BLUMEA 37 (1993) 335–340

THE TUBEROUS EPIPHYTES OF THE RUBIACEAE 6: A TAXONOMIC HISTORY OF THE HYDNOPHYTINAE

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SUMMARY

Rumphius first described the two major genera of the Hydnophytinae in 1750, but Linnaeus did not recognize the work, and Jack described *Hydnophytum* and *Myrmecodia* in 1823. These genera were briefly placed elsewhere and confused, until Beccari's admirable monograph (1884–86) when three further genera were added. Valeton's revision was sadly incomplete.

INTRODUCTION

The taxonomic history of the genera of the Hydnophytinae (Huxley & Jebb, 1991a) is presented as a separate paper in this series since it concerns the background to *Hydnophytum* Jack (Huxley & Jebb, in prep.), *Myrmecodia* Jack (Huxley & Jebb, this volume), *Myrmephytum* Becc. (Huxley & Jebb, 1991b), and *Squamellaria* Becc. (Jebb, 1991).

Pre-Linnean to the first valid publication

The first person to describe the ant-inhabited tuberous Rubiaceae was Georg Rumphius who worked for the Dutch East India Company at Ambon in the Moluccas. His classic work 'Herbarium Amboinense' was prepared during the latter half of the seventeenth century, delayed by the joint ravages of fire and blindness, and not published until 1750. Rumphius' names for the ant-plants, *Nidus formicarum niger* and *Nidus formicarum ruber*, are therefore pre-Linnean. Linnaeus, although aware of the work, did not incorporate it into his system.

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

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

Confusion 1824–1872

Two years after Jack's publication Sprengel (1825) transferred both species from their genera in the Rubiaceae to *Lasiostoma* Schreber (= *Strychnos* L.) in the Loganiaceae. They were, however, returned to their proper position by Blume (1826/27). Blume also collected a specimen of *Myrmecodia* from western Java, which he placed tentatively in *M. tuberosa* Jack, but noted that it had a spiny tuber, a feature mentioned by neither Rumphius nor Jack. He also found *Hydnophytum* in western Java and described it as a new species – *H. montanum*. This species he said had short-petioled oblong leaves, while *H. formicarum* had subsessile ovate leaves. Since, however, Jack described *H. formicarum* as having short-petioled elliptic-ovate leaves, the distinction was somewhat tenuous. Later J.D. Hooker (1881) sank *H. montanum* into *H. formicarum*.

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

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

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

Miquel (1857) recognized Blume's two species of *Hydnophytum* but he transferred the pre-Linnean name *Nidus formicarum niger* from *H. formicarum* Jack to *H. montanum* Blume; he also observed that these two species are scarcely to be distinguished. In *Myrmecodia* he removed De Candolle's superfluous name *M. inermis*, following Jack instead. He retained the name *M. echinata* Gaudich. to include Blume's collection from Java and Gaudichaud's from the Moluccas, ignoring de Candolle's name *M. armata* for these two collections. In his flora of Sumatra (1861) Miquel followed Blume.

In 1858 Asa Gray presented an account of Seemann's collections from Fiji to the American Academy of Arts and Sciences, though this was not published until 1860. He described two new species, one was *Hydnophytum longiflorum* and the other *Myrmecodia imberbis* which was later transferred by Beccari to a new genus *Squamellaria*. Gray was rather confused by the existing literature and wrote sadly "There is no small obscurity about the one or two old species of this genus and respecting

the distinction between it and *Hydnophytum* which the Dutch botanists ought to clear up." Seemann, apparently unaware of Gray's description, published in 1861 the name *M. vitiensis*, but as Gray (1862) pointed out, this was the same plant that he had called *H. longiflorum*.

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

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

From the 'Genera Plantarum' (1873) to Beccari (1884–86)

Bentham and Hooker in their 'Genera Plantarum' (1873) succeeded in clarifying the distinction between *Hydnophytum* and *Myrmecodia*, noting stem and tuber characters as well as floral ones. They also recognized that *M. inermis* A. Gray (meaning *M. imberbis* A. Gray) belongs to a distinct genus, but did not describe it.

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

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

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

Odoardo Beccari published his monumental study of ant-associated plants as the second part of his three-volume work 'Malesia' between 1884 and 1886. This volume is subtitled 'Piante Ospitatrici; ossia piante formicarie della Malesia e della Papuasia descritte ed illustrate da O. Beccari'; it deals extensively with other ant-associated plants, but the greatest part concerns the Rubiaceae. His revision of *Myrmecodia* and *Hydnophytum* was based on considerable knowledge of the plants in the field and he was familiar with the type material in Europe. He added 16 species to the existing

two of *Myrmecodia* and 29 to the six of *Hydnophytum*. One species from each genus he removed to form the new genus *Squamellaria* (*M. imberbis* A. Gray and *H. ?wilsonii* Horne ex J.G. Baker). He did not believe *Squamellaria* to be ant-associated as he missed Gray's observation of tubers. He also recognized a new genus *Myrmephytum* to accommodate his previously described *Myrmecodia selebica*. This satellite genus *Myrmephytum*, along with his other new monotypic genus, *Myrmedoma*, had a six-merous corolla and large bracts, but these genera differed in vegetative characters, resembling respectively *Hydnophytum* and *Myrmecodia*. Beccari also recorded the different species of ants present in the ant-plants, discussed their relationship with the plants, and considered the origin of the tubers.

From Beccari to Valeton (1927)

After Beccari there was a phase of piecemeal description of new species. J.D. Hooker (1886) honoured Beccari's work with *Myrmecodia beccarii*, a distinctive species from mangrove vegetation in Australia. This was the plant which had been seen but not published by Banks and Solander. Schumann in 1888 honoured Beccari with a species of *Hydnophytum*, but found that he had made an error and moved the species to *Psychotria* in 1898.

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

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

Valeton had already named several species of ant-plants from New Guinea (1911, 1912a, b) when he undertook the Rubiaceae for Lauterbach's 'Flora von Papuasien' (1927). But he was an elderly and ailing man; he saw the material neither at Florence (Beccari's) nor at Kew, and he left undescribed names in his key and on specimens. Unfortunately, many of the collections he described were not only fragmentary, but were later lost in Berlin. Thus his account of *Myrmecodia* consists of a key to species in New Guinea followed by descriptions of seven new species, of which fragments of three and photographs of two are all that survived. His 16 new species of *Hydnophytum* fared a little better. His manuscripts have survived and P. van Royen (1983) has taken up two of these names (*H. vaccinifolium* and *H. crassicaule*).

After Valeton

In the same year that Valeton's work appeared, Moore (1927) described three species collected by Brass on one of the many and important Archbold Expeditions. These three species of *Hydnophytum* were, however, all very close to species previously described by Hooker and Beccari, which Moore did not apparently examine.

In 1940 Fosberg described a new species of *Hydnophytum* from the Solomon

Islands, and in 1942 Bremekamp published *H. inerme* (Gaudich.) Bremek. as a new combination for *H. gaudichaudii* Becc. But the Gaudichaud specimen which was the type for *H. gaudichaudii* Becc. was not the type for *M. inermis* Gaudich. since this species included *H. formicarum* Jack.

In 1945 Merrill and Perry published seven species of *Myrmecodia* and 15 of *Hydnophytum* from the Brass collections. But as they did not see existing types, a number of relationships and identities with earlier species were missed. Many of the collections came from areas not explored before and little since, the variability and range of these species was therefore often under-estimated.

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

CONCLUSION

The taxonomic history of the group shows little synthesis or understanding; Beccari was the only author stimulated by an interest in the unique symbiosis of these plants. This led him to study the plants at first-hand over much of their range and to examine all the available types. His treatment is the only one which covers the group throughout its distribution, discusses subgeneric classification, attempts to define the variation of what we interpret as the ochlospecies *H. formicarum*, and which considers heterostyly and the association with ants. Valeton, Merrill, and Perry had first-hand knowledge of only the commonest species; this, together with their limited acquaintance with existing specimens led to their work being little more than a listing of new collections.

ACKNOWLEDGEMENT

I would like to thank my supervisor F. White.

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