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TUBEROUS, EPIPHYTIC, RUBIACEOUS MYRMECOPHYTES OF SINGAPORE

A. F. S. L. Lok[1] and **H. T. W. Tan**[1*]
[1]*Department of Biological Sciences, National University of Singapore*
14 Science Drive 4, Singapore 117543, Republic of Singapore
([*]Corresponding author: dbsttw@nus.edu.sg)

INTRODUCTION

There are five known genera of tuberous, epiphytic myrmecophytes belonging to the tribe Psychotrieae, subtribe Hydnophytinae of the family Rubiaceae. They are *Anthorrhiza*, *Hydnophytum*, *Myrmecodia*, *Myrmephytum* and *Squamellaria* (Huxley & Jebb, 1991). These genera are found in South East Asia to the Pacific islands of Fiji, Vanuatu and Solomon Islands, with the highest diversity in New Guinea.

Hydnophytum has the widest distribution, extending from the Andaman Islands, South Thailand, Myanmar, Cambodia, Vietnam, Malaysia, throughout the entire Indonesian Archipelago, the Philippines, Papuasia and its associated islands, the Solomon Islands, Vanuatu, Fiji, and the Cape York Peninsula in Australia (Huxley & Jebb, 1991). *Hydnophytum* means "truffle plant" and is much more xeromorphic than *Myrmecodia*, being able to withstand much more desiccating (xeric) conditions (Huxley, 1978).

Myrmecodia has the second-widest distribution, with its species are found in Malaysia, throughout the entire Indonesian Archipelago, the Philippines, Papuasia and its associated islands, the Solomon Islands, and the Cape York Peninsula in Australia (Huxley & Jebb, 1993). *Myrmecodia* means "ant-house", as their tubers are much more highly specialised and adapted to ant occupation compared to *Hydnophytum* (Huxley, 1978).

Only *Hydnophytum formicarum* (Fig. 1) and *Myrmecodia tuberosa* (Fig. 2) were recorded to occur in Singapore. The former is now listed as nationally critically endangered while the later is nationally extinct (Tan et. al., 2008). These species have long been of interest to botanists and ecologists owing to their symbiotic association with ants and these charismatic plants have recently gained favour with horticulturist-hobbyists because of their bizarre shapes and forms.

Fig. 1. *Hydnophytum formicarum* in cultivation. (Photograph by: Ang Weijen).

Fig. 2. *Myrmecodia tuberosa* on a cicada tree (*Ploiarium alternifolium*) in Bako National Park, Sarawak, Malaysia. (Photograph by: Alvin Francis Lok Siew Loon).

Hydnophytum and *Myrmecodia* species are usually associated with *Iridomyrmex* ant species but also to a lesser extent, other ant species of the genera *Anaplolepis*, *Camponotus*, *Crematogaster*, *Pedomyrma*, *Pheidole*, *Polyrachis*, *Monomorium*, *Technomyrex*, *Turneria*, and *Vollenhovia* (Huxley, 1978). Other organisms found in ant-plants include nematodes of the genus *Rhabditis*, as well as mites, dipteran larvae, and small brethid beetles which are encountered on the debris within the plant cavities. Two species of fungus, an unidentified monilialine fungus as well as *Arthrocladium* species are usually found in the cavity surfaces of *Myrmecodia tubersa* and have only been found once in *Hydnophytum formicarum*.

As mentioned above, these plants have a modified stems that house ants for protection and nutrients, and in return provide their ant colonisers with shelter and a source of food. In *Hydnophytum formicarum* and *Myrmecodia tuberosa*, the tubers are formed, after germination, by the swelling of the seedling's hypocotyl to about 0.5 cm wide during which numerous cortical vascular bundles develop in a ring around the central first vascular tissue strand (Huxley, 1978). Later, the cylindrical phellogen then develops in the cortical parenchyma beneath the ring of peripheral vascular bundles. This cylinder is closed and bent at the upper or shoot end (like an inverted sock), with its long axis parallel to the shoot axis. The shoot end cuts through the central first vascular tissue strand during development. The lower or root-end of the phellogen cylinder abuts upon the epidermis at the tuber's base. A cell layer lining the inner side of the phellogen cylinder suberises, and the tissues inside the cylinder, together with the first vascular tissue strand at the hypocotyl's centre dies, and is removed by the inhabiting ants, so forming the first cavity within the hypocotyl.

In lowland *Hydnophytum* species, these cavities are simple with no differentiation of their chambers (Huxley, 1978). The cavities are shortly branched, but the branches do not interconnect either within or between cavities. The central part of the cavity lining is usually smooth with the extremities warty. New cavities that are added laterally through growth, giving these plants distinctly lobed tubers.

The cavities of lowland *Myrmecodia* species are differentiated into those with distinct shapes, surface characteristics and functions (Huxley, 1978). The honeycombed cavities also possibly insulate the inner parts of the tubers, and occur under surfaces with openings where air can enter the tubers for ventilation, providing some advantage for their ant guests. The ant occupants, house their larvae and pupae in the smooth-walled chambers and leave waste material, and insect parts where there are small, white, lenticel-like swellings referred to as warts, which are highly absorptive. These

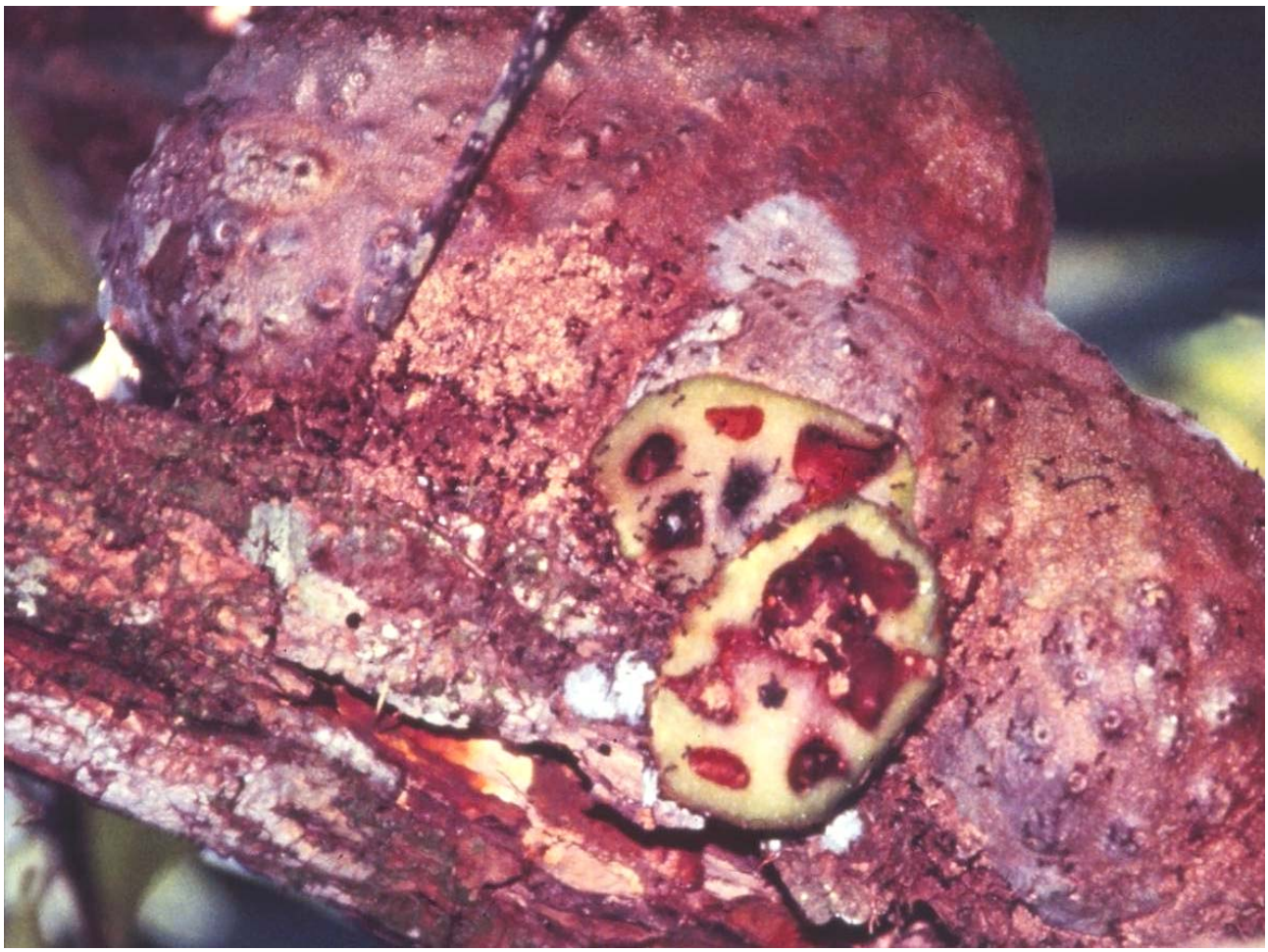

Fig. 3. Cross-section of a *Hydnophytum formicarum* tuber, showing the cavities and ant inhabitants. (Photograph by: Hugh Tan Tiang Wah).

Fig. 4. *Hydnophytum formicarum* buds and flowers. (Photograph by: Hugh Tan Tiang Wah).

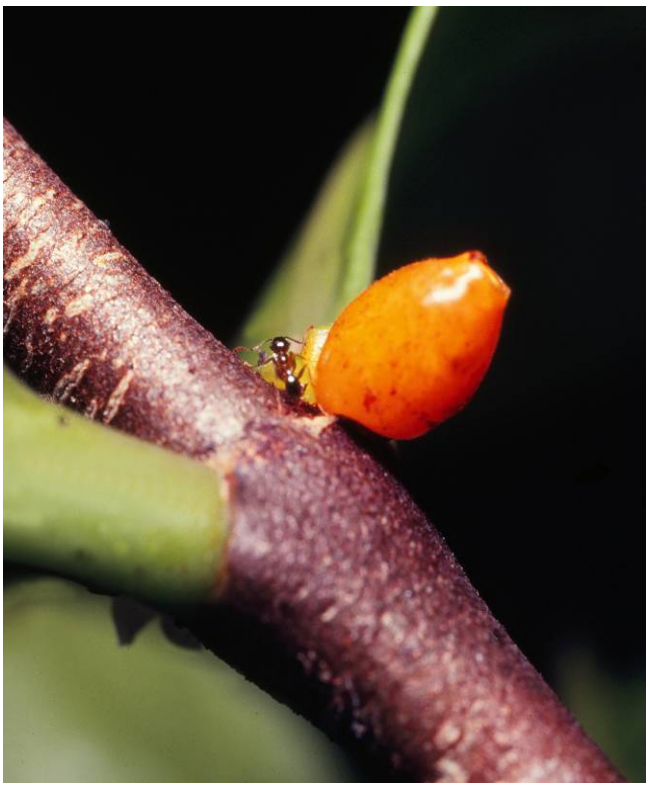

Fig. 5. *Hydnophytum formicarum* fruit with ant. (Photograph by: Hugh Tan Tiang Wah).

Fig. 6. *Hydnophytum formicarum* growing on a *Garcinia* species tree, together with a young stag's horn fern (*Platycerium coronarium*) plant at the Nee Soon Swamp Forest. (Photography by: Claudia King Sheau Horng).

Table. 1. Previous Singapore collections of *Hydnophytum formicarum* Jack and *Myrmecodia armata* Jack deposited in the herbarium, Singapore Botanic Gardens (SING).

S/No.	Bar Code No.	Species	Locality	Year	Collector	Collector' No.
1	0030237	*Hydnophytum formicarum*	Jurong	1932	E. J. H. Corner	26154
2	0030238	*Hydnophytum formicarum*	Sg. Tempei	1891	J. F. Goodenough	s.n.
3	0030236	*Hydnophytum formicarum*	Pasir Panjang	1911	J. W. Anderson	186
4	0030235	*Hydnophytum formicarum*	Changi	1889	H. N. Ridley	303
5	0030234	*Hydnophytum formicarum*	Bajau	1890	H. N. Ridley	1617
6	0030232	*Hydnophytum formicarum*	Bukit Timah	1891	H. N. Ridley	s.n.
7	0030239	*Hydnophytum formicarum*	Sungei Murai	1891	H. N. Ridley	s.n.
8	0030233	*Hydnophytum formicarum*	Pulau Seletar	1892	H. N. Ridley	s.n.
9	0030231	*Hydnophytum formicarum*	Sungei Jurong	1897	H. N. Ridley	s.n.
10	0030230	*Hydnophytum formicarum*	Sungei Murai	1899	H. N. Ridley	s.n.
11	0090261	*Hydnophytum formicarum*	Pulau Pawai	2006	S. Yang	2006-62
12	0037549	*Myrmecodia tuberosa*	Bukit Timah	?	H. N. Ridley	s.n.
13	0037550	*Myrmecodia tuberosa*	Sungei Jurong	1892	H. N. Ridley	3854
14	0037552	*Myrmecodia tuberosa*	Sungei Jurong	1894	H. N. Ridley	s.n.
15	0037551	*Myrmecodia tuberosa*	Sungei Jurong	1896	H. N. Ridley	1067

nutrients are then absorbed via the warts and are then transported to the rest of the plant.

However because of their ant associations, both *Hydnophytum* and *Myrmecodia* species are self-pollinated, and the fruits are formed without pollinator visits, because these plants are fiercely guarded by their ant tenants (Benzing, 1990). Dispersal in both genera is well-documented, with both being predominantly ant-dispersed; the ants carrying the seeds of the plants away from the parent plant, and leaving them in ant tunnels along the bark of the tree, where they later germinate into a new plant. We have however observed the fruits being eaten by flowerpeckers (*Diacaeum* species) which usually perch on a nearby branch to minimise disturbance to the myrmecophyte or sometimes they even take the fruit in flight.

HISTORICAL RECORDS AND BIOLOGY

The form of *Myrmecodia tuberosa* that occurred in Singapore was "*Myrmecodia tuberosa* 'armata'", the informally named infraspecific taxon which is used to describe a variable continuum ranging from the Gulf of Annam through Java and Borneo (Huxley & Jebb, 1993). This infraspecific taxon is highly variable with regards to stem characters, with leaf venation being the characteristic feature of this form. It has been extinct in Singapore since the early 1900s having been last collected in 1896 from Sungei Jurong (Table 1). In the past, it usually occurred on trees near the sea at Jurong as well as in the Bukit Timah area (Table 1). According to Huxley & Jebb (1993), this infraspecific taxon is characteristically an epiphytic shrub, and observed to have an extremely spiny tuber, reaching 10–20 cm across with the spines arranged in linear ridges. The tuber is tunneled and regularly perforated to allow ants entry into the tuber as well as for ventilation of the cavity systems. Plants are observed to usually being single branched, but two or more branched individuals do occur. The stalked leaves have laminas which are elliptical to slightly lanceolate and leathery, reaching 7–25 cm long and 4–11 cm wide depending on the light environment, with 10–15 lateral veins. We have observed that plants growing in shadier conditions tend to have thinner laminas which are larger compared to plants growing in full sun which have more leathery but smaller laminas. The flowers are sessile usually solitary or few together and occurs at the cup shaped cavities in the stem. The fruits are shiny orange, oblong, and fleshy, containing 3–8 seeds. This infraspecific taxon probably went extinct in Singapore owing to deforestation of lowland rainforest and primary mangrove forests, compounded by the fact that these plants do not occur in high densities in closed forest (Huxley, 1978), hence is now listed as nationally extinct (Tan et al., 2008).

Hydnophytum formicarum is currently listed as nationally critically endangered in Singapore (Tan et al., 2008). It has an irregularly lobed, smooth tuber 10–55 cm across, with numerous tunnels and perforations for ant inhabitation (Fig. 3). Its leaf laminas are subsessile, leathery, and elliptical reaching 4–10 cm long (Keng, 1990). Like *Myrmecodia tuberosa*, plants growing in shadier conditions tend to have thinner laminas which are larger compared to plants growing in full sun which have more leathery, smaller laminas. The flowers are white, four-petalled, and occur in axillary clusters of 3–10 (Fig. 4). The fruits are narrowly ellipsoid, 4–7 mm long with 1–3 seeds each (Fig. 5). At present, we have observed *Hydnophytum formicarum* in only a few localities which includes secondary forest near Rifle Range Road and Sime Road forest, Nee Soon Swamp Forest (Fig. 6), and mangrove forests along the northern shoreline of Pulau Tekong near the hot springs (Kampong Unum), and on beach forest trees on Pulau Pawai. Historical records include collections from Bajau (Western Catchment Area), Changi, Jurong, Pasir Panjang, Pulau Seletar, and Sungei Tempei (probably Sungei Tampines) (Table 1). At the Rifle Range Road, Sime Road Forest and Nee Soon Swamp Forest, *Hydnophytum formicarum* is observed to be connected by a network of myrmecophytic highways formed from the interconnection with other myrmecophytes such as the antfern (*Lecanopteris sinuosa*), button orchid (*Dischidia nummularia*), and stag's horn fern (*Platycerium coronarium*). Coastal populations such as mangrove-dwelling colonies are usually found associated with *Dischidia nummularia* and *Dischidia major*. In Singapore *Hydnophytum formicarum* plants have been associated with a few ant genera depending on the habitat and its proximity to other myrmecophytes. For example plants associated with *Platycerium coronarium* are found to be associated with *Crematogaster* species or *Camponotus* species, while plants associated with *Lecanopteris sinuosa* are usually colonised by species of *Crematogaster*, *Technomyrex* or Iridomyremex, and plants associated with *Dischidia* species usually only house *Crematogaster* species.

CONCLUSIONS

Hydnophytum formicarum is nationally critically endangered and currently only present in Singapore in very small numbers because it occurs in very low densities in closed forest such as lowland evergreen rain forest and also because most of our primary mangrove forests, where these plants usually grow in higher population densities have been cleared for coastal development since the 1960s (Johnson, 1964). *Hydnophytum formicarum* is the only remaining tuberous myrmecophytic epiphyte of the Rubiaceae remaining in Singapore, with the extinction of *Myrmecodia tuberosa* probably in the early part the 1900s. These plants not only are botanical oddities, but also represent complex interactions between plants and ants.

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