entrance holes (4–8 mm diameter) are found in arcs around the basal side of the raised areas.

The superficial chambers are of two main kinds. In most species they have a honey-combed form, consisting of numerous hexagonal cells; these are especially well developed in *M. schlechteri*. In other species the superficial chambers are formed by branching strands which arch towards the tuber surface. These dendroid chambers are well formed in *M. sterrophylla*. *Myrmecodia brassii* has dendroid superficial chambers in the apical part of the tuber but the lower part appears to be different but has not been fully examined (Fig. 18).

Stems

Myrmecodia has usually only one or a few stems, except in *M. lamii* (Fig. 19). The stems are rarely branched, and in some species not at all. The stems are thick and the internodes highly condensed except at the base in some species (e.g. *M. tuberosa*; Fig. 3). In many species a shield-shaped clypeolus is developed at the base of each petiole (e.g. Fig. 11).

In *M. melanacantha*, *M. gracilispina*, *M. horrida*, and *M. ferox* the tuber cavities connect to a few tunnels which run the length of the stem and open into the alveoli.

Leaves

The leaves are leathery (thick and fleshy only in *M. beccarii*). Some high altitude species have long narrow leaves, but the leaves are never small and xerophytic as often in *Hydnophytum* at high altitude.

The stipules are large, persistent, and split between and opposite the petioles, forming conspicuous 'ears' on the clypeoli (Fig. 11). Sometimes they extend to a wing around the upper part of the clypeolus (Fig. 20).

Inflorescence

Flowering starts when only a few internodes have been formed and then occurs at each node. The two parts of each inflorescence develop in a separate alveolus. The two alveoli may be unequal in size and differently displaced along the stem, so that in some cases (e.g. *M. tuberosa*; Fig. 6) the alveoli appear in longitudinal pairs which are in fact derived from adjacent nodes. The flower buds arise at the base of the alveoli, sometimes being sunk in the tissue there.

Each flower is subtended by a bracteole (referred to as bracts). These vary from very obscure to prominent and sometimes have hairs along the inner base. The bracts and hairs sometimes fill the alveoli with a rufous cushion.

The flowers are rarely cleistogamous and sometimes heterostylous. The calyx is usually truncate, rarely dentate, and the corolla lobes strongly unciniate.

The pollen is 1-, 2-, or 3-porate (colporate) and frequently has 1, 2, or 3 large cytoplasmic vesicles protruding from the pores.

The fruit develops within the alveolus, and elongates at the base, to protrude, only when ripe.

MYRMECODIA

[*Nidus formicarum ruber* Rumph., Herb. Amboin. (1750) 119, tab. 55.]

Myrmecodia Jack, Trans. Linn. Soc. Lond. 14 (1823) 122; Blume, Bijdr. Fl. Ned. Ind. (1826/1827) 1001; Gaudich. in Freycinet, Voyage autour du Monde (March 1830) 472, pl. 96, p.p., excl. *M. inerme* Gaudich. tantum; A.P. DC., Prod. 4 (Sept 1830) 450; Benth. & Hook., Gen. Pl. 2 (1873) 132; Becc., Malesia 2 (1884) 95; Valeton, Bot. Jahrb. 61 (1927) 144; Merr. & Perry, J. Arnold Arbor. 26 (1945) 26. — Type species: *M. tuberosa* Jack.

Lasiosoma auct. non Schreber: Sprengel, Syst. Veg. (1825) 422, p.p., quoad *L. tuberosum* (Jack) Sprengel tantum.

Epiphytic, rarely terrestrial. *Tuber* rounded, ovoid or cylindrical, often ridged. Spines (if present) simple, branched, or stellate. Chambers complex, often with arcs of entrance holes surrounding swollen honeycombed areas with pores; honeycombing forming a series of cells (or dendroid). *Stem(s)* solitary or few, little or unbranched, thick. Internodes about as long as wide. Clypeoli often present. *Leaves* mesomorphic or leathery, rarely fleshy; petioles white, green, or red; stipules splitting between the petioles and partly splitting opposite them, often persistent, usually chestnut brown. *Inflorescence* sunken in paired alveoli. Bracts inconspicuous or with hairs forming a dense mass. Corolla white (once recorded as blue and once as red), rarely with blue-black flecks, 4-lobed; lobes uncinatate, not usually spreading at anthesis; the tube with a ring of hairs at varying levels, rarely glabrous. Often heterostylous. Anthers usually enclosed within tube, white or cream, sometimes with blue-black flecks. Filaments short. Pollen 2–4 (1–5)-porate or -colporate, apertures sometimes bordered, cytoplasmic vesicles often extruded from one to all of the apertures; reticulation fine to coarse. Stigma lobed, usually as many as ovules. Ovules 2–10. Fruit a sweet fleshy drupe, developing within the alveolus and extruded when mature, white, yellow, orange, or red. Pyrenes (2–)4–6(–10).

KEY TO THE SPECIES

- 1a. Clypeoli winged for 1/3 to 1/2 their length with glossy grey extensions of the stipules. 2
- b. Clypeoli absent, or, if present, winged to less than 1/3 their length 3
- 2a. Stems 1–2, usually < 30 cm long. Leaves spatulate 22. *M. pteraspida*
- b. Stems 8–16, often > 30 cm. Leaves oblanceolate 20. *M. lamii*
- 3a. Tunnels present inside stem. Spines all simple, black or dark reddish brown at tips 4
- b. No tunnels in stems. Spines branched, or clustered on mounds at base of tuber, or simple black or brown 7
- 4a. Clypeoli clearly apparent, tuber spines slender 26. *M. gracilisipina*
- b. Clypeoli obscure or absent, tuber spines stout 5
- 5a. Petioles winged to base. Corolla glabrous 25. *M. ferox*
- b. Petioles not winged to base. Corolla with a ring of hairs 6
- 6a. Petioles (2–)3–6 cm, alveoli rims at an angle to stem 24. *M. horrida*
- b. Petioles 1–2(–3) cm, alveoli rims parallel to stem 23. *M. melanacantha*
- 7a. Leaves 9–12 cm long, fleshy. Spines on tuber simple, < 0.5 cm. Stems several, freely branched 6. *M. beccarii*

- b. Leaves usually larger, not fleshy. Spines simple or branched, usually > 0.5 cm long. Stems one or several, branched or not 8
- 8a. Spines around alveoli simple, fat; spines on stem none or few, sometimes branched. Clypeoli obscure or absent. Spines on tuber few to many, branched, club-like, or stellate 9
- b. Not with the above combination of characters 11
- 9a. Leaves > 6 cm broad. Spines on tuber simple, club-like, or clustered at base
3. *M. jobiensis*
- b. Leaves < 6 cm broad. Spines on tuber stellate 10
- 10a. Leaves > 14 cm long, margin undulately crisped 4. *M. erinacea*
- b. Leaves usually < 14 cm long, margin flat 5. *M. alata*
- 11a. Spines simple. Stems 1 (few), unbranched 12
- b. Spines sometimes branched. Stems 1-few, branched or not 20
- 12a. Leaves long and narrow, 15 × 2–30 × 4 cm 13
- b. Leaves not long and narrow 14
- 13a. Tuber spines often clustered on mounds. Petioles red. Corolla glabrous
21. *M. archboldiana*
- b. Tuber spines not clustered. Petioles green or white. Corolla with a ring of hairs
9. *M. longissima*
- 14a. Lamina 4–9.5 cm wide. Clypeoli distinct 7. *M. platytyrea*
- b. Lamina < 6.5 cm wide. Clypeoli distinct or not 15
- 15a. Tuber ridges with white edges 8. *M. pendens*
- b. Tuber ridges without white edges 16
- 16a. Mature tuber with a basal part with clustered spines and apical part with scattered spines 19. *M. brassii*
- b. Mature tuber not with distinct basal and apical parts 17
- 17a. Clypeoli well defined by a rim of spines lying in one plane, hiding the alveoli
17. *M. paradoxa*
- b. Clypeoli rimmed by spines sparse or spreading in many directions, alveoli visible, sometimes filled by bracts and hairs 18
- 18a. Lamina abruptly cuneate at base 10. *M. oblongata*
- b. Lamina cuneate or tapered at base 19
- 19a. Petioles white or green. Superficial chambers honeycombed
11. *M. longifolia*
- b. Petioles usually pink or red. Superficial chambers dendroid
15. *M. sterrophylla*
- 20a. Stem spines mostly stellate, ± dense. 21
- b. Stem spines simple or branched, often sparse 25
- 21a. Leaves long, narrow, to 45 × 2.5 cm 14. *M. angustifolia*
- b. Leaves not long and narrow 22
- 22a. Leaves oblanceolate, or narrowly elliptic, to 24 × 5 cm. Petioles 0.2–3 cm
12. *M. schlechteri*
- b. Leaves lanceolate (oblanceolate), usually larger. Petioles 2–9 cm 23
- 23a. Spines golden. Petioles 2–3.5 cm 18. *M. aureospina*
- b. Spines brown or blackish. Petioles 3–9 cm 24

- 24a. Stem solitary and unbranched. Clypeoli present. Petioles red. Tuber dark grey with blocked pores, other areas pale grey-green . . . 16. *M. oksapminensis*
 b. Stems sometimes few, branched. Clypeoli absent. Petioles green. Tuber surface pale grey to dark brown, areas with pores not markedly different in colour
 13. *M. albertisii*
- 25a. Leaves long and narrow, to 30 × 4 cm 9. *M. longissima*
 b. Leaves not long and narrow 26
- 26a. Leaves abruptly cuneate at base 10. *M. oblongata*
 b. Leaves not abruptly cuneate at base 27
- 27a. Leaves less than 4 cm wide, gradually tapered at base. Petioles 0.5–2 cm
 2. *M. kutubuensis*
 b. Leaves wider than 3 cm, usually cuneate at base. Petioles 2.5–13 cm 28
- 28a. Leaves wider than 4 cm. Petioles 4–13 cm 1. *M. tuberosa*
 b. Leaves 3–6.5 cm wide. Petioles 2.5–4.5 cm 11. *M. longifolia*

1. *Myrmecodia tuberosa* Jack

Myrmecodia tuberosa Jack, Trans. Linn. Soc. Lond. 14 (1823) 123; Blume, Bijdr. Fl. Ned. Ind. (1826) 1001; Becc., Malesia 2 (1884) 99, t. 13, 14; Merr. & Perry, J. Arnold Arbor. 26 (1945) 26. — *Lasiostoma tuberosum* (Jack) Sprengel, Syst. Veg. 1 (1825) 422. — *Myrmecodia echinata* Gaudich. in Freycinet, Voyage autour du Monde (1830) 472. — Type: Sumatra, ? Jack s.n. (no specimen known to have existed). Lectotype: in Rumphius, Herb. Amboin. (1750) 119, t. 55.

[*Nidus formicarum rubrarum* Rumph., Herb. Amboin. (1750) 119, t. 55.]

Myrmecodia inermis auct. non Gaudich.: DC., Prod. 4 (1830) 450.

Myrmecodia armata DC., Prod. 4 (1830) 450. — Types: Moluccas, *Gaudichaud s.n.* (G, P), Java; Blume 22 (L, 2 sh), syn. nov.

Myrmecodia hispida sphalm. Richard, Mém. Soc. Nat. Hist. Paris 5 (1834) 224; no description, probably an error for *M. echinata*.

Myrmecodia kandariensis Becc., Malesia 2 (1884) 100, t. 15. — Type: Sulawesi, *Beccari 5516* (FI), syn. nov.

Myrmecodia muelleri Becc., Malesia 2 (1884) 102, t. 16. — Type: Papua New Guinea, *d'Albertis 5904* (FI), syn. nov.

Myrmecodia pulvinata Becc., Malesia 2 (1884) 103, t. 17. — Type: Irian Jaya, *Beccari P.P. 769* (FI), syn. nov.

Myrmecodia bullosa Becc., Malesia 2 (1884) 108, t. 20 & 26. — Type: Irian Jaya, *Beccari P.P. 184* (FI), syn. nov.

Myrmecodia oninensis Becc., Malesia 2 (1884) 110, t. 21. — Type: Irian Jaya, *Beccari P.P. 51* (FI), syn. nov.

Myrmecodia rumphii Becc., Malesia 2 (1884) 117, t. 12: 1–6. — Type: Seram, *Beccari 5510* (FI), syn. nov.

Myrmecodia goramensis Becc., Malesia 2 (1884) 118, t. 24. — Type: Moluccas, *Beccari 5508* (FI), syn. nov.

Myrmecodia salomonensis Becc., Malesia 2 (1885) 175, t. 53: 1. — Type: Solomon Islands, *Guppy 141* (FI, K), syn. nov.

Myrmecodia menadensis Becc., Malesia 2 (1885) 176, t. 53: 2–7. — Type: Sulawesi, *Teijsmann s.n.* (CAL not seen, FI), syn. nov.

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

- Myrmecodia dahlui* Schumann, Notizbl. Bot. Gart. Berlin 2 (1898) 153. — Type: Papua New Guinea, *Dahl s.n.* (B), syn. nov.
- Myrmecodia pentasperma* Schumann, Notizbl. Bot. Gart. Berlin 2 (1898) 154. — Type: Papua New Guinea, *Dahl s.n.* (B), syn. nov.
- Myrmecodia lanceolata* Valetton, Nova Guinea 8 (1911) 510. — Type: Irian Jaya, *Versteeg 1046* (L), 1246 (L), syn. nov.
- Myrmecodia apoensis* Elmer, Leaflet. Philipp. Bot. 3 (1911) 1040. — Type: Philippines, *Elmer 11261* (?† PNH, not seen), syn. nov.
- Myrmecodia sibuyanensis* Elmer, Leaflet. Philipp. Bot. 3 (1911) 1041. — Type: Philippines, *Elmer 12336* (BM, BO, FI, G, K, L, ?† PNH not seen, W, WRS), syn. nov.
- Myrmecodia urdenatensis* Elmer, Leaflet. Philipp. Bot. 5 (1913) 1876. — Type: Philippines, *Elmer 14083* (?† PNH not seen), syn. nov.
- Myrmecodia paucispina* Valetton, Bot. Jahrb. 61 (1927) 150. — Type: Papua New Guinea, *Schlechter 14178* (B, L photo, WRS), rubbing), syn. nov.
- Myrmecodia peekelii* Valetton, Bot. Jahrb. 61 (1927) 147. — Type: Papua New Guinea, *Peekel 468* (B†), syn. nov.
- Myrmecodia sorsogonensis* Elmer, Leaflet. Philipp. Bot. 9 (1934) 3253. — Type: Philippines, *Elmer 15964* (BM, BO, FI, G, K, L, P, ?† PNH not seen), syn. nov.

Tuber variously shaped and coloured, $2 \times 6 - 40 \times 15$ cm, ridged or not. Spines present or absent, usually simple, sometimes branched or club-like. Entrance holes over the surface often in arcs, pores present or absent. *Stems* one to few, branched or unbranched. Clypeoli present or absent. Alveoli present, sometimes densely filled with cushion-like masses of bract hairs. Spines usually present, especially around the alveoli, sparsely branched. *Leaves*: Lamina $10 \times 3 - 47 \times 14$ cm, elliptic, oblanceolate or spatulate; apex acute or acuminate; base abruptly to gradually tapered; leathery or thin. Midrib prominent below, whitish or green. Petioles 2–13 cm. Stipules 0.5–1.5 cm, triangular, more or less persistent. *Inflorescence*: Bracts variable, to 8 mm, hairy. Flowers heterostylous. Calyx 0.5–3 mm. Corolla 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 c. 7 mm long, yellow, orange-red to pink.

Typology – Jack's description of his tragically lost collection from Pulo Nias resembles material from the neighbouring Siberut in its long petioles, leaf-shape, and clypeoli with strigose fibres. Jack also cites Rumphius' description and illustration of material from Ambon, and this must stand as the lectotype.

Note – The concept of *M. tuberosa* is extended here to include the whole variable continuum from Indochina and the Philippines to Australia and the Solomon Islands. This species does not fall readily into discrete, replacing units and should therefore be regarded as an ochlopecies. The material has been examined in some detail and descriptions of the main variants are given. These variants are not sufficiently discrete geographically or morphologically to name as subspecies or varieties, and are therefore given informal 'nicknames' which largely follow existing specific epithets.

a. *Myrmecodia tuberosa* 'armata'

Tuber irregularly globose to oblong, to 40×15 cm, usually ridged, brown. Spines sparse to dense, simple or once branched, stout or stiff (root-like), on ridges or scat-

tered (sometimes clustered), 1(–2) cm. Entrance holes 0.4–1 cm apart, in irregular arcs. Pores scattered or in rings over honeycombed areas. *Stem* usually solitary and unbranched, erect or curving upwards, 30 × 1–3 cm. Base of stem narrow without clypeoli or alveoli. Clypeoli obscure to distinct. Alveoli to 1.5 cm, usually filled with hairy bracts. Spines rimming alveoli, or clypeoli when present, mostly simple but often branched or root-like, to 1.2 cm. *Leaves*: Lamina 10 × 4–21 × 8.5 [–25 × 11] cm; elliptic, apex acuminate; base cuneate; thin to leathery. Midrib prominent below, it and the petiole whitish or green. Lateral veins 10–15, straight and parallel over much of their length, not strongly alternating in prominence. Petioles 3–6(–7) cm. Stipules broadly triangular, falling before the leaves, to 1.5 cm long. *Inflorescence*: Flowers (7). Corolla to 12 mm; lobes 3 mm; lobe tips 1.5 mm. Ring of hairs near base of tube, 1 mm wide. Anthers at apex of tube; filaments 0.5 mm. Pollen 2- or 3-porate, 1- or 2- (or 3-)vesiculate; reticulation medium; apertures not bordered. Stigma at or above anthers, 4- or 5-lobed. Fruit yellow or orange. Pyrenes 4–6.

Ecology – Sea level to 500 m.

Notes – The name *Myrmecodia tuberosa* 'armata' is used to cover a variable continuum ranging from the Gulf of Annam through to Java and Borneo. It varies considerably in stem characters, but the leaves are relatively uniform, the venation being characteristic. The specimen from Anamba Is. has exceptionally large leaves, to 25 × 11 cm, with petioles to 7 cm long.

The position of the stigma at the anthers, the presence of dehiscent anthers in two closed flowers, and sometimes large cytoplasmic vesicles with little sporopollenin cover, suggest a self-pollinating group.

Collections – VIETNAM. Annam, Blao, nr. Haut Douai, *Poillane* 23550 (P).

PENINSULAR MALAYSIA. NE 05° 102° Kelantan, Kampong Kubang, *Haniff* SF 10217 (BM, BRI, SING). 05° 103° Anamba Is., Sungai Ayer Maras, Jenaja, *Henderson* SF 20454 (BO, SING). 04° 100° Perak, Taiping, Simpang, Krian Rd, *Haniff* SF 13288 (SING). 04° 101° Kelantan, Gua, Panjung Ulu, *UNESCO Limestone Exped. Fl. Malaya* 668 (SING). 04° 102° Pahang, S Sat, Ulu Tembeling, *Henderson* SF 21973 (SING). 03–04° 102° Pahang, Sungai Tohan, *Holttum* SF 20827 (BO, SING, UC). 03° 103° Pahang, Kuantan, Telok, Sisik, *Henderson* s.n., 1929 (SING).

SINGAPORE. 01° 103° Sungai Jurong, *Ridley* 3854 (SING). *Ridley* 81061 (SING). 01° 103° *Waltace* s.n., 1855 (K). 01° 103° Bukit Timah, *Ridley* s.n., 6:1886 (SING). 01 103 Bukit Timah Rd, *Makoto Togashi* 622151 (TOKYO). 01° 103° Pulau Pisang, *Burkill & Kiah* 667 (SING). Kwala Pahang, *Ridley* 1462 (BM). Pahang, *Davison* s.n., 1889 (SING).

SUMATRA. NE 03° 98° Residentie S.O.K., Tingi Radja, *Jochems* 7 (BO). 02° 99° Asahan, *Yates* 1792 (UC). 00° 99° West coast, G. Taloe, *Bunnemeijer* 184 (BO). 00° 100° E of Pajakumbuh, R. Tjampo, Taram, *Meijer* 6745 (L).

BORNEO. NE 00° 116° W Kutei, Kelindjan R., near Melan, *Kostermans* 9619 (BO). SE 01° 116° Sq Wain Region, N of Balikpapan, *Kostermans* 4578 (BO). 02° 112° 10 km W of Sampit, *Buwalda* 7834a (BO, L). Danau Pentoelah, Main, emp. *Polak* 1933 (BO, L). SE 02° 112° Sampit, *Buwalda* 9113 (BO, L).

JAVA. SE 06° 106° Bantam, Tjitoiak & Moentjang, NW of Tjitvedjah, *Backer* 1844 (BO 2 sh.). 06° 106° Batavia Residentie, G. Liliang, Kp. Karangtengah, *van Steenis* 2444 (BO). 06° 106° near Buitenzorg, G. Pantjar, *Koorders* 40362 (BO); *Koorders* 40370 (BO); *Hochreutiner* 1851 (G). 06° 106° Leuwiliang, G. Sodang, *Bakhuizen van den Brink* 5291 (BO) & 77g (BO). 06° 106° Salak, Buitenzorg, *Lecomte & Finet* 11912 (P). 07° 107° Nangela, *Docters van Leeuwen* 12054 (L). G. Tjipaelih, near Tjiampba, Tjipaleuh, *Bakhuizen van den Brink* 4210 (BO). Tjibjoeroeg, Tjidadap near Tjiberber, Residentie Guangan, *Bakhuizen van den Brink* 7018 (BO). Locality unknown: *Blume* 22 (type of *M. armata*).

b. *Myrmecodia tuberosa* 'siberutensis'

Tuber semi-pendent, irregularly cylindrical, surface blackish. Spines few to many, simple, short and stiff. *Stem(s)* 1 to few, narrow at base, to 15×1.4 cm. Clypeoli distinct, elongate, densely rimmed with root-like, sometimes branched spines c. 0.4 cm long. *Leaves*: Lamina c. 11×5 cm, broadest above the middle; apex mucronate; base cuneate or tapering. Petioles 6–9.5 cm, slender. Stipules to 0.7 cm, broadly triangular. *Inflorescence*: Bracts inconspicuous. Flowers (1). Corolla 12 mm; lobes 4 mm; lobe tips 1 mm; ring of hairs 2–3 mm from base. Anthers exerted from the tube; filaments 1.5 mm. Pollen vesiculate. Stigma at or above anthers. Pyrenes 4, apex rounded.

Ecology – In lowland rain forest.

Notes – This variant is distinguished from *M. tuberosa* on mainland Sumatra by its leaf shape and clypeolate stem. The pyrenes are not horned as in *M. tuberosa* 'menadensis', but the leaf and stem characters are similar.

The single collection from Batu Is. differs from those from Siberut and the Pageh Is. in having elliptic laminae, c. 16×6 cm, widest at or below the middle; apex acute to acuminate; base cuneate; petiole 3–7 cm; spines around the clypeoli stiff; tuber and flowers not known; pyrenes 6.

Collections – MENTAWI ISLANDS. SE 00° 99° Batu Is., *Raap* 637 (BO). 01° 98–99° Siberut Is., *Iboet s.n.* (BO, L); *Boden Kloss SF 12299* (BM, BO, K, SING, UC). Pageh Is., Ka Leleu, *Loeb* 21 (UC).

c. *Myrmecodia tuberosa* 'bracteata'

Tuber irregularly obconical. Spines very few, simple. *Stem* one, unbranched. Clypeoli absent or indistinct. Alveoli elongate, densely filled with protruding, hairy bracts. Spines rimming alveoli, many, root-like, to few, simple or branched, usually less than 1 cm long. *Leaves*: Lamina $9 \times 3 - 16 \times 5.5$ cm, elliptic to oblanceolate; the apex acute to acuminate; the base cuneate; leathery to fleshy. Midrib often white, forming a large keel. Lateral veins obscure on fleshy leaves, 6–8, curving throughout their length. Petioles 2–3(–5) cm, usually white and fleshy. Stipules to 0.6 cm long, broadly triangular, persistent. *Inflorescence*: Flowers (3). Broad ring of hairs $1/3$ the way up the tube. Anthers at the apex of the tube; filaments 0.5–1.5 mm. Pollen 2-porate, 1- or 2-vesiculate, the apertures not bordered, vesiculate aperture widely stretched; reticulation fine. Stigma just above anthers. Fruit yellow. Pyrenes 4 or 5.

Ecology – Altitude 0–200 m.

Note – This variant is distinguished from *M. tuberosa* 'armata' by the dense protruding bracts and short stem spines, but it is not well-defined; for instance, the Haviland and Hose collection has thin leaves and lacks the fleshy petioles.

Collections – BORNEO. NE 05° 117° Pangkalang Westerafd, *Dunselman* 153 (BO). 04° 114° Brunei, Tutong Dist., *van Niel* 4330 (L). 04° 114° Baram, *Haviland & Hose s.n.*, Feb. 1894 (K). 04° 114° Baram, Lobok Pasir, *Anderson* 9873 (L, SING). 01° 110° Telok Asam, Bako Nat. Park, *Purseglove* P4893 (A, K, L, SING). 01° 11° Bako, *Carrick & Enoch* 167 (KLU). 01° 116° Kut-ching, *Beccari P.B.* 361 (FI).

d. *Myrmecodia tuberosa* 'apoensis'

Tuber irregularly cylindrical, ridged, to 15 cm across. Spines \pm dense along ridges, mostly simple, stout or slender, c. 0.8 cm. Stem solitary, unbranched, to 16×1.4 cm. Clypeoli round to elliptic, densely rimmed by simple spines, which are more or less stiff. *Leaves*: Lamina $5 \times 1.5 - 15 \times 6$ cm narrowly oblanceolate, apex acute, leathery. Midrib sharply keeled below, at least sometimes maroon. Lateral veins usually obscure, 4–6(–10). Petioles 1–6 cm, colour as midrib. Stipules broadly triangular. *Inflorescence*: Flowers (2). Corolla to 10 mm; lobes 3 mm; lobe tips 1 mm; ring of hairs midway up the tube. Anthers towards apex of lobes, 1.5 mm; filaments 1 or 2.5 mm. Pollen 2- or 3-porate, 1-, 2- (or 3-)vesiculate; reticulation fine to medium; wall firm; apertures not bordered. Stigma at anthers. Fruit orange-yellow, ellipsoid, 7.5 mm. Pyrenes 4–6.

Ecology – Altitude 700–2466 m, montane and mossy forest.

Notes – This is a narrow- and small-leaved montane form of *Myrmecodia tuberosa*. It is distinguished in Borneo from *M. tuberosa* 'armata' by the densely spiny clypeoli which continue to the base of the stem. In the Philippines it differs from *M. tuberosa* 'sibuyanensis' by the fewer pyrenes, and lateral veins that are not alternating markedly in size. There is considerable variation in leaf characters. Further collections may show more consistent differences between the populations in Borneo and in the Philippines.

The possibility of a relationship with *M. platytyrea* must not be ruled out. The tuber structure and pyrene number, which are unknown for the east Bornean specimens might reveal an affinity.

Collections – PHILIPPINES. NE 16°15' 121°05' Luzon, Prov. Nueva Vizcaya, nr Dupax, McGregor BS 11312 (BM). 15°40' 121°18' Luzon, Sierra Madre, WSW of Baler, Jacobs 7977 (K, L, PNH). 09°126' Mindanao, Agusan Prov., Mt Urdaneta, Cabadbaran, Elmer 14083 (type of *M. urdenatensis*). 06°58' 125°17' Mindanao, District of Davao, Mt Apo, Elmer 11261 (type of *M. apoensis*). Mindanao, Davao Prov., Mt McKinley, Edaña PNH 955 (PNH).

BORNEO. NE 05°118° Sq Susuk, N of Sanghuliang, Kostermans 6198 (BO). 03° 113–114° Dulit Ridge, Richards 2163 (K).

e. *Myrmecodia tuberosa* 'sibuyanensis'

Tuber irregularly globose to elongate, shallowly lobed; to 30 (50) cm across, smooth and lacking in spines to ridged and densely spiny. Spines usually rather weak, 0.5–1.5 cm. Entrance holes, honeycombing and pores present or absent. *Stem* solitary, rarely with short branches from the base, ascending, to 50×2 cm. Clypeoli oblong, to 3×1.5 cm. Base of stem \pm clypeolate. Alveoli usually filled with bracts. *Leaves*: Lamina $11 \times 4.5 - 20 \times 8.5$ cm, elliptic (oblanceolate); apex acute to abruptly acuminate; base usually abruptly cuneate, mostly rather leathery. Midrib prominent below to apex. Lateral veins conspicuously alternating in prominence, 8–14. Petioles 5–10 cm. Stipules broadly triangular, to 1.3 cm. *Inflorescence*: Flowers (2). Corolla 8 mm; lobes closed at anthesis, 2.5 mm; lobe tips 1 mm; ring of hairs towards base of tube. Anthers at apex of tube; filaments 1 mm. Pollen 2-porate, 2-vesiculate, apertures not bordered; reticulation medium; pollen wall thin, weak (or absent). Stigma at anthers. Fruit red, 10 mm. Pyrenes 5–8.

Ecology – Altitude 0–600 m.

Note – All the lowland material from the Philippines is placed together here although it includes considerable variation in tuber, stem, and leaf characters.

Collections – PHILIPPINES. NE 16° 121° Luzon, Mt Province, Pugu, Banue, Ifuga, *Conklin & Buwaya* PNH 78749 (A, K, L). 14° 120° Luzon, Bataan Prov., Lamao R., Mt Mariveles, *Whitford* 1144 (K, US). 14° 121° Luzon, Tayabas Prov., Lagumanoc, *Merrill* PNH 3364 (K). 13° 122° Quezon, Hina-baan, Guinayangan, *Mendoza* PNH 97950 (L, PNH, US). 12° 122° Sibuyan, Giting Giting, *Elmer* 12336 (type of *M. sibuyanensis*). 12° 124° Luzon, Mt Bulusan, Irosin, *Elmer* 15964 (type of *M. sorso-gonensis*). 9° 125° Mindanao, Surigao, *Bolster* 375 (UC). 8° 125° Mindanao, Butuan, *Fenix* BS 15892. Mindanao, Lake Lanao, Camp Keithley, *Clemens* PNH 36936-2 (F). Mindanao, Agusan Prov., Butuan, San Mateo Bo., Florida So., *Mendoza* PNH 42302 (PNH).

f. *Myrmecodia tuberosa* 'menadensis'

Tuber variable. Spines small, weak and brown (sometimes massive, stiff and black). *Stem* ?solitary, unbranched, 10 × 1.5 cm. Clypeoli 0.6 × 1 – 2.4 × 2.4 cm. Spines rimming clypeoli, fine and stiff to fleshy and weak, frequently branched and root-like. *Leaves*: Lamina to 14 × 8 cm, oblanceolate to broadly obovate; apex apiculate; base cuneate. Midrib keeled below. Lateral veins 6–10, almost perpendicular to midrib, curved. Petioles 4–9.5 cm. Stipules to 0.8 cm, broadly triangular, persistent (falling soon). *Inflorescence*: Bracts not exerted. Flowers (4). Corolla 7 mm; lobes 2.5 mm; lobe tips 1 mm. Ring of hairs a third the way up the tube. Anthers exerted above tube apex, 2.5 mm; filaments 0.5 mm. Pollen 2-porate, 2-vesiculate, apertures not bordered; reticulation medium. Stigma at or above anthers, club-like (shortly 4-lobed). Pyrenes 4–6, 4 × 2 mm; apex truncate, with three delicate horns, 1–3 mm long at the corners.

Ecology – Altitude 450–1000 m, old secondary and primary forest.

Notes – *Myrmecodia* in Sulawesi is all clypeolate with the leaves long-petioled, widest above the middle and apiculate at the apex. The pyrenes are horned wherever mature specimens are known.

Myrmecodia kandariensis is united with *M. menadensis* because 1) the pyrenes are truncate but probably not mature, 2) the flower structure falls within the range of *M. menadensis*, and 3) the large rimmed holes on the tuber are insect caused.

Pollen and flower characters are also uniform except in Van der Pijl's collection, which also differs in the massive black spines, red undersides to the leaves and caducous stipules. The final treatment of these specimens must await further material.

Collections – SULAWESI. NE 01° 124° Menado, *de Vriese & Teijsmann* s.n. (type of *M. menadensis*); *Warburg* s.n., Aug. 1888 (B alc.); *Bloembergen* 4070 (L). NE 01° 124° Tomohon, *Koorders* 18621 (BO). Central Sulawesi, Sopa Valley, Dongi Dongi Camp, Gay 1256 (FHO). SE 04° 120° Bone, Nengo, *van der Pijl* 773 (BO). 04° 122° Peninsula SE from Lepo Lepo, nr Kandari, *Beccari* 5516 (type of *M. kandariensis*).

g. *Myrmecodia tuberosa* 'rumphii'

Tuber irregularly conical or ellipsoid, ridges present except on swollen areas, rather fine. Spines mainly on ridges, few to dense, simple, filiform, 0.6–1(–3) cm. Swol-

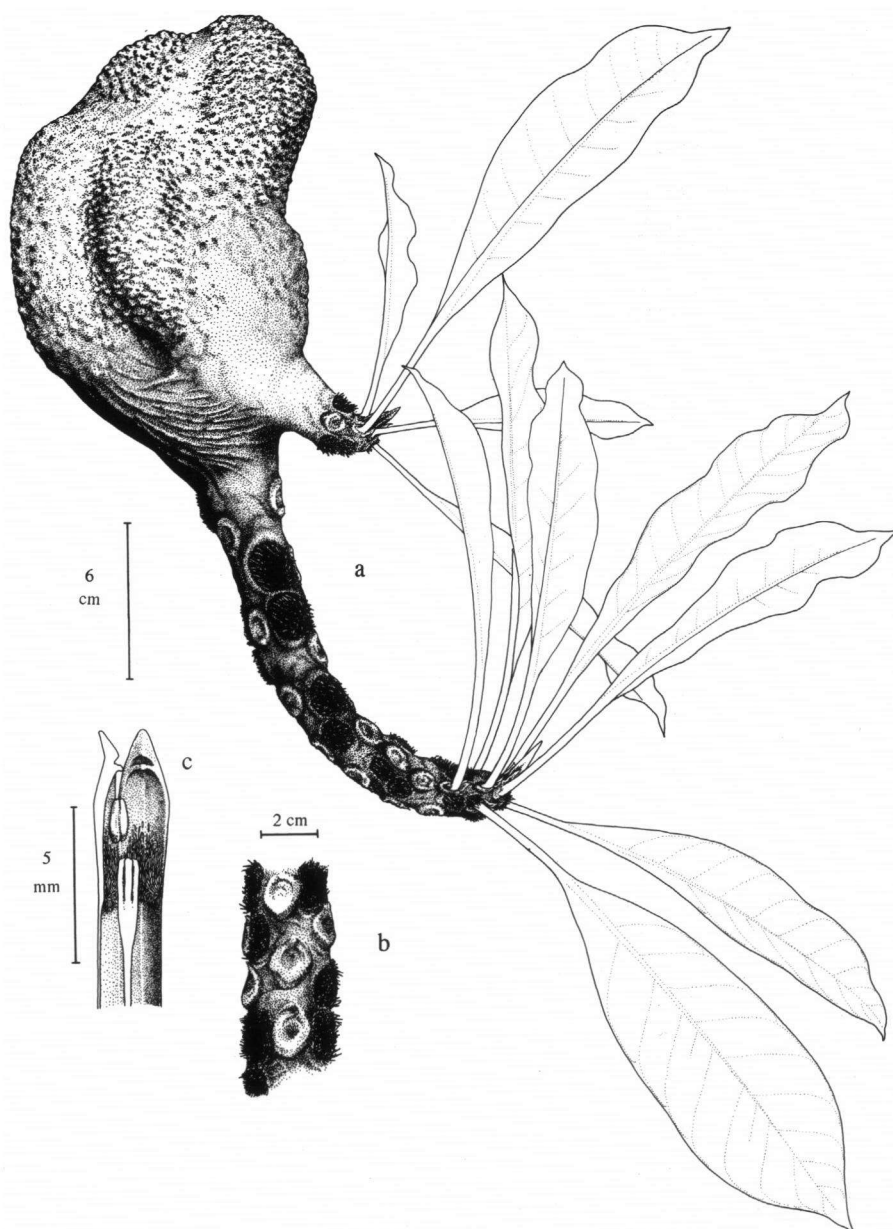


Fig. 1. *Myrmecodia tuberosa* Jack 'bullosa'. a. Habit; b. stem; c. half flower. Drawn by Eleanor Catherine.

len areas verrucose with numerous pores over cells of honeycombing; cells of honeycomb to 1.5 cm across. *Stem* solitary, usually unbranched. Clypeoli conspicuous. Alveoli obscured. Spines rimming clypeoli, simple (branched), weak, to 2.5 cm long, sparse or dense. *Leaves*: Lamina to 14×4.5 (-27×8) cm, elliptic or oblanceolate; apex acute or acuminate; base cuneate, thin or leathery. Midrib sharply keeled below. Lateral veins 6–9. Petioles 4–8 cm, sharply triangular. Stipules broadly triangular, persistent, to 1.5 cm. *Inflorescence*: Bracts more or less filling channels between clypeoli. Flowers (3). Corolla 13 mm; lobes 3 mm, lobe tips 1 mm. Ring of hairs absent, but a ridge midway up the tube sometimes present. Anthers at apex of tube, 2.5 mm; filaments 1 mm. Pollen 2-porate, 2-vesiculate, apertures bordered or not; reticulation coarse. Stigma just below unci, more or less entire. Fruit orange-red. Pyrenes 8.

Ecology – *Casuarina* and *Melaleuca* savanna, altitude 20–100 m.

Notes – *Myrmecodia rumphii* and *M. goramensis* are united as examination of Beccari's types and material from Seram shows that these plants combine the glabrous corolla of *M. goramensis* with the sparse spines of *M. rumphii*.

Specimens from the Lesser Sunda Islands are provisionally placed here; these collections are juvenile and flowers are not known. However, they have clypeoli, leathery leaves and long petioles, thus resembling young plants from Seram.

This variant is allied to two forms on the New Guinea mainland, *M. tuberosa* 'bullosa' and *M. tuberosa* 'lanceolata', see there.

Collections – EASTERN INDONESIA & MOLUCCAS. NE $04^{\circ} 127^{\circ}$ Talaud Is., Karakelang, *Lam* 2549 (L). $02^{\circ} 128^{\circ}$ Morotai, *Lam* 3663 (BO). SE $03^{\circ} 126^{\circ}$ Buru Is., *D'Urville* 97 (P). $02^{\circ} 129^{\circ}$ Seram, Tg Parigi b. Wahai, *Kornassi* 229 (BO, L). $02-03^{\circ} 129^{\circ}$ W Seram, Batoe Lhinia, *Eyma* 2463 (BO). $02-03^{\circ} 128^{\circ}$ W Seram, Salahoetoe, Biv. III, *Eyma* 3100 (BO); Hatoe Walkone, *Eyma* 2572 (BO). $02-03^{\circ} 129^{\circ}$ Seram, *Eyma* 2979 (BO). $03^{\circ} 129^{\circ}$ S Seram, Rohua Village, *UPNG* 3451 (UPNG). $03^{\circ} 128^{\circ}$ Amboina, Soya di Atas *Wiljes-Hissink* 27 (A, L). $03^{\circ} 128^{\circ}$ Ambon, *Robinson* 152 (UC). Ambon, *Beccari* 5510 (type of *M. rumphii*); *Jebb* 1 (A); *van der Pijl* 779 (BO). $04^{\circ} 131^{\circ}$ Goram, *Beccari* 5508, Apr. 1872 (type of *M. goramensis*). Seram, Moerkele Ketjil, *Eyma* 2115 (BO).

LESSER SUNDA ISLANDS. SE $08^{\circ} 120^{\circ}$ Flores, Kae Valley, Puangkeko Ck, *Schmutz* 3084 (L). Mt Mandusawa to Rana Ka, *Schmutz* 3390 (L). $08^{\circ} 119-122^{\circ}$ Flores, Tempat, Pong Nggeok, *Verheijen* 2348 (L). $09^{\circ} 124^{\circ}$ Timor, Naepesu-Mutis, *Schmutz* 2322 (L). Sumba, *Verheijen* 4091 (L). East Timor, Fuiloro, *van Steenis* 18331 (L). Timor, Bioba-Oi Poela, *Bloembergen* 3419 (L).

h. *Myrmecodia tuberosa* 'bullosa' – Fig. 1

Tuber horizontal to pendulous, irregularly cylindrical, c. 24×11 cm, grey or pale brown, slightly ridged towards apex. Spines very few (sometimes absent) short, simple. Entrance holes few, circular to 0.2 cm across, surrounding swollen, honey-combed areas. Cells of the honeycomb to 1.5 cm across, each with one or a few pores on blister-like mounds. *Stem(s)* 1–5, sometimes laterally produced, ascending, branched, to 25×2 cm. Clypeoli slight. Alveoli conspicuous, bract filled. Spines rimming alveoli, few, stubby, simple or root-like. *Leaves*: Lamina $13 \times 4.5 - 22 \times 7$ cm, thin, oblanceolate; apex acute to acuminate; base cuneate. Midrib pale, sharply keeled below. Lateral veins 6–12. Petioles 3.5–5.5(–9) cm. Stipules broadly triangular, persistent, to 0.7 cm. *Inflorescence*: Bracts not conspicuous. Flowers (2).

Corolla 11 mm, widest at apex of tube; lobes 2 mm; lobe tips 1 mm tearing. A broad ring of hairs midway up the tube, sometimes arranged in four bundles. Anthers at apex of tube, 1.5 mm; filaments 0.5 mm. Pollen 2-porate, 2-vesiculate, apertures broadly bordered; reticulation medium. Stigma between ring of hairs and anthers, 4-lobed, lobes 2 mm. Fruit orange-red, to 15 mm. Pyrenes 4–7.

Ecology — On mangroves.

Note — This variant is characterised by the rather prominent swollen areas over the large honeycombing, which has only one or a few pores over each 'cell'. It resembles *Myrmecodia tuberosa* 'rumphii' except that the spines are shorter and not filiform on the stem, and the clypeoli are small and indistinct. *Myrmecodia tuberosa* 'lanceolata' is also similar, but has longer petioles, and the corolla hairs are never in four bundles.

Collections — IRIAN JAYA. SE 00° 55' 131° 15' Sorong, *Beccari P.P. 184* (type of *M. bullosa*). Sorong, *Pleyte 489* (L). 00° 51' 131° 54' 4 km NW of Sorong, nr Tampogaram, *Jebb 10* (A) & 11 (K). Onin, Kulo Kadi, *Beccari P.P. 51* (type of *M. oninensis*).

i. *Myrmecodia tuberosa* 'lanceolata'

Tuber ovoid, slightly ridged, pale grey, to 20 × 10 cm. Spines few simple, short, 3–5 mm. Entrance in irregular arcs surrounding swollen areas with pores over honeycombing. *Stem* solitary or few, branched, pale grey. Clypeoli absent. Alveoli more or less filled by bracts. Spines small, 0.2–0.5 cm, simple or root-like, rimming alveoli. *Leaves*: Lamina 11 × 4 – 19 × 5.5 (–30 × 11) cm, elliptic to oblanceolate; apex acute or less often acuminate; base gradually attenuate, rather thin. Midrib sharply keeled below. Lateral veins 8–10. Petioles (4–)5–12 cm. Stipules broadly triangular, persistent. *Inflorescence*: Flowers (7), heterostylous. Corolla 12 mm, a narrow ring of hairs near the base of the tube; blue-black flecks in anthers. In longistyle flowers, lobes 3 mm; lobe tips 2 mm. Anthers just above the ring of hairs. Pollen 2-porate, 1-vesiculate, apertures bordered; reticulation fine. Stigma just below unci, lobed, lobes 2 mm. In brevistyle flowers, corolla lobes 4.5 mm. Anthers at tube apex. Pollen 2- or 3-porate, 1-, 2- (or 3-)vesiculate, apertures bordered; reticulation medium. Stigma at hairs, ?4-lobed, lobes 1 mm. Ovary 4 locular. Fruit unknown.

Ecology — In *Acacia-Melaleuca* woodland at low altitudes.

Note — This variant is characterised by the pale grey stems and tubers, rather narrow, long-petioled leaves, persistent stipules and bordered pollen apertures. These characters distinguish it from *M. tuberosa* 'papuana'. *Myrmecodia tuberosa* 'rumphii' is rather similar but lacks hairs in the corolla. *Myrmecodia tuberosa* 'bullosa' is vegetatively similar, but the flower is different. The collections from Aru Is., though having shorter petioles and wider, more acuminate laminae, fit best here as they share the bordered pollen apertures. This character is found again, more strongly, in *M. tuberosa* 'bullosa', but is absent from *M. tuberosa* 'muelleri'.

Collections — IRIAN JAYA. SE 05° 01' 138° 39' Bivak Eiland, *Pulle 31* (L). 06° 134° Aru Is., Trangan, Ngaibor, *Buwalda 5313* (BO). 08° 06' Merauke, Okaba, *Branderhorst 85* (BO, WRS�). 08° 15' 140° 44' Merauke, Mopa, *van Royen 4551* (L). 08° 15' 140° 44' Senajo, *Wentholt 128* (BO). Nordfluss, Nepenthes Hugel, *Versteeg 1046, 1246* (types). Locality unknown, *von Römer 77* (BO).

PAPUA NEW GUINEA. Locality unknown: Western Prov., *WLL 1312* (UPNG).

j. *Myrmecodia tuberosa* 'muelleri'

Tuber irregularly spherical to cylindrical, grey, to 30 × 15 cm. Ridges fine to prominent. Spines sparse to many, never dense, on ridges, simple, occasionally branched or somewhat club-like, stout, 0.2–0.5 cm. Entrance holes in irregular arcs surrounding raised areas of honeycombing. Pores solitary or clustered, to 0.1 cm across. *Stem* solitary, often branched, narrow at base widening to 2 cm across when fertile, to 50 cm long. Clypeoli absent. Alveoli large, elliptic, filled with hairy bracts which sometimes protrude, cushion-like especially when young. Fine, root-like spines rim the alveoli; short, simple or branched spines are absent or few and scattered on the stem 0.2–0.4 cm; short clustered spines are common around the leaf bases. *Leaves*: Lamina to 18 × 8 (29 × 11) cm, elliptic; apex acute or acuminate; base attenuate, thin to subleathery. Midrib sharply keeled below. Lateral veins 7–10. Petioles (2–)2.5–7 (–10) cm. Stipules 1(–2) cm, falling early. *Inflorescence*: Flowers (8). Corolla 10 mm; lobes 5 mm; lobe tips 1.4–4 mm long by 1.5 mm wide at base. Unci strongly hooked; ring of hairs near base to halfway up the tube. Anthers 0.9–1.5 mm at tube apex; filaments short. Pollen 2-porate, 1- (or 2)-vesiculate; apertures rarely slightly bordered; reticulation fine (medium). Stigma at anthers, 4–6-lobed. Fruit pink. Pyrenes 4–6.

Ecology – Rain forest, savanna and disturbed areas, altitude 0–700 m.

Note – *Myrmecodia tuberosa* 'muelleri' includes a wide range of material from most parts of lowland New Guinea. It forms a continuum which approaches *M. tuberosa* 'pulvinata', *M. tuberosa* 'lanceolata' and *M. tuberosa* 'papuana'. These three variants are perhaps only local forms of *M. tuberosa* 'muelleri'. They are defined by combinations of characters which overlap to some extent, e.g. the numerous stem spines of *M. tuberosa* 'papuana', the club-like spines of *M. tuberosa* 'pulvinata', or the 1-vesiculate pollen of both those taxa. There are also differences in habitat preference.

Collections – IRIAN JAYA. SE 01° 08' 136° 05' Biak, Oregon Trail, *Brongersma s.n.*, 15 Feb. 1952 (L). 02° 31' 140° 41' Base G beach, Jayapura, *Jebb 20* (A). Locality uncertain: *Schultze 27* (B).

PAPUA NEW GUINEA. SE 05° 41' 141° 43' Western Prov., Palmer R. 3 km below Black R. junction, *Brass 6936* (A). 06° 30' 147° 46' Morobe Prov., Sattelberg, *Clemens 281* (BR, L). 06° 31' 143° 10' Southern Highlands, 20 km SW of Lake Kutubu, Waro, *Jacobs 9234* (L). 06° 36' 147° 51' Morobe Prov., Finschhafen, Viehpark, *Hellwig 375* (type of *M. vivipara*). 06° 40' 146° 47' 20 km SW of Lae, *Hartley 9782* (A, LAE). 06° 54' 146° 38' Perakles Pass, *UPNG 3462* (UPNG). Patep Creek, 1 km NW of Perakles Pass, *Jebb 344* (LAE 2 sh), *Jebb 345* (L), *346* (LAE). 07° 20' 146° 50' c. 6 km E of Kaisenik, *UPNG 5946* (L, UPNG). 09° 22' 147° 22' Central Prov., Hombrom Bluff, *UPNG 3434* (K, UPNG). 09° 25' 147° 22' entrance to Varirata Nat. Park, *UPNG 5943* (A, UPNG). 09° 26' 147° 36' Musgrave R., *UPNG 3427* (BRI, UPNG). Madang Prov., on route from Ramu to coast, *Schlechter 14178* (type of *M. paucispina*). Morobe Prov., Lae, 3 mi Agricultural Stn, *NGF 5392* (LAE). Western Prov., Fly R., *d'Albertis 5504* (type of *M. muelleri*). Gulf Prov., Purari R., *UPNG 3481* (A, BO, BRI, CANB, FHO, K, L, LAE, UPNG). 9° 8' 147° 44' Central Prov., Sogeri Subdistr., Kokoda Trail, 100 m below N side of Imita Gap, *Jebb 153, 154* (LAE).

k. *Myrmecodia tuberosa* 'versteegii' – Fig. 2

Tuber pendent, irregularly cylindrical, to 30 × 12 cm. Ridges absent. Spines absent to dense, especially numerous around the entrance holes, usually branched, more or

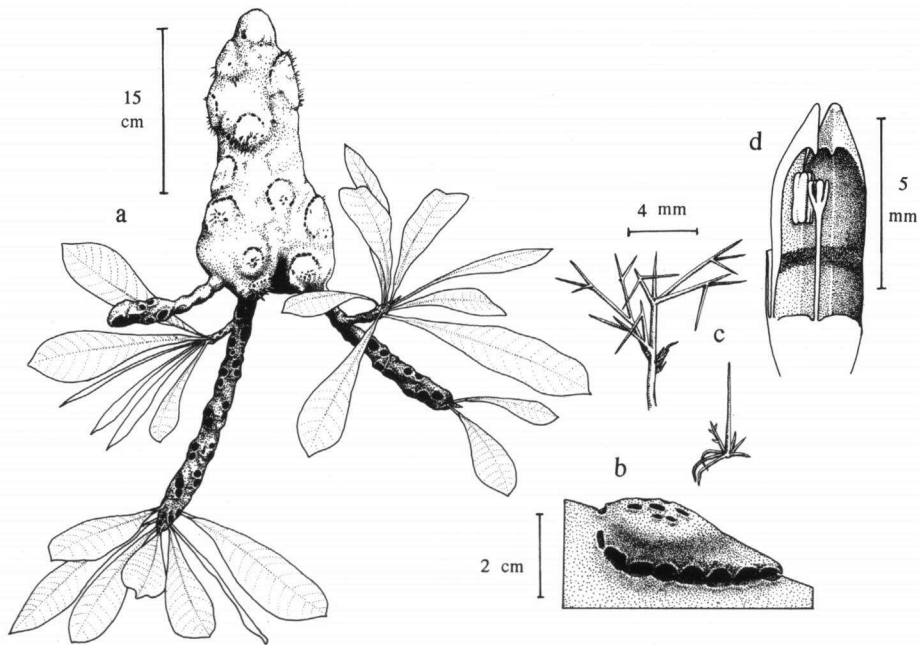


Fig. 2. *Myrmecodia tuberosa* Jack 'versteegii'. a. Habit; b. tuber surface; c. spines; d. half flower. Drawn by Eleanor Catherine.

less club-like, stout, to 1 cm or more long. Raised areas prominent, surrounded by horseshoe-shaped arcs of adjacent entrance holes which sometimes join together. Entrance holes also scattered over raised areas. Honeycombing slight. Pores absent. *Stem(s)* one to several, pendent or upturned, sometimes branched near base, narrow at base, widening to 2.5 cm when fertile, reaching 40 cm long. Clypeoli absent. Ridges decurrent from leaf attachment and transverse ridges joining alveoli pairs. Alveoli circular, with thick, constricted, raised rims, bracts not exerted. Spines absent or few, scattered. *Leaves*: Lamina to 28 × 8 cm, subleathery, broadest above the middle; apex acuminate; base narrowly spatulate. Midrib sharply keeled below, prominent to apex. Lateral veins 9–14. Stipules to 0.6 cm, falling early. Leaf scars rhomboidal. Petioles 1–2 cm, sharply winged. *Inflorescence*: Flowers (5). Corolla 6 mm, lobes 2 mm; unci strongly hooked; a ring of hairs midway up the tube. Anthers at tube apex; filaments short. Pollen 1- or 2-porate, 1-vesiculate, apertures not bordered; reticulation fine. Stigma at or just below anthers, 4-lobed. Fruit yellow-orange. Pyrenes 4.

Ecology – In swamp or riverine rain forest at 50–1070 m altitude.

Notes – This variant is distinguished by its spatulate leaves and the raised areas on the tubers surrounded by horseshoe-shaped arcs of entrance holes which are sometimes fused. Further entrance holes are found over the raised areas but pores are ab-

sent. This tuber type is approached in rain forest specimens of *M. tuberosa* 'pulvinata' and *M. tuberosa* 'muelleri'. The stem and leaf characters sometimes resemble those of *M. tuberosa* 'pulvinata', but the alveoli are more rimmed, spines not club-like, and the fruit is yellow-orange.

Valeton (1911) placed *Versteeg 1177* in *M. jobiensis* but the stem and pollen characters are quite different.

Collections – IRIAN JAYA. SE 03° 32' 139° 14' Bernhard Camp, *Brass 13829* (A, BO, L). 04° 30' 139° 15' Baliem Valley, Holluwon, *Jebb 115* (LAE). 04° 45' 138° 48' Van Weels camp, *Versteeg 1177* (BO). Rouffaer R., *Docters van Leeuwen 10361* (A, BO, K, L).

PAPUA NEW GUINEA. SE 06° 08' 145° 08' Gulf Prov., Purari R., Wabo Ck, *UPNG 3479* (L, UPNG). 08° 31' 147° 00' Central Prov., Mafulu, *Brass 5496* (A, BO, BRI).

1. *Myrmecodia tuberosa* 'pulvinata' – Fig. 3

Tuber irregularly spherical to cylindrical, grey. Ridges fine (sometimes absent). Spines on the ridges, almost all well-developed, regular, club-like, 0.3–1 cm. Entrance holes in semicircular arcs surrounding swollen areas. Pores absent. Honey-combing slight. *Stem* solitary, unbranched, narrow and square in section at base for up to 10 cm, then widening to c. 1.7 cm when fertile. Clypeoli absent. Alveoli thickly rimmed, occasionally filled with bracts. Spines few, simple, club-like or short and clustered, 0.4–0.8(–1.3) cm. *Leaves*: Lamina 14 × 5 – 20 × 8 cm, obovate; apex bluntly acuminate; base narrowly attenuate. Midrib sharply keeled below. Lateral veins 9–13. Stipules 0.4–1.1 cm, falling early. Petioles (1–)2–5(–7) cm. *Inflorescence*: Flowers (4), heterostylous. Corolla 12 mm; lobes 4 mm; lobe tips 3 mm; a narrow ring of hairs less than a third of the way up the tube. Anthers just above and touching the hairs. Pollen 2-porate, 1-vesiculate; apertures unbordered; reticulation fine. In longistyle flowers stigma at the tube apex. In brevistyle flowers stigma at the same level as the anthers. Stigma 5- or 6-lobed. Fruit pink. Pyrenes 4–6.

Ecology – Rain forest, disturbed forest, and *Eucalyptus-Melaleuca* savanna at 100–500 m altitude.

Note – *Myrmecodia tuberosa* 'pulvinata' is characterised by its club-like spines and absence of pores. The position of the hairs and the anthers in the corolla and the one vesiculate pollen are constant features. *Myrmecodia tuberosa* 'muelleri' and *M. tuberosa* 'versteegii' are the most closely related variants. *Myrmecodia tuberosa* 'muelleri' also quite often has slightly club-like spines, but is distinguished by the fact that only a small proportion of the tuber spines are club-like, and by the presence of pores. The leaf is more attenuate at the base than *M. tuberosa* 'muelleri' but not spatulate as in *M. tuberosa* 'versteegii'.

Collections – IRIAN JAYA. SE 00° 53' 134° 05' Manokwari, *Gibbs 6197* (ref. only, Gibbs, 1917). 00° 55' 134° 00' Fak Fak, Andai, *Beccari P.P. 769* (type). 02° 20' 138° 00' Mamberamo R., Albatros Bivak, *Docters van Leeuwen 9642* (A, BO, K, L). 02° 40' 141° 14' West Sepik Prov., Vanimo Timber lease, 5 km W of Vanimo *Jebb 541* (LAE).

PAPUA NEW GUINEA. 03° 12' 141° 21' West Sepik, Amanab, nr Kilifas *NGF 48201* (LAE). 03° 143' 8 km SE of Wewak, *UPNG 5904* (K, UPNG). 04° 145' Madang Prov., Karkar Is., *UPNG 5928* (OXF, UPNG), *Jebb 113* (LAE). 08° 50' 147° 45' Central Prov., Kokoda, Millar, *TNG 23536* (LAE). 08° 53' 147° 44' Kokoda, *Carr s.n.*, 8 Apr. 1936 (L).

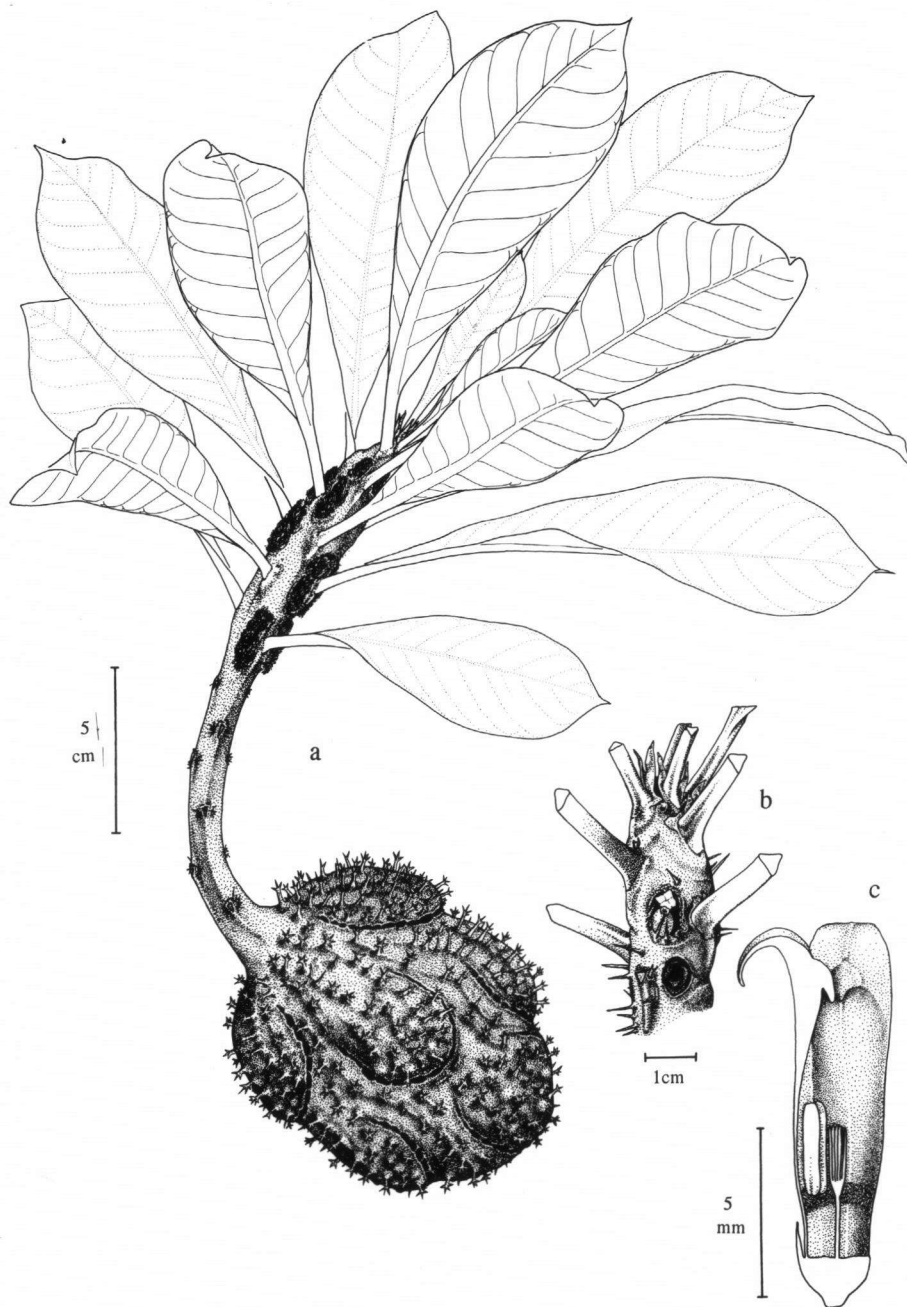


Fig. 3. *Myrmecodia tuberosa* Jack 'pulvinata'. a. Whole plant; b. stem apex; c. half flower. Drawn by Rosemary Wise.

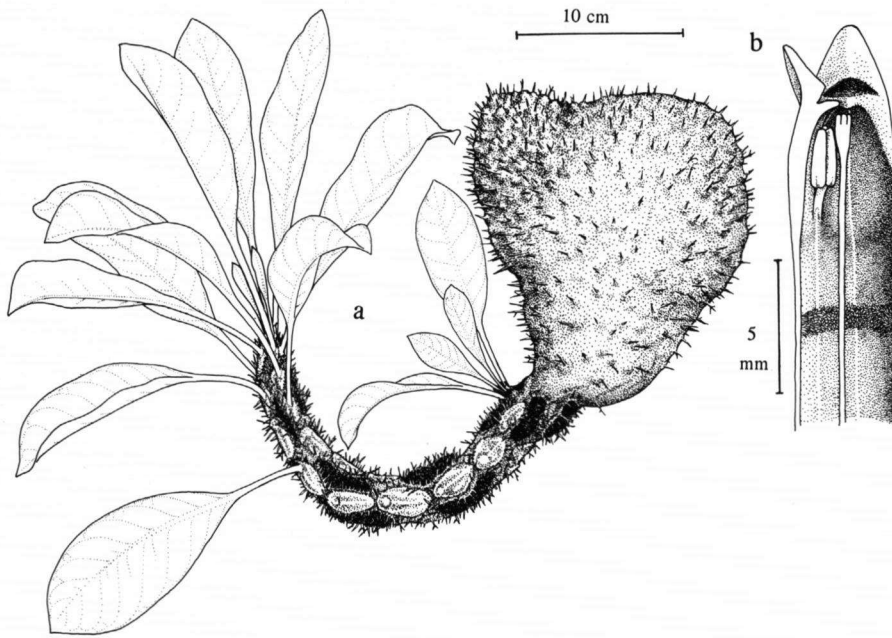


Fig. 4. *Myrmecodia tuberosa* Jack 'papuana'. a. Habit; b. half flower. Drawn by Eleanor Catherine.

m. *Myrmecodia tuberosa* 'papuana' – Fig. 4

Tuber irregularly conical to cylindrical, grey, c. 20 × 15 cm. Ridges absent to weak. Spines few to numerous, stout, simple, occasionally branched, 0.3–0.8 cm. Entrance holes 0.2–0.4 cm across, few and scattered or in irregular arcs surrounding raised honeycombed areas. Pores few, to 0.1 cm across. *Stem* solitary (few), branching near base and commonly with frequent short branches above, sometimes narrow at base, widening to 2 cm when fertile, to 30 cm long. Clypeoli absent to slight. Alveoli large, elliptical, pulvinate or more or less filled with sparse to dense, hairy bracts, which are commonly absent from older alveoli. Simple or branched stiff spines occur along the alveoli rims, on the stems and around the leaf base, 0.6–0.8 cm long. Root-like spines occasional around the alveoli. *Leaves*: Lamina to 15 × 7 cm, oblanceolate to obovate; apex acuminate; base attenuate, thin to subleathery. Mid-rib sharply keeled below. Lateral veins 7–10. Petioles stout, 2–5 cm. Stipules to 0.8 (–1) cm, falling early. *Inflorescence*: Flowers (7). Corolla 12 mm, lobes 3 mm; lobe tips tearing, 2.5 mm long, 2 mm wide at base, unci strongly hooked. A ring of hairs a quarter the way up the tube. Anthers 1–2 mm long, at tube apex; filaments long or short. Pollen 2- or 3-porate, 1–3-vesiculate; apertures unbordered; reticulation (fine) medium to coarse; pollen grains large, wall very stretched and thin or globular. Stigma at apex of tube, indistinctly lobed. Fruit orange-red (pink). Pyrenes 4–7.

Ecology – In *Eucalyptus*/*Melaleuca* savanna and mangrove swamp; 0–700 m altitude.

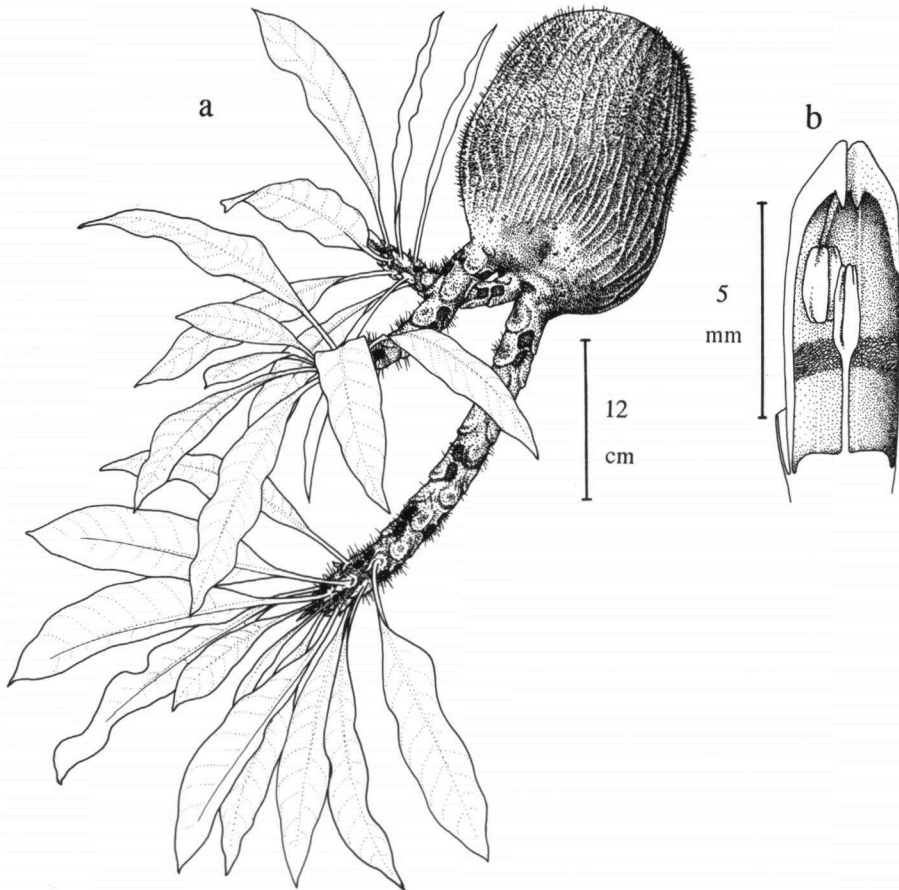


Fig. 5. *Myrmecodia tuberosa* Jack 'dahlii'. a. Habit; b. half flower. Drawn by Eleanor Catherine.

Note — *Myrmecodia tuberosa* 'papuana' is restricted to savanna vegetation in SE New Guinea and northern Cape York. It is unique in the large pollen grains with a very stretched wall which sometimes consists only of globules. This variant is distinguished from the closely related *M. tuberosa* 'muelleri' by the smaller, more leathery leaves, more stem spines, and the corolla lobe tips being less than one and a half times as long as wide. It also resembles *M. tuberosa* 'pulvinata', which has distinctive flowers and vesiculate pollen, as well as club-like spines.

Collections — PAPUA NEW GUINEA. SE 09° 01' 146° 57' Central Prov., Kanosia, Carr 11517 (A, K, L, SING). 09° 15' 147° 13' 5 km SE of Brown R., UPNG 3477 (K, LAE, UPNG). 09° 22' 147° 22' Hombrom Bluff, UPNG 3432 (A, CANB, L, UPNG), UPNG 5944 (FHO, L, UPNG). 09° 23' 147° 17' Port Moresby, Ilimo Farm, UPNG 3414 (UPNG). 10° 10' 148° 28' Kubiano Subprov., Cape Rodney UPNG 3474 (BO, BRI, L, LAE, UPNG). 10° 42' 152° 9' Louisiade Arch., Missima, S slopes Mt Sisa, Jebb 394 (LAE).

AUSTRALIA. SE 12° 40' 143° 20' Cape York, Iron Ra., *Brass* 19305 (A, G, K, L, TY), *Dunlop* 1707 (CBG). 12° 45' 143° 15' Cook Dist., Tozers Gap, *Gittins* 1072 (BRI). 13° 50' 143° 10' McIlwraith Ra., 11 km NE of Coen, *Wrigley N. Q.* 1655 (CBG). Cape York, *Jones* 2051 (BRI).

n. *Myrmecodia tuberosa* 'dahlii' – Fig. 5

Tuber horizontal to pendulous, irregularly conical or cylindrical, to 25 × 20 cm, pale grey/brown, ridged. Spines mostly on ridges, sparse to numerous, simple, rarely branched, to 1.5 cm. Entrance holes to 0.5 cm across, in arcs, round honeycombed areas with pores. Stem(s) one to several, pendent to slightly curving upwards, occasionally branched near base, to 30 × 1.5 cm. Clypeoli indistinct, to 2 × 1 cm. Alveoli circular. Spines quite dense around alveoli, simple (branched), usually stiff, to 1.5 cm. *Leaves* thin. Lamina to 18 × 5–8 cm, widest near the middle; apex acute; base attenuate. Midrib sharply keeled below, prominent to apex. Lateral veins 7–9. Petiole 1–6.5 cm. Stipules to 0.8 cm, soon falling. *Inflorescence*: Bracts sparse. Flowers (7). Corolla 8–10 mm; lobes 3 mm; lobe tips 1–2 mm; ring of hairs 1 mm broad, a third to half the way up the tube. Anthers at tube apex, 1–2 mm long; filaments 0.5 mm. Pollen 2-porate, 1-vesiculate; apertures not bordered; reticulation fine to medium. Stigma at anthers or at hairs, 4- or 5-lobed. Fruit red. Pyrenes 4–6.

Ecology – Disturbed and undisturbed forest and in plantations, 0–1000 m.

Notes – *Myrmecodia* in New Britain and New Ireland is rather uniform in stem and floral characters and is therefore placed together as *M. tuberosa* 'dahlii'. Leaf shape is somewhat variable, but not in a way that correlates with the pyrene number, which was formerly used to define species.

In southern New Ireland *M. tuberosa* 'dahlii' grades into *M. tuberosa* 'salomonensis', and several intermediate specimens are known.

Collections – PAPUA NEW GUINEA. SE 01° 40' 150° 00' New Ireland, Kavieng Subdistr., Emira Is., Mussan, *NGF* 40467 (L, LAE). 02° 22' 150° 12' Lavongai (New Hanover), Cape Entrance, N coast, *LAE* 65398 (A, L, LAE). 02° 40' 150° 56' 10 km S of Kavieng on coast road, *UPNG* 3440 (K, UPNG). 03° 07' 151° 42' New Ireland, Konos on E coast, c. 4 km inland, *UPNG* 3443 (BO, K, L, UPNG), *UPNG* 3447 (BO, CANB, K, L, NY, UPNG), *UPNG* 3448 (L, UPNG). 03° 20' 151° 50' Lelet plateau, Limbim Village, *UPNG* 5947 (A, BRI, FHO, L, UPNG). Paremecho Village, NW coast, *UPNG* 5949 (FHO, UPNG). SE 04° 13' 151° 50' New Britain, Gazelle Peninsula, Mas-sava, *Schlechter* 13732 (WRS�, drawings). 04° 15' 152° 08' Gazelle Peninsula, Simsonhafen, *Rechinger* 3987 (W). 04° 18' 152° 13' Gazelle Peninsula, Ralum, *Dahl* 1834 (type of *M. dahlii*), 8427 (type of *M. pentasperma*), 1845 (B, alc). 04° 20' 151° 00' Baining, Kaia Mt, *Rechinger* 3648 (W), 4820 (W). 04° 20' 151° 40' Gazelle Peninsula, road from Rabaul to Keravat, *UPNG* 3416. Near Vunakanau Village, Rabaul to Keravat road, *Jebb* 531 (LAE), 532 (A, K, L). 04° 23' 152° 10' Gazelle Peninsula, near Toma, *Rechinger* 3624 (W). 04° 56' 151° 26' W New Britain, Hoskins Subdistr., crater rim of North Son, *LAE* 58513 (A, L). 05° 01' 150° 08' W side of central Peninsula of Lake Dakataua, Willameuz Pen., 5 km S of Cape Hollmann, *LAE* 66565 (LAE). 05° 20' 150° 30' 16 km N of Kimbe, *UPNG* 3466 (UPNG). 05° 30' 150° 28' near Hoskins, *UPNG* 3449 (UPNG).

o. *Myrmecodia tuberosa* 'salomonensis' – Fig. 6

Tuber pendulous, cylindrical, to 60 × 35 cm. Ridges slight, over non-honeycombed areas. Spines absent or sparse, mainly on ridges, simple or root-like, weak, to 0.6 cm. Entrance holes to 0.5 cm across, in arcs or rings around honeycombed areas.

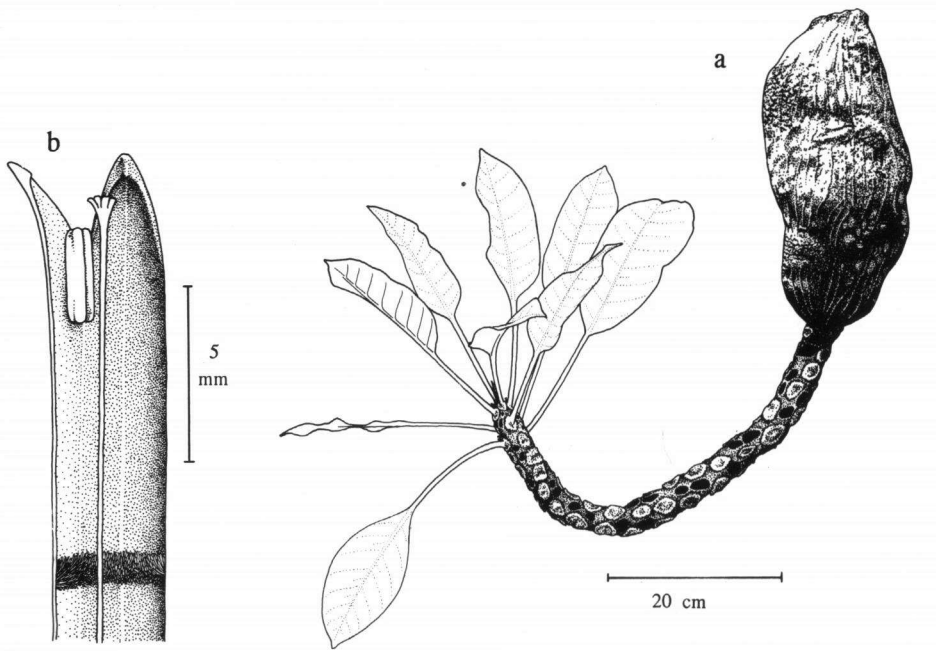


Fig. 6. *Myrmecodia tuberosa* Jack 'salomonensis'. a. Habit; b. half flower. Drawn by Eleanor Catherine.

Honeycombing well-developed with mounds bearing pores over each cell of the honeycomb. Stem(s) one to several, rarely branched, pendulous to slightly curved upwards, to 4 cm across. Clypeoli to 2.3×1.5 cm. Alveoli \pm circular to 1.5 cm across. Spines around alveoli and clypeoli, weak, to 0.6 cm. *Leaves*: Lamina (13×4) $17 \times 5 - 30 \times 10.5$ cm, broadly (narrowly) elliptic; apex acuminate (acute); base more or less abruptly cuneate. Midrib sharply keeled below, prominent to apex. Lateral nerves c. 10. Petiole green (pale orange) (4–)8–15 cm. Stipules (1–)1.3–2 cm. *Inflorescence*: Bracts filling alveoli or not. Flowers (8); flowers from the Solomon Islands (4): Corolla 13–15 mm; lobes 4 mm, broadly acute; lobe tips less than 1 mm. Ring of hairs near the base of the tube. Anthers at tube apex, 2–3 mm; filaments 0.5 mm. Pollen 2-porate, 2-vesiculate; apertures bordered; reticulation coarse, usually incomplete. Stigma above anthers, with 4 or 5 spreading lobes. Fruit orange. Pyrenes 6 or 7. Flowers from New Ireland (4): usually smaller. Anthers 1.5–2 mm; filaments rarely 1.5 mm. Pollen reticulation complete. Stigma at or above anthers. Pyrenes 4 or 5.

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

Notes — This variant is distinguished by its long petioles, large laminae, massive tubers, and large flowers with 2-vesiculate pollen. The New Ireland material appears to be a variable population tending to resemble *M. tuberosa* 'dahlia', but also plants with long narrow leaves. At higher altitude some plants have markedly smaller leaves.

The collection made by Rechinger in Bougainville has short petioles, but is too juvenile to be identified as a distinct form.

Collections – PAPUA NEW GUINEA. SE 03° 07' 151° 43' New Ireland, Konos on E coast, *UPNG* 3442 (A, BRI, CAMB, FHO, K, L, LAE, UPNG), *UPNG* 3446 (UPNG). 03° 20' 151° 50' Lelet plateau, Limbim Village, *UPNG* 5948 (BO, UPNG). 03° 40' 152° 26' Namatanai, *Peekel* 468 (type of *M. peekelii*). 04° 11' 152° 57' Namatanai Subprov., Daufu R. basin, *Coode s.n.*, 31 Jan. 1970 (LAE). SE 04° 30' 154° 15' Bougainville, Nissan Is., *Nachman* 554 (LAE). 06° 10' 155° 20' Taki Village, SE of Toiunonapu Plantation, *NGF* 16410 (A, BO, BRI, K, L, LAE). 06° 15' 155° 37' Kieta, *Rechinger s.n.*, Sep. 1905 (W). 6° 15' 155° 31' Kieta, Subprov. Panguna to Arawa Rd, *Jebb* 499 (LAE), 501 (L). Loloho to Arawa Rd, *Jebb* 523 (LAE).

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

p. *Myrmecodia tuberosa* 'manusensis' – Fig. 7

Tuber pendulous, irregularly cylindrical, to 30 × 10 cm. Ridges absent or slight. Spines very sparse, root-like, to 1 cm. Entrance holes surrounding raised honey-

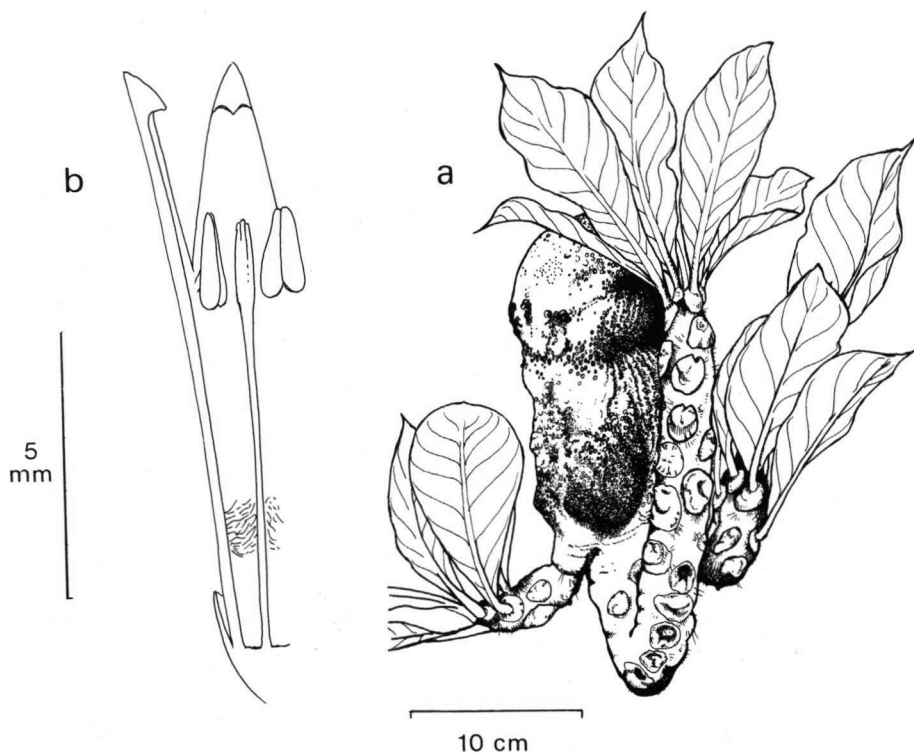


Fig. 7. *Myrmecodia tuberosa* Jack 'manusensis'. a. Habit; b. half flower. Drawn by Eleanor Catherine.

combed areas. Pores in rings on mounds over cells of honeycomb. *Stems* several, unbranched, curving upwards, to 30 × 3.5 cm. Clypeoli ± round to 2 cm across. Alveoli present. Spines rimming clypeoli and alveoli, weak, irregular. *Leaves* thin, wavy along the edges. Lamina 15 × 7 – 24 × 9 cm, oblanceolate; apex acuminate; tapering to the base. Midrib sharply keeled below. Lateral veins 7–9. Petiole 1–2 cm. Stipules to 1.6 cm. *Inflorescence*: Flowers (2). Corolla 12 mm; lobes 4–5 mm, narrowly acute; lobe tips less than 1 mm. A ring of hairs a quarter of the way up the tube. Anthers at apex of tube; filaments short. Pollen 2-porate, 2-vesiculate; apertures not bordered; reticulation coarse. Stigma at anthers, indistinctly lobed. Fruit ? Pyrenes 7.

Ecology – On trees in mangrove swamps.

Note – The few collections from Manus Island all have distinctive 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'.

Collections – PAPUA NEW GUINEA. Manus Island. SE 02° 01' 147° 16' half way between Lorengau and airport, UPNG 3437 (A, K, L, UPNG). 02° 10' 146° 45' Metaphor Village, South coast, 21 km W of Pelikawa, LAE 59269 (BRI, CANB, L, LAE, not seen). Locality uncertain: Sands 2927 (K).

2. *Myrmecodia kutubuensis* Huxley & Jebb, *spec. nov.*

Differt ab aliis *Myrmecodiis* cavitatis tuberis arcis foraminorum, spinis simplicis vel stellatis, clypeolis absens, labris alveolorum spinis stellatis gerentes, et foliis usque ad 18 × 3 cm. — Typus: Papua New Guinea, Gay 23 (holo LAE).

Tuber pendent, irregularly cylindrical, to 12 × 5 cm, ridged, pale brown. Spines sparse, simple or less often stellate, or root-like when close to entrance holes. Entrance holes forming conspicuous arcs. Pores in clusters over honeycombed areas. Inner, smooth walled chambers not shelf-like. *Stem* solitary, unbranched, curving upwards, narrow at base where sterile. Clypeoli absent. Alveoli elliptic. Spines rimming the alveoli, mostly stellate, axis before branching 2–4 mm, branches 2–3 mm. *Leaves* clustered at stem apex. Lamina 9 × 1.7 – 18 × 3 cm, narrowly oblanceolate apex acute to acuminate, base tapered. Lateral veins 5–7, midrib prominently triangular below. Petioles 1–2 cm. Stipules to 0.8 cm. *Inflorescence*: Bracts forming a ± dense mass. Flowers (1). Calyx c. 1 mm. Corolla 8 mm, lobes 5 mm; lobe tips 1 mm; tufts of hairs 1 mm from tube base. Anthers above hairs and below tube apex, 1.5 mm, with blue-black flecks at apex and along opening. Pollen 2-porate, 2-vesiculate, reticulation fine. Stigma at anthers ?fid. Fruit orange. Pyrenes 5.

Ecology – Open and lakeside communities.

Note – The arcs of entrance holes and cavity arrangement indicate a relationship with *M. tuberosa* as does the narrow base to the stalk. The narrow leaves however resemble *M. schlechteri*. The nearest collection of *M. tuberosa* comes from within 20 km and has much larger leaves.

Collections – PAPUA NEW GUINEA. Southern Highlands, Lake Kutubu, Gay 23 (type), 57 (LAE), 58 (UPNG), 60, 65 (BULOLO), 73 (K).

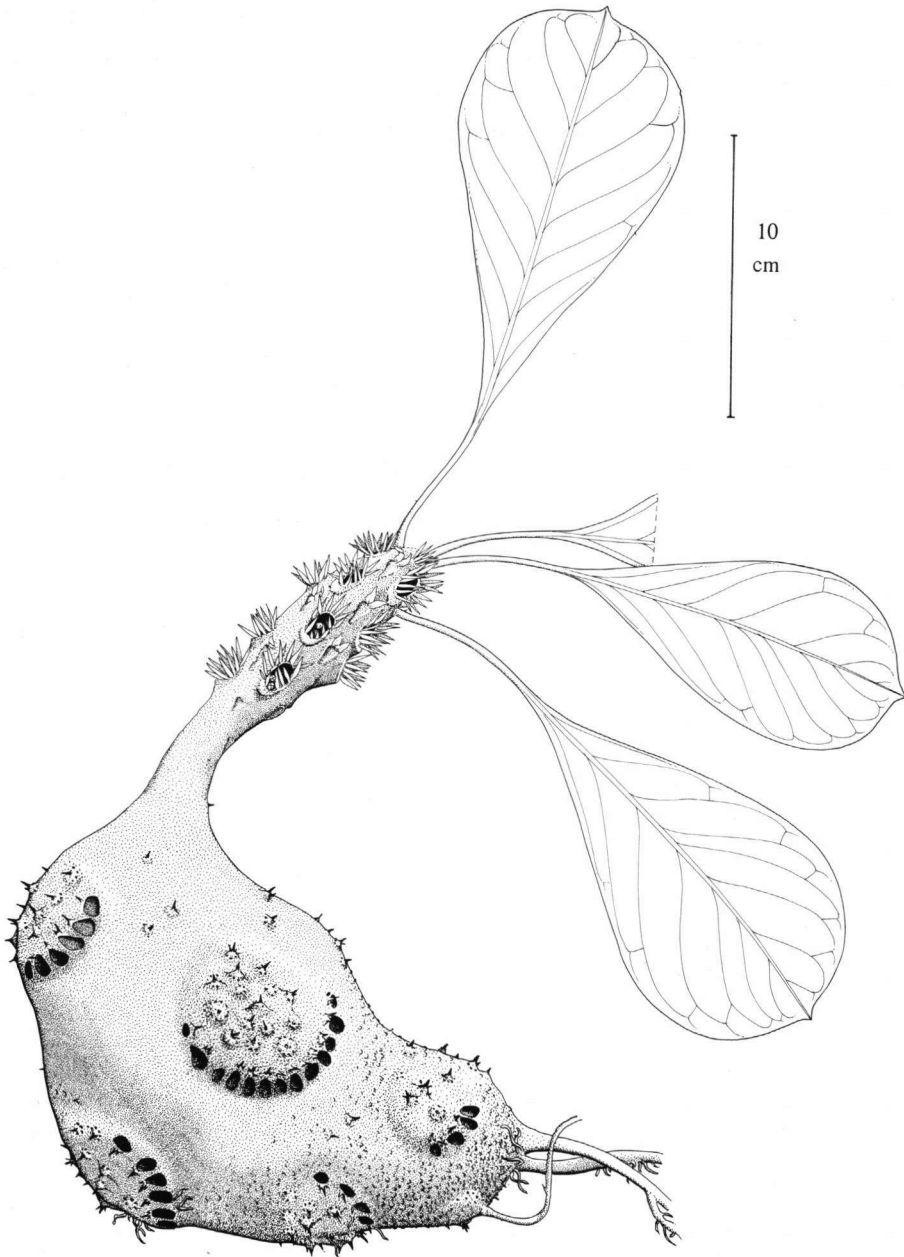


Fig. 8. *Myrmecodia jobiensis* Becc. Drawn by Rosemary Wise.

3. *Myrmecodia jobiensis* Becc. — Fig. 8

Myrmecodia jobiensis Becc., *Malesia* 2 (1884) 111. — Type: Irian Jaya, *Beccari 5507* (holo FI).

Tuber horizontal to pendulous, irregularly cylindrical, to 25 × 14 cm, unridged, drying rough and dark grey or brown. Spines sparse, on mounds in honeycombed areas, stout, black, simple or club-like branched at apex, or clustered at base, 0.3–0.6 cm long. Areas over honeycombing swollen and verrucose. Pores in rings, often surrounding spines. Entrance holes 0.7–0.5 cm, close together in semicircles. *Stem* solitary (2), ascending, unbranched, c. 21 cm long, narrow at base for 10 cm, wider above, to 2.5 cm. Clypeoli obscure, c. 1 × 0.5 cm. Alveoli round with thick, fleshy rims. Spines around the alveoli and a few around the clypeoli, simple, thick, widest just above the barrow base, fleshy, grooved when dry, 0.9–1.2 cm long. *Leaves*: Lamina 11 × 6–23 × 9 cm, leathery, broadly obovate, apex abruptly acuminate; base attenuate. Midrib sharply keeled below. Lateral veins 7–11. Petiole 3.5–7 cm. Stipules persistent, to 1.4 cm. *Inflorescence*: Bracts ± conspicuous. Flowers (2). Corolla to 20 mm, widest below the unci; lobe tips 3 mm, tearing; unci remain closed. Ring of hairs broad (narrow), near the base of the tube. Anthers at apex of tube, 2 mm; filaments 0.5 mm. Pollen 2-porate, 2-vesiculate; pores broadly bordered; reticulation fine. Stigma at or just below anthers, 4-lobed. Fruit orange. Pyrenes 4–6.

Ecology — At 200 m in hill forest with dense canopy.

Note — This species resembles *M. tuberosa* in its tuber entrance holes and club-shaped spines, and in the stem being narrow at the base. However the strongly bordered pollen and the arrangement of spines on the stem are features shared by *M. erinacea* and *M. alata*. The unbranched stems and orange-yellow fruits also unite these three species.

Collections — IRIAN JAYA. SE 01° 35' 135° 42' Japen Is., *Ansus, Beccari 5507* (type). 01° 52' 131° 16' 2 km N of Sorong, *Jebb 4* (A, 2 sh.).

4. *Myrmecodia erinacea* Becc.

Myrmecodia erinacea Becc., *Malesia* 2 (1884) 105, tab. 12: 7–11; *Valeton, Nova Guinea* 8 (1911) 514; *Bot. Jahrb.* 61 (1927) 145; *Merr. & Perry, J. Arnold Arbor.* 26 (1945) 29. — Type: Irian Jaya, *Beccari 5506*, 14 Apr. 1875 (holo FI; iso BM, K).

Tuber to 15 × 4.5 cm, cylindrical, not ridged. Spines stellate, moderately dense. Swollen areas with pores and honeycombing usually present; entrance holes few. *Stem* solitary, unbranched. Clypeoli absent. Alveoli round, densely rimmed by simple spines. Spines on stem surface few to many, usually branched. *Leaves*: Lamina 14 × 1.8–31 × 4 cm, blade narrowly elliptic to oblanceolate; apex acute (acuminate); base long attenuate; margin undulate-crisped. Midrib keeled below, lateral veins 16–22, prominent below, depressed above, sometimes making the surface bullose. Petioles 0.5–1 cm. Stipules narrow at the tip broad below, caducous. *Inflorescence*: Bracts obscure. Flowers (4), heterostylous. Corolla greenish-blue or white; a ring of hairs halfway up the tube. In brevistyle flowers anthers among hairs or at apex of tube; stigma at hairs. In longistyle flowers anthers at tube apex; stigma above anthers. Pollen 2- (or 3-)porate, 2- (or 1–3-)vesiculate; apertures very broadly bordered. Stigma 2–4-lobed. Fruit yellow-orange. Pyrenes 4.

Ecology – In mangrove, swamp and river-plain forest, and on *Quercus* in *Dillenia* forest at 50 m; altitude 0–100 m.

Note – *Myrmecodia erinacea*, *M. alata* and *M. jobiensis* are distinguished from other species by the arrangement of simple spines around the alveoli and branched and simple spines on the stem surface and tuber. They also have 2-vesiculate pollen with very broad borders to the apertures. In *M. jobiensis* the borders are not so broad.

Collections – IRIAN JAYA. SE 00° 52' 131° 14' 2 km NW of Sorong *Jebb 16* (LAE). 01° 44' 135° 49' Japen Is., Ansum, *Beccari 5006*, 14 Apr. 1875 (type). 02° 20' 138° 00' Mamberamo R., Albatros Bivak, *Docters 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). 03° 50' 134° 40' Etna Bay, *Koch 706* (BO, L). E coast of Geelvink Bay, Manipawei, *Janowsky 17* (BO, L).

PAPUA NEW GUINEA. SE 02° 40' 141° 14' West Sepik, 5 km W of Vanimo, above Warima Vanimo Timber lease, *Jebb 537* (LAE).

5. *Myrmecodia alata* Becc. – Fig. 9

Myrmecodia alata Becc., *Malesia* 2 (1884) 106, t. 18 & 25. — Type: Irian Jaya, *Beccari P.P. 758* (holo FI; iso BM).

Myrmecodia prolifera Merr. & Perry, *J. Arnold Arbor.* 26 (1945) 30. — Type: Irian Jaya, *Brass 13935* (A, BM, BO, BRI, L).

Myrmecodia aruensis Becc., *Malesia* 2 (1884) 108, t. 19b; *Valeton, Bot. Jahrb.* 61 (1927) 145. — Type: Aru Is., *Beccari 5517*, March 1873 (FI).

Tuber c. 15 × 7 cm, cylindrical, not ridged, greyish brown. Spines simple to stellately branched, more or less dense, stiff, to 1.2 cm. Rings of pores conspicuous; entrance holes few. *Stem* solitary (2), usually unbranched, to 18 × 1.3 cm. Clypeoli absent. Alveoli rounded, densely rimmed by fat, usually simple spines. Simple or branched spines occasional on stem surface. *Leaves*: Lamina 7 × 1.2 – 18 × 5 (28 × 7) cm, thin, ± flat; narrowly oblanceolate to spatulate. Apex acuminate; base long attenuate. Midrib keeled below, white; lateral veins 8–11. Petiole 0.6–3.2 cm, white. Stipules 0.7 cm, thin, soon falling. *Inflorescence*: Bracts not conspicuous. Flowers (5) white or greenish-blue. Corolla 15 mm, lobes 4–5 mm. Broad ring of hairs below or at mid tube. Anthers almost sessile, among hairs; or filaments 1.5 mm, anthers above hairs. Pollen 2- (or 3-)porate, 2- (1–3-)vesiculate; apertures very broadly bordered. Stigma shortly 4–6-lobed, at, below, or above anthers. Fruit yellow. Pyrenes 4.

Ecology – Swamp and hill forest, 80–170 m.

Notes – This species differs from *M. erinacea* in its shorter, wider, flat leaves with fewer lateral veins. Floral characters are rather variable and may lead to different interpretations of the group. Although the two species coexist and are distinct at some localities, not all collections fall readily into one or other species.

The geographical variant from the Aru Islands, formerly recognized as a separate species, has large leaves (to 28 × 7 cm) which are, however, comparable to recent collections from West Sepik.

Collections – IRIAN JAYA. SE 00° 53' 131° 15' Sorong, Mlasoen Hill, *van Royen 3079* (L). 00° 53' 131° 16' Sorong, 0.5 km N of town, *Jebb 7* (LAE), 8 (LAE), 9 (A). 00° 55' 134° 00' Andai, *Beccari P.P. 758* (type of *M. alata*). Arfak Mts, Minyan Gou, *Menzies s.n.*, 25 Aug. 1988 (L, UPNG). 03° 17' 138° 35' Idenburg R., Bernhard Camp, *Brass 13935* (type of *M. prolifera*). Aru Is., GiabuLengan, *Beccari s.n.*, March 1873 (type of *M. aruensis*).

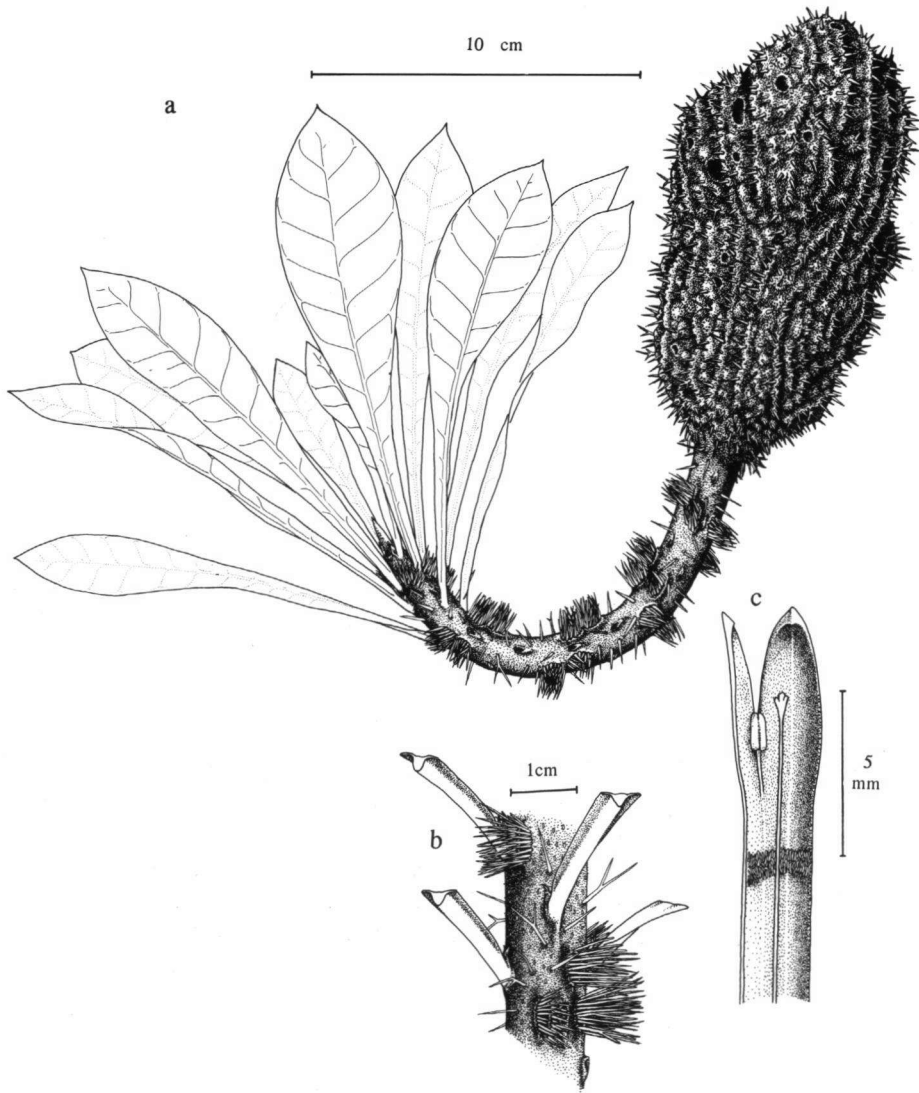


Fig. 9. *Myrmecodia alata* Becc. a. Habit; b. stem; c. half flower. Drawn by Rosemary Wise.

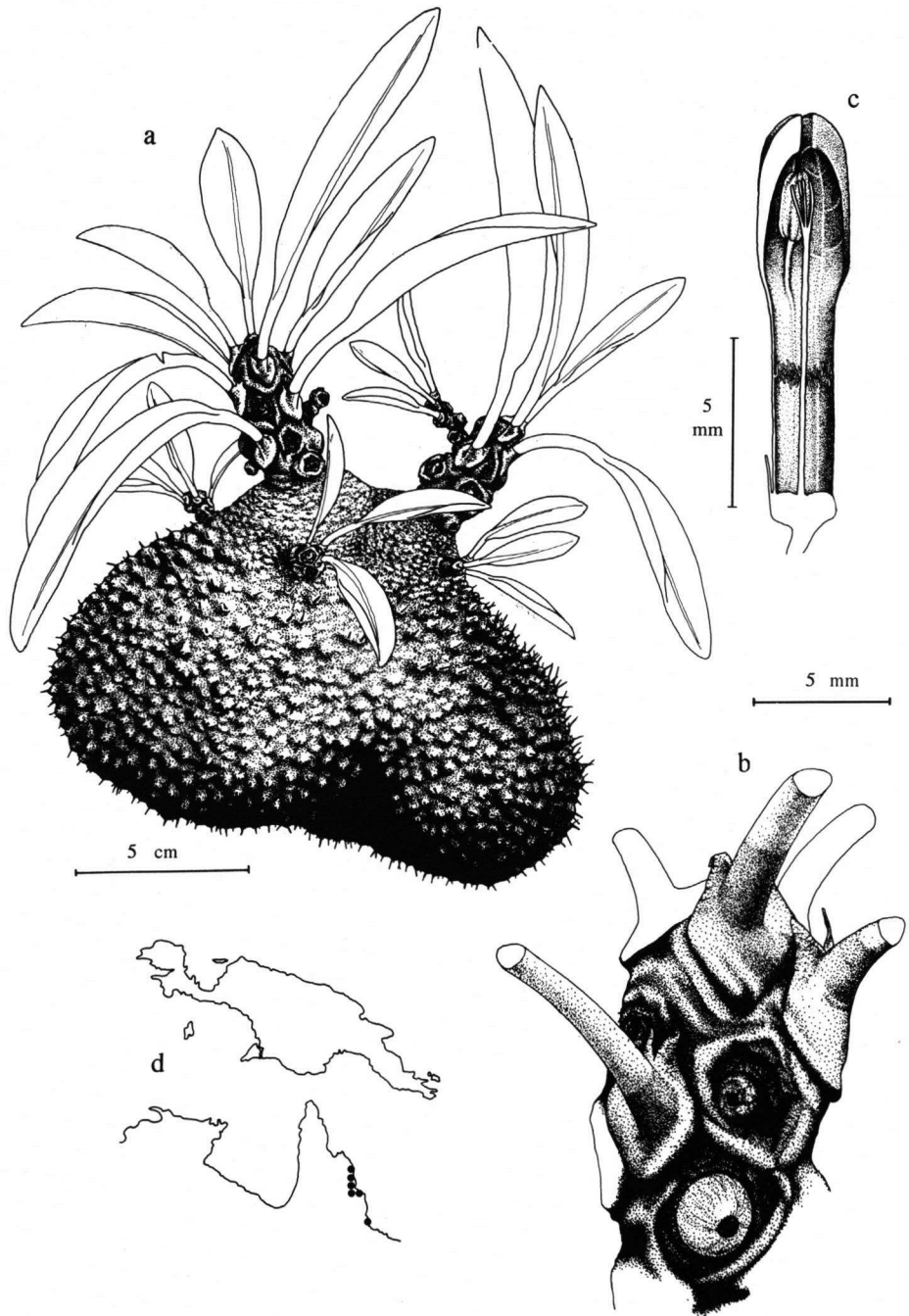


Fig. 10. *Myrmecodia beccarii* Hook. f.. a. Habit; b. stem apex, with one immature and one mature fruit; c. half flower; d. distribution. Drawn by Eleanor Catherine.

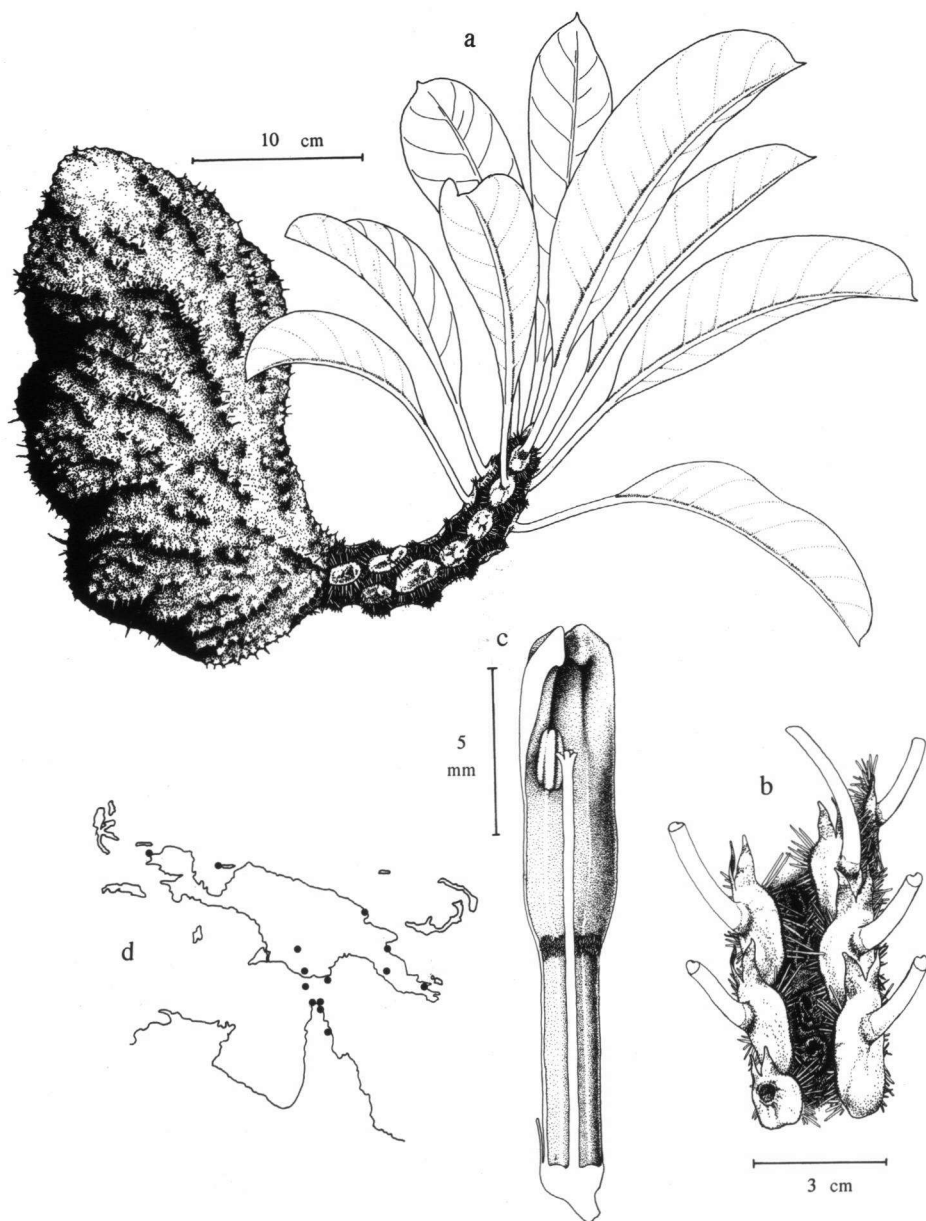


Fig. 11. *Myrmecodia platytyrea* subsp. *platytyrea* Becc. a. Habit; b. stem; c. half flower; d. distribution of *M. platytyrea* subsp. *platytyrea* and *M. platytyrea* subsp. *antoinii*. Drawn by Eleanor Catherine.

6. *Myrmecodia beccarii* J.D. Hooker – Fig. 10

Myrmecodia beccarii J.D. Hooker, Bot. Mag. (1886) t. 6883. — Type: Australia, *Veitch s.n.*, 1884 (holo K; iso FI).

Tuber irregularly cylindrical to 30 × 21 cm, pale grey. Spines simple, stout, to 0.4 cm, bourne on mounds. Pores and entrance holes absent. Chambers rarely more than 1 cm across, tissue between chambers broad, 0.5–1.5 cm. *Stems* several, freely branched, pale grey, to 10 × 3 cm. Alveoli more or less round, with broad fleshy rims. Clypeoli obscure. Spines sometimes present, scattered, simple or root-like. *Leaves*: Lamina 9 × 2 – 12 × 3.5 cm, elliptic; apex acute; base tapering, fleshy, pale green. Petiole 1–2 cm, rounded in cross section. Stipules triangular, 0.3 cm long, caducous. *Inflorescence*: Bracts to 0.4 cm, straw-coloured, not exerted. Flowers (2). Calyx 1 mm. Corolla white, 11 mm; lobes 3 mm; lobe tips 1 mm. A ring of hairs just below the middle of the tube. Anthers at the mouth of the tube, blueish; filaments 1.5 mm. Pollen 2-porate, 2-vesiculate; reticulation medium. Stigma of 4 narrow lobes, at level of anthers. Fruit pink. Pyrenes 4.

Ecology – On mangrove trees and in coastal *Melaleuca* savanna.

Note – This species is distinctive in its small fleshy leaves and richly branched stems. The stems and inflorescences resemble *M. tuberosa* more than any other species, but entrance holes and pores are absent.

Collections – AUSTRALIA. SE 15° 20' 145° 10' Cooktown, *French s.n.* (QRS). 15° 25' 145° 72' Endeavour R., *Volck 4561* (BRI). 15° 30' 145° 10' 5 km from Pt. Archer towards Cooktown, *Wrigley NQ 1311* (CBG). 16° 10' 145° 20' Bailey's Ck, N of Daintree R., *Wrigley NQ 939* (CBG). 16° 50' 145° 40' Cairns Inlet, Wah Day Ck, *Flecker & Pearson NQ 2103* (BRI). 16° 50' 145° 40' Cairns Inlet, Cairns, *UPNG 3492* (A, BO, CANB, K, LAE, OXF, QRS, UPNG), *UPNG 3493* (L, UPNG), *NQ 82* (BRI). 18° 30' 146° 10' Forest beach, east of Ingham, *Anonymus s.n.*, (CBG). Gulf of Carpenteria (?), *Veitch s.n.*, 1884 (type).

7. *Myrmecodia platytyrea* Becc. – Fig. 11

Myrmecodia platytyrea Becc., Malesia 2 (1884) 115, t. 23: 1–3; Valetton, Nova Guinea 8 (1911) 513. — Type: Irian Jaya, *Beccari 5502* (holo FI).

Myrmecodia antoinii Becc., Malesia 2 (1884) 116, t. 19: 2–4; Hook., Bot. Mag. (1897) t. 7517. — Type: Torres Straits, *Antoine s.n.* (K), syn. nov.

Tuber globose to cylindrical, to 20 cm long, grey or brown. Spines simple, stout, on ridges or mounds, 0.3–0.6 cm. Honeycombing present with pores and entrance holes. Flesh whitish or red. *Stem* solitary (few), unbranched. Clypeoli well-developed, 1 × 0.6 – 2 × 1.3 (–3 × 1.6) cm, grey or brown. Spines rimming clypeoli in a dense fringe, stout or fine, simple, (0.3–)0.5–1.3 cm. *Leaves*: Lamina 12 × 4 – 20 × 9.5 cm, more or less elliptic; apex acuminate (acute); base abruptly cuneate, veins 6–10. Petiole 2–9(–11) cm, often reddish. Stipules 0.5–1.3 cm, broadly to narrowly triangular, united for about half their length. *Inflorescence*: Bracts short. Corolla white, 16 mm; lobes 5 mm, unci 1.5 mm. A ring of hairs halfway up the tube. Anthers at apex of tube, with or without blue-black flecks. Pollen 1- or 2-vesiculate; apertures not bordered; reticulation fine to medium. Stigma 4-lobed, at anthers. Fruit 1.7 cm, red or orange. Pyrenes 6 (8).

Ecology — Commonest in savanna areas of southern Papua New Guinea, but also in gallery and other evergreen forest in lowland areas.

a. subsp. platytyrea

Tuber globose to cylindrical, brown to grey. Spines on ridges, to 0.6 cm long. Pores few. Entrance holes in arcs or scattered. Stem usually solitary. Clypeoli longer than broad. Spines thick, to 1.3 cm long. *Leaves*: Lamina elliptic or broadest below the middle 12 × 5 – 20 × 9 cm, apex short- to long-acuminate, base abruptly narrowed. Petioles 5–11 cm, sometimes orange or red. Stipules to 1.5 cm. *Inflorescence*: Pollen 1- (or 2-)vesiculate; reticulation fine to medium.

Ecology — Lowland rain forest.

Note — This subspecies occurs mainly in the wetter, northwestern part of New Guinea. It is not always clearly defined from *M. platytyrea* subsp. *antoinii*. The population at Telefomin is rather anomalous in having short petioles.

Collections — MOLUCCAS. SE 00° 20' 131° 10' Waigeu, Rawak *Gaudichaud s.n.* (G).

IRIAN JAYA. SE 0° 45' 131° 17' Vogelkop, 2 km N of Sorong, *Jebb 3* (LAE). 01° 35' 135° 42' Japen Is., Ansum, *Beccari 5902* (type of *M. platytyrea*). 07° 13' 141° 03' Merauke, Lake Wam, *van Royen 4764* (BO, K, L, LAE). *Nepenthes* Hügel, *Versteeg 1299* (BO, L).

PAPUA NEW GUINEA. SE 04° 30' 145° 50' Madang Prov., N side Karkar Is, *UPNG 5929* (A, L, UPNG). 07° 25' 147° 10' Morobe Prov., opposite Lasanga Is., *Jacobs 9588* (L). 08° 50' 147° 00' Central Prov., Kuriva, *UPNG 3428* (A, L, UPNG). 09° 22' 147° 28' Sogeri Subdist., 1 km S of Ower's Corner, *Jebb 151* (L).

b. subsp. antoinii (Becc.) Huxley & Jebb, *stat. nov.*

Myrmecodia antoinii Becc., *Malesia* 2 (1884) 116.

Tuber irregular, globose, grey. Spines on mounds, to 1 cm long. Pores many. Entrance holes few. Stems few. Clypeoli more or less isodiametric. Spines fine, to 1 cm. *Leaves*: Lamina elliptic to obovate, apex acute to acuminate, base cuneate. Petioles 2–6 cm. Stipules to 1 cm. *Inflorescence*: Pollen 2-vesiculate; reticulation medium.

Ecology — Coastal and inland hill savannas, to 600 m. High epiphyte in rain forest on Cape Vogel.

Note — This subspecies is found in the more seasonally dry region of the south and east of the range of the species.

Collections — PAPUA NEW GUINEA. 07° 49' 145° 05' Gulf Prov., Maipenairu, *UPNG 5921* (L, UPNG). 08° 50' 141° 54' Western Prov., Tarara, Wasi Kussa R., *Brass 8670* (A, BO, BRI, L). 09° 05' 143° 10' Daru Is., *Brass 6447* (A, BM, BO, L) & *LAE 51701* (L). 09° 22' 147° 20' Central Prov., Hombrom Bluff, *UPNG 3433* (A, BO, BRI, CANB, FHO, K, L, LAE, UPNG), *UPNG 5941* (UPNG), *UPNG 5942* (UPNG). 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 s.n.* (type of *M. antoinii*). 10° 40' 142° 30' Newcastle Bay, 3 km S of Somerset, *Brass 18725* (A). 11° 01' 142° 30' Bamaga, 27 km SW of Cape York., *Smith 12668* (BRI). 12° 40' 143° 20' Iron Range, *UPNG 3491* (L, UPNG). Scrubby Ck, Cook Dist., *Whitehouse s.n.* (BRI). Bamara, Cape York, *Jones 2501* (BRI).

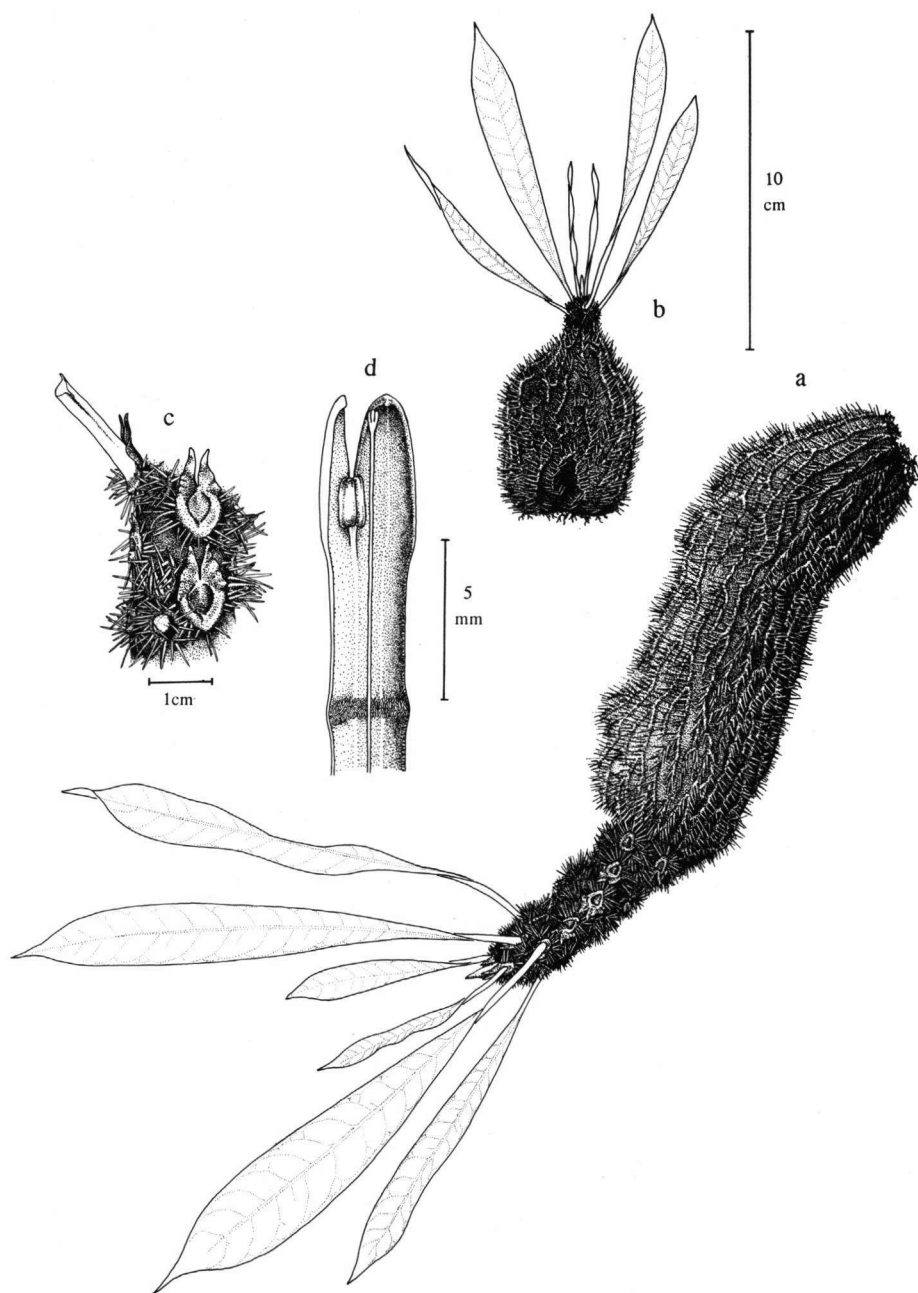


Fig. 12. *Myrmecodia pendens* Merr. & Perry. a. Mature plant; b. immature plant; c. stem; d. half flower. Drawn by Rosemary Wise.

8. *Myrmecodia pendens* Merr. & Perry — Fig. 12

Myrmecodia pendens Merr. & Perry, J. Arnold Arbor. 26 (1945) 32. — Type: Papua New Guinea, Brass 5401 (holo p.p. A).

Tuber cylindrical, pendent in mature specimens, c. 17 × 6 cm, shiny dark brown, the ridges have white edges and tend to run the whole length of the tuber. Spines mainly on the ridges, simple, straight, stiff, finely tapered, pale brown, 0.5–0.8(–1.5) cm. Swollen areas with pores over honeycombing. Entrance holes absent. Central smooth chambers transversely flattened. Flesh turns brown on cutting. *Stem* solitary, usually straight, unbranched, to 17 × 1.7 cm. Clypeoli distinct, fleshy, to 1.2 × 0.8 cm; upper part winged by an extension of the stipules, lower part densely rimmed by simple (branched), stiff, rather broad spines, to 1.3 cm long. Alveoli rimmed and more or less concealed by similar spines. *Leaves* clustered at stem apex. Lamina 13 × 2.5 – 28 × 5(–7) cm, mid to dark green, glossy above, narrowly oblanceolate; apex acuminate; base tapered from widest point. Midrib sharply keeled below. Lateral veins curved, clearly visible, prominent below, 9–13. Petiole 0.5–3 cm, winged to the base. Petiole and midrib whitish. Stipules 1–2 cm, narrowly tapered at apex, divided for half their length, more or less persistent. *Inflorescence*: bracts not conspicuous. Flowers (3). Calyx 0.7–1 mm. Corolla white, 13 mm; lobes 3 mm; lobe tips 0.5–1 mm. A ring of hairs 1 mm wide, 3–4 mm from base of tube. Anthers at apex of tube or exserted; filaments 1–2.5 mm. Pollen 2-porate, 2-vesiculate; apertures not bordered, only slightly constricted; reticulation coarse. Stigma at or above anthers, 4-lobed. Fruit orange. Pyrenes 4.

Ecology — Edge of upper mixed forest, oak forest, and *Nothofagus* forest. Also in secondary or disturbed forest, savanna or isolated trees; altitude 1200–1700 m.

Notes — This rather delicate species is readily recognized by the white crests on the ridges. It is rather uniform in leaf-shape, tuber and in flower characters. It often grows with *M. schlechteri* and has the same general appearance but is completely different in its clypeolate stem and simple spines.

The duplicates of Brass 5401 at BO, BRI and NY belong to *M. schlechteri* subsp. *pendula*, see there.

Collections — PAPUA NEW GUINEA. SE 06° 40' 143° 53' Southern Highlands, 2 km N of Sawmilli on path from Erave to Samberigi, *Jebb* 424 (L, LAE), 425 (A). 06° 42' 145° 38' Eastern Highlands Prov., Okapa, nr Awarosa, *Jebb* 96 (LAE), 97 (L). 08° 18' 146° 58' Central Prov., 2 km N of Tapini, UPNG 5938 (A, BO, BRI, FHO, K, L, UPNG). 08° 33' 147° 00' Mafulu, Brass 5401 (p.p. type). 09° 05' 147° 38' Boridi, Carr 14659 p.p. (K). 09° 09' 147° 33' Efogi, *Jebb* 161 (LAE), 165 (L), 166 (A). 09° 45' 149° 04' Milne Bay Prov., Mayu R., Mt Suckling, Stevens LAE 55708 (A, BRI, CANB, K, L, LAE); nr Agaun, UPNG 3465 (UPNG).

9. *Myrmecodia longissima* Valetton — Fig. 13a, b, c, g

Myrmecodia longissima Valetton, Bot. Jahrb. 61 (1927) 148. — Type: Papua New Guinea, Ledermann 12623 (holo B; iso L drawing).

Tuber cylindrical, hanging downwards, to 40 × 9 cm, dark grey; ridges slight, running most of the length of the tuber. Spines sparse to numerous, simple, black, c. 0.8 cm

(rarely with root-like branched spines). Rings of pores covering most of the tuber surface. Entrance holes few, scattered. *Stem* solitary, unbranched, straight, hanging downwards, c. 15 × 1.8 cm. *Clypeoli* c. 1.5 cm across, isodiametric, upper part winged, lower part rounded, jutting out from stem. Spines around alveoli and clypeoli numerous to very few, simple, dark brown, to 1.5 cm. *Leaves* hanging downwards. Lamina to 30 × 4 (42 × 1.5) cm; apex acute to finely tapered; base gradually tapered. Midrib whitish or purple-brown, prominent below. Petiole 6–18 cm, white or red. Stipules united for half or less of their length, chestnut brown, c. 1.8 cm. *Inflorescence*: reddish-brown bract remains and calyces forming dense cushions. Bracts hat-like, covering the flower bud and subsequent bract and bud, which again encloses the next and so on. Bracts splitting irregularly or the apex broken off. A dense fringe of hairs as long as the bract are attached along its inner base. Flowers (8) heterostylous. Calyx reddish brown, rather barrel-shaped, persistent and thickened in fruit, to 4 mm long. Corolla 10–15 mm, white (? pink). Anthers without blue-black flecks. In brevistyle flower (type) a ring of hairs at the base of tube, anthers at the tube apex. Pollen unknown. Style short. Stigma and anthers at tube apex. In the Lake Kopiago population corolla lobes above the unci projecting as horns to 2.5 mm long, unci remaining tightly closed. Lobes 5 mm long. Anthers just below unci, 1.5 mm. Filaments 0.5–1 mm. Pollen 2-porate, 1- (or 2-)vesiculate. Vesicles large, apertures not bordered. Vesiculate apertures not constricted. Reticulation fine. Stigma at anthers. Lobes 4, appressed, 1.5 mm long. In longistyle flowers corolla lobes 6 mm; ring of hairs midway up the tube. Anthers at hairs, 2 mm. Pollen 2-porate, 2-vesiculate; apertures slightly bordered, vesiculate apertures slightly constricted; reticulation fine. Stigma 2- or 4-lobed, 3 mm above the anthers. Pyrenes 4, 3.4 mm.

Ecology – Rain forest or open areas, roadside casuarinas; altitude (70–)1300–1500 m.

Notes – *Myrmecodia longissima* can be recognized by its rounded clypeoli which jutt out at the base, and long narrow leaves. The narrowly cylindrical tuber with a single straight stem and simple spines is similar to *M. pendens*. Stem, calyx, and pollen characters suggest a close affinity to *M. oblongata*.

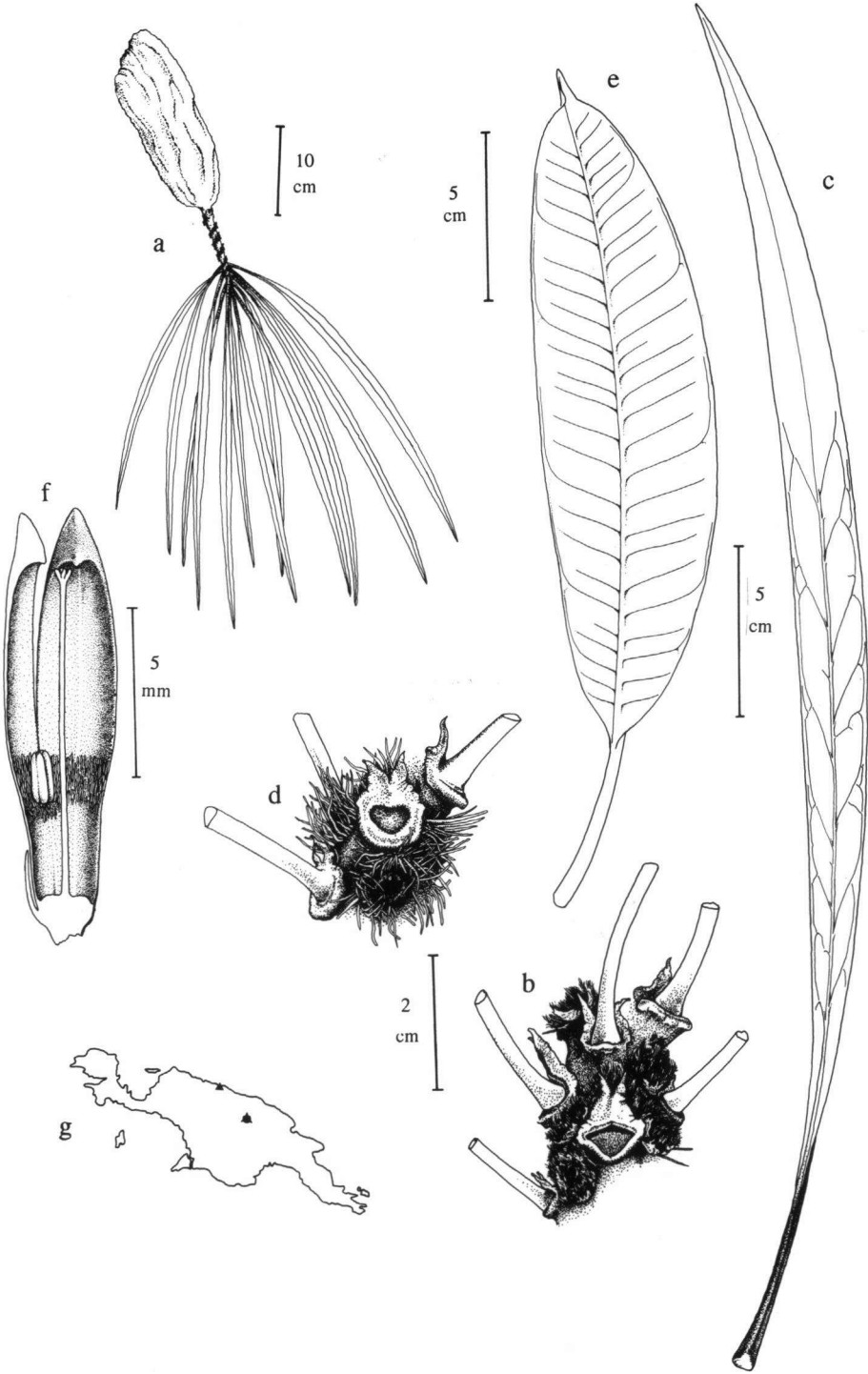
The collection from Irian Jaya differs in its very long narrow leaves and paucity of stem spines. It also comes from a much lower altitude than the other collections.

Collections – IRIAN JAYA. SE 02° 25' 140° 24' Djayapura Dist., hill NE of Tablasoefoe, *van Royen & Sleumer 6484* (K, L).

PAPUA NEW GUINEA. 04° 00' 141° 10' Sepik Prov., Sepik R., Station Felsspitze, *Ledermann 12623* (type). 04° 30' 142° 40' Ambunti Subdist., eastern ridge of Sumset (Mt Hunstein), *Hoogland & Craven 10920* (CANB not seen, LAE). 05° 24' 142° 31' Western Highlands, 3 km SE of Lake Kopiago on eastern road to Koroba, *Jebb 214* (L), *215* (LAE 2 sh, K), *216* (A). 05° 25' 142° 31' 6 km SE of Lake Kopiago, on eastern road to Koroba, *Jebb 204* (BRI), *205* (BULOLO), *206* (LAE 2 sh). 05° 26' 142° 33' 10 km SE of Lake Kopiago, on eastern road to Koroba, *Jebb 208* (FHO), *209* (UPNG), *210* (LAE), *211* (CANB, 2 sh), *212* (L).

10. *Myrmecodia oblongata* Valetton – Fig. 13 d–g

Myrmecodia oblongata Valetton, Bot. Jahrb. 61 (1927) 149. — Type: Papua New Guinea, *Ledermann 11225* (B†, holo L fragment & photo).



Tuber without ridges. Spines mostly simple, fine, short, quite dense. Pores over honeycombed areas. *Stem* 16 × 2.5 cm, unbranched. Clypeoli ± circular, 2.3 cm across, without spines, base rounded protruding. Alveoli irregularly rimmed by simple (branched), rather weak spines, 0.6–1.5 cm long. *Leaves* fleshy to leathery. Lamina 19 × 4.7 cm, narrowly oblong; apex abruptly acuminate; base cuneate. Midrib rounded below. Lateral veins conspicuous, c. 25, straight, joined to a submarginal vein which is more conspicuous above than below. Petioles c. 2.5 cm. Stipules 1 cm. *Inflorescence*: Bracts hairy. Flowers (1). Calyx bell-shaped, 3 mm. Corolla 10 mm; lobes 5 mm; lobe tips 1 mm. A ring of hairs midway up the tube. Anthers at and above hairs, 2 mm. Pollen unknown. Stigma 4-lobed, just below unci. Pyrenes 4.

Ecology – At 1400 m altitude.

Note – 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.

Collections – PAPUA NEW GUINEA. SE 04° 30' 142° 40' Sepik Prov., Hunsteinspitze, *Ledermann 11225* (type).

11. *Myrmecodia longifolia* Valetton

Myrmecodia longifolia Valetton, Nova Guinea 8 (1911) 509. — Type: Irian Jaya, *Versteeg 1522* (holo BO; iso L).

Tuber irregularly cylindrical, ridged, blackish. Spines numerous, simple, c. 0.4 cm. Pores ? Entrance holes ? Superficial chambers honeycombed. *Stem* solitary, bending to point upwards, unbranched, c. 20 cm. Clypeoli to 1 cm across, rounded, base prominent. Alveoli and clypeoli rimmed by simple, occasionally branched, spines, 0.4–0.8 cm long. *Leaves*: Lamina 12 × 3 – 25 × 6.5 cm, oblanceolate, leathery; apex acute to acuminate; base gradually tapered. Midrib prominent above and below. Lateral veins 8 or 9. Petioles 2.5–4.5 cm, white. *Inflorescence*: Bracts chestnut brown, sometimes protruding, cushion-like. Flowers (3) heterostylous. Calyx c. 1 mm. Corolla 9–12 mm; lobes c. 3 mm, lobe tips 1 mm. In brevistyle flowers (type) ring of hairs 2 mm from tube base. Anthers 2 mm long, at tube apex. Style 2.5 mm. Stigma 5-lobed; ovules 5. In longistyle flowers ring of hairs 3–4 mm from base of tuber. Anthers at tube apex, 1 mm. Filaments 2 mm. Stigma just above anthers, 4-lobed. Ovules 4.

Ecology – Rain forest, 1500 m altitude.

Note – Although the Jebb collections are 600 km geographically disjunct from the type and the leaves are not very similar, the agreement in stem and tuber features suggests they are conspecific.

Collections – IRIAN JAYA. SE 04° 40' 138° 39' Nord Fluss, nr foot of Geluks Hügel, Bivak Alkmaar, *Versteeg 1522* (type).

PAPUA NEW GUINEA. 06° 37' 143° 51' Southern Highlands, 3 km SW of Erave on ridge top, to E of path from Erave to Sawmilli, *Jebb 430* (L), *431* (A), *432* (LAE).

Fig. 13. *Myrmecodia longissima* Valetton. a. Habit; b. stem; c. leaf. — *M. oblongata* Valetton. d. Stem; e. leaf; f. half flower; g. distribution: *M. longissima* triangles, *M. oblongata* disc. Drawn by Rosemary Wise.

12. *Myrmecodia schlechteri* Valetton — Fig. 14

Myrmecodia schlechteri Valetton, Bot. Jahrb. 61 (1927) 146. — Type: Papua New Guinea, *Schlechter* 17033 & 17275 (B†); neotype: Papua New Guinea, *Jebb* 63 (holo LAE).

Myrmecodia longispina Valetton, Bot. Jahrb. 61 (1927) 145. — Type: *Schlechter* 18682, p.p. (B†).

Myrmecodia pendula Merr. & Perry, J. Arnold Arbor. 26 (1945) 32. — Type: Papua New Guinea, *Brass* 5401, p.p.(BO, BRI, NY).

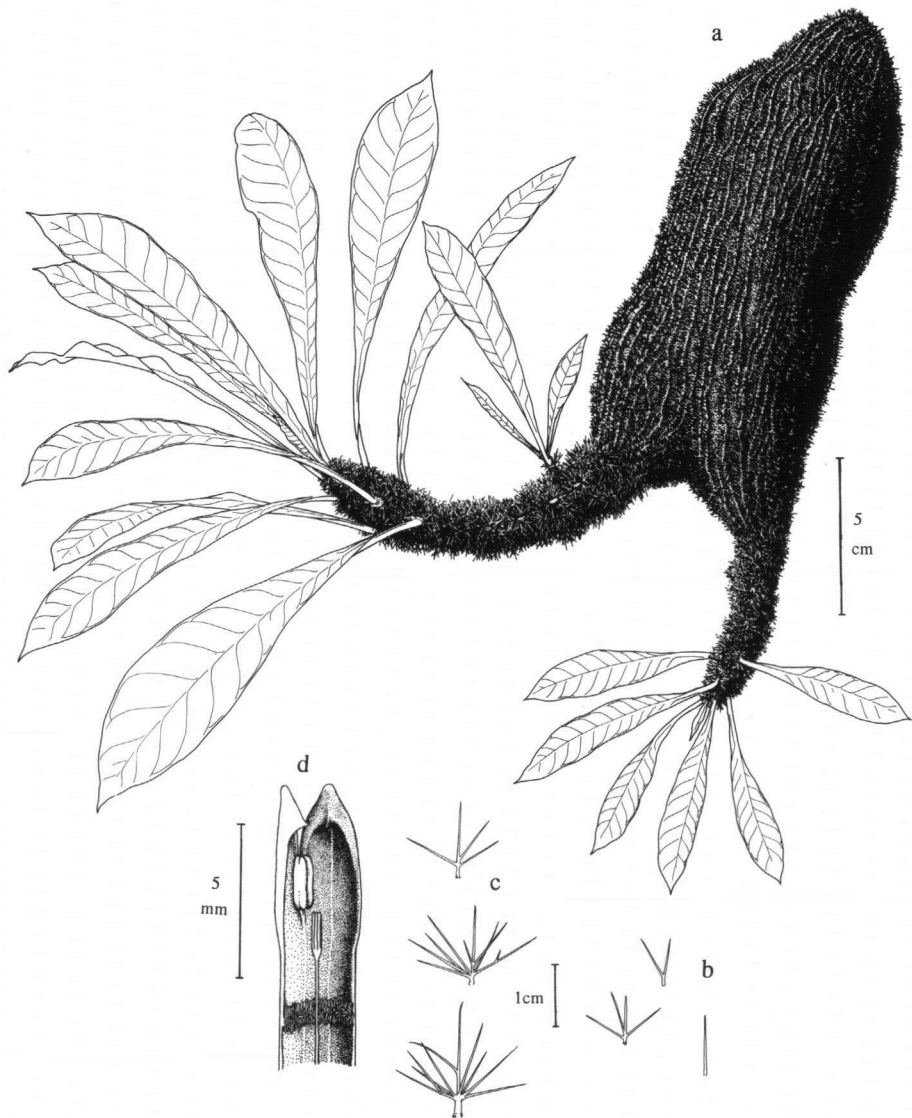


Fig. 14. *Myrmecodia schlechteri* subsp. *schlechteri* var. *schlechteri* Valetton. a. Habit; b. spines on tuber; c. spines on stem; d. half flower. Drawn by Eleanor Catherine.

Tuber pendent, irregularly cylindrical or ovoid, pale to dark brown, $17 \times 7 - 57 \times 11$ cm; ridges not usually running whole length of tuber. Spines mostly on ridges, few to dense, 0.5–1.2 cm, firm or weak, yellowish-brown, (simple) irregularly or more or less stellately branched. Entrance holes absent (scattered) on tuber surface. Swollen areas with pores over honeycombing. Cavity walls 0.2–0.5 cm. Superficial chambers with strong honeycombing, inner smooth-walled chambers shelf-like. *Stem(s)* one to few, downward pointing or curved upwards, not to often branched, to 20×1.5 cm. Alveoli rounded to elongate, filled by bracts. Clypeoli absent. Spines sparse or dense rimming alveoli and between them, irregularly or stellately branched, to 2.2 cm. *Leaves* more or less clustered at stem apex. Lamina more or less leathery, $9 \times 2.5 - 27 \times 7$ (31×8) cm, (elliptic) oblanceolate; apex acute to acuminate; narrowly attenuate at base. Midrib prominent below; lateral veins 6–13, midrib sharply keeled below. Petioles 0.2–3 cm, sharply triangular. Stipules 0.6–1.2 cm, broadly triangular. *Inflorescence*: Bracts hairy, more or less filling the alveoli. Calyx 1–2 mm, truncate or slightly toothed. Corolla 6–15 mm; lobes 4–7 mm; lobe tips $2 \times 2 - 3$ mm, rarely tearing above the unci; ring of hairs a third to midway up the tube, sometimes sparse or absent. Anthers 1.5 mm, halfway up the tube, with or without blue-black flecks. Pollen 2-porate, 1- or 2-vesiculate; apertures not rimmed; reticulation fine or medium. Stigma at or below anthers, 4–6-lobed, lobes adnate. Fruit orange-yellow to red. Pyrenes 4–8, 4×2.5 mm, obovate, apex rounded or with an apiculus.

Distribution – Papua New Guinea.

Ecology – In upper edge of mixed forest, *Castanopsis* forest, and isolated trees in agricultural areas; altitude 800–2300 m.

Notes – *Myrmecodia schlechteri* differs from *M. albertisii* in its short petioles and from *M. angustifolia* in its leaf-shape. The pollen, although similar to that of *M. albertisii*, differs in relative thickness of the exine to intine (1:2 in *M. albertisii*, 1:1 in *M. schlechteri*).

This species is divided here into three subspecies and two varieties following former division into species. The subspecies occupy distinct geographical areas and the varieties distinct altitudinal zones. The distinctions are not sharp, however. Variety *longispina* was separated at specific level by Valeton, though he admitted it was perhaps only a variant. However, Jebb observed the same morphological changes occurring over the same altitudinal range, c. 80 km west; intermediates are not known. Subspecies *pendula* differs in floral characters, but also has the vegetative characters of both the other taxa. It is connected by a somewhat intermediate collection from Morobe Province, Menyama.

Taxonomic note: Although the Valeton types are lost and at the type locality not recollected, the Jebb collections are from the same area and lead to the conclusion that *M. pendula* and *M. longispina* should be regarded as subspecific variants of *M. schlechteri*.

a. subsp. *schlechteri*

Tuber cylindrical to ovoid, to 57 cm long by 11 cm wide. Spines weak to firm. *Stem(s)* one to three, branched or not. Spines moderately to very dense. *Leaves*: Lamina usually $9 \times 2.6 - 23 \times 4.5$ cm, narrowly oblanceolate, apex acute-acuminate. Petiole

0.2–3 cm. *Inflorescence*: Flowers (17). Calyx 2 mm. Corolla 11–15 mm; lobes 4–5 mm; lobe tips 2 × 2 mm. Ring of hairs 3–4 mm from tube base. Anthers 1–3 mm above hairs, blue-black flecks present. Pollen 2-porate, 1-vesiculate; reticulation fine. Stigma between hairs and anthers or overlapping either. Fruit orange. Pyrenes 4 or 5.

Distribution – Central Papua New Guinea.

Ecology – Common in open forest and agricultural areas between 800 and 1550 m, mostly in regions with less than 250 mm rainfall p.a. It is especially frequent on *Casuarina* and *Castanopsis*.

a¹. subsp. schlechteri var. schlechteri

Tuber cylindrical, to 57 × 11 cm. Spines sparse to dense, weak, with 2–4 side branches, 0.5–0.8 cm. *Stem(s)* one to three, branched, upturned, apex tapered, not overtopped by spines. Spines to 1.2 cm. *Leaves* not usually clustered. Lamina 9 × 2.6–18 × 4.5 cm, oblanceolate, apex acuminate, leathery; lateral veins prominent below. Petiole 0.2–3 cm. *Inflorescence*: Flowers (17). Stigma at hairs.

Ecology – Often abundant in disturbed forest and agricultural areas between 800 and 1550 m, mostly in regions with less than 250 mm rainfall p.a. It is especially frequent on *Casuarina* and *Castanopsis*.

Note – This variety differs from var. *longispina* in its branched, upturned stems with thinner, acuminate, distinctly petioled leaves.

Collections – PAPUA NEW GUINEA. SE 05° 40' 144° 11' Western Highlands, N end of Baiyer Gorge, *Jebb* 599 (LAE, 2 sh). 05° 40' 144° 25' Fatima High School, 5 km W of Banz, *Jebb* 302 (K, L), 303 (LAE), 304 (A), 305 (BULOLO, LAE, UPNG), 306 (BRI). Angeliap Subdist., 4 km W of Roguts Village, *Gay* 800 (LAE). 05° 45' 145° 12' Madang Prov., Bundi, Bundikara Village, *Jebb* 46 (type), 47 (A, 3 sh), 48 (K), 50 (UPNG), 51 (BULOLO). 05° 45' 145° 13' Bundi, *Jebb* 52 (LAE), 53 (CANB), 54 (FHO), 55 (UPNG, 2 sh), 60 (L), 61 (BRI), 62 (A), 63 (neotype, K), 64 (L 2 sh), 65 (BRI). 05° 45' 145° 14' Bundi, *Jebb* 56 (BO), 57 (L), 58 (FHO 3 sh), 59 (LAE). 06° 01' 144° 59' Chimbu Prov., nr Kundiawa at beginning of road to Kegelsugul, *UPNG* 5922 (BRI, UPNG). 06° 01' 145° 55' Eastern Highlands, 20 km N of Kainantu, *Sayers* 63 (K). 06° 05' 145° 25' Goroka, *NGF* 15912 (BRI, L), *UPNG* 3456 (CANB, FHO, NY, UPNG). 06° 10' 147° 06' Morobe, Kabwum Subdist., 3 km SSE Derim, 200 m S of Molon, *Jebb* 187 (K), 189 (A), 190 (LAE), 191 (BULOLO, UPNG), 192 (L), 193 (BRI). 06° 14' 145° 59' Eastern Highlands, Kassam Pass, Undoe Bridge, *UPNG* 3454 (FI, UPNG). 06° 22' 145° 58' Yanku, off road to Ukarumpa, *UPNG* 3455 (K, L, UPNG). 06° 30' 145° 32' nr Okapa, *UPNG* 3459 (BO, K, L, LAE, UPNG). 06° 42' 145° 38' Okapa 1 km E of Awarosa, *Jebb* 98 (LAE); 99 (L). 06° 46' 146° 47' Morobe Prov., off Lae to Bulolo road, on logging tracks SE of Oomsis, *Jebb* 435 (L), 436 (BULOLO), 437 (LAE), 438 (K), 439 (UPNG), 440 (A). 07° 10' 146° 00' Menyamya, *NGF* 35885 (L, LAE).

a². subsp. schlechteri var. longispina (Valeton) Huxley & Jebb, stat. nov.

Myrmecodia longispina Valeton. – Neotype: Papua New Guinea *Jebb* 67 (holo LAE).

Tuber ovoid, to c. 20 × 9 cm. Spines dense, firm, 0.8–1.2 cm, with 2–5 side branches. *Stem(s)* one (or few), occasionally branched, to 19 × 1.2 cm, hanging. Apex not apparently tapered because it is overtopped by the very dense spines 1.6–2.2 cm long. *Leaves* clustered at stem apex. Lamina 17 × 3–23 × 4.5 cm, narrowly oblanceolate, thick, leathery, apex acute. Lateral veins obscure; midrib channelled

above when dry. Petioles 0.2–2.0. *Inflorescence*: Flowers (3). Lobes 4 mm. Lobe tips 2 mm. Ring of hairs 2 mm from tube base. Anthers midway up tube, with blue-black flecks. Pollen 2-porate, 1-vesiculate; reticulation fine. Stigma at anthers; lobes 4, adnate. Fruit orange. Pyrenes 4.

Ecology – In forest above agricultural land, growing with *Myrmecodia melancantha*; altitude 1600–1960 m.

Note – This variety occurs at higher altitude than *M. schlechteri* subsp. *schlechteri*. It is distinguished by its solitary downward pointing stem, apparently thickest at the apex, surmounted by a dense cluster of longer leathery leaves.

Collections – PAPUA NEW GUINEA. Madang Province. SE 05° 45' 145° 11' Bundi Subdist., 2 km S of Bundikara Village *Jebb* 66 (L), 67 (type), 69 (A), 70 (BULOLO), 72 (K).

b. subsp. pendula (Merr. & Perry) Huxley & Jebb, *stat. nov.*

Tuber cylindrical, to 30 × 9 cm. Spines 0.4–1 cm. *Stem(s)* one to few, sometimes branched, upturned at apex. Spines scattered to dense, to 1.2 cm. *Leaves* clustered. Lamina 9–23 × 2.5–5.5 cm, thin, apex acuminate. Petioles 0.5–1 cm. *Inflorescence*: Alveoli densely filled by bracts. Flowers (3). Corolla 7 mm. Lobes 4 mm. Lobe tips 1 mm. Ring of hairs very slight or absent, 1.5 mm from tube base. Anthers 2 mm from tube base, without blue-black flecks. Pollen 2-porate, 2-vesiculate. Reticulation medium. Stigma at anthers, 4- or 5-lobed. Fruit orange. Pyrenes 4–6.

Ecology – At 760–1400 m altitude in the Owen Stanley Range, but lower, 80 m, in Milne Bay Province. In open, secondary or primary forest.

Note – Subsp. *pendula* is distinguished from subsp. *schlechteri* by its shorter corolla usually lacking a ring of hairs, and 2-vesiculate pollen.

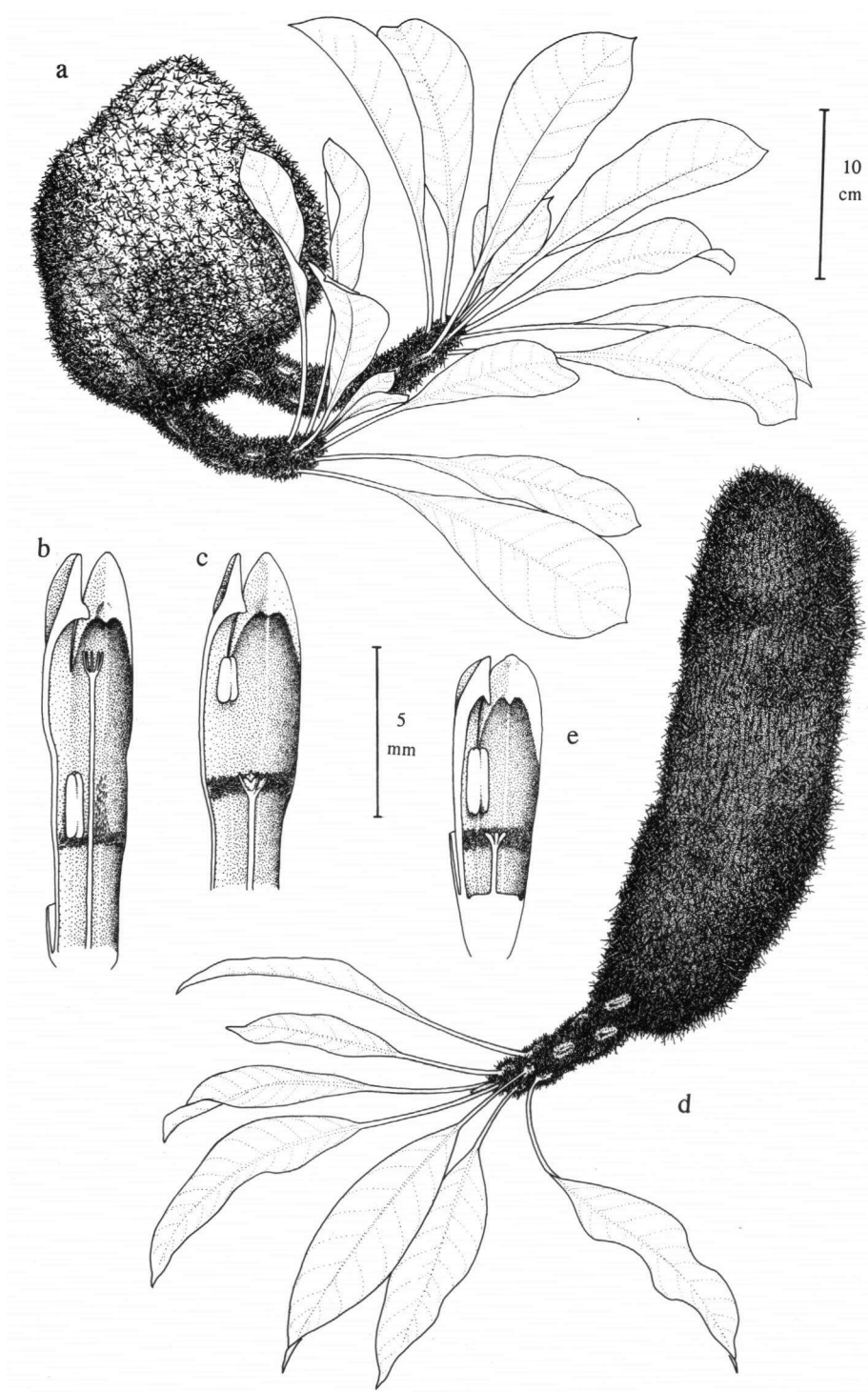
Collections – PAPUA NEW GUINEA. SE 08° 33' 147° 00' Central Prov., Mafulu, *Brass* 5401 (type). 09° 07' 147° 41' Kokoda Trail, 1 km E of Kagi, *Jebb* 167 (LAE 3 sh), 168 (UPNG). 09° 11' 147° 37' Kokoda Trail, 100 m N of Manari airstrip, *Jebb* 159 (LAE). 10° 22' 150° 15' Milne Bay Prov., N Sagarai Valley, *Henty* NGF 16894 (A, BRI, CANB, LAE).

c. subsp. eraveensis Huxley & Jebb, *subsp. nov.*

Ab aliis subspeciebus M. schlechteri foliis longioribus, latioribus, et lobis corollae longioribus differt. — Typus: Papua New Guinea, *Jebb* 410 (holo LAE).

Tuber broadly cylindrical, to 27 × 9 cm. Spines firm. *Stem(s)* one or two, occasionally branched, not or scarcely upturned, to 25 cm long. Apex gradually narrowed, well exceeding the uppermost spines. Spines densely rimming the alveoli, few on stem surface. *Leaves*: Lamina 10 × 3.5 to 27 × 6.8 cm, widest 1/3 from apex, not leathery, apex acuminate. Petioles 1–2(–4) cm. Stipules prominent, 1–1.5 cm. *Inflorescence*: Alveoli filled by bracts. Flowers (4). Calyx 2 mm, truncate. Corolla 14 mm, lobes 7 mm, lobe tips 2 mm. Ring of hairs 3–4 mm from tube base. Anthers just above hairs, edges with blue-black flecks. Pollen 2-porate, 2-vesiculate; reticulation fine to medium. Stigma 3–6-fid, at anthers. Fruit ? Pyrenes 5 or 6.

Ecology – In open forest and isolated trees in agricultural land; altitude 1000–1400 m.



Note – Subsp. *eraveensis* is larger than subsp. *schlechteri*, and the leaves are longer and wider (to 27 × 6 cm). The corolla lobes are longer and the pollen 2-, not 1-vesiculate.

Collections – PAPUA NEW GUINEA. Southern Highlands. SE 06° 36' 143° 53' 4 km W of Erave, on road to Kagua, *Jebb* 409 (L), 410 (type). 06° 40' 143° 53' 2 km N of Sawmilli on path from Erave to Samberigi, *Jebb* 426 (A 3 sh). 06° 41' 143° 51' Erave Subdistr., on ridge top, 7 km WNW of Samberigi, *Jebb* 423 (BULOLO).

d. subsp. *kopiagoensis* Huxley & Jebb. subsp. nov.

Ab aliis subspeciebus *M. schlechteri* foliis ellipticus et lobis corollae latoribus differt. — Typus: Papua New Guinea, *Jebb* 218 (holo LAE 2 sh).

Tuber c. 17 × 12 cm, spines not very dense, to 0.5 cm. *Stem* solitary, occasionally branched; apex tapered. Spines sparse, to 1.1 cm long, not developed on stem apex. *Leaves* not clustered. Lamina 15 × 4.5 – 25 × 6.5 cm; elliptic, apex acuminate; base cuneate. Lateral veins 10–12. Petioles 1–3 cm, caniculae above. Stipules reddish brown, conspicuous. *Inflorescence*: Flowers (6). Calyx 2 mm tall with slight teeth. Corolla 6–13 mm, lobes 4–5 mm, ring of hairs midway up tube. Anthers above hairs 1.5 mm, no blue-black flecks. Pollen 1- or 2-vesiculate; reticulation fine. Stigma at or just below anthers, c. 4-lobed. Fruit? Pyrenes 5–8.

Ecology – On trees in open grassland; altitude 1300–2200 m.

Note – This subspecies is distinctly different from the other ones in the leaves being sharply elliptic or widest only shortly above the middle.

Collections – PAPUA NEW GUINEA. Western Highlands Province. SE 05° 24' 142° 28' 2 km SE of Lake Kopiago on eastern road to Koroba, *Jebb* 217 (A), 218 (type), 219 (L), 220 (BRI). 05° 24' 142° 31' Lake Kopiago, *Jebb* 201 (K), 202 (L), 203 (LAE). 05° 25' 142° 31' 5 km SE of Lake Kopiago on eastern road to Koroba, *Jebb* 213 (LAE). Angeliap Subdist., Roguts Village, *Gay* 800 (LAE).

13. *Myrmecodia albertisii* Becc. – Fig. 15

Myrmecodia albertisii Becc., Malesia 2 (1884) 112, t. 11; Valetton, Bot. Jahrb. 61 (1927) 145; Merr. & Perry, J. Arnold Arbor. 26 (1945) 31. — Type: Papua New Guinea, *d'Albertis* 5503, 1877 (holo FI).

Tuber conical to cylindrical, to 50 × 23 cm, pale grey to dark brown. Ridges sometimes present, slight. Spines sparse to dense, stellate or irregularly branched, stout or weak, pale or dark brown, 0.4–0.7(–1) cm. Honeycombing well developed, pores sometimes present. *Stem(s)* solitary (or few), sometimes branched. Spines as on tuber mostly around alveoli. Clypeoli absent. Alveoli, empty to densely filled with hairy bracts, obscured by spines. *Leaves* 13 × 3 – 13 × 9, or – 32 × 6.5 cm. Lamina narrowly to broadly elliptic or oblanceolate, base cuneate. Midrib sharply prominent be-

Fig. 15. *Myrmecodia albertisii* Becc. subsp. *albertisii*. a. Habit; b. half longistyle flower; c. half brevistyle flower. — *M. albertisii* subsp. *incompta* Huxley & Jebb. d. Whole plant; e. half flower. Drawn by Rosemary Wise.

low. Petioles 3–9 cm, triangular. Stipules to 1.2 cm, sharply triangular. *Inflorescence*: Calyx 1–1.5 mm. Flowers heterostylous, at least in part of the range. Corolla white, often with blue black flecks, with a ring of hairs at mid tube or lower. Anthers among hairs or towards tube apex. Pollen 2-porate, 1- or 2-vesiculate, apertures not bordered; reticulation fine to coarse. Stigma 2–6-lobed. Fruit orange-red. Pyrenes 4–6.

Distribution – Southern Papua New Guinea; see under the subspecies.

Ecology – Low altitude swamp savanna to mossy forest at 1900 m.

Note – This taxon is extended here to include not only the type form from lowland southwestern Papua New Guinea, but also collections from Central Province and the D'Entrecasteaux Islands off the eastern tip of the mainland. Plants from these three areas are recognized as subspecies.

a. subsp. *albertisii* – Fig. 15a–c

Tuber conical, pale grey, to 50 × 23 cm. Spines dense, usually c. 0.6 cm and stout. *Stem* rarely branched. Alveoli densely filled by hairy bracts. Spines slightly longer and more freely branched than on tuber. *Leaves* 15 × 4 – 34 × 9 cm, leathery. Lamina oblanceolate to elliptic; apex acuminate to apiculate. Petioles (3–)4–9 cm. *Inflorescence*: Flowers (4) heterostylous. In brevistylous flowers (2) a narrow ring of hairs near the base of the tube. Anthers blue-black, at the apex of the tube. Pollen 2-vesiculate; reticulation medium to coarse. Stigma broadly 4-lobed, just above ring of hairs. In longistyle flowers (2) a broad ring of hairs just below the middle of the tube. Anthers among hairs. Pollen 1-vesiculate; reticulation fine. Stigma narrowly 6-lobed, above apex of corolla tube. Pyrenes 6.

Ecology – In lakeside trees and savanna of *Tristania*, *Acacia*, and *Xanthostemon*.

Note – *Myrmecodia albertisii* subsp. *albertisii* is found over quite a wide area in Western Province, and is vegetatively uniform over that area. The flowers are dimorphic in respect of anther and stigma position and pollen morphology.

Collections – PAPUA NEW GUINEA. Western Province. 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, UC). Fly R., d' *Albertis s. n.*, 1877 (type). Western Prov., UPNG 5924 (L, UPNG).

b. subsp. *valida* Huxley & Jebb, subsp. nov.

Differt ab aliis subspeciebus *M. albertisii* tubere conico usque cylindrico, spinis c. 0,6 cm, validis, rubro-brunneis, lamina foliorum usque ad 19 × 6,5 cm, elliptica, apice late acuto, stipulis usque ad 0,7 cm longis. — Typus: Papua New Guinea, Jebb 163 (holo LAE).

Tuber conical to cylindrical, brown, to c. 24 × 11 cm. Spines stout, dark reddish brown. *Stem* unbranched; spines reddish. *Leaves*: Lamina 12 × 3 – 17 × 6.5 cm, elliptic; apex broadly acute; base cuneate. Petioles 3–5(–6) cm. Stipules 0.5–0.8 cm. *Inflorescence*: Flowers (2). Calyx c. 1 mm. Corolla 12 mm, lobes 2 mm tearing above the unci. Ring of hairs midway up tube. Anthers 3/4 way up tube, without blue-black flecks. Pollen 2-porate, 1-vesiculate, vesiculate aperture splayed, not thickened, vesicle large; reticulation fine. Stigma 4-lobed between hairs and anthers. Pyrenes 4 or 5, 4 mm long.

Ecology – In secondary or dry sclerophyll forest at 1200–1900 m.

Note – The morphological characters and geographical distribution of *Myrmecodia albertisii* subsp. *valida* are intermediate between subsp. *albertisii* and subsp. *incompta*. The duplicate of Carr 14659 at A belongs to *Anthorrhiza chrysacantha* Huxley & Jebb (Huxley & Jebb, 1991b), which is distinguished by its longer, fine spines, obconical corolla, and triporate pollen. Removal of the spines reveals the unpaired inflorescence characteristic of that genus.

Collections – PAPUA NEW GUINEA. SE 09° 05' 147° 38' Central Prov., Boridi, Carr 14659 p.p. (K, L, LAE, SING). 09° 08' 147° 40' Kokoda Trail, 1 km N of Efogi 2, Jebb 162 (L), 163 (type). 09° 09' 147° 40' N facing slope of mountain between Efogi and Launumu, LAE 60555 (A, L, LAE). 09° 09' 147° 41' near Launumu, LAE 52469 (A, L, LAE). Milne Bay Prov., Daga Subdist., Mt Mon, Bonenau Village, Gay 901 (L, LAE).

c. subsp. *incompta* Huxley & Jebb, subsp. nov. – Fig. 15d, e

Differt ab aliis subspeciebus *M. albertisii* tubere fusco spinas imbecillas, c. 0.8 cm longas gerente, foliis usque ad 32 × 6.2 cm, lamina anguste elliptica, apice acuto, stipulis usque ad 1.2 cm longis. — Typus: Papua New Guinea, *Menzies UPNG 3499* (holo UPNG; iso L).

Tuber reaching 41 × 13 cm, dark, glossy brown, cylindrical. Spines weaker and mostly longer than in the other subspecies, c. 0.8 cm. *Stem* unbranched, to 16 cm. *Leaves* 13 × 3.5 – 32 × 6.2 cm. Lamina narrowly elliptic; apex acute. Petioles 4.5–8 cm. Stipules 1.2 cm, dull brown. *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- (or 2-)vesiculate, aperture border not thickened; reticulation fine. Stigma broadly 4-lobed, between the anthers and the ring of hairs (or ? below the ring of hairs). Pyrenes 4.

Ecology – Rain forest to mossy forest; altitude 300–1600 m.

Note – The collections from Goodenough and Normanby Islands differ in leaf size, but are closely related. The collection from Missima is highly anomalous and may require separate nomenclature. Many of the stem spines and all of the tuber ones are simple; the leaf size and shape resemble *M. albertisii* subsp. *valida*; the stigma is at the anthers and there are six pyrenes.

Collections – Islands of Milne Bay Prov. SE 09° 19' 150° 15' D'Entrecasteaux Islands, Goodenough Is., NE slopes of Mt Oriadamawaia, UPNG 3499 (type). 09° 21' 150° 16' Goodenough Is., E slopes, Brass 24889 (A, L). 10° 39' 152° 48' Louisiade Archipelago, Missima Is., S slopes of Mt Sisa, Jebb 394 (LAE). Normanby Is., Mt Pabinama, Brass 25657 (A, L).

14. *Myrmecodia angustifolia* Valetton – Fig. 16

Myrmecodia angustifolia Valetton, Bot. Jahrb. 61 (1927) 144, in key. — Type: Irian Jaya, *Pulle 566* (lecto L).

Tuber 20 × 5 cm, oblong, drying blackish, hanging by up to 50 cm of root. Spines dense, brown, (simple) stellate-branched, on ridges, 0.5–1.4(–1.8) cm. Pores and entrance holes not apparent. Superficial chambers not developed. *Stem* solitary, usually unbranched, to 46 × 2 cm. Clypeoli indistinct. Alveoli elliptic with cushion-like masses of bract hairs. Spines dense to very dense, mostly irregularly or stellately

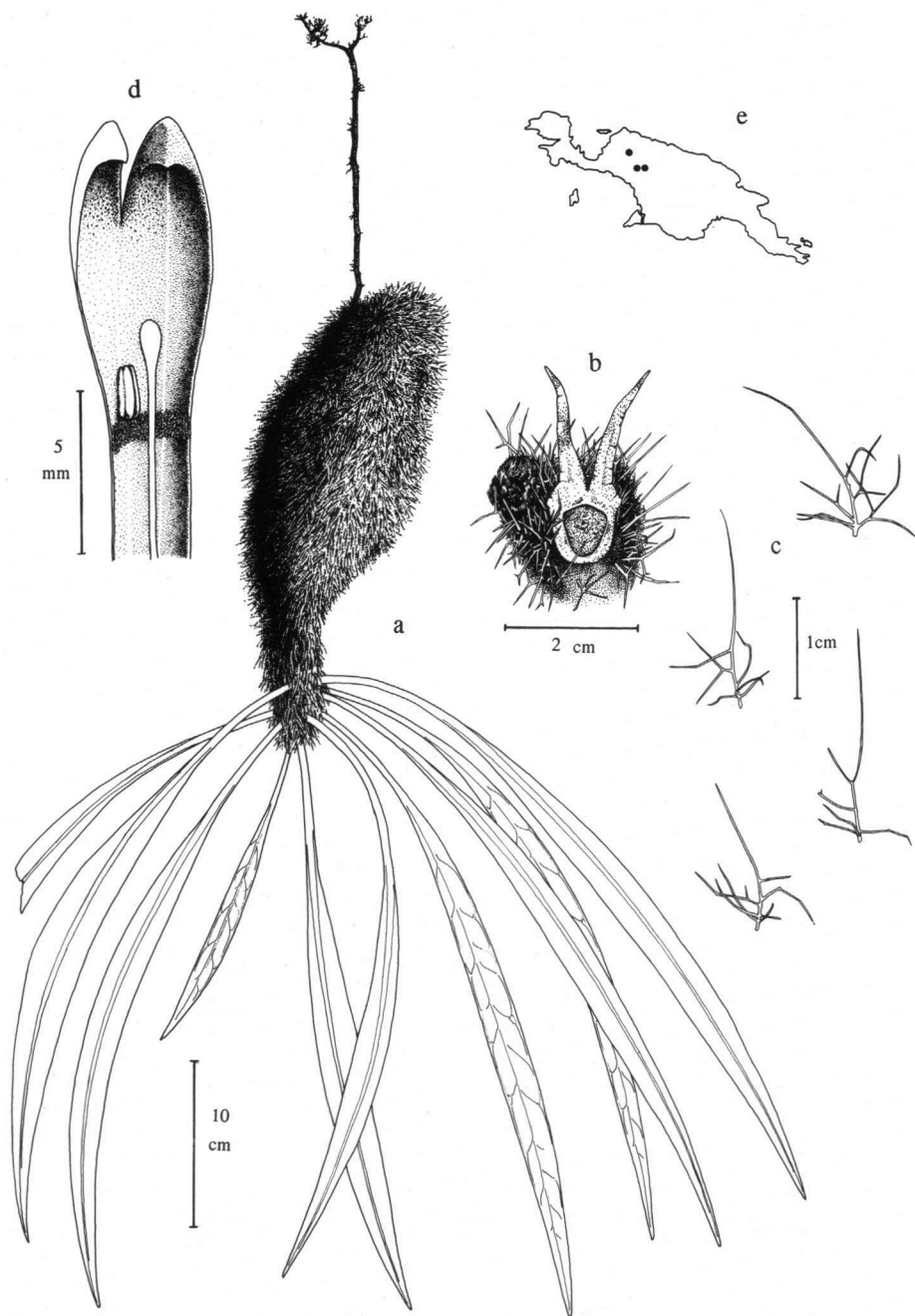


Fig. 16. *Myrmecodia angustifolia* Valetton. a. Habit; b. stem; c. stem spines; d. half flower; e. distribution. Drawn by Rosemary Wise.

branched, sometimes with central branch much longer than side branches. *Leaves*: Lamina to 45×2.3 cm, leathery, tapering gradually at both ends. Midrib prominent below; lateral veins obscure, 6–9. Petioles to 10 cm, bluntly triangular, red. Stipules c. 0.6 cm, united at the base only, forming a slight wing on the clypeoli. *Inflorescence*: Bracts dense, hairy. Flowers (1). Calyx 1.5 mm. Corolla 13 mm, white with blue-black flecks along margins of lobes below unci; lobes 3 mm; ring of hairs midway up tube. Anthers above and among hairs. Pollen 2-porate, 1-vesiculate, reticulation medium, germinating in closed flower. Stigma ? 4-lobed, above anthers. Fruit pink. Pyrenes 4.

Ecology – Forest from 300 to 1830 m altitude, abundant in higher part of range (Lam, 1924).

Notes – This species is characterized by its combination of \pm stellate spines and linear leaves. The very narrow tuber and red petioles make it distinctive. The corolla colour, pollen, and spines suggest a relationship with *M. albertisii*. The Lam specimen is immature and has many simple spines; the Jebb specimen differs in having a very long central branch to the spines, especially on stem and upper part of the stem.

Taxonomic note: The key given by Valeton (1927) makes an unambiguous diagnosis of *M. angustifolia*. The name is also written and signed by Valeton on both the Pulle specimens at L. The more complete of the two is selected as a lectotype.

Collections – IRIAN JAYA. SE 03° 20' 138° 20' hill near Doormantop, *Lam 1536* (BO). 04° 20' 138° 40' Mamberamo R., Perameles Bivak, *Pulle 471* (L), *566* (type). 04° 25' 139° 17' Baliem R., 8 km S of Ninya, *Jebb 119* (LAE).

15. *Myrmecodia sterrophylla* Merr. & Perry – Fig. 17

Myrmecodia sterrophylla Merr. & Perry, J. Arnold Arbor. 26 (1945) 28. — Type: Irian Jaya, *Brass 12138* (holo A).

Epiphytic or terrestrial. *Tuber* broadly cylindrical or conical, often curved downwards, ridged. Surface mostly greenish, smooth, swollen areas over honeycombing black with blocked pores. Spines on the ridges, or in clusters especially at base, simple, fine, black at the base, reddish or orange at the tip, 0.5–1.3 cm long. Pores appearing like lenticels because blocked. Entrance holes few. Superficial chambers dendroid. Warted chambers large, pale-walled. Smooth inner chambers forming a lattice. *Stem(s)* one to several unbranched, curved upwards, to 60×2.5 cm. Clypeoli distinct, longer than broad, to 1.5×1.2 cm. Alveoli hidden. Stem apex blunt, usually overtopped by spines. Spines rimming the clypeoli in a dense mass, simple, slender (stout), 0.5–1.3 cm long, orange or reddish brown. *Leaves* thick, leathery, or mesomorphic. Lamina 12×2.5 – 23×7 cm, narrowly elliptic to slightly oblanceolate; apex acuminate; base cuneate. Midrib prominent, rounded or triangular below. Lateral veins 8–13, more or as conspicuous above than as below when dry. Petiole 2–7 cm, rounded below, white, pink or red. Stipules to 1.9 cm long, narrowly triangular, persistent, as long as leaves. *Inflorescence*: Bracts inconspicuous, hairy. Flowers (8), heterostylous. Calyx 2–3 mm. Corolla white, 14 mm; lobes 3 mm; lobe tips 1 mm. Brevistyle flower (type); a narrow ring of 0.3 mm long hairs a quarter the way up the tube. Anthers towards apex of tube. Pollen 2-porate, 1- (or 2-) vesiculate; apertures slightly bordered; reticulation fine. Stigma half the way up the

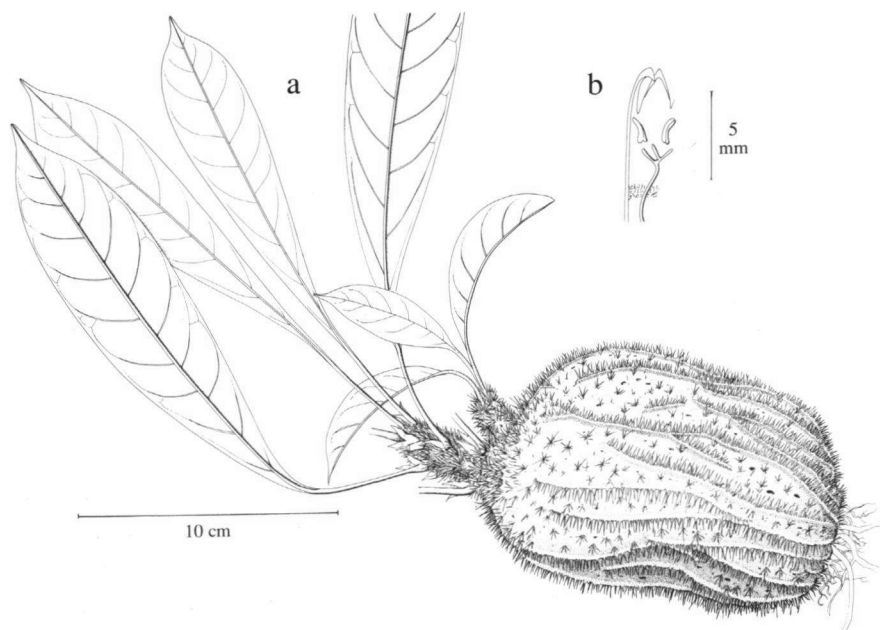


Fig. 17. *Myrmecodia sterrophylla* Merr. & Perry. a. Habit; b. half flower. Drawn by Rosemary Wise.

tube, 4-lobed. Longistyle flowers: hairs forming a narrow or 4 mm broad band or in 8 clusters in the upper half of the tube. Anthers among and/or above the upper part of the ring of hairs, 3 mm long; filaments 0.5 or 3 mm. Pollen 2-porate; 1- or 2-vesiculate; apertures bordered; reticulation fine. Stigma at apex of tube, above anthers, 6-lobed. Fruit red. Pyrenes (4-)6-8, curved towards the fruit axis.

Ecology – Epiphytic or terrestrial in nutrient poor, herbaceous vegetation, at 1500–2200 m altitude. At Bernhard Camp a high epiphyte in mossy forest.

Note – Specimens from a wide area are included here and the floral and pollen characters are rather variable. However, on vegetative characters, this appears to be a natural group. The material from Anggi Gigi differs in having 3-porate pollen; and the tuber of *Pulle 781* is unknown.

Collections – IRIAN JAYA. SE 01 22' 133 55' 2 km E of Anggi Gigi Lake, *Jebb 887* (LAE), 888 (BO). On summit of Anggi Gigi Mt, *Kostermans 2500* (BO). 03° 35' 139° 08' 15 km SW of Bernhard Camp, *Brass 12138* (type). 04° 28' 139° 16' Heluk Gorge, 5 km N of Holuwon, *Jebb 118* (L). 04° 40' 138° 40' Hellwig Gebirge Zuid, *Pulle 781* (L).

PAPUA NEW GUINEA. SE 05° 141' Western Prov., Upper Ok Tedi, *UPNG 3478* (K, UPNG 2 sh), *UPNG 3488* (L, UPNG), *UPNG 3489* (BRI, UPNG), *UPNG 3490* (L, UPNG). 05° 04' 141° 39' West Sepik Prov., 6 km N of Telefomin, on path to Elipatmin, *Jebb 251* (K, LAE 2 sh), 252 (UPNG). 05° 06' 141° 39' 2 km NE of Telefomin, on path to Elipatmin, *Jebb 240* (L, LAE 2 sh), 241 (A), 242 (BULOLO), 243 (BO). Mt Fubilan, Ok Tedi mine, Camp Edinburgh, *Gay 502* (FHO 2 sh, K, LAE).

16. *Myrmecodia oksapminensis* Huxley & Jebb, *spec. nov.*

Myrmecodiae sterrophyllae similis, praesertim cavitatis tuberis structura; spinae in tubere simplices, clypeoli rotundi; alveoli massis bractearum et pilorum protrudentibus referti; spinae alveolos et clypeolos marginantes simplices usque ramosae. — Typus: Papua New Guinea, *Jebb* 230 (holo LAE).

Tuber irregularly cylindrical, to 12 × 5 cm, dark grey with scattered blocked pores over honeycombing, other areas smooth, grey-green. Ridges running most of the length of the tuber but absent at the base. Spines on ridges or mounds, sometimes to mostly branched, fine, 0.5–0.8 cm, black. Warty chambers large, pale. Smooth inner chambers forming a lattice work. Flesh pink-purple. *Stem* solitary, unbranched, curving upwards. Base narrow for c. 1 cm. Clypeoli round, c. 0.7 cm across. Alveoli with dense protruding masses of reddish golden bracts and hairs. Spines fine, dark brown, simple to irregularly branched, c. 1 cm long. *Leaves*: Lamina 10 × 3.5 to 17 × 4.5 cm, oblanceolate; apex abruptly acuminate; base cuneate, leathery. Lateral veins 6–8, obscure when dry; midrib sharply prominent below. Petioles 4–7 cm, deep red. Stipules c. 1 cm, reddish brown. *Inflorescence*: Flowers (2). Corolla 13 mm, lobes 5 mm, lobe tips 1 mm, a narrow ring of hairs 4 mm from base of tube, with lines of hairs between the anthers. Anthers just above hairs, 3 mm long, with blue-black flecks throughout. Pollen 2-porate, 2-vesiculate, apertures the thickened borders; reticulation fine. Stigma just below unci, 4-lobed. Fruit? Pyrenes?

Ecology — In tall open forest on steep limestone slopes; altitude 1890 m.

Notes — The tuber structure, flowers and pollen suggest a relationship with *M. sterrophylla*, but the occurrence of branched spines, prominent cushions of bract hairs and isodiametric clypeoli indicate a distinct taxon.

Collections — PAPUA NEW GUINEA. SE 05° 13' 142° 12' West Sepik Prov., S of the road to Tekin, 3 km W of Oksapmin, *Jebb* 221 (K), 230 (type), 231 (L), 232 (UPNG), 233 (BULOLO), 545 (LAE).

17. *Myrmecodia paradoxa* Huxley & Jebb, *spec. nov.*

Myrmecodiae sterrophyllae similis, praesertim cavitatis tuberis structura; distinguitur clypeolis prominentibus armatis denso ordine spinarum simplicium (pro parte maxima 0.5–0.8 cm longarum), et stigmate infundibuliformi. — Typus: Papua New Guinea, *Jebb* 249 (holo LAE).

Tuber pendent, irregularly cylindrical, 15 × 8 cm, ridged, dark brown. Spines simple mostly on ridges, fine, dark brown, 0.4–0.7 cm long. Semicircular arcs of entrance holes. Pores present. Cavities like *M. sterrophylla*. *Stem* solitary, unbranched, ascending, tapered over 3–4 cm at apex. Clypeoli very prominent, longer than wide, densely rimmed by simple spines, to 1 cm long. *Leaves* clustered at stem apex. Lamina 13 × 4 – 19 × 4 (–4.5) cm, elliptic, apex acuminate, base cuneate. Midrib prominent below, lateral veins 6–8. Petiole 2–4 × 0.2–0.3 cm. Stipules usually broken to 0.4 cm when the leaves fall, chestnut brown. *Inflorescence*: Bracts rim-like, brown hairs short. Flowers (1 immature). Calyx 2 mm, truncate. Anthers above ring of hairs. Pollen 1- or 2-vesiculate, wall thin, aperture not bordered; reticulation fine. Stigma above anthers, funnel-shaped. Fruit red. Pyrenes 7 or 8.

Ecology — Low epiphyte on *Casuarina* or montane forest; 1720–1880 m altitude.

Notes — This species is superficially similar to *M. platytyrea*, but examination of the tuber reveals the wide warty chambers surrounded by open network areas of

smooth chamber, similar to those of *M. sterrophylla*. This tuber structure and the clypeol it shares with the little known species from Lake Wissel, but the stipules, stigma, and pollen are quite different.

Myrmecodia paradoxa grows with *M. sterrophylla* from which it is distinguished by its broader clypeoli, neatly rimmed by shorter (0.5–0.8 cm) spines which tend to lie in the same plane as the clypeolus, the stem apex is tapered over 3–4 cm, not overtopped by spines, and the tuber spines are shorter (mostly 0.4–0.7 cm). The leaf with petiole is 12–22 cm long, as opposed to 20–32 cm in *M. sterrophylla*.

Collections – PAPUA NEW GUINEA. SE 05° 04' 141° 39' West Sepik Prov., 6 km NE of Telefomin on path to Eliptamin, *Jebb* 249 (type), 250 (L), 252 (A). 05° 06' 141° 39' 2 km NE of Eliptamin, *Jebb* 259 (LAE).

18. *Myrmecodia aureospina* Huxley & Jebb, *spec. nov.*

Myrmecodiae sterrophyllae similis, praesertim cavitatis tuberis structura; distinguitur spinis brevibus, validis, stellatis usque irregulariter ramosis, et pilis bractearum aliquando prominentibus. — Typus: New Guinea, *Kalkman* 4268 (holo L; iso LAE).

Tuber pendent, to 50 × 20 cm, cylindrical, ridged, part of surface dark brown, part of surface pale grey-green. Spines on ridges, golden, 0.7–1.1 cm, robust, irregularly stellate, central branch often much longer than side branches. Superficial chambers dendroid, warted tunnels wide and pale, inner smooth walled chambers highly dissected. *Stems* solitary to few, unbranched, to 90 × 1.5 cm. Spines dense, as on tuber or slightly larger. *Leaves*: Lamina 20 × 3.5 – 27 × 6.5 cm, leathery, oblanceolate to narrowly ovate; apex narrowly long-acuminate. Petiole 2–3.5 cm. Stipules c. 1.4 cm, narrowly triangular, drying reddish. *Inflorescence*: Corolla with blue-black flecks on inner surface below unci. Flowers (5) heterostylous; in longistyle flowers (4) hairs forming a broad band midway up the tube. Anthers among hairs. Stigma either 4-fid halfway up lobes, or bifid just below unci. Pollen 1- (or 2-)vesiculate, slightly thickened aperture borders; reticulation fine. In brevistyle flower hairs lower in tube, forming a narrow band; anthers at apex of tube. Pollen 1-vesiculate, borders not thickened; reticulation fine. Stigma 4-fid, above ring of hairs.

Ecology – In lowland forest, stunted forest on white sand, or *Araucaria* forest; 160–2300 m altitude, sometimes terrestrial.

Note – The golden, stellate to irregularly branched spines of *M. aureospina* resemble those of *M. albertisii* and *M. schlechteri*. However, the tuber cavities resemble those of *M. sterrophylla*, with dendroid cavities, wide, pale-walled, warted tunnels and highly dissected, not shelf-like inner smooth-walled cavities. *Myrmecodia aureospina* can be distinguished externally from *M. albertisii* by the narrower leaves, narrow stipules and the tuber surface which is partly very dark brown, partly pale grey-green. The five populations included under *M. aureospina* vary considerably and three subspecies may need to be recognized.

Collections – IRIAN JAYA. SE 04° 30' Baliem Valley, Holluwon, *Jebb* 116 (BO, L). 04° 55' 140° 37' Star Mts, Sibil Valley, *Kalkman* 4268 (type).

PAPUA NEW GUINEA. SE 05° 04' 141° 39' West Sepik, 5 km NE of Telefomin on path to Eliptamin, *Jebb* 253 (LAE 2 sh), 254 (A, L 2 sh), 255 (K), 256 (UPNG), 257 (BULOLO, FHO). 05°

13' 142° 12' 3 km W of Oksapmin, S of road to Tekin, *Jebb* 223 (LAE), 224 (L), 225 (BULOLO), 226 (A), 227 (BRI), 228 (BO). Near summit of Mt Dekempkin, on track from Telefomin to Elip-tamin, Gay 536 (K, L, LAE). 05° 38' 141° 00' Western Prov., Ingembit Village, *Henty*, *Riddsdale* & *Galore NGF 1855* (A, BRI, CANB, K, LAE not seen).

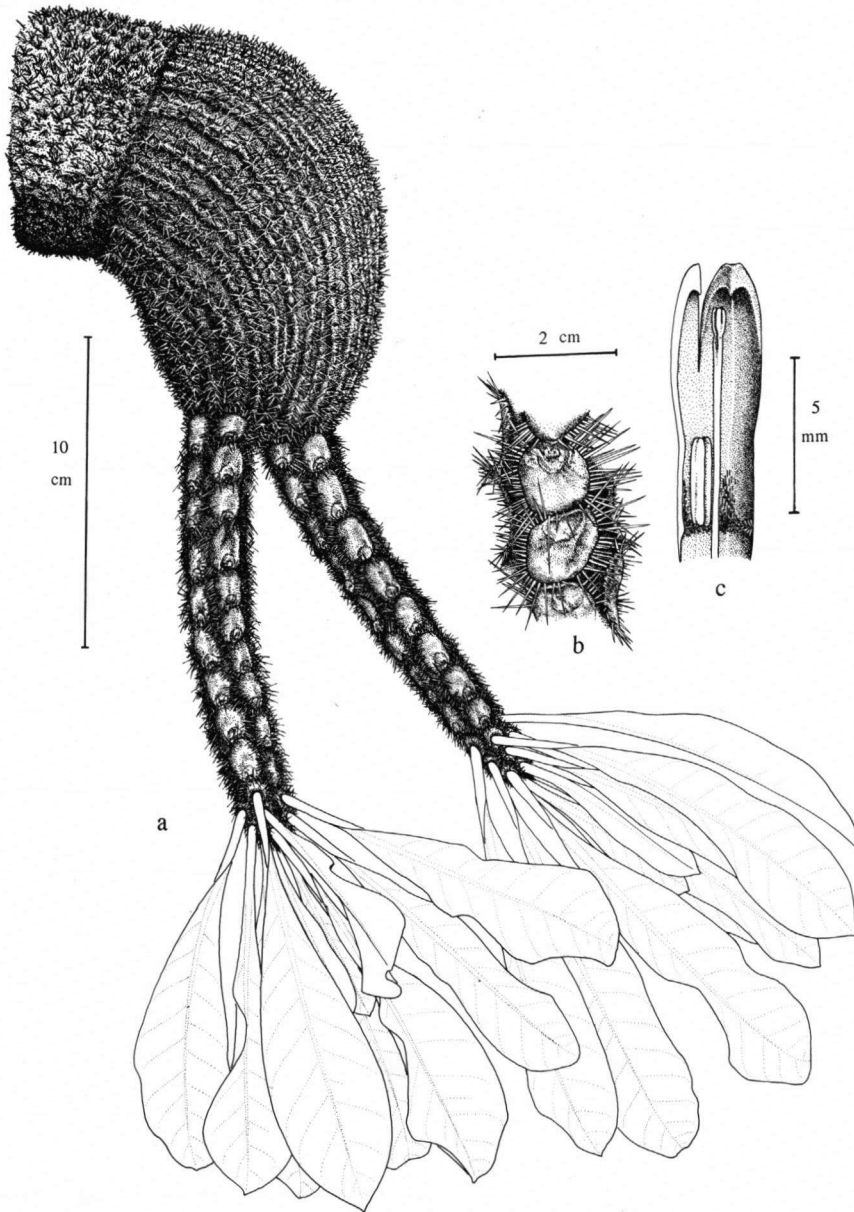


Fig. 18. *Myrmecodia brassii* Merr. & Perry. a. Habit; b. stem; c. half flower. Drawn by Rosemary Wise.

19. *Myrmecodia brassii* Merr. & Perry — Fig. 18

Myrmecodia brassii Merr. & Perry, J. Arnold Arbor. 26 (1945) 28. — Type: Irian Jaya, Brass 9446 (holo A; iso BM, BO, BRI, L; LAE photo).

Epiphyte, rarely terrestrial. *Tuber* cylindrical when young, older tubers 'humpbacked' with two distinct parts: Basal part typically horizontal, not ridged, drying dark brown, rough; spines in compact clusters which are not spreading and not on mounds; spines simple, straight, broad, c. 0.6 cm. Apical part of tuber ridged, drying shiny black; spines on ridges and in spreading clusters on mounds, simple, fine, often curved, 0.5–1.5 cm. Pores not seen. Entrance holes not seen. Superficial chambers slightly dendroid. *Stems* several, unbranched, curved upwards or straight, c. 17 × 2.2 cm. Clypeoli circular or slightly elongate, c. 1.2 cm across. Alveoli distinct. Spines densely inserted on clypeoli margins and basal edge, simple, fine, often curved, 1(–2) cm, black. *Leaves* leathery. Lamina 11 × 2.5 – 15 × 3.6 (– 26 × 4) cm, broadest 3/4–4/5 the way along the lamina; apex broadly acute; base tapering. Midrib prominent below. Lateral veins 9–11, rather obscure. Petioles triangular, 1–2(–4) cm, white. Stipules c. 0.8(–2) cm long, narrow, usually falling before the leaves. *Inflorescence*: Bracts hairy, inconspicuous. Flowers (2). Calyx 3 mm. Corolla white, 12 mm; lobes 4 mm; lobe tips 1 mm. A broad ring of hairs midway up the tube. Anthers blue, among and above hairs; filaments 0.5 mm. Pollen 3-porate, 3-vesiculate, vesicles small, apertures slightly bordered; reticulation fine. Stigma midway up corolla lobes, 4–6-lobed. Pyrenes 4–6.

Ecology — Epiphytic in upper montane forest and lower subalpine forest at 2100–3600 m, seldom terrestrial, often associated with *M. lamii*.

Notes — *Myrmecodia brassii* resembles the often terrestrial *M. lamii* in its bipartite tuber and numerous unbranched clypeolate stems with short, clustered leaves. The absence of broad persistent stipules winging the clypeoli readily distinguishes it, however. The flowers and pollen are also distinctive.

Young plants with only one stem and lacking the tuber differentiation and flowers might be confused with *M. archboldiana* or *M. sterrophylla*. The leaves of *M. brassii* can be distinguished, though, as they are widest close to the broadly acute apex.

Collections — IRIAN JAYA. SE 03° 50' 137° 50' Kemabu Plateau, 15 km N of Carstensz Mts, Hope ANU 16059 (CANB not seen, L). 04° 09' 138° 40' Lake Habbema, 3225 m Camp, Brass 9446 (type). 04° 22' 139° 05' Baliem R., 15 km from Soba, Jebb 120 (LAE).

20. *Myrmecodia lamii* Merr. & Perry — Fig. 19

Myrmecodia lamii Merr. & Perry, J. Arnold Arbor. 26 (1945) 27. — Type: Irian Jaya, Brass 9445 (holo A; iso BM, BO, BRI, G, K, L; LAE photo).

Often terrestrial, standing erect, when epiphytic usually smaller. *Tuber* relatively elongate and projecting horizontally and sometimes curving downwards c. 70 × 45 cm. Basal part of tuber with a thick unridged wall; spines not spreading, in dense clusters which are not on mounds, spines simple (branched), thick, 0.6–0.8 cm long. Apical part of tuber with thin walls, ridged; spines on ridges or in spreading clusters on mounds, simple, fine, sometimes bristle-like, 1–2(–3) cm. Entrance holes and pores not seen. *Stems* 8–16, unbranched, upturned, at least at tip, to 100

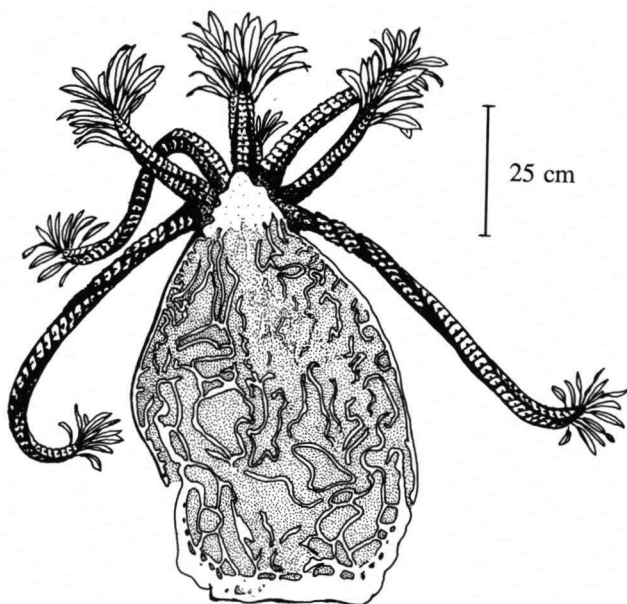


Fig. 19. *Myrmecodia lamii* Merr. & Perry. Habit, with tuber sectioned. Drawn by Eleanor Catherine.

$\times 2.5$ cm. Clypeoli prominently winged to half their length. Alveoli shallow, hidden. Spines in small clusters on the lower margins of the clypeoli, simple, bristle-like, to 1.7 cm. *Leaves* densely clustered at stem apices. Lamina $9 \times 2 - 20 \times 5$ cm, leathery, oblanceolate; apex broadly acute or shortly acuminate; base tapered. Midrib prominent, rounded below; lateral veins 10–12. Petioles white or pale green, 1–2 cm. Stipules divided to base, c. 1.1 cm long with a 0.5 cm wide wing around the upper part of the clypeoli, drying dark, glossy grey. *Inflorescence*: Bracts small, hairy. Flowers (2). Corolla white or pale blue, glabrous, 12 mm, lobes 4 mm; lobe tips 1 mm. Anthers in upper part of tube, 2.5 mm; filaments 0.5 mm. Pollen 3-porate, vesicles absent, apertures not bordered; reticulation coarse. Stigma just above anthers, 4-lobed. Pyrenes 4.

Ecology – Epiphytic in medium or stunted forest, or terrestrial, especially above the tree-line, 1900–3600 m. Often associated with *M. brassii* when epiphytic (Lam, 1924).

Notes – This species shares with *M. brassii* the bipartite tuber and numerous stems but the clypeoli have broad dark grey wings. The spine and tuber differentiation suggest a close relationship with *M. brassii*, while the 3-porate pollen and glabrous corolla suggest affinity with *M. archboldiana*. Although the winged clypeoli are reminiscent of *M. pteroaspida*, the floral and tuber 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. Valetton, but the name was not published.

Collections — IRIAN JAYA. SE 03° 30' 138° 26' Doormantop, *Lam* 1804 (BO, L). 03° 59' 138° 46' 18 km NE of Lake Habbema, 2200 m Camp, *Brass* 11554 (A, BO, L). 04° 01' 138° 43' 9 km NE of Lake Habbema, 2800 m Camp, *Brass* 10689 (A, BO, BRI, L). 04° 03' 138° 41' Lake Habbema, 3225 m Camp, *Brass* 9445 (type). 04° 20' 138° 40' Wichmansberg, *Pulle* 1058 (L).

21. *Myrmecodia archboldiana* Merr. & Perry

Myrmecodia archboldiana Merr. & Perry, J. Arnold Arbor. 26 (1945) 29. — Type: Irian Jaya, *Brass* 11216 (holo A; iso BO, BRI, L).

Tuber hanging downwards, conical, bottle-shaped or cylindrical, drying dark brown, c. 30 × 16 cm. Spines on ridges or in spreading clusters on mounds, simple, narrow and finely tapered, but stiff, pale brown, 0–6 – 1.2(–1.8) cm. Pores present over slightly dendroid superficial chambers. Entrance holes not seen. Dendroid superficial chambers. *Stem* solitary, unbranched, straight, probably hanging downwards, c. 20 × 1.2 cm. Clypeoli drying with prominent 'shoulders'. Spines dense, spreading, on clypeoli margins, simple, or irregularly branched, weak. *Leaves* leathery. Lamina 15 × 2 – 30 × 4 cm, narrowly oblanceolate, widest 1/2–3/4 along the lamina; apex acute; base tapering. Midrib reddish. Lateral veins 10–20. Petioles red, 2–9 cm. Stipules c. 0.5 cm, soon falling. *Inflorescence*: Bracts inconspicuous. Flowers (3). Corolla glabrous, 12 mm; lobes 4 mm; lobe tips 0.5 mm. Anthers at apex of tube, 2–3 mm; filaments 1 mm. Pollen 3-porate, vesicles small, 3, apertures not bordered; reticulation coarse. Stigma at or below anthers, 2(–4)-lobed. Pyrenes 2–4.

Ecology — In mossy and stunted forest on oaks, and on other trees in secondary forest; altitude 1800–220 m.

Note — The stem characters and clustered tuber spines are similar to those of *M. brassii*, while floral characters resemble *M. lamii*. However, the single stem and large tuber cavities are very different. The little-known species from Doormantop is similar.

Collections — IRIAN JAYA. SE 03° 30' 139° 00' 15 km SW of Bernhard Camp, Idenburg R., *Brass* 12047 (A, BO, L). 04° 04' 138° 46' 18 km NE of Lake Habbema, *Brass* 11216 (type). Baliem Valley, Wellesey, *Kostermans & Soegeng* 752 (A, BO, K, L).

22. *Myrmecodia pteroaspida* Huxley & Jebb, *spec. nov.* — Fig. 20

Myrmecodia lamii imitatur clypeolis alas prominentes brunneas vel argenteo-nigras gerentibus quae ab stipulis usque ad 1/2–2/3 circum clypeolos excurrunt quae ab stipulis excurrente 1/2 usque ad 2/3 clypeolorum ambiunt; distinguitur caulibus una vel duabus, tubere uniformi (non bipartito), corolla annulo pilorum instructa, polline 2-porato. — Typus: Papua New Guinea, UPNG Huxley & Worthing 3461 (holo UPNG; iso A, K, L).

Tuber c. 18 × 10 cm, irregularly cylindrical, grey, slightly downward pointing. Ridges prominent. Spines on ridges and on mounds, simple, stout, black, conical, 0.3–0.6 cm. Pores irregularly present on swollen areas over dendroid chambers. Entrance holes generally few, 2–4 at apex of tuber close to stem. *Stems* 1 or 2, unbranched, ascending, c. 19 × 2 cm. Clypeoli 1.7(–2.5) × 1.5 cm; upper third to half winged by brown, drying glossy grey, extensions of the stipules, c. 0.6 cm wide; central and lower part of clypeoli green drying matt brown. Alveoli concealed by clypeoli. Spines few on the edges and rarely the median ridge of the clypeoli, simple. *Leaves* clus-

tered at apex of stem, somewhat leathery, bright green. Lamina $7.5 \times 3 - 14 \times 5.5$ cm, spatulate; apex acuminate. Midrib prominent below, pale green. Lateral veins 7–10. Petioles slightly winged, 0.5–1 cm long, white. Stipules 1.5 cm, divided to base, triangular, persistent. *Inflorescence*: Bracts inconspicuous, hairy. Flowers (2). Calyx 2 mm. Corolla 11 mm; lobes 4–5 mm; lobe tips 1 mm; narrow ring of hairs near base of tube. Anthers at apex of tube, blue, 2 mm; filaments 1 mm. Pollen 2-porate, 1- or 2-vesiculate, apertures unbordered; reticulation medium. Stigma at anthers, 4- or 5-lobed. Pyrenes 5 or 6.

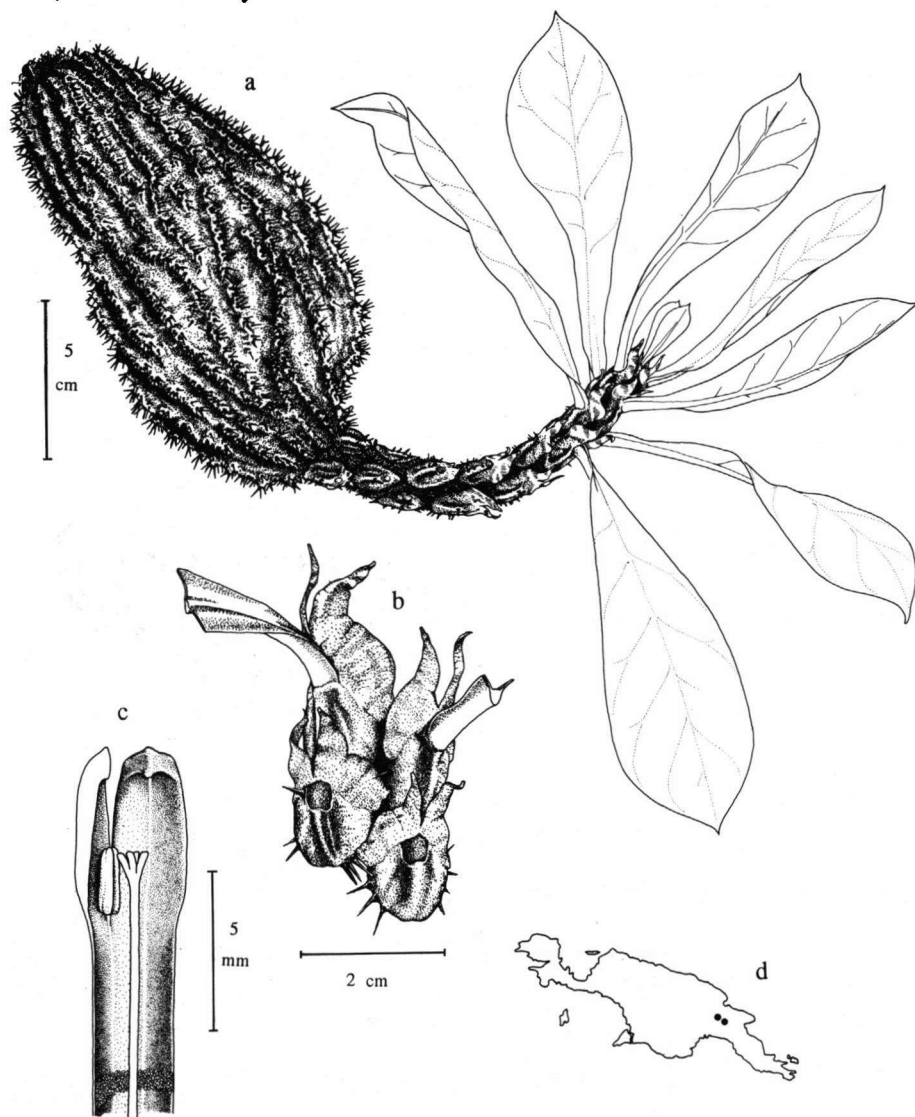


Fig. 20. *Myrmecodia pteroaspida* Huxley & Jebb. a. Habit; b. stem; c. half flower; d. distribution. Drawn by Rosemary Wise.

Ecology — In secondary forest and forest margins; altitude 1600–2300 m.

Note — This species resembles *M. lamii* in its winged clypeoli, but differs in tuber structure and pollen type. The stout black spines are similar to those of the *M. melanacantha* group. Apical entrance holes are sometimes found in *M. platytyrea*.

Collections — PAPUA NEW GUINEA. SE 06° 01' 145° 24' Eastern Highlands, Mt Gahavisuka National Park, *Jebb* 603 (LAE), 604 (FHO). 06° 22' 145° 17' Mt Michael, near Lufa, *Jebb* 105 (A), 107 (L). 06° 30' 145° 32' near Okapa, c. 45 km S of Goroka, UPNG 3460 (UPNG), UPNG 3461 (type). 06° 43' 145° 37' 22 km S of Okapa, Lamari Gorge, *Jebb* 92 (LAE), 95 (K).

23. *Myrmecodia melanacantha* Huxley & Jebb, *spec. nov.* — Fig. 21

Cuniculi intracaulini jugunt cava tuberis cum alveolis; clypeoli obscuri; alveolorum labra elevata, tumida, parallela ad superficiem caulis; spinae in labris alveolorum breves, validae, nigrae; folia elliptica usque oblancoolata, basi cuneata; petiolus viridus vel albus (ruber), 1–2(–3) cm longus. — Typus: Papua New Guinea, *Jebb* 85 (holo LAE).

Tuber upright or horizontal, irregularly ellipsoid or ovoid, to 22 × 14 cm, grey, smooth with black areas, rough with blocked pores over the swollen dendroid chambers to 2 cm apart, running less than half the length of the tuber. Spines simple, stout, black, usually on ridges or black swellings, 0.5–0.9 cm. Pores blocked; entrance holes absent. Warted chambers large, pale. Inner smooth chambers forming a lattice. *Stem* solitary, sometimes branched, horizontal, 1.8–2.5 cm across to 30 cm long. Tuber cavities connecting with the alveoli by four tunnels. Clypeoli indistinct, scarcely raised from the tuber surface. Alveoli rounded with swollen rims raised 0.4 cm off the stem surface and parallel to it. Spines simple, stout, black, mostly on alveoli and clypeoli rims. Four tunnels running the length of the stem interconnect to alveoli. *Leaves* clustered at stem apex. Lamina 13 × 3.5–17 × 6 cm, elliptic to obovate; apex acute to acuminate; base cuneate. Midrib green (red), rounded or triangular below. Lateral veins 6–9, obscure below. Petioles 1–2(–3) cm, green-white (red). Stipules c. 1 cm, strap-shaped, falling before or soon after they have split. *Inflorescence*: Bracts scale-like. Flowers (7). Calyx 1–2 mm. Corolla 10–15 mm; lobes 3–4 mm; lobe tips 1 mm. Ring of hairs c. 1 mm wide, a third the way up the tube. Anthers at apex of tube. Pollen 2-porate, 2-vesiculate, borders thickened; reticulation medium or coarse. Stigma indistinctly 7-lobed, at anthers (or just above the hairs). Fruit red, 2 cm long. Pyrenes 7 or 8, yellow when fresh.

Ecology — Primary and secondary montane forest at 1700–2400 m altitude.

Note — This and the following three species form a closely related group characterized by the fact that the tuber cavities are connected by tunnels in the stems to the alveoli. These four species are also distinguished by the simple, stout, short, dark spines on the tuber and stems. The species are sympatric but prefer different altitudinal ranges, they are confined to the central highland area of Papua New Guinea. Characters of the tuber, stem, leaf, and pollen distinguish the four species, though the definition is not sharp.

Collections — PAPUA NEW GUINEA. SE 05° 04' 141° 39' West Sepik, 6 km NE of Telefomin on path to Eliptamin, *Jebb* 247 (LAE), 248 (L). 05° 13' 142° 12' 3 km W of Oksapmin, S of road to Tekin, *Jebb* 222 (LAE), 229 (L). 05° 29' 143° 30' Enga Prov., 3 km along road to Wabag from Laigam, *Jebb* 297. 05° 30' 144° 12' Western Highlands, Jimmi divide, on road from Baiyer R. to

the Jimmi Valley, *Jebb* 593 (LAE), 594 (K), 595 (A). 05° 48' 145° 10' Madang Prov., Bundi Sub-dist., on road from Kegelsugul to Bundi, *Jebb* 38 (A), 42 (BO), 43 (BULOLO), 44 (LAE), 68 (FHO), 71 (BULOLO), 76 (CANB), 79 (CANB), 82 (BRI), 84 (K), 85 (type), 87 (L). 05° 51' 144° 17' Western Highlands, near Wirup, N of Kubor Ra., *Jebb* 601 (LAE). 05° 57' 143° 59', E of Mt Giluwe, 10 km SSE of Tambul, on road to Lalibu, *Jebb* 196 (LAE), 197 (L), 198 (A), 200 (LAE). 06° 01' 145° 26' Eastern Highlands, Goroka Trout Farm, N of Goroka, *Jebb* 91 (LAE). 06° 03' 145° 15' Daulo Pass, 200 m on Goroka side of buildings at top of Pass, *Huxley, Worthing & Turton UPNG* 3458 (L 2 sh, UPNG).



Fig. 21. *Myrmecodia melanacantha* Huxley & Jebb. Habit. Drawn by Eleanor Catherine.

24. *Myrmecodia horrida* Huxley & Jebb, *spec. nov.* — Fig. 22

Differt a *Myrmecodia melanacantha* labris alveolorum a caule eminentibus, foliis obovatis, et petiolis rubris, 3–6 cm longis. — Typus: Papua New Guinea, *Jebb 80* (holo LAE).

Tuber irregularly cylindrical, to 26 × 14 cm. Ridges to 4 cm apart, running almost the length of the tuber. Surface grey-green when young, later grey-brown, with numerous lenticel-like blocked pores which are sunken when live and raised when dry.

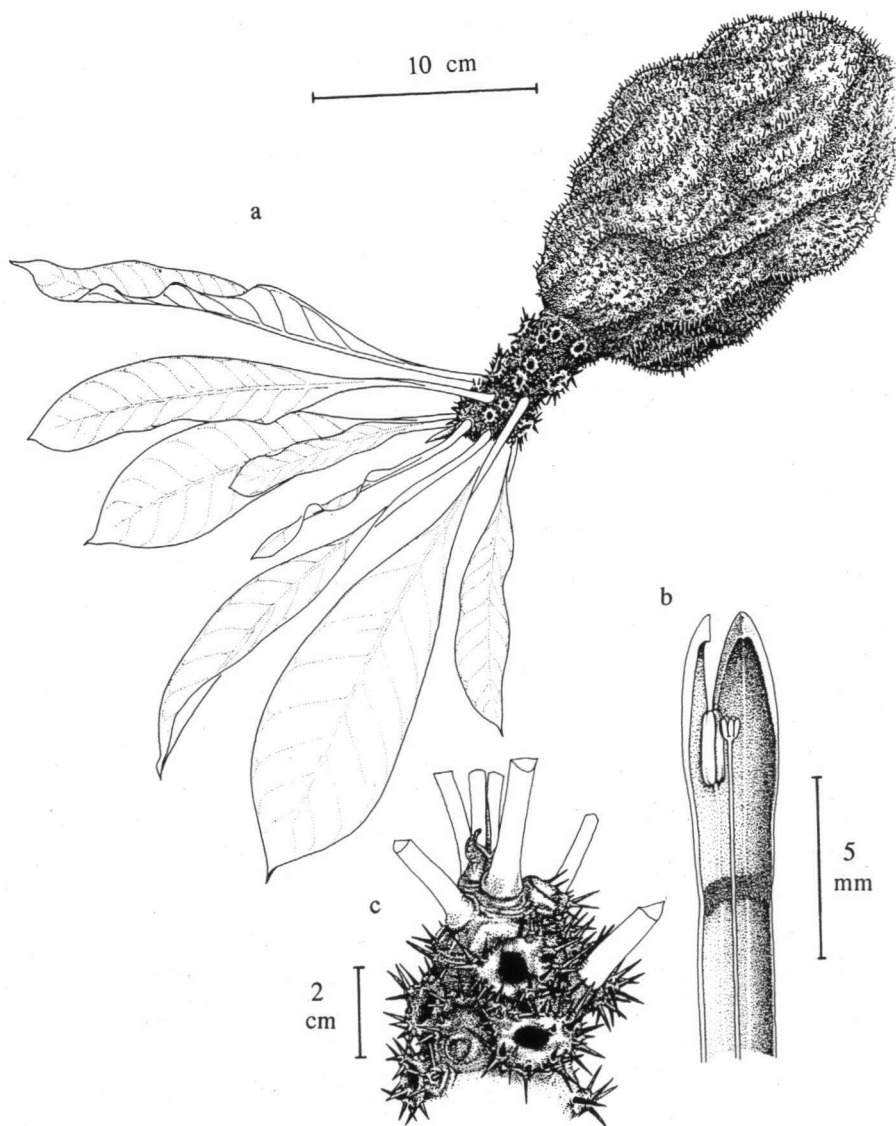


Fig. 22. *Myrmecodia horrida* Huxley & Jebb. a. Habit; b. stem; c. half flower. Drawn by Rosemary Wise.

Spines mainly on ridges, simple, stout, black, with rounded flattened bases, 0.4–0.8 cm. Superficial chambers little developed. Tunnels connect the tuber cavities to the alveoli. *Stem* solitary, unbranched, horizontal to ascending, 1.5–3.8 cm across. Clypeoli absent. Alveoli round with swollen red-brown rims, prominently raised at an angle to the stem. Spines mostly on the alveoli rims, those on the outer edges being parallel to the stem. Tunnels within the stem interconnect the alveoli. *Leaves*: Lamina 11 × 4 – 18 × 9 cm, obovate; apex acute to acuminate; base tapering. Midrib rounded below, red. Lateral veins 8 or 9, prominent below. Petioles (2–)3–6 cm, red. Stipules c. 1 cm, soon falling. *Inflorescence*: Flowers (5). Corolla 14 mm; lobes 3–4 mm; lobe tips 1–2 mm; ring of hairs (1/3–)1/2 the way up the tube. Anthers at apex of tube. Pollen 2- or 3-porate, 2- or 3-vesiculate, apertures slightly bordered; reticulation fine (coarse). Stigma at (above) anthers, irregularly lobed. Fruit red. Pyrenes 8.

Ecology – Disturbed and secondary montane forest at 1900–2400 m altitude.

Note – This species is closely related to *M. melanacantha*, but is more massively built, the spines are shorter and stouter. The alveoli rims are prominently swollen and set at an angle to the stem. The stem is stouter and unbranched, and the petioles are longer. *Myrmecodia ferox* is also similar, see there.

Collections – PAPUA NEW GUINEA. SE 05° 30' 144° 12' Western Highlands, Jimmi divide, on road from Baiyer R. to the Jimmi Valley, *Jebb 596* (LAE). 05° 45' 145° 10' Madang Prov., Bundi Subdist., road to Kegelsugul, *Jebb 73* (L), 77 (K), 78 (A), 80 (type), 83 (LAE), 86 (LAE). 05° 56' 143° 58' Western Highlands, Hagen Subdist., Kepaka, Upper Kaguel, Alipe Many, *Bowers 463* (K, LAE 2 sh). 05° 56' 143° 58' Hagen Subdist., Kepaka, Upper Kaguel, Alipe Creek, *Bowers 883* (LAE). 05° 57' 143° 59' E of Mt Giluwe, 10 km SSE of Tambul, on road to Lalibu, Kiripia Mission, *Jebb 194* (FHO, L), 195 (LAE 2s h). 06° 01' 145° 26' Eastern Highlands, Goroka Trout Farm, *UPNG 5939* (UPNG); *Jebb 90* (LAE). 06° 07' 145° 00' Chimbu, Kundiawa, Sinasina, c. 1.5 km SW of Koge Mission, *Hide 239* (LAE). 06° 08' 145° 51' Eastern Highlands, c. 20 km N of Kainantu, *Sayers 46* (K). 06° 10'–20' 143° 50'–59' Southern Highlands, Lalibu Subdist., SE of Mt Giluwe, near Onim, *UPNG 3476* (BULOLO, L, UPNG). 06° 12' 143° 57' on Mt Hagen to Mendi road, 10 km before Onim, *Jebb 583* (LAE), 584 (K). 06° 41' 154° 34' Eastern Highlands, Okapa Subdist., near Parosa, near Mt Taniloa, 2 km SSE of Ai, *Jebb 100* (LAE). 07° 13' 146° 30' Morobe, Aseki divide, on road from Bulolo to Aseki, *Jebb 570* (LAE).

25. *Myrmecodia ferox* Huxley & Jebb, *spec. nov.*

Differt a *Myrmecodia melanacantha* et *M. horrida* foliis longioribus, angustioribus, basi sensim attenuatis, spinis sparsis, longioribus, et corolla glabra. — Typus: Papua New Guinea, *Jebb 299* (holo LAE).

Tuber semi-pendent, irregularly cylindrical to slightly wider at base than at apex, curved, 28 × 14 cm, black over raised dendroid areas, pale grey-green in between. Ridges sometimes running the whole length of the tuber. Spines simple, stiff, black, on ridges or scattered on dark bosses which become contiguous along the ridges. Entrance holes few. Pores blocked. Dendroid superficial chambers over upper surface. *Stem(s)* one (or two), unbranched, hanging downwards or upcurved, to 25 cm long and 2.5 cm wide. Spines stout, black, 0.5–1.4 cm long, mainly around alveoli, also around leaf bases and scattered. Clypeoli absent. Alveoli with thick prominent rims. Tunnels run along the stem connecting the tuber cavities to the alveoli. *Leaves*

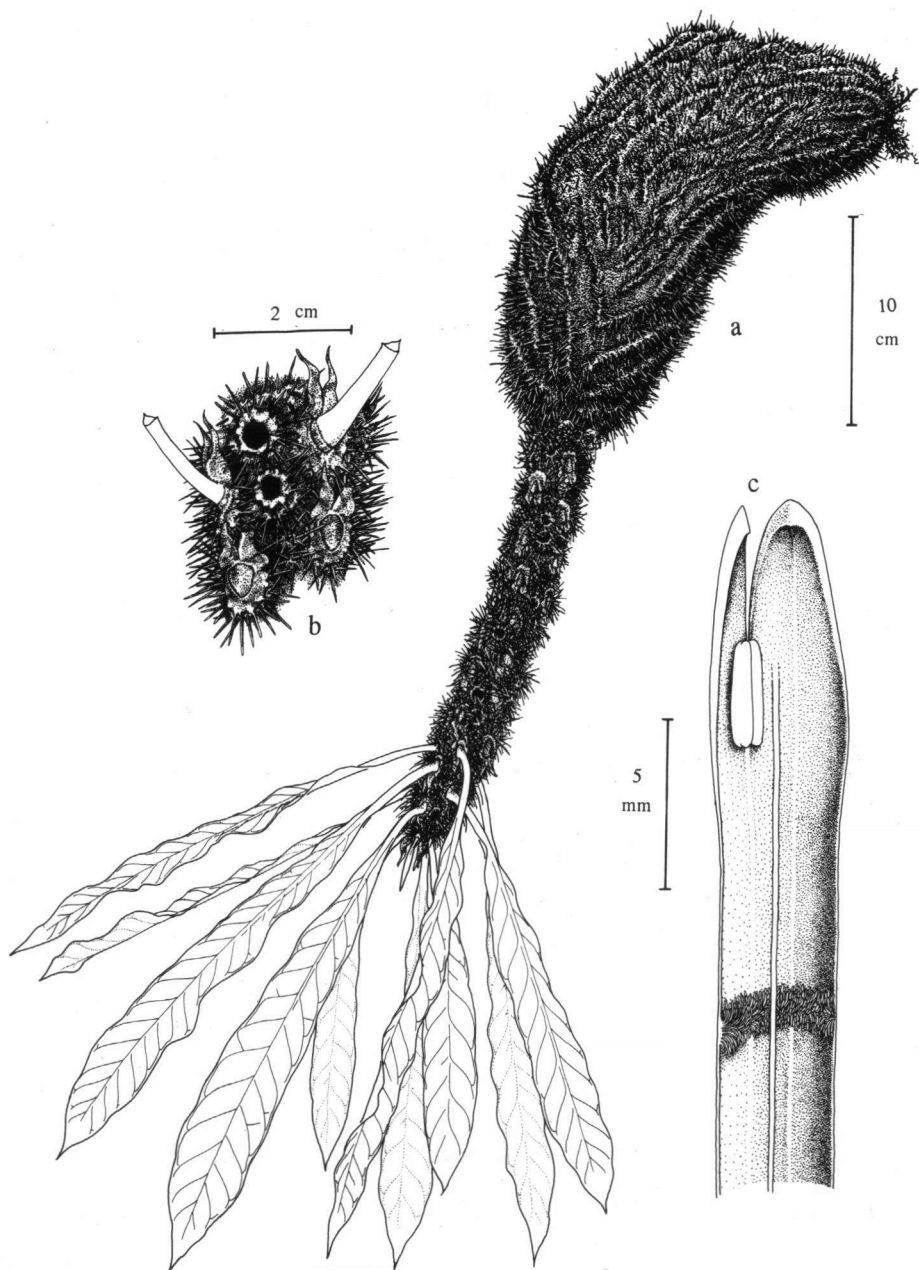


Fig. 23. *Myrmecodia gracilispina* Huxley & Jebb. a. Habit; b. stem; c. half flower. Drawn by Rosemary Wise.

usually hanging downwards. Lamina $14 \times 3.8 - 31 \times 7$ cm, oblanceolate, apex acuminate, sometimes abruptly so with a fine leaf tip; base very gradually tapered. Margin sometimes wavy, sometimes with a narrow translucent border. Midrib red, sharply prominent below; lateral veins 10–16. Petioles 1–2 cm, winged, red. Stipules 1.2–1.8 cm, reddish brown, falling almost as soon as they have opened. *Inflorescence*: Bracts to c. 4 mm, hairy. Flowers (4). Calyx 0.5 mm. Corolla to 10 mm, glabrous; lobe tips c. 1 mm, spreading at maturity; lobes, c. 3 mm, not spreading. Anthers at tube apex, 2 mm long, with blue-black flecks. Pollen 2-porate, 2-vesiculate; reticulation large; apertures not bordered. Stigma at anthers, 5- or 6-lobed. Fruit red or orange. Pyrenes 6.

Ecology – At 1880–2400 m in *Casuarina*, *Castanopsis*, and regrowth forest.

Notes – *Myrmecodia ferox* is distinguished from *M. melanacantha* and *M. horrida* by its long narrow leaves which taper very gradually at the base. It differs from *M. gracilispina* in the absence of clypeoli and the caducous stipules.

Collections – PAPUA NEW GUINEA. SE 05° 04' 141° 39' West Sepik Prov., 6 km N of Telefomin on path to Eliptamin, *Jebb* 247 (LAE), 248 (L). 05° 13' 142° 12' 3 km W of Oksapmin, S of road to Tekin, *Jebb* 222 (LAE), 229 (L). 05° 29' 143° 30' Enga Prov., 3 km along road from Laiagam to Wabag, *Jebb* 296 (K), 297 (A), 298 (K, L, LAE), 299 (type). 05° 46' 142° 45' Southern Highlands, Koruba Subdist., 3 km from Guala Mission, or Mt Alubudna, *Huxley & Matiahe UPNG 5918* (A 2 sh, BULOLO, K, L, LAE, OXF, UPNG 2 sh).

26. *Myrmecodia gracilispina* Huxley & Jebb, *spec. nov.* – Fig. 23

Differt a *Myrmecodia melanacantha*, *M. horrida* et *M. feroxi* clypeolis prominentibus, spinis densis, gracilibus, foliis longis, anguste oblanceolatis, et petiolis viridibus, 1–3 cm longis. — Typus: Papua New Guinea, *Jebb* 106 (holo LAE).

Tuber hanging downwards ovoid to obpyriform, widest near the base, to 30×15 cm. Ridges to 1 cm apart. Surface smooth, dark brown. Spines dense, usually on ridges, simple, slender, black to reddish brown at tip, 0.8–1.2 cm. Dendroid chambers present. *Stem* solitary, unbranched, 1.5–2.5 cm across, to 30 cm long, pointing downwards. Clypeoli rounded, fleshy, raised from stem surface, 1.2–1.7 cm across. Alveoli round with narrow brown rims. Spines on black swellings, clypeoli rims and in two concentric rings around alveoli, simple, slender, black, 0.9–1.5 cm. Tunnels within the stem connect the alveoli to the tuber cavities. *Leaves*: Laminae $13 \times 3.3 - 22 \times 4$ (– 38×6) cm, narrowly oblanceolate; apex acuminate; base tapered. Midrib green. Petioles green, 1–3 (–4.5) cm. Stipules brown, persistent, 1.2–2 cm. *Inflorescence*: Bracts short, hairy. Flowers (8). Calyx 3 mm. Corolla 20 mm; lobes 4–5 mm; lobe tips 1 mm. Ring of hairs 5–6 mm from base of tube. Anthers at apex of tube. Pollen 2-porate, 1- (or 2-)vesiculate; vesiculate apertures not constricted; reticulation fine to coarse. Stigma at anthers, 7-lobed. Fruit slender, red, 2 cm long. Pyrenes 6–8.

Ecology – Disturbed or undisturbed lower montane forest, 2000–2700 m, generally on *Nothofagus*.

Notes – *Myrmecodia gracilispina*, like *M. ferox*, has a downward hanging growth pattern. It is more densely spinous and the spines are finer than in *M. melanacantha* and *M. horrida*. The clypeoli are prominent though small – not covering the whole

stem as in *M. pteroaspida*. The stipules are persistent, and the leaves longer and relatively narrower than in *M. melanacantha* and *M. horrida*.

A number of collections (Jebb 40, 41, 45, 81, 88) from the Bundi area are distinctive in their narrower, less crinkled leaves. Though overlapping in altitude and habitat with the typical form, they were not found growing with it.

Collections — PAPUA NEW GUINEA. SE 05° 45' 145° 11' Bundi Subdist., on road from Kegelsugul to Bundi, *Jebb* 81 (BULOLO), 88 (L). SE 05° 48' 145° 09' Madang Prov., Bundi Subdist., on road from Kegelsugul to Bundi, *Jebb* 30 (BRI), 31 (L), 32 (K), 33 (LAE), 34 (BO), 35 (OXF 2 sh), 36 (UPNG), 37 (LAE). 05° 48' 145° 10' Bundi Subdist., on road from Kegelsugul to Bundi, *Jebb* 39 (FHO), 40 (A), 41 (UPNG), 45 (LAE). 05° 59' 145° 30' Mt Otto, *Schlechter* 18682 (p.p. K). 06° 21' 145° 17' Eastern Highlands Prov., Lufa Subdist., near Duto, *Jebb* 102 (BULOLO), 103 (A), 104 (L 2 sh), 106 (type).

UNCERTAIN AND LITTLE KNOWN SPECIES

a. *Myrmecodia decasperma* Valetton

Myrmecodia decasperma Valetton, Bot. Jahrb. 61 (1927) 145. — Type: Papua New Guinea, Bismarck Mts, *Schlechter* 18682, p.p. (B).

The type has not been found, nor the type locality re-collected. The description suggests a similarity to *Anthorrhiza caerulea* Huxley & Jebb (Huxley & Jebb, 1991b), but simple spines have not been found in that species, and there are only 7 pyrenes per fruit.

b. *Myrmecodia* species 1 'mamberamoensis'

Irian Jaya, Mamberamo R., opposite Albatros Bivak, *Docters van Leeuwen* 9540 (A, B, L), Rouffaer R., *Docters van Leeuwen* 10134 (A, BO, K, L), ? Japen Is., *Barclay* s.n. (BM). The two *Docters van Leeuwen* specimens are unique in their *Hydnophytum*-like tubers; stems without spines; leaves to 40 × 10 cm; flowers with 2-lobed stigma; pollen 3- or 4-porate, apertures bordered; reticulation coarse. The Barclay specimen is similar though the tuber is unknown and the pollen apertures not bordered.

c. *Myrmecodia* species 2 'rouffaerensis'

Irian Jaya, hills near Rouffaer R., *Docters 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 round spineless clypeoli resemble those of *M. longissima* and *M. oblongata*.

d. *Myrmecodia* species 3 'wisselensis'

Irian Jaya, Maiari Is. in Wissel Lake, *Eyma* 4514 (BO, K, L). Although resembling *M. archboldiana* in its clypeoli and spines, the leaves of this collection only reach 16 cm, the stipules are much narrower and the pollen apertures are bordered. *Myrmecodia sterrophylla* occurs in the same area but differs in other characters.

e. Myrmecodia species 4

Irian Jaya, near Doormantop, *Lam 1517* (L). This collection resembles *M. archboldiana* in its single, clypeolate stem, narrow leaves, and triporate pollen. However, the tuber and flower structure are different.

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INDEX OF SPECIFIC EPITHETS

Extant names of *Myrmecodia* species are given in Roman, synonyms in italics and new names are in bold. Numbers refer to the species reference in this work.

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apoensis Elmer 1
archboldiana Merr. & Perry 21
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aruensis Becc. 5

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beccarii J.D. Hooker 6
brassii Merr. & Perry 19
bullosa Becc. 1
dahlia Schumann 1
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longifolia Valeton 11
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longissima Valeton 9
melanacantha Huxley & Jebb 23
menadensis Becc. 1
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oksapminensis Huxley & Jebb 16
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rumphii Becc. 1
salomonensis Becc. 1
schlechteri Valeton 12
sibuyanensis Elmer 1
sorsogonensis Elmer 1
sterrophylla Merr. & Perry 15
tuberosa Jack 1
urdenatensis Elmer 1
vivipara Warb. 1