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Ant-tended scale insects (Hemiptera: Coccidae: *Myzolecanium*) within lowland rain forest trees in Papua New Guinea

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ABSTRACT. Eight species of *Myzolecanium* Beccari (Hemiptera: Homoptera: Coccoidea: Coccidae) are reported from ant nests in stem cavities of living lowland rain forest trees in Papua New Guinea. The coccids are confined to this microhabitat but are associated with a taxonomically broad range of ants and host trees. Attendant ants belonged to six species in three genera and two subfamilies: *Anonychomyrma* Donisthorpe (Dolichoderinae), *Crematogaster* Lund (Myrmicinae) and *Podomyrma* F. Smith (Myrmicinae). Host plants belonged to at least five families and included both apparently specialized (with domatia) and unspecialized species. Saplings containing the nests of *Anonychomyrma scrutator* (F. Smith), *Anonychomyrma* sp. 1 and *Podomyrma laevifrons* F. Smith were dissected and the structure of nest chambers and their contents recorded. Only some chambers had entrance holes, but many were interconnected by transverse passages. The coccids were in low numbers and fairly evenly distributed between ant-occupied chambers. The characteristics of the *Myzolecanium*-ant association, the role of the coccids as trophobionts, and the nature of the plant associations are discussed. Taxonomically, new combinations are proposed by P. J. Gullan for three species previously placed in *Cryptostigma* Ferris: *Myzolecanium endoeucalyptus* (Qin & Gullan), *M. magnetinsulae* (Qin & Gullan), and *M. robertsi* (Williams & Watson).

KEY WORDS: ants, Coccidae, coccids, domatia, mutualisms, *Myzolecanium*, Papua New Guinea, rain forest, scale insects, trophobiosis.

INTRODUCTION

Scale insects of the genus *Myzolecanium* Beccari (Hemiptera: Homoptera: Coccoidea: Coccidae) have a specialized life history, inhabiting only hollow chambers in living trees in association with ants. Some aspects of their taxonomy and biogeography were reviewed recently by Qin & Gullan (1989) who described the first two Australian species (then placed in the genus *Cryptostigma* Ferris). *Myzolecanium* was first collected in New Guinea by Beccari (1877, 1884) who described and illustrated *M. kibarae* inhabiting cavities in the swollen internodes of two species of Monimiaceae in association with ants, apparently *Anonychomyrma* *scrutator* (F. Smith). Recently, another species was described from New Guinea by Williams & Watson (1990). However, there is very little published information on the general ecology of the four described species of *Myzolecanium*.

Ants tend scale insects to obtain their sugary excreta or honeydew and such tending protects the scale insects from their natural enemies, a relationship termed trophobiosis (Hölldobler & Wilson 1990). Reciprocal benefits have been well documented for other ant–homopteran associations in which the homopterans are tended externally on plant structures (Beattie 1985, Buckley 1987, Way 1963), but the *Myzolecanium*–ant association is unusual in that the coccids appear to be obligate myrmecophiles in the nests of ants throughout their lives. Although attached to the inner, often hardened, surfaces of plant cavities, the females of *Myzolecanium* can easily tap the phloem of the stem because they have very long, thread-like stylets (Targioni Tozzetti 1877). Furthermore, as noted by Williams & Watson (1990), the anal area of *Myzolecanium* is modified, suggesting that these scales may have lost the ability to eject honeydew, instead relying completely on ants to remove it.

Although the close relationships of scale insects (coccoids, superfamily Coccoidea), especially mealybugs (family Pseudococcidae) and soft scale insects (coccids, family Coccidae), with tropical ants and plants have been noted or discussed previously (e.g. Hölldobler & Wilson 1990, Longino 1991, Maschwitz *et al.* 1991b, Stout 1979, Wheeler 1942), the significance of coccoids to the evolution of ant–plant associations has been largely ignored. Benson (1985), McKey (1989) and Ward (1991), however, have considered the role of coccoids and other homopterans in the evolution of plant domatia – specialized structures, such as leaf pouches and swollen hollow stems, petioles, roots or pseudobulbs, that serve no obvious function other than the housing of ants (Beattie 1985, Hölldobler & Wilson 1990). In fact, scale insects may have been crucial to the inception of some ant–plant mutualisms because they provide the food which draws the ants into a closer relationship with the plant (Benson 1985, Ward 1991).

A major unknown factor in the interactions between ants, plants, coccoids and (in plants without domatia) the stem-boring insects which produce cavities, is the specificity of the coccoids to particular plants or ants (Ward 1991). Here we document the ant and host-plant associations of *Myzolecanium* in Papua New Guinea (PNG) and describe the distribution of stem chambers, coccids and attendant ants in lowland rain forest trees near Madang, PNG.

METHODS

Coccid taxonomy

Recent literature (Qin & Gullan 1989, Williams & Watson 1990) dealing with *Myzolecanium* species refers to them as taxa in *Cryptostigma*, a genus which was erected by Ferris (1922) for certain Neotropical coccids. Examination of the recently located type specimens of *M. kibarae* Beccari has established the identity of the obscure and older name *Myzolecanium* (C. J. Hodgson, pers. comm.). One of our PNG species is clearly *M. kibarae* and here is considered congeneric with our other Australasian species. A decision as to whether the Neotropical species also belong in *Myzolecanium* (making *Cryptostigma* a junior synonym of *Myzolecanium*) must await a systematic revision of the group. Three new combinations are proposed here for Australasian species previously placed in *Cryptostigma*: *Myzolecanium endoeucalyptus* (Qin & Gullan), *M. magnetinsulae* (Qin & Gullan), and *M. robertsi* (Williams & Watson). Responsibility for these taxonomic changes should be attributed solely to P. J. Gullan.

Study sites and specimens collected

Field work was carried out during May 1989 at three rain forest localities in PNG: 24 km N, 40 km N and 25 km SSW of Madang (5°01′S 145°46′E, 4°52′S 145°45′E, and 5°25′S 145°41′E, respectively). Trees were examined for active ants or for small entrance holes, and stems were cut open close to these entrance holes in seven trees to reveal ants and coccids in internal chambers. Most of the host plants sampled were saplings 5–8 m tall, with few branches, though a few were larger and strongly branched. For three unidentified saplings, at sites subject to logging, the entire host plant was cut into sections and quickly placed into plastic bags with ethyl acetate to kill the insects. The chambers were dissected later to allow the ants and coccids to be counted and identified.

Additional information on *Myzolecanium* and associated ants came from collections made by one of us (P.S.W.) in several localities in Madang and Wewak Provinces, PNG, in January and February, 1989.

The coccids from hollow stems in rain forest trees all belonged to *M. kibarae* or one of seven undescribed species of *Myzolecanium*, which are referred to as species B, C, D, F, G, H and I. All specimens will be deposited in the Australian National Insect Collection (ANIC), Division of Entomology, CSIRO, Canberra, Australia, upon completion of taxonomic research. Ants have been deposited in the ANIC and in the collection of P. S. Ward, Department of Entomology, University of California, Davis, USA. A voucher collection of ants has been retained by the Christensen Research Institute (CRE), Madang, PNG. We prepared samples of most plant specimens as herbarium specimens, referred to by a code, e.g. CRI 759, and have deposited them in the CRI collection; most of these specimens were identified, at least to family level, by M. Jebb of CRI and subsequently were examined by staff at the Papua New Guinea National Herbarium, Forest Research Institute, Lae, but apparently further determinations were not possible (M. Jebb, pers. comm.).

RESULTS

Eight species of *Myzolecanium* were collected from ant nests in hollow stems of living lowland rain forest trees in Madang Province in PNG, bringing to nine the number of species known from PNG (Figure 1). Two pairs of species (*M. kibarae*

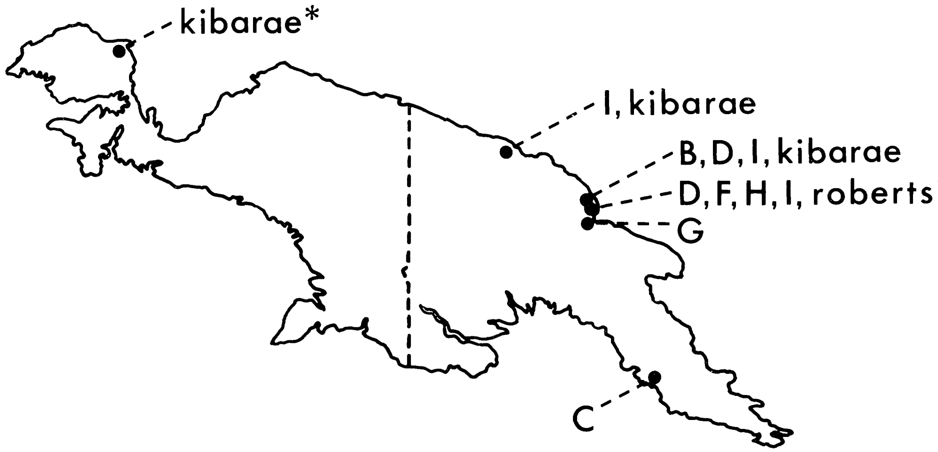

Figure 1. Map of New Guinea showing distribution of species of *Myzolecanium*. *Beccari's (1877) locality for the type species, *M. kibarae*.

plus *M.* sp. B, and *M. kibarae* plus *M.* sp. I) were collected together in the same chambers. Six ant species, belonging to three genera, *Anonychomyrma* Donisthorpe (until recently part of *Iridomyrmex* Mayr; Shattuck 1992) (Dolichoderinae), *Crematogaster* Lund (Myrmicinae) and *Podomyrma* F. Smith (Myrmicinae), were observed co-habiting with and tending populations of *Myzolecanium*. There was no evidence of a close taxonomic partnership between ant and *Myzolecanium* species (Table 1). Furthermore, the coccids were collected from a broad range of host plants, including at least five families, and host-plant specificity was not indicated by the available data (Table 1).

The three fully dissected saplings each contained a nest of *Anonychomyrma scrutator* (F. Smith) and coccids of either *Myzolecanium* spp. G or H. One sapling contained a small ant colony, apparently confined to a single chamber, whereas the other two housed larger colonies of >1000 workers and roughly half this number of eggs, larvae and worker pupae within multiple chambers (Table 2).

Four other trees each contained a nest of either *Anonychomyrma* sp. 1 or *Podomyrma laevifrons* F. Smith, which housed one or two species of *Myzolecanium* (*M. kibarae* and *M.* sp. B, or *M.* spp. D or I) (Figure 2; Table 1). The cavities generally were restricted to stems and branches <20 mm in diameter. Entrance holes were oval or circular and small 1.5–3 mm in maximum dimension, and hence more uniform than those in the three fully dissected trees.

In all nests, occupied chambers were typically cylindrical, several times broader than the central pith, often offset from the stem axis, and frequently interconnected by transverse passages. Uninhabited chambers had pale green to black inner surfaces and often lacked entrance holes, whereas inhabited chambers had brown or black inner surfaces and usually one hole. The chambers did not contain any conspicuous accumulations of food, although accumulations of fungal-infected detritus and dead female coccids were found in a few occupied chambers.

Table 1. Ant and host-plant associations of *Myzolecanium* species from Papua New Guinea. Voucher herbarium specimens in the Christensen Research Institute, Madang, are identified by a code, e.g. CRI 750. [a]Data from Beccari (1877), Philipson (1986) and Targioni Tozzetti (1877); ant identified by S.O. Shattuck from Beccari's figure. [b]Data from Huxley (1986). [c]Data from William & Watson (1990).

Myzolecanium species	Associated ant species	Host-plant family (genus and species, if known)
M. kibarae	*Anonychomyrma scrutator*	Monimiaceae (*Kibara* and *Steganthera* spp.)[a]
	Anonychomyrma sp. 2	Myristicaceae (?*Myristica*)
	Podomyrma laevifrons	Meliacae (?*Aglaia* sp., CRI 750)
B	*Podomyrma laevifrons*	Meliaceae (?*Aglaia* sp., CRI 750)
C	*Anonychomyrma* sp. 1	Myristicaceae (*Myristica* sp.)
D	*Crematogaster (Orthocrema)* sp. 1	Rubiaceae *(Timonius sericeus)*
	Podomyrma basalis	Rubiaceae (*T. sericeus*)
	Podomyrma laevifrons	?Lauraceae (CRI 751)
F	*Crematogaster (Orthocrema)* sp. 1	Unidentified
G	*Anonychomyrma scrutator*	Unidentified (CRI 757, 759)
H	*Anonychomyrma scrutator*	Meliaceae (CRI 761)
I	*Anonychomyrma* sp. 1	Myristicaceae (*M. subalulata*)
	Anonychomyrma sp. 2	Myristicaceae (?*Myristica*)
	Podomyrma laevifrons	Sterculiaceae (?*Sterculia*, CRI 752)
	Anonychomyrma cf. *scrutator*[b]	Meliaceae (*Aphanamixis myrmecophila*)[b]
M. robertsi[c]	No data on ants	Combretaceae (*Terminalia brassii*)[c]
Unident. sp.	*Anonychomyrma* cf. *scrutator*[b]	Lauraceae (*Cryptocarya* sp.)[b]

Mature coccid females ranged from 3–8 mm in length and varied correspondingly in colour from yellow to dark brown, presumably reflecting age. Individual nest chambers rarely contained more than 15 adult female coccids and at least half contained none. Most occupied chambers contained adult females and earlier instars, including first-instar nymphs; none contained first-instar nymphs alone. For the three fully dissected saplings, 40% of the total 32 chambers were occupied by adult coccids, which ranged in number from 0–22 (3.5 ± 5.8 SD) per chamber. Larger females occurred on woody platforms conforming to the outline of the coccid, and raised 0.2–0.3 mm above the general surface of the chamber. These individuals may have remained stationary over a period of time, whilst the ants excavated the chamber around them.

Diurnal foraging by the ants was not observed at the three rain forest sites near Madang, although aggressive defence by *Anonychomyrma* sp. 1 occurred when their *Myristica subalulata* Miq. tree was disturbed. The interconnection of chambers meant that ant workers were free to move between chambers without using the surface entrance holes. We did not observe ants carrying food items, although ants frequently picked up their eggs, larvae or pupae when their nest

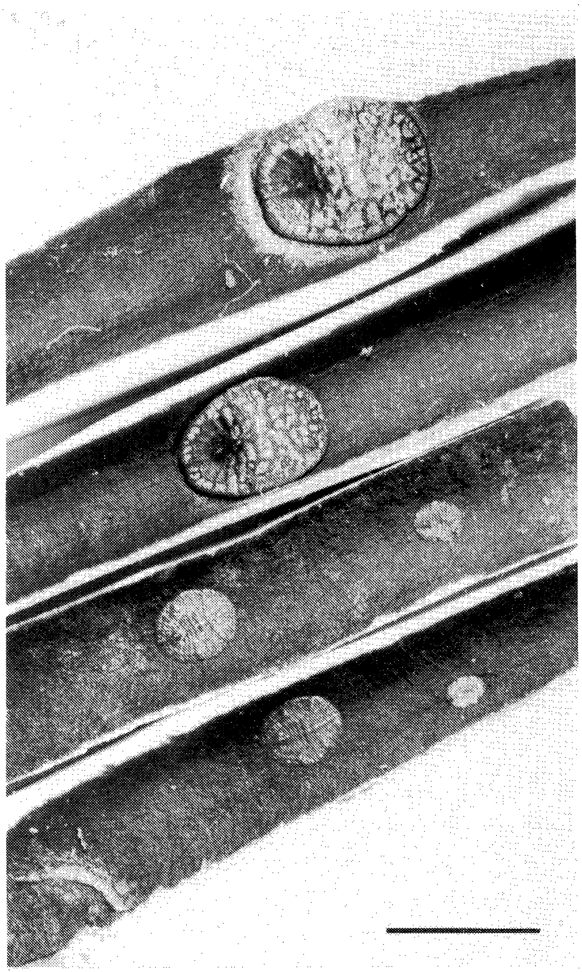

Figure 2. Stem sections of *Myristica subalulata* Miq. (Myristicaceae) cut open to show scale insects of *Myzolecanium* sp. I attached to cavity wall. The two largest scale insects are mature adult females, the two smallest ones are nymphs and the other two are young adult females. Scale line = 5 mm.

was cut open and, on one occasion, we observed ants of *P. laevifrons* attempting to carry two coccids that had been dislodged.

DISCUSSION

Populations of *Myzolecanium* appear to be common inhabitants of ant nests in stem cavities of live plants in PNG rain forests. Several previously unrecognized reports of undoubted *Myzolecanium* from New Guinea supplement Beccari's (1877, 1884) and our findings. Individuals of *Myzolecanium* are evident in Warburg's (1897, plate XI: figure 1) illustration of the internodes of *Myristica subalulata*, and Hölldobler & Wilson's (1990, p. 540) listing of scale insects associated with '*Iridomyrmex*' ants in the hollow internodes of *Myristica* species

Table 2. Data for three fully dissected unidentified saplings each housing a nest of *Anonychomyrma scrutator* plus coccids of a *Myzolecanium* species. The CRI numbers in column 1 refer to herbarium voucher specimens held at the Christensen Research Institute, Madang, PNG. Abbreviations for ants: al., alate; deal., dealate; w., worker; w.p., worker pupae.

Tree	Tree height: m (Basal diameter: mm)	Height above ground of 1st chamber: mm	No. of chambers	Chamber lengths: mm	External stem diameter: mm	Internal max. chamber diameter: mm	Number of entrance holes	Shape of entrance holes	Dimensions of entrance holes mm	Ants	Scale insects
25 km SSW of Madang CRI 759	5.5 (23)	20	1	120	20	7–9	1	oval	1.2 × 3.5	1 deal. queen 200 workers 7 larvae 5 queen pupae	16 adults 1 nymph (*M.* sp.G)
25 km SSW of Madang CRI 757	5.5 (37)	25	7	90–117	25–30	12–16	3 in lowest chambers only	2 slits, 1 knothole	1–1.5 × 4–7 6.5 × 10	60 al. queens c. 1000 w. c. 500 eggs, larvae & w. p. 22 queen pupae	73 adults 38 nymphs (*M.* sp. G)
24 km N of Madang CRI 761	8 (32)	90	12 empty 12 occupied	10–260	9–18	3–10	12	9 round or oval, 3 slits	< 1–2 1–2 × 7–8	1 deal. queen c. 2000 w. c. 1700 eggs, larvae & w. p.	23 adults 18 dead adults 2 nymphs (*M.* sp. H)

probably refers to *Myzolecanium*. Furthermore, two photographs that clearly show individuals of *Myzolecanium* attended by ants of '*Iridomyrmex* cf. *scrutator*' are published in Huxley (1986, p. 268); her figure 4A shows our *M*. sp. I in a hollowed-out stem of *Aphanamixis myrmecophila* Harms (Meliaceae); the *Myzolecanium* species of her figure 4B, in a stem of *Cryptocarya* sp. (Lauraceae), cannot be identified with certainty. Philipson (1986) reported scale insects (probably *Myzolecanium*) and ants from the hollow stems and swollen internodes of four species of *Kibara* Endl. and four species of *Steganthera* Perkins, which are either conspecifics or congeners of the host plants named in Beccari's (1877) original description of *Myzolecanium*. There are only two definite records of other coccoids from New Guinean rain forest myrmecophytes: *Psoraleococcus browni* Lambdin & Kosztarab (Lecanodiaspididae) has been described from within the pseudobulbs of *Myrmecodia* Jack (Rubiaceae) (Lambdin & Kosztarab 1988), and P. S. Ward has collected *Saissetia vivipara* Williams & Watson (Coccidae; det. P. J. Gullan) from the nest of an unidentified species of *Crematogaster* (*Orthocrema*) in a *Myristica*-like sapling in rain forest near Wewak.

The species of *Crematogaster* (*Orthocrema*), *Anonychomyrma* and *Podomyrma* studied here nest entirely in arboreal situations, as do many of their congeners, but their associations with *Myzolecanium* appear to be facultative. Our *Crematogaster* (*Orthocrema*) sp. 1 is widespread in New Guinea and commonly occupies dead twigs, unaccompanied by coccids (P. S. Ward, pers. obs.). *Anonychomyrma scrutator* sometimes inhabits epiphytic myrmecophytes of the genus *Myrmecodia*, in which scales generally are absent (P. S. Ward, pers. obs., M. Jebb, pers. comm.). It is unclear to what extent other *Anonychomyrma*, or any *Podomyrma* species, nest preferentially in live plant cavities in association with coccoids. Both of these genera occur in Australia and Melanesia, with *Anonychomyrma* confined to mesic forests and *Podomyrma* more widely distributed (Shattuck, 1992, Taylor & Brown 1985).

Our PNG studies have revealed ants in association with *Myzolecanium* both in understorey myrmecophytes (e.g. *Myristica*) and in insect-bored twigs of unspecialized plants (e.g. *Timonius sericeus*). In some collections, however, it is uncertain whether the ants occupied true domatia (i.e. cavities that form independently of ants), constructed the chambers by hollowing out pithy stems, or utilized hollow stems excavated by other insects. The variability in the shape and dimensions of the entrance holes in the seven saplings described here suggests heterogeneous origins of the nest entrances and hence the cavities.

In keeping with their Neotropical and Australian counterparts (Qin & Gullan 1989), the PNG *Myzolecanium* species are not specific to particular plant genera or families, but are confined to a specialized microhabitat in their host plants. To date, seven plant families have been recorded as hosts to *Myzolecanium* and four other families are known hosts to Neotropical *Cryptostigma*. Furthermore, these coccids have been found in the nests of many ant genera: three from PNG, two of these plus an additional two from Australia (Qin & Gullan 1989, Ward 1991) and several others, including *Azteca* Forel and *Pseudomyrmex* Lund

(Wheeler 1942), from the Neotropical region (see references in Qin & Gullan 1989). More than one species of *Cryptostigma* may associate with one ant species (Wheeler 1942). Similarly in PNG, two to four species of *Myzolecanium* were associated with each of five of the six ant species reported here (Table 1) and in two instances two *Myzolecanium* species were found in the same ant nest.

Both adults and nymphs of *Myzolecanium*, usually of more than one size or stage, occurred in all the ant nests that we dissected. Thus *Myzolecanium* species fulfil Hölldobler & Wilson's (1990, p. 524) criterion for ideal trophobionts, in that their life cycles are 'not tightly synchronized so that stages capable of producing honeydew are available throughout the year'. It is not known whether the ants feed solely on the honeydew of the coccids or whether they also kill and consume some individuals, as has been reported for a few other ant–coccoid associations (e.g. Bailey 1922, Way 1954). The numbers of coccids in any nest chamber were always quite low, suggestive of either culling by the ants or dispersal of the coccids from the nests.

There are no positive records of *Myzolecanium* from external plant surfaces or outside ant nests, although *M. magnetinsulae* Qin & Gullan apparently was collected under loose bark of a tree (Qin & Gullan 1989) and the data label for *M. robertsi* states only that the coccids were collected on the trunk of *Terminalia brassii* (Williams & Watson 1990). It seems that *Myzolecanium* coccids are obligate inhabitants of ant nests, although it is possible that ants remove all individuals of *Myzolecanium* from external plant surfaces, as observed for weaver ants of *Camponotus* and *Dolichoderus* species associated with other scale insects in Malaysian rain forest (Maschwitz *et al.* 1985, 1991a).

There is no evidence that queen ants carry nymphs of *Myzolecanium* to new nests. Carriage of coccoids by colony-founding queens has never been documented in arboreal-nesting ants, which presumably need unencumbered mandibles to chew into plant tissue. Instead, nymphs of *Myzolecanium* presumably enter ant nests as a result of active dispersal, after nest establishment. The lack of specificity between ant species and *Myzolecanium* species supports this suggestion, since transport by queen ants should lead to more species-specific associations.

Myzolecanium and *Cryptostigma* appear closely related to the African genus *Houardia* Marchal, with three species known from woody plants in galleries of cavities probably made by ants (Hodgson 1990). Little is known of the ant associations of *Houardia*, except that *H. troglodytes* Marchal was found in the galleries of a *Crematogaster* species. Phylogenetic studies of *Cryptostigma*, *Myzolecanium*, *Houardia* and other morphologically similar genera, many of which also associate with ants, may cast some light on the interrelationships and origins of these peculiarly modified coccids.

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LITERATURE CITED

BAILEY, I. W. 1922. The anatomy of certain plants from the Belgian Congo, with special reference to myrmecophytism. *Bulletin of the American Museum of Natural History* 45:585–621.

BEATTIE, A. J. 1985. *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, Cambridge. 182 pp.

BECCARI, O. 1877. Piante nuove o rare dell'Arcipelago Malese e della Nuova Guinea, raccolte, descritte ed illustrate da Odoardo Beccari. *Malesia (Genova)* 1:167–192.

BECCARI, O. 1884. Raccolta di osservazioni botaniche intorno alle piante dell'Arcipelago Indo-Malese e Papuano pubblicata da Odoardo Beccari. *Malesia (Genova)* 2:1–340.

BENSON, W. W. 1985. Amazon ant-plants. Pp. 239–266 in Prance, G. T. & Lovejoy, T. E. (eds). *Amazonia*. Pergamon Press, Oxford.

BUCKLEY, R. C. 1987. Ant-plant-homopteran interactions. *Advances in Ecological Research* 16:53–85.

FERRIS, G. F. 1922. Notes on Coccidae. IX. (Hemiptera). *Canadian Entomologist* 54:156–161.

HODGSON, C. J. 1990. The scale insect genus *Houardia* Marchal (Homoptera: Coccidae). *Systematic Entomology* 15:219–226.

HÖLLDOBLER, B. & WILSON, E. O. 1990. *The ants*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts. 732 pp.

HUXLEY, C. R. 1986. Evolution of benevolent ant–plant relationships. Pp. 257–282 in Juniper, B. & Southwood, R. (eds). *Insects and the plant surface*. Edward Arnold, London.

LAMBDIN, P. & KOSZTARAB, M. 1988. *Psoraleococcus browni*: a new species of pit scale from Papua New Guinea (Homoptera: Coccoidea: Lecanodiaspididae). *Annals of the Entomological Society of America* 81:724–727.

LONGINO, J. T. 1991. *Azteca* ants in *Cecropia* trees: taxonomy, colony structure, and behaviour. Pp. 271–288 in Huxley, C. R. & Cutler, D. F. (eds). *Ant–plant interactions*. Oxford University Press, Oxford.

McKEY, D. 1989. Interactions between ants and leguminous plants. Pp. 673–718 in Stirton, C. H. & Zarucchi, J. L. (eds). *Advances in legume biology*. Monographs in Systematic Botany from the Missouri Botanical Garden, Number 29.

MASCHWITZ, U., DUMPERT, K. & SCHMIDT, G. 1985. Silk pavilions of two *Camponotus (Karavaievia)* species from Malaysia: description of a new nesting type in ants (Formicidae: Formicinae). *Zeitschrift für Tierpsychologie* 69:237–249.

MASCHWITZ, U., DUMPERT, K., BOTZ, T. & ROHE, W. 1991a. A silk-nesting weaving Dolichoderine ant in a Malayan rain forest. *Insectes Sociaux* 38:307–316.

MASCHWITZ, U., FIALA, B., MOOG, J. & SHAW, L. G. 1991b. Two new myrmecophytic associations from the Malay Peninsula: ants of the genus *Cladomyrma* (Formicidae, Camponotinae) as partners of *Saraca thaipingensis* (Caesalpiniaceae) and *Crypteronia griffithii* (Crypteroniaceae). 1. Colony foundation and acquisition of trophobionts. *Insectes Sociaux* 38:27–35.

PHILIPSON, W. R. 1986. Monimiaceae. *Flora Malesiana. Series I. Spermatophyta (Flowering Plants)* 10(2):255–326.

QIN, T. K. & GULLAN, P. J. 1989. *Cryptostigma* Ferris: a coccoid genus with a strikingly disjunct distribution (Homoptera: Coccidae). *Systematic Entomology* 14:221–232.

SHATTUCK, S. O. 1992. Review of the dolichoderine ant genus *Iridomyrmex* Mayr with descriptions of three new genera (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society* 31:13–18.

STOUT, J. 1979. An association of an ant, a mealy bug, and an understory tree from a Costa Rican rain forest. *Biotropica* 11:309–311.

TARGIONI TOZZETTI, A. 1877. *Myxolecanium kibarae* Beccari (Lecaniti). *Bulletino della Società Entomologica Italiana (Florence)* 9:317–320. [note *lapsus calami* in generic name]

TAYLOR, R. W. & BROWN, D. R. 1985. Formicoidea. Pp. 1–149 in Walton, D. W. (ed.). *Zoological Catalogue of Australia. Volume 2. Hymenoptera.* Australian Government Publishing Service, Canberra.

WARBURG, O. 1897. Monographie der Myristicaceen. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosum, Halle* 68:1–680.

WARD, P. S. 1991. Phylogenetic analysis of pseudomyrmecine ants associated with domatia-bearing plants. Pp. 335–352 in Huxley, C. R. & Cutler, D. F. (eds). *Ant-plant interactions.* Oxford University Press, Oxford.

WAY, M. J. 1954. Studies on the association of the ant *Oecophylla longinoda* (Latr.) (Formicidae) with the scale insect *Saissetia zanzibarensis* Williams (Coccidae). *Bulletin of Entomological Research* 45:113–134.

WAY, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology* 8:307–344.

WHEELER, W. M. 1942. Studies of Neotropical ant-plants and their ants. *Bulletin of the Museum of Comparative Zoology* 90:1–262.

WILLIAMS, D. J. & WATSON, G. W. 1990. *The scale insects of the tropical South Pacific region. Part 3. The soft scales (Coccidae) and other families.* CAB International, Wallingford. 267 pp.

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