



# The tuberous epiphytes of the *Rubiaceae* 7: a revision of the genus *Hydnophytum*

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## Key words

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**Abstract** *Hydnophytum* (*Psychotrieae* *Hydnophytinae*) is revised. A key is provided, and an informal infrageneric grouping is proposed. Variation in tuber structure is discussed. Fifty-five species are recognised, of which 19 are described as new. For one species a number of varieties are also described. Forty-four species are found in New Guinea, of which 41 are endemic. The recent transfer of a number of taxa into an expanded concept of *Squamellaria* based on a molecular phylogeny is addressed. Three taxa of *Squamellaria* are included in this revision to complete the series of papers on the tuberous epiphytes of the *Rubiaceae*.

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## INTRODUCTION

*Hydnophytum* Jack is the largest of the five genera of tuberous ant-plants in the subtribe *Hydnophytinae* (*Rubiaceae*) (Huxley & Jebb 1991a). The other four genera have been revised (Huxley & Jebb 1991b, c, 1993, Jebb 1991b, 1993, Chomicki & Renner 2016). During the revision work, substantial new collections were made in Papua New Guinea; however, major problems still remain with the understanding of the genus in the Indonesian archipelago. The taxonomic history of the whole group has been described by Beccari (1884) and Huxley (1993).

Of the 111 species names and 14 subspecific names of *Hydnophytum* that have been published, 36 are retained here, while a further 19 species are described as new. Eleven species remain known from their holotype alone; a problem with a number of species in New Guinea. Six further species remain inadequately known, either through loss of the type, or paucity of material, and these are retained as 'little known species'. Five names are excluded from the genus. Apart from Beccari (1884–1886) few authors have illustrated new taxa, and therefore all the species have been illustrated here.

## METHODS

This paper is based on morphological characters. The authors examined all known collections from the herbaria in A, ABD, BISH, BM, BO, BRI, BSIP, CANB, CGE, E, F, FHO, FI, FU, G, GH, K, L, LAE, P, PNH, SING, SUVA, UC, UPNG, US and WRSL. Extensive field-based studies, including dissection of tubers, were conducted by the authors in Papua New Guinea, Indonesia, and Fiji. Of the 55 species recognised, 25 were examined in the field. The arrangement of synonyms is organised chronologically in homotypic paragraphs. All cited specimens were examined by the authors unless explicitly indicated as 'not seen' or 'presumed lost'. We have also had the benefit of using Theodorice Valeton's (1855–1929) manuscript material

on *Hydnophytum* from Leiden, which contains many unpublished drawings and descriptions of species he had intended publishing.

## PHYLOGENETIC CONSIDERATIONS

Huxley & Jebb (1991a) formed the subtribe *Hydnophytinae* to include the five epiphytic myrmecophilous genera of the *Psychotrieae*. Sohmer (1988) had hypothesized that the *Hydnophytinae* were derived directly from climbing species of Malesian *Psychotria* L. Based on evidence from DNA sequence variation (e.g., Andersson & Rova 1999, Nepokroeff et al. 1999, Andersson 2002) the *Hydnophytinae* are monophyletic, and are nested within the tribe *Psychotrieae*. Nepokroeff et al. (1999) suggested the *Hydnophytinae* would be better ranked as a subgenus of *Psychotria*.

The analysis by Andersson (2002), utilising rps16 (cpDNA) data, identified the *Hydnophytinae* as belonging to a diverse Pacific clade which excluded *Psychotria* s.str., but included several other distinctive genera (*Amaracarpus*, *Calycosia*, *Dolianthus*, *Straussia* and *Streblosa*). Andersson (2002) concluded that the question of how to treat the Pacific clade taxonomically remained open, however, as recognising strongly supported groups such as the *Hydnophytinae* taxonomically leads to consequences for the remaining groups.

Andersson's work (2002) indicated that *Hydnophytum* was paraphyletic, with the endemic Fijian genus *Squamellaria*, closely related to the Fijian taxon *H. grandiflorum* Becc. Morphology of the inflorescence and pollen supports this view. Andersson (2002) has proposed that all species of the *Hydnophytinae* are united into the single genus *Hydnophytum*, since this is the choice that leads to the smallest number of new combinations. Razafimandimbison et al. (2014) using gene trees based upon two nuclear and five plastid regions, have recently made the generic combinations making all the members of the tribe *Psychotrieae* synonymous with the genus *Psychotria*. Whilst this creates a monophyletic grouping (with some 4 000 taxa), the authors admit that the phylogenetic relationships are only partly resolved and continue to be a major challenge (Razafimandimbison et al. 2014).

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Recently, Chomicki & Renner (2016) have recognised an expanded concept of *Squamellaria*, based upon a molecular phylogeny. Those *Hydnophytum* species related to the former *Squamellaria* s.str. (Beccari 1885, Jebb 1991b) have been included in a sister clade to all other taxa of the *Hydnophytinae* (Chomicki & Renner 2016). The authors acknowledged that there is unfortunately no useful morphological character that can be used to distinguish the circumscribed genus other than the geographic distribution of these species in the Solomon, Vanuatu and Fijian Islands (Chomicki & Renner 2016). Whilst removing the predictive value of morphology, this satisfies a monophyletic approach to genus recognition in the subtribe.

On the criteria of monophyly, morphological diagnosability, and geographic coherence, the *Hydnophytinae* and the included genera are of utility, providing a category whereby species can be discussed from an ecological, biological or evolutionary point of view. Whether this is recognised as a subgenus, or even an informal category in the future concept of *Psychotria* remains to be seen.

Morphological studies of tuber structure have considerably improved generic delimitation within the subtribe. Using characters provided by the study of fresh material, a morphological cladistic analysis of the subtribe has been undertaken (Jebb 1985). Morphological insights from tuber and inflorescence structure in particular suggest that whilst all the remaining genera of the *Hydnophytinae* are derived, *Hydnophytum* is paraphyletic (Jebb 1985, 1991a). The derived genera, namely *Anthorrhiza* C.R.Huxley & Jebb, *Myrmecodia* Jack, *Myrmephytum* Becc. and *Squamellaria* Becc., appear to be monophyletic themselves, but share no particular affinities to one another. This conclusion is based upon the fact that, unlike *Hydnophytum*, the four latter genera each embody a characteristic tuber-cavity architecture and have various derived morphological features of the stems which appear to be related to ant-symbiosis specialisation. *Hydnophytum* on the other hand has a diverse range of tuber morphologies, and presents less atypical morphologies of the stem and inflorescence.

Two former *Hydnophytum* species confined to the Solomon Islands – *Squamellaria guppyana* (Becc.) Chomicki and *S. kajewskii* (Merr. & L.M.Perry) Chomicki – have solitary, branched inflorescences that arise apically on the stem, a form of inflorescence identical to that seen in many species of *Psychotria*, as pointed out by Beccari (1885) and Sohmer (1988). Two further species, endemic to the Fijian Islands, have solitary, terminal, but unbranched inflorescences and share pollen characters with the endemic Fijian genus *Squamellaria* (Jebb 1991b). Chomicki & Renner (2016) have taken the step to place these species, including a species from Vanuatu, within a phylogenetic concept of *Squamellaria* which differs from the morphological concept used by previous authors (Beccari 1886, Huxley & Jebb 1991a, Jebb 1991b). *Squamellaria* now encompasses a total of 12 taxa (Chomicki & Renner 2016), six of which fall into the former morphological concept of *Hydnophytum*. Chomicki & Renner (2016) identified the former as the ‘Specialised *Squamellaria* clade’. Five of these taxa are treated here as they would currently key out as *Hydnophytum* in all present taxonomic works.

The *Hydnophytinae* commend themselves as an excellent group for further molecular analysis, and any taxonomic rearrangements at the genus level are probably premature until such work has been undertaken. However, it seems more than likely that the nested, paraphyletic patterns will lead to broadly defined genera which, while phylogenetically appealing, have little predictive value to field workers.

## THE GENUS HYDNOPHYTUM

Amongst the *Hydnophytinae*, the genus *Hydnophytum* is here distinguished on the basis of its 4-merous flowers lacking squamules within the corolla, and having an unmodified stem with interpetiolar stipules (with the exception of *H. mamberamoense* Jebb & C.R.Huxley and *H. trichomanes* Jebb & C.R.Huxley). The remaining genera each have derived characters unique to their genus, whereas *Hydnophytum* is largely devoid of apomorphies and is a plesiomorphic, paraphyletic grouping, as confirmed by all molecular studies to date (see above).

## INFRAGENERIC GROUPINGS

In the absence of a complete phylogeny, besides the *Squamellaria* clade (Chomicki & Renner 2016), an informal infrageneric grouping of species was developed because of the number of species within the genus. Natural divisions are limited in that they only separate a few groups of species, leaving the remainder of the genus unresolved. Ten groupings have developed during the revision, and these provide a useful framework for examining the genus, and are practical for identifying specimens that prove difficult to key out, since in many cases we have been obliged to use combinations of flower, fruit and pyrene characters, which may well be absent from a specimen. Although the majority of these groups can be considered to be more or less natural (1, 2, 3, 4, 7, 9, 10), two groupings are purely morphological-geographic (5, 6), whilst ten species remain in a mixed bag grouping (8).

- 1) Formicarum group
- 2) Ovatum group
- 3) Petiolatum group
- 4) Moseleyanum group
- 5) Western New Guinea group
- 6) Papua New Guinea group
- 7) Red Tuber Tissue group
- 8) Melanesia group
- 9) Radicans group
- 10) The *Squamellaria* clade

1) Formicarum group  
*Hydnophytum formicarum* is found from Indochina and throughout Malaysia, the Philippines and Indonesia. Although it is a highly variable species (we have reduced 15 species and 12 varieties), the oblong blunt leaf is diagnostic and suggests a continuum through the region.

1. *H. formicarum* Jack
2. *H. puffii* Y.W.Low, Sugau & K.M.Wong

2) Ovatum group  
These species are confined to the north Mollucas and westernmost New Guinea. They have an inflorescence consisting of an irregular mass of four or more socket-like depressions spread across a much swollen node. Branches arise from within this inflorescence.

3. *H. morotaiense* Jebb & C.R.Huxley
4. *H. ovatum* Miq.
5. *H. spathulatum* Valetton
6. *H. tortuosum* Becc.

3) Petiolatum group  
Found in New Guinea and Australia, these species have sessile inflorescences which are covered by ferruginous hairy bracts, at least when young. Seven varieties are recognised under the polytypic *H. petiolatum*, which appears to be closely related to *H. ferrugineum* of Australia.

7. *H. ellipticum* Merr. & L.M.Perry
8. *H. ferrugineum* P.I.Forst.

9. *H. lauterbachii* Valetton
10. *H. magnifolium* Merr. & L.M.Perry
11. *H. petiolatum* Becc.
- 11a. *H. petiolatum* var. *petiolatum*
- 11b. *H. petiolatum* var. *argentatum* Jebb & C.R.Huxley
- 11c. *H. petiolatum* var. *auridemens* Jebb & C.R.Huxley
- 11d. *H. petiolatum* var. *contortum* (Merr. & L.M.Perry) Jebb & C.R.Huxley
- 11e. *H. petiolatum* var. *lacum* Jebb & C.R.Huxley
- 11f. *H. petiolatum* var. *ledermannii* (Valetton) Jebb & C.R.Huxley
- 11g. *H. petiolatum* var. *nigrescens* (Merr. & L.M.Perry) Jebb & C.R.Huxley
12. *H. trichomanes* Jebb & C.R.Huxley

#### 4) Moseleyanum group

*Hydnophytum moseleyanum* is a coastal species of the Philippines and much of New Guinea, reaching as far as Australia and the Solomon Islands. It has characteristically rhomboid to rounded, thick and fleshy, often pale green or yellowish green leaves, and shortly pedunculate inflorescences.

13. *H. grandifolium* Valetton
14. *H. moseleyanum* Becc.

The mountains of New Guinea (above 1400 m) support a large number of species with restricted ranges. They are characterised by small leaves and tubers that are for the most part not occupied by ants.

#### 5) Western New Guinea group

In the mountains of this region (formerly known as Irian Jaya), the leaves of *Hydnophytum* spp. are remarkably small, many species having leaves less than 2 cm long; in others the leaves are narrowly linear, barely reaching a few mm in breadth. Being poorly collected, these species remain ill-defined. *Hydnophytum kebareense*, *H. microphyllum* and *H. multituberosum* come from the Doberai Peninsula (Vogelkop) in West Papua Province, and are found at lower altitude than the remaining species.

15. *H. alboviride* Merr. & L.M.Perry
16. *H. buxifolium* Merr. & L.M.Perry
17. *H. caminiferum* Wistuba, U.Zimm., Gronem. & Marwinski
18. *H. confertifolium* Merr. & L.M.Perry
19. *H. davisii* Jebb & C.R.Huxley
20. *H. decipiens* Merr. & L.M.Perry
21. *H. kebareense* Jebb & C.R.Huxley
22. *H. microphyllum* Becc.
23. *H. multituberosum* Jebb & C.R.Huxley
24. *H. pauper* Valetton ex Jebb & C.R.Huxley
25. *H. ramispinum* Merr. & L.M.Perry
26. *H. valettonii* Jebb & C.R.Huxley
27. *H. vitis-idaea* Merr. & L.M.Perry

#### 6) Papua New Guinea group

These species have leaves somewhat larger than the Western New Guinea species, ranging from 2–5 cm or more in length. All are endemic to Papua New Guinea.

28. *H. acuminicalyx* Jebb & C.R.Huxley
29. *H. dauloense* Jebb & C.R.Huxley
30. *H. fusiforme* Jebb & C.R.Huxley
31. *H. hailans* Jebb & C.R.Huxley
32. *H. mayuense* Jebb & C.R.Huxley
33. *H. myrtifolium* Merr. & L.M.Perry
34. *H. reevii* Jebb & C.R.Huxley
35. *H. terrestris* Jebb & C.R.Huxley

#### 7) Red Tuber Tissue group

These species share the character of having distinctive red to purple-red tuber tissue when freshly cut, which dries a dark reddish brown colour. The corolla lobes also have a purple-red colouration.

36. *H. archboldianum* Merr. & L.M.Perry
37. *H. magnirubrum* Jebb & C.R.Huxley
38. *H. minirubrum* Jebb & C.R.Huxley

#### 8) Melanesia group

These species show no particular affinities either to other species or amongst themselves. They are generally of low altitude (below 1000 m), and are mostly found along the north coast and offshore islands of New Guinea.

39. *H. bracteatum* Valetton
40. *H. cordifolium* Valetton
41. *H. dentrecastense* Jebb & C.R.Huxley
42. *H. hellwigii* Warb.
43. *H. heterophyllum* Merr. & L.M.Perry
44. *H. lucidulum* Valetton
45. *H. mamberamoense* Jebb & C.R.Huxley
46. *H. orichalcum* Jebb & C.R.Huxley
47. *H. tetrapterum* Becc.

#### 9) Radicans group

These species are characterised by their paired, bifurcately branched inflorescences.

48. *H. albertisii* Becc.
49. *H. linearifolium* Valetton
50. *H. radicans* Becc.

#### 10) *Squamellaria* clade

A recent molecular phylogeny published by Chomicki & Renner (2016) highlights the close relationship between a specialised *Squamellaria* clade (*sensu* Huxley & Jebb 1991a, Jebb 1991b) and species formerly classified as *Hydnophytum* in the Solomon Islands, Vanuatu and Fiji. In this treatment the two taxa in the Solomon Islands, one in Vanuatu and two taxa in Fiji are described and illustrated, but generic placements of taxa, as diagnosed by Chomicki & Renner (2016), have not been changed for the sake of stability.

51. *Hydnophytum grandiflorum* Becc.
52. *H. longiflorum* A.Gray
53. *Squamellaria guppyana* (Becc.) Chomicki
54. *S. kajewskii* (Merr. & L.M.Perry) Chomicki
55. *S. vanuatuensis* Jebb & C.R.Huxley in Chomicki & Renner

## MORPHOLOGY

### Tuber

The tuber of all members of the *Hydnophytinae* appears to develop initially from the hypocotyl (Treub 1883, 1888, Beccari 1886, Huxley 1978, Jebb 1985). Absence of the tuber has been reported once (Beccari 1885: 130) for *H. radicans* (as *H. normale*) on Yapen Island (as Jobi island). This was possibly an individual that had arisen by stem layering, since horticultural cuttings can be made of *Hydnophytum* and these develop into shrubs without forming a tuber (MHPJ pers. obs.). Whilst most species develop just a single tuber, two recently discovered species of *Hydnophytum* are unusual in that later, subsidiary tuber tissue is derived from stem or root tissue (*H. caminiferum* and *H. multituberosum*, respectively).

Unlike the other four genera of the *Hydnophytinae*, in which cavity structure and tuber growth is characteristic of each genus, the tubers of *Hydnophytum* are varied and the majority are typically irregular and show little pattern or symmetry in their structure (Jebb 1985, 1991a). Tubers are usually poorly-preserved in herbarium material, and much of the new information has been derived from either fresh or spirit-preserved material (Jebb 1985). The tubers of less than half the species have been examined to date, and a more complete knowledge may considerably alter understanding of the genus in regard to its relationship with the other genera of the *Hydnophytinae*.

The tuber is parenchymatous and the tissue is not unlike that of a potato tuber (*Solanum tuberosum* L.) in consistency. The epidermal surface tends to be grey, silvery or brown in colour, while the flesh is green towards the periphery and white within. In montane species the tissue tends to be drier and more leathery in texture, and in some species is brown or reddish in colour when cut open.

The majority of species have tubers with a range of cavity sizes. Towards the centre of the tuber there are large, bulbous, and little-branched cavities in which the walls have densely warted surfaces, and these open by one to few entrance holes to the substrate side of the tuber. Near the surface of the tuber the cavities are narrower, more copiously branched, and have walls which tend to be warted only at their extremities, and these have few to many openings to the tuber surface. A large tuber will possess a number of cavities, each of which may be morphologically intermediate between these two extremes. Cavities may attach to one another during their initial growth as revealed by suture lines on the cavity wall surfaces (Jebb 1985). Tunnels with warted surfaces tend to accumulate debris or detritus and the warts have been shown to be absorptive structures (Huxley 1978).

In a number of species, the tuber cavities are more markedly divergent: the deep-lying chambers are spiral in shape, and occupy virtually the entire tuber volume, while the superficial cavities are few in number and are both short and little branched (myrtifolium type). In these tuber-types, all the cavity walls are usually devoid of warts, and there are no intermediate cavities.

Two species from the Solomon Islands, *Squamellaria guppyana* and *S. kajewskii*, have the most elaborated tuber-cavity architecture (Jebb 1985). Their tubers grow apically and new cavities are added apically and sequentially, much as in the specialised *Squamellaria* clade (Jebb 1991b) and *Myrmecodia* (Jebb 1991a).

Besides these, there are species which have tubers with as yet unique morphologies: *Hydnophytum acuminicalyx* has a laterally growing tuber lacking ventral entrance holes; *H. caminiferum* has upright, flask-like cavities which collect rainwater; *H. multituberosum* has numerous tubers arising in a large cluster, each tuberlet having an essentially similar cavity structure.

Six major architectural types are recognised here, and these are named after species that characterise the tuber-type. These types appear to have no systematic or taxonomic significance as yet. Not all species have been assigned to a tuber-type, and it is apparent that many of the species only known from herbarium material probably have yet other, as yet unidentified, cavity architecture. The tuber of *H. kebarensense*, for example, appears to be made up from a series of transverse lobes, each of which consists of a series of structurally similar cavities.

- a) moseleyanum type: Tubers globose, growing throughout. Cavities of two extremes, the types grading into one another; deep-lying bulbous cavities, warted throughout; and superficial, tubular, branching cavities, with warted surfaces confined to the extremities, or absent. Usually ant-inhabited. Examples include: *H. ellipticum*, *H. ferrugineum*, *H. formicarum*, *H. grandiflorum*, *H. grandifolium*, *H. longiflorum*, *H. moseleyanum*, *H. orichalcum*, *H. ovatum*, *H. puffii*, *H. petiolatum*, *H. radicans*, *H. spathulatum* and *H. tortuosum*.
- b) myrtifolium type: Tubers globose, growing throughout. Cavities of two distinct types; deep-lying, spiral-shaped, bulbous cavities which lack warts entirely; and superficial, narrow, tubular, branching tunnels which are only very sparsely warted. Rarely ant-inhabited, often water-filled. Examples include: *H. albertisii*, *H. alboviride*, *H. archboldianum*, *H. bracteatum*, *H. buxifolium*, *H. confertifolium*,

*H. dauloense*, *H. fusiforme*, *H. hailans*, *H. magnirubrum*, *H. minorubrum*, *H. myrtifolium*, *H. pauper*, *H. ramispinum*, *H. reevii*, *H. trichomanes*, *H. valetonii* and *H. vitis-idaea*.

- c) guppyana type: Tubers cylindrical, growing apically. Cavities of a single type added sequentially; cavities differentiated into separate chamber types, with a large transverse chamber from which arise narrow tubular tunnels. Ant-inhabited, or not. Examples include: *Squamellaria guppyana* and *S. kajewskii*.
- d) acuminicalyx type: Tubers flattened, growing peripherally. Cavities of a single type added sequentially in the several peripheral lobes; each cavity opens to the tuber's lower surface, and comprises a broad, flattened chamber from which arise peripheral, tubular, blind-ended and warted tunnels. Always ant-inhabited. Examples include: *H. acuminicalyx* and *H. kebarensense*.
- e) caminiferum type: Tuber developing from swollen stem tissue, and forming a conical structure like organ pipes. Cavities of one type, comprising blind-ended or U-shaped chambers, somewhat swollen in their basal parts, and tubular near the 1–3 entrance holes; smooth-walled throughout. Without ants and usually water-filled. Examples include: *H. caminiferum* and possibly *H. davisii*.
- f) multituberosum type: Initial tuber irregular in shape, with numerous subsidiary, spheroid tubers developing on the roots and forming a mat of tuberlets on the host surface. Cavities of one type, comprising flattened chambers from which arise tubular warted tunnels. Example: *H. multituberosum*.

Entrance holes to the tuber cavities are highly ordered in some species, but in others appear randomly dispersed on the tuber surface; in some species they are confined to the substrate-facing surface only. In many species they are of two distinct types, associated with the different cavity types; either large and funnel-like connecting to the deep-lying cavities, whilst those connected to the superficial cavities tend to be small, and often have a narrow, slightly raised rim. In some species the entrance holes have thickened, prominent lips (*S. kajewskii*), or elaborated rims with tubercle-like extensions (*H. reevii*) or with thin-walled cylindrical extensions which raise the entrance hole a centimetre or more above the tuber surface (*H. caminiferum*, *H. davisii*).

### Tuber contents

The term ant-plant (or ant-house plant) is something of a misnomer when applied to *Hydnophytum*. Unlike the other genera, only a small proportion of the species have tuber cavities that are regularly inhabited by ant colonies (Jebb 1985, 1991a). Whether the cavities are occupied by an ant-colony or not, the tuber cavities act as an efficient nutrient and or water-gathering organ and the tissues as a storage organ. It is not unusual to find the roots of epiphytic plants invading the cavities (Janzen 1974).

The tuber cavities of the majority of species contain a varied range of inhabitants including platyhelminthes, nematodes, annelids, Onychophora (Holthuis & Husson 1973), myriopods, thrips, mites, spiders, scorpions, orthopterans, dipteran larvae, adult beetles and their larvae, cockroaches, termites, skinks (*Emoia campbellii* Brown & Gibbons (1986) in Fiji has only ever been found in the tubers of *Hydnophytum*), geckoes (*Lepidodactylus pumilus* Boulenger (1885)), frogs (*Cophixalus riparius* Zweifel (1962) from New Guinea uses the tubers of at least two species as an arboreal breeding site Jebb (1985)). In addition, there are various chance findings of bats and small marsupials which may use damaged tubers as roosting sites. Several species have tubers in which the cavities are regularly found to

contain rainwater (*H. caminiferum*, *H. dauloense*, *H. fusiforme*, *S. kajewskii*, *H. myrtifolium* and *H. pauper*).

Only about 14 species are regularly occupied by ants, the most frequent belonging to the genera *Philidris* and *Anonychomyrma* (Huxley 1978, Shattuck 1992). Some 19 species of ants belonging to 14 genera have been recorded from *Hydnophytum* tubers (Huxley 1978, Jebb 1985). The most frequent ant inhabitants were formerly placed in the genus *Iridomyrmex* Mayr (Janzen 1974, Huxley 1976, 1978, Jebb 1985). These species have recently been reassigned to different genera, or placed in new genera (Shattuck 1992). The usual species found inhabiting the tubers of ant-plants growing in mangrove swamps as well as coastal and hill savannahs, are small orange coloured members of the genus *Philidris* Shattuck: *Philidris cordata* (F. Smith) in New Guinea and the Solomon Islands, *P. myrmecodiae* (Emery) in Borneo and *P. nagasau* (Mann) in Fiji. The larger, black, pungent-smelling species are now placed in *Anonychomyrma* Donisthorpe (Shattuck 1992). In New Guinea *Anonychomyrma scrutator* (F. Smith) is the more usual occupant of rubiaceaceous ant-plants, although at least two distinct forms are to be found in ant-plant tubers: in closed canopy forest from sea level to 2500 m, the workers are c. 3 mm in length, whilst at altitudes above 2500 m, a larger, 4 mm long form is found (Jebb 1985).

Those species with tubers occupied by *Philidris* spp. include: *H. formicarum*, *Squamellaria guppyana* and *H. moseleyanum*. *Hydnophytum acuminicalyx* has always been found to contain *Anonychomyrma* spp. Other species which are always occupied by ants, but of varied genera and species, include: *H. cordifolium*, *H. dauloense*, *H. ferrugineum*, *H. grandiflorum*, *H. hellwigii*, *H. heterophyllum*, *H. mayuense*, *H. microphyllum*, *H. multituberosum*, *H. orichalcum*, *H. ovatum*, *H. puffii*, *H. petiolatum*, *H. spathulatum*, *H. terrestris*, *H. tortuosum* and *Squamellaria vanuatuensis*.

Species in which the tuber cavities are occupied by various invertebrates other than ants include: *H. alboviride*, *H. archboldianum*, *H. buxifolium*, *H. confertifolium*, *H. davisii*, *H. ellipticum*, *H. ramispinum*, *H. radicans*, *H. reevii* and *H. valetonii*. Those in which the tuber cavities are usually filled with rainwater, but often also contain invertebrates, and in some species, arboreal frogs, include: *H. bracteatum*, *H. caminiferum*, *H. decipiens*, *H. dentrecastense*, *H. fusiforme*, *H. hailans*, *Squamellaria kajewskii*, *H. longiflorum*, *H. magnirubrum*, *H. minorubrum*, *H. myrtifolium* and *H. pauper*.

The tuber contents of the other species remain unknown, although the evidence, from herbarium material, suggests that they are probably ant-occupied, these include: *H. albertisii*, *H. grandifolium*, *H. kebareense*, *H. lauterbachii*, *H. linearifolium*, *H. lucidulum*, *H. magnifolium*, *H. mamberamoense*, *H. morotaiense*, *H. tetrapterum*, *H. trichomanes* and *H. vitis-idaea*.

### Stems

Stems are solitary only in young plants. With age, further stems may arise at the apex of the tuber, and in many species a woody boss, or stock, develops at the point of common origin. The stems may be sparsely to densely branched. In some species the stems may develop two or four, more or less prominent ridges, or wings. In some species the nodes may be swollen or have an articulated appearance. The vascular tissue comprises a cylinder. Only in *H. caminiferum* does the stem appear to develop cavitated tuber tissue, but the manner in which this occurs is not yet clear. In *H. valetonii* the stems are dimorphic, with main stems giving rise to two or four smaller side branches at each node.

### Roots

In high-humidity conditions, or when sunken under moss-cushions, many species will develop roots on their tubers. In *H. ramispinum* and *H. confertifolium* the type specimens have tuber surfaces covered by rigid, stellate spines (which are root-derived). We have taken the view that the type of *H. ramispinum* is unusual in this respect, by including a large number of spine-less specimens within this species. Whether the spines of these species is normal or exceptional remains to be determined, since collections of these and other species from western New Guinea are still very few in number.

Roots may develop at the nodes on the stems of various species, especially those with large, bract-covered inflorescences. In *Squamellaria guppyana* the tuber cavity 'warts' are distinct from those found on the cavity walls of other species, and have the appearance of clustered root tips (Beccari 1885: 135; MHPJ pers. obs.).

Roots are sometimes capable of producing small, cavitated swellings in species such as *H. radicans* (Beccari 1885), while in *H. multituberosum* it appears to be normal for such subsidiary tubers to be developed continuously by the roots.

### Leaves

Nearly all species have thick, leathery laminas. In general, the leaves are larger in low altitude species and smaller in highland species. The newly-emerged leaves of *Squamellaria kajewskii* are almost white in colour, and remain so for a number of days (MHPJ pers. obs.). Generally, all species have leaves that are glossy and dark green above, and dull and paler in colour below. The midrib is usually whitish, but in a few species it may be reddish or brownish in colour. Venation is sometimes obscure in live material and becomes more prominent on drying.

The coastal species *H. moseleyanum* has exceptionally fleshy leaves. One species, formerly only known by its type, *H. microphyllum*, was recorded as having pubescent leaves. Recent collections, however, reveal that whilst the stem surface of new shoots bear many multicellular hairs, the short black hairs covering the surface and margins of leaves, are in fact the erect conidia of a dematiaceous hyphomycete of the genus *Sporidesmium* Link ex Fr. (Howard Fox pers. comm.). It has not been possible to re-examine Beccari's specimen in the light of this finding.

The stipules of *H. trichomanes* and *H. mamberamoense* split both between and opposite the petioles, while in all remaining species the stipules are interpetiolar, small, triangular or rounded, and usually papery and caducous.

### Inflorescence

In the majority of species, the inflorescences are paired in a single leaf axil. Four species of *Hydnophytum* have solitary inflorescences, although two other species, *H. cordifolium* and *H. heterophyllum*, appear to be variable in this regard, sometimes having one of an inflorescence pair missing. Of the four species, two have branching peduncles (*Squamellaria guppyana* and *S. kajewskii*) while the other two have simple unbranched peduncles (*H. grandiflorum* and *H. longiflorum* both from Fiji). In these four species the inflorescence or flowers may emerge terminally unlike the majority of species, where flower production is delayed and they only appear laterally.

The inflorescence of *S. guppyana* is, to all intents and purposes, identical to that of a *Psychotria* species, in that it is solitary, appears terminally, becoming axillary with age and branches pseudo-dichotomously. Thus an argument can be made that the inflorescence of this species, and that of *S. kajewskii*, are ancestral states in the subtribe, while the paired, laterally appearing inflorescence of the remaining 50 species of *Hydnophytum* are

derived. The inflorescences (or at least flowers) of the Fijian species *H. grandiflorum* and *H. longiflorum* appear terminally, but have unbranched peduncles. There is therefore a reduction series from *S. guppyana* through *S. kajewskii*, with its less richly branched inflorescence, to the unbranched inflorescences of *H. grandiflorum* and *H. longiflorum*.

*Hydnophytum radicans* and other members of the Radicans group have paired, branched peduncles, whilst in the remaining species the inflorescences have either unbranched peduncles or the inflorescences are strictly sessile. Many of these latter species may have their inflorescences covered by papery or hairy bracts. In species of the Ovatum group, the inflorescence appears to be composed of several socket-like areas from which flowers arise successively. It is not clear whether this comprises a multiple inflorescence or merely a broad inflorescence area.

Beccari was puzzled by the inflorescence of *S. guppyana* and suspected that the species must have paired inflorescences, and that the specimens he examined had lost these. As he pointed out at the time, if the inflorescence was solitary, then it would be identical to a *Psychotria* species (Beccari 1885: 135). Beccari (1885: 181) also suggested a possible evolutionary series to explain the paired sessile inflorescences of *Myrmecodia* and those of the majority of *Hydnophytum* species.

### Flowers

The calyx is short and cupuliform, the margin in most species is weakly to strongly 4-dentate, in a few it is entire, more rarely it has a fringe of hairs. The calyx is persistent, and in nearly all species crowns the fruit, surrounding the likewise persistent disc.

The corolla is white except in a few species, where it may have a slight greenish or yellowish tinge, or in the case of *H. magnirubrum* and *H. minirubrum* where it has purple-red tips to the corolla lobes. *Hydnophytum archboldianum* was said to have purple flowers, but probably this referred to the lobe tips. The corolla tube is generally cylindrical, but in some species it may be globose near the calyx, narrowing to the mouth. There are four corolla lobes, and these are usually triangular with convex margins, although in a few species they are more elliptic. The lobe tip often has a prominently hooked tip referred to as the uncus (Latin for barbed), which may be up to 1 mm long. In some species the corolla lobes lie perpendicular to the tube when open, while in others they may become further reflexed and sometimes revolute.

Only in a handful of species hairs are not present within the corolla tube. These are arranged either in a continuous band around the tube, or in four distinct patches between the stamen filaments. These unicellular hairs are usually long enough to occlude the lumen of the tube, and may spread to the surface of the corolla lobes also. When the flower is open, the hairs generally appear as a connivent mass above the corolla lumen, with the anthers and stigma either submerged within the hairs, or immediately above them. All species, with the exception of two, have hermaphrodite flowers. For the 46 species for which sufficient material was available, 33 are heterostylous, whilst the remainder are not.

Two of the Fijian species (*H. grandiflorum* and *H. longiflorum*) have homogamous flowers. In both forms of flower, the stigma lies at the mouth of the corolla tube, with the anthers immediately below. In male flowers the anthers contain pollen, and although the stigma lies above the anthers, the style is detached from the disc, and the entire pistil is only a fraction of the length of the corolla tube. In female flowers the anthers are empty and the style remains attached to the disc. It may be that the full anthers physically restrain the capitate stigma, and thus, as the flower tube elongates, the style is detached from the disc,

effectively isolating the ovules, and preventing growth of the pistil. Of several flowers examined from single inflorescences, both facultatively-male or female flowers were present. Whilst Smith (1988) has reported the presence of hermaphrodite flowers in these Fijian species we did not observe any.

The anthers may be white, yellow or dark blue in colour. In long-styled flowers they are smaller, and usually lie immediately within the mouth of the tube, whilst in short-styled flowers they are larger and exerted on 1–2 mm long filaments.

The pollen grains are spherical to scarcely oblate, and vary from 25–76(–130)  $\mu\text{m}$ . They are 3-porate or 3-colpate and more rarely 4-colpate. When heterostyly is present the pollen of short-styled flowers is of a greater diameter than those from long-styled flowers, and the ratio of style length and pollen volume is found to be inversely related (Jebb 1985). In *H. hellwigii* the pores have a small border, while in *H. mamberamoense* the borders are massive. The exine is reticulate in all species, with brochi from 0.5 to 5  $\mu\text{m}$  across, and muri from 1 to 1.5  $\mu\text{m}$  thick. Vesicles are present in only a few species. The Fijian species *H. grandiflorum* and *H. longiflorum* have exceptionally large, 4-colpate pollen grains, 75 to 130  $\mu\text{m}$  across, with brochi 6 to 15  $\mu\text{m}$  across, and muri 2 to 3  $\mu\text{m}$  thick. These pollen characters are very similar to those of the Fijian genus *Squamellaria* (*sensu* Jebb 1991b). *Hydnophytum magnirubrum* and *H. minirubrum* also have large grains (75–100  $\mu\text{m}$ ) with medium reticulation (brochi 2–5  $\mu\text{m}$ ).

### Fruits

Fruits in the genus are for the most part uniform. The majority have globose, baccate drupes, between 5 and 12 mm long. *Hydnophytum longiflorum* and *S. kajewskii* have flattened turbinate fruits with a prominent disc. In colour the fruits vary from green to yellow when unripe, and orange or red when ripe. The flesh is glutinous and sweet, and is probably bird dispersed.

Pyrene number is two in the genus, with the exception of four species: *H. magnirubrum* which usually has three or four pyrenes, *H. grandiflorum* which has a tendency to have three pyrenes, whilst *H. radicans* and *H. albertsii* each have four pyrenes. Pyrenes vary from obovoid to ovoid, and the apex may be truncate, apiculate or notched. In most species the pyrenes are flattened on their adaxial surface, and in some a distinct median ridge is present abaxially. In *H. moseleyanum* and *H. grandifolium* there is an unusual club-like appendage at the centre of the apical notch, and in *H. bracteatum*, *H. magnifolium* and some variants of *H. petiolatum* the apex has both a central lobe and two lateral lobes, giving it a 3-lobed appearance.

### BIOGEOGRAPHY

The diversity of species in *Hydnophytinae* to the east of Wallace's Line is in striking contrast to that to the west. Predation by monkeys may be a significant factor in this regard (Whitten 1981). Of the 55 species of *Hydnophytum* (including three taxa of *Squamellaria*) revised here, 41 are endemic to the island of New Guinea, two are found in New Guinea and the Indonesian archipelago, whilst a further five are found in Indonesia or the Philippines alone. One species is common to Australia and New Guinea, while another is Australian only. Five species have recently been transferred to *Squamellaria* (Chomicki & Renner 2016) and of these, two are endemic to the Solomon Islands, one to Vanuatu and two in Fiji. All nine species of *Anthorrhiza* are endemic to Papua New Guinea, and three of the five species of *Myrmephytum* are from the mainland of New Guinea. Of the 25 species of *Myrmecodia* all but one is found on the island of New Guinea, and 22 are endemic there (Huxley & Jebb 1993). The revised concept of *Squamellaria*

(Chomicki & Renner 2016) includes nine species endemic to the Fijian Islands. Thus of the 101 rubiaceaceous ant-plants, 80 are found in New Guinea and 75 of these are endemic there. Eleven taxa are found west of New Guinea, two in Australia and 13 are found eastwards in the Pacific.

### Cytology

Kumar & Subramaniam (1987) record a chromosome count of  $2n = 44$  for *H. formicarum*, and Kiehn (1996) recorded a count of  $2n = 40-44$  for the Fijian species *H. longiflorum*. Robbrecht (1996) and Kiehn (1996) both report a chromosome count of  $2n = 110+1$  for *H. moseleyanum*.

### Conservation assessments

The very low collection density of the rubiaceaceous ant-plants in Indonesia and New Guinea means that we have scant information on the actual abundance, distribution and ecology of the majority of species. The allocation, with any confidence, of an IUCN Red List Category (IUCN 2001) is therefore difficult. However, the georeferencing of herbarium specimens and extrapolation of the known threats allows the application of an informed threat level, as recommended by IUCN, rather than the category of Data Deficient (DD).

Some, but not all, *Hydnophytum* species are usually tolerably common where they occur. As epiphytes, however, they are usually poorly collected, even at logging sites. Plants on felled trees are soon deserted by their ant colonies, become desiccated and decay rapidly such that their survival beyond a few weeks is usually limited. These factors conspire to provide scant information on the abundance, distribution and ecology of the majority of species. Of the 60 taxa of *Hydnophytum* and *Squamellaria* recognised here (55 species along with 7 varieties), 18 are known from just one or two specimens, while a further seven species have a known extent of occurrence scarcely greater than 10 km<sup>2</sup> making them essentially known from a single locality. Some species appear to be restricted to stunted, open-canopied forest growing on nutrient-poor soils that are at significant risk of mining activities as they have appreciable deposits of nickel, copper and/or gold present (Waigeo Island; Mount Bwebesu [Imwauna], Normanby Island; Mount Sisa, Misima Island).

A recent interest in the anti-cancer properties of ant-plants (Abdullah et al. 2010), has led to a major export business of dried tubers (as *Sarang Semut* – Ant-nests) from Papua Province, chiefly within Indonesia. The tuber tissue is claimed to cure a diversity of cancers and tumours, as well as for treating diabetes, bronchitis, hypertension, heart disease and stroke. Several dozen companies based in Java, Bali and Papua Province offer teas and other herbal products. Whilst this trade is mostly affecting *Myrmecodia* species, it seems likely that identifications are for the most part irrelevant and the trade is being supplied with tubers of all genera and species of ant-plants. Photographs of processed tubers on the internet indicate that large numbers of plants of all genera are being harvested, almost certainly in an unsustainable manner. A road network that is being developed from the Baliem Valley westwards into the subalpine forest around Lake Habbema is likely to severely impact all species in this region.

The impact of increasing human population pressure, subsistence agriculture, logging in both lowland and montane forests, and contributions from forest fires, plantation establishment and mining are considerable (Shearman et al. 2009, Margono et al. 2014). Between 1972 and 2002, logging pressure in Papua New Guinea forests (from lowland to upper montane) resulted in a 15 % net loss, with a further 8.8 % degraded through logging (Shearman et al. 2009). Fragmentation and degradation

of old-growth forest can therefore be considered to be causing a continuing decline in the area and quality of habitat, as well as the number of locations for all species. Without any knowledge of population changes or counts, however, the only metric available to assess the conservation status of species has been geographic range (criteria B and D) as determined by herbarium specimens.

Georeferencing of collections was done through the use of gazetteers, and publications such as Veldkamp et al. (1988) as well as on-line resources. Using the GeoCAT tool (Bachman et al. 2011), an IUCN Red List (IUCN 2001) compliant software, distribution data was used to calculate the extent of occurrence (EOO) and area of occupancy (AOO) for each taxon. Conservation ratings were generated using the methodology of Willis et al. (2003). The GeoCAT tool clearly exaggerates the EOO for those taxa found in particular habitats (i.e., montane forest), since extensive areas between recorded specimens will be ecologically unsuitable for the taxon. Furthermore, the paucity of collections is likely to give a severe underestimate of probable populations between collection localities. The use of AOO at a grid size of 2 km or 10 km simply gives a measure of the number of collections rather than a measure of subpopulations. Rivers et al. (2010) have demonstrated the value of using a grid size equating to 1/10th maximum inter-point distance to give a species-specific method. Under each taxon the AOO using the auto-value rule, as defined by the GeoCAT tool, is given, where appropriate, as a proxy measure of the number of localities.

Where only one or two locations are known (25 of the 61 taxa), AOO and EOO figures generated from herbarium specimens are unlikely to be a realistic measure of a natural range. Similarly, species known from only one or a few islands do not give realistic measures of EOO and furthermore may be prone to sudden habitat fluctuations. It has therefore been deemed sensible to adopt the category Vulnerable (VU) under criteria D2 in these cases, on the assumption that there is insufficient distribution data to utilise criteria B.

In summary, of the 61 taxa (55 species + 7 varieties), three are deemed to be Critically Endangered (CR), 9 Endangered (EN), 33 Vulnerable (VU), 6 as Near Threatened (NT) and 10 as of Least Concern (LC).

### Hydnophytum Jack

[*Nidus formicarum niger* Rumph. (1750) 119, t. 55: 1; Hensch. (1833)].  
*Hydnophytum* Jack (1823) 124; Blume (1826) 955; DC. (1830) 450; Endl. (1838) 539; Benth. & Hooker (1873) 132; Miq. (1869) 256 (sphalm. *Hydnophytum*); Becc. (1884) 120; K.Schum. (1891) 123; Valetton (1927) 127; Merr. & L.M.Perry (1945) 14; Darwin (1979) 35; P.Royen (1983) 2666; A.C.Sm. (1988) 192. — Type species: *H. formicarum* Jack.  
*Lasiostoma* Spreng. (1825) 423; Benth. (1843) 224; Baill. (1880) 459.  
*Myrmecodia* auct. non Jack: Gaudich. in Freyc. (1830) 472, t. 95; A.Rich. (1834) 224; Baill. (1880) 411.

Epiphytic, rarely terrestrial, woody subshrub with cavitated tuber between stem and roots. *Tuber* irregularly subglobose, occasionally flattened, fusiform or scaphoid in shape, rarely multiple. Spines usually absent, occasionally root-like or small and tubercle-like, rarely stiff and stellately branching. Entrance holes scattered on surface, or rarely arranged in discrete patterns; more numerous on substrate-facing side of tuber. Cavity shape and wall character variable within the genus. Tuber tissue fibrous to fleshy, yellowish white, rarely purplish red. Cavity surfaces either partly warted, with lenticel-like outgrowths, partly smooth, or entirely smooth. *Stems* arising from a single origin on the tuber, sometimes a woody boss, at the apex of the tuber, or rarely at several positions; numerous, occasionally one to few, branched; woody, slender, hanging to erect; often with 2 or 4 ridges, rarely winged; spines absent, rarely root-like around the inflorescences. *Leaves* rounded to lanceolate, to

20 cm in length, more usually less than 15 cm, often less than 2 cm in montane species; leathery, thick to fleshy, more rarely thin and mesophytic. Petiole 0–9 cm. Stipules interpetiolar, rarely splitting between the petioles; usually inconspicuous, occasionally large, with a prominent keel, caducous to persistent. Inflorescence axillary, rarely terminal, paired, rarely single, usually sessile, or peduncle short and unbranched or up to 12 cm in length. Bracts absent, or sometimes, when peduncle is absent, numerous and conspicuous, papery or leathery, sometimes with numerous reddish hairs on inner surfaces, these persistent. *Flowers* usually heterostylous. Corolla lobes 4, white, rarely green or red/purple tipped, usually with a ring of hairs at or below the corolla tube mouth which form a connivent mass above the corolla lumen. Anthers generally exerted in short-styled flowers, and then larger, also producing larger pollen grains, rarely pollen grains absent in long-styled flowers. Pollen 3-porate or 3- or 4-colporate, (25–)40–60(–130)  $\mu\text{m}$ ; pores and colpi rarely bordered, exine finely to coarsely reticulate, brochi 1–1.5  $\mu\text{m}$  across; vesicles rare, small. Stigma 2–4 fid, exerted in long-styled flowers, then with shorter and more papillose elements. *Fruit* baccate, rarely siccate, ovoid to globose, occasionally flattened, often with prominent calyx and disc remains, yellow, pink or red when ripe. Pyrenes 2 (rarely 3 or 4), obovoid to ovoid, and flattened adaxially, apex rounded to narrowly acute or acuminate, or 3-lobed.

**Distribution** — 55 species. Andaman Islands, Burma, Thailand, Cambodia, Laos, Vietnam, Malaysia, Brunei, Philippines, Indonesia, Papua New Guinea, Australia, Solomon Islands, Vanuatu, Fiji.

**Ecology & Habitat** — Sea level to above the timber line (3300 m). Epiphytic in seasonally dry to ever-wet forests: strand-line trees, mangrove forest, seasonal *Eucalyptus* savannah, primary and disturbed rainforest, *Casuarina* savannah, agricultural trees, heath forest and other poor-soil sites, montane forest (dry to very mossy), ridge-top forest or upper montane forest. More rarely some species are terrestrial above the tree-line (*H. archboldianum*, *H. pauper*), in heath forest or scrub at lower altitudes (*H. caminiferum*, *H. dentrecastense*), occasionally terrestrial on rocky substrates in open-canopied forest (*S. guppyana*, *H. grandiflorum*), or rarely grow in the leaf litter having fallen from the trees (*H. terrestris*).

## KEY TO THE SPECIES

1. Inflorescence peduncles > 3 times as long as broad, branched (sometimes branched so close to stem, that there appear to be 4 in each axil) . . . . . 2
1. Inflorescence peduncles < 3 times as long as broad, unbranched, 1 or 2 in each axil, or inflorescence sessile or sunken in stem . . . . . 6
2. Inflorescence solitary in each axil; peduncle slender, to 3 mm thick, usually  $\pm$  flattened . . . . . 3
2. Inflorescence paired, or apparently 4 in each axil; peduncle thick, > 3 mm thick, terete . . . . . 4
3. Lamina 5–20 cm long; peduncle trichotomously branched, with 4 or more fertile branch ends; corolla tube slender, at least 3 times as long as broad . . . . . 53. *S. guppyana*
3. Lamina 2–4 cm long; peduncle dichotomously branched, with 2 or rarely 3 fertile branches; corolla tube scarcely longer than broad . . . . . 54. *S. kajewskii*
4. Stem terete; leaves 3–10 cm wide . . . . . 50. *H. radicans*
4. Stem square; leaves 0.5–2.5 cm wide . . . . . 5
5. Stem 3–10 mm thick when dry; angles winged; pyrenes 4 . . . . . 48. *H. albertisii*
5. Stem 1–2 mm thick when dry; angles not winged; pyrenes 2 . . . . . 49. *H. linearifolium*
6. Inflorescence sessile, obscured or filled by a cushion of bracts and/or bract hairs and calyx remains . . . . . 7
6. Inflorescence sunken, sessile or pedunculate, but not obscured by bracts or bract hairs . . . . . 28
7. Lamina 16 by 6 to 40 by 14 cm; inflorescence cushion wider than thickness of stem . . . . . 8
7. Lamina never larger than 15 by 4 cm; inflorescence cushion as wide as, or narrower, than stem . . . . . 10
8. Petiole c. 9 cm long; inflorescence bract hairs coalescing to form a large mass that obscures the stem . . . . . 45. *H. mamberamoense*
8. Petiole < 3 cm long; inflorescence cushions discrete . . . . . 9
9. Lamina base tapering; petiole 0.5–1 cm; bracts mostly hairs, forming a dense cushion; roots arising from nodes . . . . . 12. *H. trichomanes*
9. Lamina base rounded or cordate; petiole < 0.5 cm; bracts triangular, papery to leathery; roots not arising at nodes . . . . . 39. *H. bracteatum*
10. Corolla lobes and tuber tissue purplish red when fresh . . . . . 11
10. Corolla lobes white or greenish white, tuber tissue not purplish red when fresh . . . . . 13
11. Lamina 1.2 by 0.6 to 2 by 1.5 cm; pyrenes 2 . . . . . 38. *H. minirubrum*
11. Lamina larger; pyrenes 2–4, usually 3 . . . . . 12
12. Lamina elliptic-lanceolate; corolla to 11 mm; fruit 8 mm. — Western New Guinea . . . . . 36. *H. archboldianum*
12. Lamina elliptic-obovate; corolla to 15 mm; fruit 5 mm. — Papua New Guinea . . . . . 37. *H. magnirubrum*
13. Tuber multiple, comprised of more than one globular cavi-tied swelling articulated by stem or roots . . . . . 23. *H. multituberosum*
13. Tuber solitary, sometimes deeply lobed, but never articulated by stems or roots . . . . . 14
14. Leaves sessile, base blunt to cordate . . . . . 17. *H. caminiferum*
14. Leaves sessile to petiolate, base tapering, always relatively narrow . . . . . 15
15. Lamina to 1.3 by 0.6 cm . . . . . 16. *H. buxifolium*
15. Lamina larger . . . . . 16
16. Tuber entrance holes numerous, thin-walled cylinders to 1.4 cm high and at least 1 cm across . . . . . 19. *H. davisii*
16. Tuber entrance holes not so . . . . . 17
17. Stem prominently winged, with wings c. as broad as stem . . . . . 47. *H. tetrapterum*
17. Stem not prominently winged . . . . . 18
18. Petiole c. 2 cm . . . . . 19
18. Petiole less than 2 cm . . . . . 20
19. Leaves succulent; bracts papery, lacking hairs, white. — Vanuatu . . . . . 55. *S. vanuatuensis*
19. Leaves not succulent, but sometimes leathery; bracts papery to leathery, brown, grey or sometimes with reddish hairs. — New Guinea . . . . . 11. *H. petiolatum*
20. Base of lamina abruptly narrowed . . . . . 21
20. Base of lamina attenuate . . . . . 24
21. Plant either a low-level epiphyte, or terrestrial; stems 4-angled; lamina 3.5 by 1 to 11 by 4 cm; apex tapering or acuminate . . . . . 35. *H. terrestris*
21. Plant epiphytic; stems angled or not; lamina relatively broader, apex blunt to acute . . . . . 22
22. Bract hairs not a prominent part of the inflorescence, papery bracts being  $\pm$  as common . . . . . 31. *H. hailans*
22. Bract hairs forming a prominent proportion of the inflorescence cushion . . . . . 23
23. Found in New Guinea . . . . . 11. *H. petiolatum*
23. Found in Australia . . . . . 8. *H. ferrugineum*



24. Lamina 7.5–15 cm long, lanceolate, midrib caniculate; pyrenes fusiform 4 by 1.5 mm. — Moluccas . . . . . 3. *H. morotaiense*
24. Lamina less than 7 cm long, midrib raised to flat above; pyrenes obovate . . . . . 25
25. Bracts triangular, papery, to 0.8 cm, without hairs . . . . . 26
25. Bracts mostly comprising a mass of hairs . . . . . 27
26. Tuber with short tubercles; leaves to 4 by 1.7 cm; pyrene with blunt apiculus . . . . . 34. *H. reevii*
26. Tuber surface smooth; most leaves greater than 4 by 2.1 cm; pyrene apex rounded . . . . . 32. *H. mayuense*
27. Midrib prominent above and below; pyrenes obovate, apex rounded . . . . . 7. *H. ellipticum*
27. Midrib prominent below, rarely above, and then pyrene apex truncate, with 3 lobes . . . . . 11. *H. petiolatum*
28. Nodes markedly wider than internodes; inflorescence socket-like, sunken into stem . . . . . 29
28. Nodes not, or scarcely, swollen; inflorescence sessile or pedunculate . . . . . 36
29. Tuber of several separate swellings on stem and roots; corolla 3.5 mm. — Waigeo Island 23. *H. multituberosum*
29. Tuber solitary, sometimes deeply lobed, but never articulated by stems or roots; corolla usually > 3.5 mm . . . . . 30
30. Tuber with scattered spines; lamina 0.5 by 0.4 cm; corolla 9.5 mm . . . . . 18. *H. confertifolium*
30. Tuber without spines; lamina greater than 0.5 by 0.4 cm; corolla various . . . . . 31
31. Lamina widest below the middle . . . . . 32
31. Lamina widest above the middle . . . . . 33
32. Lamina > 4.8 by 1.9 cm, apex acute. — New Guinea . . . . . 7. *H. ellipticum*
32. Lamina to 3.6 by 3.2 cm, apex obtuse or blunt. — Moluccas . . . . . 4. *H. ovatum*
33. Lamina spatulate. — Moluccas . . . . . 5. *H. spathulatum*
33. Lamina obovate. — Western New Guinea . . . . . 34
34. Stem not winged; petiole 0–0.3 cm . . . . . 6. *H. tortuosum*
34. Stem winged; petiole 0.3–1 cm . . . . . 35
35. Leaves 3–6 cm long; stipules to 0.1 cm, blunt . . . . . 21. *H. kebarensis*
35. Leaves 5–11 cm long; stipules to 0.6 cm, acute-triangular . . . . . 47. *H. tetrapterum*
36. Leaves narrowly ovate, apex acuminate-caudate, < 6 cm long, thin in texture; petiole 0–0.4 cm; corolla to 2 mm . . . . . 42. *H. hellwigii*
36. Not the above combination . . . . . 37
37. Leaves fleshy yellowish green, petiole-midrib base forming a pale, triangular pattern on the lamina . . . . . 38
37. Not the above combination . . . . . 39
38. Inflorescence a pair of peduncles; leaves to 13 by 7.5 cm . . . . . 14. *H. moseleyanum*
38. Inflorescence a cluster of (2–)4–6 peduncles; leaves to 24 by 16 cm . . . . . 13. *H. grandifolium*
39. Inflorescence sometimes or always solitary and ± displaced in each axil . . . . . 40
39. Inflorescence always paired . . . . . 43
40. Pyrenes apex apiculate . . . . . 43. *H. heterophyllum*
40. Pyrenes apex not apiculate . . . . . 41
41. Lamina cordate; corolla to 3.5 mm. — New Guinea . . . . . 40. *H. cordifolium*
41. Lamina elliptic to ovate; corolla 10–46 mm. — Fiji . . . . . 42
42. Corolla 15–46 mm, with a ring of hairs in throat; fruit globose, fleshy . . . . . 51. *H. grandiflorum*
42. Corolla 10–18 mm, glabrous within; fruit flattened, siccate . . . . . 52. *H. longiflorum*
43. Leaves c. 3 times as long as broad or greater . . . . . 44
43. Leaves less than 3 times as long as broad . . . . . 48
44. Internodes < 0.4 cm thick . . . . . 45
44. Internodes > 0.6 cm thick . . . . . 46
45. Leaves all more or less similar . . . . . 25. *H. ramispinum*
45. Leaves dimorphic: smaller and less ovate on side branches . . . . . 26. *H. valetonii*
46. Leaves 8–15 cm long, less than 2 cm wide; petiole 0.2–1.3 cm. — Borneo . . . . . 2. *H. puffii*
46. Leaves often longer, more than 2 cm wide; petiole various. — New Guinea . . . . . 47
47. Petiole 1–2 cm; inflorescence bracts < 1.5 mm; pyrene apex apiculate . . . . . 9. *H. lauterbachii*
47. Petiole to 1 cm; inflorescence bracts c. 2 mm long; pyrene apex 3-lobed . . . . . 10. *H. magnifolium*
48. Leaves less than 2 times as long as broad . . . . . 49
48. Leaves greater than 2 times as long as broad . . . . . 58
49. Leaves less than 3 cm long . . . . . 50
49. Leaves more than 3 cm long . . . . . 56
50. Leaf base blunt to cordate . . . . . 51
50. Leaf base attenuate or tapering . . . . . 52
51. Tuber with several upward-pointing entrance holes extended like chimneys; terrestrial . . . . . 17. *H. camiferum*
51. Tuber not as above; epiphytic . . . . . 22. *H. microphyllum*
52. Leaves less than 1 cm long . . . . . 53
52. Leaves more than 1 cm long . . . . . 54
53. Corolla 3 mm . . . . . 24. *H. pauper*
53. Corolla 10 mm . . . . . 27. *H. vitis-idaea*
54. Leaves less than 1.6 by 0.9 cm; calyx ciliate, entire; corolla glabrous internally . . . . . 15. *H. alborivide*
54. Leaves more than 1.4 by 0.7 cm; calyx dentate; corolla with a ring of hairs . . . . . 55
55. Tuber flattened, blackish above; leaves sessile, obovate; calyx markedly 4-dentate, numerous and persistent in axils . . . . . 28. *H. acuminicalyx*
55. Tuber globose, grey to brown; leaves elliptic to ovate; calyx scarcely dentate, not persistent in axils . . . . . 33. *H. myrtifolium*
56. Pyrenes apiculate at apex . . . . . 43. *H. heterophyllum*
56. Pyrenes acute to rounded at apex, but never apiculate . . . . . 57
57. Leaves usually > 5 cm; calyx entire. — Not in New Guinea . . . . . 1. *H. formicarum*
57. Leaves usually < 4 cm; calyx dentate. — New Guinea . . . . . 31. *H. hailans*
58. Leaves less than 2 cm long . . . . . 59
58. Leaves more than 2 cm long . . . . . 62
59. Tuber fusiform, widest at apex; corolla glabrous inside . . . . . 30. *H. fusiforme*
59. Tuber globose; corolla with a ring of hairs or not . . . . . 60
60. Corolla glabrous inside . . . . . 20. *H. decipiens*
60. Corolla with a ring of hairs . . . . . 61
61. Main stem bearing paired, slender side branches; leaves clustered, dimorphic, those of the side branches smaller and less ovate . . . . . 26. *H. valetonii*
61. Stem not bearing paired branches; leaves not clustered nor dimorphic . . . . . 16. *H. buxifolium*
62. Petiole 0.5–3 cm . . . . . 63
62. Petiole 0–0.5 cm . . . . . 64
63. Leaves elliptic to obovate, apex and base rounded, midrib flat above . . . . . 1. *H. formicarum*
63. Leaves lanceolate to ovate, apex and base acute, midrib prominent above and below . . . . . 44. *H. lucidulum*

64. Base of leaf blunt to cordate . . . . . 46. *H. orichalcum*  
 64. Base of leaf cuneate . . . . . 65  
 65. Stipules to 0.4 cm, leaves drying grey-purplish brown. —  
 Central highlands of Papua New Guinea . . . . .  
 . . . . . 29. *H. dauloense*  
 65. Stipules to 0.25 cm, leaves drying glaucous-green. — Milne  
 Bay and Northern Province . . . . . 41. *H. dentrecastense*

## NOTES ON THE DESCRIPTIONS

Tuber, stem, leaf, petiole, stipule and inflorescence measurements are all given in centimetres, whilst, flower, fruit and pyrene dimensions are in millimetres. Leaf sizes are given for particular leaves (smallest and largest) and not as ranges. Pollen was mounted in Kaiser's glycerol jelly and measured with an eyepiece graticule at a magnification of  $\times 100$ ; size is given in micrometres ( $\mu\text{m}$ ) and where possible is the average of 10 grains.

The number of flowers dissected for each species is given in square brackets after Flowers. Where heterostyly has not been confirmed (because only a single flower type has been seen for the species), but is probable, it is given as '?heterostylous' (11 taxa), or the opposite case as '?not heterostylous' (4 taxa: wherein the anthers and stigma are at the same level and are probably homostylous). Overall corolla length is obtained by adding the tube and lobe lengths.

Latitude and longitude is given where known, and where the locality is poorly localised, the minutes are omitted, the implication being that the specimen comes from within the degree square. Collections are enumerated, as far as is possible, in a NW to SE order within each province or region. All specimens have been seen, unless otherwise stated. An identification list is appended.

### Typification

Species placed as 'Uncertain and Little Known Species' are usually those for which the type is lost, and for which no equivalent material exists, or for which only a single fragmentary specimen is known (we have made an exception for *H. contortum* var. *ledermannii*). We have not conducted a search at Berlin or Manila, and have assumed that many of Valetton and Warburg's type specimens are lost. We have, therefore, not always selected lectotypes for material that we are synonymising. In the case of *H. formicarum* and *H. hellwigii* we have selected epitypes (Art. 9.7 of the Tokyo ICBN) to serve as discriminating elements.

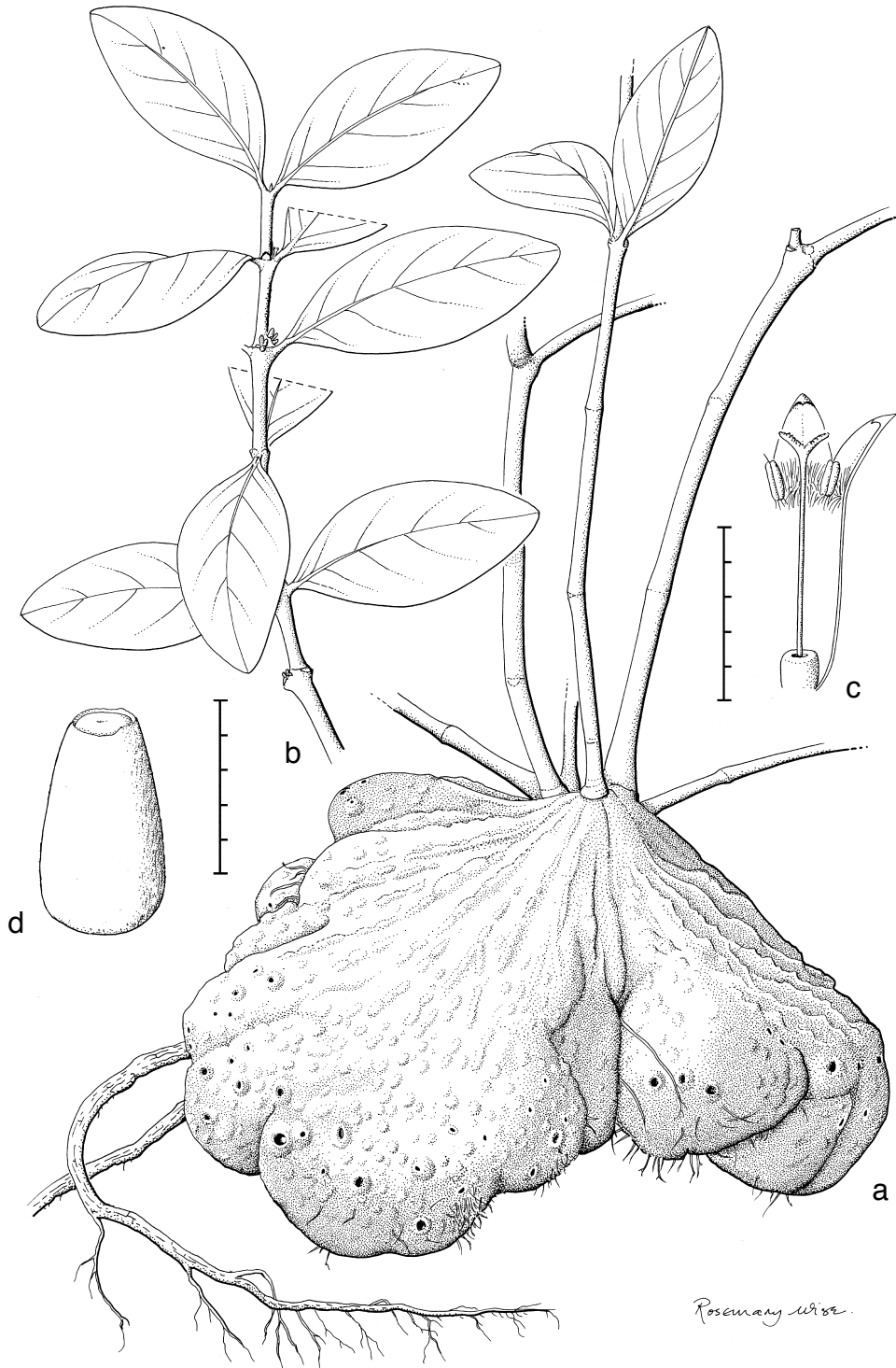
## GROUP 1 – FORMICARUM GROUP

### 1. *Hydnophytum formicarum* Jack — Fig. 1, 2

*Hydnophytum formicarum* Jack (1823) 124; DC. (1830) 451; G. Don (1834) 547; D. Dietr. (1839) 459; Endl. (1838) 539; Hassk. (1844) 110; Korth. (1851) 227; Miq. (1855) 309; Hassk. (1866) 172; Miq. (1869) 257; Benth. & Hook. f. (1873) 132; Kurz (1877) 8; Hook. f. (1881) 194; Becc. (1885) 159; Ridl. (1923) 172; Pit. (1924) 406; Craib (1934) 223. — Type: *Jack s.n.* (no specimen known to have existed), Sumatra, Nias Is. Lectotype selected here: Rumphius, Herb. Amboin. 11, 16 (1750) 119, t. 55: 1 (*Nidus formicarum niger*). Epitype nominated here: *Meijer 4602* (L), Sumatra, Mt Sago. [*Nidus formicarum niger* Rumph. (1750) 119, t. 55: 1].  
*Lasiostoma formicarum* (Jack) Spreng. (1825) 423.  
*Hydnophytum montanum* Blume (1826) 956; DC. (1830) 451; Miq. (1855) 309; Becc. (1884) 125. — Many syntypes: *Blume* (BO), Java, syn. nov.  
*Hydnophytum sumatranum* Becc. (1884) 124; (1885) 137, t. 39: 1–5. — Type: *Beccari s.n.* (F), Indonesia, Sumatra, Padang, Air Mancur, Aug. 1878, syn. nov.  
*Hydnophytum amboinense* Becc. (1884) 124; (1885) 138, t. 32: 1–7. — *Nidus formicarum niger* Rumph. (1750) 119, t. 55: 1a. — *Hydnophytum formicarum* auct. non Jack: Miq. (1855) 308 p.p. — Type: *Beccari 5530* (F, K), Indonesia, Ambon, syn. nov.

*Hydnophytum gaudichaudii* Becc. (1884) 124; (1885) 139, t. 35: 1–9. — *Hydnophytum inerme* (Gaudich.) Bremek. ex Holthuis & H.J. Lam (1942) 245. — *Myrmecodia inermis* auct. non DC. (1830) 450: Gaudich. in Freyc. (1830) 472, t. 95, 96: 2–11 (excl. all synonymy); G. Don (1834) 547; D. Dietr. (1839) 485. — Type: *Gaudichaud s.n.* (G, P), Indonesia, Waigeo, Rawak Island, syn. nov.  
*Hydnophytum selebicum* Becc. (1884) 125; (1885) 157, t. 39: 6–12. — Type: *Beccari s.n.* (F), Indonesia, Sulawesi, Kendari, syn. nov.  
*Hydnophytum coriaceum* Becc. (1884) 125; (1885) 158, t. 41. — Type: *Beccari 661* (F), Borneo, Sarawak, syn. nov.  
*Hydnophytum andamanense* Becc. (1885) 156, t. 38: 11–18. — Type: *Kurz s.n.* (CAL not seen, P), Andaman Islands, syn. nov.  
*Hydnophytum formicarum montanum*  $\alpha$  *typicum* Becc. (1885) 159, t. 47: 1–11. — *Hydnophytum montanum* Blume (1826) 956; DC. (1830) 451; Hassk. (1844) 110; G. Don (1834) 547; D. Dietr. (1839) 459; Miq. (1855) 309 (excl. syn. Rumphius); (1869) 266. — Type: *Blume s.n.* (L, P), Indonesia, Java, Buitenzorg, syn. nov.  
*Hydnophytum formicarum montanum*  $\beta$  *latifolium* Becc. (1885) 160. — *Hydnophytum montanum* var. *latifolia* [sic] Miq. (1869) 256. — Type: *Van Hasselt s.n.* (L), Indonesia, Java, Lebak, syn. nov.  
*Hydnophytum formicarum montanum*  $\gamma$  *longifolium* Becc. (1885) 161, t. 49: 1–5 (sphalm. *Hydnophytum montanum* forma *longifolium* l.c. p. 340); *Hydnophytum montanum* forma, Miq. (1869) 256; *Hydnophytum formicarum* Jack (1823) 124, excl. *Nidus formicarum niger* Rumph. — Type: *Korthals s.n.* (L), Indonesia, Sumatra, syn. nov.  
*Hydnophytum formicarum montanum*  $\delta$  *minor* Becc. (1885) 161, t. 50: 1–8; *Hydnophytum montanum* auct. non Blume: Becc. (1884) 125. — Type: *Zollinger 2607* (F), Indonesia, Java, syn. nov.  
*Hydnophytum formicarum montanum*  $\epsilon$  *borneense* Becc. (1885) 162, t. 50: 9–18; *Hydnophytum borneense* Becc. (1884) 125. — Type: *Beccari PB 711* (F), Borneo, Sarawak, syn. nov.  
*Hydnophytum formicarum montanum*  $\zeta$  *buxifolium* Becc. (1885) 163, t. 47: 12–16. — *Hydnophytum montanum* (*Celebicum*) Miq. (1869) 266 in syn. — Type: *Forsten s.n.* (L), Indonesia, Sulawesi, Tondano, syn. nov.  
*Hydnophytum formicarum montanum*  $\eta$  *cochincinense* Becc. (1885) 163, t. 49: 6–10. — *Hydnophytum blumei* Becc. (1884) 125, p.p.; Pit. (1924) 407. — Type: *Pierre 51* (A, BM, F, K, L, P), Vietnam, Ba Ria Province, Dinh mountain, Mar. 1869, syn. nov.  
*Hydnophytum formicarum montanum*  $\theta$  *lucidum* Becc. (1885) 164, t. 49: 11–15. — *Hydnophytum blumei* Becc. (1884) 125, p.p. *in clavi*. — Type: *Beccari PB 3671* (F), Borneo, Sarawak, syn. nov.  
*Hydnophytum formicarum blumei* Becc. (1885) 164, t. 48: 1–8. — *Hydnophytum formicarum* auct. non Jack: Blume (1826) 956. — *Hydnophytum ellipticum* Blume Herb. (according to Miq.) ex Becc. (1885) 164, in syn. — *Hydnophytum montanum latifolium* Miq. (partim) (1869) 257. — *Hydnophytum montanum* auct. non Blume: Burck (1884) 16, t. 4: 5. — *Hydnophytum blumei* Becc. (1884) 125, p.p. *in clavi*. — Type: *Blume s.n.* (L), Java, Buitenzorg, syn. nov.  
*Hydnophytum formicarum dubium* Becc. (1885) 165, t. 48: 9–11, t. 49: 16–19, 51, 52: 2. — *Hydnophytum blumei* Becc. (1884) 125, p.p. *in clavi*. Syntypes: *Griffith* (CAL not seen), Malacca, and *Gaudichaud* (L not seen), Singapore, syn. nov.  
*Hydnophytum formicarum siamense* Becc. (1885) 167, t. 48: 12–17; Pit. (1924) 407. — Type: *Pierre 1348* (P), Vietnam, Phu-Quoc island, syn. nov.  
*Hydnophytum formicarum zollingerii* Becc. (1885) 167, t. 57: 17–22. — Type: *Zollinger 659* (A, G, P), Java, syn. nov.  
*Hydnophytum nitidum* Merr. (1907) 307. — Type: *Merrill 6181* (PNH presumed lost), Philippines, syn. nov.  
*Hydnophytum intermedium* Elmer (1911) 1039. — Type: *Elmer 10782* (E, L), Philippines, May 1909, syn. nov.  
*Hydnophytum orbiculatum* Elmer (1913) 1860. — Type: *Elmer 15583* (BM, BO, F, FI, G, GH, L, P, UC, W), Philippines, Dec. 1915, syn. nov.  
*Hydnophytum leytenense* Merr. (1913) 390. — Type: *Wenzel 45* (G), Philippines, syn. nov.  
*Hydnophytum membranaceum* Merr. (1915) 143. — Type: *Merrill 3720* (PNH presumed lost), Philippines, syn. nov.  
*Hydnophytum mindorensis* Merr. (1915) 143. — Type: *Merrill 6182* (PNH presumed lost), Philippines, syn. nov.

**Tuber** globose to oblate, to 60 cm across; surface smooth to rugose, grey to brown. Roots confined to substrate side of tuber, occasionally numerous and throughout, then becoming  $\pm$  spinose. Entrance holes lipped or not, to 1 cm across. **Stems** few to many, sparsely to densely branched; internodes 0.5–5 by 0.2–0.6 cm. Lamina usually lanceolate-elliptic, occasionally obovate or rhomboid, rarely orbicular; 5 by 2, 8 by 1.5, to 14.5



**Fig. 1** *Hydnophytum formicarum* Jack. a. Tuber and shoots; b. shoot; c. half flower; d. immature fruit (from *Leopold s.n.* (SAN) 18 Jan. 1995, mangrove forest Sepilok, Sandakan, Sabah). — Scale bars: a, b = 5 cm; c, d = 2.5 mm. — Drawn by Rosemary Wise.

by 7 cm; apex rounded to round-acute; base cuneate, tapering to petiole; midrib prominent below; veins 3–10 oblique; chartaceous to leathery, brittle. Petiole 0–1.5 cm; stipules 0.1–0.2 cm, triangular, caducous. Inflorescence sessile to sunken, paired, axillary. *Flowers* [12] not heterostylous. Calyx to 1 mm. Corolla tube 1–3 mm, lobes 0.7–1.5 mm, with a ring of hairs below level of mouth. Anthers 1 mm, at mouth of tube. Pollen 3-colporate, 60 (50–75)  $\mu$ m, finely reticulate, vesicles and pores small. Stigma bifid, above level of anthers. *Fruit* ovoid, to 8 by 5 mm, rarely pubescent, red when ripe. Pyrenes ellipsoid-ovoid, to 2.5–3.5 by 1 mm; apex acute to acuminate, base rounded.

**Ecology & Habitat** — Mangrove swamp, savannah forest, especially common in heath forest growing on nutrient-poor soils; sea level to 1500 m. Tuber nearly always inhabited by

ants, and usually by *Pholidris cordata*. Rare in many Indonesian islands.

**Distribution** — Andaman Islands, Burma, Thailand, Vietnam, Cambodia, Sumatra, Peninsular Malaysia, Borneo, Java, Philippines, Sulawesi, Lesser Sundas and Moluccas; it has been collected once from Waigeo Island, but is apparently absent from the New Guinea mainland.

**Conservation status** — Least Concern (LC). Whilst probably Vulnerable in some parts of its range, this taxon is found throughout the Indonesian archipelago. Other information: EOO 8.5 million km<sup>2</sup>.

**Typification** — Jack’s original specimen, if it existed, was lost with the ship ‘HMS Fame’, which caught fire in the Indian Ocean (Van Steenis-Kruseman 1950); however, he also cited



Fig. 2 *Hydrophytum formicarum* as *Nidus formicarum niger* (upper left) reproduced from Rumphius (1750) book 11, chapter 11, plate 55. Courtesy of Biblioteca digital, Real Jardín Botánico-CSIC.

Rumphius' illustration (1750) of *Nidus formicarum niger* (Fig. 2). Since this latter illustration comprises part of the 'original material', it must automatically stand as the lectotype (Art. 9.9 in Turland et al. 2017). However, in view of the variable nature of *H. formicarum* this type is of no practical use – there being over 3000 km between the type locality cited by Jack (Nias Island, Sumatra) and the lectotype (Ambon). No material is available from Nias, and a specimen from mainland Sumatra has therefore been selected as an epitype (Art. 9.7), to serve as a discriminating element. Geographically, this is the closest specimen that provides a good match to the original description by Jack.

Since there is no conflict within the type material of the various synonyms, we have not lectotypified any of the material since



Fig. 3 *Hydrophytum puffii* Y.W.Low, Sugau & K.M.Wong. a. Shoot of Endert 2165; b. shoot of Endert 1647. — Scale bar = 5 cm. — Drawn by Rosemary Wise.

we feel that considerable alteration may occur to the broad species concept we have proposed here, once more methodical collecting has been undertaken in Indonesia.

Notes — A widespread and variable species, characterised by its lanceolate-elliptic leaves with a blunt apex. The concept of *H. formicarum* is broadly defined here, incorporating 15 former species and 12 forms and varieties. Neither Valetton nor Merrill and Perry investigated the Indonesian species of *Hydrophytum*, and Beccari is the only author who had extensive field knowledge of these plants in the islands west of New Guinea. The many forms and varieties that Beccari described, however, do not appear to be helpful in understanding the genus in Indonesia.

There are several island forms with much smaller leaves, and the most problematic region centres around the southern Philippines and the northern Moluccas, where this species and *H. moseleyanum* [14] are both found. On mainland New Guinea this species appears to be replaced by *H. petiolatum* [11]. In Eastern Borneo there is an exceptionally narrow-leaved species, *H. puffii* [2], that we have recognised as distinct since it appears to be co-extensive with *H. formicarum*.

Beccari (1885: 164) synonymised the name *H. ellipticum* under his *H. formicarum blumei* (which was in turn a renaming of his own *H. blumei*), citing it as being a specimen in the Blume Herbarium seen by Miquel. There are no further details of this *in sched.* name, and we have seen no specimen. The name *H. ellipticum* [7] was later used by Merrill and Perry.

## 2. *Hydnophytum puffii* Y.W.Low, Sugau & K.M.Wong — Fig. 3

*Hydnophytum puffii* Y.W.Low, Sugau & K.M.Wong (2016) 125. — Type: *KM Wong et al. WKM 2244* (holo SAN; iso L), Borneo, Sabah, Tongod, Gunung Tingkar, 26 Aug. 1992.

*Tuber* small, globose, to 20 cm; surface rugose, smooth, dark brown. Entrance holes lipped, to 1 mm across, and with or without occasional simple spines to 0.8 cm. Cavities small, regular, with smooth and warted surfaces. *Stems* 1 to few; to 50 by 0.7 cm; much branched; internodes 1.2–6 by 0.3–0.7 cm. Lamina narrowly obovate-lanceolate,  $\pm$  falcate, margins  $\pm$  parallel; 8.5 by 0.2 to 15 by 1.5 cm; apex rounded-acute, base tapering; midrib prominent below, veins c. 7 each side, often obscure; leathery to thin in texture; pale green in colour. Petiole 0.2–1.3 cm; stipules triangular to 0.05 cm, caducous. Inflorescence paired mounds to 0.4 cm across, and up to 0.4 cm long; bracts minute, caducous. *Flowers* not heterostylous. Calyx cupuliform, tube 0.6–1 mm long, glabrous on both sides; margin lobes not present. Corolla tubular, white; tube 1.5–2 mm long, outside glabrous, inside with a band of dense translucent hairs at the throat; lobes triangular, 1.5 mm long, 1 mm wide, outside surface glabrous, inside hairy at the basal-most part attached to the corolla tube; apex not uncinat. Stamens inserted at the corolla throat, basifixed; filaments subsessile; anthers 0.5 mm long, exserted. Style 2.5 mm long, densely papillate except at the basal quarter. Stigma 2-lobed, 0.5 mm long, surface densely papillate, exserted above the anthers. *Fruit* prolate, 6 by 4 mm, smooth, fleshy drupe, maturing reddish orange. Pyrenes fusiform, broadest slightly above middle, 3.5

mm long, 1.7 mm wide, with a semi-transparent fleshy thread at the base

**Ecology & Habitat** — Epiphytic in swampy forest, waterlogged *Agathis* forest, lowland to hill kerangas or heath forest over sedimentary rocks and forest over ultramafic geology; 10–500 m. Tuber inhabited by ants.

**Distribution** — Borneo (Sabah, E Kalimantan).

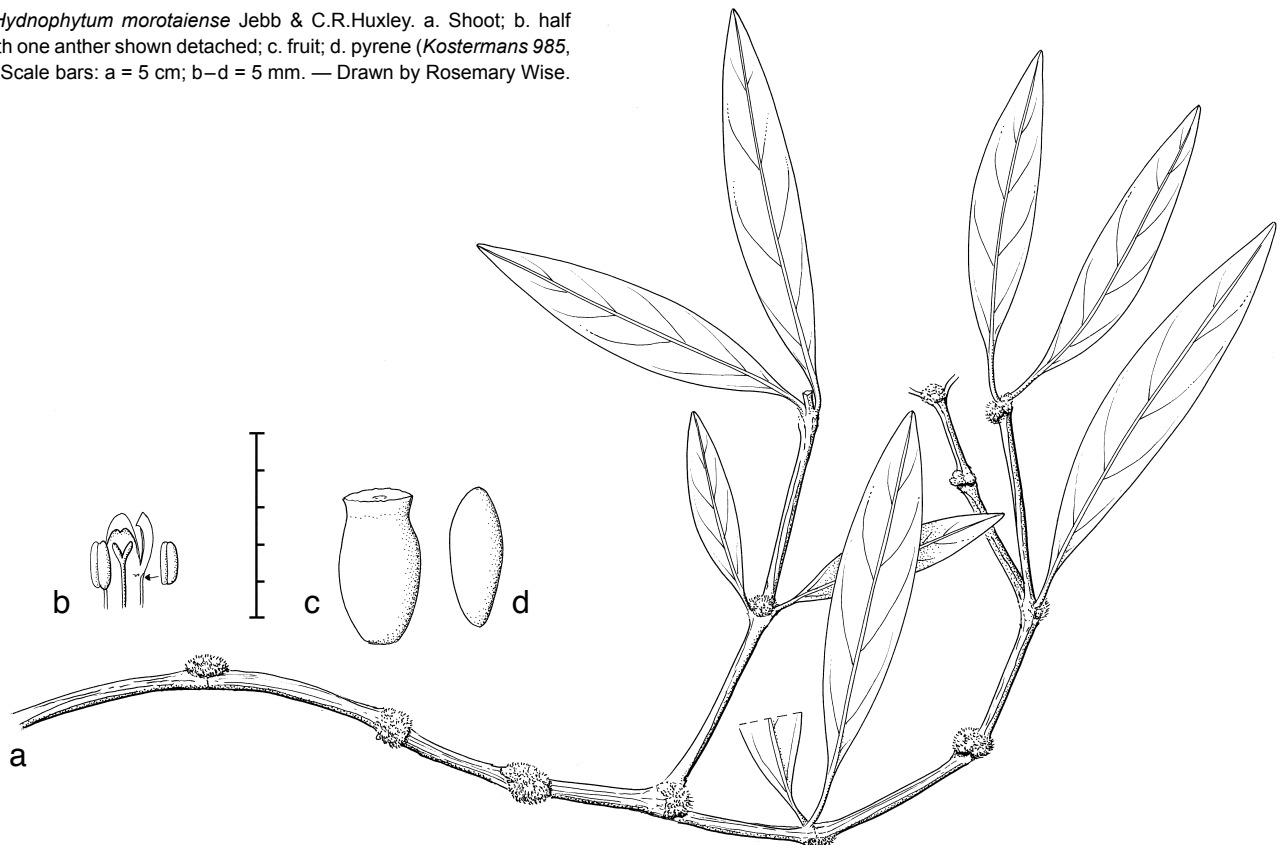
**Conservation status** — Low et al. (2016) assigned a status Vulnerable (VU) under criteria B1+2ab(iii,iv). At the time the taxon was considered to be endemic to Sabah. This is adjusted here to Near Threatened (NT) on the basis that collections from south-eastern Kalimantan raise the known extent to nearly 800 km and the former EOO from 15 000 km<sup>2</sup> to 93 000 km<sup>2</sup>. Whilst now having a larger known range, its habitat remains highly threatened by logging and clearing for oil palm plantations. Other information: georeferenced collections 12, AOO 22 500 km<sup>2</sup> (using an auto-value cell width of 50 km), indicating 9 locations.

*Additional specimens from Kalimantan.* *Endert 1647* (BO, L), Kalimantan, S0°00' E116°30', West Koetai, no. 4, near Bewaewa; *Endert 2165* (BO, L), West Koetai, no. 9, near Antjabeng; *Kostermans 13106* (BO, L), West Koetai, Mt Palimasan, near Tabang on Belajan River.

**Notes** — The exceptionally slender leaves of this species separate it from *H. formicarum* [1] with which it shares inflorescence characters. The specimens, however, are variable, some with smaller, thicker leaves (*Kostermans 13106*) others larger and more papery when dry (*Endert 2165*). *Hydnophytum angustifolium* (see Uncertain and Little Known Species) described by Merrill (1908) from the Philippines suggests a very similar facies to this species, but all the original type material is missing (see Uncertain and Little Known Species). In describing *H. puffii*, Low et al. (2016) contrasted the description of this later species in some detail.

The name *perangustum* had been proposed for this species, and was circulating in horticultural circles, but remains a *nomen*

**Fig. 4** *Hydnophytum morotaiense* Jebb & C.R.Huxley. a. Shoot; b. half flower with one anther shown detached; c. fruit; d. pyrene (*Kostermans 985*, type). — Scale bars: a = 5 cm; b–d = 5 mm. — Drawn by Rosemary Wise.



*nudum*. The name '*H. extendifolium*' has been applied to specimens at Leiden, but no publication has been traced.

## GROUP 2 – OVATUM GROUP

### 3. *Hydnophytum morotaiense* Jebb & C.R.Huxley, *sp. nov.* — Fig. 4; Map 1

Tuber laeve. Caules complures; internodia ad 7 per 0.8 cm. Lamina lanceolata, 7.5 per 1.8 ad 15 per 4.5 cm, apice acuto, basi sensim attenuata. Petiolus 1.3 cm; stipulae triangulares, 0.25 mm longae, caducae. Inflorescentia binati pulvini ad 1.5 cm in diametro. Flos non bene cognitus. — Typus: *Kostermans 985* (holo BO; iso A, K, L), Moluccas, Morotai Island, 25 May 1949.

*Etymology.* For the type locality.

*Tuber* scarcely known, probably large; surface smooth. Cavities warted and smooth-walled. *Stems* several to 1 m in length; branched, drying striate; internodes 1.5–7 by 0.4–0.8 cm, angular. Lamina narrowly lanceolate; 7.5 by 1.8 to 15 by 4.5 cm; apex acute; base tapering; midrib prominent below, canaliculate above; veins 5–7, but often obscured, arched and joined near margin; thick and leathery, drying grey-green. Petiole to 1.3 cm, drying dark; stipules triangular to 0.25 cm, caducous. Inflorescence comprising 2 or 4 circular depressions with slightly raised rims, covered by a mass of brown bract hairs to 1.5 cm across. *Flowers* [1] fragmentary. Calyx 1 mm, entire. Corolla tube 0.8 mm, with a ring of hairs below the anthers lobes 0.6 mm, uncus to 0.3 mm. Anthers 0.4 mm, filaments 0.2 mm; half exerted from mouth of tube. Stigma at level of anthers. *Fruit* to 4.5 mm, oblong, with large disc remains surrounded by calyx remains. Pyrenes fusiform to ovoid, 3–4 by 1–1.5 mm.

*Ecology & Habitat* — Forest, 100–800 m. Tuber contents not recorded.

*Distribution* — Indonesia, North Sulawesi Province (Talaud Island) and North Maluku Province (Morotai Island).

*Conservation status* — Vulnerable (VU) under criteria D2. The two island populations are over 330 km apart.

*Additional specimens examined.* *Lam 3602* (BO, L), Moluccas, Morotai Is, Mt Ligoir, Guguti, East of Pilano; *Lam 2963* (BO, L), Talaud Island, Karakelang, SW slope of G. Duata.

*Note* — The lanceolate leaves and large bract cushions covering the inflorescence are reminiscent of *Myrmephytum moniliforme* C.R.Huxley & Jebb (Huxley & Jebb 1991c), with which it could be confused. The inflorescence structure is similar to that of *H. ovatum* [4] and *H. spathulatum* [5].

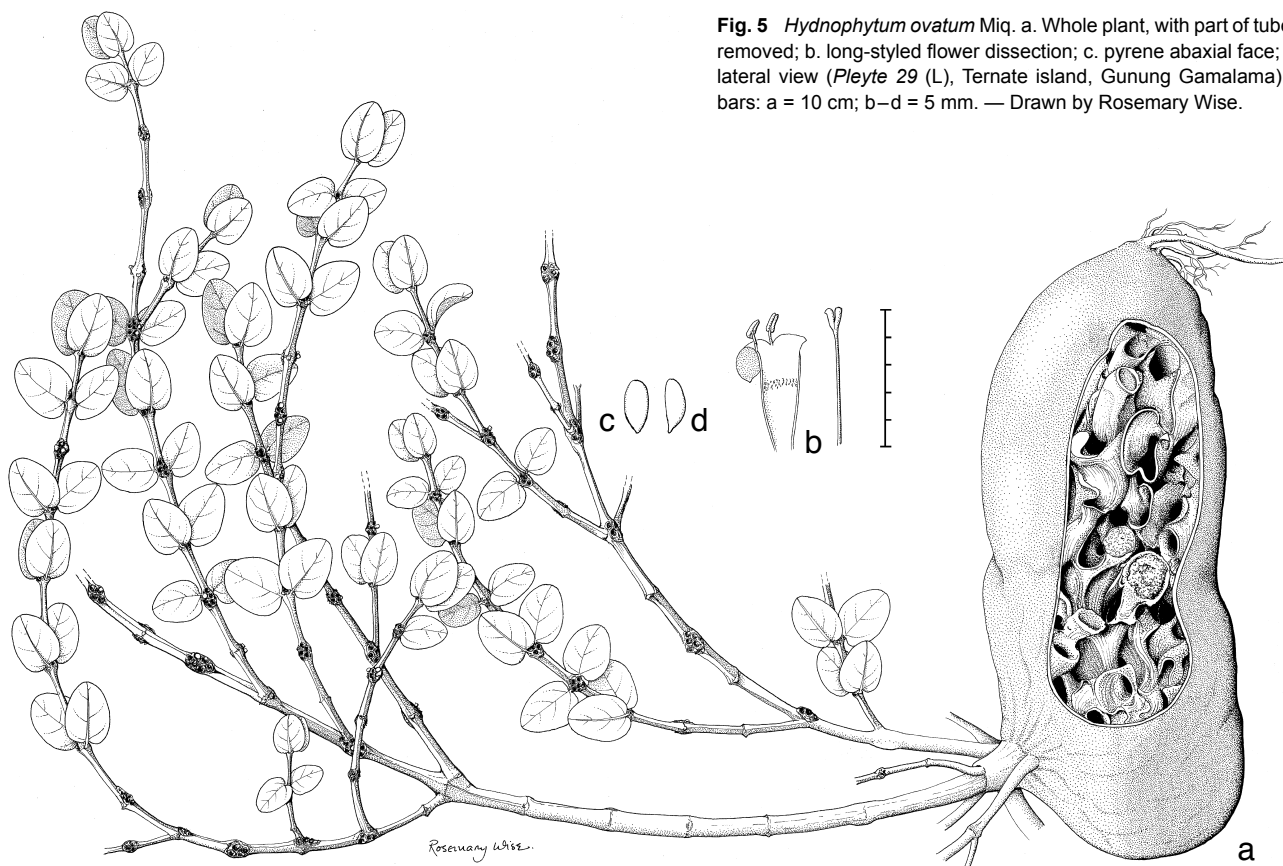
### 4. *Hydnophytum ovatum* Miq. — Fig. 5; Map 1

*Hydnophytum ovatum* Miq. (1869) 257; Becc. (1885) 143, t. 32: 8–14. — Type: *Teysmann & de Vries 20* (lectotype selected here L; CAL not seen), Indonesia, Moluccas, Ternate, Mar. 1860.

*Tuber* oblong to globose, dark brown, without ridges or spines. *Stems* several, branched to 70 cm; internodes 1.5–5 by 0.1–0.5 cm, rounded to subterete. *Leaves* sessile. Lamina ovate to orbicular, 1.6 by 1.3 to 3.6 by 3.2 cm; apex obtuse; base truncate to cordate; midrib diminishing rapidly, prominent near base; veins 4 or 5; leathery in texture, drying reddish brown. Stipules triangular, to 0.2 by 0.2 cm, caudate, caducous. Inflorescence a mass of tightly grouped sockets in a swollen node. Bracts papery to hairy, to 2 mm long. *Flowers* [3] heterostylous. Calyx to 1 mm entire. Corolla to 6.5 mm; tube 5 mm; lobes triangular to 1.5 mm; a narrow band of very short hairs at mouth of tube. Short-styled flowers with anthers exerted; pollen 63 (60–65)  $\mu$ m, brochi 1.5  $\mu$ m; stigma bifid, below mouth of tube. Long-styled flowers with anthers within mouth of tube, to 1 mm long; pollen 48 (44–53)  $\mu$ m, brochi 1  $\mu$ m; stigma exerted. *Fruit* globose, to 5 mm, calyx remains prominent. Pyrenes obovoid, 2 by 1.2 mm, rounded at apex.

*Ecology & Habitat* — Forest, 1200–1500 m. Tuber inhabited by ants.

*Distribution* — North Maluku Province (Ternate and Tidore Islands).



**Fig. 5** *Hydnophytum ovatum* Miq. a. Whole plant, with part of tuber surface removed; b. long-styled flower dissection; c. pyrene abaxial face; d. pyrene lateral view (*Pleyte 29* (L), Ternate island, Gunung Gamalama). — Scale bars: a = 10 cm; b–d = 5 mm. — Drawn by Rosemary Wise.

Conservation status — Vulnerable (VU) under criteria D2. Known from two small and adjacent volcanic islands this taxon may be prone to sudden habitat fluctuations.

Note — The inflorescence is composed of several peduncular sockets each of which produces a succession of flowers, and which together form a large swollen mass at the nodes. Where a branch arises at a fertile node, these sockets lie to each side of the branch, and above it. It is distinguished from *H. spathulatum* [5] by its leaf shape. It is restricted to the volcanic islands of Ternate and Tidore.

**5. *Hydnophyllum spathulatum* Valetton — Fig. 6; Map 1**

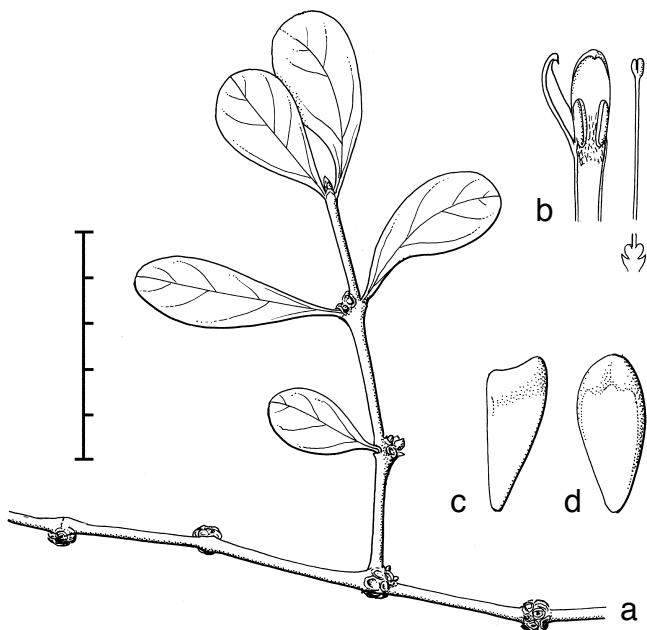
*Hydnophyllum spathulatum* Valetton (1912a) t. 340. — Type: *Smith s.n.* (lectotype selected here BO 1360-120; iso BO 1360-119), Moluccas, Batjan Is, 2 Sept. 1900.

*Tuber* oblong to conical, to 25 by 10 cm, ridged, smooth or rough; spines unbranched, flexible, root-like or recurved, on ridges; entrance holes numerous. *Stems* several, arising from a large area around tuber apex, to 50 by 0.4 cm, little branched; internodes 1–5 by 0.1–0.3 cm, terete; spines rarely present at nodes. Lamina spatulate, 3 by 1.8 to 5.5 by 2.5 cm; apex rounded, base attenuate; leathery to thin; midrib not prominent, veins obscure. Petiole 0–0.5 cm, stipules c. 0.1 cm, soon falling. Inflorescence a mass of tightly grouped sockets forming a prominent swelling at each node; bracts small, papery. *Flowers* [2] ?heterostylous. Calyx c. 0.2 mm. Corolla tube to 2.5 mm; lobes 1–1.5 mm; with a broad band of short hairs at level of anthers at mouth of tube. Anthers 1 mm, at mouth of tube. Pollen 3-porate, 53 (50–57) µm, brochi < 1 µm across; vesicles prominent. Stigma bifid, exserted. *Fruit* globose, red. Pyrenes obovoid, 3.5 by 1.5 mm; the flattened surface adpressed to the other pyrene c. 2.8 mm long, the rounded-acute apex projecting freely away from the other pyrene.

Ecology & Habitat — Forest, from sea level to 300 m. Tuber inhabited by ants.

Distribution — Indonesia, Maluku Province.

Conservation status — Vulnerable (VU) under criteria D2. Known from four collections, one from each island in the north Moluccas. Since EOO and AOO measures are inappropriate, criteria D2 is utilised.



**Fig. 6** *Hydnophyllum spathulatum* Valetton. a. Shoot; b. flower dissection; c. pyrene lateral view; d. pyrene adaxial face (a: *Boerlage & Smith 570* (L), Batjan Island; b: *Nedi 76* (BO), Batjan Island, Gunung Kewasa; c, d: *Smith s.n.*, type). — Scale bars: a = 4 cm; b–d = 4 mm. — Drawn by Rosemary Wise.

Notes — The inflorescence of this species is similar to that of *H. ovatum* [4], although the leaves are very different and it is more widely distributed in the north Moluccas.

The specimen *De Vogel 4130* from Obi Island is placed here with reservation. The leaves are lanceolate and finely attenuated at each end, reaching 10 by 1.5 cm.

**6. *Hydnophyllum tortuosum* Becc. — Fig. 7; Map 1**

*Hydnophyllum tortuosum* Becc. (1884) 124; (1885) 141, t. 37: 1–5. — Type: *Beccari 185* (lectotype selected here FI; iso K), New Guinea, West Papua Province, Sorong.

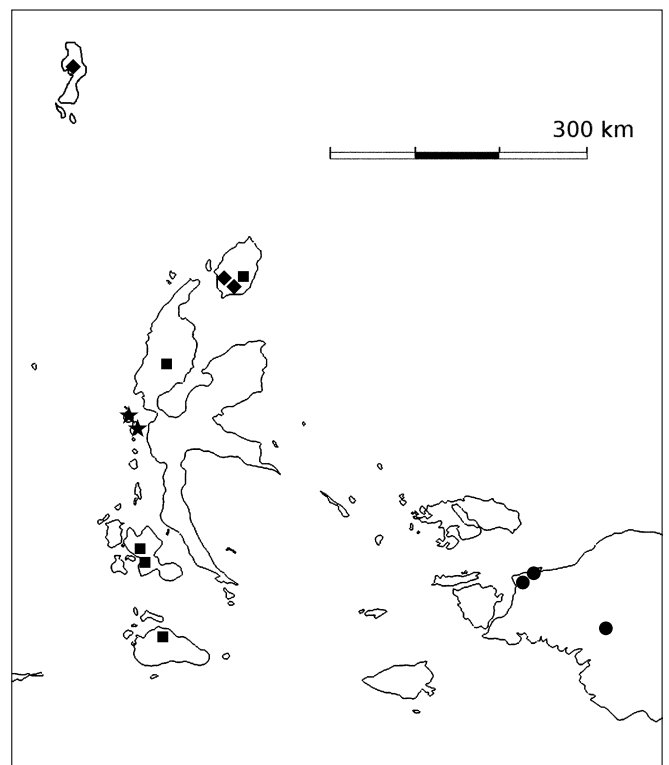
*Tuber* spherical, to 20 cm across, smooth, otherwise unknown. *Stems* numerous, to 60 cm long, little branched; internodes 1–6 by 0.1–0.3 cm, round; nodes slightly swollen. Lamina obovate; 3 by 1.6 to 4.5 by 2.5 cm; apex rounded-acute, base cuneate; veins 3–5; leaves tending to dry crinkled. Petiole 0–0.3 cm; stipules triangular, 0.1 cm, caducous. Inflorescence an area of socket-like depressions across one axil of each node, and to sides of petiole. *Flowers* [2] ?heterostylous. Calyx 1.5 mm. Corolla tube 2 mm, lobes 2 mm, a ring of hairs at mouth of tube. Anthers within throat or exserted, 1 mm long. Pollen 44 (40–48) µm diam. Stigma 2-fid, lobes long, above anthers. *Fruit* and pyrenes immature.

Ecology & Habitat — Mangrove forest to lowland forest, sea level to 300 m. Tuber inhabited by ants.

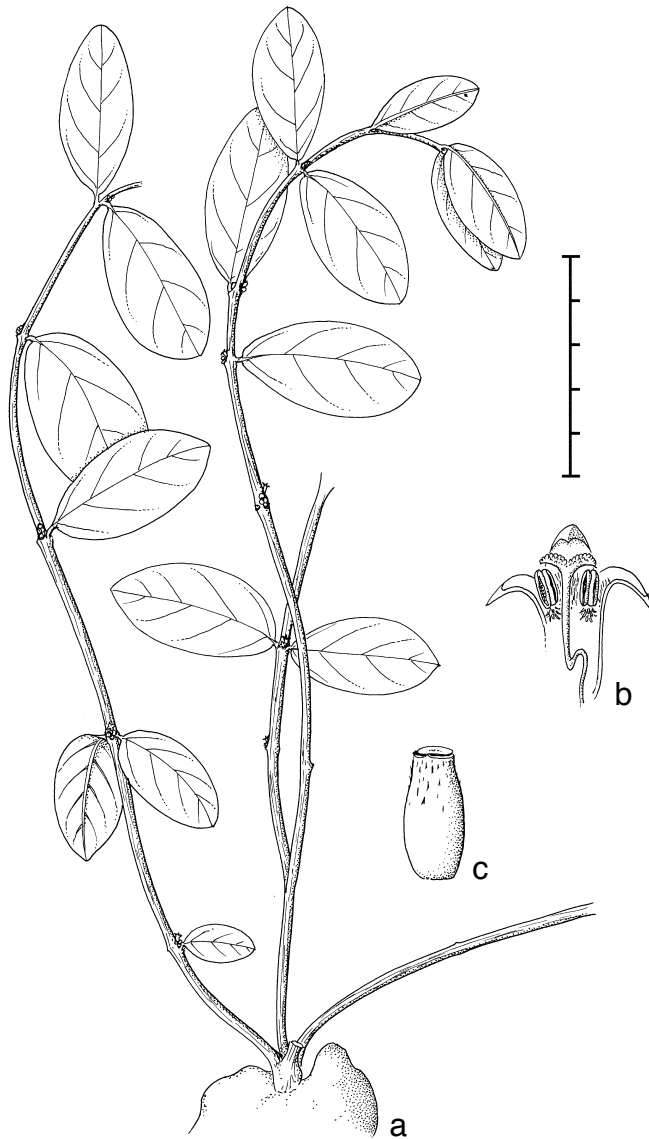
Distribution — New Guinea (West Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only two locations known c. 120 km apart.

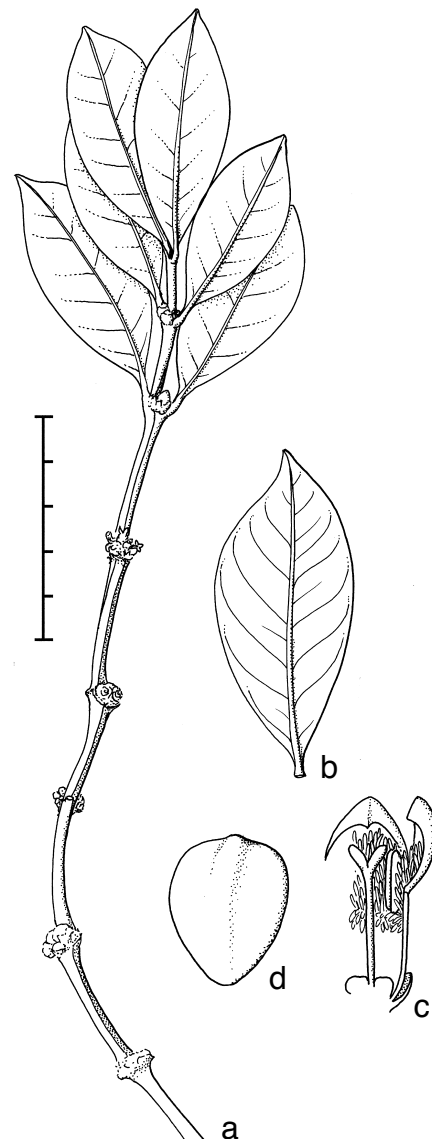
Note — The specimens included here in this species are somewhat varied, but each exhibits an inflorescence structure identical to that illustrated by Beccari (1885: t. 37), and all are found in a limited geographical area, see Map 1. The inflorescence shows similarities to those of *H. ovatum* [4] and *H. spathulatum* [5], although in these latter two species they are developed into prominently swollen nodes.



**Map 1** Distribution map of the ovatum group species. *H. morotaiense* Jebb & C.R.Huxley (◆), *H. ovatum* Miq. (★), *H. spathulatum* Valetton (■), *H. tortuosum* Becc. (●).



**Fig. 7** *Hydrophytum tortuosum* Becc. a. Shoot; b. flower; c. fruit (a: *Jebb 15* (LAE) West Papua Province, 2 km N of Sorong, 10/08/1980; b, c: Beccari (1885) *Tav 37*: 2, 3, 4, 5). — Scale bars: a = 5 cm; b, c = 5 mm. — Drawn by Rosemary Wise.



**Fig. 8** *Hydrophytum ellipticum* Merr. & L.M.Perry. a. Shoot; b. leaf; c. half flower; d. pyrene abaxial face (*Jebb 429* (LAE), Southern Highlands: S6°38' E143°51', 3 km SW of Erave on path to Samberigi). — Scale bars: a, b = 5 cm; c, d = 5 mm. — Drawn by Rosemary Wise.

### GROUP 3 – PETIOLATUM GROUP

#### 7. *Hydrophytum ellipticum* Merr. & L.M.Perry — Fig. 8; Map 2

*Hydrophytum ellipticum* Merr. & L.M.Perry (1945) 19. — Type: *Brass 12111* (A), New Guinea, West Papua Province, 15 km southwest of Bernhard Camp, Idenburg River, Jan. 1939.

*Tuber* irregularly globose, 10–22 cm across. Entrance holes numerous, of two types: the majority prominently lipped (to 0.6 mm tall), 0.15–0.8 cm diam, others fewer, funnel-like, and then 0.9–2 cm across. Roots numerous, scattered on surface, 0.1–1 cm long. Cavities largest in centre, spiral in structure, to 5 cm diam. Warts absent from all cavity walls. *Stems* several, upcurved, branching, to 40 by 0.4 cm; young stems ferruginous; internodes 3–5 cm, rounded to angular; nodes swollen, 1 cm or more across. Lamina lanceolate-elliptic; 4.8 by 1.9 to 8 by 4.3 cm; apex acute to acuminate, ultimately blunt; base attenuate; leathery; midrib prominent above and below; veins 4–8. Petiole 0.3–0.8 cm; stipules minute, caducous. Inflorescence sunken, cup-like alveoli, 0.5–0.7 cm across, with a prominent rim, filled with a dense cushion of hairy bracts to 0.4 cm, and papery bract remains. Bracts persistent on old stems. *Flowers* [3] heterostylous. Calyx entire to 1 mm, sometimes with bract

hairs attached. Corolla tube to 7.5 mm; lobes 2.5 mm; with a broad ring of hairs at mouth of tube and extending to insides of lobes, hairs to 1.6 mm. Short-styled flowers with anthers to 2 mm; exerted on filaments 1 mm long; pollen 41 (38–43)  $\mu\text{m}$  across, brochi 1–2  $\mu\text{m}$ ; stigma 2-fid, below mouth of tube. Long-styled flowers with anthers to 1.5 mm, within mouth of tube; pollen 51 (49–52)  $\mu\text{m}$  across, brochi very fine; stigma, exerted. *Fruit* 6.5 by 3 mm. Pyrenes broad-obovoid 3.5 by 2.7 mm; apex rounded truncate, with a blunt apiculus; base tapered; abaxial side with a longitudinal ridge.

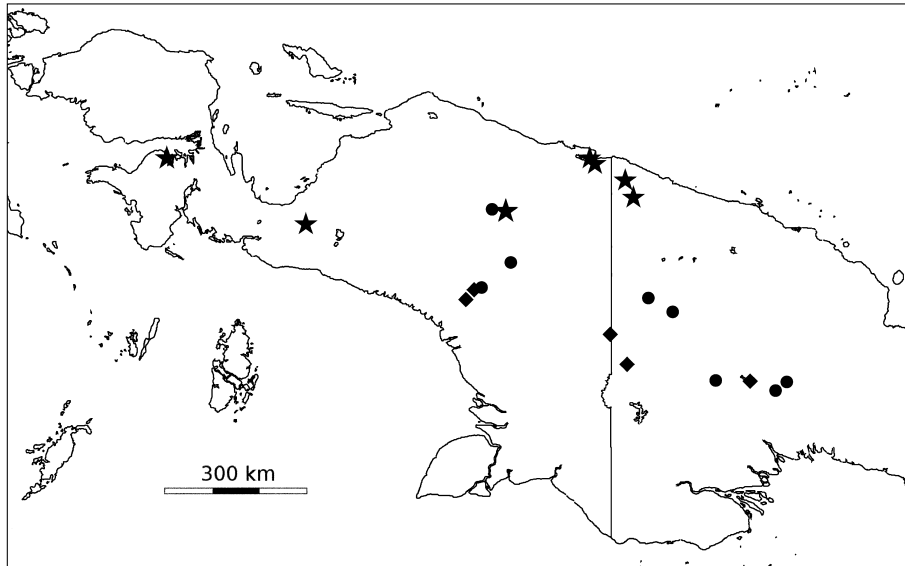
*Ecology & Habitat* — Forest, (? 80–)1070–1840 m. Tuber not inhabited by ants.

*Distribution* — Indonesia (western New Guinea), Papua New Guinea.

*Conservation status* — Least Concern (LC). Whilst probably Vulnerable in some parts of its range, this taxon is widespread across much of central New Guinea with herbarium collections indicating 7 locations (subpopulations). Other information: geo-referenced collections 8, AOO 17 500 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO c. 58 000 km<sup>2</sup>.

*Notes* — Beccari records a *H. ellipticum* in Blume's herbarium, which he synonymised with *H. formicarum blumei* (Beccari



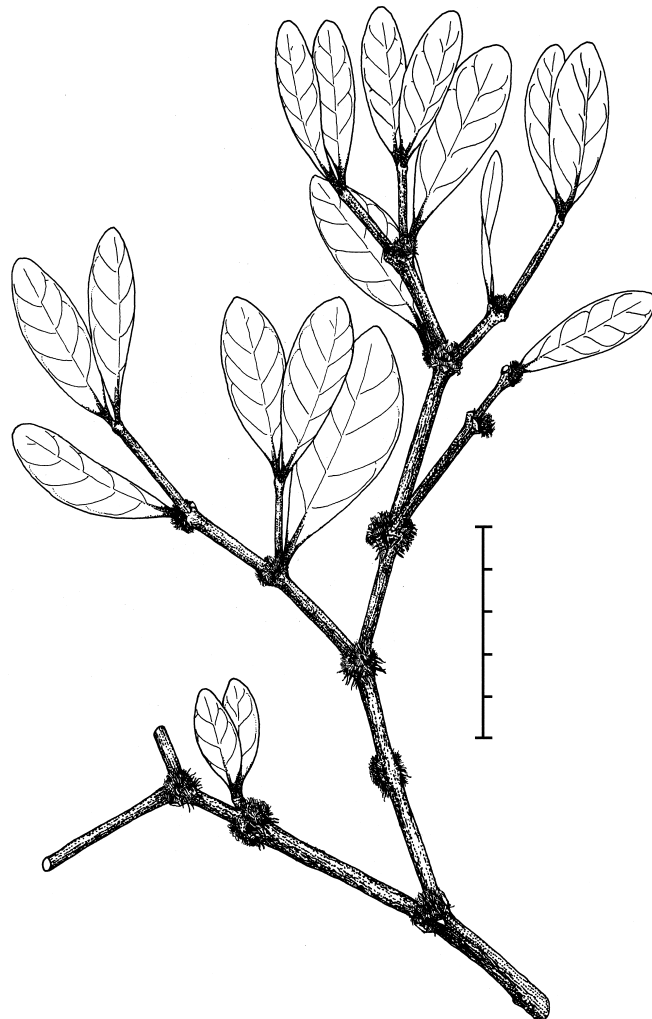


**Map 2** Distribution map of *Hydnophytum ellipticum* Merr. & L.M.Perry (●), *H. lauterbachii* Valeton (◆), *H. magnifolium* Merr. & L.M.Perry (★).

1885: 64). Since no description was given, and no specimen has been traced, we feel it unnecessary to qualify the Merrill and Perry name as a homonym.

A distinctive species with its slender stems and relatively large swollen nodes with pulvinate bract cushions. The leaves are lanceolate and have a midrib prominent above and below. It

can be distinguished from the *H. petiolatum* complex [11] by the more lanceolate leaves (although these are approached by *H. petiolatum* var. *nigrescens* [11g]), and the generally higher altitudes occupied by the present species. *Pulle 307* reputedly comes from low altitude (80 m), and although this may be correct, it is also possible that the measure represents camp data rather than the actual collection site.



**Fig. 9** *Hydnophytum ferrugineum* P.I.Forst (Brass 19885 (K), Australia, Queensland, Leo Creek, Upper Nesbit River). — Scale bar: 5 cm. — Drawn by Eleanor Catherine. Originally published in Buckley (1982).

**8. *Hydnophytum ferrugineum* P.I.Forst. — Fig. 9; Map 3**

*Hydnophytum ferrugineum* P.I.Forst. (2001) 103. — Type: *P.I. Forster* PIF21406 et al. (holo BRI (3 sheets + spirit); iso K, MEL), Australia, Queensland, Cook District, Timber reserve 14, Leo Creek, 9 July 1997. *Hydnophytum* sp.1 Huxley, in Buckley (1982) 72.

*Tuber* globose to 30 cm diam, silvery in colour, covered by entrance holes. *Stems* 1–3, branching, internodes 1.5–4.5 cm, nodes swollen. *Leaves* variable in size. Lamina oblong-lanceolate to obovate, 3.5 by 1 to 6 by 2.5 cm; apex rounded; base cuneate; midrib prominent on both sides; veins 4 or 5. *Petiole* 0–0.6 cm. *Inflorescence* sunken, with a mass of brown bract hairs to 1.2 cm across. *Flowers* [1] ?not heterostylous. *Corolla tube* 2–3.5 mm; lobes 2 by 1.5 mm; with a broad ring of hairs at mouth of tube; anthers 1.2 by 0.5mm within mouth of tube; stigma immediately above anthers.

*Ecology & Habitat* — Canopy epiphyte of ridge forest, 100 m.

*Distribution* — Endemic to Australia (Queensland).

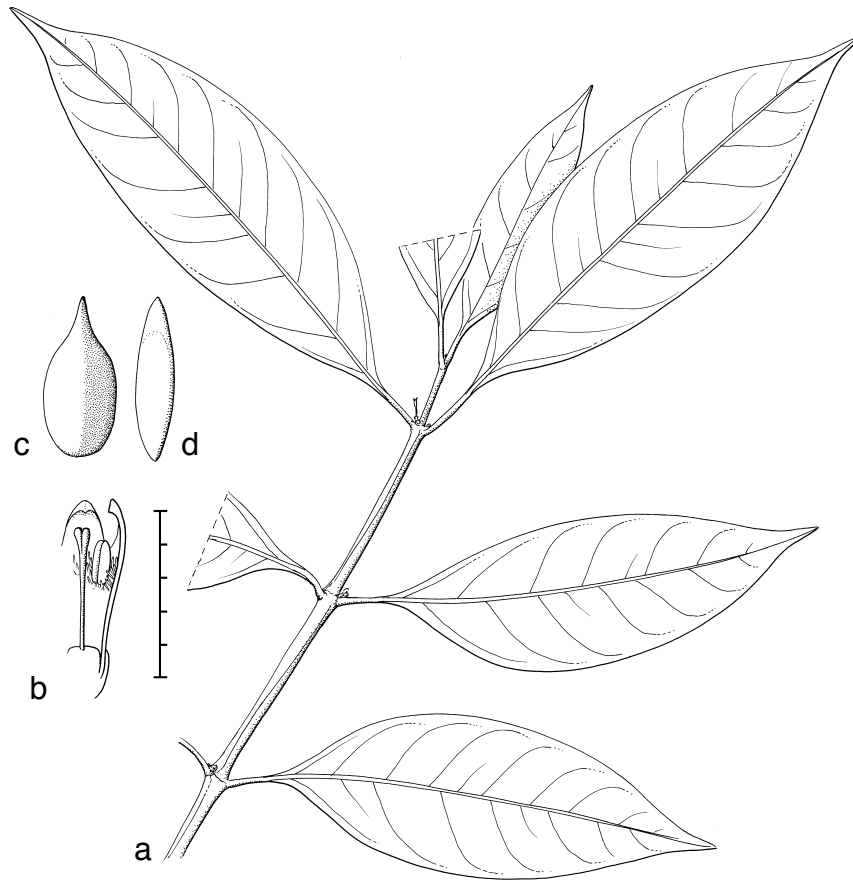
*Conservation status* — Vulnerable (VU) under criteria D2 with only the type locality known. Forster (2001) has previously classified this taxon as Vulnerable under former guidelines as VU, C2, D1, D2.

*Note* — We had intended assigning this taxon as a further variety of *H. petiolatum* [11], and *Brass 19885* is labelled as the type of '*H. petiolatum* var. *australiense*'. However, Forster (2001) has since published the taxon as a species, and the name and rank are retained here.

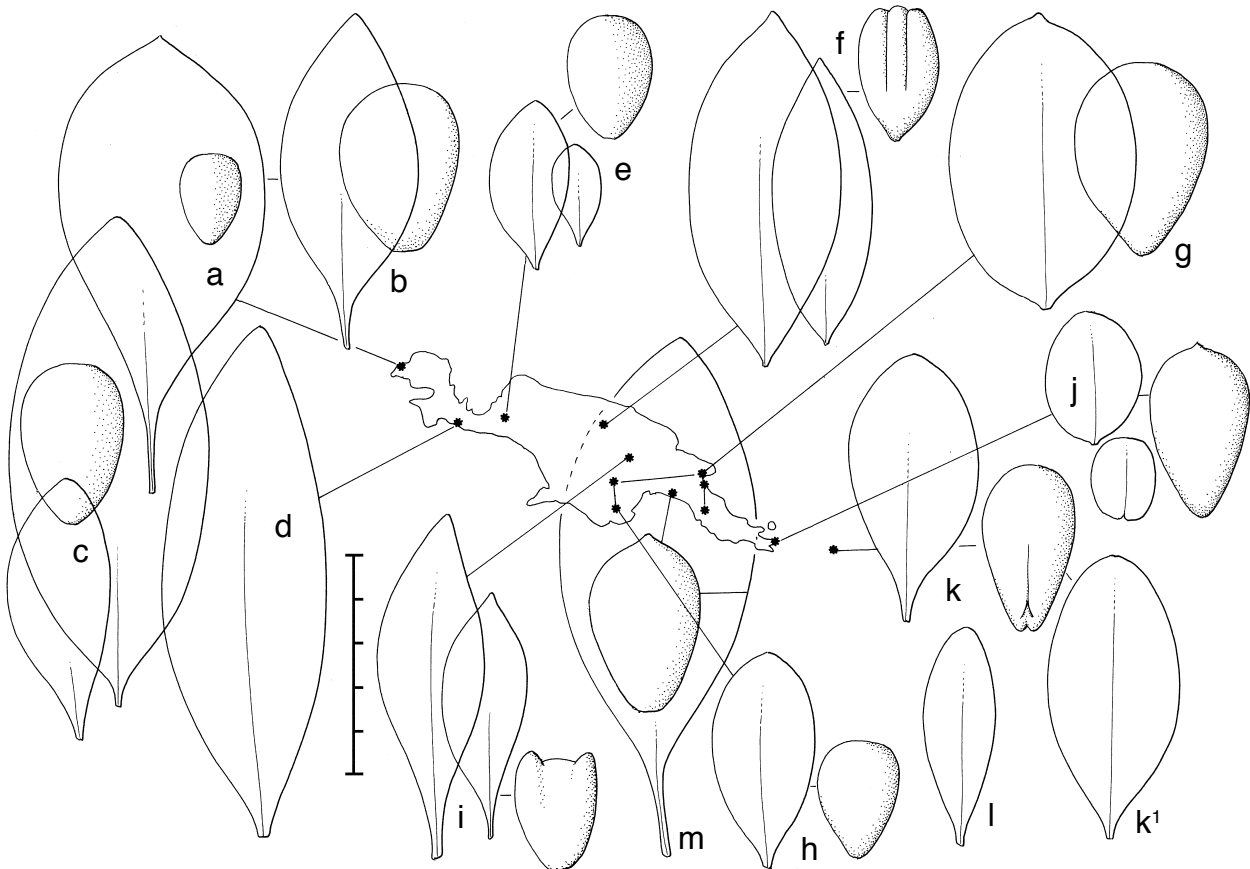
**9. *Hydnophytum lauterbachii* Valeton — Fig. 10; Map 2**

*Hydnophytum lauterbachii* Valeton (1911) 505. — Type: *Versteeg* 1226 (lectotype selected here L; iso BO, K), New Guinea, Papua Province, S5°00' E138°30' Noordrivier (= Lorentz river), Sept. 1907.

*Tuber* 15 cm or more across; surface smooth. Entrance holes few, conical, to 1 cm across. Spines occasional, scattered, erect, flexible, blunt, to 0.6 cm in length. Cavities few, tuber somewhat fleshy. *Stems* several, to 50 by 1 cm, sparsely



**Fig. 10** *Hydnoophytum lauterbachii* Valetou. a. Shoot; b. half flower; c. pyrene abaxial face; d. pyrene lateral view (a: *Versteeg 1776* (L), Papua Province, Noord-riber; b–d: *Soegeng Reksodihardjo 363* (L), Papua Province, Ingembit to Opka village). — Scale bars: a = 5 cm; b–d = 5 mm. — Drawn by Rosemary Wise.



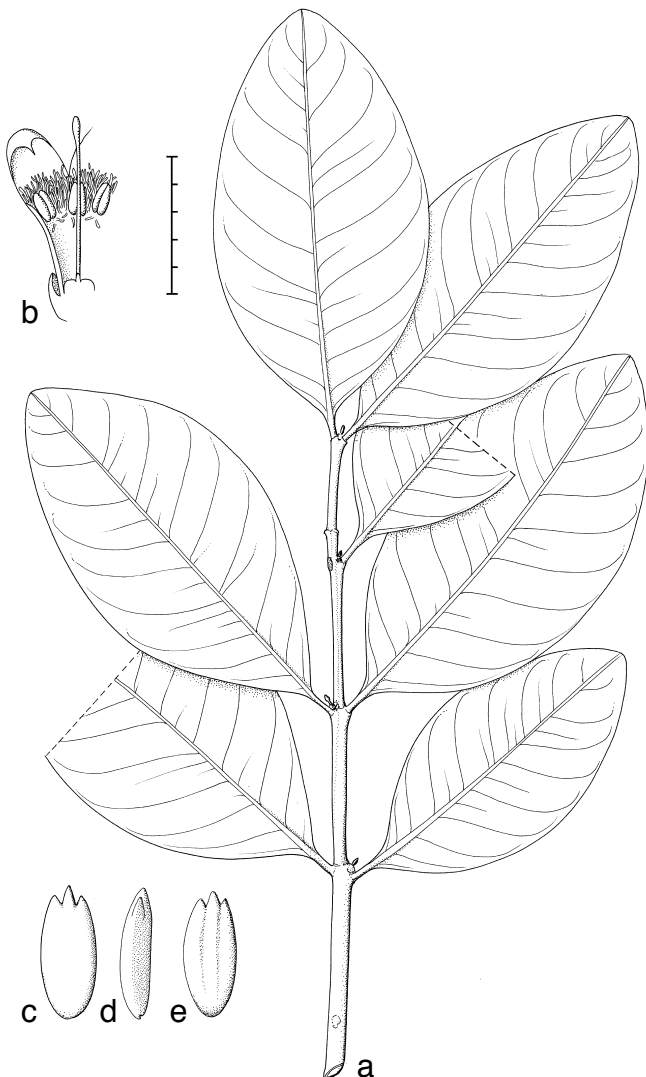
**Map 3** Leaf outlines and pyrene shapes of varieties of *Hydnoophytum petiolatum* Becc. in New Guinea. a–d. var. *petiolatum*; e. var. *lacum*; f. var. *ledermanii*; g, h. var. *contortum*; i. var. *nigrescens*; j. var. *argentatum*; k, k<sup>1</sup>. var. *auridemans*; l. *H. ferrugineum* P.l.Forst.; m. *H. petiolatum* aff. (a: *Beccari 187*; b: *Van Royen 3151*; c: *Van Royen 3090*; d: *Koch 26*; e: *Eyma 5069*; f: *Ledermann 12925*; g: *Jebb 307*; h: *Brass 5849*; i: *Brass 7171*; j: *Jebb 375*; k: *Jebb 395*; k<sup>1</sup>: *Brass 27390*; l: *Brass 19885*; m: *Gray & Floyd NGF 8024*). — Scale bars: 5 cm for leaves; 5 mm for pyrenes. — Drawn by Rosemary Wise.

branched; internodes 1.5–9.5 cm, rounded sometimes with prominent ridges. *Leaves* spreading. Lamina lanceolate, 9 by 3.5 to 17 by 5.5 cm; apex acuminate; base attenuate; thin to fleshy, dull dark green above, green below; midrib prominent below; veins 6–12. Petiole 1–2 cm; stipules minute, papery, caducous. Inflorescence paired, on small mounds to 0.5 cm across. Bracts minute, caducous. *Flowers* [4] not heterostylous. Calyx entire, to 1.5 mm. Corolla tube 3.5–4 mm, lobes 1.5–3.5 mm; with a broad ring of hairs at mouth of tube. Anthers 1.5 mm, in mouth of corolla tube. Pollen 57–63  $\mu\text{m}$ , brochi 1–1.5  $\mu\text{m}$ ; vesicles 15–20  $\mu\text{m}$ . Stigma 2-lobed, above anthers. *Fruit* to 6 mm, orange. Pyrenes ellipsoid, 5 by 2.5 mm, abaxial surface with a prominent central ridge; apex apiculate; base acute to rounded.

**Ecology & Habitat** — Unknown, low altitude. Tuber probably ant-inhabited.

**Distribution** — Indonesia (western New Guinea) and Papua New Guinea.

**Conservation status** — Vulnerable (VU) under criteria B1ab(iii)+2ab(iii). This taxon is widespread across much of the lowlands of south-central New Guinea (625 km extent) with herbarium collections indicating 5 locations (subpopulations). Other information: georeferenced collections 5, AOO 12 500 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO c. 16 000 km<sup>2</sup>.



**Fig. 11** *Hydnophytum magnifolium* Merr. & L.M.Perry. a. Shoot; b. flower; c. pyrene abaxial face; d. pyrene lateral view; e. pyrene adaxial view (a: *Brass* 13768 (A, L), Papua Province, Bernhard Camp, Idenburg river, April 1939; b–d: *Brass* 14130, type). — Scale bars: a = 5 cm; b–e = 5 mm. — Drawn by Rosemary Wise.

**Note** — A low altitude species from the southern slopes of the central cordillera of New Guinea. The large, thin, and petiolate leaves and a mound-like inflorescence are characteristic. Differs from *H. magnifolium* [10] in the larger, apiculate pyrenes which are not 3-lobed at the apex.

**10. *Hydnophytum magnifolium* Merr. & L.M.Perry** — Fig. 11; Map 2

*Hydnophytum magnifolium* Merr. & L.M.Perry (1945) 15. — Type: *Brass* 14130 (lectotype selected here A; iso L), New Guinea, Papua Province, Bernhard Camp, Idenburg river, Apr. 1939.

*Tuber* subglobose, to 50 cm diam, surface smooth. Entrance holes conical to 0.6 cm across. *Stems* several, branching, to 90 cm long. Internodes 1–6 by 0.2–0.6 cm. *Leaves* shortly petiolate. Lamina lanceolate to elliptic; 3.2 by 1 to 16 by 8 cm; apex acute-acuminate; base attenuate; midrib prominent below, veins 6–10. Petiole 0.4–1 cm; stipules inconspicuous, triangular, to 0.2 cm, papery, caducous. Inflorescence paired, sessile to mound-like. Bracts few, papery to 2 mm. *Flowers* [4] heterostylous. Calyx entire, to 2 mm. Corolla tube 4.5–6 mm; lobes 2 mm; a broad ring of hairs immediately within mouth of tube and partly exerted. Short-styled flowers with anthers exerted on filaments to 1.5 mm; pollen 3-porate, 62 (57–73)  $\mu\text{m}$ , brochi 1  $\mu\text{m}$ , vesicles and pores small; stigma 2-lobed, 1/2 way up tube. Long-styled flowers anthers 1 mm, within mouth of tube; pollen 3-porate, 52 (50–54)  $\mu\text{m}$ , brochi 1  $\mu\text{m}$ , vesicles and pores small; stigma exerted. *Fruit* 5 by 2.5 mm, red. Pyrenes ellipsoid to obovoid to obtriangular, 4.5 by 2 mm; apex truncate with three acute to rounded lobes, the middle one longest; abaxial surface prominently ribbed with 2 furrows; base tapering or rounded.

**Ecology & Habitat** — Forest, sea level to 600 m. Only once recorded with ants.

**Distribution** — Indonesia (western New Guinea) and Papua New Guinea.

**Conservation status** — Least Concern (LC). Whilst probably Vulnerable in some parts of its range, this taxon is widespread across much of the north coast of New Guinea with herbarium collections indicating 5 locations (subpopulations). Other information: georeferenced collections 10, AOO 17 500 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO c. 78 500 km<sup>2</sup>.

**Note** — Differs from *H. lauterbachii* [9] in its thicker lamina, smaller, more papery inflorescence bracts and 3-lobed pyrene apex. It is confined to the north coast of western New Guinea, while *H. lauterbachii* is a south coast species.

**11. *Hydnophytum petiolatum* Becc.** — Fig. 12, 13; Map 3

*Hydnophytum petiolatum* Becc. (1884) 124; (1885) 144, t. 34. — Type: *Beccari* PP 187 (lectotype selected here FI; iso K), Sorong, West Papua Province, 1872.

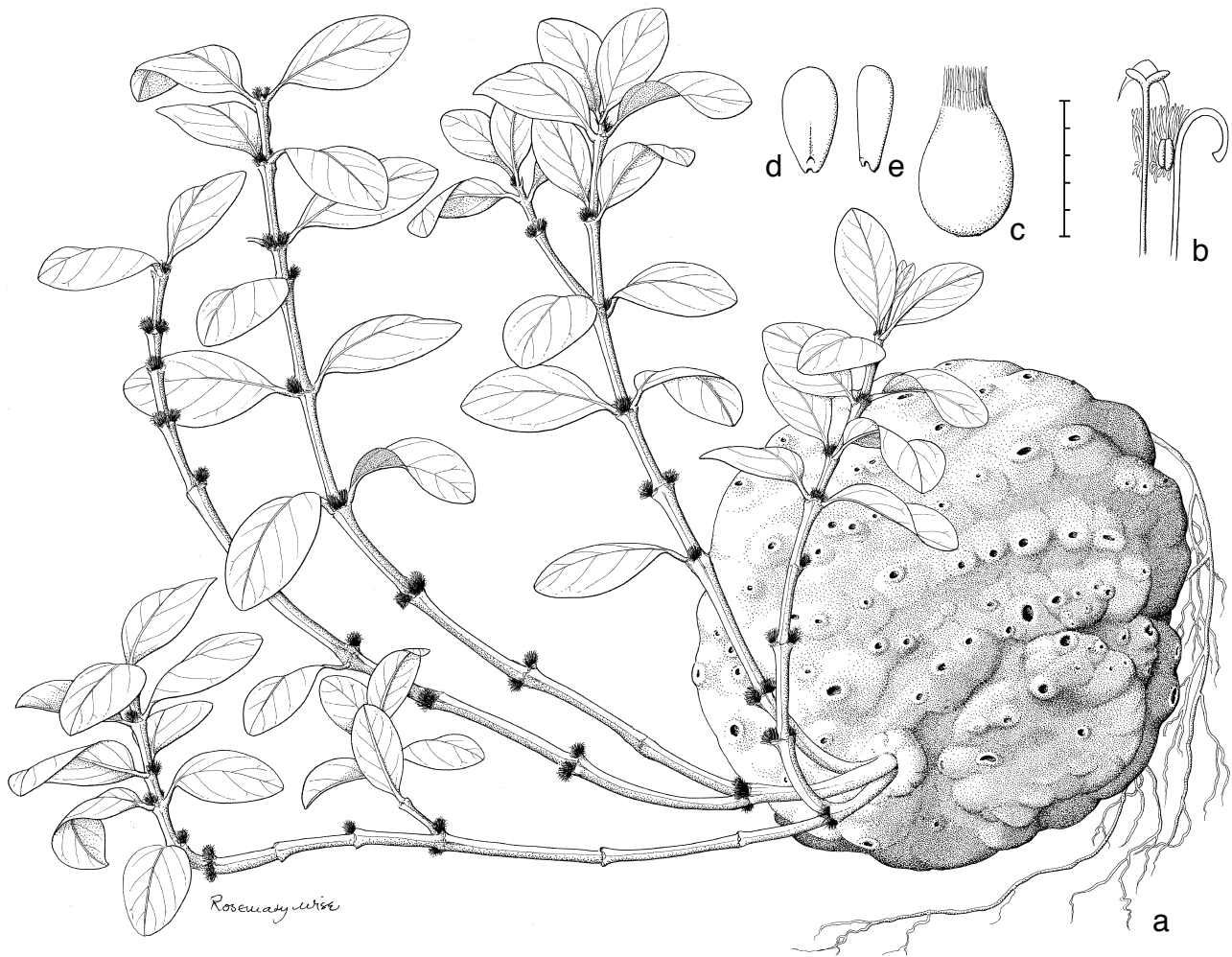
*Hydnophytum kochii* Valetton (1911) 507. — Type: *Koch* 26 (lectotype selected here L; iso BO), West Papua Province, Fakfak, 23 Nov. 1904, syn. nov.

*Hydnophytum ledermannii* Valetton (1927) 134. — Type: *Ledermann* 12925 (B presumed lost), Papua New Guinea, Sepik River, syn. nov.

*Hydnophytum nigrescens* Merr. & L.M.Perry (1945) 16. — Type: *Brass* 7171 (lectotype selected here A; iso BM, BRI), Papua New Guinea, Western Province, Palmer River, 2 miles below junction Black River, ridge forests, July 1936, syn. nov.

*Hydnophytum contortum* Merr. & L.M.Perry (1945) 17. — Type: *Brass* 5849 (lectotype selected here A; iso BO, BRI, CAL), Papua New Guinea, Western Province, Wuoi, Oriomo River, Mar. 1934, syn. nov.

*Tuber* globose, to 50 cm across; surface smooth, brown to grey to silvery. Entrance holes of various sizes, 0.1–1 cm across, rounded, lipped. Cavities warted and smooth-walled. *Stems* numerous, branching, sometimes zigzagged; nodes swollen, especially when fertile. Lamina lanceolate to cordate-ovate;



**Fig. 12** *Hydrophytum petiolatum* Becc. var. *auridemans* Jebb & C.R.Huxley. a. Whole plant; b. flower dissection; c. fruit; d. pyrene adaxial face; e. pyrene lateral view (a, b: Jebb 398; c–e: Jebb 396). — Scale bars: a = 10 cm; b–e = 10 mm. — Drawn by Rosemary Wise.

2 by 1.2 to 11 by 5 cm; apex rounded to acute, base cordate to cuneate; midrib prominent below, or more rarely prominent on both sides; leathery, often drying a reddish brown colour. Petiole 0–2 cm; stipules triangular or blunt, to 0.5 cm, persistent becoming part of inflorescence margin. Inflorescence paired, sunken, cup-like, with a mass of reddish bract hairs, sometimes with numerous papery bract remains; 0.4–1.5 cm across. *Flowers* heterostylous. Calyx 1–2 mm, entire or with a fringe of brown hairs. Corolla tube 2–6 mm, lobes 2–5 mm, tube with a broad ring of hairs at mouth and base of lobes. Anthers 1–2 mm long, exserted or within mouth of tube. Pollen 36–60  $\mu\text{m}$ , brochi 0.5–2.5  $\mu\text{m}$  across; characteristic of many of the individual varieties are the irregular vesicles, with one often larger than the remaining two. Stigma above or below anthers. *Fruit* obovoid, 3–6 mm, with prominent calyx remains, orange to red. Pyrenes obovoid, 2.5 by 1.5–4 by 2.5 mm; apex rounded to truncate, sometimes 3-lobed; base tapering, blunt.

**Ecology & Habitat** — Mangrove forest or coastal trees to forest, open or disturbed areas, including forest on nutrient-poor soils, sea level to 1800 m. Tubers sometimes inhabited by ants, sometimes not.

**Notes** — This taxon has not been satisfactorily resolved, however, it seems to us that the lumping of these five species is the most reasonable step to take with our current knowledge. Rather than obscure the variation, seven geographic varieties are recognised, three of which are illustrated. The chorology of leaf and pyrene shapes are presented on Map 3. All these varieties share the following features: stems contorted, zigzagged at nodes; leaves leathery or fleshy, drying a characteristic reddish

brown colour; inflorescences socket-like, and usually filled with dense, reddish brown bract hairs, which become more prominent on dried specimens; calyx with hairs strongly attached to its outer surface, and sometimes to its margin.

**Distribution** — Indonesia (western New Guinea) and Papua New Guinea. Individual variants are distributed as follows:

Variant	Distribution
11a. var. <i>petiolatum</i>	New Guinea.
11b. var. <i>argentatum</i>	Normanby Is., PNG.
11c. var. <i>auridemans</i>	Misima Is, PNG.
11d. var. <i>contortum</i>	Western, Central, Morobe, PNG.
11e. var. <i>lacum</i>	Wissel lakes, West Papua Province.
11f. var. <i>ledermannii</i>	Sepik, PNG.
11g. var. <i>nigrescens</i>	Western, PNG.

#### **a. var. *petiolatum***

*Hydrophytum petiolatum* Becc.

*Hydrophytum kochii* Valetton.

**Tuber** globose. **Stems** numerous, branching, nodes swollen. Lamina elliptic, 6 by 2.5 to 11 by 4 cm; apex rounded-acute; base rounded, abruptly attenuate. Petiole 0.5–2 cm; stipules triangular, to 0.2 cm, caducous. Inflorescence socket-like to somewhat pulvinate cushions of bract hairs, to 1.2 cm across. **Flowers** [4] heterostylous. Calyx 1.5 mm, entire. Corolla tube to 4 mm; lobes 2 mm; tube with a broad ring of hairs within mouth of tube. Short-styled flowers with anthers to 2 mm, exserted on 1 mm filaments; stigma within mouth of tube. Long-styled flowers with anthers to 1.5 mm, at mouth of tube; stigma exserted.

Pollen 3-porate, 57 (54–59)  $\mu\text{m}$ , pores and vesicles large, brochi 2–3  $\mu\text{m}$ . *Fruit* ellipsoid to obovoid, 5 by 4 mm. Pyrenes obovoid, 3.5 by 3 mm; apex and base rounded.

**Ecology & Habitat** — Mangrove swamp to lowland forest, to 100 m. Tuber inhabited by ants.

**Distribution** — Indonesia (western New Guinea), Papua New Guinea (Sepik Province).

**Conservation status** — Least Concern (LC). Known from just five locations but with a geographical spread of 1300 km this taxon is enigmatic. The figures for AOO and EOO are probably uninformative in view of the sparse numbers. Other information: AOO 10000 km<sup>2</sup> (using an auto-value cell width of 50 km) and EOO of 135000 km<sup>2</sup>.

**Note** — The type of *H. kochii* has somewhat oblong leaves compared to those of *H. petiolatum*, but in other characters the collections are a close match.

**b. var. *argentatum*** Jebb & C.R.Huxley, *var. nov.* — Map 3

*a Hydnophytum petiolatum* sed tuber oblongum, angulari, superficies laevis, argentum coloratum. Folia subsessilia, lamina subrotunda usque ovata, 1.1 per 0.8 ad 3.4 per 3 cm, apice obtusa vel rotundato, basi obtusa vel cordata, nervi obscurato 4–5. Petiolus brevissimus. Pyrenae obovoideae, 4 per 2.5 mm, apice rotundato vel acuminato minuto, basi attenuata. — *Typus: Jebb 376* (holo K; iso L, LAE, UPNG), Papua New Guinea, Milne Bay Province, Normanby Island, Mt Bwebwesu, 6 June 1983.

**Etymology.** For the silver colour of the tuber surface in the living plant.

*Tuber* oblong-ovoid, angular, to 25 by 14 cm, silvery-grey in colour. Entrance holes varied in size, 0.2–1.8 cm, all more or less prominently lipped. *Stems* numerous, regularly branching, rounded in section; nodes swollen, to 7 mm across, internodes 0.4–4.5 cm. *Leaves* clustered at stem apices. Lamina round-elliptic; 1.1 by 0.8 to 3.4 by 3.0 cm; apex blunt to rounded; base blunt to cordate; veins 4 or 5; drying dark above pale below. Petiole very short; stipules triangular, 0.1 cm, persistent becoming worn. Inflorescence sunken, 0.4–0.5 cm across, and densely filled with papery bract remains and bract hairs to 0.3 cm long. *Flowers* [5] heterostylous. Calyx 1.5 mm, entire, with a large number of brown bract hairs arising from its surface, and persistent in fruit. Corolla tube to 4.5 mm, lobes 2 mm, with a ring of hairs at mouth of tube. Short-styled flower with anthers exerted, to 1.5 mm, pollen 38–45  $\mu\text{m}$  diam; stigma at or slightly below anthers. Long-styled flower with anthers within tube, to 1 mm, pollen 35–37  $\mu\text{m}$  diam; stigma exerted. *Fruit* 4.5 by 3 mm, red. Pyrenes obovoid, 4 by 2.5 mm; apex rounded, minutely acuminate; base attenuate.

**Ecology & Habitat** — Only known from the stunted, scrub forest on ultrabasic soils in southern Normanby Island, from 400–600 m (*H. dentrecastense* [43] and *Anthorrhiza areolata* C.R.Huxley & Jebb (1991b) are also endemic to this area of vegetation). The tuber cavities contain rainwater and cockroaches.

**Distribution** — Papua New Guinea (Normanby Island).

**Conservation status** — Vulnerable (VU) under criteria D2 with a single population known from an area of ultramafic soils identified as a source of future nickel and gold mining. The entire area covers less than 20 km<sup>2</sup>, but it is not known whether this epiphyte is found further afield.

**Additional specimens examined.** *Jebb 375* (LAE), *Jebb 377* (A), *Jebb 378* (LAE), *Jebb 379* (LAE), Milne Bay Province, Normanby Island: S10°02' E151°00', NW slopes of Mt Bwebwesu, above Sewa Bay, 6 June 1983.

**Note** — This variant has slender, much contorted stems, and small, almost circular leaves. The tuber has a smooth surface, with prominently lipped entrance holes. It is named for the striking metallic silver-coloured surface of the tuber.

**c. var. *auridemens*** Jebb & C.R.Huxley, *var. nov.* — Fig. 12; Map 3

*a Hydnophytum petiolatum* sed tuber cum aperturae numerosae, labrosae, 0.3 ad 0.9 cm in diametro. Lamina obovata usque ovata, 6 per 3 ad 7.5 per 4 cm, apice obtusa acuta, basi sensim attenuata, nervi 6 vel 7. Petiolus ad 0.7 cm. Pyrenae obovoideae, 4 per 2 mm, apice rotundato, basi cuneata. — *Typus: Jebb 397* (holo K; iso L, LAE), Papua New Guinea, Milne Bay Province, Misima Island, Mt Sisa, 11 June 1983.

**Etymology.** Latin for gold-madness, for the human obsession with seeking gold.

*Tuber* globose, flattened, to 30 by 20 cm, light brown. Entrance holes numerous, lipped, from 0.3–0.9 cm across (internal); arranged in linear to curved arrays. *Stems* numerous, branching, to 60 cm long; internodes 1.5–8 by 0.2–0.8 cm, rounded, with 4 fine ridges; young stems ferruginous. *Leaves* spreading. Lamina obovate to ovate; 6 by 3 to 7.5 by 4 cm; apex blunt-acute, base tapering; leathery, brittle, dark glossy green above, pale below; midrib prominent above and below, and distinct to very apex, veins 6 or 7. Petiole 0.7 cm; stipules 0.2–0.3 cm, triangular, papery, caducous. Inflorescence sunken, with a dense cushion of bract hairs 0.3–0.5 cm in length, forming a mass 1–1.5 cm across. *Flowers* [4] heterostylous. Calyx 1.5 mm, densely clothed with bract hairs, and with a margin of hairs persistent in fruit. Corolla tube to 5 mm; lobes rounded-triangular, to 3 mm; with a ring of hairs within and exerted from mouth of tube. Short-styled flowers with anthers to 2 mm, exerted; pollen 44  $\mu\text{m}$  diam; stigma below anthers. Long-styled flowers with anthers 1.5 mm, within tube; pollen 37  $\mu\text{m}$  diam; stigma exerted. *Fruit* 6 mm, ovoid, orange-red. Pyrenes obovoid, 4 by 2 mm; apex rounded; base tapered, notched.

**Ecology & Habitat** — High to middle-level epiphyte in open forest, 300–400 m. Tuber inhabited by ants.

**Distribution** — Papua New Guinea (Misima Island).

**Conservation status** — Vulnerable (VU) under criteria D2 with a single population known from Misima island, the site of a major gold lode and potential mine site. The entire island is under 200 km<sup>2</sup> in extent and less than 50 % of that area remains forested.

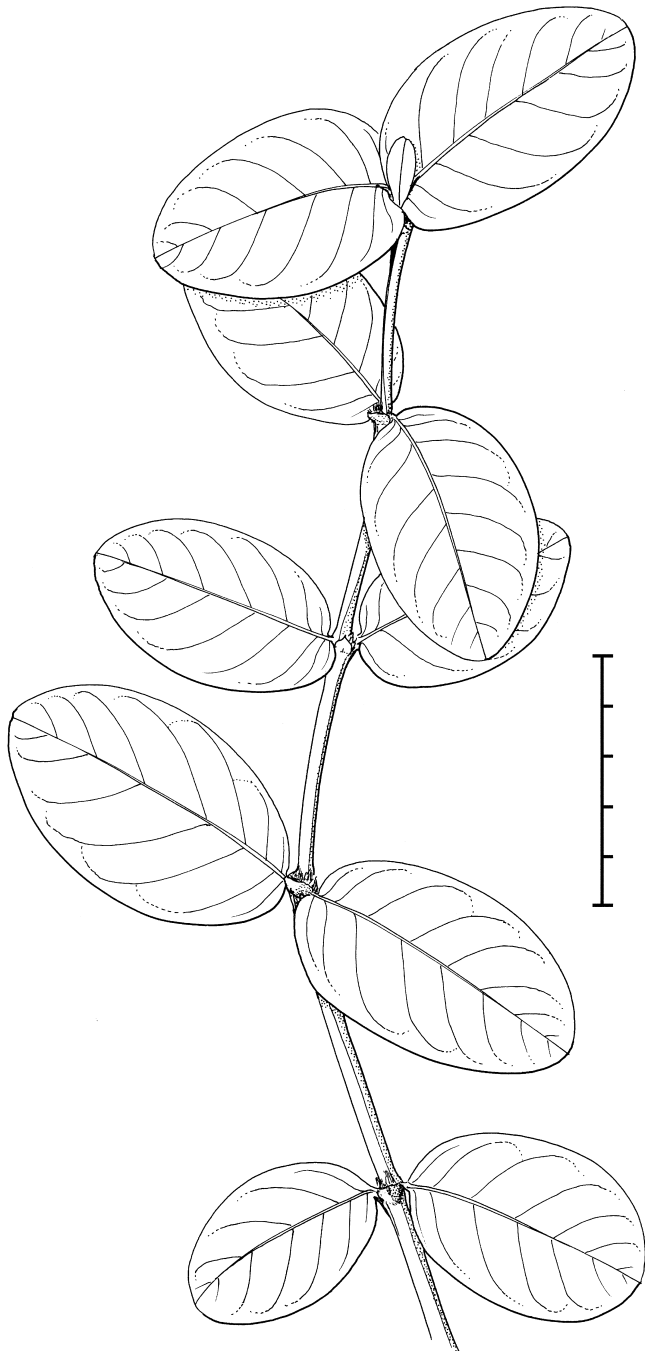
**Additional specimens examined.** *Brass 27390* (A, L), S slopes of Mt Sisa, 1956; *Jebb 395* (BRI), *Jebb 396* (CANB, LAE), *Jebb 398* (A, LAE), Louisiade Archipelago, Misima Island, S10°39' E152°48', NE slopes of Mt Sisa, 11 June 1983.

**Note** — The pulvinate cushions of bract hairs and the thinner leaves are characteristic of this variety. It is named for the gold rush currently taking place on the island, which has removed almost the entire forest cover from Mount Sisa, and which will probably exterminate much of the endemic flora.

**d. var. *contortum*** (Merr. & L.M.Perry) Jebb & C.R.Huxley, *stat. nov.* — Fig. 13; Map 3

**Basionym:** *Hydnophytum contortum* Merr. & L.M.Perry, J. Arnold Arbor. 26 (1945) 17. — *Type: Brass 5849* (lectotype selected here A; iso BO, BRI, CAL), Papua New Guinea, Western Province, Wurui, Oriomo River, Mar. 1934.

*Tuber* globose, to 30 cm across, surface smooth, grey to brown. Entrance holes of various sizes, 0.1–1 cm across, rounded, large holes lipped. *Stems* numerous, to 20(–30) by 0.5 cm, branching; internodes angular to rounded, 1–4 by 0.5 cm, nodes to 1.2 cm across, contorted. *Leaves* subsessile. Lamina elliptic to broad-obovate; 3 by 1.5 to 6 by 4 cm; apex rounded; base tapering, rounded and abruptly attenuate; midrib prominent below, veins 4–6; leathery, brittle; drying brownish red. Petiole 0–0.3 cm; stipules to 0.2 cm, caducous. Inflorescence sessile to sunken, usually with a dense cushion of bract hairs to 1 cm across. *Flowers* [4] heterostylous. Calyx 1 mm, entire, with



**Fig. 13** *Hydnophytum petiolatum* Becc. var. *contortum* (Merr. & L.M.Perry) Jebb & C.R.Huxley (Jebb 310 (LAE), Madang Province, 1 mile east of Lae). — Scale bar: 5 cm. — Drawn by Rosemary Wise.

attached bract hairs to 1.5 mm long. Corolla tube 8 mm; lobes 3 mm; tube with a broad ring of hairs at mouth. Short-styled flowers with anthers to 1 mm, exerted on 1 mm filaments; pollen 3-porate, 57 (48–60)  $\mu\text{m}$ , brochi 2  $\mu\text{m}$ ; stigma within mouth of tube. Long-styled flowers with anthers within mouth of tube; pollen 3-porate, 64 (59–66)  $\mu\text{m}$ , brochi > 2  $\mu\text{m}$ ; stigma immediately above anthers. *Fruit* ellipsoid, to 8 by 4.5 cm, with prominent hairy calyx remains. Pyrenes obovoid-obtriangular, to 4.5 by 3 cm; apex rounded; base tapering.

**Ecology & Habitat** — Mangrove forest to lowland forest, sea level to 200 m. Tuber usually inhabited by ants, and then by a range of ant species.

**Distribution** — Papua New Guinea (Western, Central and Morobe Provinces).

**Conservation status** — Least Concern (LC). Whilst probably Vulnerable in some parts of its range, this taxon is widespread across much of Papua New Guinea with herbarium collections

indicating at least six locations (subpopulations). Other information: georeferenced collections 12, EOO c. 160 000 km<sup>2</sup>.

**Note** — The almost sessile, rounded leaves, short contorted internodes and hairy calyx distinguish this variant. It has a wide distribution in Papua New Guinea.

**e. var. *lacum*** Jebb & C.R.Huxley, var. *nov.* — Map 3

*a Hydnophytum petiolatum* sed lamina ovata usque obovata, 1.6 per 1 ad 3.8 per 1.9 cm, apice acuto usque brevissime acuminato, basi rotundato usque cuneato, nervi obscurato 4 vel 5. Petiolus ad 1 cm. Stipulae ad 0.3 cm, triangulares, persistentes. Pyrenae obovoideae, 3.2 per 1.7 mm, apice rotundato. — Typus: *Eyma* 4851 (holo BO), New Guinea, Papua Province, Enarro valley, Apr. 1939.

**Etymology.** For the characteristic lakes of the type locality.

*Tuber* irregularly globose; 19 by 15 cm to much larger; often pendulous; surface brown, smooth. Entrance holes of two types: lipped and 1–1.5 cm overall; funnel-like to 4 cm across. *Stems* several, spreading to erect, to 60 by 0.3–0.7 cm; regularly branched, angular in section, internodes 0.5–6 cm, nodes slightly swollen, grey-brown in colour. Lamina ovate to obovate; 1.6 by 1 to 3.8 by 1.9 cm; apex acute to minutely acuminate; base rounded to cuneate; midrib prominent above and below, veins obscure 4 or 5. Petiole 1 cm; stipules triangular, to 0.3 cm, papery, somewhat persistent. Inflorescence sessile, bract-covered, the bracts leathery to 0.5 cm, with dense reddish brown hairs within. *Flowers* [2] heterostylous. Calyx to 1 mm, with a margin of septate hairs to 1 mm. Corolla tube to 2.5 mm; lobes 1.5 mm; with a ring of hairs at mouth of tube. Short-styled flowers with anthers to 1.5 mm, exerted from tube; pollen 3-colpate, 49 (48–51)  $\mu\text{m}$ , brochi 2–2.5  $\mu\text{m}$ ; stigma at level of anthers. Long-styled flowers with anthers within mouth of tube; pollen 3-colpate, 37–42  $\mu\text{m}$ , brochi 1–2  $\mu\text{m}$ ; stigma above level of anthers. *Fruit* ovoid, 6 mm, orange. Pyrenes obovoid, 3.2 by 1.7 mm; apex rounded; base tapering.

**Ecology & Habitat** — A low-level epiphyte of shady, mossy forest, 400–1770 m. Tuber not inhabited by ants.

**Distribution** — Indonesia (Papua Province).

**Conservation status** — Endangered (EN) under criteria B1ab(iii)+2ab(iii). The four locations occur to the north and south of the Weyland Mountain range suggesting it is likely to have a greater distribution. Other information: EOO of 770 km<sup>2</sup> and AOO of 377 km<sup>2</sup> (using an auto-value cell width of 10 km).

**Additional specimens examined.** *Kanehira & Hatusima* 12265 (A, BO, FU 2 sheets), Wissel, Dalman, 25 km inland from Nabire; *Eyma* 4851 (BO), Wissel Lakes, Upper Enarro Valley and Poeraida ridge, near Enarotali; *Eyma* 4812 (BO), *Eyma* 5069 (BO) Wissel Lakes, Cape Weremoeka.

**Note** — The minute leaves make these collections similar to several high altitude species found in western New Guinea (group 5); however, the swollen nodes with alveoli densely filled with bract hairs, and the rounded leaves which dry glossy yellow below indicate its affinity with the *H. petiolatum* complex. Named for the Wissel (Paniai) lake region from where it has been collected.

**f. var. *ledermannii*** (Valeton) Jebb & C.R.Huxley, *stat. nov.* — Fig. 14; Map 3

**Basionym:** *Hydnophytum ledermannii* Valeton, Bot. Jahrb. Syst. 61 (1927) 134. — Type: *Ledermann* 12925 (B presumed lost), Papua New Guinea, Sepik River. Epitype Valeton drawing (= Fig 14).

**Description ex Valeton.**

*Tuber* stock pendulous, 0.5 m diam. *Stems* round. Branches slightly flattened, rugose-furfuraceous, nodes thickened, internodes 2–5 cm long. *Leaves* shortly petiolate, 0.2–0.3 cm, lamina generally elliptic 45–65–75 by 22–38 mm, subacumi-

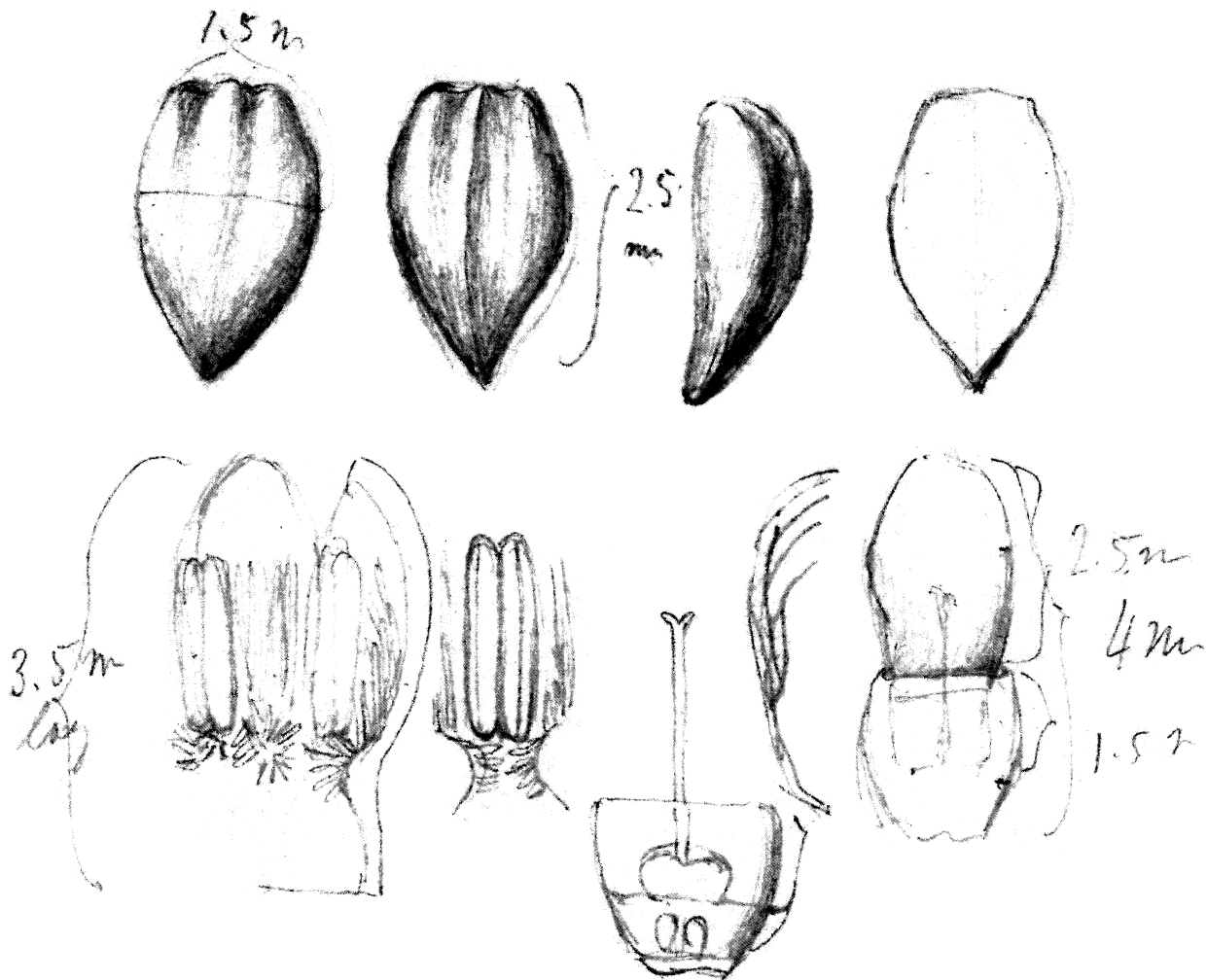


Fig. 14 *Hydnophytum petiolatum* Becc. var. *ledermannii* (Valeton.) Jebb & C.R.Huxley (MS notes of Theodore Valeton at Leiden).

nate acute, base generally obtuse or subrotund, leathery, drying reddish olive. Midrib prominent below, obliterated towards apex; nerves c. 8 inconspicuous below, scarcely visible above, erect-spreading curved. Inflorescences in prominently swollen nodes, base of leaves almost adnate to deeply immersed in slender young bracts, on the inside completely clothed with long, dense, totally enclosed, brown hairs, exerted at anthesis, opening unknown, probably long-styled. Calyx cupuliform, short 1.5 mm, much longer than disc. Corolla club-like in bud, below the anthers somewhat constricted within, with a swollen annulus, with dense hairs below the apparently sessile anthers, towards the lobes the hairs erect amongst the anthers and equally long, lobes glabrous, tube 2 mm; lobes 1.5 mm; anthers 1.5 mm. Style twice as long as tube\*. *Fruit* red. Pyrenes obovoid 2.5 by 1.5 mm, flattened; apex truncate; base acute; abaxially convex with 2 slight grooves.

Ecology & Habitat — 1500 m.

Distribution — Papua New Guinea (Sepik Province).

Conservation status — Vulnerable (VU) under criteria D2 with only the type specimen known.

Note — We have not found the type, or any matching specimen, and the description is taken from Valeton (1927) and manuscript drawings of the flower and pyrene (Leiden MS). The description clearly places this taxon in the *H. petiolatum* complex, whilst the leaf and pyrene shape isolate it from the other varieties.

\* In Valeton's drawing of the flower of *Ledermann* 12925 the style is about equal to the length of the tube.

**g. var. *nigrescens*** (Merr. & L.M.Perry) Jebb & C.R.Huxley, *stat. nov.* — Map 3

Basionym: *Hydnophytum nigrescens* Merr. & L.M.Perry, *J. Arnold Arbor.* 26 (1945) 16. — Type: *Brass* 7171 (lectotype selected here A; iso BM, BRI), Western Province, Papua New Guinea, Palmer River, 2 miles below junction Black River, ridge forests, July 1936.

*Tuber* globose. *Stems* numerous, branching, internodes 1.5–5 by 0.3 cm, nodes swollen; drying black. *Leaves* strikingly variable in size. Lamina elliptic-obovate, 3.5 by 2 to 8.5 by 4.5 cm, but mostly 4.5 by 2 to 5 by 2.5 cm; apex abruptly acute; base cuneate to attenuate; midrib prominent on both sides; veins 8 or 9. Petiole 0.4–0.7 cm. Inflorescence sunken, with a mass of brown bract hairs; 0.8–1.2 cm across. *Flowers* [1] ?heterostylous. Calyx 1.5 mm, margin irregular, thin, surface furfuraceous. Corolla tube 5 mm; lobes 2 mm; with a ring of hairs at mouth and base of lobes. Anthers 1.3 mm, within mouth of tube; pollen 3-colpate, 54 (51–62)  $\mu\text{m}$ , brochi 1  $\mu\text{m}$ ; stigma exserted. *Fruit* unknown. Pyrenes obovoid-oblong, 2.5 by 2 mm; apex truncate, with prominent lateral lobes like short horns, base rounded.

Ecology & Habitat — Canopy epiphyte of ridge forest, 100 m. Tuber not inhabited by ants.

Distribution — Papua New Guinea (Western Province).

Conservation status — Vulnerable (VU) under criteria D2 with only the type specimen known.

Note — This variety is similar to the description of var. *ledermannii*, differing in its longer petiole and the slightly 'horned' pyrenes.

***Hydnophytum petiolatum* aff.**

Several collections, which appear to fall into the *H. petiolatum* complex, are not readily assignable to the above variants, and further collections of this complex may result in alterations to our suggested categories:

Collections: NEW BRITAIN, S5°04' E151°48', Mengen Massif, S/D Pomio, Stevens & Lelean in LAE 58790 (A, BRI, CANB, EDIN, K, L). – PAPUA NEW GUINEA, Gulf Province: S7°30' E144°30', Uramu Island, Kikori S/D, Gray & Floyd NGF 8024 (Map 3m) (A, BRI, K, L). – PAPUA PROVINCE, Rouffaer (Tariku) river, Docters van Leeuwen 10300 (BO, L).

**12. *Hydnophytum trichomanes* Jebb & C.R.Huxley, sp. nov.**  
— Fig. 15

Tuber grande. Caules complures, ad 60 cm. Radices ad nodos ramorum enatae. Lamina late lanceolata usque obovata, 11 per 6.5 ad 13 per 9 cm, apice acuto usque acuminato, basi sensim attenuata, coriacea textura; nervi 6 vel 8, irregulares. Petiolus ad 1 cm. Stipulae 1 ad 1.3 cm, triangulares, persistentes, tandem attriti, findentes et inter et intra petiolus. Inflorescentia grandis, binata, obiecti ingenti pulvino pilorum bractealium ad 2 cm in diametro. Flos non bene cognitus, ad 4 mm; lobi ad 1.5 mm. Pyrenae obovoideae, 5 per 2.5 mm. — Typus: Docters van Leeuwen 9566 (holo L; iso A, BO, K), New Guinea, Papua Province, Mamberamo river, Albatross bivak, July 1926.

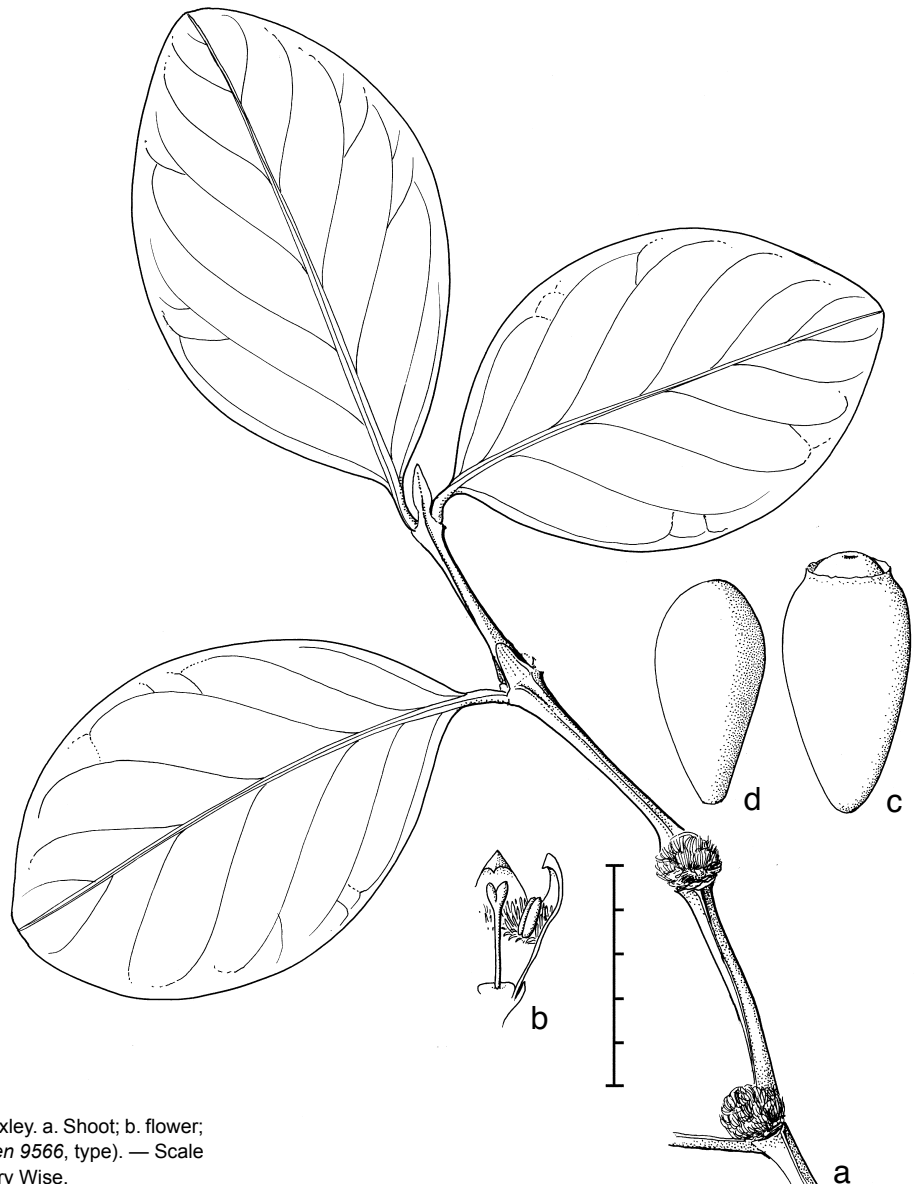
*Etymology.* For the exceptional pulvinate inflorescence hairs.

*Tuber* to 30 cm, surface smooth. Entrance holes scattered, conical 0.1–1 cm diam internally. Cavities large, to 10 cm across.

*Stems* several, to 60 by 0.3–1 cm, branching. Internodes 1–9 cm, round in section, with two narrow ridges, ferruginous when young. Roots arising at both sterile and fertile nodes, up to 20 cm in length, becoming branched and ramifying amongst the bract hairs. Lamina broadly lanceolate to obovate, 11 by 6.5 to 13 by 9 cm; apex acute to acuminate; base tapering; leathery in texture; midrib caniculate above, thickening markedly towards the petiole; veins 6–8, irregular, with secondary veins not parallel to more distinct primary veins. Petiole caniculate above, 0.5–1 cm; stipules 1–1.3 cm, triangular, persistent, becoming worn; splitting both inter- and intra-petiole. Inflorescence large, paired, obscured by a massive pulvinate cushion of bract hairs to 2 cm across, the flowers arising from an area to 0.6 cm across on the stem. *Flowers* [1 – undeveloped flower]. Calyx 1 mm, entire. Corolla to 4 mm; lobes triangular to 1.5 mm, a ring of hairs at mouth of tube. Anthers at apex of tube. Pollen 3-porate, 45 µm, brochi < 1 µm, pores unbordered, vesicles small. Stigma bifid, above level of anthers. *Fruit* 6.5 by 3 mm, obovate. Pyrenes obovoid to club-like, to 5 by 2.5 mm, rounded at apex, tapered towards base, abaxially rounded, adaxially flat to concave.

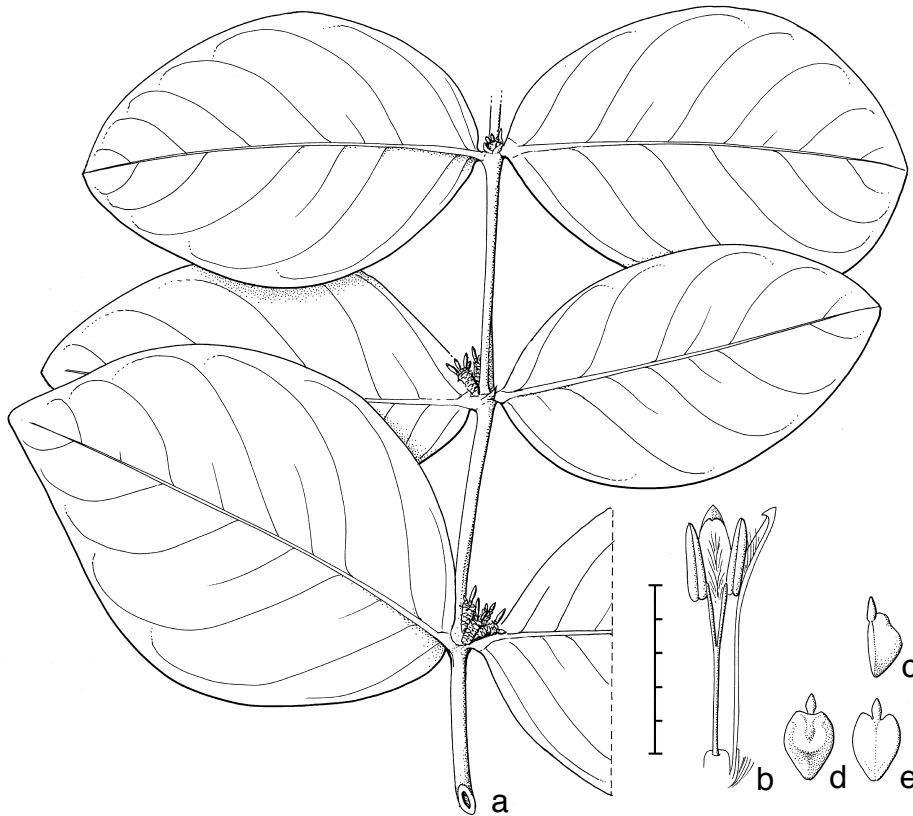
*Ecology & Habitat* — Forest, 100–250 m. Docters van Leeuwen's notes mention that the freshly collected tuber contained water in its cavities.

*Distribution* — Indonesia (Papua Province).



**Fig. 15** *Hydnophytum trichomanes* Jebb & C.R.Huxley. a. Shoot; b. flower; c. fruit; d. pyrene abaxial face (Docters van Leeuwen 9566, type). — Scale bars: a = 5 cm; b–d = 5 mm. — Drawn by Rosemary Wise.





**Fig. 16** *Hydnophytum grandifolium* Valetton. a. Shoot; b. half flower; c. lateral; d. adaxial; e. abaxial faces of pyrene (Gjellerup 226, type). — Scale bars: a = 5 cm; b–e = 5 mm. — Drawn by Rosemary Wise.

Conservation status — Vulnerable (VU) under criteria D2 with the two localities over 200 km apart.

*Additional specimen examined.* *Barclay s.n.* (K) Japen Island, Jobie.

*Note* — The very large cushions of bracts exceed two or three times the diameter of the stem.

#### GROUP 4 – MOSELEYANUM GROUP

##### 13. *Hydnophytum grandifolium* Valetton — Fig. 16

*Hydnophytum grandifolium* Valetton (1912b) 773. — Type: *Gjellerup 226* (lectotype selected here L; iso BO), New Guinea, Papua Province, Jayapura.

*Tuber* large. *Stems* numerous, to 75 cm; thickened, internodes 2.5–10 by 0.4–0.7 cm. *Leaves* subsessile. Lamina broad-elliptic; 12 by 7 to 24 by 16 cm; apex obtuse to subacuminate, base rounded; midrib broadening to base, prominent below, lateral nerves 7–9. Petiole 0–0.2 cm; stipules caducous. Inflorescence a pair, or up to 6 short, axillary peduncles to 1 by 0.4 cm. *Flowers* [1] ?heterostylous. Calyx 1.5 mm, entire. Corolla tube 4 mm, with a band of hairs at mouth, lobes 4 mm, lanceolate. Anthers 3.7 mm, exserted. Stigma 2-fid, at mouth of tube. *Fruit* ellipsoid, 5.5 by 4.5 mm, red. Pyrenes obovate-oblong, 4 by 2.5 mm; apex truncate, notched, with a central acute appendage 1.5 mm long; base truncate.

*Ecology & Habitat* — Epiphytic on *Casuarina*, 160 m. Tuber ant-inhabited.

*Distribution* — Indonesia (Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only the type specimen known.

*Note* — Like a very big-leaved *H. moseleyanum*, but the inflorescences are more numerous, with up to 6 peduncles, and the anthers are much larger. While it is very similar to *H. moseleyanum* [14] it appears to be sympatric with that species and no intermediate forms have been collected.

##### 14. *Hydnophytum moseleyanum* Becc. — Fig. 17

*Hydnophytum moseleyanum* Becc. (1884) 125; (1885) 150, t. 35: 10–14; K.Schum. & Lauterb. (1901) 587; (1905) 401; Valetton (1927) 138. — Type: *Moseley s.n.* (K), Papua New Guinea, Manus Island, Mar. 1875.

*Hydnophytum loranthifolium* (Benth.) Becc. (1884) 124; (1885) 146, t. 33: 8–13. — *Lasiostoma loranthifolium* Benth. (1843) 224. — Type: *Hinds s.n.* (K), Papua New Guinea, 1841, syn. nov.

*Hydnophytum oblongum* (Benth.) Becc. (1884) 124; (1885) 140, t. 33: 1–7. — *Lasiostoma oblongum* Benth. (1843) 225; Valetton (1927) 139. — Type: *Barclay s.n.* (K), Papua New Guinea, New Ireland, syn. nov.

*Hydnophytum papuanum* Becc. (1884) 124; (1885) 147, t. 36. — Type: *Beccari PP 186* (lectotype selected here FI; iso K), New Guinea, West Papua Province, Sorong, 20 May 1872, syn. nov.

*Hydnophytum crassifolium* Becc. (1884) 124; (1885) 148, t. 37: 6–12. — Type: *Beccari s.n.* (lectotype selected here FI; iso K), New Guinea, Maluku Province, Aru Island, Giabu-lengan, syn. nov.

*Hydnophytum philippinense* Becc. (1884) 125; (1885) 149, t. 33: 14–19. — Type: *Moseley s.n.* (K), Philippines, Zamboanga, Malanipa Island, Jan.-Feb. 1875, syn. nov.

*Hydnophytum moseleyanum* var. *teysmannii* Becc. (1885) 151, t. 35: 15–20. — *Hydnophytum montanum* auct. non Blume: Scheff. (1876) 31 p.p. — Type: *Teysmann 7510* (lectotype selected here BO; iso K not seen), New Guinea, Papua Province, Humboldt Bay, syn. nov.

*Hydnophytum longistylum* Becc. (1885) 152, t. 38: 1–10; K.Schum. & Lauterb. (1901) 587; Valetton (1927) 136. — Type: *Guppy 183* (lectotype selected here K; iso FI), Solomon Islands, Faro Island, syn. nov.

*Hydnophytum macrophyllum* Warb. (1891) 441. — Type: *Warburg 21449* (B presumed lost), Papua New Guinea, syn. nov.

*Hydnophytum forbesii* Hook.f. (1892) t. 7218; Merr. & L.M.Perry (1945) 15. — Type: *Forbes s.n.* (K), New Guinea, syn. nov.

*Hydnophytum laurifolium* Warb. (1894) 209. — Type: *Naumann s.n.* (B presumed lost), New Guinea, 17 June 1875, syn. nov.

*Hydnophytum mindanaense* Elmer (1911) 1039, as '*mindanaensis*'. — Type: *Elmer 10974*, published as *10874* (lectotype selected here L; iso E, FI), Philippines, syn. nov.

*Hydnophytum agatifolium* Valetton (1912b) 774; Merr. & L.M.Perry (1945) 15. — Type: *Gjellerup 137* (BO, L), New Guinea, Papua Province, syn. nov.

*Hydnophytum robustum* Rech. (1912) 186. — Type: *Rechinger 3751* (holo W), Papua New Guinea, syn. nov.

*Hydnophytum brachycladum* Merr. (1915) 142. — Type: *Mangubat BS 924* (K, PNH), Philippines, June 1906, syn. nov.

*Hydnophytum brassii* S.Moore (1927) 271. — Type: *Brass 1200* (holo BM not seen; iso A, BRI, K), Papua New Guinea, Gulf Province, Keuru, 23 Mar. 1926, syn. nov.

*Hydnophytum camporum* S.Moore (1927) 271. — Type: *Brass 605* (holo BM not seen; iso A, BRI), Papua New Guinea, Gulf Province, Biriatabu, 11 Nov. 1925, syn. nov.

*Hydnophytum capitatum* Valetton (1927) 129. — Type: *Schlechter 16489* (B presumed lost), Papua New Guinea, syn. nov.

*Hydnophytum cuneatum* Valetton (1927) 133. — Type: *Ledermann 6556* (holo L), Papua New Guinea, Ambunti, syn. nov.

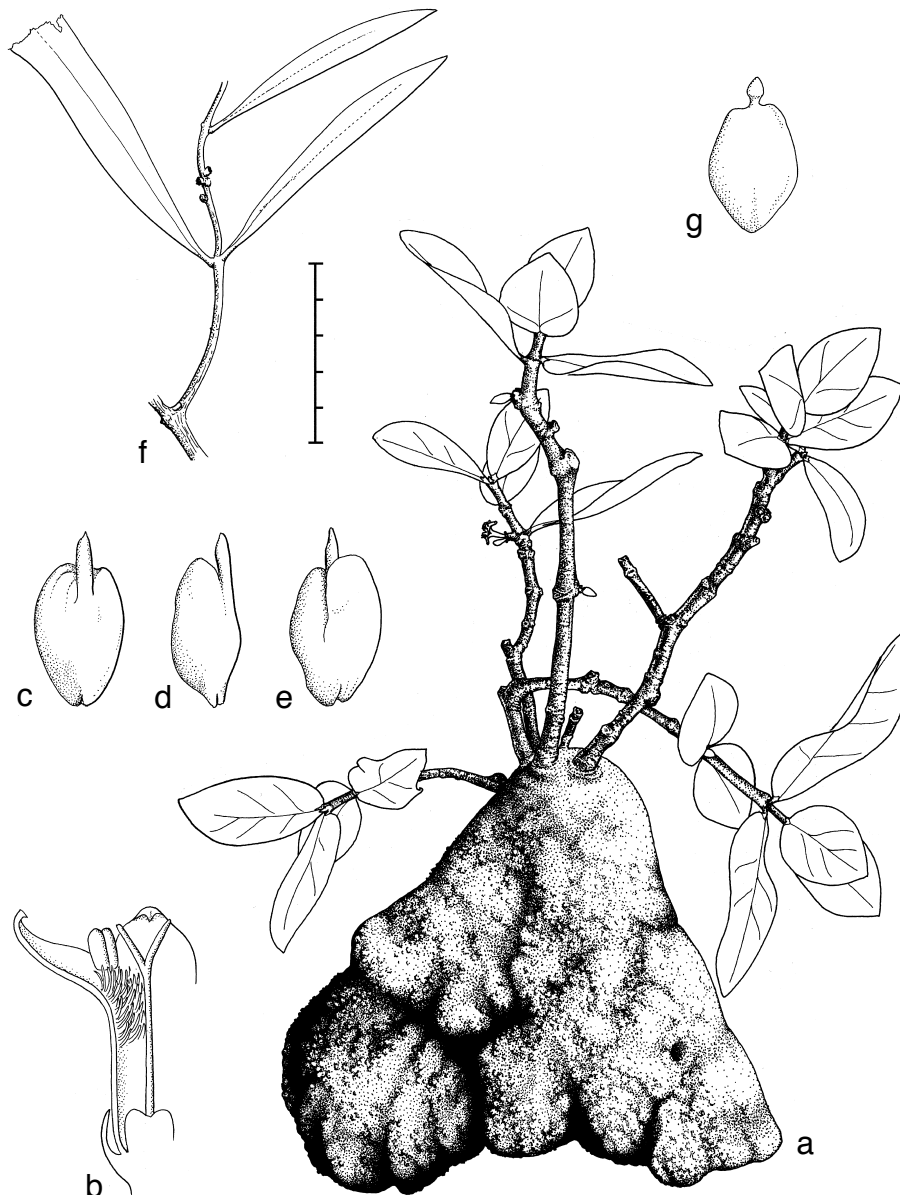
*Hydnophytum subfalcifolium* Valetton (1927) 141. — Type: *Schlechter 14202* (B presumed lost), Papua New Guinea, between Ramu and coast, Feb 1902, syn. nov.

*Hydnophytum subrotundum* Valetton (1927) 142. — Type: *Schlechter 14177* (holo WRSL), Papua New Guinea, between Ramu and coast, Feb 1902, syn. nov.

*Hydnophytum stewartii* Fosberg (1940) 123; Merr. & L.M.Perry (1945) 18. — Type: *Stewart s.n. (A)*, Solomon Islands, syn. nov.

*Tuber* globose to bell-shaped, 6 by 5 to 30 by 45 cm; green to silvery-grey in colour, the surface smooth or areolate, occasionally with tubercle-like spines to 0.5 cm in length and 0.2–0.3 cm broad at their base. Entrance holes scattered, of two types: the majority small, lipped or unlipped holes 0.2–0.6 cm across; the remainder larger, funnel-like, 1–3 cm across. Cavities larger and more globose towards centre of tuber, finer, planar and more

branched near the surface of the tuber. Cavity walls warted and smooth-walled. *Stems* numerous, branching, spreading to pendulous; to 1 m in length, 0.5–1.5 cm diam, internodes to 10 cm when sterile, 0.5–4 cm when fertile. *Lamina* variable in shape, most commonly subrotund-lanceolate, 3.5 by 1.5 to 13 by 7.5 (20 by 6.5) cm, also ranging from narrowly lanceolate (6.5 by 0.5 to 12 by 1.5 cm in *H. agatifolium*) to circular (6 by 5 cm in *H. brassii*); apex acute to rounded; base blunt; venation obscure; fleshy and leathery. *Petiole* 0.2–0.3 cm, rarely to 1 cm, pale green to white in colour, and this colouration characteristically extending as a slender triangle to a third or more of the length of the lamina; stipules triangular, papery, to 0.4 cm, caducous. *Inflorescence* paired, rarely 4 or 6, tubercle-like peduncles, extending with age and bearing flowers at their apex only; to 3 cm long, and 0.4–0.6 cm diam; bracts minute. *Flowers* [7] heterostylous. *Calyx* obovoid-cupuliform, somewhat narrowed at margin, to 1.5 mm. *Corolla* tube 4–7.5 mm, lobes 2.5–4.5 mm, with a broad ring of hairs within the mouth, and usually over lower half of lobes. *Short-styled* flowers with anthers to 2 mm, exserted; stigma 2-fid, below anthers, within mouth of corolla tube. *Long-styled* flowers with anthers to 1.5 mm, scarcely within mouth of tube; stigma exserted. *Pollen* 3-porate, 47 (43–55)  $\mu\text{m}$  diam. *Fruit* globose, to 6 by 5 mm, with



**Fig. 17** *Hydnophytum moseleyanum* Becc. a. Whole plant; b. flower; c. adaxial; d. lateral; e. abaxial faces of pyrene. f–g. *Hydnophytum agatifolium*. f. shoot tip; g. pyrene (c–e: *Brass 8851* (L), Papua Province, Jautefa Bay; f: *Huxley* in *UPNG 5902*; g: *Gjellerup 137* (L), Papua Province, Jayapura). — Scale bars: a = 7.5 cm; b = 10 mm; c–e = 5 mm; f = 5 cm; g = 10 mm. — Drawn by: a, b. Eleanor Catherine; c–g. Rosemary Wise.

prominent calyx remains. Pyrenes oblong-obovoid, 4.5 by 2.5 mm, abaxial surface with a central groove; apex truncate to notched, and with a flattened, filiform or more rarely inflated, central appendage to 2 mm long; base rounded.

**Ecology & Habitat** — Common in mangrove swamps and other coastal forests, rarely to 400 m. Tuber nearly always inhabited by ants.

**Distribution** — Philippines, Indonesia (North Maluku, western New Guinea), Papua New Guinea and the Solomon Islands.

**Conservation status** — Least Concern (LC). Whilst probably Vulnerable in some parts of its range, this taxon is spread across over 5000 km with herbarium collections indicating over 50 locations (subpopulations). Other information: georeferenced collections 66, EOO c. 4 million km<sup>2</sup>.

**Notes** — This widespread species has characteristically, fleshy, yellowish green leaves, with a short petiole. On drying they remain thick and leathery. The midrib often dries in a characteristic manner, forming a paler or, more rarely, darker-coloured triangular pattern on the upper surface of the leaf. The notched pyrene with an apical appendage is a characteristic but variable feature of this and the closely related species *H. grandifolium* [13].

The great variation in leaf shape, from the narrowly lozenge-shaped leaves of *H. agatifolium* to the almost perfectly orbicular leaves of *H. brassii* has led to an unnecessary proliferation of names. Valetton (MS at L) intended describing a large number of varieties that were never published.

Some of the foregoing names could be retained as varietal names, however, for the most part it forms a more unified grouping than that of *H. petiolatum*, and is restricted to coastal forests throughout its range. We had considered retaining a single variety based on *H. agatifolium* and *H. subfalcifolium* since these collections do show a correlation of lozenge-shaped leaves, which are frequently falcate also, and a tuber surface with regular short fleshy tubercles. In the end we have decided that such a solitary and somewhat isolated variety provides no benefit to understanding the species as here defined. According to his notes (MS Leiden), Valetton had planned to name the species '*H. agathifolium*' in reference to the leaves resembling those of *Agathis* spp. (*Araucariaceae*) in shape. The altered spelling in the final publication obscures the intended etymology.

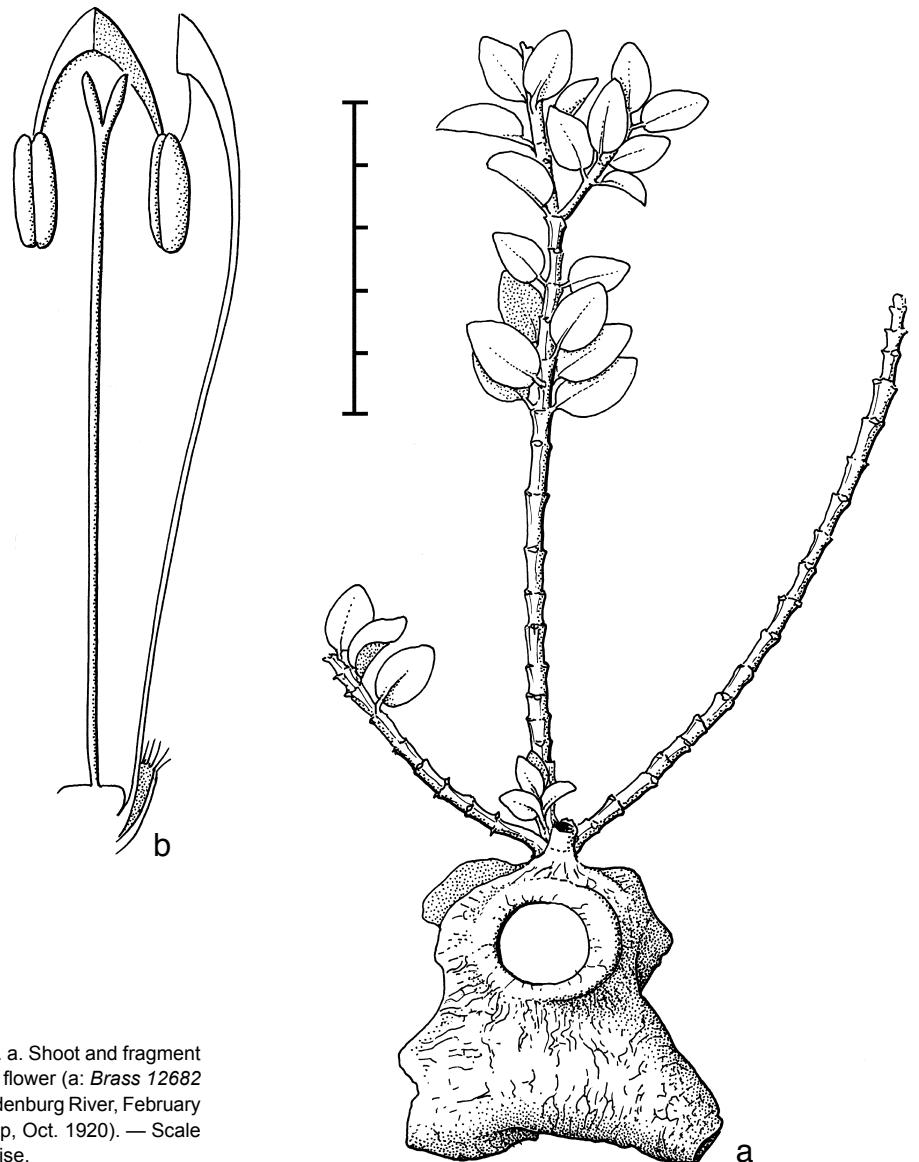
## GROUP 5 – WESTERN NEW GUINEA GROUP

### 15. *Hydnophytum alboviride* Merr. & L.M.Perry — Fig. 18

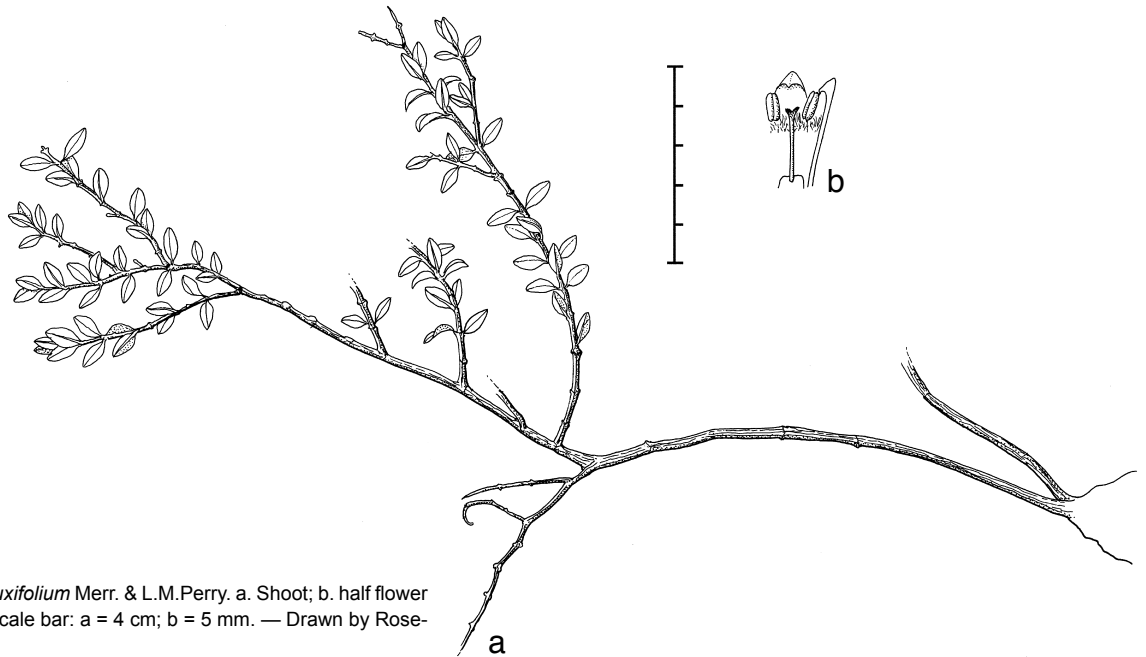
*Hydnophytum alboviride* Merr. & L.M.Perry (1945) 21. — Type: *Brass* 12683 (lectotype selected here A; iso BO, BRI, L), New Guinea, Papua Province, 18 km southwest of Bernhard Camp, Idenburg River, Feb. 1939.

*Hydnophytum crassicaule* P.Royen (1983) 2672, f. 770. — Type: *Lam* 1796 (holo L; iso BO), New Guinea, Papua Province, Doorman Top, 29 Oct. 1920, syn. nov.

*Hydnophytum vacciniifolium* P.Royen (1983) 2668, f. 769. — Type: *Lam* 1641 (holo L; iso BO), New Guinea, Papua Province, on ridge to Doorman Top, 18 Oct. 1920, syn. nov.



**Fig. 18** *Hydnophytum alboviride* Merr. & L.M.Perry. a. Shoot and fragment of tuber showing large, lipped entrance hole; b. half flower (a: *Brass* 12682 (L), Papua Province, 18 km SW of Bernhard Camp, Idenburg River, February 1939; b: *Lam* 1796 (L) Papua Province, Doorman Top, Oct. 1920). — Scale bar: a = 5 cm; b = 5 mm. — Drawn by Rosemary Wise.



**Fig. 19** *Hydnophytum buxifolium* Merr. & L.M.Perry. a. Shoot; b. half flower (*Brass* 12681, type). — Scale bar: a = 4 cm; b = 5 mm. — Drawn by Rosemary Wise.

*Tuber* globose, to 24 by 9 cm, surface smooth. Entrance holes large, funnel-like, often lipped. Cavities all smooth-walled and bulbous-ended. *Stems* several, to 1 m long; internodes 0.5–4 cm, nodes somewhat thickened; when short, internodes appearing as an imbricated series of small cones. Lamina ovate to subrotund; 0.7 by 0.4 to 1.6 by 0.9 cm; apex acute; base abruptly attenuate to truncate; thick. Petiole 0.1 cm; stipules triangular, 0.2 cm, persistent. Inflorescence paired, sessile; bracts sparse, triangular to 0.3 cm. *Flowers* [5] ?not heterostylous. Calyx ciliate or entire, 2 mm. Corolla greenish white, tube 7–10 mm, glabrous within, lobes 3 mm, unci 1 mm. Anthers to 2 mm, at mouth of tube. Pollen 52–76  $\mu\text{m}$ . Stigma 2-fid, exserted, above anthers or at level of anthers. *Fruit* red, but otherwise unknown.

**Ecology & Habitat** — Ridge top, mossy forest, 2150–3250 m. Tuber not inhabited by ants.

**Distribution** — Indonesia (Papua Province).

**Conservation status** — Vulnerable (VU) under criteria D2 with only two locations known about 55 km apart.

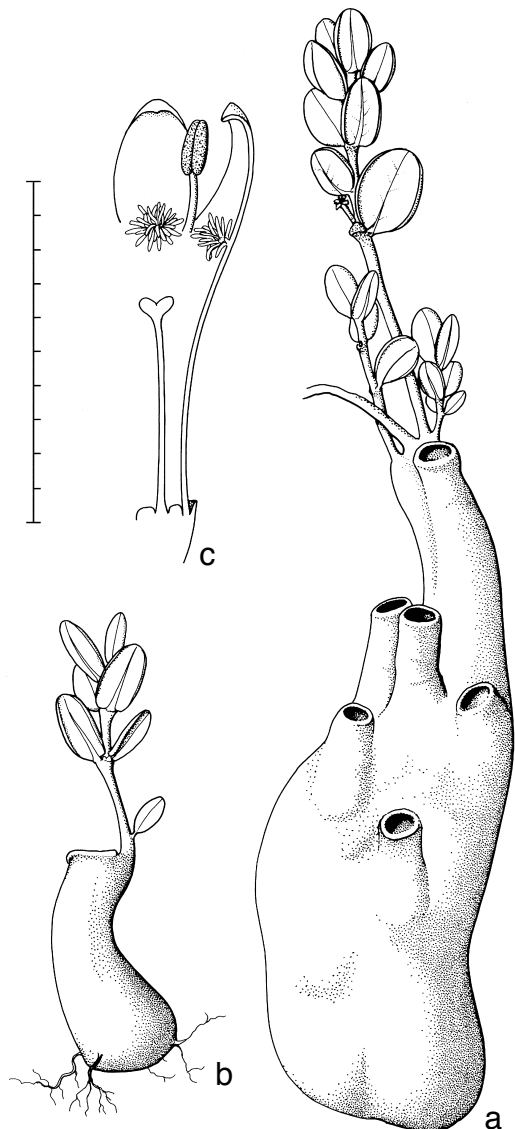
**Note** — The thickened stems and ovate leaves characterise this high altitude species. Van Royen recognised two manuscript names of Valeton's, albeit applying one to a different entity (Valeton's 'vaccinifolium' falls under *H. decipiens*). Valeton had planned (MS Leiden) to use *Lam* 1641 as the type for his manuscript name 'condensatum'. We have reduced both taxa until such time as further collections become available.

#### 16. *Hydnophytum buxifolium* Merr. & L.M.Perry — Fig. 19

*Hydnophytum buxifolium* Merr. & L.M.Perry (1945) 22. — Type: *Brass* 12681 (A), New Guinea, Papua Province, 18 km southwest of Bernhard Camp, Idenburg River, Feb. 1939.

*Tuber* subglobose, to 10 cm or more across. Entrance holes conical, 0.3–1 cm across. *Stems* few, branched, to 30 by 0.4 cm; internodes 0.5–1 cm, up to 3 cm when sterile,  $\pm$  quadrangular. Lamina elliptic-rhomboid; 0.6 by 0.3 to 1.3 by 0.6 cm; apex acute; base tapered; leathery. Petiole 0.1 cm; stipules minute, caducous. Inflorescences surrounded by bracts. *Flowers* [1] not heterostylous. Calyx to 1.5 mm, margin undulate. Corolla tube to 3 mm, lobes 1.5 mm, a ring of hairs within mouth of tube. Anthers exserted, < 1 mm in length. Stigma obscurely 2-lobed, at level of anthers. *Fruit* and pyrenes not known.

**Ecology & Habitat** — High-level epiphyte in mossy forest, 2150–2600 m. Tuber not inhabited by ants.



**Fig. 20** *Hydnophytum caminiferum* Wistuba, U.Zimm., Gronem. & Marwinski. a. Whole plant with some shoots; b. whole young plant; c. half flower (*Jebb* 890 (BO, K, L, LAE) West Papua Province, Vogelkop, ridge between Anggi Gigi and Anggi Gita lakes, Dec. 1990). — Scale bar: a, b = 10 cm; c = 10 mm. — Drawn by Rosemary Wise.

Distribution — Indonesia (Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only two locations known about 110 km apart.

*Additional specimens examined.* *Mangen 1763* (A, L), S4°25' E139°40', Valentijn Mts, S slopes of main range, trail from base camp to Koruppun village; *Mangen 2163* (A, L), S4°17' E139°30', Valentijn Mts trail from Koruppun to Angguruk, 'Angolagna' forest camp.

**17. *Hydnophytum caminiferum*** Wistuba, U.Zimm., Gronem. & Marwinski — Fig. 20

*Hydnophytum caminiferum* Wistuba, U.Zimm., Gronem. & Marwinski (2014) 45. — Type: *Wistuba 2014-001* (M not seen) from cultivated material (ex New Guinea, West Papua Province, Manokwari, Anggi Lakes), 8 Mar. 2014. *Hydnophytum cecilia* Jebb & C.R.Huxley, Naturalis Biodiversity Center (NL), <http://bioportal.naturalis.nl/> (accessed 17 Oct. 2017); JSTOR, <http://plants.jstor.org/stable/10.5555/al.ap.specimen.k000761975> (accessed 17 Oct. 2017); GBIF Backbone Taxonomy, Checklist Dataset <https://doi.org/10.15468/39omei> (accessed via GBIF.org on 17 Oct. 2017, <https://www.gbif.org/species/8943207>), *nom nud*.

Terrestrial shrub. *Tuber* upright, to 60 cm high, an aggregation of amphora-shaped tubers with upwardly opening cavities each with 1 or 2 entrances. Entrance holes 1–2 cm across; lipped and ± oriented upwards, standing prominently from surrounding tuber surface. Cavities all smooth-walled, new tuber tissue arising as swollen stems which eventually become hollow, opening at their apex; the majority of cavities comprise U-shaped chambers opening by two openings, one opening higher than the other. *Stems* mostly confined to apex of tuber, but also arising laterally from tuber and on side tubers; solitary to numerous, little branched, straight to zigzagged; to 40 by 0.2–0.4 cm; internodes 0.5–1.5 cm in length. *Leaves* sessile, clustered at apices, falling by the 5th or 6th node; held upright close to stem. Lamina cordate, 1.3 by 1.1 to 1.6 by 1.3 cm; apex blunt to acute, base cordate; thick, fleshy, margin recurved; white below; midrib prominent below, becoming inconspicuous in upper 1/3, veins c. 5 indistinct. Stipules to 0.15 cm, triangular, persistent. Inflorescences paired swollen tubercles, to 0.5 cm across, a prominent cushion of papery and brown bract hairs to 3 mm in length. *Flowers* [1] ?heterostylous. Calyx to 2 mm; margin with a fringe of septate hairs to 2 mm. Corolla white, 14 mm long; tube 10 mm; lobes 4 mm; with four patches of hairs at the mouth of the tube. Anthers dark purplish brown, exerted, 1.5 mm long; filaments 2.5 mm. Pollen 56 µm, 3-colpate, coarse vermiculate reticulation. Stigma 2-lobed, about 1/3rd the way down the corolla tube; style 5–7 mm. *Fruit* red, to 5 mm. Pyrenes obovoid, 4 by 2 mm; apex rounded; base attenuate.

*Ecology & Habitat* — Terrestrial in open scrub and woodland on quartzite soils surrounding the Anggi Lakes in the Arfak Mountains, between 2000–2600 m. The tuber is once reported with ants, but usually the cavities contain rainwater and various arthropods other than ants.

Distribution — Indonesia (West Papua Province).

Conservation status — Critically Endangered (CR) under criteria B1ab(i,ii,iii,v)+2ab(i,ii,iii,v). This taxon is terrestrial on the ridge tops around the Anggi lakes, this habitat has a total area of under 10 km<sup>2</sup> and is prone to regular fires. It is inferred that the EOO and AOO of this taxon will decline as well as being degraded. A species of *Myrmephytum*, *M. arfakianum* (Becc.) C.R.Huxley & Jebb, is also found as a terrestrial plant on these ridges, but it is also found epiphytically in the surrounding forest, while *H. caminiferum* is not.

*Additional specimens examined.* *Jebb 890* (BO, K, L, LAE), S1°23' E133°55', ridge between Anggi Gigi and Anggi Gita lakes, Dec. 1990; *Sleumer & Vink* in *BW 14216* (L) S1°25' E133°51', Anggi Gigi lakes, Mt Sensenemes, 18 Jan. 1962; *Kanehira & Hatusima 14062* (FU), Mt Koebre, Anggi lakes.

*Notes* — The tuber of this species is remarkable in form, and unique within the genus. The flask-shaped tuber comprises a

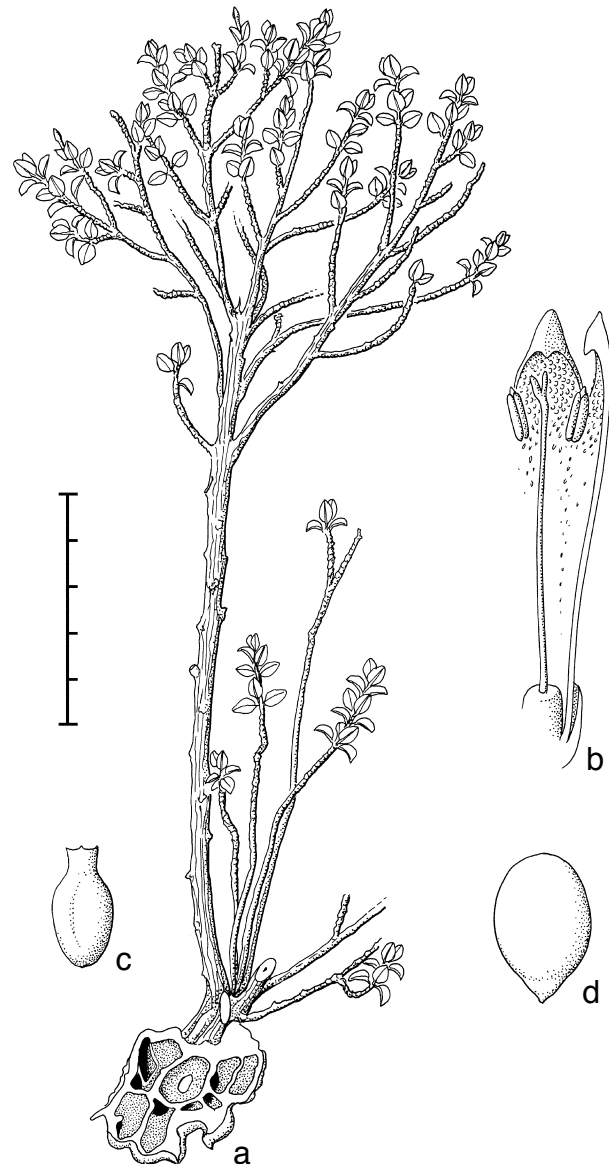
number of unconnected, U-shaped cavities, with upward-facing entrance holes 1–2 cm diam. Each cavity has 2 openings, at different heights, rarely, in young plants they may have only a single opening. Cavities are added both apically, apparently through swelling of the stems, and basally, along the lower perimeter of the tuber. The cavities contain trapped rainwater and detritus, but as pointed out by Wistuba et al. (2014) the positioning and structure of the entrance holes does not appear to be efficient at capturing rainfall.

Three other species of *Hydnophytum* have small cordate leaves: — *H. cordifolium* [40] has larger leaves and pedunculate inflorescences; *H. orichalcum* [46] has linear-cordate leaves; *H. ovatum* [4] has swollen nodes with a socket-like inflorescence. We had intended to publish this species with the name *H. cecilia* and the proposed type material (*Jebb 890*) was distributed under that name.

**18. *Hydnophytum confertifolium*** Merr. & L.M.Perry — Fig. 21

*Hydnophytum confertifolium* Merr. & L.M.Perry (1945) 17. — Type: *Brass 12680* (lectotype selected here A; iso L), New Guinea, Papua Province, Idenburg (Taritatu) river, 18 km SW of Bernhard Camp, Feb. 1939.

*Tuber* small, c. 5–10 cm across. Spines scattered, simple to branched, to 1 cm long. *Stems* several, densely branched, to



**Fig. 21** *Hydnophytum confertifolium* Merr. & L.M.Perry. a. Shoot and fragment of tuber; b. half flower; c. fruit; d. pyrene abaxial face (*Brass 12680* (A) type). — Scale bars: a = 5 cm; b, c = 10 mm; d = 5 mm. — Drawn by Rosemary Wise.

20 by 0.5 cm; internodes short, to 0.1 cm towards stem apices. Leaves clustered at stem apices and recurved along their length and width. Lamina subrotund, 0.3 by 0.2 to 0.5 by 0.4 cm; apex blunt to acute; base truncate to cuneate. Petiole 0.1–0.2 cm; stipules triangular, papery, caducous. Inflorescence a pair of small alveoli, bearing a single flower or fruit. Flowers [1] not heterostylous. Calyx 1.5 mm, margin 4-cuspidate. Corolla tube 7.5 mm, lobes 2 mm, inner surface of lobes with very short papillae, which grade into short hairs at the mouth of the tube; unci to 0.7 mm. Anthers within mouth of tube, to 1 mm. Stigma 2-fid, at same level as anthers. Fruit red, to 6 mm long. Pyrenes hemispherical, 3 by 2 mm; apex rounded; base tapered.

Ecology & Habitat — High-level epiphyte of mossy forest, 2150–2600 m.

Distribution — Indonesia (Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only two locations known about 110 km apart.

Additional specimen examined: *Mangen 2128* (A, L) S4°24' E139°37', Valentijn Mts Trail between Koruppun and Angguruk.

Note — The tuber spines of the type specimen are unusual for *Hydnophytum*, a character only shared by the type specimen of *H. ramispinum* [25], which comes from the same mountain.

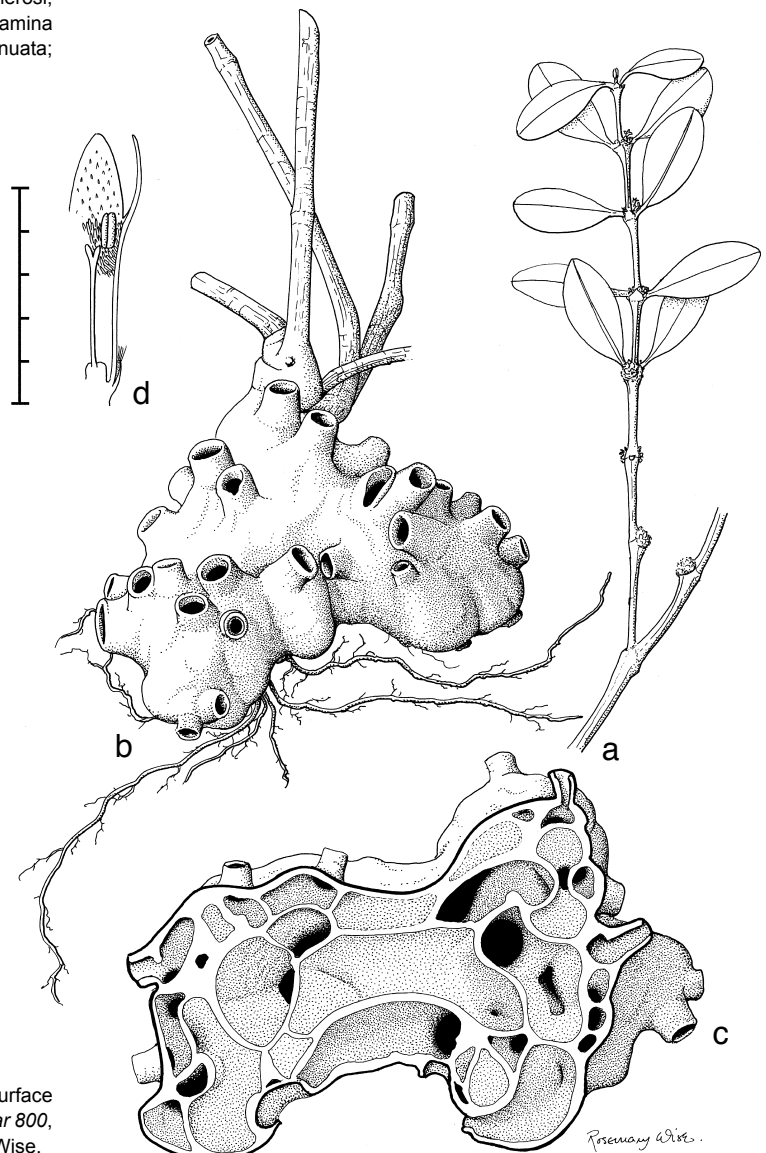
**19. *Hydnophytum davisii*** Jebb & C.R.Huxley, *sp. nov.* — Fig. 22

Tuber oblatum, ad 30 per 20 cm; superficies laevis, cum plurumque aperturis 1 ad 1.3 cm latis et 1 ad 1.5 cm altis, cum mura tenuis. Caules numerosi, ramosi, ex stirpe communi enati, ad 1 m longi; internodia terete. Lamina obovata, 2 per 1 ad 4.5 per 1.9 cm, apice rotundato basim sensim attenuata;

nervi obscuram; petiolus 0.1 ad 0.2 cm; stipula ad 0.1 cm, caduca. Inflorescentia binata, sessilis, oblecta pulvino pilorum bractealium ad 1 cm in diametro, pili bracteales ad 0.5 cm. Corollae tubus ad 3.5 mm, annulo pilorum ad faucem inductus, lobi 2.8 mm longis. Antherae 1.3 mm, ad faucem exsertae. Stigma bifidum, 2.5 mm. Fructus et pyrenae ignota. — Typus: *Davis & Mayar 800* (holo K; iso BO, L, MAN), New Guinea, West Papua Province, Kebar valley, 7 May 1995.

*Etymology.* Named in honour of Aaron Davis of Kew, collector of the type specimen and *Rubiaceae* expert.

*Tuber* globose, to 30 by 20 cm across; surface smooth, dark brown. Entrance holes throughout, conspicuous, abrupt cylinders 1–1.3 cm across and 1–1.5 cm tall, with thin walls 0.1–0.3 cm thick. Cavities globose, 0.8–4 cm across, all smooth-walled. *Stems* several, to 1 m long, branched; internodes 1.7–7 by 0.2–0.6 cm, rounded, ultimate internodes furfuraceous. Lamina obovate; 2 by 1 to 4.5 by 1.9 cm; apex rounded, base tapering, ultimately attenuate; midrib prominent below; veins obscured; lathery; pale brown when dry; margin recurved. Petiole 0.1–0.2 cm; stipules triangular, 0.1 cm, caducous. Inflorescence paired, sessile, covered by cushions of bract hairs to 1 cm across. Bract hairs pale brown, to 0.5 cm long. *Flowers* [1] ?heterostylous, iridescent white. Calyx 0.5 mm entire, with adherent bract hairs. Corolla tube 3.5 mm, with a broad ring of hairs at mouth of tube, and exserted to 1 mm long; lobes 2.8 by 1.5, without an uncus, with many raphides. Stamens exserted, filaments 1 mm, anthers 1.3 mm. Style 2.5 mm long; stigma 2-lobed, lobes c. 0.7 mm, immediately below anthers. *Fruit* and pyrenes unknown.



**Fig. 22** *Hydnophytum davisii* Jebb & C.R.Huxley. a. Shoot; b. tuber surface and stem bases; c. section through tuber; d. half flower (*Davis & Mayar 800*, type). — Scale bar: a–c = 5 cm; d = 5 mm. — Drawn by Rosemary Wise.

Rosemary Wise.

Ecology & Habitat — Stunted ridge top *Nothofagus* forest, at 1740 m. Tuber not inhabited by ants.

Distribution — Indonesia (West Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only the type specimen known.

Note — The tuber is remarkable for the many cylindrical entrance holes. These are taller and thinner-walled than those of *H. reevii* [34], and are far more numerous and disposed on a quite dissimilar shaped tuber than *H. caminiferum* [17]. The collector noted an iridescent quality to the flowers, the corolla of which is rich in raphides.

**20. *Hydnophytum decipiens* Merr. & L.M.Perry — Fig. 23**

*Hydnophytum decipiens* Merr. & L.M.Perry (1945) 20. — Type: Brass 12684 (lectotype selected here A; iso BO, BRI, L), New Guinea, Papua Province, 18 km southwest of Bernhard Camp, Idenburg River, Feb. 1939.

*Tuber?* 5–10 cm, spherical; surface smooth. *Stems* several, weak and pendulous, to 60 cm, much branched. Internodes 0.3–3 by 0.1–0.3 cm, thickest towards apices. Lamina ovate-lanceolate, 1.5 by 0.6 to 2.5 by 1.1 cm; apex blunt-acute to rounded; base tapered to acuminate. Petiole to 0.2 cm; stipules minute, caducous. Inflorescence paired, sessile. Bracts inconspicuous, to 0.1 cm. *Flowers* [2] heterostylous, club-shaped in bud. Calyx weakly dentate, 2 mm. Corolla tube 3–5.5 mm, glabrous within;

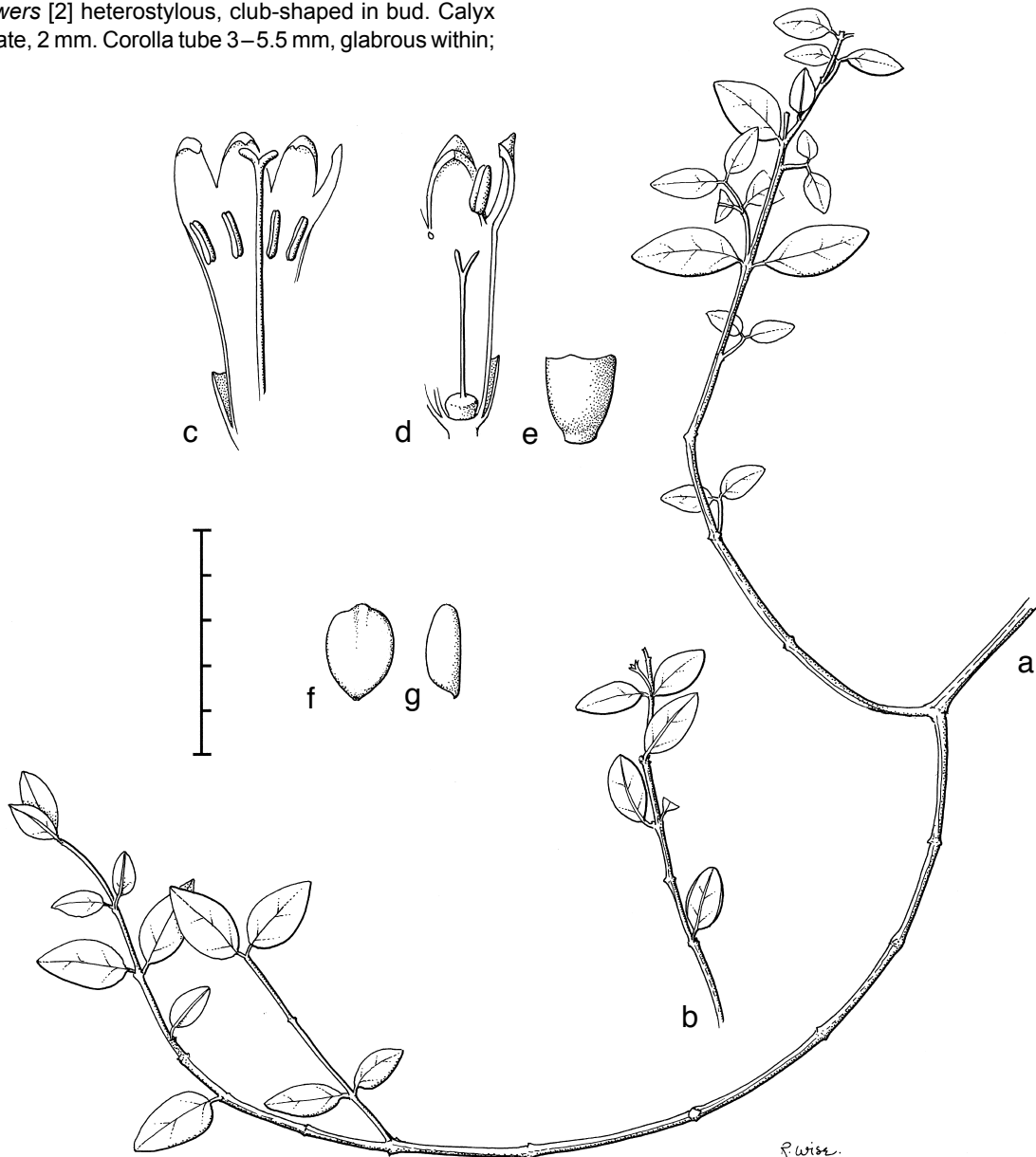
lobes with a prominent apiculum at the tip. Short-styled flowers with corolla tube 4 mm, lobes 2 mm, anthers at mouth of tube; pollen 3-porate, 69 (67–75)  $\mu$ m, brochi 1.5  $\mu$ m; style 2.6 mm. Long-styled flowers with corolla tube 5.5 mm, lobes 1–2 mm, anthers 3/4 way up tube, 1 mm long, sessile; pollen 47 (45–49)  $\mu$ m, style 6 mm, stigma exserted. *Fruit* 4 mm. Pyrenes ellipsoid, 2.5 by 2 mm; apex rounded with central rounded protuberance and slight abaxial ridge; base cuneate.

Ecology & Habitat — Mossy forest, 1420–2150 m; on branches of large trees. Tuber not inhabited by ants.

Distribution — Indonesia (Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only two locations known about 55 km apart.

Note — This species is distinguished from *H. alboviride* [15] by its more elliptic leaves with a rounded apex, more slender stem and various floral characters. We include a Lam specimen from Doorman Top under this species. Valetton had intended to make this specimen, *Lam 1475*, the type for his manuscript species ‘*vaccinifolium*’ (*auct. non* P.Royen). In using this name, however, Van Royen cited *Lam 1641* as the type, a specimen we identify with *H. alboviride*, and which Valetton had intended (MS Leiden) as the type of a further manuscript species ‘*condensatum*’.



**Fig. 23** *Hydnophytum decipiens* Merr. & L.M.Perry. a, b. Shoots; c. long-styled flower; d. short-styled flower; e. calyx and ovary; f. pyrene abaxial face; g. lateral view (a–c, e–g: Brass 12684, type; d: *Lam 1475* (L), Papua Province, ridge to Doorman top). — Scale bar: a, b = 5 cm; c–g = 5 mm. — Drawn by Rosemary Wise.

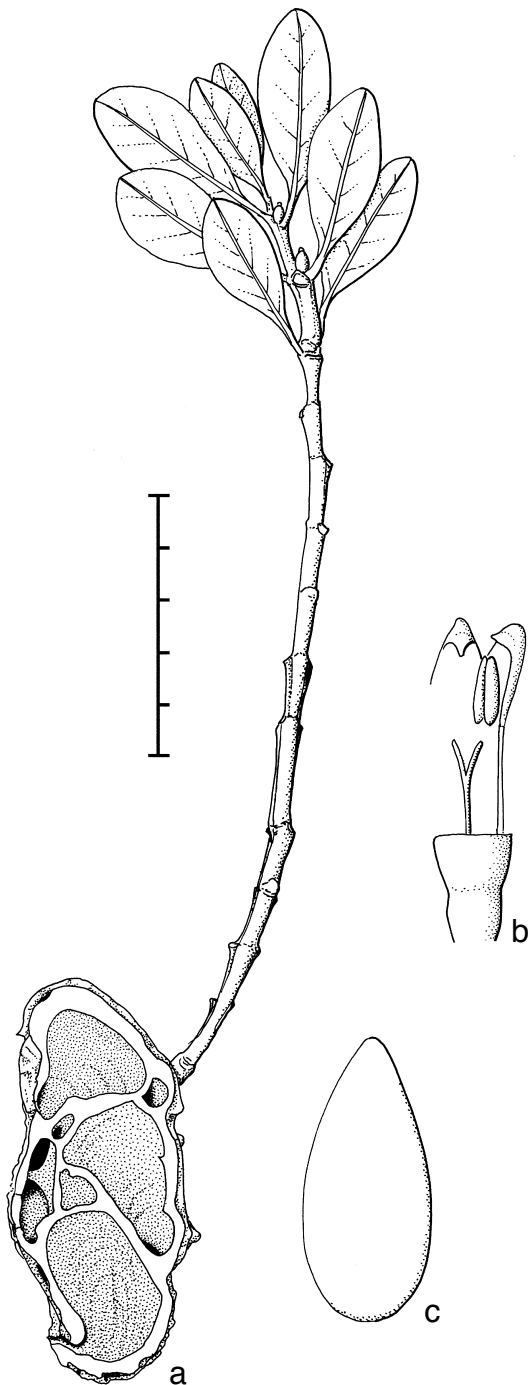
**21. *Hydnophytum kebareense* Jebb & C.R.Huxley, sp. nov. — Fig. 24**

Tuber complanatum, ad 15 cm in diametro; superficies laevis, aliquot obtusis spinis ad 0.3 cm longis armata. Caules ex compluribus locis in tubere enati, ad 40 cm longi; internodia alata. Lamina obovata, 3 per 1.4 ad 6 per 2.5 cm, apice rotundato usque acuto-acuminato, basi sensim attenuata; nervi c. 4 vel 6 utrinque; petiolus 0.3 ad 0.8 cm; stipula ad 0.1 cm, processu centrali instructa, caduca. Inflorescentia binata, in caule impressa. Corollae tubus ad 2.5 mm, glaber, lobis ad 1.5 mm longis. — Typus: *Van Royen 5012* (holo L), New Guinea, West Papua Province, Manokwari, Kebar valley, range of hills south of Anjai airstrip, 11 Nov. 1954.

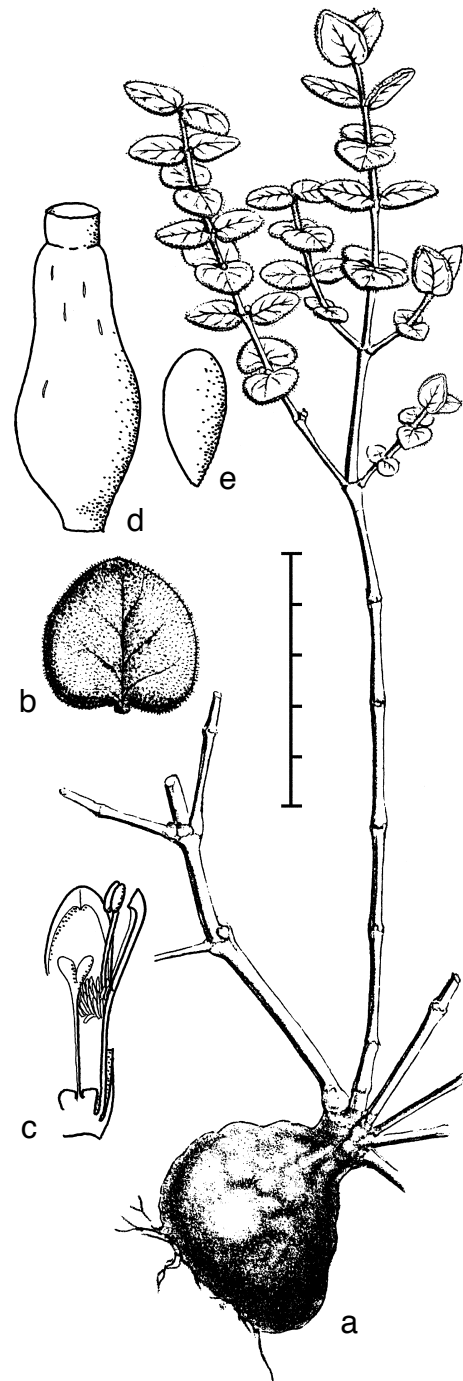
*Etymology.* After the type locality.

*Tuber* flattened, to 15 cm across; with transverse lobing surface smooth, grey to dark-grey. Spines few, obtuse, to 0.3 cm long. Entrance holes scattered, largest on lower surface, ± hidden between adjacent lobes of tuber, darker in colour than surround-

ing tuber surface, neither lipped nor funnel-like. Cavities large and planar with both smooth-walled and warted surfaces. *Stems* arising from several places on tuber, to 40 cm long; sparsely branched; internodes strongly winged towards apex, to 2.5 by 0.6 cm. Lamina obovate; 3 by 1.4 to 6 by 2.5 cm; apex rounded to acute-acuminate, base tapering; midrib prominent below; veins 4–6 on each side; papery in texture; bright green in colour. Petiole 0.3–0.8 cm; stipules blunt, to 0.1 cm, with a central process, caducous. Inflorescence paired, shallow alveoli somewhat paler than surrounding stem, to 0.5 cm across on herbarium specimen (expanding on drying?). *Flowers* [1] ?heterostylous, borne in small cluster at centre of alveolus. Calyx to 1 mm, entire. Corolla tube to 2.5 mm, glabrous within; lobes to 1.5 mm, with a hooked uncus to 0.5 mm. Anthers exerted from tube, to 1.2 mm; pollen 45 µm, pores prominently lipped, brochi 1–1.5 µm. Stigma 2-fid, within mouth of tube. *Fruit* to 6 by 3



**Fig. 24** *Hydnophytum kebareense* Jebb & C.R.Huxley. a. Shoot with tuber fragment; b. flower; c. pyrene abaxial face (*Van Royen 5012*, type). — Scale bars: a = 5 cm; b = 4 mm; c = 2.5 mm. — Drawn by Rosemary Wise.



**Fig. 25** *Hydnophytum microphyllum* Becc. a. Habit; b. leaf upper surface; c. flower; d. fruit; e. pyrene abaxial surface (a, b: reproduced from Beccari (1885) t. 42; c: *Polak 970*; d, e: *Polak 1152*). — Scale bars: a = 5 cm; b = 2 cm; c–e = 5 mm.



mm, with prominent calyx remains. Pyrenes ovoid, 2.8 by 1.2 mm; apex acute; base rounded.

**Ecology & Habitat** — Waterlogged riverine forest, *Quercus-Castanopsis* forest, 550–840 m. Ants not mentioned in collecting notes, but frass in tuber suggests it is ant-inhabited.

**Distribution** — Indonesia (West Papua Province).

**Conservation status** — Endangered (EN) under criteria B1ab(iii)+2ab(iii). The two locations are c. 120 km apart. Other information: AOO 385 km<sup>2</sup> (using an auto-value cell width of 12 km), EOO 800 km<sup>2</sup>.

*Additional specimens examined.* *Van Royen 6764* (L), Manokwari, Kebar valley, Nettoti, opposite Anjai, 7 Oct. 1961; *Ridsdale 2440* (BO, L) S1.14° E132.12°, surroundings of Ayawasi, 2 Apr. 1996.

**Notes** — The tuber is lobed and reminiscent of the tubers of both *H. acuminicalyx* [28] and *H. multituberosum* [23]. Unlike the foregoing, however, it appears to be composed of transverse lobes, which are interconnected by a central element. The surface appearance suggests that the tubers may be partially buried beneath mosses in life, with roots or short spine-like protuberances on the surface. The cavities form a series of transverse chambers, suggesting that the tuber is composed of repeated cavity units. The prominently winged stem and sunken inflorescences are also characteristic to this species and scarcely matched by other species. *Hydnophytum tetrapterum* [47] was collected at low altitude, and although it possesses similar wings on its stem, the leaves are different. *Hydnophytum davisii* [19] also from the Kebar valley has a quite distinct tuber, thicker leaves with obscure venation which dry brown, and the corolla has a ring of hairs, and the corolla lobes lack an unculus.

**22. *Hydnophytum microphyllum* Becc. — Fig. 25**

*Hydnophytum microphyllum* Becc. (1884) 126; (1885) 174, t. 42: 4–9. — Type: *Beccari 5528* (FI), New Guinea, West Papua Province, Sorong, Wa-Samson river, Feb. 1875.

**Tuber** globose, small to large; surface smooth or covered by numerous small fleshy papillae c. 1 mm diam and 2 mm tall. **Stems** numerous, to 23 by 0.1–0.3 cm; branched; slender, woody, cylindrical, pilose in young parts. Internodes 2–4 cm

when sterile, 0.4–1 cm when fertile. Nodes swollen, and articulated in appearance. Lamina ovate-subrotund; 0.4 by 0.4 to 1.1 by 1.1 cm; apex acute to blunt; base subcordate, obtuse; margin revolute; veins 4; lower lamina with minute, stellate hairs, upper surface finely pubescent with simple hairs. Petiole very short. Inflorescence sessile. **Flowers** [1] ?heterostylous. Calyx to 1 mm, entire. Corolla tube to 2.5 mm, with a band of hairs at mouth; lobes to 1.5 mm, with a hooked unculus to 0.5 mm. Anthers exerted from tube, 0.6 mm. Stigma 2-fid, within mouth of tube. **Fruit** obpyriform, to 6 by 2.5 mm, with prominent calyx remains to 1 mm. Pyrenes ovoid, 2.5 by 1.3 mm; apex rounded; base cuneate.

**Ecology & Habitat** — Primary rainforest, sea level to 450 m.

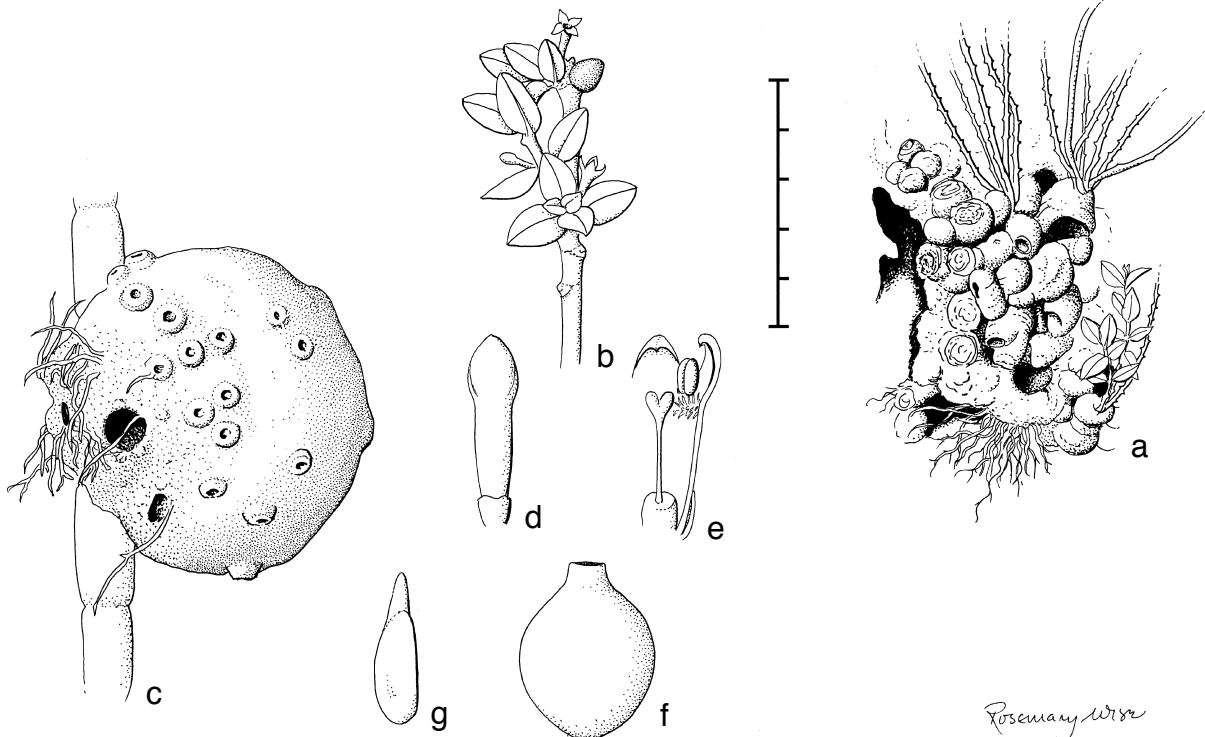
**Distribution** — New Guinea (West Papua Province).

**Conservation status** — Vulnerable (VU) under criteria D2 with the only two known locations 90 km apart.

**Note** — The pubescent leaves were considered to be a unique character, however, recent collections from the Birds Head area by Marcel Polak (*Polak 970 & 1152*, collected near Ayawasi, deposited at L) have allowed microscopic examination of the hairs illustrated by Beccari. They can be seen to be fungal hyphae of a dermitaceous hyphomycete, probably a *Sporidesmium* (Howard Fox, pers. comm.). Considering the historic gap between the collections, of over 100 years, this suggests a consistent relationship between the two taxa.

**23. *Hydnophytum multituberosum* Jebb & C.R.Huxley, sp. nov. — Fig. 26**

Tuber initio solitarium, postea cum numerosis subsidiariis sphaeroideis tuberibus 1 ad 5 cm latis crescens. Caules numerosi, ramosi, quadrangulares. Lamina lanceolato-oblonga, 0.9 per 0.5 ad 2 per 0.9 cm, apice rotundo, basi obtusa, brevissime attenuata; petiolus 1 mm. Inflorescentia binati alveoli paucis papyraceis bractearum reliquiis ornati. Flores heterostyli. Calyx late obovoideus, ad 0.7 mm. Corollae tubus 2.5 mm, annulo pilorum ad faucem instructus; lobi rotundati, 1 mm. Antherae 0.6 ad 0.8 mm, intra faucem vel exsertae. Stigma 2-fidum, exsertum vel infra faucem tubi. Fructus globosus, 3.5 per 3 mm; disci reliquiae prominentes. Pyrenae, ovoideae, 2.5 per 1 mm. — Typus: *Jebb 998* (holo BO; iso K, L), New Guinea, West Papua Province, Waigeo Island, 2 km NE of Go village, 8 Sept. 1992.



**Fig. 26** *Hydnophytum multituberosum* Jebb & C.R.Huxley. a. Habit; b. shoot; c. single tuberlet; d. whole flower; e. half flower; f. fruit; g. pyrene, lateral view (*Jebb 998*, type). — Scale bars: a = 20 cm; b = 2 cm; c = 3 cm; d–f = 5 mm. — Drawn by Rosemary Wise.

*Etymology.* The only taxon where the tuber comprises multiple separate parts.

*Tuber* initially solitary, irregular in outline, brown; 10–20 cm across; further tubers develop from both stem and roots, each spheroid, 1–5 cm across. Entrance holes small, conical. *Stems* numerous, branching; internodes 0.6–2 by 0.2 cm, quadrangular. *Leaves* clustered, upright. Lamina lanceolate-oblong; 0.9 by 0.5 to 2 by 0.9 cm; apex round; base blunt, shortly-attenuate; midrib sunken above ± prominent below; veins 2 or 3, curving towards apex; thick, sclerophyllous. Petiole 0.1 cm; stipules minute, caducous. Inflorescence a socket-like depression to 2 mm across, with few, papery bract remains. *Flowers* [2] heterostylous. Calyx broad-obovoid, to 0.7 mm, thick-edged. Corolla tube 2.5 mm, with a band of short hairs below mouth of tube; lobes rounded, 1 mm. Anthers 0.6–0.8 mm, within mouth or exserted. Pollen 25.6 µm across in long-styled flowers, 35.6 µm in short-styled flowers, brochi c. 1.2–1.5 µm. Stigma 2-fid, exserted, or below mouth of tube. *Fruit* red, globose, 3.5 by 3 mm, disc remains prominent. Pyrenes ovoid, 2.5 by 1 mm.

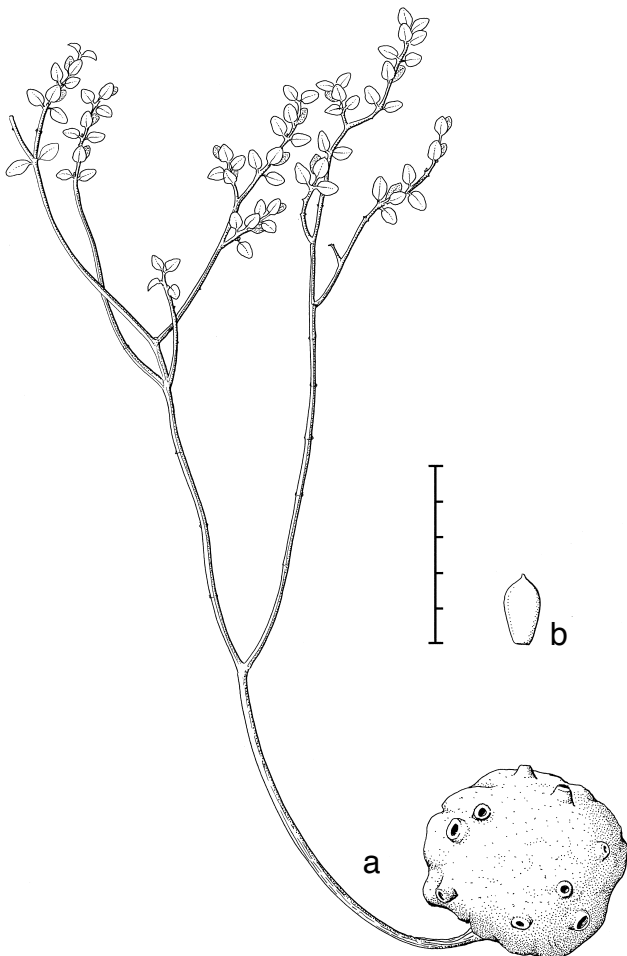
*Ecology & Habitat* — Epiphytic in open scrub-like forest on ultrabasic soils, 200–400 m above sea level. Tuber inhabited by ants.

*Distribution* — New Guinea (West Papua Province).

*Conservation status* — Vulnerable (VU) under criteria D2, only known from Waigeo Island.

*Additional specimens examined.* *Jebb 1006* (BO, L), *Jebb 1007* (L), Waigeo Island, 4 km NE of Waifeo, 9 Sept. 1992.

*Note* — The manner in which the tuber grows is remarkable, and unmatched by any other member of the *Hydnophytinae*.



**Fig. 27** *Hydnophytum pauper* Valetton ex Jebb & C.R.Huxley. a. Whole plant; b. pyrene abaxial face (*Lam 2550*). — Scale bars: a = 5 cm; b = 5 mm. — Drawn by Rosemary Wise.

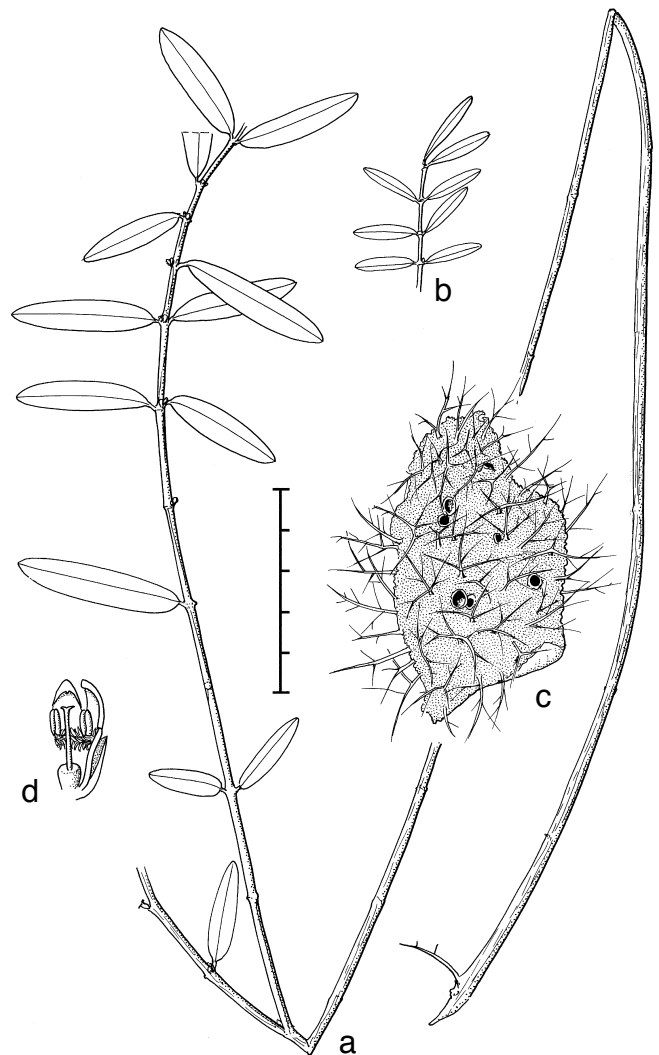
Each tuberlet has an ordered arrangement of several enveloping cavities, each of which opens near the point of attachment to the root.

**24. *Hydnophytum pauper* Valetton ex Jebb & C.R.Huxley, sp. nov. — Fig. 27**

*Tuber* subglobosus parvus. *Caulis* gracilis pedalis a medio dichotomus ramis laxè parce ramosis. *Folia* minuta secus ramos numerosa, brevissime petiolata elliptica vel suborbicularia apice acuta vel obtusa, basi cuneata, crasse membranacea, supra rugulosa siccando brunnea costa paullum prominente percursa. *Stipulae* caducissimae lanceolatae minutae. *Flores* solitariae in axillis, calyx cupularis 4 denticulatus, corollae tubus ad 0.5 mm, lobi ad 1.5 mm, glabri. *Drupa* succosa, pyrena laevis obovoidea, apice truncata, fibris coronata. — *Typus:* *Lam 1969* (holo L), New Guinea, Papua Province, Mount Doorman Top, 11 Nov. 1920.

*Etymology.* After the somewhat diminutive specimens (lat. Pauper = poor).

*Tuber* spherical, 6–7 cm across; surface smooth or rugose, silvery-grey in colour. Entrance holes large, conical, 0.4–0.8 cm across, with a prominent lip. *Stems* to 30 by 0.3 cm, sparsely branched; internodes to 3 cm when sterile, to 0.5 cm when fertile. Lamina elliptic to suborbicular, just longer than wide; 0.6 by 0.4 to 0.9 by 0.8 cm; apex acute to obtuse, base tapered to cordate; midrib prominent throughout length of blade. Inflorescence with minute papery bracts < 1 mm long. *Flowers* [2],



**Fig. 28** *Hydnophytum ramispinum* Merr. & L.M.Perry. a, b. Shoots; c. tuber surface showing spines and entrance holes; d. flower (a, c: *Brass 12858*, type; b: *Docters van Leeuwen 10359*, Papua Province, Rouffaer river; d: *Brass 13403* (A), Papua Province, 4 km SW of Bernhard Camp, Idenburg river). — Scale bars: a–c = 5 cm; d = 5 mm. — Drawn by Rosemary Wise.

not heterostylous. Calyx 4-dentate, 1–1.5 mm. Corolla tube 0.5–1.5 mm, lobes 1.5 mm, with or without a dense ring of hairs in the mouth of the tube. Anthers 1 mm at mouth of tube; pollen 3-colpate, 62 (59–73)  $\mu\text{m}$ , brochi < 1  $\mu\text{m}$ , pores lacking borders. Stigma obscurely 2-lobed, at level of anthers. *Fruit* light red. Pyrenes obovoid, 2 by 1.5 mm.

**Ecology & Habitat** — Terrestrial or epiphytic, 2550 m. Apparently housing frogs in the cavities, and also once with *Paraperipatus* (Lam 1945).

**Distribution** — Indonesia (Papua Province).

**Conservation status** — Vulnerable (VU) under criteria D2 with only two locations known over 250 km apart.

*Additional specimen examined.* *Eyma* 5143 (BO) S3° E136°, Paniai (Wissel Lakes), slopes of Mt Barara.

**Notes** — The name and Latin diagnosis were found amongst Valeton’s manuscript material at Leiden. Lam (1945) found the tuber occupied by frogs as well as a new species of velvet worm: *Paraperipatus vanheurnii* Horst.

The collection *Eyma* 5143 is placed here with doubt; the flowers are larger and hairy within, and the leaves and stems are only a tolerable match; possibly it is a distinct taxon. As with other species in this group, collections are few and the present taxonomy must be considered tenuous at best.

**25. *Hydnophytum ramispinum* Merr. & L.M.Perry** — Fig. 28; Map 4

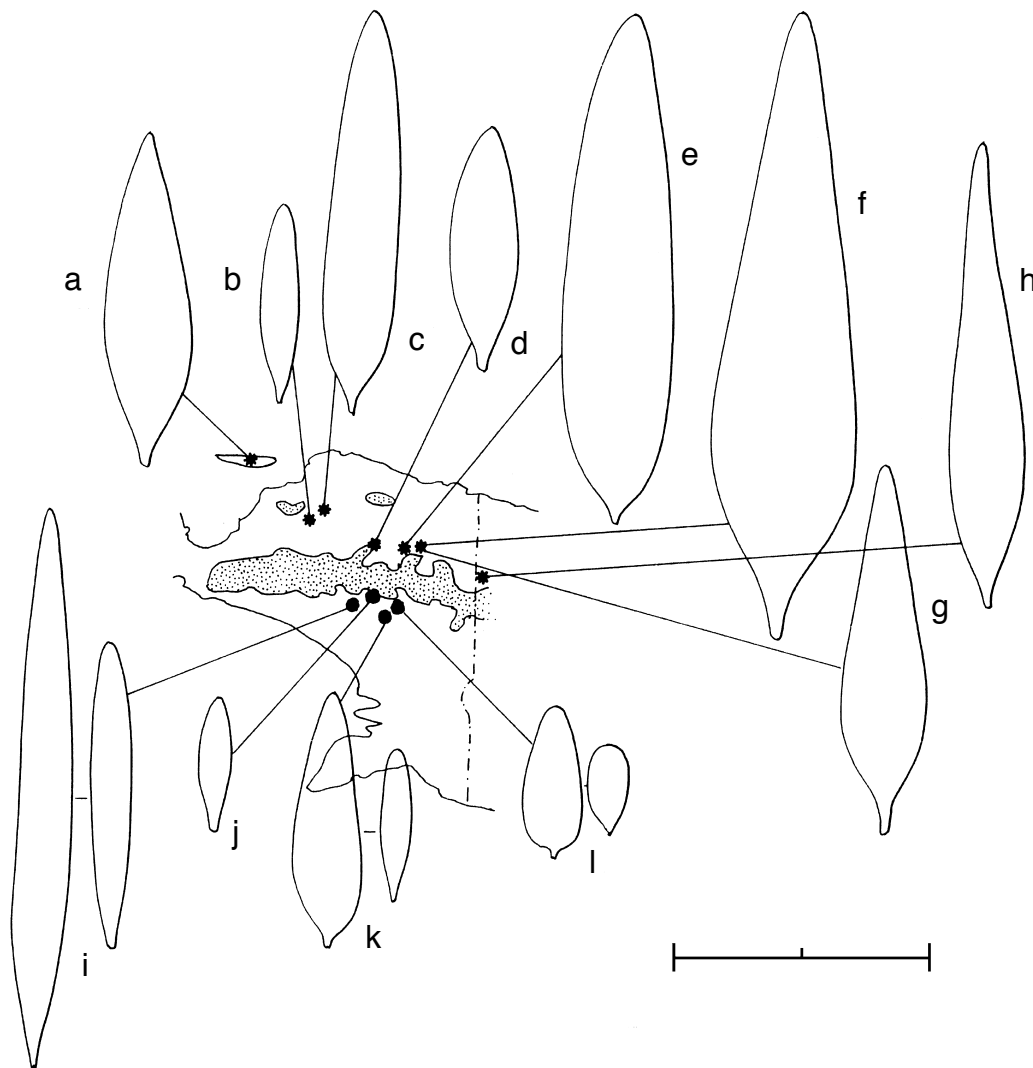
*Hydnophytum ramispinum* Merr. & L.M.Perry (1945) 22. — Type: *Brass* 12858 (lectotype selected here A; iso L), Papua Province, Idenburg River, 6 km southwest of Bernhard Camp, Feb. 1939.

*Tuber* spherical to cylindrical-ellipsoid, to 28 by 8 cm; smooth, or with irregularly branched spines. *Stems* several, pendent to upcurved, to 40 cm or more. Internodes (0.5–)1–5 by 0.1–0.4 cm. *Leaves* scattered, spreading. Lamina narrow linear, linear-oblong to linear-ovate, and then broadest at 1/3 length; 1.1 by 0.2 to 5 by 1.4 (4 by 0.15) cm. Inflorescences paired, sessile. *Flowers* [7] heterostylous. Calyx 1 mm, entire or with a ciliate margin. Corolla tube 1.5 mm, with a ring of hairs towards the mouth, lobes 1–1.5 mm. Short-styled flowers with anthers to 0.8 mm, exerted from tube; pollen 3-porate, 46  $\mu\text{m}$ , brochi 1  $\mu\text{m}$ ; stigma not lobed, at level of anthers. Long-styled flowers with anthers to 0.5 mm, at mouth of tube; pollen 42  $\mu\text{m}$ , brochi 1  $\mu\text{m}$ ; stigma 2-lobed, exerted above anthers. *Fruit* and pyrenes unknown.

**Ecology & Habitat** — Forest, 100–1420 m. Tuber with or without ants.

**Distribution** — Indonesia (Papua Province) and Papua New Guinea.

**Conservation status** — Near Threatened (NT). Whilst probably Vulnerable in some parts of its range, this taxon is widespread across much of the north coast of New Guinea with her-



**Map 4** Leaf outlines of *Hydnophytum ramispinum* and *H. valetonii*. a–h: *H. ramispinum* (a: Vink BW 11306; b: Docters van Leeuwen 10359; c: Docters van Leeuwen 9980; d: Lam 1516; e: Brass 12858; f: Brass 13403; g: Brass 13008; h: Reeve 1065). — i–l: *H. valetonii* (i: Kloss s.n.  $\times 2$ ; j: Pulle 513; k: Versteeg 1644  $\times 2$ ; l: Jebb 121  $\times 2$ ). Shaded area is land over 1500 m. — Scale bar: 2 cm. — Drawn by Rosemary Wise.

barium collections indicating 5 locations (subpopulations). Other information: georeferenced collections 10, AOO 12 500 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO c. 44 000 km<sup>2</sup>.

Notes — This species is characterised by its narrow linear-ovate leaves. The type is unusual for *Hydnophytum* in that it possesses stiff, branched spines, a feature found in only one other species (*H. confertifolium* [18]). Although the remaining collections all lack spines, the leaf shape and flower characters are constant.

The Docters van Leeuwen collections (9980, 10279 & 10359) come from low altitudes in the Rouffaer (Tariku) river valley (175 m), whilst the remainder are from 1 000–1 400 m. These collections differ in their ciliate-margined calyx.

*Hydnophytum vaeletonii* [26] which is found on the southern side of the central Papua Province highlands, differs in its dimorphic leaves, these being smaller on the side branches than on the main stem. Leaf outlines of the two species are mapped.

**26. *Hydnophytum vaeletonii* Jebb & C.R.Huxley, sp. nov. — Fig. 29; Map 4**

Tuber parvum. Caulis complures. Caulibus biniati (raro usque quaterni) tenues surculi laterales ad nodum quemque enati; caules primarii ad 3 mm crassi, quadrangulares, internodia 0.5 ad 2 cm; surculi laterales ad 1 mm crassi, quadrangulares, internodia 0.1 ad 0.8 cm, nodi prominentes tumores ad 1.5 mm latas formantes; surculi laterales longitudine crescente bifurcati. Folia fasciculata ut videtur in surculis lateralibus, recurva. Lamina in surculo primario cordata usque ovata, subtendens surculum lateralem, 1.1 per 0.3 ad 1.6 per 0.5 cm; lamina in surculis lateralibus elliptica usque orbicularis, 0.3 per 0.15 ad 0.9 per 0.2 cm. Inflorescentiae solum in surculis lateralibus gestae, sessiles, binatae. Flores ad 3 mm, lobi 1 mm. Pyrenae obovoidea, ad 3.5 per 2.5 mm. — Typus: *Pulle 513* (holo L L0000509; iso BO, L L0000507, L0000508), New Guinea, Papua Province, Mt Perameles, 1 Dec. 1912.

*Etymology.* Named in honour of Theodore Valeton (1855–1929) author of numerous *Hydnophytum* names.

*Tuber* small, 10 cm, spherical, irregular. Entrance holes conical, 0.5–1 cm across. *Stems* ascending to pendulous, several to 50 cm long, with paired, rarely up to 4, slender side shoots at

each node; main stems to 3 mm thick, quadrangular, internodes 0.5–2 cm, side shoots to 1 mm thick, quadrangular, internodes 0.1–0.8 cm, nodes prominent swellings to 1.5 mm across, side shoots bifurcating with length. *Leaves* appearing to be clustered on side shoots, recurved. Lamina cordate to ovate on main shoot, subtending side shoot, 1.1 by 0.3 to 1.6 by 0.5 cm; elliptical to orbicular on side shoots 0.3 by 0.15 to 0.9 by 0.2 cm; dark glossy green above, pale below, stiff. *Petiole* short to absent, to 0.1 cm; stipules rounded with an apical apiculum, to 0.08 cm, caducous. *Inflorescences* confined to side shoots, sessile, paired. *Flowers* [2] ?heterostylous. Calyx 1 mm, minutely 4-dentate. Corolla tube 1.5–2 mm, lobes 1 mm, with a short unicus at tip, and a narrow ring of hairs in tube. Anthers 0.7 mm, at mouth of tube, sessile or on 1 mm filaments. Pollen 3-porate, 44 (35–50) µm, brochi 1–1.5 µm. Stigma, bifid, immediately below anthers. *Fruit* glossy red, to 12 by 9 mm, calyx remains prominent. Pyrenes obovoid, to 3.5 by 2.5 mm; apex and base rounded.

*Ecology & Habitat* — Mossy forest, once on nutrient-poor soil, 900–1 070 m. Tuber not inhabited by ants, recorded with spiders.

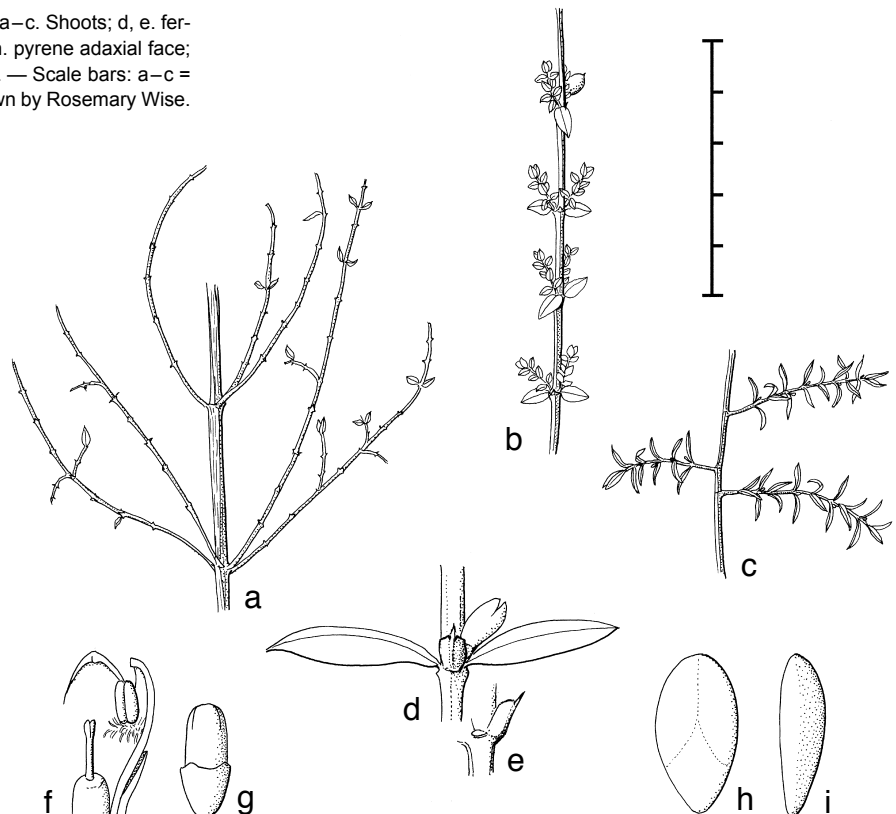
*Distribution* — Indonesia (Papua Province).

*Conservation status* — Endangered (EN) under criteria B1ab(iii)+2ab(iii). The four known localities indicate 4 subpopulations within 400 km of one another. Other information: AOO 6 200 km<sup>2</sup> (using an auto-value cell width of 40 km), EOO 4 900 km<sup>2</sup>.

*Additional specimens examined.* *Kloss s.n.* (BM, K), Utakwa expedition to Mt Carstenz; *Jebb 121* (LAE), S4°30' E139°15' near Holuwon, 60 km SE of Wamena; *Versteeg 1644* (BO), Mimika, Resi Mts.

Note — The apparent dimorphism of leaves, and the quadrangular main stem with long internodes and short, much-contracted side shoots are characteristic of this species. It appears to represent a southern entity to the *H. ramispinum* complex which is restricted to the northern slopes of the Papua Province highlands. Valeton had planned to make *Pulle 513* the type for his manuscript name 'minutifolium', we have preferred not to adopt this somewhat confusing name because of the number of small-leaved species in the West Papua highlands,

**Fig. 29** *Hydnophytum vaeletonii* Jebb & C.R.Huxley. a–c. Shoots; d, e. fertile node with stipule; f. half flower; g. whole flower; h. pyrene adaxial face; i. lateral view (a, b: *Jebb 121*; c–g: *Pulle 513*, type). — Scale bars: a–c = 5 cm; d, e = 3 mm; f, h, i = 5 mm; g = 10 mm. — Drawn by Rosemary Wise.



and instead have named the species in honour of Theodore Valeton (1855–1929) for his taxonomic work on the ant-plants, unfortunately curtailed by his premature death. Leaf outlines of this species and *H. ramispinum* [25] are mapped.

### 27. *Hydnophytum vitis-idaea* Merr. & L.M.Perry — Fig. 30

*Hydnophytum vitis-idaea* Merr. & L.M.Perry (1945) 21. — Type: Brass 12046 (lectotype selected here A; iso BM, BRI, K, L), New Guinea, Papua Province, 15 km SW of Bernhard Camp, Jan. 1939.

*Tuber* globose, smooth, to 15 cm diam. Entrance holes conical 0.4–0.6 cm diam. *Stems* several, branching, to 45 cm long. Internodes rounded to angular, to 5 by 0.4 cm when sterile, 0.3–0.8 by 0.1–0.2 cm towards apices. *Leaves* scattered. Lamina broadly elliptic to orbicular; 0.3 by 0.2 to 1 by 0.5 cm; apex rounded, base tapered to obtuse; thick, recurved when dry, drying glossy below, wrinkled above, venation obscure. Petiole 0.05–0.1 cm; stipules minute, caducous. Inflorescences paired, sessile. *Flowers* [2] heterostylous. Calyx 4-dentate, to 2 mm. Corolla tube to 7 mm, with a narrow band of hairs below mouth of tube or glabrous; lobes 3 mm; unicus < 1 mm. Short-styled flowers with anthers exserted, to 1.5 mm on 1 mm filaments; pollen 3-colpate, 84 µm, brochi 3 µm; stigma at level of anthers, not lobed. Long-styled flowers with anthers within tube at level of hairs, stigma exserted 2-lobed. *Fruit* to 4 mm, pink. Pyrenes oblong-obovoid, 2.5 by 1.5 mm; apex truncate; base tapered.

*Ecology & Habitat* — Mossy forest, 1770–1800 m. Tuber not inhabited by ants.

*Distribution* — Indonesia (Papua Province).

*Conservation status* — Vulnerable (VU) under criteria D2 with only two locations known about 300 km apart.

*Additional specimen examined.* *Eyma* 5069A (BO), Papua Province, Wissel lakes, Cape Weremoeka.

Note — The loose spreading branches and relatively large flowers characterise this species.

### GROUP 6 – PAPUA NEW GUINEA GROUP

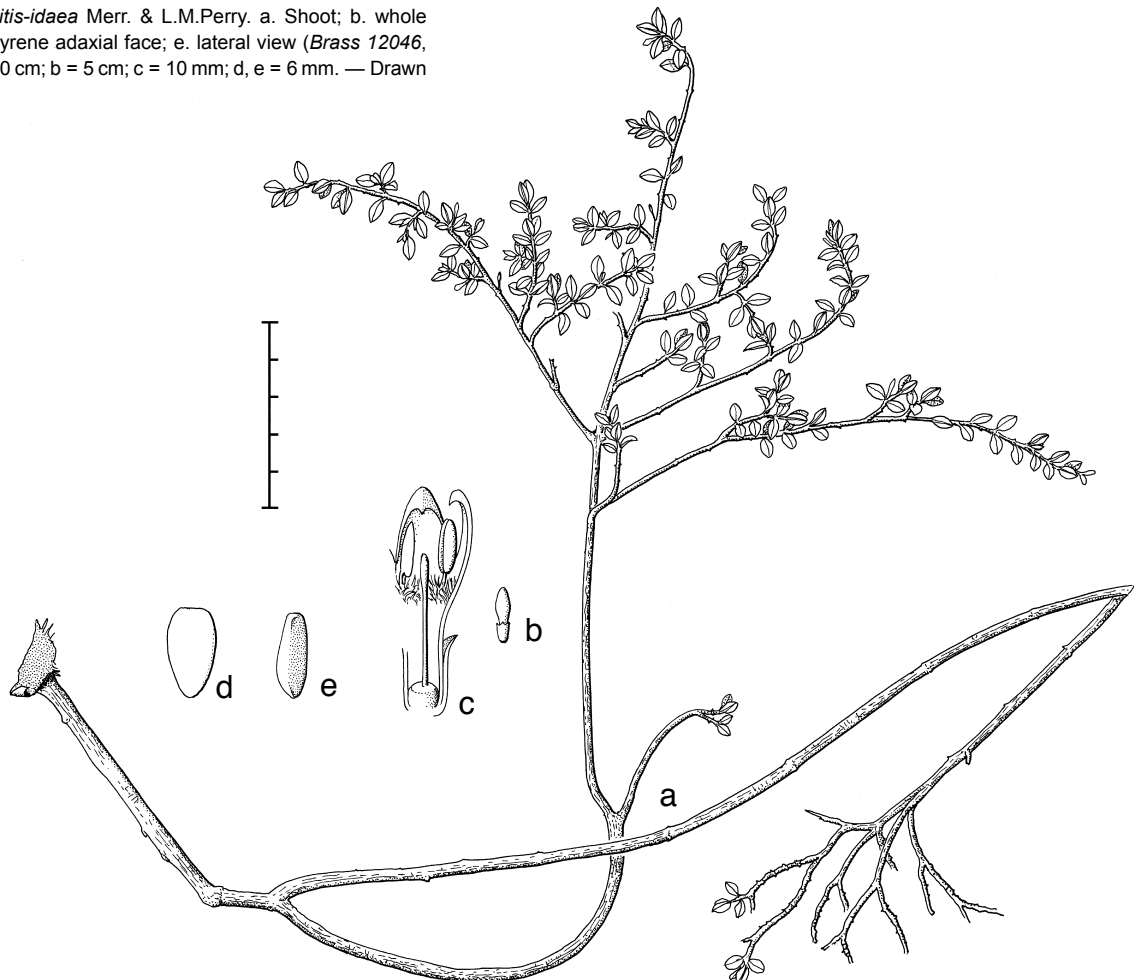
### 28. *Hydnophytum acuminicalyx* Jebb & C.R.Huxley, *sp. nov.* — Fig. 31; Map 5

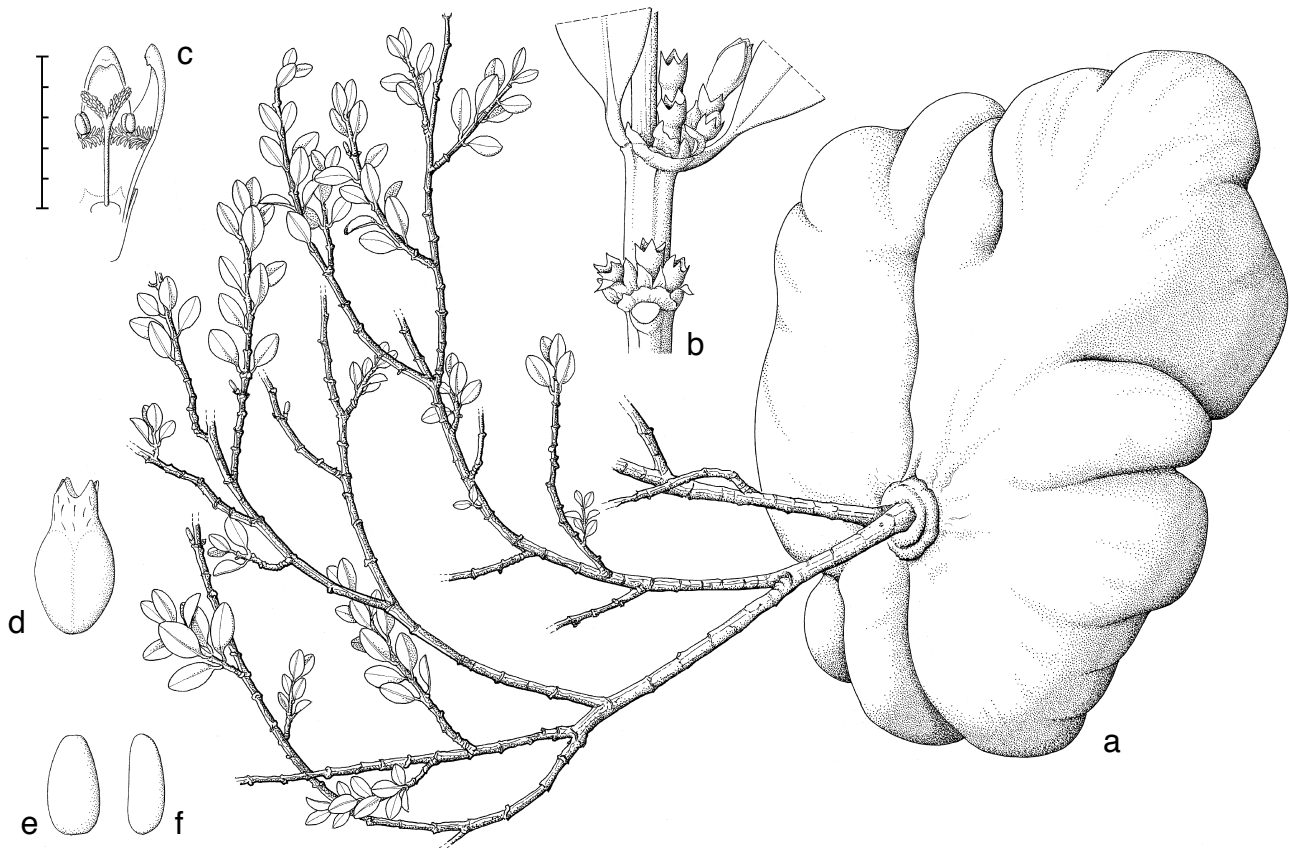
*Tuber* amplexans, complanatum, circulare usque oblongum ambitu, iocineriforme, lobis distinctis, saepe profunde divis, rotundatis circum marginem ornatum, rotundatis circum marginem ornatum, ad 30 cm in diametro. Aperturæ supra omnino nullae, solum in pagina substrata tuberis, ad 2 cm in diametro. Caules numerosi, ramosi, ex stirpe communi enati, in centro tuberis. Folia subsessilia. Lamina obovata, 2 per 1.1 cm sed varia magnitudine, apice acuto, basi cuneata usque sensim attenuata. Inflorescentia binata, sessilibus usque breviter pedunculata, instructa bracteis minutis, papyraceis, sed plurimis reliquis calycum fasciculum distinctum ad nodum quemque formantibus. Calyx 2 mm, irregulariter 4-acumino-dentatus. Flores heterostyli. Corollae tubus 4.5 mm, annulo brevium pilorum ad faucem instructus, lobi 2–3 mm. Pyrenae oblongo-ovoideae, 3.4 per 1.8 mm. — *Typus*: Jebb 327 (holo LAE; iso A, BRI, CANB, K, L, UPNG), Papua New Guinea, Lufa subdistrict, Frigano Timber Lease, Habu River, S6°28' E145°26', 11 May 1983.

*Etymology.* For the prominent and persistent calyx remains with their 4 sharp teeth.

*Tuber* clasping, flattened, circular to oblong in outline, liver-shaped, with distinct, often deeply divided, rounded lobes around edge, to 8 by 30 cm; silvery to grey-brown, reddish brown underneath, matt, roughened by minute grooves, sometimes becoming lichen-encrusted, barely corrugated towards edge of lobes and at common stem stock, otherwise smooth

**Fig. 30** *Hydnophytum vitis-idaea* Merr. & L.M.Perry. a. Shoot; b. whole flower; c. half flower; d. pyrene adaxial face; e. lateral view (Brass 12046, type). — Scale bars: a = 10 cm; b = 5 cm; c = 10 mm; d, e = 6 mm. — Drawn by Rosemary Wise.





**Fig. 31** *Hydnophytum acuminicalyx* Jebb & C.R.Huxley. a. Habit; b. detail of shoot; c. flower; d. fruit; e. pyrene abaxial face; f. pyrene lateral view (a–c: *Jebb 320*; d–f: *Jebb 323*). — Scale bars: a = 5 cm; b = 1 cm; c–f = 5 mm. — Drawn by Rosemary Wise.

and gently undulating. Entrance holes to 2 cm diam, confined to substrate side of tuber only. Cavities numerous, not interconnected, planar to digitate, clasping, warted in their extremities. Flesh white. Roots largely confined to edge of substrate surface. *Stems* numerous, branching; arising from a common stock at centre of the tuber; to 60 cm long, 0.3–1 cm diam; upcurving, silvery-brown, often lichen-encrusted. Longer shoots with numerous short branches. Internodes on main shoots 0.5–5 cm in length, on secondary shoots 0.1–0.6 cm. *Leaves* subsessile, clustered at apex, held erect, curving outwards. Lamina obovate, 0.3 by 0.2 to 3.5 by 1.7 cm (most often c. 2.0 by 1.1 cm); apex acute; base cuneate to tapering; fleshy, dark green above, paler below, midrib white, nerves obscure c. 4–6. Petiole 0–0.2 cm, white, rounded; stipules membranous, blunt, 0.1 cm. Inflorescence paired, sessile to shortly pedunculate, bracts minute papery, often bearing numerous calyx remains (fruit apparently not always produced) forming a distinctive cluster at each node. *Flowers* [7] heterostylous, lobes apiculate in bud. Calyx 2 mm, irregularly 4 acumino-dentate, 2 longer than others (1 and 0.4 mm, respectively). Corolla white to yellow-green; tube 4.5 mm, lobes 2–3 mm, a ring of short hairs at mouth of tube. Short-styled flowers with anthers c. 1 mm long, exerted on 1 mm filaments; pollen 60–75  $\mu$ m, pores 12–14  $\mu$ m, brochi < 1  $\mu$ m; stigma 2-lobed, at or below level of mouth. Long-styled flowers with anthers 0.6 mm, below level of mouth; pollen 40–50  $\mu$ m; stigma with 2 papillose lobes c. 1.5 mm long, exerted. *Fruit* ovoid, to 6 mm overall, crowned by persistent calyx; red, calyx green. Pyrenes oblong-ovoid, 3.4 by 1.8 mm.

*Ecology & Habitat* — Mid-level epiphyte in closed forest, 2000–2400 m; often in large numbers in a single tree. Invariably inhabited by a large form of the aggregate ant species *Anonychomyrma scrutator*.

*Distribution* — Papua New Guinea (Eastern Highlands Province).

*Conservation status* — Critically Endangered (CR) under criteria B1ab(iii)+2ab(iii). The collections indicate just a single location. Other information: AOO 8 km<sup>2</sup> (based on a cell width of 2 km).

*Additional specimens examined.* *Streimann & Kairo NGF 45256* (A, BRI, CANB, K, L, LAE), Eastern Highlands Province: S6°25' E145°22' Lufa sub-district, Frigano Timber Lease; *Jebb 316* (LAE), *Jebb 317* (LAE), *Jebb 318* (BO, CANB, LAE, UPNG), *Jebb 319* (BULOLO), *Jebb 320* (LAE), *Jebb 321* (FHO), *Jebb 322* (BRI, K, LAE), *Jebb 323* (LAE), *Jebb 324* (L, LAE), *Jebb 325* (BISH), *Jebb 326* (SUVA), S6°27' E145°26' Lufa sub-district, Frigano Timber Lease.

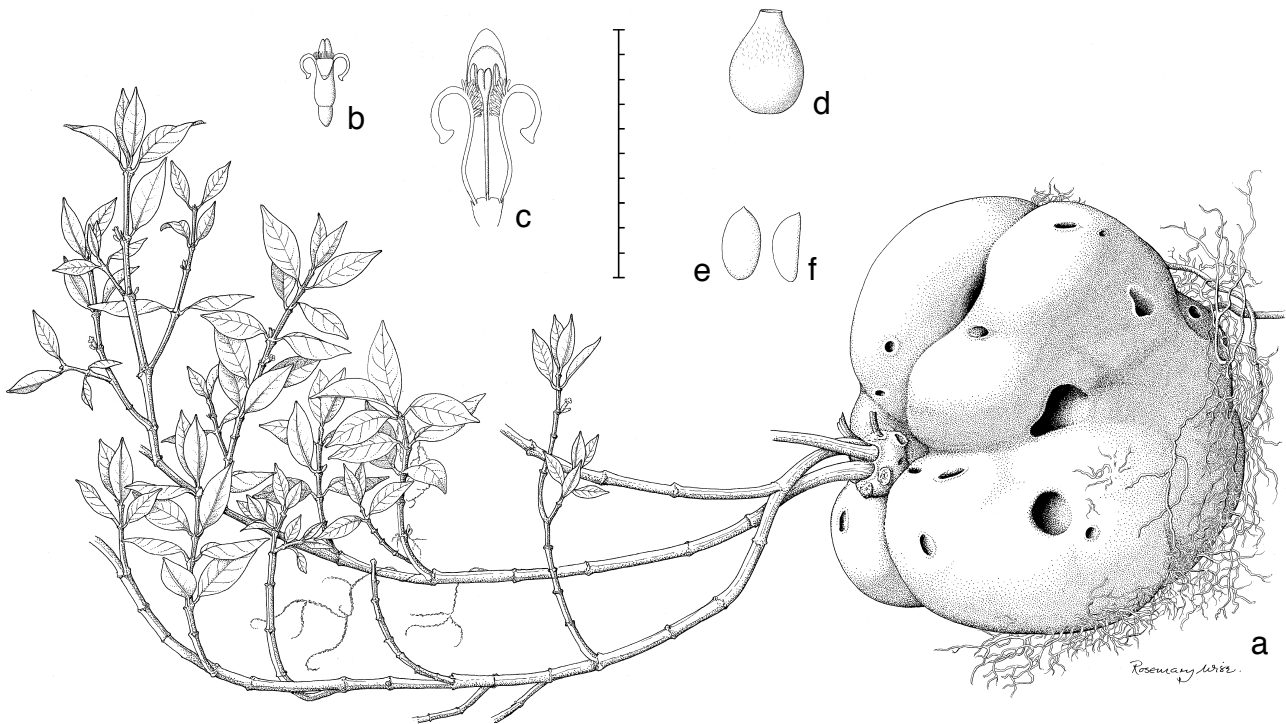
*Note* — The laterally growing tuber of this species, with its smooth, pale to dark-brown, unbroken upper surface, and the prominent and persistent 4-dentate calyces clustered in the axils are unique.

**29. *Hydnophytum dauloense* Jebb & C.R.Huxley, sp. nov. — Fig. 32; Map 5**

Tuber irregulariter globosum. Aperturæ duo generum, vel grandes infundibuliformes vel parvae et conicae. Caudes numerosi, ex stirpe communi enati, libere ramosi. Lamina lanceolata, latissima infra medium, 2.2 per 0.9 ad 7 per 3 cm; apex longe acuminiatus, ultimo rotundatus; basis abrupte angustata. Petiolus 1–5 mm. Inflorescentia sessilis, binata. Calyx ad 1.5 mm, margine integro. Corolla alba vel flavida apice dilute viridi; tubus ad 5 mm, basi ventricosus, angustatus ad faucem, qua annulo pilorum ornatus est; lobi ad 2.5 mm. Antherae exsertae, < 1 mm. Stigma multifidum, pari libra ad altitudinem antherarum. Pyrenae hemisphaericae, ad 3 per 1.6 mm, apice acuto, basi rotundata. — *Typus*: *Jebb 338* (holo LAE; iso A, BRI, CANB, K, L), Papua New Guinea, Chimbu Province, Mt Elimbari, 14 May 1983.

*Etymology.* After the Dauilo Pass, where the species is common.

*Tuber* irregularly globose with rounded lobes; to 30 by 25 cm. Entrance holes of two kinds, large and funnel-like or small and conical. Flesh white, firm. Cavity walls unwarted. *Stems*



**Fig. 32** *Hydnophytum dauloense* Jebb & C.R.Huxley. a. Whole plant; b. whole flower; c. half flower; d. fruit; e. pyrene abaxial face; f. lateral view (a–c: *Jebb 337*; d–f: *Jebb 334*). — Scale bars: a = 8 cm; b = 1 cm; c–f = 5 mm. — Drawn by Rosemary Wise.

numerous; to 100 by 0.3–0.6 cm; arising from a common stock; branching freely, ascending to upcurved. Internodes to 10 cm or more when sterile, 0.3–3 cm when fertile, with 2 prominent, rounded ridges running from below stipule. *Leaves* loosely clustered. Lamina lanceolate, widest below middle; 2.2 by 0.9 to 7 by 3 cm; apex long acuminate, ultimately rounded; base abruptly attenuate; midrib prominent; glossy dark green above pale below, drying grey/purplish/brown; margin recurved, strongly so when dry. Petioles 0.1–0.5 cm; stipules triangular, white, to 0.4 cm. Inflorescence sessile, paired. *Flowers* [3] ?not heterostylous. Calyx to 1.5 mm above level of disc; margin entire. Corolla white or yellowish with a faintly green tip. Corolla tube to 5 mm, ventricose at base, narrowing to mouth, and with a ring of hairs there; lobes to 2.5 mm, uncus < 1 mm, fully reflexed in open flower. Anthers exserted, < 1 mm, filaments to 1 mm, closely appressed to one another. Pollen 51–60  $\mu$ m, walls 2.5–3  $\mu$ m thick, brochi 1  $\mu$ m, pores 15–18  $\mu$ m, vesicles small. Stigma multi-fid, at level of anthers. *Fruit* ovoid to 5 by 3 mm, red. Pyrenes to 3 by 1.6 mm, more or less hemispherical; apex acute; base rounded.

**Ecology & Habitat** — Low to high-level epiphyte in montane forest, 2400–2800 m. Tuber not inhabited by ants, but collecting rainwater and occupied by a range of invertebrates including cockroaches, centipedes, spiders and on Mt Elimbari the arboreal frog *Cophixalus riparius*.

**Distribution** — Papua New Guinea (Eastern Highlands and Chimbu Province).

**Conservation status** — Endangered (EN) under criteria B1ab(iii)+2ab(iii). The five known localities occurring in one of the most densely populated regions of the Papua New Guinea highlands. Whilst the strict EOO covers some 340 km<sup>2</sup>, the actual remaining habitat is a fraction of this. Other information: AOO 28 km<sup>2</sup> (2 × 2 (using a cell width of 2 km)), using an auto-value grid size is likely to be erroneous given the restricted habitat area.

*Additional specimens examined.* *Kerenga & Baker* LAE 56924 (K, L, LAE), Eastern Highlands, S5°90' E144°05', NE of Kamus village; *Grubb & Edwards* 206 (CGE, L, LAE), S6°00' E145°11', near (W of) Fatima river, Marafunga Sawmill, Goroka subdistrict; *Cruttwell s.n.* 1980 (LAE), S6°00' E145°25', Mt

Gahavisuka National Park, c. 10 km NW of Goroka; *C.R.Huxley & Worthing* UPNG 3457 (UPNG) S6°02' E145°13', Daulo Pass, Goroka side; *Phillipson* 3529 (L), summit of Daulo Pass; *Cruttwell* in UPNG 5945 (×3), Daulo Pass; *Pullen* 457 (A, CANB, L), S6°03' E145°13', Asaro-Mairifutca divide, S of Daulo Camp; *Jebb 333* (A, BISH, K, L), *Jebb 334* (BRI, CANB), *Jebb 335* (LAE), *Jebb 336* (LAE), *Jebb 337* (L, SUVA), *Jebb 339* (BRI, CANB, K, L, LAE), *Jebb 340* (A, L, LAE), Chimbu Province, S6°11' E145°09', NE side of Mt Elimbari, 2 km S of pass on road from Nambaiyufa to Chuave.

**Note** — This species has a characteristic ovate leaf that is broadest below the middle and tapers to a slender, ultimately rounded, acuminate apex. The leaves approach those of *H. terrestris* [35], which is distinguished by its large bracts and distinct tuber anatomy.

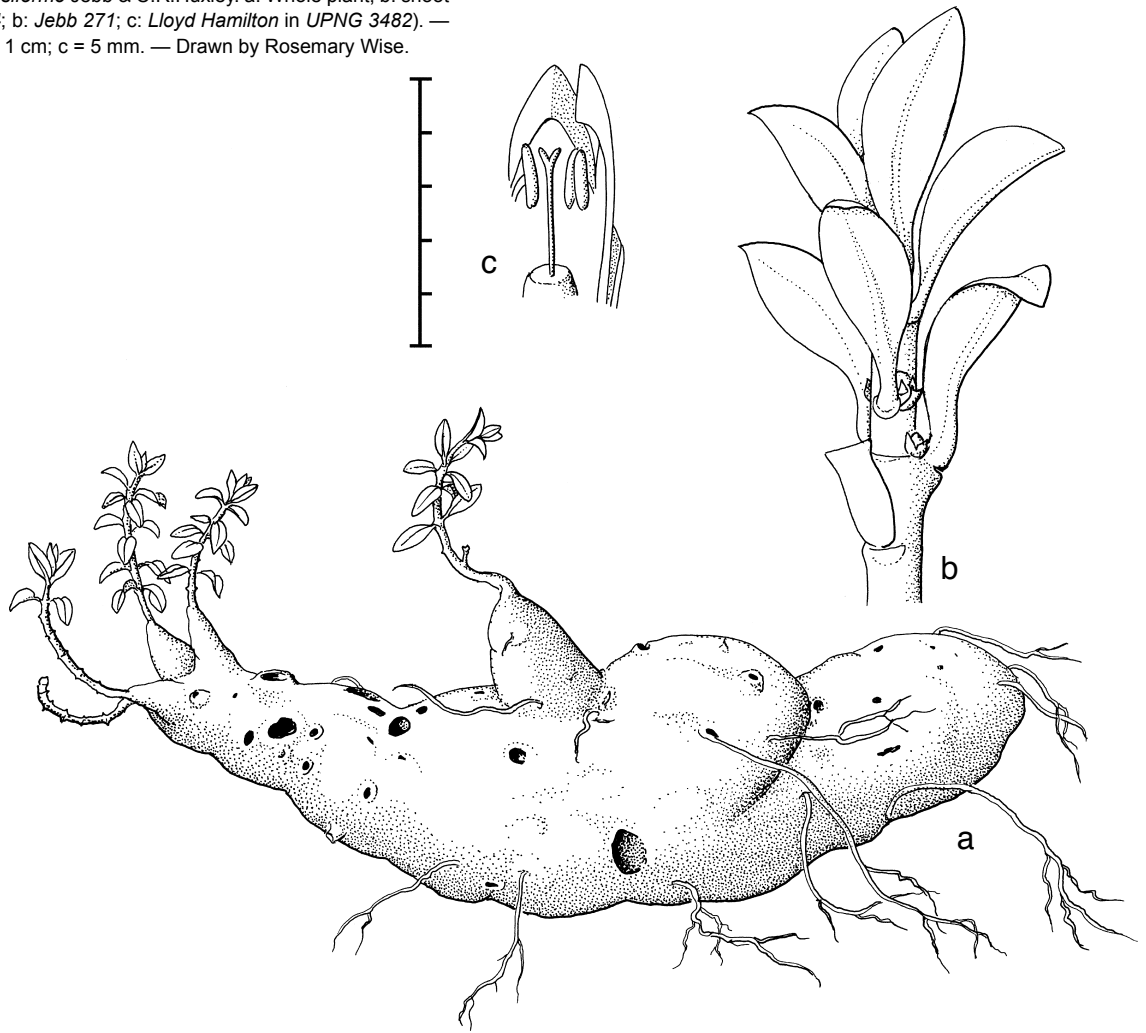
### 30. *Hydnophytum fusiforme* Jebb & C.R.Huxley, *sp. nov.* — Fig. 33; Map 5

Tuber initio fusiforme, aetate procedente apice grandescens; superficie grisea, spinis tenuibus, flexibilibus armatum. Aperturae duo generum, vel infundibuliformes vel parvae et conicae. Caules numerosi, ramosi, ex variis locis in apice tubere enati. Lamina parva, ovata usque elliptica, 0.6 per 0.25 ad 1.2 per 0.5 cm, apice obtuso usque acuto, basi sensim attenuata. Petiolus brevissimus. Stipulae triangulares, ad 0.5 mm, satis persistentes. Inflorescentia binata, sessilis. Calyx 4-dentatis, ad 2 mm. Corollae tubus ad 2 mm, glabrum; lobi ad 2 mm. Antherae ad 1.5 mm. Stigma bifidum, pari libra cum antheris. Fructus et pyrenae ignota. — *Typus: Lloyd Hamilton* in UPNG 3482 (holo UPNG; iso LAE), Papua New Guinea, West Sepik Province, Nong river.

**Etymology.** For the fusiform shape of the tuber in young plants.

*Tuber* fusiform, initially narrowly cylindrical, to 1 cm diam, becoming larger at apex with age, to 25 by 12 (30 by 30) cm, pale brown to grey. Spines slender, finely tapering and flexible, to 0.5 cm. Entrance holes of two kinds, funnel-like to 2 cm across, or small and conical to 0.2 cm internally. Cavities few, large, to 15 cm across, bulbous, smooth-walled. *Stems* numerous, branching, arising from various places on tuber, usually short, some to 40 cm, erect to pendulous. Internodes of main stems to 5 by 0.3 cm; those of side shoots 0.1–1.5 by 0.1–0.2 cm, nodes swollen, with a marked petiole base articulation, and a minute ridge running from below stipule. *Leaves* erect, recurved, clustered at apex, and often obscuring such. Lamina ovate to elliptic; 0.6

**Fig. 33** *Hydnophytum fusiforme* Jebb & C.R.Huxley. a. Whole plant; b. shoot tip; c. flower (a: *Jebb 294*; b: *Jebb 271*; c: *Lloyd Hamilton in UPNG 3482*). — Scale bars: a = 5 cm; b = 1 cm; c = 5 mm. — Drawn by Rosemary Wise.



by 0.25 to 1.2 by 0.5 cm; apex blunt to acute; base tapering; dark glossy green. Petiole very short; stipules triangular, to 0.5 mm, with a hooked central process c. 0.03 cm long; somewhat persistent, though often partly detached. Inflorescence paired, sessile. *Flowers* [2] not heterostylous. Calyx 4-dentate, to 2 mm. Corolla tube to 2 mm, glabrous within; lobes to 2 mm, unicus to 1.5 mm. Anthers to 1.5 mm. Pollen to 75  $\mu\text{m}$ , thin-walled (c. 1  $\mu\text{m}$ ), brochi 1.5–2.5  $\mu\text{m}$ . Stigma slender, bifid, at level of anthers. *Fruit* and pyrenes unknown.

**Ecology & Habitat** — Mossy forest, 2000–2400 m. Tuber not inhabited by ants.

**Distribution** — Papua New Guinea (Southern Highlands and West Sepik Province).

**Conservation status** — Endangered (EN) under criteria B1ab(iii)+2ab(iii). The three known localities indicate only 2 sub-populations some 400 km distant from one another. Whilst the strict EOO covers some 820 km<sup>2</sup>, the potential habitat is far greater. Other information: AOO 2280 km<sup>2</sup> (using an auto-value cell width of 34 km).

**Additional specimens examined.** *Jebb 271* (LAE), *Jebb 272* (LAE), *Jebb 293* (LAE), *Jebb 294* (LAE), Southern Highlands Province, S6°07' E143°57', SE of Mt Giluwe, above Onin, 'Beechwoods No. 2' logging track; *UPNG 3483* (LAE, UPNG), *UPNG 3484* (UPNG), *UPNG 3485* (UPNG), *UPNG 3486* (LAE, UPNG), West Sepik Province, Nong river.

**Note** — Small specimens of this taxa have their tubers entirely buried in cushions of moss. Young tubers are narrow and fusiform in shape, later they develop a broad, blunt apical region, with stems arising from several positions. No *in situ* observations have been made (collections from felled trees only), but the tuber probably grows in a manner to retain its stems at the

surface of the growing moss layer. Fine roots develop over the whole tuber surface, becoming short and spine-like on exposed surfaces. Some stems may grow to 30–40 cm, bearing many short side shoots. In Papua New Guinea the minute leaves readily distinguish it from all other *Hydnophytum* species, it differs from *H. vitis-idaea* [27] in its much shorter flowers.

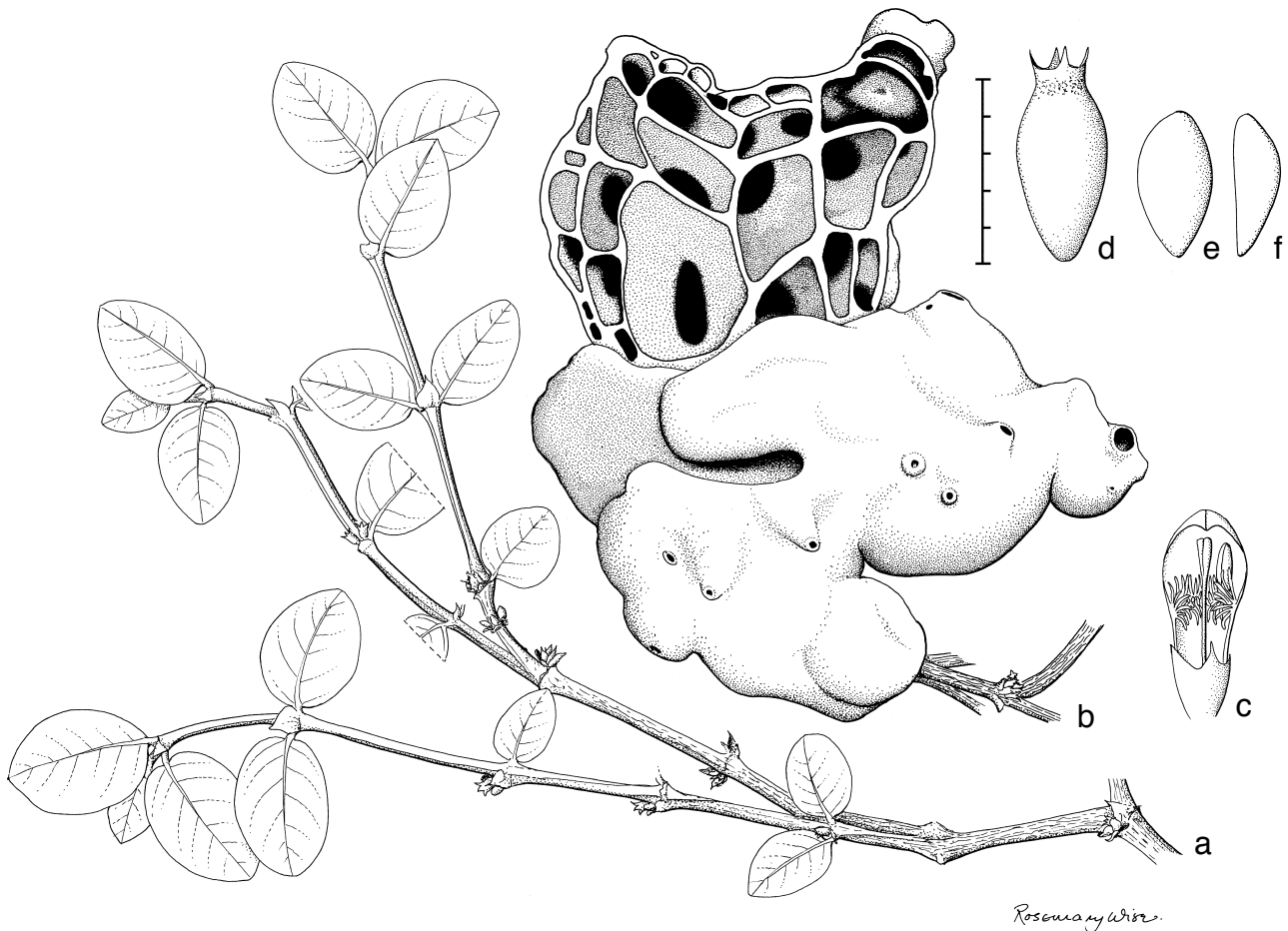
**31. *Hydnophytum hailans* Jebb & C.R.Huxley, *sp. nov.* — Fig. 34; Map 5**

Tuber irregulariter globosum, superficie laevi. Aperturæ dispersae, duo generum, pleraeque labrosae, ad 0.5 cm in diametro, pauciores infundibuliformes, ad 2 cm in diametro. Caules pauci, parce ramosi, quadrangulares. Lamina ovata, 2.1 per 1.6 (1.5 per 1) ad 4 per 3 cm, apice obtuso usque acuto, basi rotundata usque cordata. Petiolus 0–0.2 cm. Inflorescentia sessilis; bracteis obiecta, quae bracteae papyraceae, ad 0.8 cm, triangulares. Calyx 2 mm, margine 4 vel 5 dentato. Corollae tubus 2.5 mm, annulo pilorum ad faucem instructus. Lobi 1.5 mm. Antherae exsertae, ad 1.3 mm. Stigma 2-lobatum, pari libra ad altitudinem antherarum. Pyrenae obovoideae, 3.5 per 2.5 mm, apice rotundato-acuto, basi sensim attenuata. — **Typus:** *Huxley & Turton in UPNG 5919c* (holo LAE; iso A, BRI, CANB, K, L, UPNG), Papua New Guinea, S5°57' E143°51', Southern Highlands Province, foothills of Mt Giluwe on Mendi-Hagen Road.

**Etymology** The *lingua franca* of the Papua New Guinea highlands region is Melanesian Pidgin, and 'Hailans' is the pidgin name for that region.

**Tuber** irregularly globose, to 20 cm diam, surface smooth, brown; roots numerous, short, throughout surface. Entrance holes of two kinds: some prominently rimmed, 0.2–0.5 cm internally; others funnel-like, to 2 cm diam, scattered throughout surface. Cavities 1–7 cm across, largest towards centre of tuber. Tuber tissue buff in colour. **Stems** few, upcurving, spreading,





**Fig. 34** *Hydnophytum hailans* Jebb & C.R.Huxley. a. Shoot; b. tuber with upper half sectioned to show cavities within; c. flower; d. fruit; e. pyrene abaxial face, lateral view (a: Huxley & Turton in *UPNG 5919C*, type; b–f: Jebb 572 (Lae), Morobe Province, beside road from Bulolo to Aseki). — Scale bars: a, b = 5 cm; c–f = 5 mm. — Drawn by Rosemary Wise.

occasionally branching to 60+ cm; internodes 0.5–4 by 0.2–0.4 cm, 4-angled; nodes swollen. *Leaves* spreading. Lamina ovate; (1.5 by 1) 2.1 by 1.6 to 4 by 3 cm; apex blunt to acute, base rounded to cordate; mid-green above, pale below; leathery; midrib prominent above and below; veins 5–7. Petiole 0–0.2 cm; stipules to 0.6 cm, rounded to triangular, with a prominent central appendage, persistent. Inflorescence paired, sessile, bract-covered, bracts triangular, to 0.8 cm, papery. *Flowers* [2] ?not heterostylous. Calyx 2 mm, margin 4 or 5 dentate. Corolla tube 2.5 mm, with a ring of hairs at mouth; lobes with a minute crest at tip, 1.5 mm. Anthers exserted, 1.3 mm. Pollen 55 (53–57)  $\mu\text{m}$ , colpate, brochi < 1  $\mu\text{m}$  across. Stigma 2-lobed, at same level as anthers. *Fruit* ovoid, to 5 mm, with prominent calyx remains; orange-red. Pyrenes obovoid, 3.5 by 2.5 mm; apex rounded-acute; base tapering.

**Ecology & Habitat** — Forest, 2000–2700 m. Tuber not inhabited by ants.

**Distribution** — Papua New Guinea (Southern Highlands to Morobe).

**Conservation status** — Vulnerable (VU) under criteria B1ab (iii)+2ab(iii). Two main populations exist, one in the central highlands and one in Morobe Province with a geographical spread of 470 km. Whilst the strict EOO covers some 18 000 km<sup>2</sup>, the actual habitat is a fraction of this. Other information: AOO 40 km<sup>2</sup> (2×2 km squares) or 14 400 km<sup>2</sup> (using an auto-value cell width of 42 km).

**Additional specimens examined.** Jebb 597 & 598 (LAE), Western Highlands Province, S5°30' E144°12', Jimmi divide, on road from Baiyer River to the Jimmi Valley; Ash in *UPNG 3469* (UPNG), Southern Highlands Province, S6°10' E143°57', Onin, SE of Mt Giluwe, Ialibu subprovince; Jebb 287, 291 & 292 (LAE), SE of Mt Giluwe, on logging track above Onin; Jebb 591 (LAE),

S6°11' E143°54', Beechwoods logging track c. 8 km after Onin, S of Mt Giluwe, off Mt Hagen to Mendi road; Jebb 571, 572, 573, 574, 575, 576, 577, 578 & 579 (LAE), Morobe Province, Aseki divide, beside road from Bulolo to Aseki; Huxley in *UPNG 3453* (UPNG), Wau, near Eddie Creek turning, Mt Kaindi summit road; Jebb 26 (LAE), Wau, Mt Kaindi summit road; Höft 3612 (L, LAE), Mt Kolorong Wildlife Conservation Area, Kuper Range.

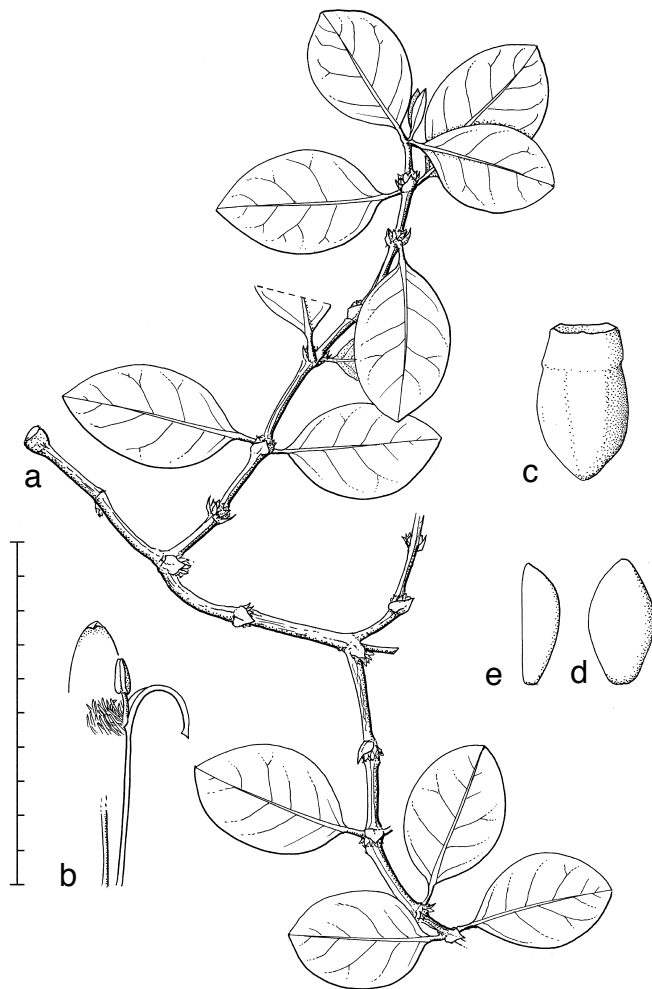
**Note** — A somewhat nondescript species that can be distinguished by its rounded leaves with prominent midrib above and below that often dries to a pinkish tinge. The tuber is irregular, and the stems are often distorted.

**32. *Hydnophytum mayuense* Jebb & C.R.Huxley, sp. nov.** — Fig. 35; Map 5

Tuber complanatum; superficies laevis, aperturis elevatis. Caules complures, rotundati. Lamina ovata, 3.6 per 2.1 ad 6 per 3.9 cm, apice acuto, basi sensim attenuata. Petiolus 0.7 cm. Inflorescentia sessilis, bracteis obiecta; quae bractee densae, triangulares, papyraceae, ad 0.8 cm, siccando brunneae, caulem ad nodos fertiles obtegentes. Calyx integer, ad 1 mm. Corollae tubus ad 5.5 mm, lobis 2.5 mm, annulo pilorum ad faucem instructus. Antherae exsertae, 1 mm, filamenta ad 1 mm. Pyrenae obovoideae, 3.5 per 2 mm, apice rotundato, basi angulari cuneatae, tum abrupte truncatus. — **Typus:** Stevens in *LAE 55653* (holo L; iso A, BRI, CANB, K, LAE), Papua New Guinea, Milne Bay Province, Scarp of Tantam Plateau overlooking Mayu River, 18 July 1972.

**Etymology.** For the type locality.

**Tuber** flattened, to 20 cm across, surface smooth with slightly raised entrance holes. **Stems** several, spreading, to 40 by 0.5 cm; internodes 1–5 cm. Lamina ovate; 3.6 by 2.1 to 6 by 3.9 cm; apex acute, base tapering; midrib prominent below, less so above; veins 5 or 6; dark shiny green above, pale below. Petiole 0.7 cm; stipules to 0.2 cm, triangular to rounded,



**Fig. 35** *Hydrophytum mayuense* Jebb & C.R.Huxley. a. Shoot; b. flower; c. fruit; d. pyrene abaxial face; e. lateral view (Stevens LAE 55653, type). — Scale bars: a = 5 cm; b–e = 5 mm. — Drawn by Rosemary Wise.

caducous. Inflorescence sessile, bract-covered, these dense, triangular, papery to 0.8 cm, drying brown, obscuring stem at fertile nodes. *Flowers* [1] ?heterostylous. Calyx entire, to 1 mm. Corolla tube to 5.5 mm, lobes 2.5 mm; with a ring of hairs at mouth of tube. Anthers to 1 mm; exserted, filament to 1 mm. Stigma missing, but apparently below corolla mouth. *Fruit* spherical, red, to 5 mm, with prominent calyx remains. Pyrenes obovoid, 3.5 by 2 mm; apex rounded; base angular, cuneate then abruptly truncate.

**Ecology & Habitat** — Forest, 2010 m. Occasionally ant-occupied (P. Stevens notes).

**Distribution** — Papua New Guinea (Morobe, Milne Bay and Northern Provinces).

**Conservation status** — Vulnerable (VU) under criteria D2 with only two locations known almost 400 km apart.

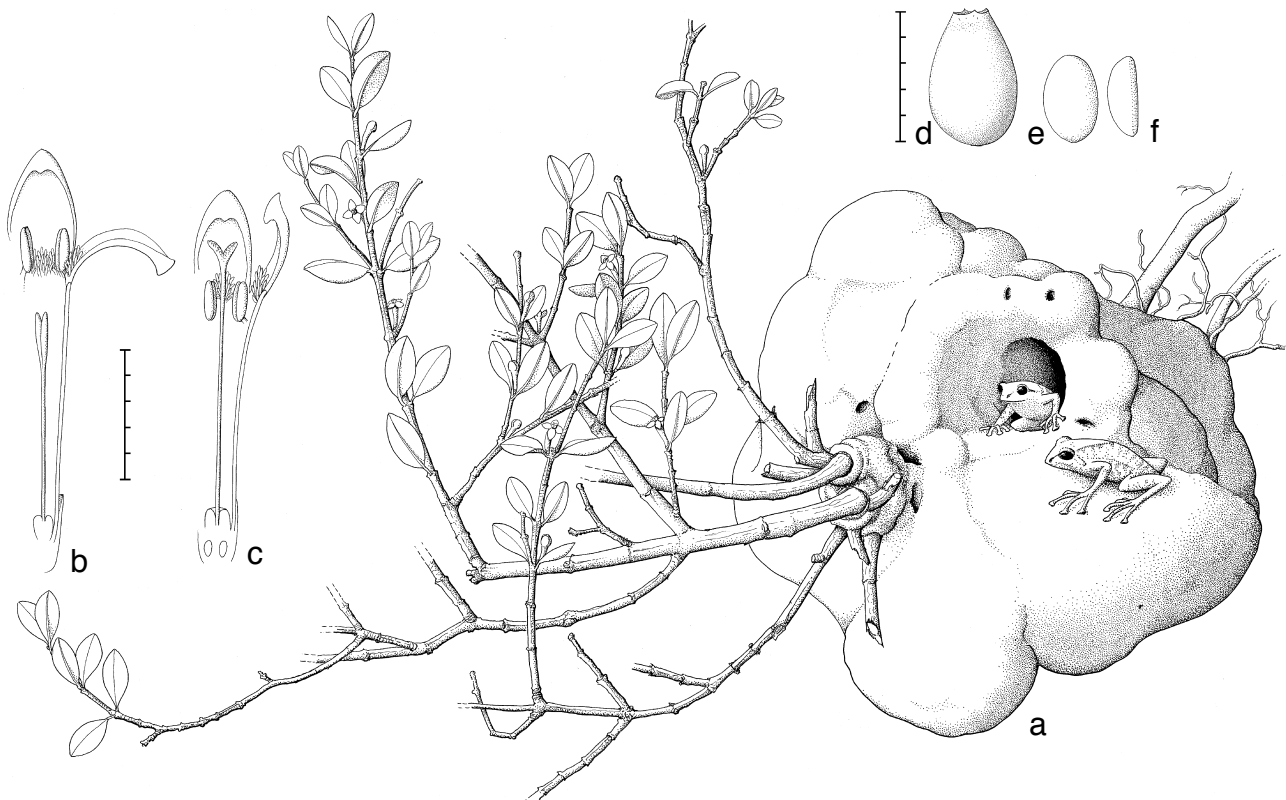
*Additional specimens examined.* Höft 2822 (L) Morobe Province, Mt Kolorong Wildlife Conservation Area, Kuper Range.

**Note** — Resembles *S. vanuatuensis* [55], but has petiolate leaves, and more robust bracts.

**33. *Hydrophytum myrtifolium* Merr. & L.M.Perry** — Fig. 36; Map 5

*Hydrophytum myrtifolium* Merr. & L.M.Perry (1945) 19. — Type: Brass 4093 (lectotype selected here A; iso BO, BRI, K, L), Papua New Guinea, Central Province, Mt Tafa, May 1933.

*Tuber* irregularly subglobose to fusiform, 25 by 30 cm, sunken in moss-cushions or pendent by one to few roots to 1 m or more, surface smooth to rough, occasionally areolate, reddish brown. Entrance holes of two types: small and conical, 0.3–1 cm across; large funnel-shaped, 2–8 cm diam. Cavities of two types: large, spiral-shaped and blind-ended 2–9 cm across; or narrow, tubular, and much branched tunnels 0.1–0.5 cm across; all smooth-walled, occasionally with internally produced roots. Tuber tissue white. *Stems* one to many, arising from a woody stock, branching, to 1 m or more, 0.2–0.8 cm diam; pendent to



**Fig. 36** *Hydrophytum myrtifolium* Merr. & L.M.Perry. a. Habit with the frog *Cophixalus riparius*; b. short-styled flower; c. long-styled flower; d. fruit; e. pyrene abaxial face, lateral view (a, b: Jebb 352; c: Jebb 348; d–f: Jebb 349). — Scale bars: a = 5 cm; b–f = 5 mm. — Drawn by Rosemary Wise.

upcurving. Internodes 0.5–6 cm, nodes angular, with prominent ridges decurrent from stipules. Bark grey-brown, smooth, drying ridged. Lamina elliptic to ovate, usually widest at middle; 1.4 by 0.7 to 3 by 1.7 cm; apex acute to blunt; base attenuate; gently recurved along their length; midrib prominent below, sunken above, pale green; margin recurved; stiff, leathery; dark, glossy green above, pale, dull below. Petiole short or absent, to 0.5 cm; stipules green-brown, persistent, to 0.3 cm, with central spur to 0.1 cm. Inflorescence paired, virtually sessile near stem apex, becoming shortly pedunculate with age; bracts small, papery. *Flowers* [5] heterostylous, club-shaped in bud. Calyx to 2.5 mm, entire to slightly dentate, much longer than disc. Corolla tube to 10 mm; lobes 4.5 by 2.5 mm, apiculate; with a dense ring of hairs at mouth of tube. Short-styled flowers with anthers to 1.8 mm, exserted; pollen 43–49 µm, wall c. 3.75 µm, brochi 1.5–2 µm, pores small; stigma 2-lobed, lobes to 2.5 mm, c. 1/2 way down corolla tube. Long-styled flowers with anthers to 1.6 mm; immediately within mouth of corolla tube; pollen 49–59 µm; stigma exserted, with lobes to 1 mm. *Fruit* ellipsoid, to 5 by 3.5 mm; red, with a prominent orange calyx. Pyrenes hemispherical, 3 by 2.3 mm; apex and base rounded.

*Ecology & Habitat* — An epiphyte of mossy forest, from 2000–2900 m. Tuber not inhabited by ants, but usually containing rainwater, cockroaches, myriopods and sometimes arboreal frogs and their eggs.

*Distribution* — Papua New Guinea (Morobe, Central and Northern Provinces).

*Conservation status* — Vulnerable (VU) under criteria B1ab (iii)+2ab(iii). This taxon has a geographical spread of 250 km

along the Owen Stanley range. Other information: georeferenced collections 12, EOO c. 10 000 km<sup>2</sup>, AOO 5790 km<sup>2</sup> (using an auto-value cell width of 27 km), herbarium collections suggest 6 locations (subpopulations).

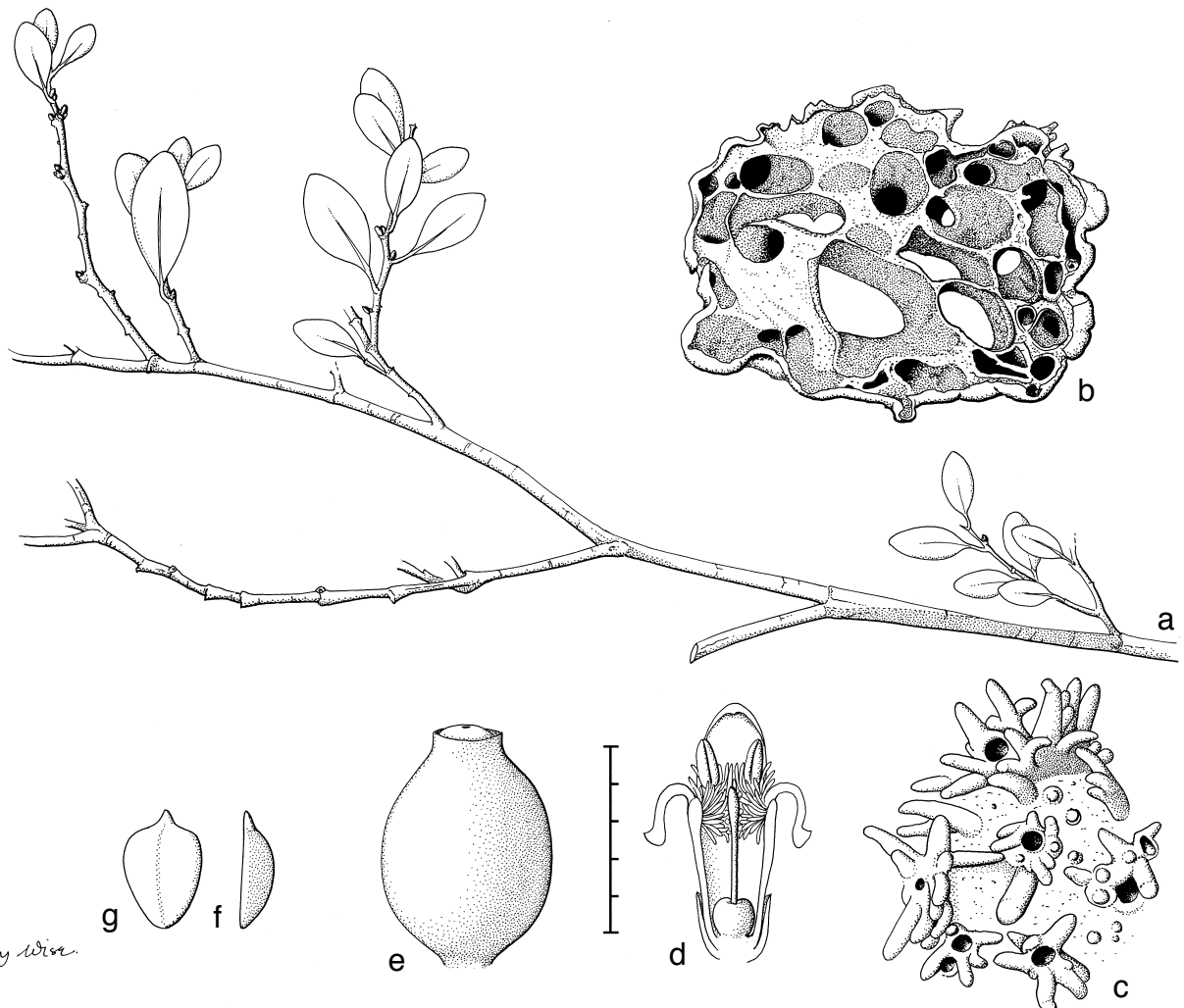
*Note* — The cavities are well adapted for collecting rainwater, with large funnel-like entrance holes. Several collectors have noticed frogs in these chambers, and MHPJ has found adults and eggs of the tree frog *Cophixalus riparius* Zweifel on Mt Shungol. Two other *Hydnophytum* species have been recorded as regularly containing frogs: *H. pauper* [24] and *H. dauloense* [29].

**34. *Hydnophytum reevii* Jebb & C.R.Huxley, sp. nov.** — Fig. 37; Map 5

Tuber irregulariter globosum. Aperturæ numerosæ, 0.2 ad 0.6 cm, labrosæ, instructæ quæque 1–5 lobis digitiformibus. Caules juvenes 4-angulati. Lamina elliptica usque obovata, ad 4.2 per 2.3 cm, apice rotundo-acuminato, basi sensim attenuata. Petiolus ad 0.6 cm. Inflorescentia binata, sessilis, bracteis obtecta; quæ bracteæ ad 0.7 cm longæ, ad 0.4 cm latæ. Flores heterostylii. Calyx 2 mm, integer usque 4-dentatus. Corolla ad 9 mm; lobi triangulares, ad 3.5 mm; annulus pilorum exsertus ex faucem. Pyrenæ obovatae, 3.5 per 2.2 mm, apice truncato-apiculato. — *Typus*: *Reeve 1069* (holo LAE; iso CBG, FHO, K, L), Papua New Guinea, Enga Province, Porgera district, Tukulanga-Tombena ridge, Paiela C/D, July 1983.

*Etymology*. Named in honour of Tom Reeve, former agricultural officer at Laiagam in Enga Province of Papua New Guinea and orchidologist.

*Tuber* irregularly globose, to 30 by 15 cm. Entrance holes numerous, often densely covering tuber, 0.2–0.6 cm within, with

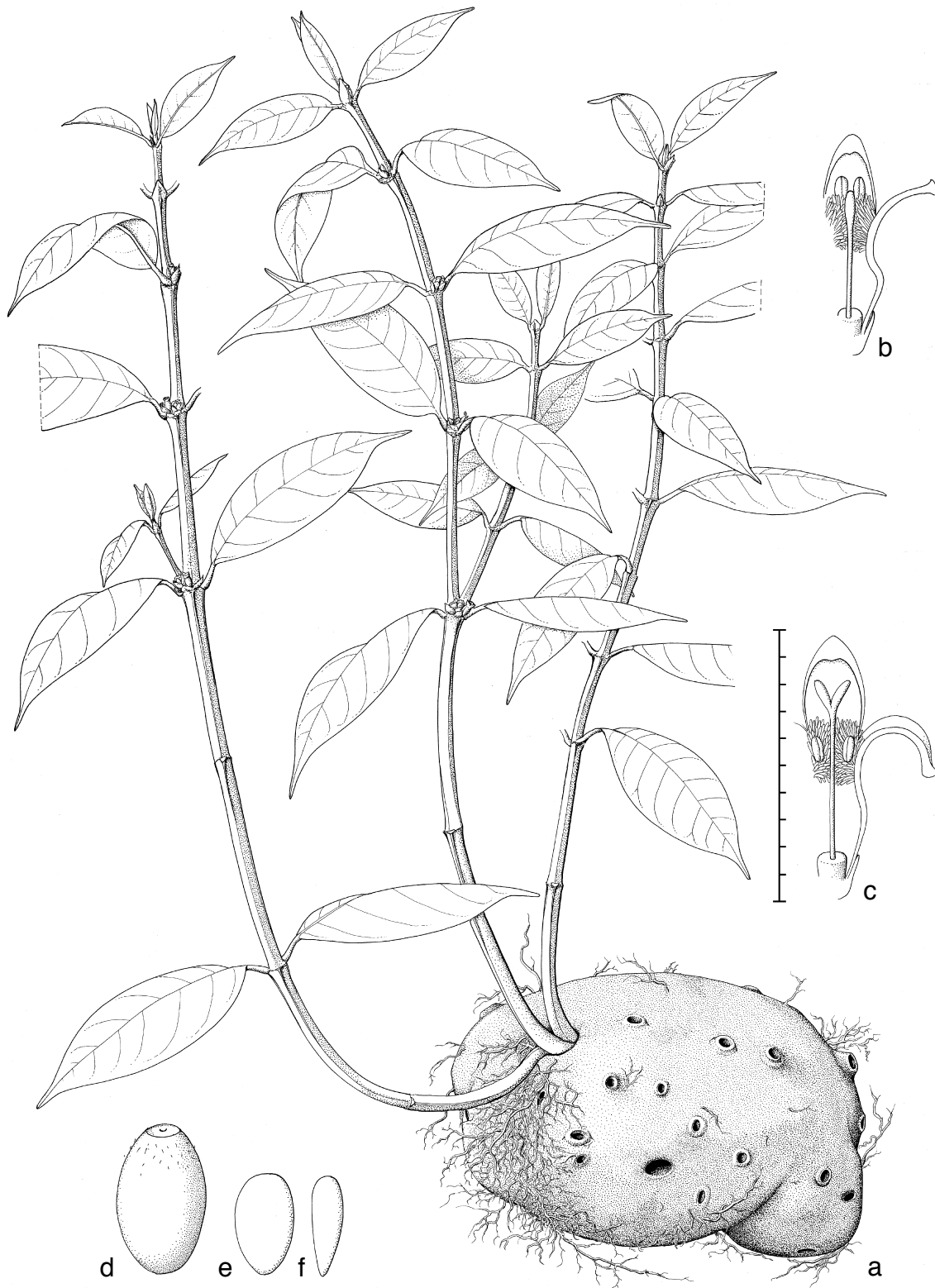


**Fig. 37** *Hydnophytum reevii* Jebb & C.R.Huxley. a. Shoot; b. tuber section; c. tuber surface; d. flower; e. fruit; f. pyrene abaxial face; g. lateral view (*Reeve 1069*, type). — Scale bars: a, b = 4 cm; c = 2 cm; d–g = 5 mm. — Drawn by Rosemary Wise.

a thick raised rim, often with 1–5, fleshy, upright to spreading, finger-like lobes, 0.2–1 by 0.2–0.3 cm along its margin. *Stems* several, to 60 cm, pendent to upcurved, branching, 4-angled, becoming rounded; internodes up to 12 by 1 cm when sterile, 0.5–4 by 0.2–0.4 cm when fertile. Lamina elliptic to obovate; 1.5 by 0.8 to 4.2 by 2.3 cm; apex round-acute; base tapering; leathery; midrib obscure towards apex; veins 4 or 5, obscure. Petiole 0.2–0.6 cm; stipules 0.2–0.3 cm, ± persistent. Inflorescences sessile, paired, bract-covered, to 0.8 cm across, bracts papery to leathery, triangular, to 0.7 by 0.4 cm. *Flowers* [3] ?heterostylous. Calyx to 2 mm, margin entire to 4-dentate.

Corolla tube to 6 mm, with a broad ring of hairs at mouth of tube, and spreading to the lobes; lobes triangular, to 3.5 mm, fully reflexed in open flower, uncus narrow to 1 mm. Only short-styled flower known. Anthers 2 mm, exserted, filaments 1.5 mm. Pollen 47–49 µm, brochi 1.5–2.5 µm, walls 1.5–3 µm thick, vesicles small. Stigma 2-fid to obscurely lobed, within mouth of corolla tube. *Fruit* globose, to 6 by 5 mm, calyx and disc prominent at apex. Pyrenes obovoid, 3.5 by 2.2 mm; apex truncate with an abrupt, rounded to acute, central process to 0.5 mm long.

*Ecology & Habitat* — Mid to low-level epiphyte in mossy forest, 1800–1900 m.



**Fig. 38** *Hydnophytum terrestris* Jebb & C.R.Huxley. a. Whole plant; b. short-styled flower; c. long-styled flower; d. fruit; e. pyrene abaxial face; f. lateral view (a, b: Jebb 314; c–f: Jebb 315). — Scale bars: a = 10 cm; b–f = 10 mm. — Drawn by Rosemary Wise.

Distribution — Papua New Guinea (Enga and West Sepik Province).

Conservation status — Vulnerable (VU) under criteria D2 with the only two known locations about 200 km apart.

*Additional specimen examined.* Jebb 244 (K, L, LAE), Jebb 245 (LAE), West Sepik Province, S5°05' E141°39', on path from Telefomin to Eliptamin.

Note — The extraordinary entrance hole extensions are not as well marked in the Telefomin specimens, and nor is the leaf shape in these latter two specimens a perfect match to the type, however, the inflorescence, flower and fruit characters are all constant.

**35. *Hydnophytum terrestris* Jebb & C.R.Huxley, sp. nov. — Fig. 38; Map 5**

Saepe terrestre. Tuber irregulariter globosum. Caules numerosi, ramosi. Internodia 4-angulata, alata. Lamina lanceolata usque ovata, latissima ad tertiam partem longitudinis, 3.5 per 1 ad 11 per 4 cm, apice sensim attenuato usque acuminato, basi abrupte angustata. Petiolus ad 1 cm. Stipulae grandes, triangulares, obtusae, ad 1 cm. Inflorescentia binata sessilis, raro quadruplex, tandem pedunculata. Bractee densae, inflorescentiam obtegentes, triangulares, ad 0.8 cm. Flores heterostyli. Calyx ad 1.5 mm. Corollae tubus ad 4.5 mm, lato annulo pilorum instructus; lobi ovati, ad 4.5 per 2 mm. Antherae ad 1 mm. Stigma 2-fidum. Fructus ellipsoideus. Pyrenae complanatae, ellipsoideae. — Typus: *Kairo 459* (holo LAE; iso A, Bulolo, CBG, K, L, UPNG), Papua New Guinea, Lufa, track to Mt Michael, S6°21' E145°17', 5 km SW of Lufa.

*Etymology.* For the unusual terrestrial nature of the species.

Epiphytic or terrestrial. *Tuber* globose, highly irregular in outline when growing terrestrially or beneath leaf litter, more regular when epiphytic, to 25 by 30 cm, pale brown. Entrance holes numerous, prominent, conical, 0.3–1 cm across. Cavity surfaces pale brown, warted at extremities. Tuber tissue white. *Stems* numerous, branching, erect, to 1 m, rarely with tuberous swellings with cavities, particularly when stems lie beneath leaf litter; internodes to 10 cm or more near tuber, becoming more condensed when fertile, 4-angled, winged immediately below nodes, wings running from between the petiole bases largest.

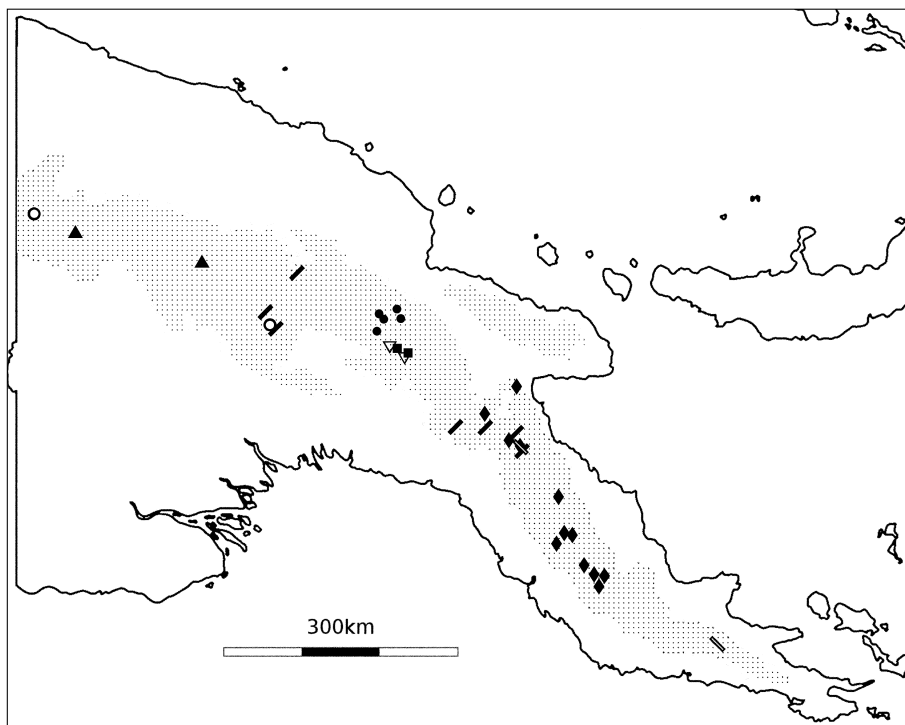
*Leaves* squarrose, stiff, leathery. Lamina ovate to lanceolate, widest at 1/3 length; 3.5 by 1 to 11 by 4 cm; apex tapering to acuminate; base narrowing abruptly. Dark glossy green above, paler below; drying grey-green with purple markings in herbarium specimens. Petiole to 1 cm; stipules large, triangular, blunt, to 1 cm, with a prominent wing, caducous. Inflorescence sessile, paired, rarely 4, becoming pedunculate. Bracts dense, covering inflorescence, triangular, to 0.8 cm, keeled, papery; drying grey/brown, persistent. *Flowers* [7] heterostylous. Calyx to 1.5 mm, entire, dentate or minutely ciliate. Corolla tube to 4.5 mm, widest at middle; with a broad ring (2 mm) of hairs at mouth, exerted in open flower; lobes ovate, to 4.5 by 2 mm, unicus < 1 mm. Short-styled flowers with anthers to 1 mm, filaments to 1.5 mm; pollen 3-colporate, 42–54 µm, walls to 2.5 µm, colpi to 35 µm long, 7 µm wide, brochi to 1 µm; stigma 2-fid, immediately within mouth of tube. Long-styled flowers with anthers at mouth of tube; filament < 0.5 mm; pollen 35–42 µm diam; stigma exerted. *Fruit* ellipsoid, to 6 by 3 mm. Pyrenes flattened, ellipsoid, 3.8 by 2.2 mm; apex and base rounded.

*Ecology & Habitat* — A low-level epiphyte, regularly becoming terrestrial by falling from tree, becoming buried in leaf litter, and then appearing as a shrub. Often growing at the very base of tree trunks. Tuber sometimes deeply buried, with upper surface 5–10 cm below surface. In *Castanopsis-Nothofagus* forest, 1800–2100 m. Abundant around Mt Michael. Tuber inhabited by a range of ant species.

Distribution — Papua New Guinea (Eastern Highlands Province).

Conservation status — Critically Endangered (CR) under criteria B1ab(iii)+2ab(iii). The collections indicate just 3 locations within a range of 20 km. This taxon is confined to lower montane forests around Mt Michael, a habitat that probably comprises less than 40 km<sup>2</sup> in total area. Other information: AOO 8 km<sup>2</sup> (using an auto-value cell width of 3 km), EOO 15 km<sup>2</sup>.

*Additional specimens examined.* Jebb 101 (LAE), Jebb 328 (LAE), Jebb 329 (K, L), Jebb 330 (LAE), Jebb 331 (LAE), Jebb 332 (LAE), S6°21' E145°16', Eastern Highlands Province, just past Duto, on road beyond Lufa, Mt Michael, Lufa subdistrict, 12 May 1983; Jebb 311 (LAE), Jebb 312 (LAE), Jebb 313 (LAE), Jebb 314 (BRI, K, L), Jebb 315 (LAE), S6°28' E145°26',



**Map 5** Distribution of the Papua New Guinea group. *H. acuminicalyx* Jebb & C.R.Huxley (■), *H. dauloense* Jebb & C.R.Huxley (●), *H. fusiforme* Jebb & C.R.Huxley (○), *H. hailans* Jebb & C.R.Huxley (/), *H. mayuense* Jebb & C.R.Huxley (\), *H. myrtifolium* Merr. & L.M.Perry (◆), *H. reevii* Jebb & C.R.Huxley (▲), *H. terrestris* Jebb & C.R.Huxley (▽). Shaded area is above 1000 m.

SW of Lufa, on logging track in the Frigano Timber Lease, Habu river, Lufa subdistrict, 11 May 1983; *Brass* 31377 (A, L), Mt Michael, NE slopes; *Jebb* 123 (LAE), Lamari valley.

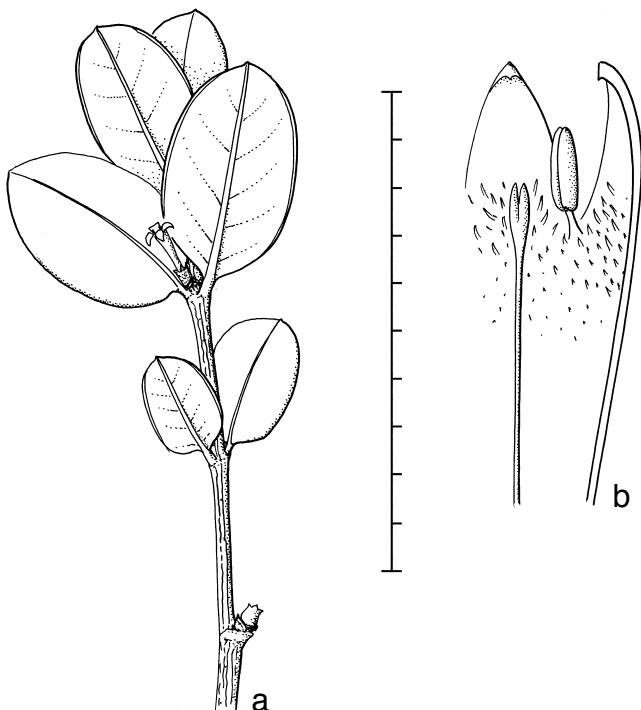
**Note** — The name refers to the unique habit of this species being found at the base of trees, or with its tuber buried in the leaf litter, having fallen from the trees above. Most species rot rapidly in such situations, while those other species found terrestrially are either in open, scrub-like habitats (*H. caminiferum* [17] and *H. dentrecastense* [41]) or are only terrestrial above the tree-line (*H. archboldianum* [36] and *H. pauper* [24]).

## GROUP 7 – RED TUBER TISSUE GROUP

### 36. *Hydnophytum archboldianum* Merr. & L.M.Perry — Fig. 39

*Hydnophytum archboldianum* Merr. & L.M. Perry (1945) 16. — Type: *Brass* 9506 (lectotype selected here A; iso L), New Guinea, Papua Province, Lake Habbema, Aug. 1938.

Terrestrial to epiphytic. *Tuber* large, surface rugose, brownish yellow. Entrance holes rimmed to 1 cm across. Tuber tissue purple. *Stems* several, branching and spreading, to 30 by 0.6 cm. Internodes 0.5–6 cm. Lamina elliptic-lanceolate; 2.3 by 1 to 5 by 3.3 cm; apex round apiculate to acute; base rounded; leathery; midrib prominent above and below, veins 4–6, more prominent above, slightly impressed below. Petiole to 0.2 cm; stipules to 0.2 cm, triangular, more or less persistent, falling before leaves. Inflorescence paired, sessile; bracts 0.5–0.8 cm, papery, with numerous reddish hairs within. *Flowers* [2] heterostylous. Calyx to 1.5 mm, 4-cuspidate. Corolla tube 7–8 mm, lobes 3 mm, pale purple to purple-red, with a broad band of short hairs from lobes to well within corolla tube. Short-styled flowers with anthers 1.8 mm, exserted on 1 mm filaments, stigma 2-fid at mouth of tube. Long-styled flowers with anthers 1.8 mm, within mouth of tube, stigma 2-fid, exserted above anthers. Pollen 3-colpate, 74 (68–78)  $\mu\text{m}$ , brochi 2–3  $\mu\text{m}$ . *Fruit* obovate, 8 mm, red. Pyrenes 2 or 3, obovoid, 3 by 2 mm; apex rounded; base tapering.



**Fig. 39** *Hydnophytum archboldianum* Merr. & L.M.Perry. a. Shoot tip; b. flower (a: *Brass* 9492; b: *Brass* 9240). — Scale bars: a = 10 cm; b = 10 mm. — Drawn by Rosemary Wise.

**Ecology & Habitat** — Terrestrial or epiphytic in alpine scrub, above 3000 m. Tuber not inhabited by ants.

**Distribution** — Indonesia (Papua Province).

**Conservation status** — Vulnerable (VU) under criteria D2 with only the type location known, a previously remote area, that is now accessible by 4WD with the concomitant risk of ecological degradation.

*Additional specimens examined.* *Brass* 9240 (A, BO, BRI, L), *Brass* 9492 (A, BO, BRI, L), S4°07' E138°40', Lake Habbema, 3225 m camp.

**Notes** — The tuber tissue is purplish red, and the flowers are said to be purple in colour, although this probably applies to the lobes only. These characters are shared by two species of *Hydnophytum* from Papua New Guinea: *H. magnirubrum* [37] and *H. minirubrum* [38]. *Hydnophytum archboldianum* has more leathery, oblong leaves and flowers with less fleshy lobes.

According to Merrill & Perry (1945), *Brass* suspected that certain plants lacked a tuber, all his numbers are annotated as shrubs, and for *Brass* 9240 and 9492 no tuber is mentioned. It seems improbable that this species sometimes lacks a tuber, and it is more likely that after an extended period of growth, the stems may appear at some distance from the original tuber, which becomes buried in leaf litter or moss.

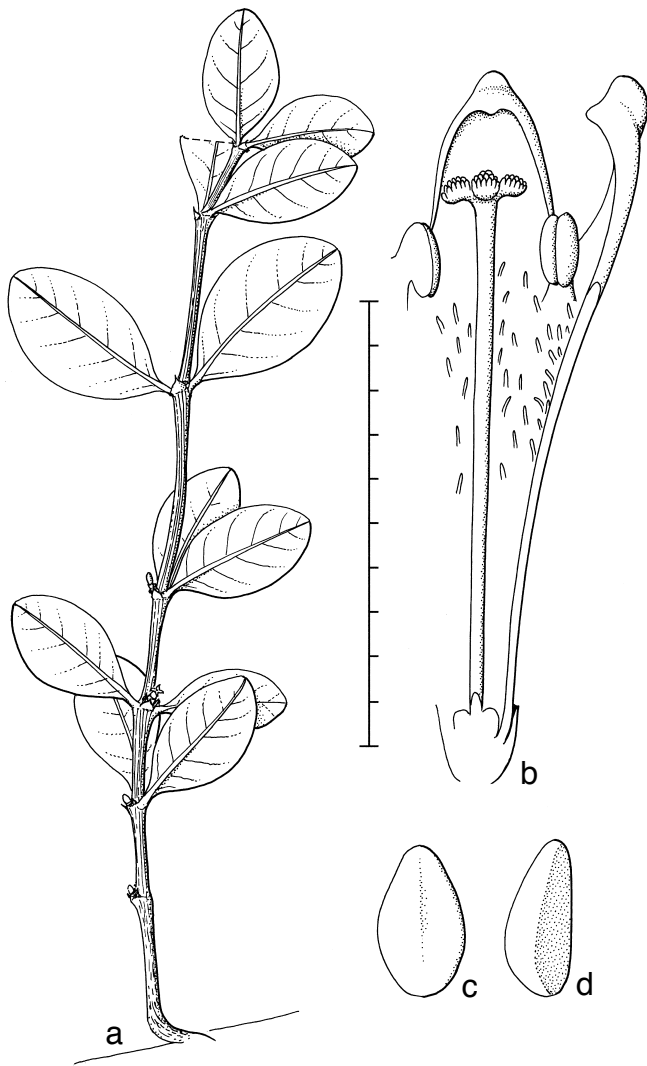
### 37. *Hydnophytum magnirubrum* Jebb & C.R.Huxley, *sp. nov.* — Fig. 40

Tuber globosum, superficie laevi. Aperturæ duo generum, vel infundibuliformes, ad 4 cm in diametro, vel parvæ et conicæ, ad 0.5 cm in diametro. Tuberis contextus badius. Caules numerosi, libere ramosi. Lamina elliptica usque obovoidea, 3 per 1.4 ad 6 per 3 cm, apice rotundato usque acuto, basi sensim attenuata. Petiolus ad 0.3 cm. Inflorescentia sessilis, binata, bracteis oblecta; quæ bracteae papyraceae usque coreaceae, ad 0.5 cm. Calyx ad 3.5 mm, margine irregulariter dentato. Corollæ tubus ad 10 mm, albus, intus pilis conspersus. Lobi ad 5 mm, rubello-purpurei. Antheræ ad 1.5 mm, exsertæ ex fauce corollæ. Stigma 3-lobatum. Pyrenæ (2–)3(–4), hemisphericæ usque obovoideæ, 3 per 2 mm. — Typus: *Jebb* 261 (holo LAE; iso A, BRI, CANB, K, L), Papua New Guinea, S6°07' E143°57', SE of Mt Giluwe, above Onin, 'Beechwoods No. 2' logging track, 23 Apr. 1983.

**Etymology.** There are two taxa in Papua New Guinea with red tuber tissue and red-tipped corollas, of the two this has the larger leaves.

*Tuber* globose, to 30 by 19 cm; surface smooth, grey. Entrance holes of two kinds, some conical, or lipped, to 0.5 cm diam; others more numerous and funnel-like, to 4 cm diam. Cavity walls partly silver-grey in colour, partly purplish brown. Tuber tissue reddish brown. *Stems* numerous, to 100 by 0.8 cm, freely branching, spreading and upcurving. Internodes to 7 by 0.8 cm when sterile, 0.4–3 by 0.2–0.4 cm when fertile. *Leaves* erect to spreading. Lamina, elliptic to obovoid; 3 by 1.4 to 6 by 3 cm; apex rounded to acute; base shortly-attenuate; sclerophyllous, dark green, glossy above, pale below; margin downcurved; veins 5–7; midrib prominent below, pale yellow. Petiole to 0.3 cm, rounded, yellow to reddish in colour; stipules 0.2–0.3 cm, triangular, with a central process, caducous. Inflorescence paired, sessile, bract-covered, these papery to leathery, to 0.5 cm. *Flowers* [7] incompletely heterostylous. Calyx to 3.5 mm, margin irregularly toothed. Corolla tube to 10 mm, white; lobes to 5 mm, with a crest at apex, reddish purple; with scattered hairs within. Anthers to 1.5 mm, just exserted from corolla mouth. Pollen 94 (73–120)  $\mu\text{m}$ , 3-colpate, brochi irregular, 1–2.5  $\mu\text{m}$ , vesicles small. Stigma 3-lobed at or barely above level of anthers, or exserted. *Fruit* globose, to 5 mm, red. Pyrenes (2–)3(–4), hemispherical to obovoid, then triangular in section, 3 by 2 mm.

**Ecology & Habitat** — Mid- to high-level epiphyte in *Nothofagus* forest, 2400–2800 m. Tuber cavities not inhabited by ants, instead occupied by spiders, myriopods and other arthropods.



**Fig. 40** *Hydnophyllum magnirubrum* Jebb & C.R.Huxley. a. Shoot; b. flower; c. pyrene adaxial face; d. lateral view (a: *Jebb 300*; b, c: *Jebb 278*). — Scale bars: a = 10 cm; b–d = 10 mm. — Drawn by Rosemary Wise.

**Distribution** — Papua New Guinea (Enga and Southern Highlands Provinces).

**Conservation status** — Endangered (EN) under criteria B1ab (iii)+2ab(iii). The four known localities lie within 100 km of one another. Other information: AOO 365 km<sup>2</sup> (using an auto-value cell width of 10 km), EOO 2500 km<sup>2</sup>.

**Additional specimens examined.** *Jebb 300* (BRI, K, L, LAE), Enga Province: S5°36' E143°30', Kandep Pass, on road from Laiagam; *Huxley & Turton in UPNG 5919B* (A, UPNG), Southern Highlands Province, S5°57' E143°51', NW Foothills of Mt Giluwe, on Mendi-Hagen Road; *Jebb 264* (L), 265 (K), 266 (LAE), 269 (LAE), 270 (K), 273 (L), 274 (A, BRI), 276 (LAE), 277 (CANB, LAE), 278 (A), 279 (LAE, UPNG), 281 (LAE), 282 (LAE), 285 (LAE), 286 (LAE, SUVA), *Ash UPNG 3467* (BRI, CANB, LAE, UPNG), *Ash UPNG 3468* (UPNG), *Ash UPNG 3475* (UPNG), *Schodde 1701* (L, A), S6°07' E143°57', SE of Mt Giluwe, above Onin, 'Beechwoods No. 2' logging track; *NGF 28276* (LAE), Mt Ambua.

**Note** — This species is closely related to *H. minirubrum* [35] with which it is sympatric, and to *H. archboldianum* [33].

**38. *Hydnophyllum minirubrum* Jebb & C.R.Huxley, sp. nov.** — Fig. 41

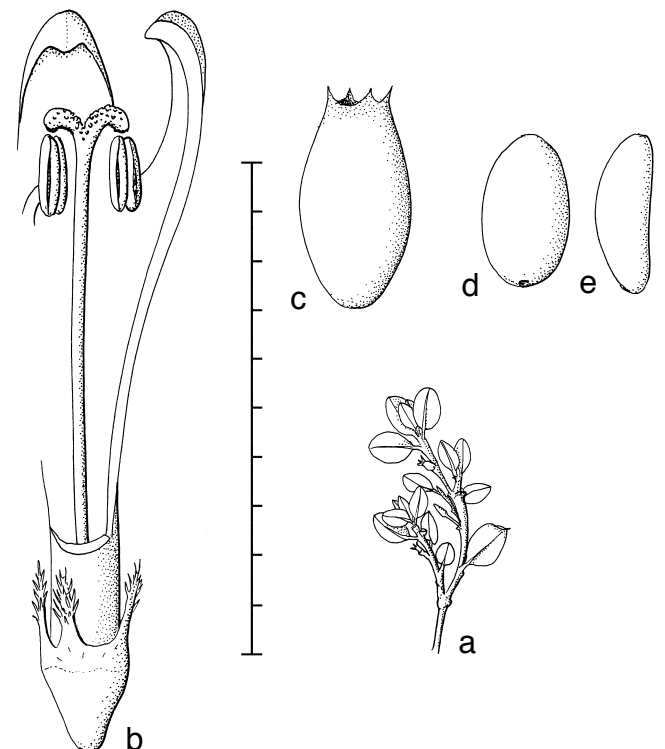
Tuber sphaericum usque ellipsoideum, contextu rubello-purpurea; superficies sparsis tuberculis et radicibus oblecta. Aperturæ numerosae, grandes, labrosae, ad 2 cm in diametro. Caules numerosi, libere ramosi; internodia fertilia contorta. Lamina ovata usque subrotunda, 1.2 per 0.6 ad 2 per 1.5 cm, apice acuto, basi rotundata usque sensim attenuata. Petiolus minus quam 2 mm. Inflorescentia binata, sessilis. Bracteae ad 0.4 cm, papyraceae,

triangulares; nonnulli ex pilis bractealibus ad 0.3 cm. Calyx 3.5 mm; margo 4 vel 5 dentato acuminatis, ad 2 mm longis, interdum fimbriatis instructus. Corollae tubus albus, ad 7.5 mm, pilis in fauce dimidio superiore conspersus, vel glaber. Lobi rubello-purpurei, ad 2.5 mm. Antherae exsertae ex fauce, 1.5 mm. Pyrenae hemisphaericae, 3.5 per 2 mm. — Typus: *Jebb 289* (holo LAE; iso A, BRI, CANB, K, L), Papua New Guinea, Southern Highlands Province, S6°07' E143°57', SE of Mt Giluwe, above Onin, 'Beechwoods No. 2' logging track, 24 Apr. 1983.

**Etymology.** There are two taxa in Papua New Guinea with red tuber tissue and red-tipped corollas, of the two this has the smaller leaves.

**Tuber** regularly spherical to ellipsoid, to 30 by 18 cm. Surface covered by numerous scattered tubercles to 0.15 cm, and roots. Entrance holes numerous; 0.2–1.2 cm across internally, overall to 2 cm; rimmed, the rims to 0.4 cm across. Cavity walls silvery or dull reddish brown. Tuber tissue reddish purple. **Stems** numerous, to 70 by 0.8 cm, freely branching, elliptic in section towards node, cylindrical elsewhere; upcurved to ascending. Internodes 2–4 by 0.3–0.8 cm when sterile, shorter, 0.15–1.5 cm and contorted when fertile. **Leaves** clustered, more or less erect, recurved. Lamina ovate to subround; 1.2 by 0.6 to 2 by 1.5 cm; apex acute; base rounded to tapered; glossy green above, yellowish green below; venation obscure. Petiole < 0.2 cm, rounded, yellow-green; stipules 0.1–0.2 cm, triangular, acute, with a small central process, papery and caducous. Inflorescence paired sessile. Bracts to 0.4 cm, papery, triangular, some bract hairs to 0.3 cm. **Flowers** [4] ?not heterostylous. Calyx 3.5 mm; margin with 4 or 5 acuminate, sometimes fringed appendages to 2 mm long. Corolla white, lobes reddish purple, tube to 7.5 mm, with short scattered hairs in upper half, or glabrous, lobes 2.5–3 mm. Anthers to 1.5 mm, exserted from mouth of corolla tube. Pollen 3 or 4 colpiate, 86 (80–100) µm, brochi irregular 1–5 µm; vesicles absent. Stigma 2- or 3-lobed, exserted. **Fruit** globose to 4 mm, orange-red. Pyrenes hemispherical, 3.5 by 2 mm.

**Ecology & Habitat** — Mid- to high-level epiphyte in *Nothofagus* forest, 2400–2800 m. Tuber not inhabited by ants, occupied by spiders, myriopods or other arthropods.



**Fig. 41** *Hydnophyllum minirubrum* Jebb & C.R.Huxley. a. Shoot apex; b. flower; c. fruit; d. pyrene adaxial face; e. lateral view (*Jebb 301*). — Scale bars: a = 10 cm; b–e = 5 mm. — Drawn by Rosemary Wise.

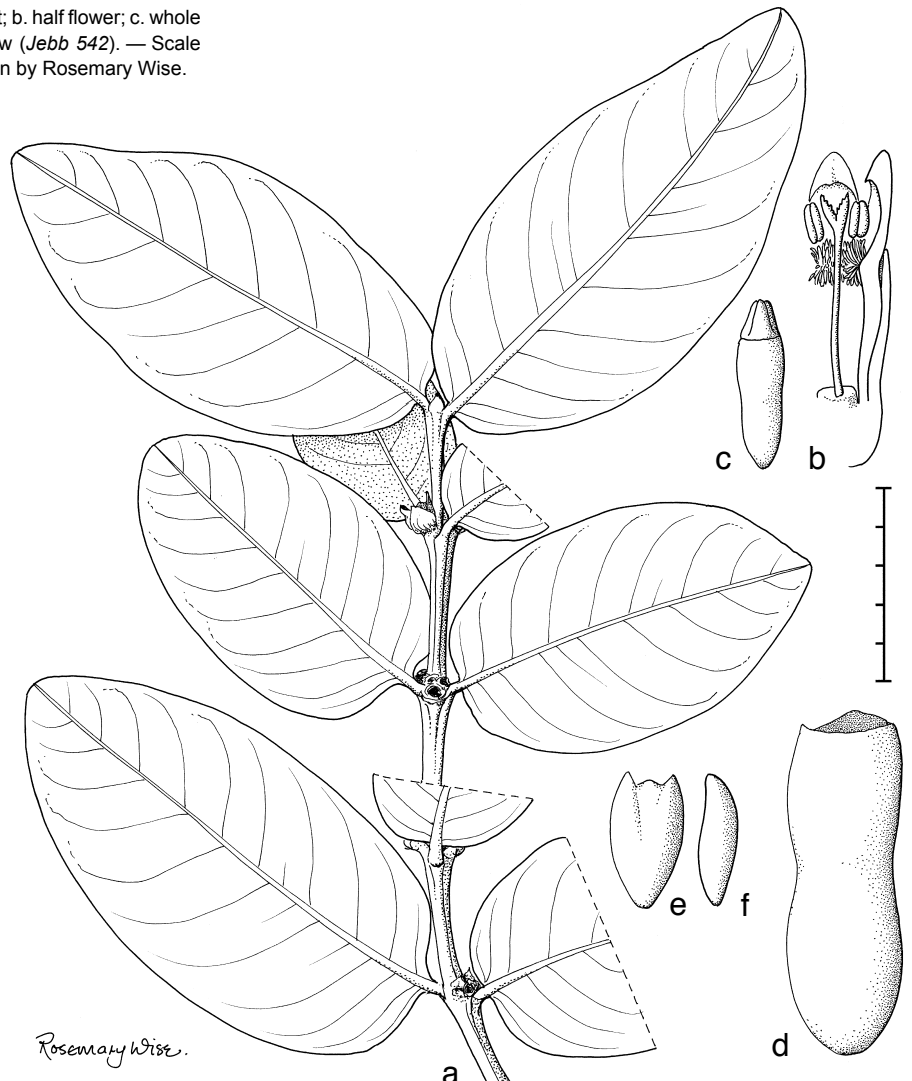
Distribution — Papua New Guinea (Western Highlands and Southern Highlands Province).

Conservation status — Endangered (EN) under criteria B1ab (iii)+2ab(iii). The three known localities lie within 40 km of one another in the montane forests of Mt Giluwe and Mt Hagen. Other information: AOO 43 km<sup>2</sup> (using an auto-value cell width of 4 km), EOO 247 km<sup>2</sup>.

*Additional specimens examined.* *Jebb 301* (CANB, K, L, LAE), Western Highlands Province: S5°47' E143°59', Tomba Pass, on road from Wabag to Hagen; *Huxley & Turton* in *UPNG 5919A* (A, BRI, K, L, UPNG), Southern Highlands: S5°57' E143°51', foothills of Mt Giluwe, on Mendi-Hagen Road; *Jebb 267* (LAE), *Jebb 268* (LAE), *Jebb 283* (L, LAE), *Jebb 288* (FHO), S6°07' E143°57', SE of Mt Giluwe, above Onin, 'Beechwoods No. 2' logging track.

**Note** — This species is very similar to *H. magnirubrum* [37] with which it occurs co-extensively. Each has a reddish purple fleshed tuber, contorted and contracted nodes, small leaves and a reddish purple tipped flower. The two species are sympatric throughout their range. The two species can be distinguished by a combination of characters: the leaves of *H. minirubrum* are smaller, the apex in particular being more acute, the venation of the leaves is less apparent; the tubers of *H. minirubrum* are more regular in outline, with a roughened surface covered by numerous small tubercles; the entrance holes of this species are also striking for their large regular rims, reaching up to 2 cm across, in *H. magnirubrum* the rimmed entrance holes are smaller, and the surface is mostly smooth while the larger entrance holes are distinctly funnel-shaped; lastly *H. magnirubrum* may have up to 3 pyrenes in each fruit.

**Fig. 42** *Hydnophytum bracteatum* Valeton. a. Shoot; b. half flower; c. whole flower; d. fruit; e. pyrene abaxial face; f. lateral view (*Jebb 542*). — Scale bars: a = 7 cm; b, d, e = 5 mm; c = 10 mm. — Drawn by Rosemary Wise.



## GROUP 8 – MELANESIA GROUP

### 39. *Hydnophytum bracteatum* Valeton — Fig. 42

*Hydnophytum bracteatum* Valeton (1911) 506. — Type: *Versteeg 1765* (lectotype selected here BO; iso L), New Guinea, Papua Province, Lorentz River, 28 Sept. 1907.

**Tuber** to 35 cm across, irregular; surface rough, areolate. Entrance holes few, prominently lipped, and raised as much as 1 cm above tuber surface; to 2.5 cm internally. Cavities bulbous, from 0.5–15 cm across; without ants. **Stems** several, unbranched, to 100 cm; rounded in section, with 2 prominent, winged ridges, running from below stipule. Internodes 3–11 by 0.7 cm. **Leaves** sessile, spreading. Lamina, elliptic; 13.5 by 6 to 19 by 8.5 cm; apex acute; base rounded to cordate; thick and brittle; dark glossy green above, pale below. Midrib prominent above and below. Veins 15–18 including prominent secondary veins. Stipules 0.6 cm, triangular, falling before leaves. Inflorescence paired; consisting of 2 or 3 flower-producing locules covered by a dense mass of triangular leathery bracts to 1 cm long. **Flowers** [2] heterostylous. Calyx 3–6 mm, membranous, margin 4-cuspidate. Corolla tube to 5 mm, with a broad ring of hairs at mouth; lobes to 3 mm overall, with an apical crest to 1.5 mm. Short-styled flowers with anthers to 1 mm, exerted; filaments to 1 mm; pollen 56 µm 3-colpate; stigma 2-lobed, at same level as anthers. Long-styled flowers with anthers to 1.5 mm, below ring of hairs; stigma above anthers, and at mouth of tube. **Fruit** to 5 mm, pink; calyx remains prominent to 4 mm, brown. Pyrenes obovoid to rhomboid, flattened, 3.5 by 2 mm;



apex truncate-notched, with 2 lateral horns as long as or longer than true apex, giving appearance of three short teeth; abaxial surface with 2 furrows; base tapered, rounded.

Ecology & Habitat — Closed forest, 100–1000 m. Tuber rarely ant-inhabited.

Distribution — Indonesia (Papua Province) and Papua New Guinea.

Conservation status — Least Concern (LC). This taxon is remarkably widespread (2000 km) but represented by just six locations (subpopulations). Removing the outlying island populations (Manus & New Britain) leaves the New Guinea collections with an EOO of over 100 000 km<sup>2</sup>. Other information: georeferenced collections 7, AOO 12 500 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO 415 200 km<sup>2</sup>.

Note — The large leaves and inflorescence bracts, thick stem, and large-cavities, lightweight tuber of this species distinguish it from all others. It is remarkable that such a morphologically uniform species has been collected so rarely and from such widespread localities (from the south coast of New Guinea to Manus island and New Britain). It is probably a high-level epiphyte of primary forest, accounting for its infrequent discovery.

#### 40. *Hydnophytum cordifolium* Valetton — Fig. 43

*Hydnophytum cordifolium* Valetton (1927) 129. — Type: *Schlechter 19636* (lectotype selected here K; iso G), Papua New Guinea, Morobe Province, Dischore, 30 May 1909.

*Tuber* not known. *Stems* numerous, to 40 cm, branching, angular, with 4 ridges, grey. Internodes to 4 by 0.3 cm. Lamina ovate to round-cordate, 2 by 1.8 to 6.5 by 4.2; apex blunt to abruptly acuminate; base cordate; leathery to slightly fleshy when fresh, dull dark green above. Midrib impressed above, prominent below, lateral veins 4 or 5. Petiole 0.3–1 cm; stipules triangular, to 0.25 cm, with a central ridge, falling before the leaves. Inflorescence solitary or paired, unbranched, to 0.7 cm long. Bracts minute. *Flowers* [2]. Calyx truncate. Corolla 4–5.5 mm, lobes 2 mm, ring of hairs either at tube apex, around anthers or midway up tube below anthers. Anthers 1 mm. Pollen 36–42 µm, 3-colporate. Stigma just above anthers, bifid. *Fruit* not known. Pyrenes ovate to elliptic, rounded on inner adaxial face, strongly ridged on abaxial side, 3–5 by 2.5 mm; apex long or short acuminate; base rounded.

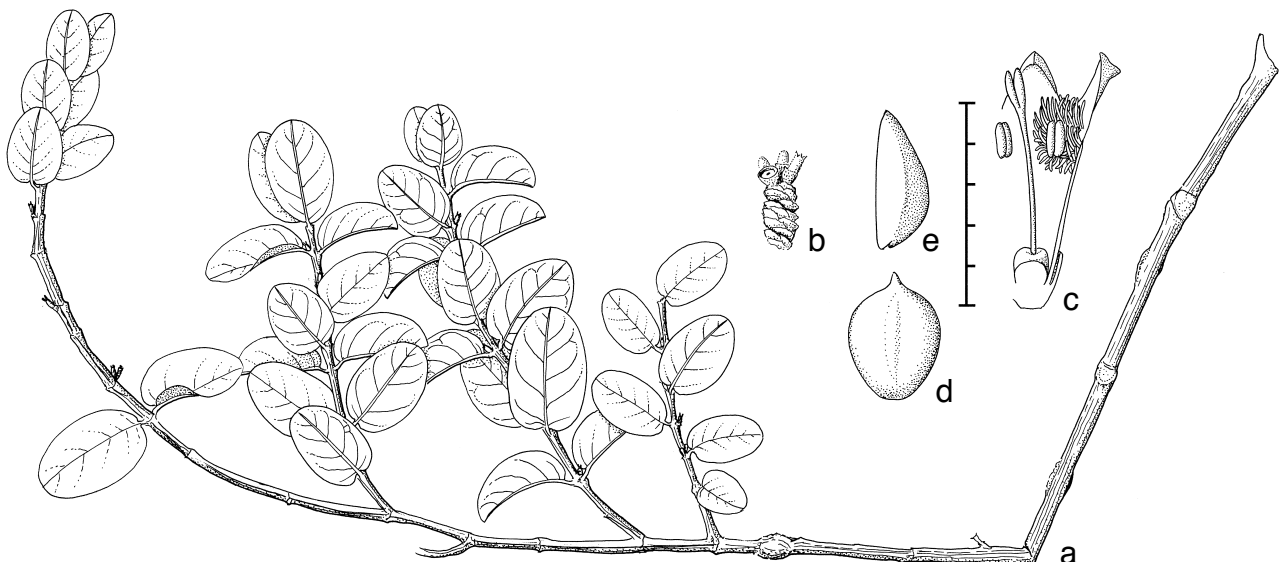


Fig. 43 *Hydnophytum cordifolium* Valetton. a. Shoot; b. inflorescence; c. flower; d. pyrene abaxial face; e. lateral view (a, d, e: *Schlechter 19636*; b, c: *Streitmann* in *NGF 44307*). — Scale bars: a = 8 cm; b = 3 cm; c–e = 5 mm. — Drawn by Rosemary Wise.

Ecology & Habitat — Forest, sea level to 300 m.

Distribution — Papua New Guinea (Morobe Province).

Conservation status — Endangered (EN) under criteria B1ab (iii)+2ab(iii). The three locations have a geographic spread of 80 km. Other information: EOO 249 km<sup>2</sup>, AOO 175 km<sup>2</sup> (using an auto-value cell width of 8 km).

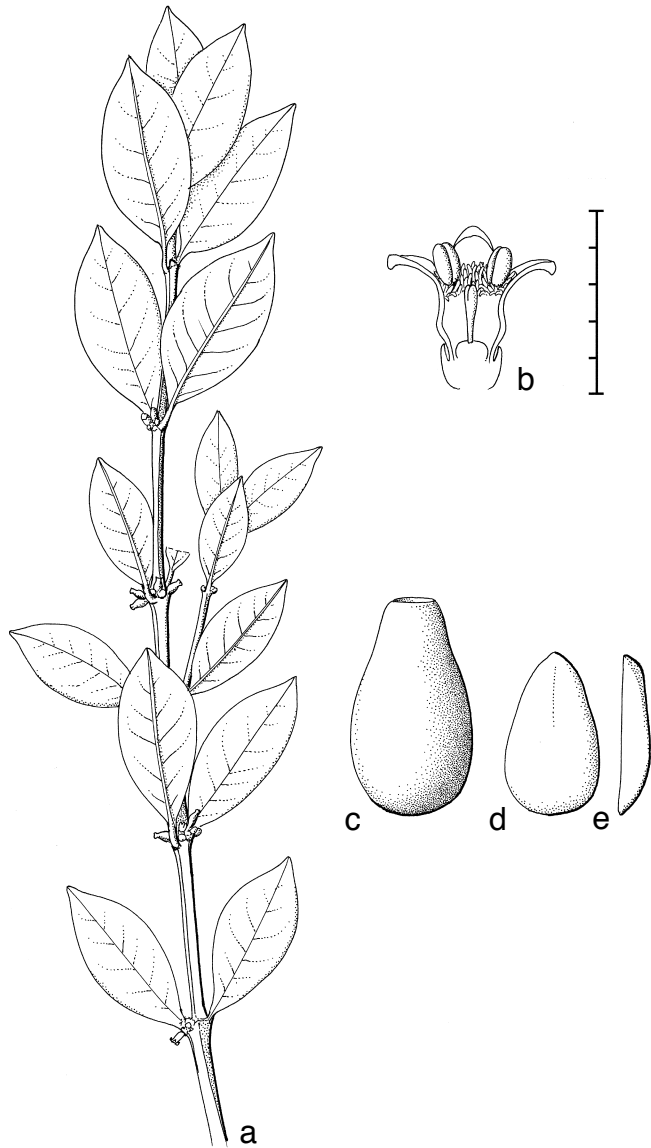
Note — Resembles *H. heterophyllum* [43], but the leaves are always cordate, less than 6 cm long and the pyrenes lack the characteristic shouldered apex of this latter species. *Hydnophytum orichalcum* [46] can be distinguished by its longer, sessile leaves, longer flowers and blunt pyrenes. The two specimens differ somewhat in inflorescence number, flower structure and pyrene shape.

#### 41. *Hydnophytum dentrecastense* Jebb & C.R.Huxley, sp. nov. — Fig. 44

"Tuber parvum. Caules quadrati. Lamina lanceolata, 4 per 1.2 cm ad 6.5 per 2.8 cm, apice acuminato, basi cuneata. Petiolus ad 0.4 cm. Inflorescentia binata, sessilis usque pedunculata, ad 1 cm longa. Calyx ad 1 mm. Corolla ad 3 mm, annulo pilorum ad faucem instructa. Antherae 1 mm longae. Pyrenae ovoideae, 4.5 per 2.5 mm, complanatae. — Typus: *Jebb 387* (holo LAE; iso A, BRI, CANB, K, L), Papua New Guinea, Milne Bay Province, Normanby Island, Mount Bwebwesu, 600 m, 6 June 1983.

*Etymology*. For the d'Entrecasteaux islands from where the species was first recognised.

Terrestrial to epiphytic. *Tuber* relatively small, 15 by 15 cm, irregularly globose. Entrance holes conical, to 1 cm, scattered and prominent. *Stems* 1 to several, branching, square in section; upright to subpendent, to 60 by 0.15–0.7 cm. Internodes 1–7 cm. Lamina lanceolate, widest at or slightly below middle; 4 by 1.2 to 6.5 by 2.8 cm; apex acuminate to acute; base cuneate; leathery; margins strongly recurved; glaucous-green, and drying darker below. Midrib prominent below, occasionally caniculate above. Veins 7–9. Petiole to 0.4 cm; stipules to 0.25 cm, triangular, caducous. Inflorescence paired, sessile to pedunculate, to 1 cm. Bracts minute, papery. *Flowers* [2] heterostylous. Calyx to 1 mm, margin entire. Corolla tube to 3 mm; lobes 1.5 mm; a ring of hairs at mouth of tube. Short-styled flowers with anthers to 1 mm long, exerted; pollen 3-colpate, 45 µm, brochi 1 µm; stigma 2-lobed, within mouth of tube. Long-styled flowers with anthers to 0.5 mm; within mouth of tube; pollen 54 µm; stigma exerted. *Fruit* to 6 mm, conical-ovoid, red. Pyrenes ovoid, 4.5 by 2.5 mm; flattened; apex blunt-acute, base rounded.



**Fig. 44** *Hydnophytum dentrecastense* Jebb & C.R.Huxley. a. Shoot; b. flower; c. fruit; d. pyrene abaxial face; e. lateral view (a: Brass 25789; b–e: Jebb 387). — Scale bars: a = 5 cm; b–e = 5 mm. — Drawn by Rosemary Wise.

**Ecology & Habitat** — This species is found terrestrially on the upper slopes of Mts Pabinama and Bwebwesu of Normanby Island, at c. 600–800 m altitude. This is an area of ultrabasic soils with sparse, stunted forest cover. The tuber is not inhabited by ants and nor does it collect rainwater.

**Distribution** — Papua New Guinea (Milne Bay and Northern Province).

**Conservation status** — Vulnerable (VU) under criteria D2. The habitat on Normanby Island is an area of ultramafic soils identified as a source of future nickel and gold mining. The entire area covers less than 20 km<sup>2</sup>, but it is not known whether this epiphyte is found further afield on that island. Two other localities are on islands and one in Northern Province, a range of over 700 km. Other information: AOO 20 km<sup>2</sup> (using a cell width of 2 km), EOO c. 32 900 km<sup>2</sup>.

**Additional specimens examined.** Woods 350 (E), Northern Province, ridge above Doma; Brass 25682 (A, L), Brass 25698 (A, L), Brass 25786 (A, L), Brass 25789 (A, L), Milne Bay Province; Croft NGF 71018 (LAE, L), Fergusson Island, E slopes of Mt Kilkerran, Normanby Island, Mt Pabinama; Jebb 380 (LAE), Jebb 388 (BRI), Jebb 389 (LAE), Jebb 390 (LAE), Normanby Island, west slopes of Mt Bwebwesu; Brass 28403 (A, BO, K, L), Rossel Island, South slopes of Mt Rossel.

**Note** — The fresh leaves of this species have a glaucous-green look, and dry to a grey-green colour, darker below.



**Fig. 45** *Hydnophytum hellwigii* Warb. a. Shoot; b. flower; c. fruit; d. pyrene lateral view; e. adaxial face (a: Schlechter 16799 (K); b–e: Streimann NGF 45105). — Scale bars: a = 9 cm; b = 2 mm; c = 5 mm; d = 4 mm. — Drawn by Rosemary Wise.

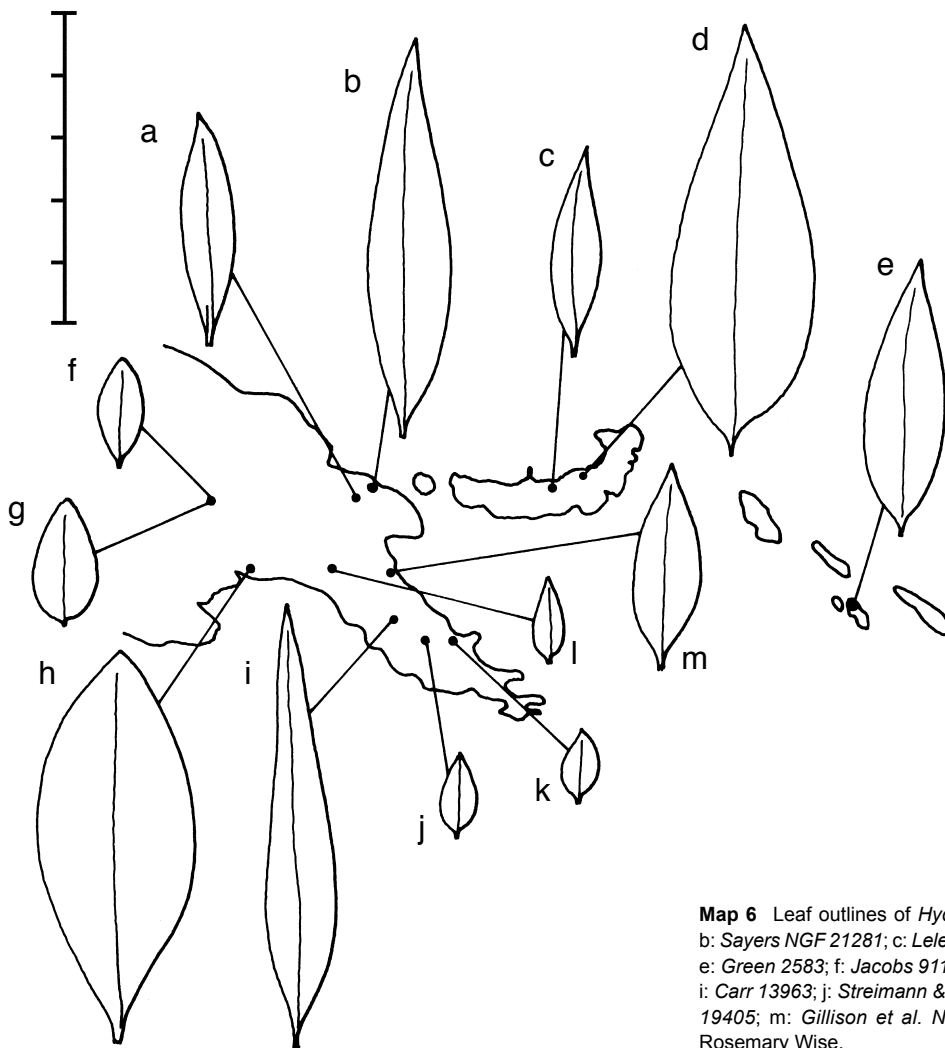
#### 42. *Hydnophytum hellwigii* Warb. — Fig. 45; Map 6

*Hydnophytum hellwigii* Warb. (1894) 209. — Type: *Hellwig 469* (Lectotype selected here B presumed lost). Epitype selected here, *Gillison & Streimann 25662* (K; isoepitypes A, BO, BRI, CANB, L, LAE, SING), Papua New Guinea, Morobe Province, Buso River, 16 Aug. 1968.

*Hydnophytum parvifolium* Valeton (1927) 140. — Type: *Schlechter 19405* (lectotype selected here K; iso F, G, L), Papua New Guinea, Morobe Province, Waria River, Pema, 11 May 1909, syn. nov.

*Hydnophytum punamense* Lauterb. in K.Schum. & Lauterb. (1905) 401; Valeton (1911) 508; (1927) 140; Merr. & L.M.Perry (1945) 23. — Type: *Schlechter 14671* (WRSL), Papua New Guinea, New Ireland, Punam, June 1902, syn. nov.

**Tuber** globose, to 20 cm, regular, smooth. Entrance holes numerous, conical with narrow rims, 0.3–0.6 cm diam. Cavities small. **Stems** several, branching, pendulous to erect, quadrangular in section, with 4 narrow ridges. Internodes 0.5–6 by 0.05–0.3 cm. **Leaves** sessile to barely petiolate, distichous. Lamina linear-ovate; 3 by 0.7 to 6.2 by 2.4 cm; apex acute, but blunt at its extremity; base rounded; midrib prominent below, veins 4–6; thin, mid-green. Petiole to 0.4 cm; stipules triangular, papery to 0.2 cm, ± persistent. Inflorescence paired, sessile. Bracts inconspicuous, < 1 mm. **Flowers** [4] not heterostylous.



**Map 6** Leaf outlines of *Hydnophytum hellwigii* Warb. a: Clemens 11094; b: Sayers NGF 21281; c: Lelean & Stevens LAE 51204; d: Henty NGF 38505; e: Green 2583; f: Jacobs 9116; g: Jacobs 9233; h: Gray & Floyd NGF 8026; i: Carr 13963; j: Streimann & Kairo NGF 35950; k: Carr 16416; l: Schlechter 19405; m: Gillison et al. NGF 25662. — Scale bar: 5 cm. — Drawn by Rosemary Wise.

Calyx to 1 mm. Corolla tube to 1 mm, lobes to 0.5 mm, with a minute ring of hairs within mouth of tube. Anthers 0.3 mm, partly exserted. Pollen colpiolate, 36 (30–41)  $\mu\text{m}$ , brochi 1  $\mu\text{m}$ . Stigma 2-lobed, reaching to top of anthers. Fruit 4 by 2 mm, red. Pyrenes ellipsoid to ovoid, 3 by 2 mm; apex rounded to acute; base rounded.

**Ecology & Habitat** — A coastal species, forest, from sea level to 600 m (once at 1800 m). Tuber only occasionally not inhabited by ants.

**Distribution** — Papua New Guinea and the Solomon Islands.

**Conservation status** — Least Concern (LC). Whilst probably Vulnerable in some parts of its range, this taxon is spread across 1400 km with herbarium collections indicating at least 12 locations (subpopulations). Other information: georeferenced collections 15, EOO c. 510 000 km<sup>2</sup>.

**Notes** — This species has delicate, long-ovate leaves, which taper into an ultimately rounded apex. The stems are slender, and the leaves are usually disposed at right angles to the stem in a strikingly distichous manner for the genus. The north coast specimens, especially those from the Bismarck Archipelago and Milne Bay Province, as well as those from the coasts of Madang and Morobe Province are all fairly uniform. However, a number of collections from Southern Highlands and Gulf Province have been provisionally included here, and these may represent separate taxa (Map 6). Clemens 11094 from Wantoat has a more lanceolate, thicker leaf, while Carr 13963 from Northern Province has exceptionally long leaves compared to other collections from the same area. Of the five collections from the Southern Highlands and Gulf Provinces,

Gray & Floyd NGF 8026 has large elliptic leaf blades, while the others all have smaller, cordate-elliptic blades. All these specimens share stem and inflorescence characters as well as the delicate leaf texture of the north coast specimens. A map of leaf outlines is presented in Map 6.

There are no recent collections from Finschhafen, and we have decided not to neotypify this species, since collections from the type locality could be readily made. In the meantime, we have adopted an epitype to serve as a discriminating element until such time as suitable topotype material becomes available.

#### *H. hellwigii* aff.

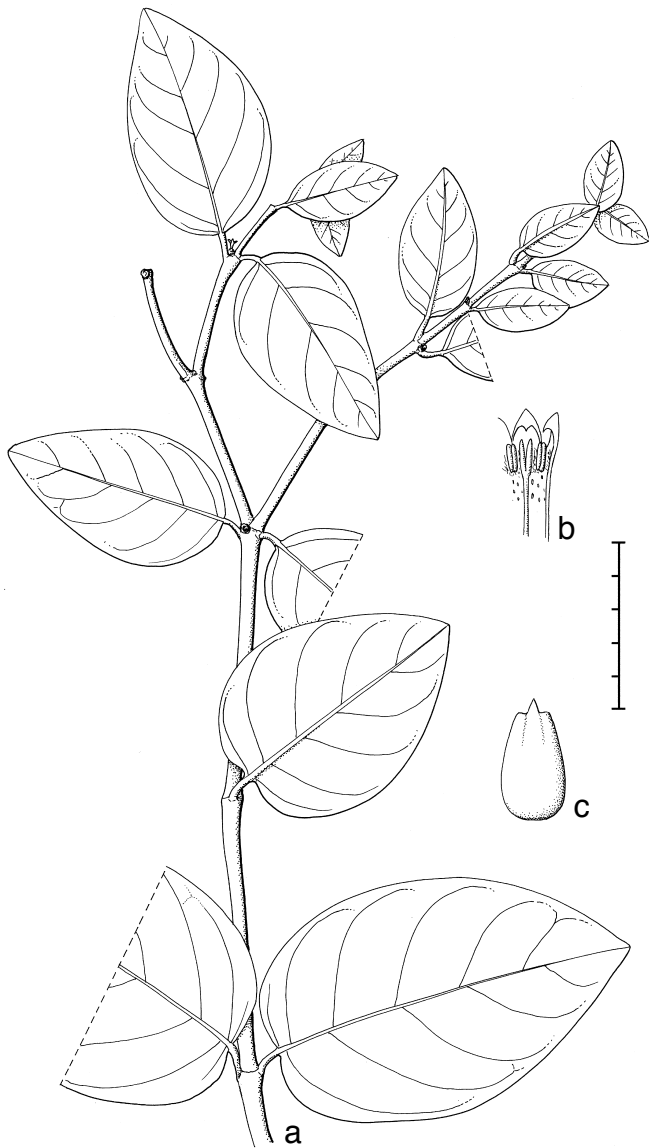
A number of collections from southern Papua New Guinea have broad, elliptic leaves, but in other respects closely match *H. hellwigii*.

Papua New Guinea: Gay 487 (LAE), Western Province, Ok Tedi area, Ok Menga valley. Jacobs 9116 (L), Jacobs 9233 (L), Southern Highlands Province, Waro airstrip, 20 km SSW of Kutubu, S6°31' E143°10'. Streimann & Kairo NGF 35950 (A, BRI, BULOLO, CANB, K, L, LAE), Gulf Province, Titamunga, Kukipi subdistrict, S7°22' E146°03'. Gray & Floyd NGF 8026 (A, BRI, L, LAE); S7°30' E144°30', near Kinomeri, Uramu Island.

#### 43. *Hydnophytum heterophyllum* Merr. & L.M.Perry — Fig. 46

*Hydnophytum heterophyllum* Merr. & L.M.Perry (1945) 15. — Type: Brass 12857 (A), New Guinea, Papua Province, 6 km southwest of Bernhard Camp, Idenburg River, Feb. 1939.

**Tuber** small. Spines few, slender, not sharp  $\pm$  1 cm. **Stems** solitary, pendulous to 1 m long, branched towards apex. Inter-



**Fig. 46** *Hydrophytum heterophyllum* Merr. & L.M.Perry. a. Shoot; b. flower; c. pyrene abaxial face (Brass 12857 (A)). — Scale bars: a = 5 cm; b, c = 5 mm. — Drawn by Rosemary Wise.

nodes terete, 1–4 cm. Leaves strikingly varied in size; larger, ovate and cordate based on the lower stem, smaller and elliptic towards the apex. Lamina 2 by 1.3 to 13 by 7.6 cm; midrib distinct above and below, thick towards base; lateral veins 5 or 6, inconspicuous. Petiole (0.5–)0.7–1 cm; stipules minute, caducous. Inflorescence solitary or paired, shortly pedunculate. Bracts minute. Flowers [1 – bud only]. Calyx membranous, truncate. Corolla tube with a ring of sparse hairs from midway to mouth of tube; lobes 1.5 mm long. Anthers just within tube, c. 1 mm long. Stigma not known. Fruit to 6 mm, orange. Pyrenes ovate, 4 by 2 mm; apex abruptly shouldered with a prominent apiculum forming a fine point 0.5–1 mm in length, which is contiguous with a prominent abaxial ridge that runs to base of pyrene; base rounded.

Ecology & Habitat — High epiphyte in forest, at 1200 m.

Distribution — Indonesia (Papua Province).

Conservation status — Vulnerable (VU) under criteria D2 with only the type specimen known.

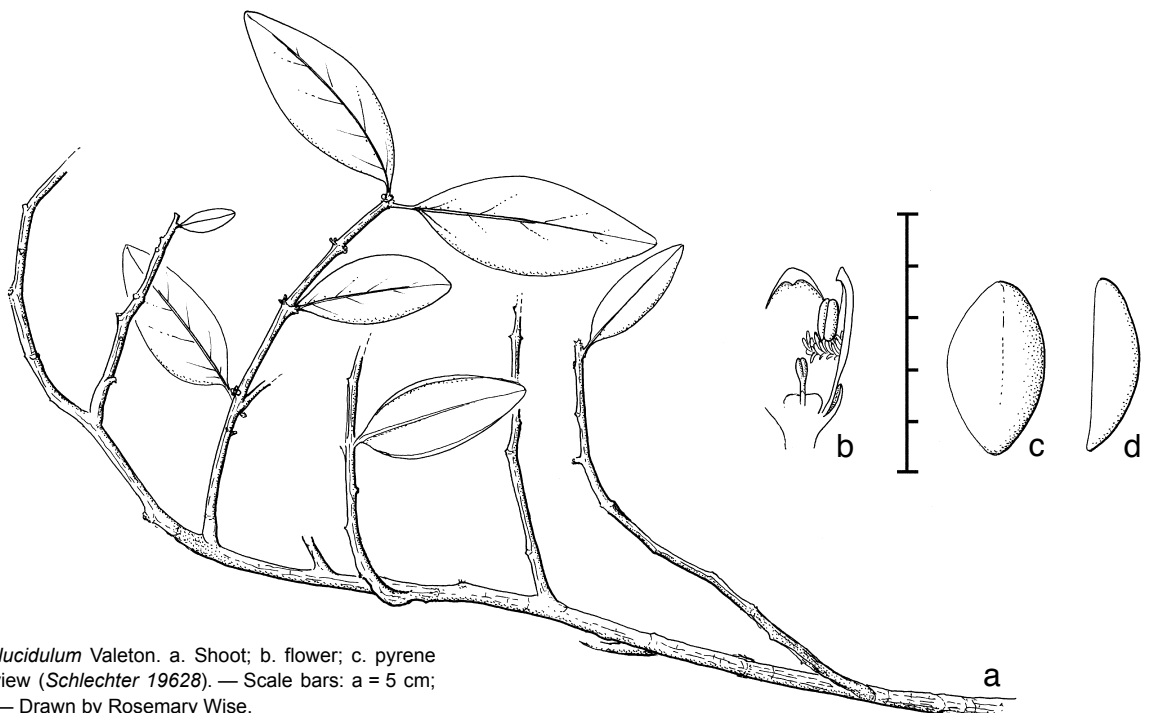
Note — The variable size and shape of the leaves are a striking feature of this specimen. For differences from *H. cordifolium* [40] see notes for that species.

#### 44. *Hydrophytum lucidulum* Valetton — Fig. 47

*Hydrophytum lucidulum* Valetton (1927) 137. — Papua New Guinea, Schlechter 19628 (lectotype selected here L; iso BM, G, K), Morobe Province, Dischore.

Tuber size and appearance unknown. Stems several, much branched, to 40 cm or more. Internodes 0.5–5 by 0.2–0.5 cm; rounded to angular. Lamina lanceolate to ovate-lanceolate, 2.5 by 1–6 by 2.5 cm; apex acute to blunt; base cuneate; midrib prominent above and below; veins c. 5 obscure; leathery; margin recurved. Petiole 0.2–0.5 cm; stipules 0.1 cm, triangular, papery, caducous. Inflorescence paired peduncles to 0.5 cm. Bracts minute. Flowers [2] ?heterostylous. Calyx entire 1.5 mm. Corolla tube 2 mm; lobes 1 mm, with a ring of hairs 2/3rds way up tube. Anthers < 1 mm; at mouth of tube. Pollen 3-colporate, 44  $\mu$ m, walls thick. Stigma 2-lobed, below ring of hairs, style 1 mm. Fruit 4 mm, with prominent calyx remains. Pyrenes ovoid, 3 by 1.5 mm.

Ecology & Habitat — Forest, 350–1650 m.



**Fig. 47** *Hydrophytum lucidulum* Valetton. a. Shoot; b. flower; c. pyrene abaxial face; d. lateral view (Schlechter 19628). — Scale bars: a = 5 cm; b = 5 mm; c, d = 4 mm. — Drawn by Rosemary Wise.

Distribution — Papua New Guinea (Central & Morobe Provinces)

Conservation status — Endangered (EN) under criteria B1ab(iii)+2ab(iii). Other information: AOO 342 km<sup>2</sup> (using an auto-value cell width of 14 km), EOO 567 km<sup>2</sup>.

Note — The small lanceolate leaves with prominent midribs both above and below are quite unlike those of *H. moseleyanum* [14] with which it shares shortly pedunculate inflorescences. Although the collections imply a large geographic spread, it remains known from just two locations some 140 km apart.

**45. *Hydnophytum mamberamoense* Jebb & C.R.Huxley, sp. nov.** — Fig. 48

*Myrmecodia* species 1 'mamberamoensis' C.R.Huxley & Jebb (1993) 332.

Tuber oblongum, laeve. Aperturae 0.2–0.6 cm, labrosae, arcuatim vel seriatim dispositae. Caules complures; internodia fertilia 2–9 cm. Stipulae triangulares, ad 1.6 per 0.6 cm, papyraceae, mox caducae. Lamina ovato-elliptica, 19 per 9 ad 40 per 14 cm, apice acuto, basi cuneato-attenuata, nervis 12–19, coreacea textura. Petiolus 9 cm. Inflorescentia binata, sessilis, obiecta pulvino pilorum bractealium et plurimorum fructuum ineffectorum, omnia ad 3.5 cm in diametro, plus minus contigua, ad instar densae spirae caulem ascenditis; pili bracteales ad 1.3 cm, badii. Calyx 1.5 mm, integer, supra altitudinem disci. Corollae tubus 8 mm, annulo pilorum infra faucem instructus; lobi anguste triangulares, ad 5 mm, unci ad 2.5 mm. Antherae 1.5 mm, ad faucem tubi. Stigma bifidum, supra antheras. Fructus et pyrenae ignota. — Typus: *Docters van Leeuwen 9540* (holo L; iso A, BO, K, SING), New Guinea, Papua Province, Mamberamo river opposite Albatros biv, July 1926.

*Etymology.* For the type locality.

*Tuber* oblong, 18 by 11 cm; smooth-surfaced. Entrance holes 0.2–0.6 cm, rimmed; often in arcs or lines. *Stems* several, unbranched? to 50+ by 1.5 cm; internodes 2–9 cm when fertile. *Lamina* ovate-elliptic; 19 by 9 to 40 by 14 cm; apex acute; base cuneate, ultimately attenuate; veins 12–19; leathery in texture.

Petiole 9 cm; stipule intrapetiolar, triangular, to 1.6 by 0.6 cm, papery, soon falling. Inflorescence paired, sessile, covered by a mass of bract hairs, to 3.5 cm across; more or less contiguous, appearing as a thick spiral up stem. Bract hairs to 1.3 cm, reddish brown, with numerous undeveloped fruits. *Flowers* [1] ?heterostylous. Calyx 1.5 mm, entire, above level of disc. Corolla tube 8 mm; with a ring of hairs below level of mouth; lobes narrow-triangular to 5 mm, unci to 2.5 mm. Anthers 1.5 mm, at mouth of tube. Pollen 3- (or 4-)colpate; 100–120 µm; colpi with large swollen borders to 20 µm across; brochi 1–2 µm. Stigma bifid, above anthers. *Fruit* undeveloped and pyrenes unknown.

*Ecology & Habitat* — In forest on trees or rockwalls, 100–175 m. Apparently not inhabited by ants.

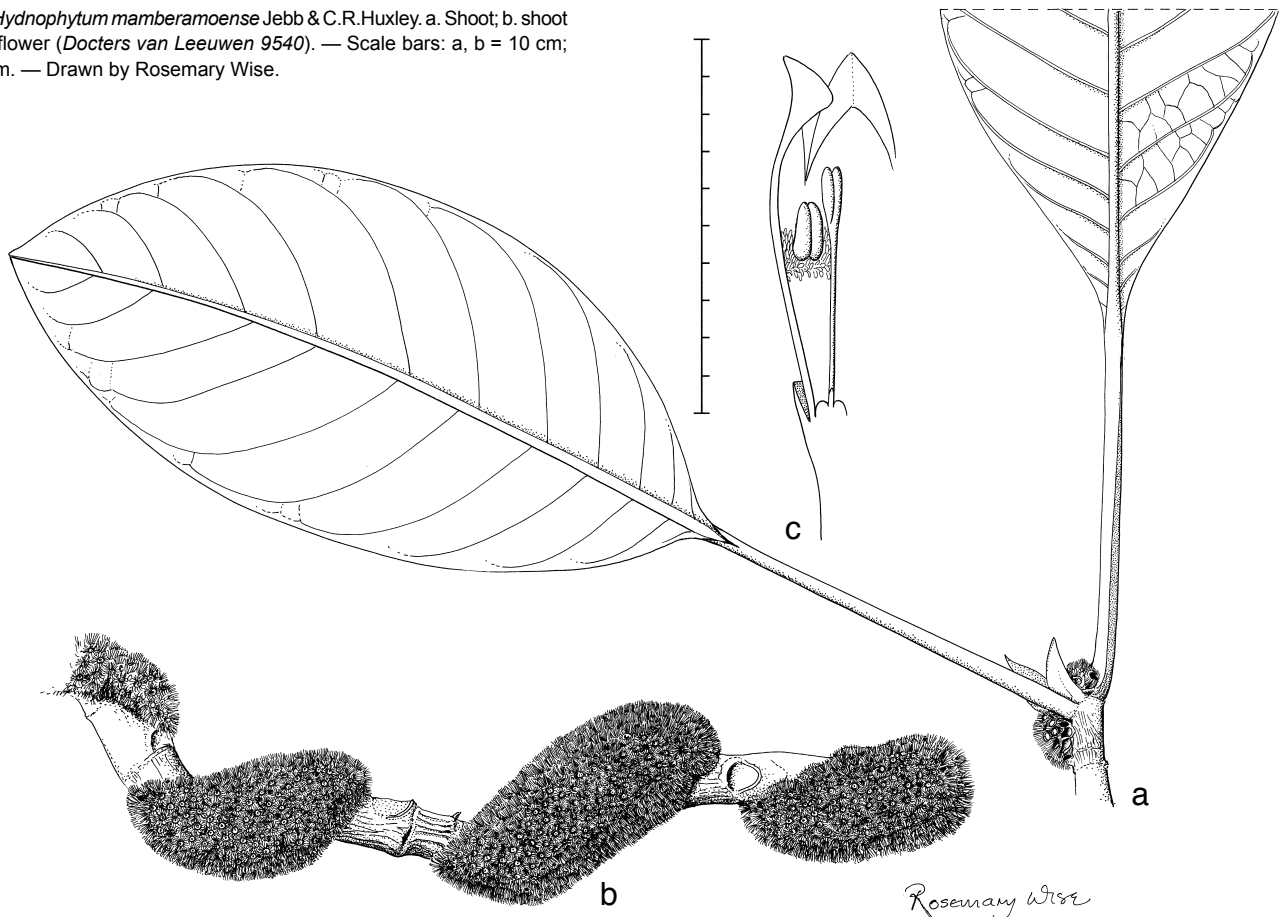
*Distribution* — Indonesia (Papua Province).

*Conservation status* — Vulnerable (VU) under criteria D2 with only three locations known. These locations are widespread (350 km) along the northern coastal plains of Papua Province.

*Additional specimens examined.* *Kanehira & Hatusima 12293* (FU), Dalman, 45 km inland from Nabire; *Docters van Leeuwen 10134* (A, K, L), S3°00' E138°00', Rouffaer (Tariku) river.

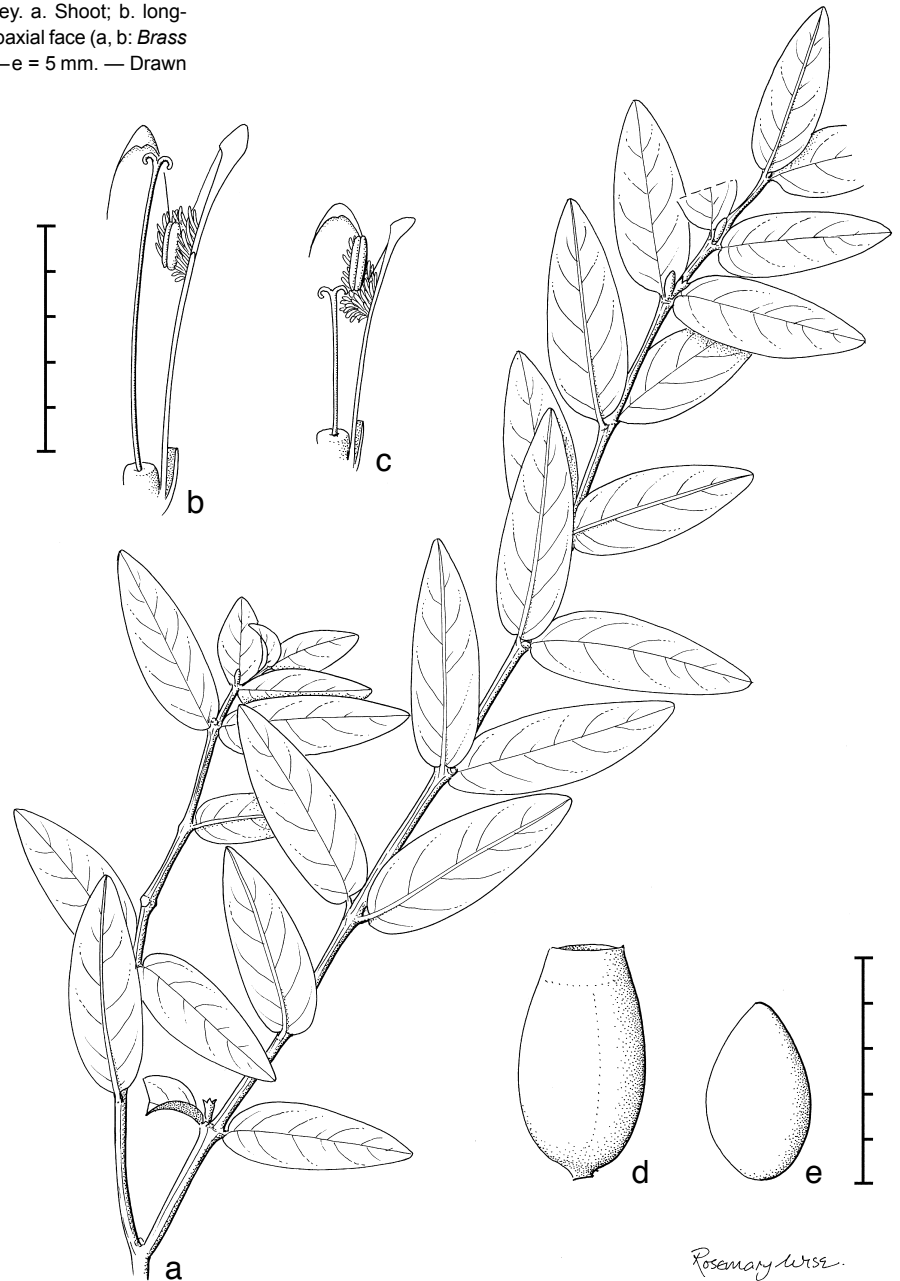
Note — This species has been difficult to place to a genus, chiefly because of its large intrapetiolar stipules, a character otherwise not known in *Hydnophytum*. The large inflorescences, pollen grains with thick bordered pores, a coarse reticulation, and large petiolate leaves are more like *Myrmecodia* (as suggested in Huxley & Jebb 1993), however, the tuber lacks the characteristic *Myrmecodia*-type cavity arrangement (Jebb 1985, 1991a), and the species is placed in *Hydnophytum* more by default than by diagnosis.

**Fig. 48** *Hydnophytum mamberamoense* Jebb & C.R.Huxley. a. Shoot; b. shoot detail; c. flower (*Docters van Leeuwen 9540*). — Scale bars: a, b = 10 cm; c = 10 mm. — Drawn by Rosemary Wise.



Rosemary Wise

**Fig. 49** *Hydnophytum orichalcum* Jebb & C.R.Huxley. a. Shoot; b. long-styled flower; c. short-styled flower; d. fruit; e. pyrene abaxial face (a, b: *Brass* 28005; c–e: *Brass* 28248). — Scale bars: a = 5 cm; b–e = 5 mm. — Drawn by Rosemary Wise.



**46. *Hydnophytum orichalcum* Jebb & C.R.Huxley, sp. nov. — Fig. 49**

Tuber amplum. Caules numerosi, ramosi, quadrati in sectione. Folia sessilia. Lamina lanceolato-cordata, 3.5 per 1.3 ad 5 per 2 (8.5 per 3.5) cm, apice acuto, basi cordata usque obtusa, nervo medio supra et subtus prominente, badia in statu sicco. Inflorescentia binata, pedunculis haud ramosis, ad 2 mm longis. Flores heterostylii. Calyx 1.5 mm, integer. Corollae tubus ad 6 mm, lato annulo pilorum intra faucem instructus; lobi 3 mm. Pyrenae ovoideae, 4 per 2.5 mm, basi rotundata, apice obtuso-acuto, ventraliter complanatae. — Typus: *Brass* 28005 (holo A; iso BO, K, L), Papua New Guinea, Milne Bay Province, Sudest Island, Mt Riu, west slopes, 4 Sept. 1956.

*Etymology.* From the Greek for brass, derived from oros = mountain and chalkos = copper.

*Tuber* large. *Stems* numerous, to 80 by 0.5 cm, branching; erect to subpendent. Internodes 1–5 cm, ± square in section. *Leaves* scattered, sessile. Lamina lanceolate-cordate, 3.5 by 1.3 to 5 by 2 (8.5 by 3.5) cm; apex acute; base cordate to blunt; midrib prominent above and below, veins 5 or 6; margin recurved when dry; reddish brown in colour when dry. Stipules to 0.2 cm, triangular, papery, caducous. Inflorescence paired, peduncles unbranched, to 0.2 cm long. Bracts minute, < 0.1 cm, papery, persistent. *Flowers* [3], heterostylous. Calyx 1.5 mm,

entire. Corolla tube to 6 mm, lobes to 3 mm, a broad ring of hairs within mouth of tube, and partly exserted. Short-styled flowers with anthers 1.3 mm, exserted; pollen 3-colpate, to 58 µm; stigma 2-fid, immediately below anthers. Long-styled flowers with anthers to 1.5 mm; within mouth of tube; pollen 41–45 µm; stigma exserted. *Fruit* to 6 by 3.5 mm, orange. Pyrenes ovoid, 4 by 2.5 mm; apex blunt-acute; base rounded.

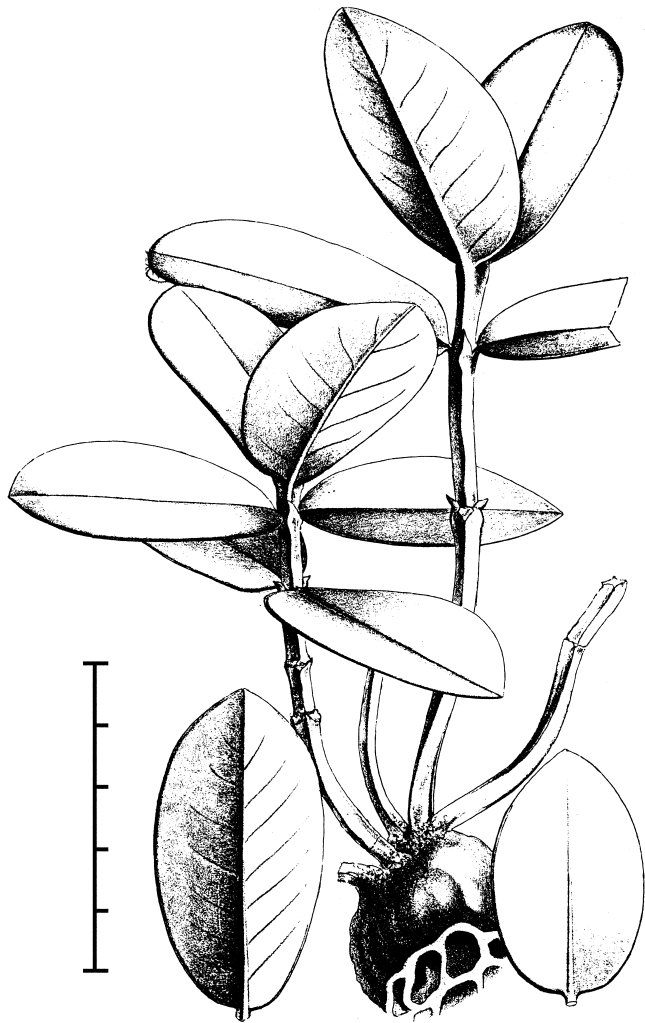
*Ecology & Habitat* — Low to mid-level epiphyte in forest, 100–500 m. Tuber with or without ants.

*Distribution* — Papua New Guinea (Milne Bay Province).

*Conservation status* — Vulnerable (VU) under criteria D2 with only the two island locations known.

*Additional specimens examined.* *Brass* 27955 (A, K, L), Louisiade Archipelago, Sudest Island, Mt Riu, W slopes; *Brass* 28248 (A, L), Rossel Island, Abaleti.

*Note* — This species has distinctive, apetiolate long-cordate leaves. It differs from *H. cordifolium* [40] in its sessile or shortly pedunculate (< 0.2 cm) inflorescence. Leonard Brass (1900–1971) was one of the most prolific ant-plant collectors, and it is fitting that we name this species, only ever collected by him, it being unfortunate that the species named in his honour has been reduced to a synonym of *H. moseleyanum* in this revision.



**Fig. 50** *Hydnophytum tetrapterum* Becc. Reproduced from Beccari (1885) t. 42. — Scale bar: 5 cm.

**47. *Hydnophytum tetrapterum* Becc. — Fig. 50**

*Hydnophytum tetrapterum* Becc. (1884) 126; (1885) 173, t. 42: 1–3. — Type: Beccari 5529 (Fl), New Guinea, West Papua Province, Sorong, Wa-Samson river, Feb. 1875.

*Tuber* not known. *Stems* numerous, spreading, to 40 cm long, 0.6 cm diam. Internodes to 9 cm, to just 1 cm when fertile; quadrangular and winged, especially immediately below nodes. Lamina lanceolate to obovate; 5 by 2 to 11 by 5.5 cm; apex blunt to acute; base acuminate to tapered; thin to leathery, light green in colour; midrib pronounced below, veins 5–7. Petiole short, 0.3–1 cm; stipules to 0.6 cm, triangular, caducous. Inflorescence paired, sessile, sometimes bract-covered. *Flowers* unknown. *Fruit* to 7 mm, ovoid. Pyrenes to 4.5 mm.

*Ecology & Habitat* — Forest at low altitude.

*Distribution* — Indonesia (West Papua Province).

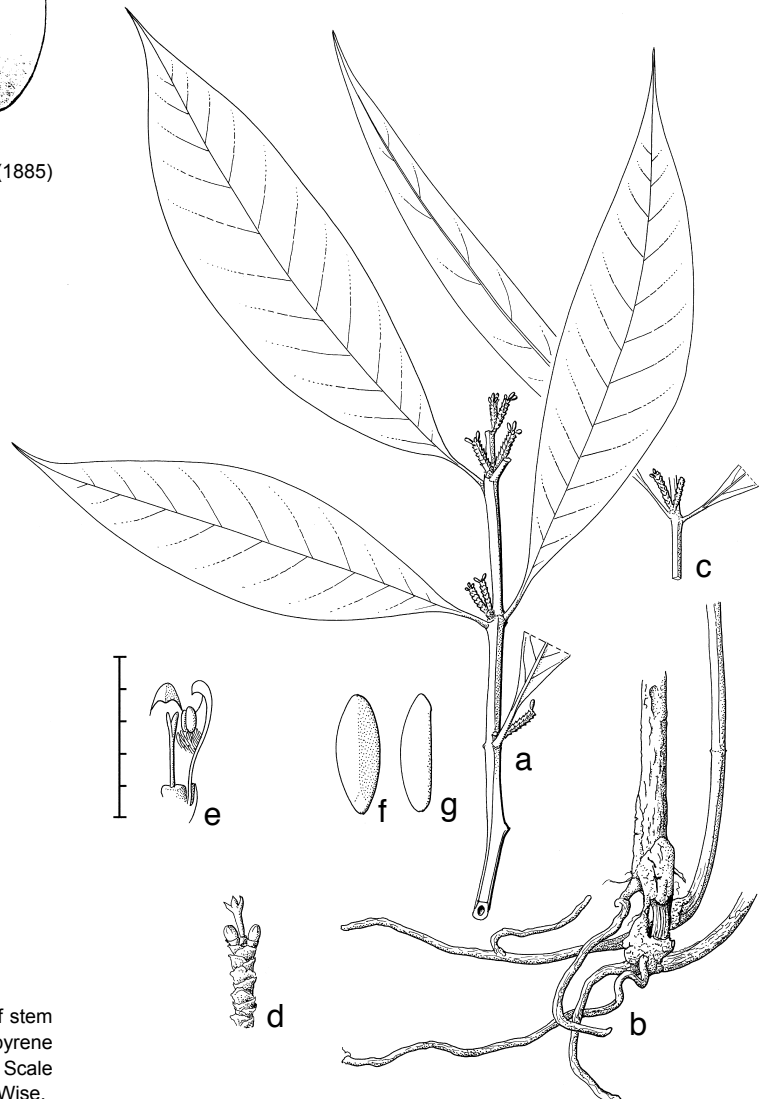
*Conservation status* — Vulnerable (VU) under criteria D2 with the two specimens 125 km apart.

*Note* — The winged internodes and leaf shape resemble *H. kebarense* [21], but the tuber is quite distinct.

**GROUP 9 – RADICANS GROUP**

**48. *Hydnophytum albertisii* Becc. — Fig. 51**

*Hydnophytum albertisii* Becc. (1884) 124; (1885) 136, t. 45: 8–14; Valetton (1912b) 772; Merr. & L.M.Perry (1945) 24. — Type: d'Albertis s.n. (Fl), Papua New Guinea, Fly River, 1877.



**Fig. 51** *Hydnophytum albertisii* Becc. a. Shoot; b. detail of base of stem lacking tuber; c. stem; d. inflorescence peduncle; e. half flower; f. pyrene abaxial face; g. lateral view (a, d–g: Brass 6599; b, c: Jacobs 8785). — Scale bars: a–c = 5 cm; d = 2.5 cm; e–g = 5 mm. — Drawn by Rosemary Wise.

*Tuber* small, to 15 cm across, smooth. Entrance holes scattered, prominently lipped; 0.3–1 cm across internally. *Stems* several, little branched to 60 by 0.3–1 cm. Internodes 1–11 cm, square in section, with four  $\pm$  prominent wings, these contracting at nodes. *Leaves* spreading. Lamina oblong-lanceolate, margins more or less parallel; 10 by 0.5 (11.5 by 2.7) to 17 by 4.7 (27 by 3.5) cm; apex acuminate; base attenuate; midrib prominent below; veins 7–10. Petiole 0.5–2 cm; stipules to 0.2 cm, triangular, caducous. Inflorescence comprising 2–4 unbranched peduncles bearing flowers towards their tips; to 1.5 cm in length. *Flowers* [5] heterostylous. Calyx entire, to 1 mm. Corolla tube to 3 mm, with a ring of hairs at mouth of tube; lobes to 1.5 mm. Short-styled flowers with anthers < 1 mm; exserted, filaments to 1 mm; pollen 40–42.5  $\mu$ m, 3-colpate, colpi unbordered, reticulation medium; stigma 2-lobed, style 1.5 mm. Long-styled flowers with anthers < 1 mm; below ring of hairs; pollen 31–34  $\mu$ m, reticulation medium to fine; stigma exserted. *Fruit* to 5 mm, red. Pyrenes 4, fusiform, 3.5 by 1.5 mm, triangular in section.

**Ecology & Habitat** — Closed or open forest, from 80–1000 m. Tuber contains various arboreal predators including centipedes and spiders, only occasionally with ants.

**Distribution** — Papua New Guinea (Western, Southern Highlands and Gulf Provinces).

**Conservation status** — Near Threatened (NT). This taxon is widespread (1000 km) across much of the southern foothills of the central highlands of New Guinea. Herbarium collections indicate at least six locations (subpopulations). Other information: georeferenced collections 8, AOO 15000 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO 38800 km<sup>2</sup>.

**Note** — The 4-angled stem, narrow-lanceolate leaves and pedunculate inflorescence, in which the initial peduncle is much reduced are diagnostic for this species.

#### 49. *Hydnophytum linearifolium* Valetton — Fig. 52

*Hydnophytum linearifolium* Valetton (1927) 135. — Type: *Ledermann 9700* (lectotype selected here L; iso B presumed lost), Papua New Guinea, Sepik April River, Lager 18, Nov. 1912.

*Hydnophytum linearifolium* Valetton var. *pedunculata* Valetton (1927) 136. — Type: *Ledermann 12455* (not seen), Papua New Guinea, Sepik Province, Felsspitze, July 1913, syn. nov.

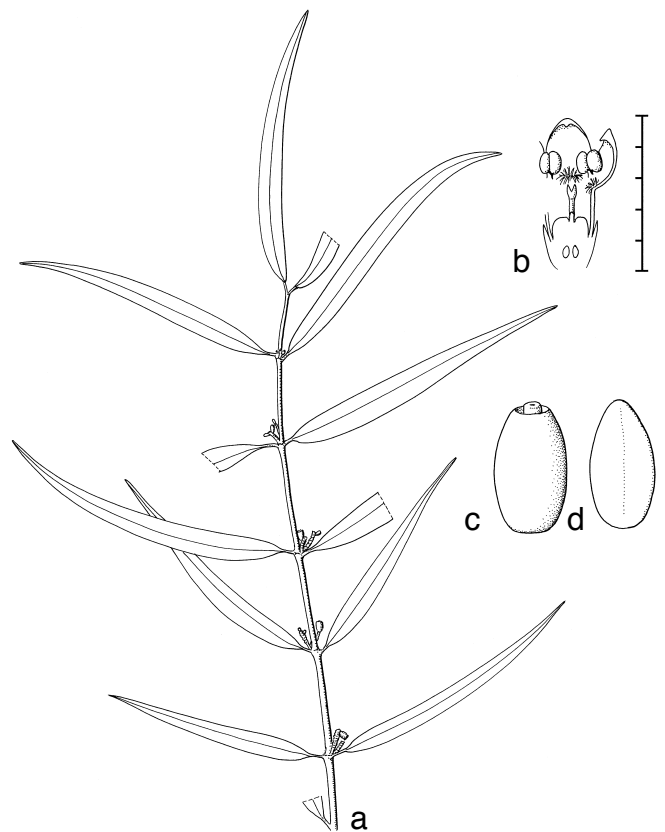
*Hydnophytum dolichophyllum* Valetton (1927) 130. — Types: *Ledermann 9889* (L), Papua New Guinea, Sepik Province, Lordberg, Dec. 1912 & *Ledermann 12723* (L), Papua New Guinea, Sepik Province, Felsspitze, Aug. 1913, syn. nov.

*Tuber* unknown. *Stems* several (?); to 40 cm; unbranched (?); internodes 1.5–2.5 by 0.1–0.2 cm,  $\pm$  quadrangular in section, but scarcely winged. Lamina linear-lanceolate to lanceolate, broadest near base; 9 by 0.8 (7 by 1.8) to 19.5 by 3.8 cm; apex acuminate-acute; base attenuate; midrib prominent below, venation obscure; matt green above, grey-green below. Petiole 0.4–2 cm; stipules minute, papery, caducous. Inflorescence paired peduncles to 1 cm. *Flowers* [1] ?heterostylous. Calyx 0.7 mm, entire to 4-cuspidate, at level of disc. Corolla tube 1.5 mm; with a ring of hairs within mouth of tube; lobes triangular, 1.25 mm. Anthers 0.3 mm, exserted from corolla tube. Stigma bifid, below level of anthers. *Fruit* ovoid; to 4.5 by 2.5 mm; apex broad with prominent swollen disc surrounded by calyx remains. Pyrenes 2, ellipsoid, to 4 by 2 mm, flattened.

**Ecology & Habitat** — Forest (?), 200–1500 m.

**Distribution** — Papua New Guinea (Sepik and Enga Provinces).

**Conservation status** — Near Threatened (NT). This taxon is widespread (560 km) across much of the northern Bismarck Mountains of Papua New Guinea, with herbarium collections indicating 5 locations (subpopulations). Other information: georeferenced collections 8, AOO 12500 km<sup>2</sup> (using an auto-value cell width of 50 km), EOO 20200 km<sup>2</sup>.



**Fig. 52** *Hydnophytum linearifolium* Valetton. a. Shoot; b. flower; c. fruit; d. pyrene adaxial face (*Ledermann 9700*). — Scale bars: a = 5 cm; b–d = 5 mm. — Drawn by Rosemary Wise.

**Additional specimen examined.** *Reeve 1121* (LAE), Western Highlands, Enga, Pogera.

**Note** — This species appears to represent an analogue to *H. albertisii* on the northern slopes of the central mountain ranges of Papua New Guinea. As with that species it has a narrow leaf, a square stem, much reduced inflorescence peduncles, and it also belongs to the *H. radicans* group. We have combined a second species described from the Sepik by Valetton – *H. dolichophyllum* – which, although it has larger leaves and branched inflorescences, shares the same diminutive flower size. Valetton also described the variety *pedunculata* based on *Ledermann 12455*, with slightly larger leaves and pedunculate inflorescences.

#### 50. *Hydnophytum radicans* Becc. — Fig. 53

*Hydnophytum radicans* Becc. (1884) 123; (1885) 132, t. 30; Valetton (1911) 503; (1912b) 774; H.J.Lam (1928) 204; Merr. & L.M.Perry (1945) 24. — Type: *Beccari 793* (FI), New Guinea, West Papua Province, Andai.

*Hydnophytum simplex* Becc. (1884) 123; (1885) 129, t. 28. — Type: *Beccari s.n.* (FI), Indonesia, Maluku Province, Aru Is., Vokan, syn. nov.

*Hydnophytum normale* Becc. (1884) 123; (1885) 130, t. 29. — Type: *Beccari s.n.* (FI), New Guinea, Papua Province, Japen Island, Ansum, syn. nov.

*Hydnophytum keiense* Becc. (1884) 123 (as *H. kejense*); (1885) 131, t. 31. — Type: *Beccari s.n.* (lectotype selected here FI; iso K), Indonesia, Maluku Province, Kei Island, Weri, Aug. 1873, syn. nov.

*Hydnophytum subnormale* K.Schum. in K.Schum. & Lauterb. (1905) 400; Valetton (1927) 142; Merr. & L.M.Perry (1945) 24. — Type: *Nyman 725* (not seen), New Guinea, syn. nov.

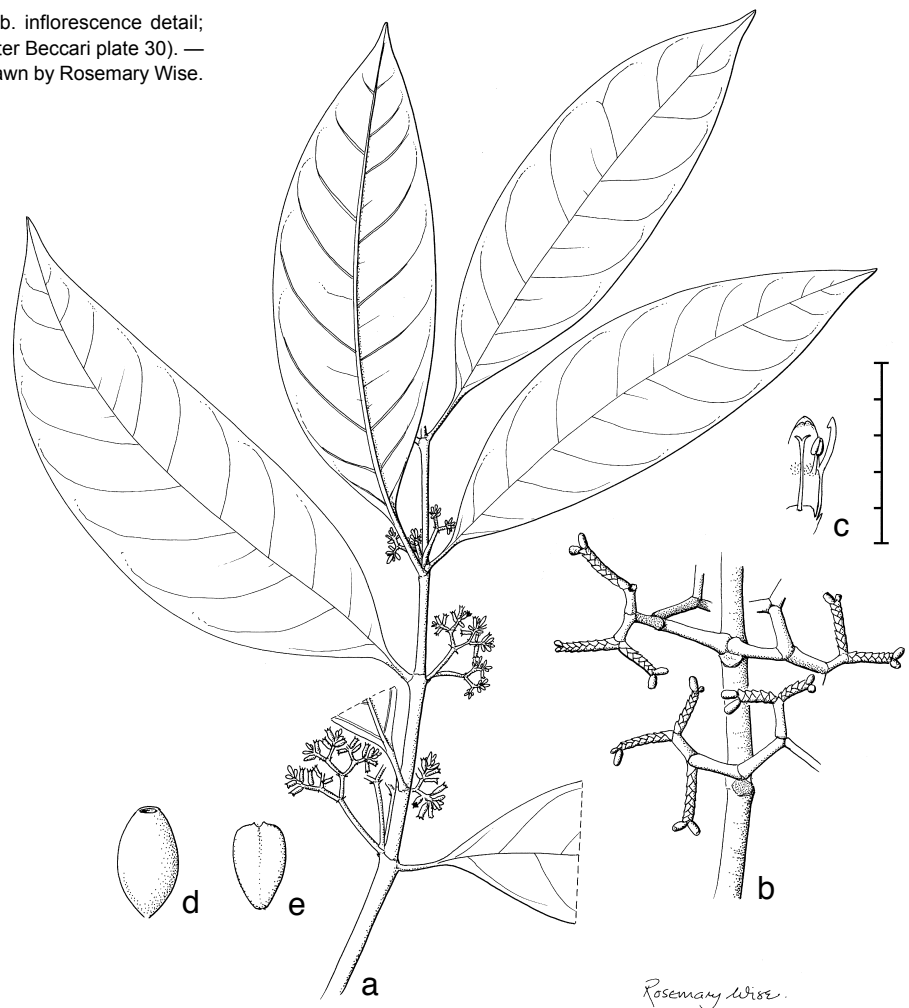
*Hydnophytum albense* Valetton (1927) 128; Merr. & L.M.Perry (1945) 24. — Type: *Schlechter 16164* (B presumed lost), New Guinea, Madang Province, Albu, syn. nov.

*Hydnophytum kelelense* Valetton (1927) 134. — Type: *Schlechter 16237* (B presumed lost), New Guinea, Madang Province, Kelel, June 1907, syn. nov.

*Hydnophytum montis-kani* Valetton (1927) 138 (as *H. kaniensis* in key, p. 128). — Type: *Schlechter 17056* (K), New Guinea, Madang Province, Kani Mountains, 26 Dec. 1907, syn. nov.



**Fig. 53** *Hydnophytum radicans* Becc. a. Shoot; b. inflorescence detail; c. flower; d. fruit; e. pyrene (a, b: *Jebb 427*; c–e: after Beccari plate 30). — Scale bars: a = 4 cm; b = 2 cm; c–e = 5 mm. — Drawn by Rosemary Wise.



*Hydnophytum amplifolium* S. Moore (1927) 270. — Type: *Brass 1151* (lectotype selected here A; iso BRI), Papua New Guinea, Gulf Province, Upoia, Vailala River, 15 Mar. 1926, syn. nov.

*Tuber* variable, globose to fusiform-cylindric; up to 60 cm broad; surface smooth, grey to brown. Entrance holes few, lipped. Tubers either small and then fleshier with small cavity volume, or larger with very thin cavity walls and large spiral cavities. *Stems* 1 to several, to 150 cm or more, sparsely branched, thickening towards base; internodes 1.5–15 by 0.2–2 cm. Lamina lanceolate to lanceolate-obovate; 12 by 3 to 27 by 10 cm; apex acuminate, acumen c. 1 cm, rarely to 2 cm, rarely apex acute-acuminate; base rounded to cuneate, attenuate to petiole; midrib occasionally prominent; veins 7–12, oblique; papery to leathery; glossy to dull green. Petiole 1–3 cm long, scarcely winged; stipules triangular, to 0.4 cm. Inflorescence variable; a pair of dichotomously branched (sometimes asymmetrically so) peduncles, branching 1–4 times; terminal branches (numbering 2–8), which are fasciculated and bract-covered, bearing flowers; this terminal portion continues to produce flowers ultimately becoming quite long; in some populations entire inflorescence falling after 4 or 5 nodes from apex; entire inflorescence from 1–15 cm overall, and 0.1–0.5 cm thick at base; rarely bearing a single flower in first or later bifurcations. *Flowers* [20] not heterostylous. Calyx 1–1.5 mm entire. Corolla 4–7.5 mm overall; lobes 1.5–2 mm; with a ring of hairs in throat. Anthers 1–2 mm; at mouth of tube, 1/2 exerted. Stigma 2-fid, at level of anthers. *Fruit* globose, to 7 by 5 mm. Pyrenes 2–4, obovoid to oblong, to 4(–5) by 2 mm, flattened; apex notched, blunt or rounded; base rounded.

*Ecology & Habitat* — In open savannah to closed forest, from sea level to 1200(–1800) m, then often a low-level epiphyte. With or without ants, but since there is probably more than one

species involved in this complex, each may exhibit a somewhat different ecology in their relationship with ants.

*Distribution* — Indonesia: Maluku Province (Seram, Kei and Aru islands); West Papua and Papua Provinces (including Yapen Island), Papua New Guinea (mainland only, including Karkar and Normanby Island).

*Conservation status* — Least Concern (LC). Found across the whole island of New Guinea with herbarium collections indicating over 45 locations (subpopulations). Other information: georeferenced collections 72, EOO over 1 million km<sup>2</sup>.

*Notes* — A very widespread and variable species. Although found throughout the New Guinea mainland, and on some of the offshore islands, *H. radicans* is absent from the Bismarck Archipelago and the Solomon Islands. We have been unable to resolve any pattern to the variation in this species, and present collections have enabled us to distinguish only two other species: *H. albertisii* [48] and *H. linearifolium* [49].

Whilst *H. albense*, *H. amplifolium*, *H. keiense*, *H. kelelense*, *H. montis-kani*, *H. normale*, *H. simplex* and *H. subnormale* readily fall into a single variable taxon (even though we have seen no authentic specimens for several of these species), other specimens which are somewhat more extreme in appearance may represent distinct taxa.

Some notable variations are the high altitude collections from the Eastern Highlands Province of Papua New Guinea, which have a large, fusiform tuber with spiral cavities and little tuber flesh (*Jebb 93 & 94*, *Brass 31936 & 32048*). It is not occupied by ants, but instead by a range of arthropods, and skinks. The leaves are leathery, with prominent midrib and veins. Another unusual specimen, *Brass 7172* (from Western Province, PNG) has remarkably long, slender inflorescences.

## GROUP 10 – SQUAMELLARIA CLADE

51. *Hydnophytum grandiflorum* Becc. — Fig. 54

*Hydnophytum grandiflorum* Becc. (1884) 126; (1885) 171, t. 44: 13–25; Gibbs (1909) 153; Parham (1964) 193; (1972) 271; A.C.Sm. (1988) 242, f. 90: a–b, 129. — Type: *Graeffe s.n.* (K) Fiji, Ovalau, Mt Tana Lailai, Dec. 1864. *Myrmecodia vitiensis* Seem. (1861) 256, *nom. nud.*; A.Gray (1862b) 36; Seem. (1862) 438. — Type: *Seemann 216* (lectotype selected here P; iso BM, CAL, G, GH, K), Fiji, Kandavu, Mt Mbuke Levu.

*Hydnophytum longiflorum* auct. non A.Gray (1858): A.Gray (1862a) 318; (1862b) 36; Seem. (1862) 438, p.p.; (1866) 138; Drake (1890) 99, p.p.; Becc. (1885) 172, t. 45: 1–7; Parham (1964) 193, p.p.; (1972) 272.

*Squamellaria jebbiana* Chomicki in Chomicki & S.S.Renner (2016) 14, f. 2: i, 3: N–P, 9. — Type: G. Chomicki, J. Aroles & A. Naikatini 74 (holo SUVA; iso GH, K, L, M barcode M-0274837, MO, NOU, NSW, P, S), Fiji, Taveuni, Des Voeux peak, 450 m alt., 22 Mar. 2015.

**Tuber** broadly conical, to 35 by 30 cm, slightly lobed at periphery; surface dark brown, smooth. Entrance holes of two types, conical to 1 cm across, with a prominent rim, or large and funnel-like to 4 cm across. **Stems** numerous, to 40 by 0.6 cm, branching freely, spreading to upcurved. Internodes to 7 cm when sterile, 0.4–2(–4) cm when fertile, with 2 slight ridges running from below stipules. **Leaves** clustered, erect to spreading. Lamina elliptic to ovate, 1.6 by 1 to 7 by 3.1 cm; apex rounded to acute; base rounded to truncate, abruptly attenuate; midrib prominent above and below; veins 4–6 pairs; leathery and brittle. Petiole to 0.2 cm; stipules rounded, 0.1–0.3 cm, with a prominent central process to 0.3 cm, continuous with stem ridge, caducous. Inflorescence terminal, becoming axillary, solitary, shortly pedunculate. Bracts c. 1 mm, papery. **Flowers** [7] heterogamous. Calyx entire, to 2 mm. Disc at or slightly above level of calyx, not prominent in fruit. Corolla tube 15–46 mm long, lobes to 10 by 5.5 mm, elliptic; uncus 1–2 mm;

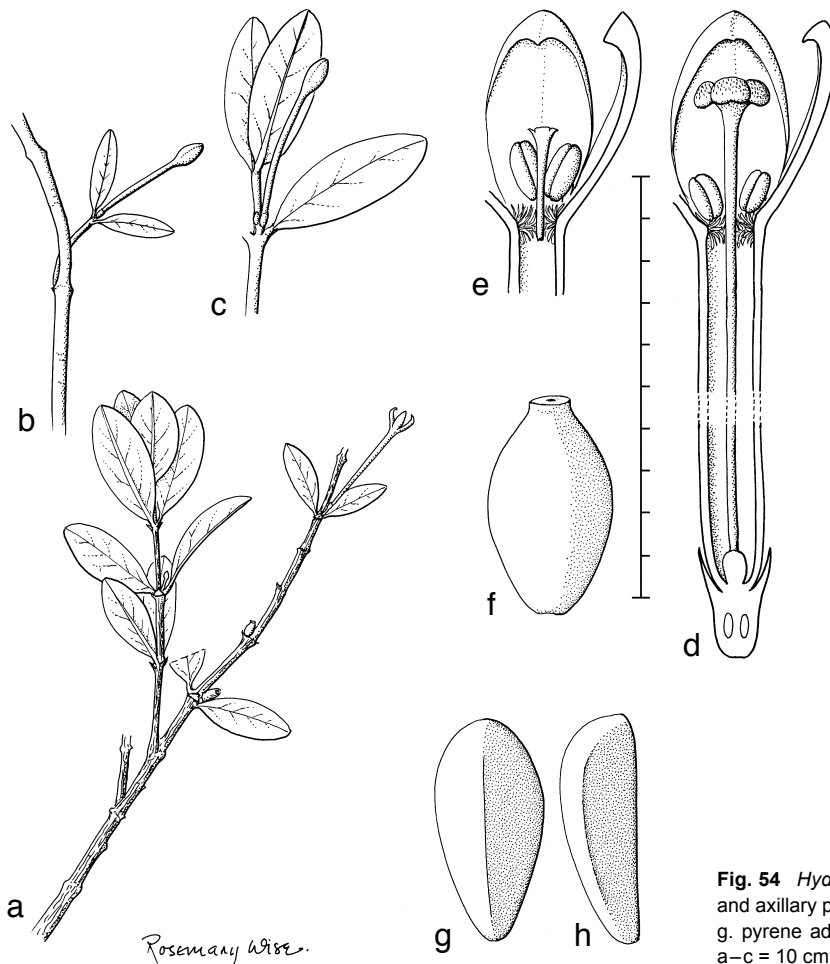
with a ring of hairs at mouth of corolla tube. Anthers exerted from mouth of tube. In female-sterile flowers anthers 2.5–3.5 mm long, containing 4-colpate pollen, 105–130  $\mu\text{m}$  diam, with walls 7.5  $\mu\text{m}$  thick, brochi 8–15  $\mu\text{m}$  across; style to 6 mm, not attached to disc; stigma < 1 mm across, above anthers. In male-sterile flowers, anthers 1.2–2.5 mm long, lacking pollen; stigma capitate, broadly 4-lobed, and exerted from corolla mouth, to 3 mm across. **Fruit** globose to 12 by 9 mm, baccate, pink when ripe. Pyrenes 2 or 3, obovoid-oblong; 5.5 by 2.5 mm; semi-circular to triangular in section, rounded at apex and base.

**Ecology & Habitat** — Lowland to montane forest, 200–1 100 m. The tuber appears to be less regularly occupied by ants than *H. longiflorum* [52], and is often found to be occupied by skinks, geckoes and their eggs, and invertebrates, in particular spiders, myriopods and cockroaches.

**Distribution** — Fiji (Viti Levu, Ovalau, Kandavu, Vanua Levu and Taveuni).

**Conservation status** — Near Threatened (NT). This species is found on all 5 of the larger islands in the Fijian archipelago. Other information: georeferenced collections 20, AOO 68 km<sup>2</sup> (using a cell width of 2 km), EOO on Viti Levu alone 1 000 km<sup>2</sup>.

**Notes** — Gray created confusion when he redescribed his 1858 *H. longiflorum* when specimens of *H. grandiflorum* came to hand in 1862. Beccari compounded this error and described *H. longiflorum* purely from Seeman's description of *Myrmecodia vitiensis*. Albert Smith unravelled the nomenclature in *Flora Vitiensis Nova* (1988). The present species is distinguished from *H. longiflorum* [52] by its larger flowers with pubescent throats, and globose, fleshy fruits. Whilst the tubers of *H. grandiflorum* tend to be smooth-surfaced, this is not a consistent or reliable identification feature to distinguish it from *H. longiflorum* (Chomicki & Renner 2016).



**Fig. 54** *Hydnophytum grandiflorum* Becc. a. Shoot; b, c. buds in terminal and axillary positions; d. female-sterile flower; e. male-sterile flower; f. fruit; g. pyrene adaxial face; h. pyrene lateral view (Jebb 493). — Scale bars: a–c = 10 cm; d–f = 20 mm; g, h = 10 mm. — Drawn by Rosemary Wise.

The flowers of both *Hydnophytum* species in Fiji demonstrate a remarkable form of heterogamy, with staminate and pistillate flowers. This was not understood by Beccari, when working with herbarium material alone. From field observations (by MHPJ) it seems that flowers of both sexes may occur on a single inflorescence, while in other plants only one sex can be found. Smith reports finding hermaphrodite flowers (1988), but we have not seen this. When anthers contain pollen, it seems that their size physically results in the stigma being unable to pass between them, and as the corolla tube elongates, apparently faster than the style can grow, it is presumably plucked from the disc, in effect, a process of female neutering.

The pollen of all *Hydnophytinae* in Fiji share characteristic pollen. The majority of *Hydnophytum* spp. have 3-porate (more rarely 3-colpate) pollen 40–70 µm across, with a mean of 52 µm and a punctate surface. Two exceptions are *H. magnirubrum* [37] and *H. minorubrum* [38], which have pollen grains up to 100 µm across, with a coarsely reticulate exine with brochi c. 1–5 µm across. The pollen of Fijian *Hydnophytinae* is 3–5-colpate, and 70–160 µm diam with a coarse reticulation with brochi 6–15 µm across.

Chomicki & Renner (2016: 14) described a further species of *Squamellaria* from Taveuni Island, *S. jebbiana* Chomicki. They acknowledged that the species cannot be morphologically distinguished except for its occurrence on Taveuni Island. The species was taxonomically diagnosed by having a consistently elliptic lamina and a single base substitution in two genes; a C in position 354 of the ITS gene (GenBank # KU586342) instead of an A or T, and a C at position 278 of rps16 (GenBank # KU586438) instead of an A as in all other Fijian *Squamellaria* specimens (n = 13) examined (Chomicki & Renner 2016).

## 52. *Hydnophytum longiflorum* A.Gray — Fig. 55

*Hydnophytum longiflorum* A.Gray (1858) 42; Seem. (1866) 138 p.p.; Drake (1890) 199; Hook.f. (1894) t. 7343; Parham (1964) 193 p.p.; (1972) 272 p.p.; A.C.Sm. (1988) 244, f. 90: c–f. — Type: *US Expl. Exp.* 62267 (US), Fiji, Ovalau, 1840.

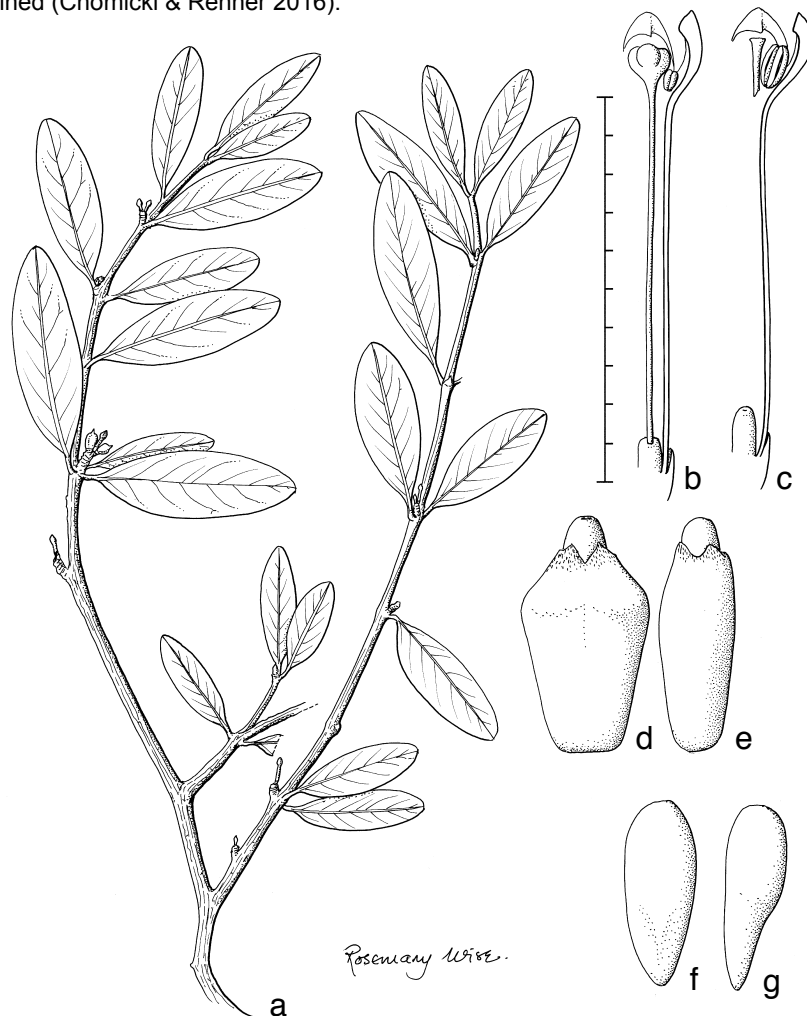
*Squamellaria wilkinsonii* (Horne ex Baker) Chomicki in Chomicki & S.S. Renner (2016) 20. — *Hydnophytum wilkinsonii* Horne ex Baker (1883) 365, as *H. wilkinsonii*; Horne (1881) 263, *nom. nud.*; Becc. (1884) 125; (1885) 170, t. 44: 1–12; Drake (1890) 200; Parham (1964) 193; (1972) 272; A.C.Sm. (1988) 245. — Type: *Horne 1077* (erroneously published as 1078 in Beccari 1885) (lecto K barcode K000761990; iso GH, K barcode K000761991), Fiji, Vanua Levu, Mbua, Sept. 1878, *syn. nov.*

*Hydnophytum horneanum* Becc. (1884) 125; (1885) 168, t. 43: 15–25 (legend on plate as '*H. horneianum*'); Parham (1964) 193; (1972) 272. — *Hydnophytum borneanum* Becc. *Sphalm.* Govaerts et al. (2015). — Type: *Horne 282* (K), Fiji.

*Squamellaria tenuiflora* (Becc.) Chomicki in Chomicki & S.S. Renner (2016) 20. — *Hydnophytum tenuiflorum* Becc. (1884) 125; (1885) 169, t. 43: 1–14; Parham (1964) 193; (1972) 272. — Type: *Graeffe 1573* (lectotype selected by Smith (1988) K), Fiji, Ovalau.

non *Hydnophytum longiflorum* auct. non A.Gray (1858); A.Gray (1862a) 318; (1862b) 36 p.p.; Seeman (1862) 438; (1866) 138 p.p.; Drake (1890) 99; Becc. (1885) 172, t. 45: 1–7 p.p.; Parham (1964) 193; (1972) 272. *quae* = *H. grandiflorum*.

*Tuber* clasping, flattened to rounded, irregular, to 30 by 27 cm. Surface brown, usually sparsely bearded with flexible, slightly recurved spines. Entrance holes scattered, of two types, conical to 4 mm, or funnel-like and irregular. *Stems* several to numerous, branching freely, erect to upcurving, to 40 by 0.8 cm. Internodes to 7 cm when sterile, 0.5–3 cm when fertile. *Leaves* erect to spreading. Lamina elliptic, 3 by 1 to 11.4 by 4 cm; apex



**Fig. 55** *Hydnophytum longiflorum* A.Gray. a. Shoot; b. male-sterile flower; c. female-sterile flower; d. fruit broad axis; e. fruit narrow axis; f. pyrene abaxial face; g. pyrene lateral view (a: *Jebb 446*; b–g: *Jebb 441*). — Scale bars: a = 7.5 cm; b, c = 5 mm; d–g = 10 mm. — Drawn by Rosemary Wise.

rounded to acute; base tapered, attenuate; midrib prominent below; veins 4–6; leathery. Petiole 0–1 cm; stipules rounded, to 0.2 cm, with a short, recurved central process to 0.1 cm, which is contiguous with stem ridge; caducous. Inflorescence terminal and axillary, solitary, shortly pedunculate, to 1.5 cm. Bracts to 1 mm papery, more or less persistent. Flowers [6] heterogamous. Calyx 4-cuspidate or entire, to 1 mm. Corolla tube 10–18 mm; lobes elliptic to rounded, 2.5–4 mm; unicus < 1 mm; entirely glabrous within. Anthers exerted at mouth of corolla tube. In female-sterile flowers, anthers 1.5–2 mm, containing 4-colpate pollen, 74–94  $\mu\text{m}$ , wall 7.5  $\mu\text{m}$  thick, reticulation coarse, brochi 6–12  $\mu\text{m}$  across, with fine spines within reticulations. In male-sterile flowers anthers 0.5–1 mm, containing no pollen, stigma exerted, capitate, broadly 4-lobed, to 1.5 mm across. Disc prominent to 1 mm above level of calyx, persistent in fruit. Fruit turbinate, flattened, to 7 by 4 mm; with prominent disc at apex; siccate; green and pink or red in colour when ripe. Pyrenes wedge-shaped, to 5 by 2 mm, blunt and rounded at apex, truncate and flattened at base.

**Ecology & Habitat** — Mangroves to montane forest, sea level to 900 m. Usually ant-inhabited, with about 50 % of individual tubers occupied by the ant species *Philidris nagasau* Mann.

**Distribution** — Fiji Islands (Viti Levu, Ovalau and Vanua Levu).

**Conservation status** — Vulnerable (VU) under criteria B1ab (iii)+2ab(iii). This species is found on three islands, with herbarium specimens indicating eight locations (subpopulations) and an AOO of 76 km<sup>2</sup> (using a cell width of 2 km). Other information: georeferenced collections 21, EOO on Viti Levu 1900 km<sup>2</sup>.

**Notes** — *Squamellaria wilkinsonii*, as interpreted by Beccari (1884), with a cuspidate fruit, is regarded, by us, as an artefact of drying, and here synonymised with *H. longiflorum*. Smith (1988) has already reduced *H. borneanum* and *S. tenuiflora*, which were based on inconsequential differences in calyx shape and corolla length, respectively.

More regularly ant-inhabited than *H. grandiflorum*, this species is distinguished by having a tuber that is more usually (but not invariably) covered by numerous slender roots, a shorter corolla, that is quite glabrous within, and a flattened, turbinate fruit.

Two of the taxa we recognise as synonymous with *H. longiflorum* – *S. tenuiflora* and *S. wilkinsonii* – have been transferred to *Squamellaria* by Chomicki & Renner (2016). They indicated that they considered three taxa as possible synonyms of *S. tenuiflora* (Becc.) Chomicki, namely *H. longiflorum*, *H. grandiflorum* and *H. borneanum*. They did not make the specific transfer pending DNA sequences from the type specimens. However, the dates of publication for these taxa – *H. longiflorum* (1858), *H. tenuiflorum* (1884), *H. grandiflorum* (1884) and *H. borneanum* (1884) – leaves no doubt that the name *H. longiflorum* has priority and is therefore used here.

The misspelling of the name *H. borneanum*, instead of *H. borneanum*, by Govaerts in the Kew Checklist for Rubiaceae (2015) has entered IPNI (2015) and The Plant List (2015), as pointed out by Low et al. (2016)

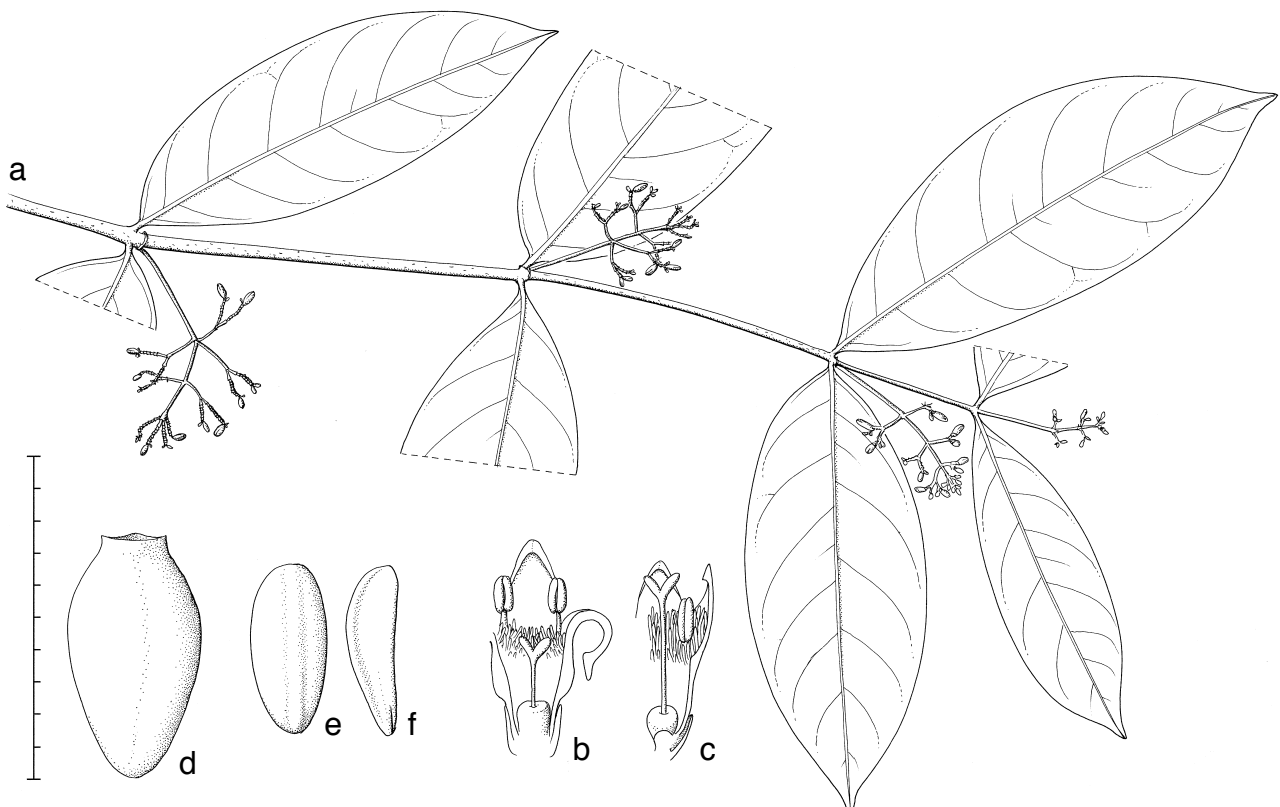
### 53. *Squamellaria guppyana* (Becc.) Chomicki — Fig. 56

*Squamellaria guppyana* (Becc.) Chomicki in Chomicki & S.S. Renner (2016) 20; *Hydnophytum guppyanum* Becc. (1885) 133, t. 40 *partim.*; H.B. Guppy (1887) 297; Rech. (1913) 612; Merr. & L.M. Perry (1945) 25. — Type: *Guppy s.n. partim.* (lecto FI barcode FI008898; iso K, L), Solomon Islands, Shortland Island, Mar. 1884.

*Hydnophytum hahlili* Rech. (1912) 186; (1913) 612, t. 2, f. 3a; Merr. & L.M. Perry (1945) 25. — Type: *Rechinger 3552* (holo W), Bougainville, Djup, syn. nov.

*Hydnophytum longipes* Merr. & L.M. Perry (1945) 23. — Type: *Kajewski 1571* (lectotype selected here A; iso BRI), Bougainville, Kieta, 21 Mar. 1930, syn. nov.

**Tuber** oblong-ovoid; 30 by 15 cm; pendent to clasping (on vertical trunks); fawn to deep brown in colour. Entrance holes numerous; 0.2–0.4 cm diam; arranged in concentric circles



**Fig. 56** *Squamellaria guppyana* (Becc.) Chomicki. a. Shoot; b. short-styled flower; c. long-styled flower; d. fruit; e. pyrene abaxial face; f. pyrene lateral view (a, b: Jebb 514; c–f: Whitmore BSIP 1462). — Scale bars: a = 10 cm; b–f = 10 mm. — Drawn by Rosemary Wise.

about long axis of tuber; in some tubers occluded by corky plugs; often with 1 or more large, funnel-like openings along side of tuber to 2 by 5 cm. Roots numerous on substrate side of tuber, and around base of stem. Cavities pale to dark-walled, some chambers with root-like warts in clusters, 1–2 mm long. *Stems* several, to 3 m; little branched. Internodes 1–13 cm, with a prominent ridge descending from below stipule on each side of stem. Bark grey, green towards apex. *Leaves* lax, drying thin. Lamina lanceolate, ovate or obovate; 5.5 by 2 to 20 by 11 cm; apex blunt to acute; base attenuate; dark green, somewhat brittle. Petiole 0–1 cm, usually winged throughout; stipules triangular, acuminate to 0.3 cm. Inflorescence solitary, initially terminal, becoming axillary; pseudodichotomously branched; primary peduncle to 6 by 0.5 cm, winged, with 2(–4) secondary, dichotomously branching axes, these up to 10 cm in length; main axis continuing with up to 2 further branch points. *Flowers* [27] heterostylous. Calyx 1.5 mm, as long as disc. Corolla tube 3 mm, widest near base, with a ring of hairs in corolla mouth; lobes to 2.5 mm, fully reflexed in open flower, unicus 0.5 mm. Short-styled flowers with anthers to 1.5 mm; exserted from corolla mouth; filaments to 2 mm; pollen 37–47 (43)  $\mu\text{m}$ , wall 3.75  $\mu\text{m}$  thick, brochi 1  $\mu\text{m}$ , pores 9–12  $\mu\text{m}$  across, vesicles very small; style 2 mm, stigma within corolla tube, 2-lobed. Long-styled flowers with anthers to 1 mm; below corolla mouth, filaments to 0.5 mm; pollen 31–41 (37)  $\mu\text{m}$ ; style 3.5 mm, stigma exserted. *Fruit* obovoid, 8 by 4 mm, with prominent calyx and disc remains. Pyrenes obovoid to oblong; to 5.5 by 2.5 cm; flattened dorsoventrally; apically rounded; base rounded to tapered, abaxial face with a longitudinal ridge.

*Ecology & Habitat* — Common throughout the Solomon Islands in mangrove swamps, riverside forest etc., sea level to 600 m. Often ant-inhabited, by a extensive range of ant species, but some cavities capable of collecting rainwater.

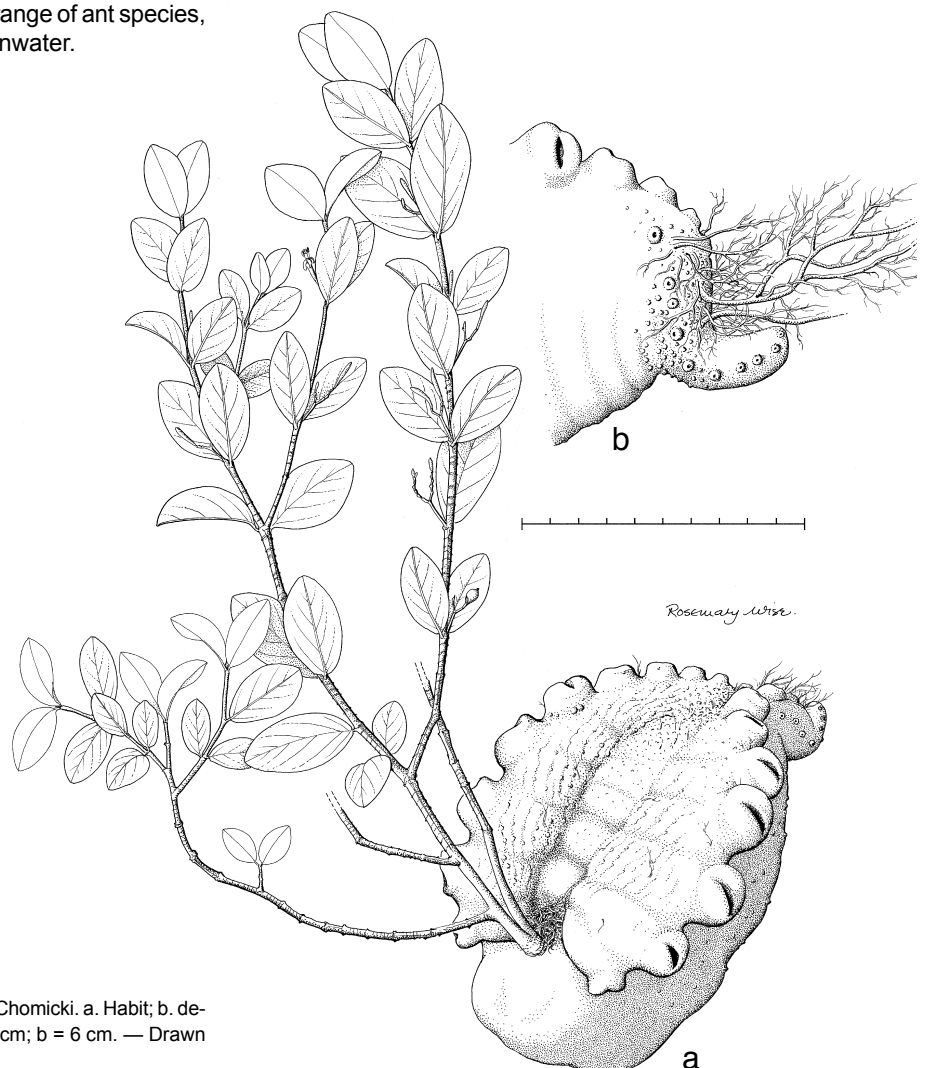
*Distribution* — Papua New Guinea (Bougainville), Solomon Islands (Shortland, Choiseul, New Georgia group, Kolombangara, Santa Isabel, Guadalcanal and San Cristobal).

*Conservation status* — Least Concern (LC). This species is found on seven islands with a geographical spread of 700 km. Other information: georeferenced collections 20, AOO 80 km<sup>2</sup> (using a cell width of 2 km), EOO 62 100 km<sup>2</sup>.

*Notes* — Beccari described this species from a Guppy collection, which is unfortunately a mixture of two species – the tuber collected by Guppy, and illustrated by Beccari (1885: t. 40: 1) is that of *S. kajewskii* [54]. All other material is of *S. guppyana*, and there is no confusion in the original diagnosis.

The inflorescence is remarkable in its resemblance to that of a *Psychotria* species. It arises terminally, is solitary, and has a pseudodichotomously branching peduncle. Beccari was convinced that the specimens he examined must have lost the opposite inflorescence of the pair, which would otherwise, as he pointed out, have been identical to a *Psychotria* (Beccari 1885: 135). He was anxious enough to have even got the draftsman to tentatively add the base of the 'missing' inflorescence in the plate (Beccari 1885: t. 40: 2). *Squamellaria kajewskii* shares this inflorescence structure, although in this latter species the size and degree of branching is much reduced.

The corky plugs that occlude the entrance holes in some tubers are unique in the subtribe. It appears that this makes the tuber cavities water-tight in some individuals, and may allow a tuber not occupied by an ant-colony to act as a water-collecting organ. The tuber-cavity structure comprises encircling chambers that



**Fig. 57** *Squamellaria kajewskii* (Merr. & L.M.Perry) Chomicki. a. Habit; b. detail of tuber base (Jebb 507). — Scale bars: a = 10 cm; b = 6 cm. — Drawn by Rosemary Wise.

girdle the tuber, with rings of entrance holes that form encircling lines on the tuber surface. This morphology is identical to that seen in the Fijian *Squamellaria* species and lends weight to the decision by Chomicki & Renner (2016) to place this species in the latter genus.

**54. *Squamellaria kajewskii* (Merr. & L.M.Perry) Chomicki — Fig. 57, 58**

*Squamellaria kajewskii* (Merr. & L.M.Perry) Chomicki in Chomicki & Renner (2016) 20; *Hydnophytum kajewskii* Merr. & L.M.Perry (1945) 25. — Type: *Kajewski 1716* (lectotype A; iso BM, BO, BRI, G, P), Bougainville, Kupei Gold Field, 14 Apr. 1930.

**Tuber** scaphoid, with a flattened to sunken upper surface, and a broad, keeled, swollen and bellying lower surface; obovate from above, and triangular-obovate to cordate in transverse section; to 19 cm long, 12 cm wide and 10 cm deep. Initial tuber (basal) cylindrical, with small lipped entrance holes 1–4 mm diam in a row along each side. Initially horizontal, ascending and becoming almost vertical, and then thickening greatly, and becoming triangular in section with a flattened dorsal surface, before turning sharply downwards and horizontal once more. Mature part of tuber with 2 rows of prominently lipped entrance holes along upper, outer edges, 1–2.5 cm diam, and 1 cm apart, with lips to 0.5 cm thick, pointing outwards to downwards. Older tubers may lose this symmetry and become more rotund with additional rows of entrance holes. Tuber surface smooth, dark-brown, dull, with small roots and tubercle-like swellings, especially on upper surface and towards base; keel with very slight corrugations corresponding to cavities within. Entrance holes

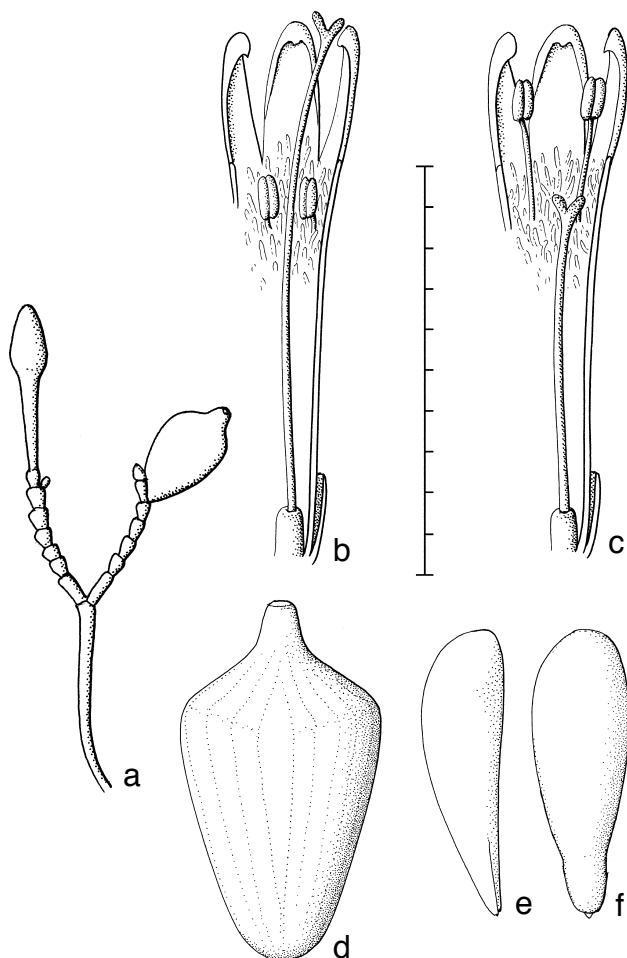
each giving rise to a transverse warted chamber, and paired to an entrance hole on the opposite side of tuber; each chamber having 2 entrance holes. Cavity walls dark in upper parts, pale below; warted throughout, warts root-like in clusters of 2–5, most numerous above, on dark-coloured walls. **Stems** several, arising from a common stock; to 80 by 0.3 cm; branching; older stems with annular furrows, younger stems drying ridged, dark-brown to black. Internodes 0.5–7 cm in length, generally shortest towards shoot apex, nodes swollen. A pair of rounded ridges descending from stipules. **Leaves** sessile. Lamina subrotund, 2 by 1.2 to 4 by 3 cm; apex acute to blunt; base blunt to cordate; midrib prominent below, less so above; veins 5–7 prominent above and below. New leaves white to very pale green, when mature medium green, upper surface dull, lower surface with a slight sheen; drying dark green above, pale below, new leaves drying translucent. Stipules acuminate to 0.1 cm, persistent. Inflorescence solitary, pedunculate; initially terminal, becoming axillary, slightly offset to petiole. Peduncle to 2.5 by 0.2 cm; flattened; with two narrow and opposite ridges; with two, or rarely three, terminal, flower-bearing branches. Occasionally a single flower may be borne at centre of branch point. Side branches are narrow at their base, to 0.1 cm, becoming thicker above to c. 0.25 cm diam, when fertile. **Flowers** produced sequentially from individual sections of this peduncle, bracts minute. Flowers [8] heterostylous. Calyx to 1.5 mm, entire. Corolla tube 9 mm long, with a broad ring of hairs to 2 mm in breadth at mouth; lobes to 3 by 1 mm, recurved in open flower, uncut to 0.5 mm. Short-styled flowers with anthers to 1 mm, exserted; filaments to 3 mm; pollen 53–60(–69)  $\mu\text{m}$ , walls c. 4.4  $\mu\text{m}$  thick, brochi 1  $\mu\text{m}$ , pores 15–23  $\mu\text{m}$  across; style 7 mm in length, stigma 2-fid, below mouth of tube. Long-styled flowers with anthers to 1 mm; within mouth of corolla tube; filaments < 0.5 mm; pollen 47–53 (51)  $\mu\text{m}$ , walls c. 3.75  $\mu\text{m}$  thick, pores 11–16  $\mu\text{m}$ , reticulation fine, brochi to 1  $\mu\text{m}$ , lacking vesicles; stigma 2-fid, well exserted from mouth, stigma 2-fid, papillose. **Fruit** flattened turbinate; to 9 by 5 mm; with prominent calyx remains; red, with distinct white lines when ripe. Pyrenes obovoid, to 7 by 2.5 mm; apex rounded, base tapered.

**Ecology & Habitat** — Ants have been recorded in certain collection notes, but are not present in the tubers which collect rainwater (being water-filled when collected, MHPJ pers. obs.). Although the cavity openings do not appear ideally suited for this (they point sideways or downwards, and have a large swollen lip), there seems little doubt they function as such. Cockroaches are commonly found in these cavities along with their egg cases. The species is found in similar habitats to *S. guppyana*, but tends to be observed higher in the canopy.

**Distribution** — Papua New Guinea (Bougainville), Solomon Islands (Santa Isabel).

**Conservation status** — Vulnerable (VU) under criteria B1ab(iii)+2ab(iii). This species is found on Bougainville with a single outlier on Santa Isabel island 500 km away. The Bougainville collections represent five locations (subpopulations) and taken alone they have an AOO (using an auto-value cell width of 5 km) of 112 km<sup>2</sup> and an EOO of 270 km<sup>2</sup>. Other information EOO 7500 km<sup>2</sup>.

**Notes** — The tuber of this species is unique in its bilateral symmetry, having no parallel within the *Hydnophytinae*. However, with age the tuber acquires a more irregular appearance and loses its strikingly scaphoid form. It is commonly found growing with *S. guppyana* [53] from which it can be distinguished by its tuber, its smaller, more slender stems, smaller leaves, and its smaller, less-branched inflorescence, with long slender flowers. As a consequence, it is no surprise that Guppy collected both species as a mixed collection (see notes under *S. guppyana*).



**Fig. 58** *Squamellaria kajewskii* (Merr. & L.M.Perry) Chomicki. a. Inflorescence detail; b. long-styled flower; c. short-styled flower; d. fruit, e. pyrene lateral view; g. pyrene abaxial face (a, b: *Jebb 507*; c–f: *Jebb 509*). — Scale bars: a = 3 cm; b–f = 10 mm. — Drawn by Rosemary Wise.

The cavity architecture of this species and *S. guppyana* have much in common, even though externally they are quite unlike. Both have a series of independent transverse cavities, each of which is added apically to the tuber. Each of these cavities comprises a broad chamber occupying almost the entire breadth of the tuber, from this arise narrow, tubular tunnels which run towards the tuber base (Jebb 1985, 1991a).

**55. *Squamellaria vanuatuensis* Jebb & C.R.Huxley — Fig. 59**

*Squamellaria vanuatuensis* Jebb & C.R.Huxley in Chomicki & S.S.Renner (2016) 17. — Type: G. McPherson, M. Tuiwawa, & R. Rigault 19437 (holo PVNH; iso MO, NOU, P, SUVA), Vanuatu, Espiritu Santo Island, West coast of Cumberland Peninsula above village of Penarouf, 17 Nov. 2006.

*Etymology.* For the type locality.

*Tuber* flattened, to 40 cm across, red-brown in colour. Cavities relatively large. *Stems* several, to 60 by 0.2–0.5 cm. Internodes 1.5–5 cm. Lamina ovate; 4 by 2.2 to 5.5 by 3.3 cm; apex acute; base rounded; succulent; pale green; venation obscure, 6 or 7. Petiole 2 cm; stipules to 0.15 cm, rounded, papery, caducous. Inflorescence paired, sessile, covered by papery, triangular

bracts to 1 cm in length, forming a mass 1.5 cm across. *Flowers* [1] ?heterostylous. Calyx 4-dentate, 3 mm, teeth to 1 mm. Corolla in bud 2.5 mm overall. Anthers 1.2 mm. Pollen 3-colpate, 57.5 µm across; reticulation medium, brochi 1–2 µm. Stigma 2-fid, above level of anthers. *Fruit* and pyrenes unknown.

*Ecology & Habitat* — Forest.

*Distribution* — Vanuatu (Espiritu Santo Island, Maewo, Pentecost, Efate and Erromanga islands).

*Conservation status* — Near Threatened (NT). This species is found on five of the islands of Vanuatu. These islands are still covered by some 75 % forest cover and conservation at community level is a high government priority. Other information: AOO 847 km<sup>2</sup> (using an auto-value cell width of 11 km).

*Additional specimens examined.* L. Bernardi 13238 (G), Erromanga, in the vicinity of the Nouankao Camp, 5 Aug. 1971; Green in RSNH 1274 (K), S18°54' E169°11', Erromanga; Morrison s.n. (K), Efate, summit of Mt Macdonald, Undine Bay; P. Cabalion 2731 (P), Efate, Mt McDonald; Bourdy 532 (K) Maewo, Saritamita; P. Cabalion 2528 (P), Pentecoste, Eikol.

*Note* — This species is geographically isolated. Although superficially similar to *H. mayuense* [32], it differs in its short petiole, and pale-coloured, delicate bracts. Bourdy 532 (K), which was intended to be the type, has been annotated as '*Hydnophytum vanuatuense*'.

**UNCERTAIN AND LITTLE KNOWN SPECIES**

**a. *Hydnophytum angustifolium* Merr.**

*Hydnophytum angustifolium* Merr. (1908) 162. — Types: Clemens s.n., May, June 1907, April 1906 (PNH not seen, presumed lost), Philippines, Mindanao, Lake Lanao, Camp Keithly; Copeland s.n., March 1905 (PNH not seen, presumed lost), Philippines, District of Zamboanga, San Ramon, March 1905.

Description taken from Merrill (1908): "Tuber irregular, at least 15 cm diameter, brown or greyish, unarmed. Stems several, diffusely branched, slender at least 60 cm long grey or brown, the branches elongate, brown furfureaceous and angled when young. Leaves lanceolate or narrow-lanceolate, 5 by 0.6 to 10 by 1.8 cm, base and apex gradually narrowed, tip acute or blunt; midrib prominent beneath, lateral veins obscure, leathery; pale green when dry, somewhat shining. Petiole ± absent. Inflorescence slightly raised. Calyx 1 mm, truncate. Corolla 2 mm, slight ring of hairs at the middle. Anthers 0.7 mm. Style 1.2 mm. *Fruit* to 10 mm long, about 4 mm wide at base gradually narrowed upwards, red, somewhat fleshy."

*Ecology & Habitat* — Unknown.

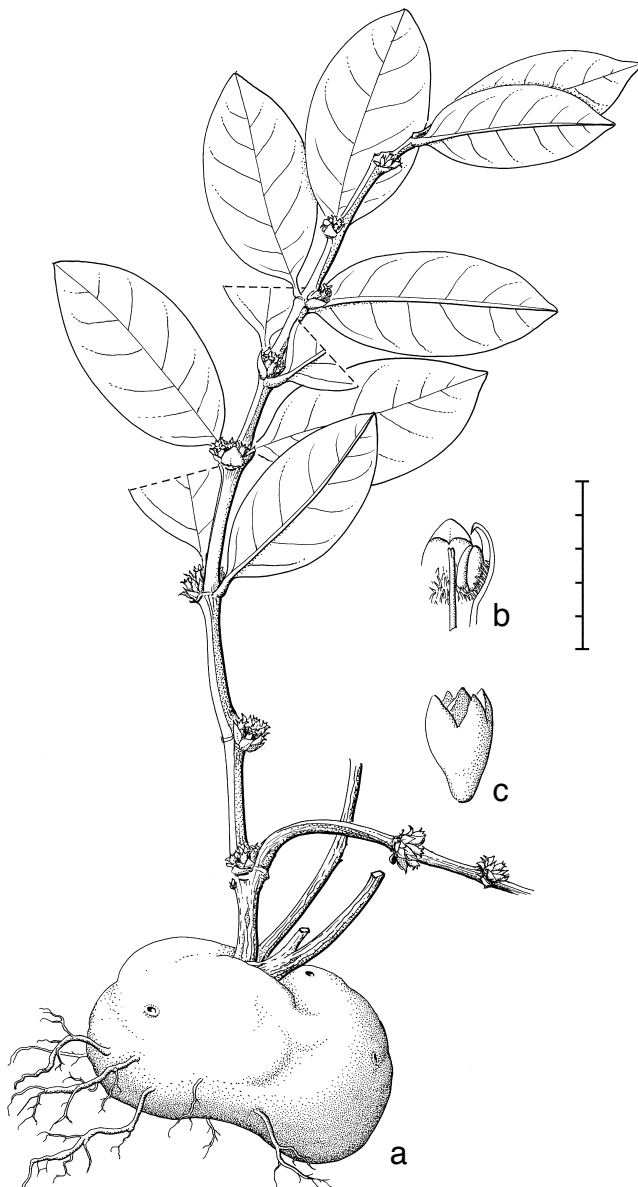
*Distribution* — Philippines (Mindanao).

*Note* — Originally distinguished by its narrow leaves and elongate fruits. We have seen none of the material mentioned by Merrill, which may be lost, and are therefore unable to give a view of the tenability of this species with regard to *H. mo-seleyanum* [14], *H. formicarum* [1] or most especially *H. puffii* [2]. The taxon appears to differ from the latter species in the combination of furfureaceous twigs, obscure secondary veins, a sparse ring of hairs in the corolla and a narrow fruit. Satellite imagery suggests that forest still survives near the type locality so recollecting the taxon would probably be feasible.

**b. *Hydnophytum stenophyllum* Valetton**

*Hydnophytum stenophyllum* Valetton (1927) 140. — Type: Schlechter 18173 (K not seen, presumed lost), Papua New Guinea, Madang Province, Finisterre Mts.

Description taken from Valetton (1927): "Tuber? Stem? Branch apices slender acute-quadrangular internodes short (10–20 mm) nodes not at all swollen (2–5 mm thick). Leaves less than subsessile (petiole 1–2 mm), linear-lanceolate (4–9 by 0.5–1.4 cm)



**Fig. 59** *Squamellaria vanuatuensis* Jebb & C.R.Huxley in Chomicki & Renner. a. Habit; b. flower; c. calyx (a: Bernardi 13238; b, c: Green RSNH 1274). — Scale bars: a = 3.5 cm; b, c = 5 mm. — Drawn by Rosemary Wise.

often slightly falcate gradually acute to apex, base attenuate and acute, softly coriaceous, margin strongly recurved, midrib prominent below, sunken above, veins inconspicuous. Flowers minute in axils, scarcely congregated, bracts small glabrous not encasing inflorescence. Calyx cupuliform, short. *Fruit* flask-shaped (4.5 mm long), calyx remains coronate. Pyrenes lanceolate-ovate (3 by 1 mm); apex attenuate-acute.”

Ecology & Habitat — Unknown.

Distribution — Papua New Guinea (Madang Province).

Note — Amongst the Valeton archive material at Leiden there was no drawing of *H. stenophyllum*, so the description is all that is available. The leaf and quadrangular stem would suggest a relationship to *H. linearifolium* [49], but the inflorescence appears to be sessile and not pedunculate, in this respect it is similar to *H. virgatum* below.

### c. *Hydnophytum subsessile* Valeton

*Hydnophytum subsessile* Valeton (1927) 142. — Type: *Lauterbach 3164* (B not seen, presumed lost), Papua New Guinea.

Description taken from Valeton (1927): “Tuber 9 cm diam. Branches thick (8 mm), bark smooth. Leaves subsessile, obtuse-ovate, base rounded. Inflorescences sessile.”

Ecology & Habitat — Unknown.

Distribution — Papua New Guinea (Sepik Province).

Note — This species is only very sparsely described in Valeton (1927), and there are no manuscript drawings. We have not seen the type, and the description is inadequate to identify it with a known taxon. There are no further details to a location.

### d. *Hydnophytum virgatum* Valeton

*Hydnophytum virgatum* Valeton (1927) 143. — Types: *Ledermann 11646, 11701, 11849* (B not seen, presumed lost), Papua New Guinea, East Sepik Province, Schrader Mountains.

Description taken from Valeton (1927): “Tuber small, single-stemmed? Branches long and slender, little branched, bark thick, black, branches sharply tetragonal, newest branches flattened (internodes 60 by 2–4 mm). Stipules minute, ovate. Leaves short-petiolate (3–6 mm); lamina narrow-lanceolate (5–9 by 1.5–2 cm), base and apex attenuate-acute, rigid

subcoriaceous, olive-green when dry, midrib prominent below, sunken above, remainder veinless. Flowers in cushion-like or tuberculate, sessile, minute aggregations. Bracts inconspicuous, glabrous. Calyx glabrous, short, disc overtopping it. Corolla tube about twice as long as calyx (3.5 mm overall), petals spreading and recurved a little from tube. From throat to insertion of anthers densely hairy, these shortly erect above, exerted from throat, spreading below. Anthers exerted, anthers and filaments equally long. Submature drupes oblong-ovate (4 mm), calyx coronate. Pyrenes ovoid, 3.5 by 1.75 mm, flattened, abaxial surface convex; apex obtuse; base rounded.”

Ecology & Habitat — Forest, at 2070 m.

Distribution — Papua New Guinea, Schrader Mts.

Note — We have not seen the specimens mentioned by Valeton, and have been unable to satisfactorily understand this species. In its narrow leaves and sessile inflorescence, it matches *H. stenophyllum*, another little known species.

### e. *Hydnophytum zippelianum* Becc.

*Hydnophytum zippelianum* Becc (1885) 174, t. 54: 8–11. — Type: *Zippelius s.n.* (L), New Guinea?

Base tuberous? *Leaves* lanceolate-elliptic, 8 by 2.1 cm, apex and base attenuate-acute, petiole 0.6–0.9 cm. Inflorescence sessile in axils. Corolla lobes long. Flower illustrated in Beccari (1885: t. 54).

Ecology & Habitat — Unknown.

Note — Type locality uncertain, possibly New Guinea. This species is illustrated by Beccari, and we have seen the Zippel collection, however, since the locality is dubious, and it equates to no other species, we have left it as little known. Interestingly *H. stenophyllum*, *H. virgatum* and *H. sp.1*, three other little known species share the combination of narrow leaf and sessile or shortly pedunculate inflorescence.

### f. *Hydnophytum* sp. 1 — Fig. 60

*Tuber* unknown. *Stem* to 60 cm or more; internodes to 3–7 by 0.2–0.6 cm. Lamina lanceolate, ± falcate; 10 by 1.3 to 15 by 2.6 cm; apex acute-acuminate, base cuneate; midrib prominent below, veins c. 8 each side; coriaceous in texture, stipules

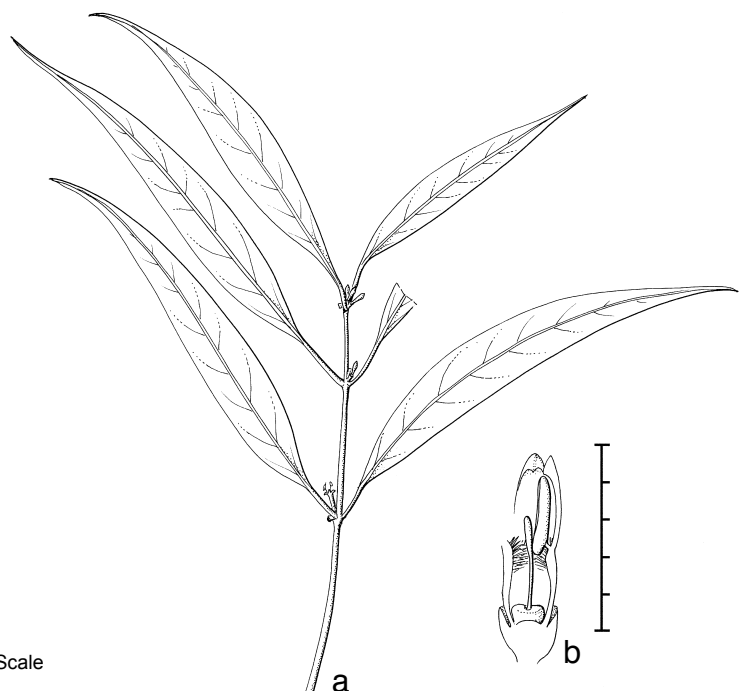


Fig. 60 *Hydnophytum* sp. 1. a. Shoot; b. flower (Janowski 68). — Scale bars: a = 5 cm; b = 5 mm. — Drawn by Rosemary Wise.



unknown; petiole 1–1.3 cm. Inflorescence paired, pedunculate; to 4 mm long. Flower [1], calyx 1.5 mm, entire at same level as disc; corolla tube 2.5 mm, lobes narrow, 2.5 mm long, a ring of hairs within the mouth of the tube 1 mm broad; anthers 2.5 mm long, exserted. Pollen 53 µm diam, reticulation large, brochi 3–4 µm, lacking vesicles; style scarcely exserted from tube. *Fruit* to 4 by 3 mm with prominent calyx remains.

**Ecology & Habitat** — Unknown.

**Distribution** — Indonesia, West Papua Province, Manokwari, middle Legari R., *Janowski* 68 (L).

**Note** — Only the single collection is known. The combination of petiolate, lanceolate leaves and shortly pedunculate inflorescences fits no other species, and Valeton prepared a manuscript name 'falcatum'. The paucity of the available material makes us cautious to establish a new species.

## SPECIES EXCLUDENDA

a. *Hydnophytum beccarii* K.Schum. (1888) 221. — Type: *Hollrung* 238 (not seen, presumed lost), New Guinea. = ***Psychotria leptothyrsa*** Miq. (1869) 208; Sohmer (1988) 157. — *Psychotria beccarii* (K.Schum.) K.Schum. in K.Schum. & Hollrung (1889) 135.

b. *Hydnophytum costatum* Drake (1895) 240. — Type: *Balansa* 685 (P), Indochina. = ***Scyphiphora hydrophyllacea*** C.F. Gaertn. (1805) 91, t. 196; Pit. (1923) 280.

c. *Hydnophytum dipteropodum* (Lauterb. & K.Schum.) Valeton (1927) 130 (as '*diplopoda*'). — Type: *Lauterbach* 1056 (WRSL), Papua New Guinea, Madang, Gogol River, 24 Nov. 1890. — *Psychotria dipteropoda* K.Schum. & Lauterb. (1901) 576. = ***Psychotria dipteropoda*** K.Schum. & Lauterb.; Sohmer (1988) 90, f. 31.

**Note** — It is not clear why Valeton decided to transfer this species to *Hydnophytum*. The inflorescence is distinct, with a single, winged peduncle with three short fertile branches at its apex. Sohmer (1988) gives a photograph of the type (which we have not seen), demonstrating its quite distinct facies from *Hydnophytum*.

d. *Hydnophytum? lanceolatum* Miq. (1869) 257; Scheff. (1876) 31; F.Muell. (1875) 26; Becc. (1885) 175, 213, t. 54: 1–7. — Type: *Zippelius s.n.* (not seen), New Guinea. = non *Hydnophytinae*.

**Note** — Originally excluded from *Hydnophytum* by Beccari, who suggested it should belong to a new genus, we have not been able to trace any later publication, which places it into a genus. The illustration in Beccari (1885) shows a stem with large stipules, the inflorescences borne in both axils of a node, and the flowers as 5-lobed. Beccari reports the material as too fragmentary for the establishment of a new genus.

e. *Hydnophytum wilsonii* Horne ex Baker (1883) 365; Horne (1881) 263, *nom. nud.*; Drake (1890) 200. — Type: *Horne* 1139 (K), Fiji. — ***Squamellaria wilsonii*** (Horne ex Baker) Becc. (1884) 92; (1885) t. 46: 13–21; (1886) 229. = ***Squamellaria imberbis*** (A.Gray) Becc. (1886) 228; Jebb (1991b) 55.

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## REFERENCES

- Abdullah H, Pihie AHL, Hohmann J, et al. 2010. A natural compound from *Hydnophytum formicarium* induces apoptosis of MCF-7 cells via up-regulation of Bax. *Cancer Cell International* 10: 14. doi: <https://doi.org/10.1186/1475-2867-10-14>.
- Andersson L. 2002. Relationships and generic circumscriptions in the *Psychotria* complex (Rubiaceae, Psychotriaceae). *Systematics and Geography of Plants* 72: 167–202.
- Andersson L, Rova JHE. 1999. The rps16 intron and the phylogeny of the Rubioideae (Rubiaceae). *Plant Systematics and Evolution* 214: 161–186.
- Bachman S, Moat J, Hill AW, et al. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117–126.
- Baillon HE. 1880. *Historie des Plantes*. Vol. 7. Hachette & Cie, Paris.
- Baker JG. 1883 '1884'. Recent additions to our knowledge of the flora of Fiji. *Journal of the Linnean Society Botany* 20: 358–373.
- Beccari O. 1884–1886. *Malesia*. Vol. 2 (piante ospitatrici). Tip. del R. Istituto Sordo-Muti, Genoa.
- Bentham G. 1843. Enumeration of the plants collected by R.B. Hinds Esq., and by Mr. Barclay in the Feejee Islands, Tanna, New Ireland and New Guinea: to which are added a few species gathered in Amboyna by Mr. Barclay. *The London Journal of Botany* 2: 211–240.
- Bentham G, Hooker JD. 1873. *Genera plantarum*. Vol. 2. Reeve & Co., London.
- Blume CL. 1826. *Bijdragen tot de flora van Nederlandsch Indië*. Ter Lands Drukkerij, Batavia.
- Buckley RC (ed). 1982. *Ant-plant interactions in Australia*. Junk, The Hague.
- Burck MW. 1884. Sur l'organisation florale chez quelques Rubiacées. *Annales du Jardin botanique de Buitenzorg* 4: 12–87.
- Chomicki G, Renner SS. 2016. Evolutionary relationships and biogeography of the ant-epiphytic genus *Squamellaria* (Rubiaceae: Psychotriaceae) and their taxonomic implications. *PLoS ONE* 11 (3): e0151317. doi: <https://doi.org/10.1371/journal.pone.0151317>.
- Craib WG. 1934. *Flora Siamensis enumeratio*. Vol. 2. Siam Society, Bangkok.

- Darwin SP. 1979. A synopsis of the indigenous genera of Pacific Rubiaceae. *Allertonia* 2: 1–44.
- De Candolle AP. 1830. *Prodromus systematis naturalis regni vegetabilis*. Vol. 4. Treuttel & Würtz, Paris.
- De Freycinet LCD. 1826–1830. *Voyage autour du monde, entrepris par ordre du roi*. Chez Pillet Aîné, Paris.
- Dietrich DNF. 1839. *Synopsis plantarum*. Vol. 1. BF Voigt, Weimar.
- Don G. 1834. A general history of the dichlamydeous plants. Vol. 3. JG & F Rivington, London.
- Drake del Castillo E. 1890. *Illustrationes florae insularum maris Pacifici*. Vol. 6. Masson, Paris.
- Drake del Castillo E. 1895. Contribution a la flore du Tonkin: Énumération des Rubiacées trouvées au Tonkin par M. Balansa en 1885–89. *Journal de botanique* 9: 234–241.
- Elmer ADE. 1911. New and noteworthy Rubiaceae. *Leaflets of Philippine Botany* 3: 971–1046.
- Elmer ADE. 1913. Rubiaceae from Mount Urdaneta. *Leaflets of Philippine Botany* 5: 1855–1905.
- Endlicher SFL. 1838. *Genera plantarum secundum ordines naturales disposita*. Vol. 7. Fr. Beck Universitatis, Vienna.
- Forster PI. 2001. *Hydnophytum ferrugineum* (Rubiaceae: Hydnophytinae), a new species of ant-plant from Cape York Peninsula, Queensland. *Austrobaileya* 6 (1): 103–106.
- Fosberg FR. 1940. Melanesian vascular plants. *Lloydia: A Quarterly Journal of Biological Science* 3: 109–124.
- Gaertner, C.F. 1805. *Supplementum carpologiae: seu continuati operis Josephi Gaertner de Fructibus et seminibus plantarum*. Sumtibus Carol. Frid. Enoch Richter Bibliopolae Lipsiensis.
- Gibbs LS. 1909. A contribution to the montane flora of Fiji (including cryptogams) with ecological notes. *The Journal of the Linnean Society Botany* 39: 130–212.
- Govaerts R, Ruhsam M, Andersson L, et al. 2015. World checklist of Rubiaceae. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; <http://apps.kew.org/wcsp/> (accessed 26 Feb. 2015).
- Gray A. 1858. Notes upon some Rubiaceae, collected in the United States south sea exploring expedition under Captain Wilkes, with characters of new species. *Proceedings of the American Academy of Arts and Sciences* 4: 33–50.
- Gray A. 1862a. Notes upon a portion of Dr. Seeman's recent collection of dried plants gathered in the Feejee Islands. *Proceedings of the American Academy of Arts and Sciences* 5: 314–321.
- Gray A. 1862b. *Plantae Vitiensis Seemannianae*. Remarks on the plants collected in the Vitian or Fijian islands by Dr Berthold Seemann. *Bonplandia, Zeitschrift für die gesammte Botanik* 10: 34–37.
- Guppy HB. 1887. *The Solomon Islands and their natives*. Sonnenschein, Lowrey & Co., London.
- Hasskarl JC. 1844. *Catalogus plantarum in horto botanico Bogoriensi cultarum alter*. Ter Lands-Drukkerij, Batavia.
- Hasskarl JC. 1866. *Neuer schlüssel zu Rumph's herbarium Amboinense*. Schmidt, Halle.
- Henschel AWET. 1833. *Clavis Rumphiana botanica et zoologica: accedunt vita G.E. Rumphii, Plinii indicii, specimenque materiae medicae Amboinensis*. Breslau, Vratislaviae.
- Holthuis LB, Husson AM. 1973. *Jonkheer Drs. Willem Cornelis van Heurn (1887–1972)*. *Zoologische Bijdragen* 16: 3–67.
- Holthuis LB, Lam HJ. 1942. A first contribution to our knowledge of the flora of the Talaud islands and Morotai. *Blumea* 5: 93–256.
- Hooker JD. 1881. *The flora of British India*. Vol. 3 (Caprifoliaceae to Apocynaceae). Reeve & Co., London.
- Hooker JD. 1892. Tab 7218 *Hydnophytum forbesii* native of New Guinea. *Curtis's Botanical Magazine*. Vol. 118. Reeve & Co., London.
- Hooker JD. 1894. Tab 7343 *Hydnophytum longiflorum* native of the Fiji Islands. *Curtis's Botanical Magazine*. Vol. 120. Reeve & Co., London.
- Horne J. 1881. *A year in Fiji*. Stanford, London.
- Huxley CR. 1976. The ant-plants Myrmecodia and *Hydnophytum* (Rubiaceae). MSc thesis, University of Papua New Guinea.
- Huxley CR. 1978. The ant-plants Myrmecodia and *Hydnophytum* (Rubiaceae), and the relationships between their morphology and occupants, physiology and ecology. *The New Phytologist* 80: 231–268.
- Huxley CR. 1993. The tuberous epiphytes of the Rubiaceae 6: A taxonomic history of the Hydnophytinae. *Blumea* 37: 335–340.
- Huxley CR, Jebb MHP. 1991a. The tuberous epiphytes of the Rubiaceae 1: A new subtribe – The Hydnophytinae. *Blumea* 36: 1–20.
- Huxley CR, Jebb MHP. 1991b. The tuberous epiphytes of the Rubiaceae 2: The new genus *Anthorrhiza*. *Blumea* 36: 21–41.
- Huxley CR, Jebb MHP. 1991c. The tuberous epiphytes of the Rubiaceae 3: A revision of Myrmephytum to include Myrmedomia. *Blumea* 36: 43–52.
- Huxley CR, Jebb MHP. 1993. The tuberous epiphytes of the Rubiaceae 5: A revision of Myrmecodia. *Blumea* 37: 271–334.
- IPNI. 2015. The International Plant Names Index. Published on the Internet <http://www.ipni.org> (accessed 25 Feb. 2015).
- IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. 2nd ed. IUCN, Gland, Switzerland.
- Jack W. 1823. Account of the *Lansium* and some other genera of Malayan plants. *Transactions of the Linnean Society of London* 14: 114–130.
- Janzen DH. 1974. Epiphytic myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. *Biotropica* 6 (4): 237–259.
- Jebb MHP. 1985. Taxonomy and tuber morphology of the rubiaceous ant-plants. DPhil thesis, University of Oxford.
- Jebb MHP. 1991a. Cavity structure and function in the tuberous Rubiaceae. In: Huxley CR, Cutler DF (eds), *Ant-plant Interactions*: 374–389. Oxford University Press, Oxford.
- Jebb MHP. 1991b. The tuberous epiphytes of the Rubiaceae 4: A revision of *Squamellaria*. *Blumea* 36: 53–61.
- Jebb MHP. 1993. *Anthorrhiza camilla*, a new species of rubiaceous ant-plant. *Blumea* 37: 341–344.
- Kiehn M. 1996. Chromosomes of Rubiaceae occurring in Malesia, the Philippines, New Guinea, and the Pacific. *Opera Botanica Belgica* 7: 249–260.
- Korthals PW. 1851. *Overzicht der rubiaceën van de Nederlandsch-oost-indische kolonien*. *Nederlandsch Kruidkundig Archief* 2 (4): 145–269.
- Kumar V, Subramaniam B. 1987. Chromosome atlas of flowering plants of the Indian subcontinent. Botanical Survey of India, Calcutta.
- Kurz WS. 1877. *Forest Flora of British Burma*. Vol. 2 (Caprifoliaceae to Filices). Office of the superintendent of Government Printing, Calcutta.
- Lam HJ. 1928. *Fragmenta Papuana IV: Meervlakte en heuvelvoet*. *Natuurkundig tijdschrift voor Nederlandsch-Indië* 88: 187–227.
- Lam HJ. 1945. *Fragmenta Papuana* [observations of a naturalist in Netherlands New Guinea] translated by Perry LM. *Sargentia: Contributions from the Arnold Arboretum of Harvard University* 5: 1–197.
- Low YW, Sugau JB, Wong KM. 2016. *Hydnophytum puffii* (Rubiaceae: Psychotriaceae), a new ant-plant from Sabah, Malaysian Borneo. *Plant Ecology and Evolution* 149 (1): 123–130.
- Margono BA, Potapov PV, Turubanova S, et al. 2014. Primary forest cover loss in Indonesia over 2000–2012. *Nature Climate Change* 4: 730–735. doi: <https://doi.org/10.1038/nclimate2277>.
- Merrill ED. 1907. The flora of Mount Halcon. *The Philippine Journal of Science, C Botany* 2: 251–309.
- Merrill ED. 1908. New Philippine plants from the collections of Mary Strong Clemens I. *The Philippine Journal of Science, C Botany* 3: 129–165.
- Merrill ED. 1913. *Plantae Wenzeliana*. *The Philippine Journal of Science, C Botany* 8: 363–390.
- Merrill ED. 1915. Studies on Philippine Rubiaceae II. *The Philippine Journal of Science, C Botany* 10: 99–144.
- Merrill ED, Perry LM. 1945. *Plantae Papuanae Archboldiana* XV. *Journal of the Arnold Arboretum* 26: 1–36.
- Miquel FAG. 1855. *Flora van Nederlandsch Indië*. Van der Post, Amsterdam.
- Miquel FAG. 1869. *Annales musei botanici lugduno-batavi*. Vol. 4. Van der Post, Amsterdam.
- Moore S. 1927. New Rubiaceae collected by Mr. L. Brass in British New Guinea. *Journal of Botany* 65: 265–272.
- Nepokroeff N, Bremer B, Sytsma KJ. 1999. Reorganization of the genus *Psychotria* and tribe Psychotriaceae (Rubiaceae) inferred from ITS and rbcL sequence data. *Systematic Botany* 24: 5–27.
- Parham JW. 1964. *Plants of the Fiji Islands*. Government Press, Suva.
- Parham JW. 1972. *Plants of the Fiji Islands, second edition*. The Government Printer, Suva.
- Pitard J. 1923. Rubiacées. In: Lecomte H, *Flore générale de l'Indochine* 3 (2): 145–288. Masson & Cie, Paris.
- Razafimandimbison SG, Taylor CM, Wikström N, et al. 2014. Phylogeny and generic limits in the sister tribes Psychotriaceae and Palicoureae (Rubiaceae): evolution of schizocarps in *Psychotria* and origins of bacterial leaf nodules of the Malagasy species. *American Journal of Botany* 101: 1102–1126.
- Rechinger K. 1912. *Plantae novae Papuanae*. *Feddes repertorium novarum specierum regni vegetabilis* 11: 179–187.
- Rechinger K. 1913. *Botanische und zoologische ergebnisse einer wissenschaftlichen forschungsreise nach den samoainseln*. *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse* 89: 443–708.
- Richard A. 1834. *Mémoire sur la famille des Rubiacées*. In: *Memoires de la Société d'Histoire Naturelle de Paris* 5: 81–304.
- Ridley HN. 1923. *The Flora of the Malay Peninsula*. Vol. 2. Reeve & Co., London.

- Rivers MC, Bachman SP, Meagher TR, et al. 2010. Subpopulations, locations and fragmentation: applying IUCN red list criteria to herbarium specimen data. *Biodiversity and Conservation* 19 (7): 2071–2085.
- Robbrecht E. 1996. Chromosomes of Rubiaceae occurring in Malesia, the Philippines, New Guinea, and the Pacific. *Opera Botanica Belgica* 7: 249–260.
- Rumphius GE. 1750. *Herbarium Amboinense* 11 (16). Franciscum Changuion, Joannem Catuffe, Hermannum Uytwerf, Amsterdam.
- Scheffer RHCC. 1876. Énumération des plantes de la Nouvelle-Guinée, avec description des espèces nouvelles. *Annales du Jardin botanique de Buitenzorg* 1: 1–60.
- Schumann KM. 1888. Die Flora des Deutschen ost-asiatischen Schutzgebietes. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 9: 189–223.
- Schumann KM. 1891. In: Engler A, Prantl K, Die natürlichen Pflanzenfamilien 4 (4): 1–156.
- Schumann KM, Hollrung UM. 1889. Die Flora von Kaiser Wilhelms Land Kommissias-Verlag. Asher & Co., Berlin.
- Schumann KM, Lauterbach K. 1901. Die Flora der deutschen Schutzgebiete in der Südsee. Verlag van Gebrüder Borntraeger, Leipzig.
- Schumann KM, Lauterbach K. 1905. Nachträge zur Flora der deutschen Schutzgebiete in der Südsee (mit Ausschluss Samoa's und der Karolinen). Verlag van Gebrüder Borntraeger, Leipzig.
- Seemann B. 1861. *Plantae Vitiensis*. Bonplandia, Zeitschrift für die gesammte Botanik 9: 253–262.
- Seemann B. 1862. Viti: An account of a government mission to the Vitian or Fijian Islands. Macmillan & Co., Cambridge.
- Seemann B. 1866. *Flora vitiensis: a description of the plants of the Viti or Fiji Islands, with an account of their history, uses, and properties*. Reeve & Co., London.
- Shattuck SO. 1992. Review of the Dolichoderine ant genus *Iridomyrmex* May with descriptions of three new genera (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society* 31: 13–18.
- Shearman PL, Ash J, Mackey B, et al. 2009. Forest conversion and degradation in Papua New Guinea 1972–2002. *Biotropica* 41 (3): 379–390. doi: <https://doi.org/10.1111/j.1744-7429.2009.00495.x>.
- Smith AC. 1988. *Flora Vitiensis Nova* volume 4. Pacific Tropical Botanic Garden, Hawaii.
- Sohmer S. 1988. The nonclimbing species of the genus *Psychotria* (Rubiaceae) in New Guinea and the Bismark archipelago. *Bishop Museum Bulletin in Botany* 1. Bishop Museum Press, Honolulu.
- Sprengel K. 1825. *Systema vegetabilium* 1. Librariae Dieterichianae, Göttingen.
- The Plant List. 2015. Version 2. Published on the Internet; <http://www.the-plantlist.org/> (accessed 25 Feb. 2015).
- Treub M. 1883. Sur le Myrmecodia echinata Gaudichaud. *Annales du Jardin Botanique de Buitenzorg* 3: 129–157.
- Treub M. 1888. Nouvelles recherches sur le Myrmecodia de Java. *Annales du Jardin Botanique de Buitenzorg* 7: 191–221.
- Turland NJ, Wiersema JH, Barrie FR, et al. (eds.). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). *Regnum Vegetabile* 159. Glashütten, Koeltz Botanical Books.
- Valeton T. 1911. Rubiaceae. *Nova Guinea* 8: 437–519.
- Valeton T. 1912a. *Hydnophytum spathulatum*. *Icones Bogorienses* 4: 129–130, t. 340.
- Valeton T. 1912b. Rubiaceae. *Nova Guinea* 8: 772–774.
- Valeton T. 1927. Die Rubiaceae von Papuasien II (*Hydnophytum*). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 61: 127–143.
- Van Royen P. 1983. *The Alpine Flora of New Guinea*. Vol. 4. Cramer Verlag, Lehre.
- Van Steenis-Kruseman MJ. 1950. *Cyclopaedia of collectors*. In: Van Steenis CGGJ (ed), *Flora Malesiana* I, 1. Noordhoff-Kolff N.V., Jakarta.
- Veldkamp JF, Vink W, Frodin DG. 1988. Ledermann's and some other German localities in Papua New Guinea. *Flora Malesiana Bulletin* 10 (1): 32–38.
- Von Gaertner CF. 1805 '1807'. *De fructibus et seminibus plantarum* volume 3, supplementum carpologiae. Carol FE Richter, Leipzig.
- Von Mueller FJH. 1875. Descriptive notes on Papuan plants volume 2: 17–34. George Skinner, acting Government printer, Melbourne.
- Warburg O. 1891. Beiträge zur Kenntnis der papuanischen Flora. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 13: 230–455.
- Warburg O. 1894. *Plantae Hellwigianae*. Beiträge zur Flora von Kaiser Wilhelms-Land. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 18: 184–212.
- Whitten AJ. 1981. Notes on the ecology of *Myrmecodia tuberosa* Jack on Siberut Island, Indonesia. *Annals of Botany* 47: 525–526.
- Willis F, Moat J, Paton A. 2003. Defining a role for herbarium data in Red List assessments: a case study of *Plectranthus* from eastern and southern tropical Africa. *Biodiversity and Conservation* 12: 1537–1552.
- Wistuba A, Zimmermann U, Marwinski D, et al. 2014. *Hydnophytum caminiferum*, eine einzigartige neue *Hydnophytum*-Art von der Vogelkop-Halbinsel in West Papua (Indonesien). *Das Taublatt* 78: 45–50. [http://www.bio-schmidhol.ch/domains/bio-schmidhol\\_ch/data/free\\_docs/Taublatt\\_April\\_2014.pdf](http://www.bio-schmidhol.ch/domains/bio-schmidhol_ch/data/free_docs/Taublatt_April_2014.pdf).

## IDENTIFICATION LIST

Specimens with a collector name and number can be identified by the following numbers or codes after the colons:

1 = <i>H. formicarum</i>	11h = <i>H. petiolatum</i> aff.	29 = <i>H. dauloense</i>	45 = <i>H. mamberamoense</i>
2 = <i>H. puffii</i>	12 = <i>H. trichomanes</i>	30 = <i>H. fusiforme</i>	46 = <i>H. orichalcum</i>
3 = <i>H. morotaiense</i>	13 = <i>H. grandifolium</i>	31 = <i>H. hailans</i>	47 = <i>H. tetrapterum</i>
4 = <i>H. ovatum</i>	14 = <i>H. moseleyanum</i>	32 = <i>H. mayuense</i>	48 = <i>H. albertisii</i>
5 = <i>H. spathulatum</i>	15 = <i>H. alborivide</i>	33 = <i>H. myrtifolium</i>	49 = <i>H. linearifolium</i>
6 = <i>H. tortuosum</i>	16 = <i>H. buxifolium</i>	34 = <i>H. reevii</i>	50 = <i>H. radicans</i>
7 = <i>H. ellipticum</i>	17 = <i>H. caminiferum</i>	35 = <i>H. terrestris</i>	51 = <i>H. grandiflorum</i>
8 = <i>H. ferrugineum</i>	18 = <i>H. confertifolium</i>	36 = <i>H. archboldianum</i>	52 = <i>H. longiflorum</i>
9 = <i>H. lauterbachii</i>	19 = <i>H. davisii</i>	37 = <i>H. magnirubrum</i>	53 = <i>S. guppyana</i>
10 = <i>H. magnifolium</i>	20 = <i>H. decipiens</i>	38 = <i>H. minirubrum</i>	54 = <i>S. kajewskii</i>
11 = <i>H. petiolatum</i>	21 = <i>H. kebarensis</i>	39 = <i>H. bracteatum</i>	55 = <i>S. vanuatuensis</i>
11a = var. <i>petiolatum</i>	22 = <i>H. microphyllum</i>	40 = <i>H. cordifolium</i>	LKa = <i>H. angustifolium</i>
11b = var. <i>argentatum</i>	23 = <i>H. multituberosum</i>	41 = <i>H. dentrecastense</i>	LKb = <i>H. stenophyllum</i>
11c = var. <i>auridemans</i>	24 = <i>H. pauper</i>	42 = <i>H. hellwigii</i>	LKc = <i>H. subsessile</i>
11d = var. <i>contortum</i>	25 = <i>H. ramispinum</i>	42.1 = <i>H. hellwigii</i> aff.	LKd = <i>H. virgatum</i>
11e = var. <i>lacum</i>	26 = <i>H. valetonii</i>	43 = <i>H. heterophyllum</i>	LKe = <i>H. zippelianum</i>
11f = var. <i>ledermanni</i>	27 = <i>H. vitis-idaea</i>	44 = <i>H. lucidulum</i>	LKf = <i>H. sp.1</i>
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*papuanum* Becc. 14  
*parvifolium* Valeton 42  
**pauper** Valeton ex Jebb & C.R.Huxley 24  
*perangustum nom. nud.* 2

### Hydnophytum (cont.)

*petiolatum* Becc. 11  
var. **argentatum** Jebb & C.R.Huxley 11b  
var. **auridemens** Jebb & C.R.Huxley 11c  
var. **contortum** (Merr. & L.M.Perry) Jebb & C.R.Huxley 11d  
var. **lacum** Jebb & C.R.Huxley 11e  
var. **ledermannii** (Valeton) Jebb & C.R.Huxley 11f  
var. **nigrescens** (Merr. & L.M.Perry) Jebb & C.R.Huxley 11g  
var. *petiolatum* 11a  
*philippinense* Becc. 14  
*puffii* Y.W.Low, Sugau & K.M.Wong 2  
*punamense* Lauterb. 42  
*radicans* Becc. 50  
*ramispinum* Merr. & L.M.Perry 25  
**reevii** Jebb & C.R.Huxley 34  
*robustum* Rech. 14  
*selebicum* Becc. 1  
*simplex* Becc. 50  
sp. 1 Huxley 8  
sp. 1 LK-f  
*spatulatum* Valeton 5  
*stenophyllum* Valeton LK-b  
*stewartii* Fosberg 14  
*subfalcatifolium* Valeton 14  
*subnormale* K.Schum. 50  
*subrotundum* Valeton 14  
*subsessile* Valeton LK-c  
*sumatranum* Becc. 1  
*tenuiflorum* Becc. 52  
**terrestris** Jebb & C.R.Huxley 35  
*tetrapterum* Becc. 47  
*tortuosum* Becc. 6  
**trichomanes** Jebb & C.R.Huxley 12  
*vaccinifolium* P.Royen 15  
**valetonii** Jebb & C.R.Huxley 26  
*vanuatuense* Jebb & C.R.Huxley 55  
*virgatum* Valeton LK-d  
*vitis-idaea* Merr. & L.M.Perry 27  
*wilkinsonii* Horne ex Baker 52  
*wilsonii* Horne excl.-e  
*zippelianum* Becc. LK-e  
*Lasiostoma formicarum* (Jack) Spreng. 1  
*loranthifolium* Benth. 14  
*oblongum* Benth. 14  
*Myrmecodia inermis* auct. 1  
*vitiensis* Seem. 51  
*Nidus formicarum niger* Rumph. 1  
*Psychotria dipteropoda* K.Schum. & Lauterb. excl.-c  
*leptothyrsa* Miq. excl.-a  
*Scyphiphora hydrophyllacea* C.F.Gaertn. excl.-b  
*Squamellaria guppyana* (Becc.) Chomicki 53  
*imberbis* (A.Gray) Becc. excl.-e  
*jebbiana* Chomicki 51  
*kajewskii* (Merr. & L.M.Perry) Chomicki 54  
*tenuiflora* (Becc.) Chomicki 52  
*vanuatuensis* Jebb & C.R.Huxley 55  
*wilkinsonii* (Horne ex Baker) Chomicki 52  
*wilsonii* (Horne ex Baker) Becc. excl.-e