

Colonial system of *Philidris* ants (Formicidae; Dolichoderinae) occupying epiphytic myrmecophytes in a tropical mangrove forest

T. MAEYAMA & T. MATSUMOTO

*Matsumoto Laboratory, Department of Biology, Graduate School of Arts & Sciences
The University of Tokyo, 3-8-1, Komaba, Meguro, Tokyo 153-8902, Japan*

Abstract: The colonial system and territoriality of *Philidris* (Formicidae; Dolichoderinae) ants occupying dominantly epiphytic myrmecophytes, *Hydnophytum moseleyanum* (Rubiaceae: Hydnophytinae), in a mangrove forest in Papua New Guinea were investigated using a test measuring ant aggressiveness. One ant colony occupied several *H. moseleyanum* plants on plural mangrove trees. The ants were polydomous and monogynous as the colonies always had a single queen. It was suggested that the arboreal ant fauna in the mangrove forest canopy revealed an ant mosaic distribution pattern. As the main food resource, the *Philidris* ants obtained honeydew secreted by the diaspidid scale insects on the shoot tips of the host mangrove trees of *H. moseleyanum*.

Resumen: El sistema colonial y la territorialidad de hormigas *Philidris* (Formicidae; Dolichoderinae) que ocupan predominantemente la mirmecófita epífita *Hydnophytum moseleyanum* (Rubiaceae: Hydnophytinae) en un manglar en Papúa Nueva Guinea fueron investigados por medio del uso de una prueba de agresividad de las hormigas. Una colonia de hormigas ocupó varias plantas de *H. moseleyanum* en varios árboles del manglar. Las hormigas fueron polidomias y monóginas ya que las colonias siempre tuvieron una única reina. Se sugiere que la fauna mirmecófila arbórea en el dosel del manglar revela un patrón de distribución en mosaico. Como fuente de alimento principal, las *Philidris* colectaron gotitas de miel secretadas por los insectos escamosos diaspididos en las puntas de las ramillas en los árboles de manglar hospederos de *H. moseleyanum*.

Resumo: O sistema de colônia e a territorialidade das formigas *Philidris* (Formicidae; Dolichoderinae) ocupando de forma dominante a epífita mirmercophite *Hydnophytum moseleyanum* (Rubeacea: Hydnophytinae), numa floresta de mangal na Papua, Nova Guiné foi investigada usando um método de medida da agressividade das formigas. Uma colônia de formigas ocupavam várias plantas de *H. moseleyanum* num mangal plural. Como as colônias tinham uma única rainha, as formigas apresentavam abobadadas múltiplas e eram monogamas. Foi sugerido que a fauna de formigas arbóreas na copa da floresta de mangal apresentava um padrão de distribuição em mosaico. Como principal recurso alimentar, as formigas *Philidris* obtêm a solução açucarada segregada pelos insectos diaspididos de escamas nos rebentos terminais do mangal parasitado pela *H. moseleyanum*.

Key words: Aggression test, ant mosaic, colony structure, *Hydnophytum moseleyanum*, New Guinea, territoriality.

Introduction

Numerous ant species have complicated symbiotic relationships with plants (Buckley 1982; Keeler 1989). One of the most developed symbioses is the mutualism between ants and myrmecophytes (Jolivet 1996). However, there is little knowledge about the ecology of the ant species inhabiting myrmecophytes, although some studies clarified several ecological aspects such as behaviour against herbivores, food resources, colony foundation, territoriality of the associated ants, e.g., *Crematogaster* spp. in *Macaranga* plants (Fiala *et al.* 1989), *Pseudomyrmex* ants in *Acacia* trees (Janzen 1966, 1973).

The epiphytic myrmecophytes in Hydnophytinae (Rubiaceae) can absorb the nutrients from the debris stored inside the cavities in plant tubers by the occupant ants, and the plants appear to utilize it for their living (Huxley 1978; Rickson 1979). Though two studies observed the behavior of *Iridomyrmex* ants occupying *Myrmecodia tuberosa* (Huxley 1978) and *Hydnophytum formicarum* (Janzen 1974), knowledge obtained was lacking about the ants' colonial system or food resources because investigation of high trunks or branches of the host tree where these epiphytic myrmecophytes occur is so difficult. It is occasionally observed that ants carry their broods from one plant-nest to another (Maeyama 1995). However, colonial structure and territoriality are unknown. Thus, we examined the colonial nest system using aggression tests for the most dominant ants *Philidris* sp. (Formicidae; Dolichoderinae) inhabiting *Hydnophytum moseleyanum* (Rubiaceae; Hydnophytinae) in a mangrove forest in Papua New Guinea. The queen number per colony (monogyny or polygyny) and food resources were also investigated.

Materials and methods

Organism

H. moseleyanum is a myrmecophytic epiphyte distributed in/around New Guinea Island (Jebb 1985; Maeyama *et al.* 1997a). The plants have a swollen tuber which has very complex cavities inside which some arboreal ant species inhabit. Our previous study clarified the species composition of ants occupying *H. moseleyanum* in the mangrove forest in this study (Maeyama *et al.* 1997b). Ele-

ven ant species from 9 genera were detected there. The dominant ant species were *Philidris* sp. (detected in 34.2% of the plants), *Camponotus* sp. (10.3%) and *Crematogaster* sp. (4.2%). The other 8 species appeared very rarely (0.3-3.0% of each, 12.6% in total). No ants were found in 38.5% of the plants.

Study area

All research was carried out from October 16 to November 2 in 1993 in a 10 m x 10 m quadrat set up in a mangrove forest about 800 m south of Christensen Research Institute (CRI) in Papua New Guinea. CRI is situated about 9 km north of Madang town in northern Papua New Guinea. The height of the mangrove trees was 8-9 m on average. The roots of the trees got entangled with one another and some boughs were in contact with those of other trees, enabling ants to cross from one tree to the next directly. The region is situated in the tropics with little seasonal variation in temperature. The rainy season in this area is usually from December to April or May. The dry season is from May to November.

Internest aggression tests in Philidris sp.

The workers of *Philidris* sp. attack members of different colonies severely, while aggressive behavior is never observed between workers in the same colony (Maeyama 1998). To investigate the nest structure and the territoriality of *Philidris* sp., levels of aggression were tested between the ant workers inhabiting each plant-nest. For *H. moseleyanum* occupied by *Philidris* sp., all mature plants whose tubers were more than 7 cm in diameter were recorded on the quadrat map, and the plant-nests were numbered (Fig. 1). About 200 *Philidris* sp. workers per plant-nest were collected using an aspirator. The collected plant-nest groups of ants were maintained in plastic cases (19 x 26 x 4) in the CRI laboratory. They were fed on honey diluted with water. The inner sides of the rearing cases were coated with fluon (I.C.I. United States, Inc.) to prevent ants from escaping. These artificial nests were maintained at room temperature (23-27°C) during the experimental period.

Internest aggression was tested by the following method which was time consuming but very sensitive. One worker selected randomly from nest A was picked up lightly by the legs using forceps and painted on its thorax. The painted indi-

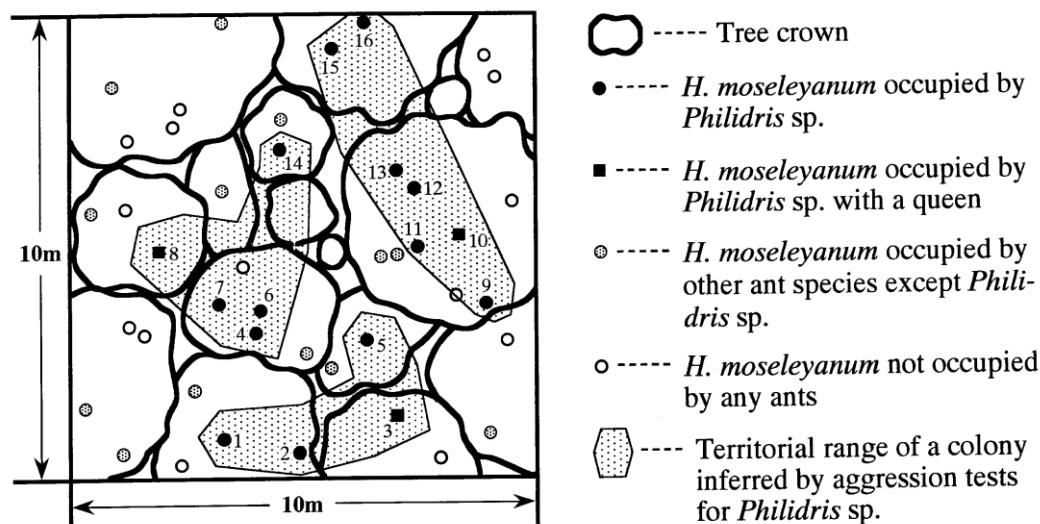


Fig. 1. Horizontal distribution of *Hydnophytum moseleyanum* used as nests by *Philidris* sp. in the study area. All plant-nests are numbered.

vidual was transferred into the cases of nest B, and the encounters between workers of the different nests were observed. Except when severe fighting began, at least five encounters were observed in each trial. In the case of a full attack, group B was calmed for at least about 20 minutes after the removal of the immigrant from group A, because group B became very agitated. With one combination, the same trials (transfer from group A into group B) were repeated five times, and opposite trials (transfer from group B into group A) were also repeated five times. Thus, trials of any combination were performed ten times in total.

The level of aggression was scored on an arbitrary scale (Table 1) which was slightly modified from Carlin & Hölldobler (1983). Such a trial was repeated ten times with different individuals for each nest combination. This test was also performed within the same nest as a control, and

Table 1. Aggression scale used in scoring the responses of ant workers from different nests.

0) Acceptance	: Mutual tolerance, grooming, trophallaxis
1) Avoidance	: Retreat back, escape from the opponent
2) Alarm	: Open-mandible threat, posture of spraying formic acid
3) Weak attack	: Nipping, leg pulling, body jerking
4) Full attack	: Locking together, biting, spraying formic acid

workers always accepted each other (aggression score is zero). All tests were performed within two weeks from collection. The observed distributions of scores were compared by the Mann-Whitney U-test with the control to detect any statistical difference in aggressiveness.

Furthermore, the food sources of *Philidris* sp. were investigated in the field. The observations were done day and night for a week. All the myrmecophytes were collected after the aggression tests were over, and tubers occupied by the ants were sliced open to survey the number of queens in each ant colony.

Results

Colonial nest structure of Philidris sp.

Sixteen plant-nests in mature *H. moseleyanum* occupied by *Philidris* sp. were detected in the study quadrat. On all the combinations between the plant-nests, the total scores of aggression levels were clearly separated into two types (Table 2). One had non- or slightly aggressive response (score ≤ 4 , e.g. the combinations of 1 x 2, 1 x 3) which were not significantly different from the control ($P > 0.05$, Mann-Whitney U-test), and the other had extremely high aggressive responses (score ≥ 32 , e.g. the combinations of 1 x 4, 1 x 6) which revealed a significant difference from the control ($P < 0.001$, Mann-Whitney U-test). Because the combinations of the plant-nests which showed

Table 2. Aggressive responses between plant-nests of *Philidris* sp. The observed number of each response is shown. In statistical tests, distribution of scores was compared with the control by Mann-Whitney U-test.

Combinations	Level of aggression					Total score	Mann-Whitney U-test with control
	accept (0)	avoid (1)	alarm (2)	quarrel (3)	flight (4)		
Control	10	0	0	0	0	0	
1x2	10	0	0	0	0	0	P>0.1
1x3	9	1	0	0	0	1	P>0.1
1x4	0	0	1	1	8	37	P<0.001
1x5	10	0	0	0	0	0	P>0.1
1x6	0	0	2	2	6	34	P<0.001
1x7	0	0	1	0	9	38	P<0.001
1x8	0	1	1	2	6	33	P<0.001
1x9	0	0	0	2	8	38	P<0.001
1x10	0	0	2	1	7	35	P<0.001
1x11	0	0	1	1	8	37	P<0.001
1x12	0	1	1	2	6	33	P<0.001
1x13	0	0	0	2	8	38	P<0.001
1x14	0	0	2	1	7	35	P<0.001
1x15	0	1	0	4	5	33	P<0.001
1x16	0	0	0	3	7	37	P<0.001
2x3	9	0	1	0	0	2	P>0.1
2x4	0	0	1	3	6	35	P<0.001
2x5	9	1	0	0	0	1	P>0.1
2x6	0	0	1	0	9	38	P<0.001
2x7	0	0	2	2	6	34	P<0.001
2x8	0	0	1	1	8	37	P<0.001
2x9	0	0	1	0	9	38	P<0.001
2x10	0	0	0	2	8	38	P<0.001
2x11	0	0	1	2	7	36	P<0.001
2x12	0	0	2	1	7	35	P<0.001
2x13	0	0	0	1	9	39	P<0.001
2x14	0	0	1	0	9	38	P<0.001
2x15	0	0	0	2	8	38	P<0.001
2x16	0	0	4	0	6	32	P<0.001
3x4	0	1	0	3	6	34	P<0.001
3x5	10	0	0	0	0	0	P>0.1
3x6	0	0	0	2	8	38	P<0.001
3x7	0	0	0	3	7	37	P<0.001
3x8	0	0	1	1	8	37	P<0.001
3x9	0	0	0	1	9	39	P<0.001
3x10	0	1	0	1	8	36	P<0.001
3x11	0	0	0	0	10	40	P<0.001
3x12	0	0	0	2	8	38	P<0.001
3x13	0	0	0	2	8	38	P<0.001
3x14	0	0	1	3	6	35	P<0.001
3x15	0	0	0	1	9	39	P<0.001
3x16	0	0	1	0	9	38	P<0.001
4x5	0	0	1	1	8	37	P<0.001
4x6	10	0	0	0	0	0	P>0.1
4x7	8	0	2	0	0	4	P>0.1
4x8	10	0	0	0	0	0	P>0.1
4x9	0	0	0	3	7	37	P<0.001
4x10	0	0	2	1	7	35	P<0.001
4x11	0	0	0	1	9	39	P<0.001
4x12	0	0	0	0	10	40	P<0.001
4x13	0	0	0	3	7	37	P<0.001

Table 2. (contd.)

Combinations	Level of aggression					Total score	Mann-Whitney U-test with control
	accept (0)	avoid (1)	alarm (2)	quarrel (3)	flight (4)		
Control	10	0	0	0	0	0	
4x14	10	0	0	0	0	0	P>0.1
4x15	0	0	0	3	7	37	P<0.001
4x16	0	0	0	2	8	38	P<0.001
5x6	0	0	2	2	6	34	P<0.001
5x7	0	0	0	2	8	38	P<0.001
5x8	0	0	1	0	9	38	P<0.001
5x9	0	0	1	2	7	36	P<0.001
5x10	0	0	1	1	8	37	P<0.001
5x11	0	1	0	3	6	34	P<0.001
5x12	0	0	0	2	8	38	P<0.001
5x13	0	1	0	4	5	33	P<0.001
5x14	0	1	1	2	6	33	P<0.001
5x15	0	0	1	0	9	38	P<0.001
5x16	0	0	4	0	6	32	P<0.001
6x7	10	0	0	0	0	0	P>0.1
6x8	10	0	0	0	0	0	P>0.1
6x9	0	0	2	1	7	35	P<0.001
6x10	0	0	0	3	7	37	P<0.001
6x11	0	0	1	1	8	37	P<0.001
6x12	0	0	0	1	9	39	P<0.001
6x13	0	0	0	2	8	38	P<0.001
6x14	9	0	1	0	0	2	P>0.1
6x15	0	0	2	1	7	35	P<0.001
6x16	0	0	1	3	6	35	P<0.001
7x8	10	0	0	0	0	0	P>0.1
7x9	0	0	1	0	9	38	P<0.001
7x10	0	0	0	3	7	37	P<0.001
7x11	0	0	2	1	7	35	P<0.001
7x12	0	0	1	0	9	38	P<0.001
7x13	0	0	0	2	8	38	P<0.001
7x14	9	1	0	0	0	1	P>0.1
7x15	0	1	0	1	8	36	P<0.001
7x16	0	0	0	0	10	40	P<0.001
8x9	0	0	0	3	7	37	P<0.001
8x10	0	0	0	1	9	39	P<0.001
8x11	0	0	1	1	8	37	P<0.001
8x12	0	0	0	2	8	38	P<0.001
8x13	0	0	0	1	9	39	P<0.001
8x14	10	0	0	0	0	0	P>0.1
8x15	0	0	1	1	8	37	P<0.001
8x16	0	0	1	3	6	35	P<0.001
9x10	10	0	0	0	0	0	P>0.1
9x11	10	0	0	0	0	0	P>0.1
9x12	10	0	0	0	0	0	P>0.1
9x13	10	0	0	0	0	0	P>0.1
9x14	0	0	0	0	10	40	P<0.001
9x15	10	0	0	0	0	0	P>0.1
9x16	8	1	1	0	0	3	P>0.1
10x11	9	1	0	0	0	1	P>0.1
10x12	10	0	0	0	0	0	P>0.1
10x13	10	0	0	0	0	0	P>0.1
10x14	0	0	0	3	7	37	P<0.001
10x15	9	1	0	0	0	1	P>0.1

Table 2. (contd.)

Combinations	Level of aggression					Total score	Mann-Whitney U-test with control
	accept (0)	avoid (1)	alarm (2)	quarrel (3)	flight (4)		
Control	10	0	0	0	0	0	
10x16	9	0	1	0	0	2	P>0.1
11x12	10	0	0	0	0	0	P>0.1
11x13	10	0	0	0	0	0	P>0.1
11x14	0	0	0	2	8	38	P<0.001
11x15	10	0	0	0	0	0	P>0.1
11x16	10	0	0	0	0	0	P>0.1
12x13	10	0	0	0	0	0	P>0.1
12x14	0	1	1	2	6	33	P<0.001
12x15	8	1	1	0	0	3	P>0.1
12x16	10	0	0	0	0	0	P>0.1
13x14	0	0	2	1	7	35	P<0.001
13x15	10	0	0	0	0	0	P>0.1
13x16	9	1	0	0	0	1	P>0.1
14x15	0	0	0	3	7	37	P<0.001
14x16	0	0	1	1	8	37	P<0.001
15x16	10	0	0	0	0	0	P>0.1

low aggressiveness were judged to belong to the same colony and the combinations showing high aggressiveness were judged to belong to different colonies, three colonies were detected in the quadrat (Fig. 1). This result revealed that these colonies had utilized several plant-nests on 2-3 mangrove trees; therefore *Philidris* sp. were polydomous. Three queens were collected from plant-nests No. 3, 8 and 10 (one queen from each). Therefore, it was clarified that each of three colonies had a single queen; *Philidris* sp. were monogynous.

Food materials of the ants

It was observed that *Philidris* sp. visited two species of scale insects, type 1, type 2 (Homoptera: Diaspididae) and one species of pit scale (Homoptera: Cerococcidae). The diaspidid scale insect type 1 existed along the midribs on leaves or on the tips of shoots of the mangrove trees. This species was the most popular among the three homopterans, and was visited most frequently by *Philidris* sp. to obtain the honey dew secreted by these scale insects. The ants often constructed carton runways on the routes from the plant-nests to the places where the scale insects lived. Because the runways were also constructed over the scale insects, they should play the role of protecting the scale insects from predators. The other two homopterans, diaspidid scale insect type 2 and cerococcid pit scales, appeared very rarely. The dias-

pidid scale insect type 2 existed on the surface of the branches or trunks, or in the cracks between the bark of the mangrove trees. They were also visited by *Philidris* sp. and provided honeydew to the ants. Although the cerococcids existed on the cavity surface inside the tubers of *H. moseleyanum*, the visiting behavior of *Philidris* sp. on the cerococcids has never been observed. Also, it was observed that the *Philidris* sp. workers carried small dead insects (flies, mosquitoes, moths, etc.) into their plant-nests.

Discussion

We succeeded in clarifying the colonial structure and territoriality of *Philidris* sp. with analysis using their aggressive responses. It was shown that one colony of *Philidris* sp. occupied several *H. moseleyanum* plants on plural trees in a mangrove forest; this ant species exhibited a polydomous colonial structure. The number of queens from each colony revealed the monogyny of *Philidris* sp. Therefore, all the myrmecophytes, except the plant containing an ant queen, were used as satellite nests in the ant colonies. Because it was observed that the ants carried their broods between the plant-nests, they would appear to breed them from a queen-bearing plant-nest at the satellite plant-nests.

On myrmecophytic *Macaranga* trees, one colony of the associated ant *Crematogaster borneensis*

occupies only one tree (Fiala & Maschwitz 1990). The ants rarely leave the plant and their lifetimes are spent on and inside the plant. On the other hand, one colony of *Philidris* sp. in this study occupied several *H. moseleyanum* plants. This epiphytic myrmecophyte species has less space for ant inhabitation, whereas terrestrial myrmecophytic trees like *Macaranga* have lots of space in their long trunks and branches. *Philidris* sp. may need to occupy several myrmecophytes to maintain their large colony size.

In tropical forests, arboreal ant colonies often exhibit mosaic distribution (called ant mosaic) in the forest canopy due to intraspecific and interspecific competition and strong hostility (Morrison 1996; Dejean *et al.* 1997). Although territoriality and colonial structure are unclear for the other 10 ant species except *Philidris* sp. found in *H. moseleyanum*, the distribution of the colonies of *Philidris* sp. showed a mosaic distribution pattern. Our results suggest that arboreal ant fauna in the mangrove forest in this study also exhibit an ant mosaic. More detailed study is needed on the overall interspecific correlations of arboreal ant species inhabiting the mangrove forest canopy.

Philidris ants mainly utilized honeydew from the diaspidid scale insect type 1 as their food resource. Honeydew from scale insects is generally poor as a nitrogen source (Jolivet 1996). It is possible that the small dead insects carried into the plant-nests by *Philidris* sp. were used to compensate for this lack of nitrogen. With the myrmecophytic trees, it is known that the associated ants often gather protein grains made by the plant on the leaves and/or stems, collect nectar from extrafloral nectaries (Buckley 1982), and rear scale insects inside the plant cavities to obtain honeydew (Longino 1991; McKey 1991; Fiala & Maschwitz 1992). *H. moseleyanum*, however, do not provide any food for the ants. *Philidris* ants may rear the cerococcid pit scales on the cavity surface of *H. moseleyanum* to get honeydew.

The presence of *H. moseleyanum* plants unoccupied by any ant species suggests that ant occupation is not obligatory for the plants. The reason for ant absence may not be due to factors related to the plants and ants, but due to the relationship between the diaspidid scale insect type 1 and the ants. Most unoccupied plants existed on dead branches of mangrove trees (Maeyama 1998).

The diaspidid scale insect type 1 is unable to suck sap from dead branches. If the scale insects

were absent from the branches, *Philidris* sp. might also be unable to live there. Thus, ant behavioral observation in the field has to be conducted to clarify the relationship and interaction between *Philidris* sp. and the diaspidid scale insect type 1.

Acknowledgements

The authors would like to thank Dr. M.H.P. Jebb and Dr. L. Orsak, the previous and present Directors of Christensen Research Institute in Papua New Guinea, for various support. We also thank Dr. M. Terayama for identification of all the New Guinean ant specimens. We gratefully acknowledge many people in Papua New Guinea for their support and encouragement.

T. Maeyama was supported by the fellowships of the Japan Society for the Promotion of Science for Young Scientists (No. 07-3895). This study was also partly supported by Grant-in-Aid Scientific Research Program (Nos. 10440231 and 11142204) from the Ministry of Education, Science, and Culture of Japan.

References

- Buckley, R.C. 1982. Ant-plant interactions: a world review. pp. 111-141. *In*: R.C. Buckley (ed.) *Ant-Plant Interactions in Australia*. Dr. W. Junk Publishers, The Hague.
- Carlin, N.F. & B. Hölldobler. 1983. Nestmate and kin recognition in interspecific mixed colonies of ants. *Science* **222**: 1027-1029.
- Dejean, A., C. Djieto-Lordon & J.L. Durand. 1997. Ant mosaic in oil palm plantations of the Southwest Province of Cameroon: Impact on leaf miner beetle (Coleoptera: Chrysomelidae). *Journal of Economic Entomology* **90**: 1092-1096.
- Fiala, B., U. Maschwitz, Y.P. Tho & A.J. Helbig. 1989. Studies of a South East Asian ant-plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia* **79**: 463-470.
- Fiala, B. & U. Maschwitz. 1990. Studies on the South East Asian ant-plant association *Crematogaster borneensis*/*Macaranga*: adaptations of the ant partner. *Insectes Sociaux* **37**: 212-231.
- Fiala, B. & U. Maschwitz. 1992. Domatia as most important adaptations in the evolution of myrmecophytes in the paleotropical tree genus *Macaranga* (Euphorbiaceae). *Plant Systematics and Evolution* **180**: 53-64.
- Huxley, C.R. 1978. The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships

- between their morphology and occupants, physiology and ecology. *New Phytologist* **80**: 231-268.
- Janzen, D.H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* **20**: 249-275.
- Janzen, D.H. 1973. Evolution of polygynous obligate acacia-ants in western Mexico. *Journal of Animal Ecology* **42**: 727-750.
- Janzen, D.H. 1974. Epiphytic myrmecophytes in Sarawak: mutualism through the feeding of plants by ants. *Biotropica* **6**: 237-259.
- Jebb, M.H.P. 1985. *Taxonomy and Tuber Morphology of the Rubiaceae Ant-Plants*. Ph.D. Thesis, University of Oxford.
- Jolivet, P. 1996. *Ant and Plants: An Example of Coevolution*. Backhuys Publishers, Leiden.
- Keeler, K.H. 1989. Ant-plant interactions. pp. 207-242. In: W.G. Abrahamson (ed.) *Plant-Animal Interactions*. McGraw-Hill, New York.
- Longino, J.T. 1991. *Azteca* ants in *Cecropia* trees: taxonomy, colony structure, and behaviour. pp. 271-288. In: C.R. Huxley & D.F. Cutler (eds.) *Ant-Plant Interactions*. Oxford University Press, Oxford.
- Maeyama, T. 1995. *Ecology and Symbiotic Relationship between Ants and Rubiaceae Epiphytic Ant-Plants*. M.Sc. Thesis, University of Tokyo.
- Maeyama, T., O. Kitade & T. Matsumoto. 1997a. The diverse occupant fauna in epiphytic ant-plants, *Hydnophytum moseleyanum* (Rubiaceae) in New Guinea. *Tropics* **7**: 91-101.
- Maeyama, T., M. Terayama & T. Matsumoto. 1997b. Comparative studies of the various relationships between rubiaceae myrmecophytes and their inhabitant ant species. *Sociobiology* **30**: 169-174.
- Maeyama, T. 1998. *Studies of Symbiotic Relationships between Epiphytic Myrmecophytes in Hydnophytinae (Rubiaceae) and Their Occupant Ants*. Ph.D. Thesis, Univ. of Tokyo.
- McKey, D. 1991. Phylogenetic analysis of the evolution of a mutualism: *Leonardoxa* (Caesalpiniaceae) and its associated ants. pp. 310-334. In: C.R. Huxley & D.F. Cutler (eds.) *Ant-Plant Interactions*. Oxford University Press, Oxford.
- Morrison, L.W. 1996. Community organization in a recently assembled fauna: The case of Polynesian ants. *Oecologia* **107**: 243-256.
- Rickson, F.R. 1979. Absorption of animal tissue breakdown products into a plant stem-the feeding of a plant by ants. *American Journal of Botany* **66**: 87-90.