

Squamellaria: Plants domesticated by ants

1 | INTRODUCTION

Plants across 50 families have evolved modified structures to host ants in return for defense or nutrients—sometimes both (Chomicki & Renner, 2015). Recently some astounding discoveries have been made in the complex interactions between ants and plants, none more so than in the genus *Squamellaria*. The genus comprises 12 species in Oceania: nine in Fiji, one on Vanuatu, and two on the Solomon Islands (Chomicki & Renner, 2016a). They belong to the coffee family (Rubiaceae) in the subtribe Hydnophytinae, which is the largest ant-plant clade, containing approximately 105 species distributed across Southeast Asia and Oceania from Indonesia, the Philippines, and New Guinea, to the Solomon Islands, Vanuatu and Fiji (Chomicki & Renner, 2017; Huxley & Jebb, 1991). All are epiphytic (living on tree branches) and produce a drastically modified, and highly specialised, hollow nesting structure derived from the hypocotyl (the stem portion below the cotyledons at the seedling stage), called the *domatium*, which is specifically adapted for habitation by ants.

The genus *Squamellaria* was named by the Italian botanist Odoardo Beccari (1884–1886), who examined plants collected during the Wilkes United States Exploring Expedition in 1840. The first species was described by Asa Gray as *Myrmecodia imberbis* (Wilkes Expl. Exped. s.n.; US Catalog No.: 62266, barcode: 00129869). A second species, placed formerly in the genus *Hydnophytum* (Horne, 1881) was collected by John Horne (1848–1928), a British forester living in Fiji in 1876/1877. Beccari himself never visited Fiji, but while examining the specimens collected by Gray and Horne, concluded that they were sufficiently distinct from those of the other ant-plant genera *Myrmecodia* and *Hydnophytum*, which he had described previously from Sarawak and West Papua, to be placed in a separate genus Beccari (1884–1886). The name he gave the new genus, *Squamellaria*, refers to the presence of fringed scales—or squamellae—which are produced within the petals in some species. Beccari knew only the specimens collected by Gray and Horne, which were preserved without their tubers. He therefore assumed that *Squamellaria* plants lack the substantial tubers present in *Myrmecodia* and *Hydnophytum* and concluded that they were not ant-plants. The Fijians, however, were well aware that *Squamellaria* plants form large tubers, as testified by the name *theke theke nkau* (among many local variants), meaning “testicle of the trees.”

Like other Hydnophytinae, *Squamellaria* has a large domatium, which develops from a modified hypocotyl and contains a network

of self-formed, hollow galleries connected to the external environment via entrance holes. Most Hydnophytinae engage in nutritional symbioses whereby they obtain nutrients derived from ant feces or detritus brought in by the ants. Six closely related species of *Squamellaria* are endemic to two Fijian islands (Vanua Levu and Taveuni) and all have evolved an obligate symbiosis with the ant species *Philidris nagasau* (Dolichoderinae). The ants fertilize the plants by defecating inside the domatia (see Section 2) and also defend the individual that they inhabit against herbivory by attacking insect herbivores. This combination of “services” is unusual in ant-plant symbioses. Four of the 12 species of *Squamellaria* were described as new to science in 2016, as was the extraordinary farming mutualism itself (Chomicki & Renner, 2016b).

2 | ECOLOGY AND EVOLUTION OF THE SYMBIOSIS

So-called “cultivation mutualisms” have evolved multiple times across the tree of life, but only certain social insects that cultivate fungi engage in true agriculture—defined by habitual planting, cultivation, harvesting and dependence on the crop (Mueller, Gerardo, Aanen, Six, & Schultz, 2005). Nonhuman agriculture is not restricted to fungus-farming by ants (Mueller, Rehner, & Schultz, 1998), termites and beetles (Mueller et al., 2005) it also occurs in plant-farming ants, namely in the ant species *P. nagasau* (subfamily Dolichoderinae), which farms *Squamellaria* in Fiji (Chomicki & Renner, 2016b). This ant species forms extensive “farms” encompassing dozens of *Squamellaria* plants cultivated high up in the forest canopy. The ants collect seeds from the fruits before they ripen (circumventing their removal by birds) and insert them into sunken pockets underneath the tree bark. They plant several seeds (up to 10) after which a small group of workers remain under the bark, presumably to protect seeds from predation (Figure 1a). The ants later harvest food rewards produced by the plants, and also depend upon the plants obligately for nesting since they have lost their nest-building behavior (Chomicki & Renner, 2016b, 2019). In order to emerge from their sunken sites under the tree bark, the seedlings have evolved an elongated “foot” of the hypocotyl, which delays domatium development until the seedling has emerged fully (Chomicki & Renner, 2016b). Once the seedling has a domatium of about 1.5 cm across, with its first entrance hole, ant workers enter the seedling and fertilize it

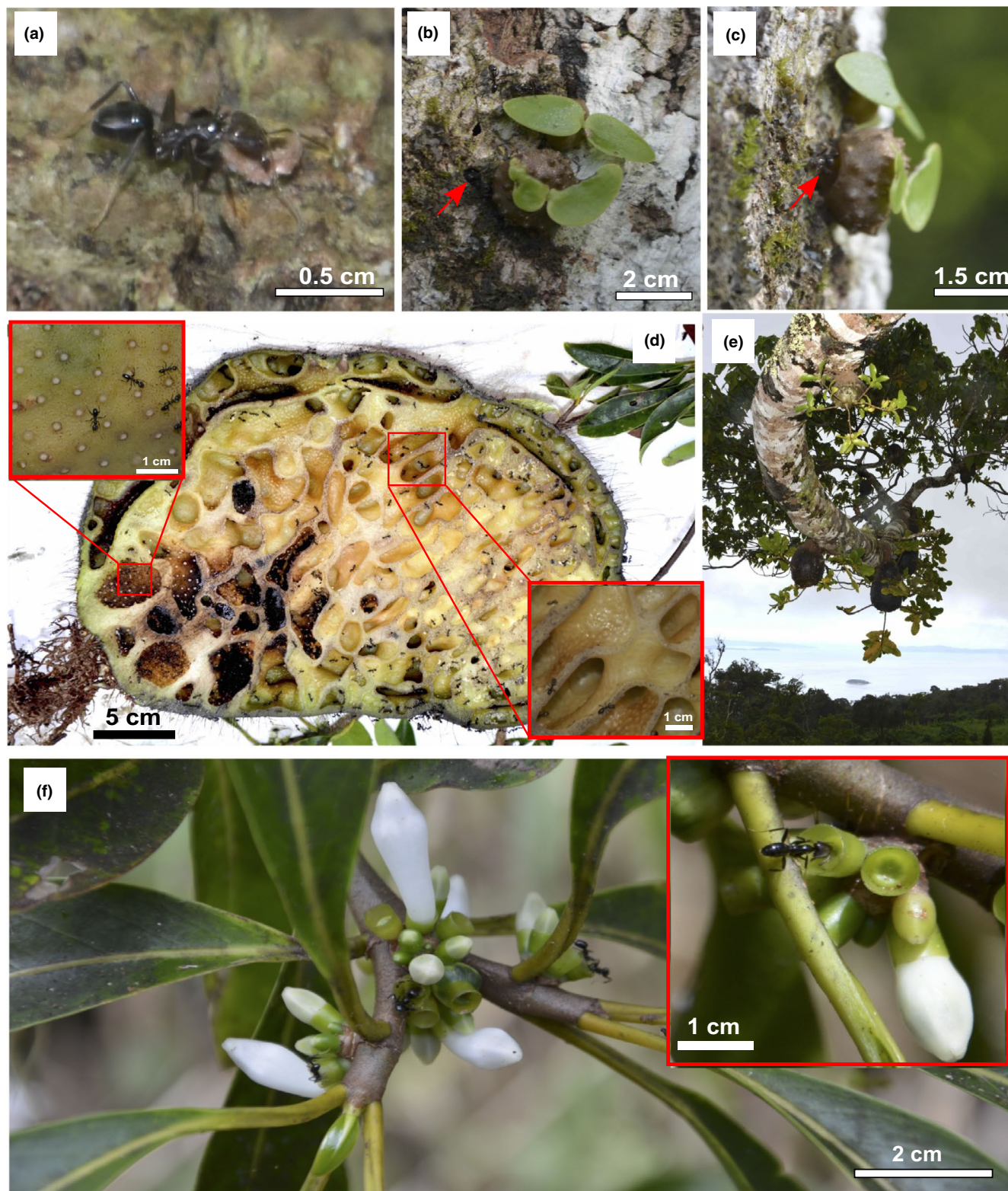


FIGURE 1 The farming symbiosis between Fijian *Squamellaria* and *Philidris nagasau* ants. (a) *P. nagasau* worker dispersing a *Squamellaria* seed; (b) *Squamellaria* "nursery" where a sunken site has been planted with seeds and two seedlings are emerging (arrowheads show holes in the bark where a worker emerges, bark removal revealed that many seeds were present, guarded by *P. nagasau* workers); (c) *P. nagasau* worker (arrowhead) visiting the tiny domatium of a *Squamellaria* seedling to fertilize it; (d) longitudinal section through a large *Squamellaria wilsonii*, revealing two types of inner wall structures: the warted walls (left inset) where ants defecate and place detritus and the smooth walls (right inset) where ants rear their brood; (e) *Squamellaria* "farm" with dozens of individuals, here *S. major* and *S. thekii*, overlooking a bay, in Taveuni island, Fiji and; (f) food rewards (nectary in old flowers) in *Squamellaria wilsonii*, Taveuni island, Fiji. Photographs: Guillaume Chomicki

actively by defecation (Chomicki & Renner, 2016b, Figure 1b,c). The fertilization by ants continues throughout the life of the plant and occurs only on hyper-absorptive structures on the inner domatium walls that look like warts (Figure 1d). Similar warty domatium walls are found in several ant-housing Hydnophytinae, such as those of the genus *Myrmecodia* (Huxley, 1978). In all cases, plants of different ages are occupied by the same ant colony (Figure 1e). Sexually mature, farmed specimens of *Squamellaria* produce food rewards that consist of nectar offered in old flowers (after the corolla has fallen and the flower has been pollinated). The nectar is concealed and is rich in sugar and amino acids (Chomicki, Staedler, Schönenberger, & Renner, 2016, Figure 1f). As young and old *Squamellaria* plants are farmed together from the seedling stage onward, ants looking for a new home, and plants that need to be detected by ants, are able to encounter one another reliably. In other ant-plant symbioses involving bird-dispersed trees or shrubs, each young plant must first be detected by founder queens before it can receive any defense and nutritional benefits from its ant mutualists.

The *Squamellaria*-*P. nagasau* agriculture is restricted to two islands of Fiji, and both plants and ants evolved some 3 million years ago in the archipelago (Chomicki & Renner, 2016b). The young geological age of Taveuni island (~800,000 years) implies that the symbiosis first evolved on the ~4 million-year-old island of Vanua Levu, before *Squamellaria* and *P. nagasau* colonized Taveuni, which is only 6.5 km away (Chomicki, Janda, & Renner, 2017). Comparative analyses have revealed that this obligate farming symbiosis evolved from facultative symbioses with generalist ants (Chomicki & Renner, 2016b, 2017).

3 | FOCUS ON SQUAMELLARIA MAJOR, THE “DODO” OF THE GENUS

Squamellaria major is an outlier among the ant-farmed species of *Squamellaria*. It has large and conspicuous succulent leaves, often longer than 15 cm, rounded at the apex and undulate throughout (Figures 1e and 2), by contrast with the smaller, thinner, flat-edged leaves of other species in the genus. In a revision of the genus written almost 30 years ago when only three species were known, Jebb (1991, p. 59) noted: “The leaves of this species always appear chlorotic and diseased.” In nature, the plants with their large, often chlorotic leaves exposed to full sun, give the impression of being diseased or somehow maladapted—a metaphorical “dodo” that struggles in the competition of life. Furthermore, *S. major* is an obligate CAM species (Chomicki & Renner, 2016a), with a type of photosynthesis shared by cacti and other succulents in which the stomata close during the day and open at night. Owing to its succulent habit, *S. major*, by contrast to most other *Squamellaria* species, is restricted to low altitudes (300–400 m) on the island of Taveuni, since higher elevations are too humid for it to survive. In the lowlands, deforestation is rife, to make way for the cultivation of the local crops taro, cassava and kava. As a result, *S. major* is on the verge of extinction with perhaps only 100 individuals or fewer



FIGURE 2 *Squamellaria major*, a threatened ant-farmed epiphyte endemic to Taveuni island, Fiji. A virtual section through the domatium shows the inner cavity channels. A longitudinal section is shown in the bottom right corner. Illustration: Chris J. Thorogood

remaining, and with a very small area of occupancy (<10 km²). As such, it qualifies for the International Union for Conservation of Nature (IUCN) criterion “critically endangered” and its formal red-listing is underway. The few remaining plants are found on large trees standing on cleared land, far apart from one another. The uniqueness of *Squamellaria* and its symbiosis with ants should put a spotlight on Fijian rainforests as a place in dire need of greater conservation focus.

4 | CONCLUDING REMARKS

The speed at which plants can take up nitrogen is a key limitation to plant growth rate. Most plants, including our crops, take up nitrogen from the soil and are thus not naturally exposed to very high nitrogen concentrations. However, for millions of years, ants have deposited nitrogen-rich feces directly inside *Squamellaria*—which suggests that deciphering this mechanism of nitrogen uptake, and transferring it to cultivated crops, could potentially help boost plant growth rates. Hence, the complex nutritional physiology that has evolved

in *Squamellaria*-*P. nagasau* agriculture might help humankind's own challenge for food security (Chomicki & Renner, 2019).

Four new species of *Squamellaria* have been identified in the past 5 years (Chomicki & Renner, 2016a; b) and as some Fijian islands still remain to be fully explored it seems likely that more species of *Squamellaria* await discovery. The complex symbiotic relationship between *Squamellaria* and *P. nagasau* warrants further exploration, and raises more questions than we have answers. For example, do microbes play an important role in the system as they do for leafcutter ants that farm fungi? Similarly, since *P. nagasau* ant workers are responsible for the cultivation of *Squamellaria*, what role does the ant queen play in the symbiosis, and do symbiotic ant colonies spread other than by "budding" (the clonal separation of one ant colony into several colonies)? Further research into this fascinating and complex symbiosis will shed light on these, and other questions, and enlighten our understanding of obligate mutualisms in ant-plants and beyond.

ACKNOWLEDGEMENTS

Research from the first and senior author described in this paper has been supported by the German Science Foundation (DFG, grants RE 603/20, RE 603/20-2). GC is supported by a Glasstone Research Fellowship and a Junior Research Fellowship at the Queen's college, both at the University of Oxford.

AUTHORS CONTRIBUTION

GC designed and wrote the paper, with edits from all coauthors; CJT drew plate; AN was involved in the fieldwork of the research described in this study; SSR was involved in various aspects of the research described in this paper..

Guillaume Chomicki^{1,2*} 

Chris J. Thorogood^{3*} 

Alivereti Naikatini⁴

Susanne S. Renner⁵ 

¹Department of Plant Sciences, University of Oxford, Oxford, UK

²The Queen's College, University of Oxford, Oxford, UK

³Oxford University Botanic Garden, Oxford, UK

⁴South Pacific Regional Herbarium, Institute of Applied Sciences, The University of the South Pacific, Suva, Fiji

⁵Systematic Botany and Mycology, Department of Biology, University of Munich (LMU), Munich, Germany

Correspondence

Guillaume Chomicki, Department of Plant Sciences, University of Oxford, Oxford, UK.

Email: guillaume.chomicki@gmail.com

*Guillaume Chomicki and Chris J. Thorogood contributed equally.

ORCID

Guillaume Chomicki  <https://orcid.org/0000-0003-4547-6195>

Chris J. Thorogood  <https://orcid.org/0000-0002-2822-0182>

Susanne S. Renner  <https://orcid.org/0000-0003-3704-0703>

REFERENCES

- Beccari, O. (1884–1886). *Piante ospitatrici, ossia piante formicarie della Malesia e della Papuasias*. Malesia (Genoa) vol. II, fasc. 1–2 (1884), fasc. 3 (1885), fasc. 2 (1886).
- Chomicki, G., Janda, M., & Renner, S. S. (2017). The assembly of ant-farmed gardens: Mutualism specialization following host broadening. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20161759. <https://doi.org/10.1098/rspb.2016.1759>
- Chomicki, G., & Renner, S. S. (2015). Phylogenetics and molecular clocks reveal the repeated evolution of ant-plants after the late Miocene in Africa and the early Miocene in Australasia and the Neotropics. *New Phytologist*, 207, 411–424. <https://doi.org/10.1111/nph.13271>
- Chomicki, G., & Renner, S. S. (2016a). Evolutionary relationships and biogeography of the ant-epiphytic genus *Squamellaria* (Rubiaceae: Psychotrieae) and their taxonomic implications. *PLoS ONE*, 11, e0151317. <https://doi.org/10.1371/journal.pone.0151317>
- Chomicki, G., & Renner, S. S. (2016b). Obligate plant farming by a specialized ant. *Nature Plants*, 2, 16181. <https://doi.org/10.1038/nplants.2016.181>
- Chomicki, G., & Renner, S. S. (2017). Partner abundance controls mutualism stability and the pace of morphological change over geologic time. *Proceedings of the National Academy of Sciences of the USA*, 114, 3951–3956. <https://doi.org/10.1073/pnas.1616837114>
- Chomicki, G., & Renner, S. S. (2019). Farming by ants remodels nutrient uptake in epiphytes. *New Phytologist*, 23(4), 2011–2023. <https://doi.org/10.1111/nph.15855>
- Chomicki, G., Staedler, Y. M., Schönnenberger, J., & Renner, S. S. (2016). Partner choice through concealed floral sugar rewards evolved with the specialization of ant-plant mutualisms. *New Phytologist*, 211, 1358–1370. <https://doi.org/10.1111/nph.13990>
- Horne, J. (1881). *A year in Fiji, or an inquiry into the botanical, agricultural, and economical resources of the colony*. London, UK: Eyre GE & Spottiswoode W.
- Huxley, C. R. (1978). The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships between their morphology, ant occupants, physiology and ecology. *New Phytologist*, 80, 231–268. <https://doi.org/10.1111/j.1469-8137.1978.tb02285.x>
- Huxley, C. R., & Jebb, M. H. P. (1991). The tuberous epiphytes of the Rubiaceae 1: A new subtribe: The Hydnophytinae. *Blumea*, 36, 1–20.
- Jebb, M. H. P. (1991). The tuberous epiphytes of the Rubiaceae: 4. A revision of *Squamellaria*. *Blumea*, 36, 53–61.
- Mueller, U. G., Gerardo, N. M., Aanen, D. K., Six, D. L., & Schultz, T. R. (2005). The evolution of agriculture in insects. *Annual Review of Ecology, Evolution and Systematics*, 36, 563–595. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152626>
- Mueller, U. G., Rehner, S. A., & Schultz, T. R. (1998). The evolution of agriculture in ants. *Science*, 281, 2034–2038. <https://doi.org/10.1126/science.281.5385.2034>

How to cite this article: Chomicki G, Thorogood CJ, Naikatini A, Renner SS. *Squamellaria*: Plants domesticated by ants. *Plants, People, Planet*. 2019;1:302–305. <https://doi.org/10.1002/ppp3.10072>