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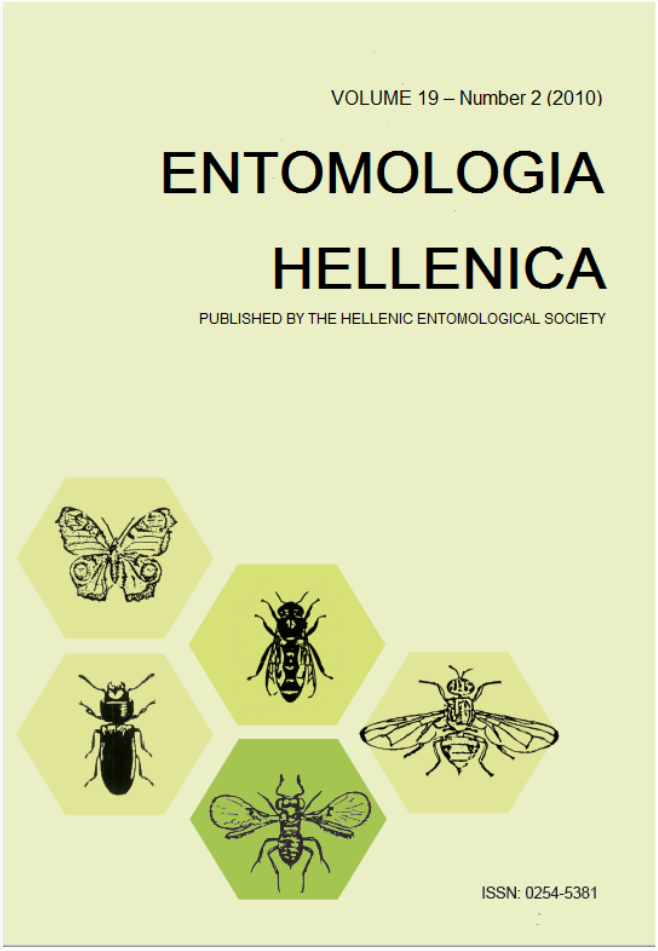

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Y. Ben-Dov, B.L. Fisher

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The mutualism of *Melissotarsus* ants and armoured scale insects in Africa and Magadascar: distribution, host plants and biology

Y. BEN-DOV[1*] AND B.L. FISHER[2]

[1]*Department of Entomology, Agricultural Research Organization, The Volcani Center, P.O. Box 6, Bet Dagan, 50250, Israel*
[2]*Department of Entomology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA*

ABSTRACT

Species of the ant genus *Melissotarsus* Emery are widespread in the Afrotropical region (three species, namely *M. beccarii* Emery, *M. emeryi* Forel and *M. weissi* Santschi) and in the Madagascar region (one species, namely *M. insularis* Santschi). The ants of all these species tunnel their galleries in live wood of various dicotyledonous trees, close to the bark surface. The ants maintain within these galleries populations of different species of armoured scale insects. A review is presented on the geographical distribution of mutualism, of the *Melissotarsus* species, the associated 10 species of armoured scale insects, and the host plants on which the mutualism takes place. The ecology of the mutualism is discussed also, together with suggestions on the benefits that the partners gain from the associations.

KEYWORDS: Coccoidea, Diaspididae, scale insects, *Melissotarsus*, ants, mutualism, Africa, Madagascar.

Introduction

The ant genus *Melissotarsus* (Hymenoptera: Formicidae) was described by Emery in 1877 for the species *Melissotarsus beccarii,* which was collected in Ethiopia. Three additional species were described during following years, namely, *M. emeryi* Forel, 1907 (from Ethiopia), *M. weissi* Santschi, 1910 (from Congo), and *M. insularis* Santschi, 1911 (from Madagascar). The genus was regarded as unique, and placed in the tribe of its own, Melissotarsini, but this was based purely on morphological features of the ants. In the 1970's it was verified that the *Melissotarsus* ants are also unique in their ecology and biology, as they maintain in their bark-galleries in close association with live populations of armoured scale insects, Diaspididae. This mutualism was discovered almost concurrently, by Delage-Darchen et al. (1972) in the Ivory Coast, by Prins et al. (1975) and by Ben-Dov (1978) in South Africa.

This paper presents an up-to-date review on the mutualism structure, its geographical distribution, host plants, the *Melissotarsus* species involved, and the armoured scale partners.

Geographical Distribution

Ants of the genus *Melissotarsus* are widely distributed in the Afrotropical region - Saudi Arabia, West Africa (Ivory Coast), Central

**Corresponding author, e-mail: yairbd@netvision.net.il*

Africa (Burundi, Cameroon, Congo), South Africa and in Madagascar (see Table 1; Bolton 1982).

Structure and Biology of the Mutualism

Colonies of *Melissotarsus* species live in a network of galleries that are tunneled by the workers (Fig. 1) in both bark and live wood. Each gallery is 5-6 mm in diameter. Although the galleries are tunneled very close to the external surface of the bark, their presence can be detected only by cutting the bark (Fig. 2, 3). Workers never forage outside their nest galleries. These colonies can become extremely large, for example about 43000 individuals of *M. beccarii* were counted in $1m^2$ of bark (Mony et al. 2002). The *Melissotarsus* ants are uniquely adapted to living in galleries: (1) the workers walk with their mesothoracic legs pointing upwards in contact with the ceiling of the galleries (Fig. 1). Workers taken out of the galleries and placed on a flat surface will stagger (Delage-Darchen 1972). (2) Their large head glands produce silk that is excreted around the hypo stoma, corresponding to the only known case of silk production by adult ants (Fisher and Robertson 1999). The modified protarsi of their forelegs are used to pull and spin the silk to line and plug the galleries. (3) Within the galleries, *Melissotarsus* workers tend live populations of armoured scale insects (Hemiptera: Coccoidea: Diaspididae) (Fig. 4) (Delage-Darchen et al. 1972, Prins et al. 1975, Ben-Dov 1990, Mony et al. 2007)

FIG. 1. Scanning electron microscope (SEM) micrograph of worker of *M. beccarii*..

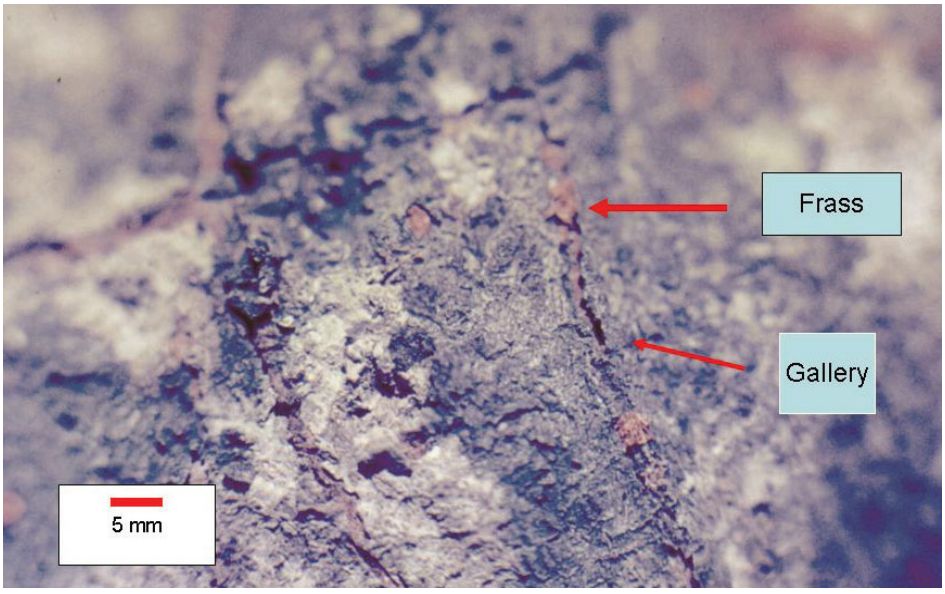

FIG. 2. External surface of bark of *L. praemorsum* infested with tunnels of *M. beccarii*.

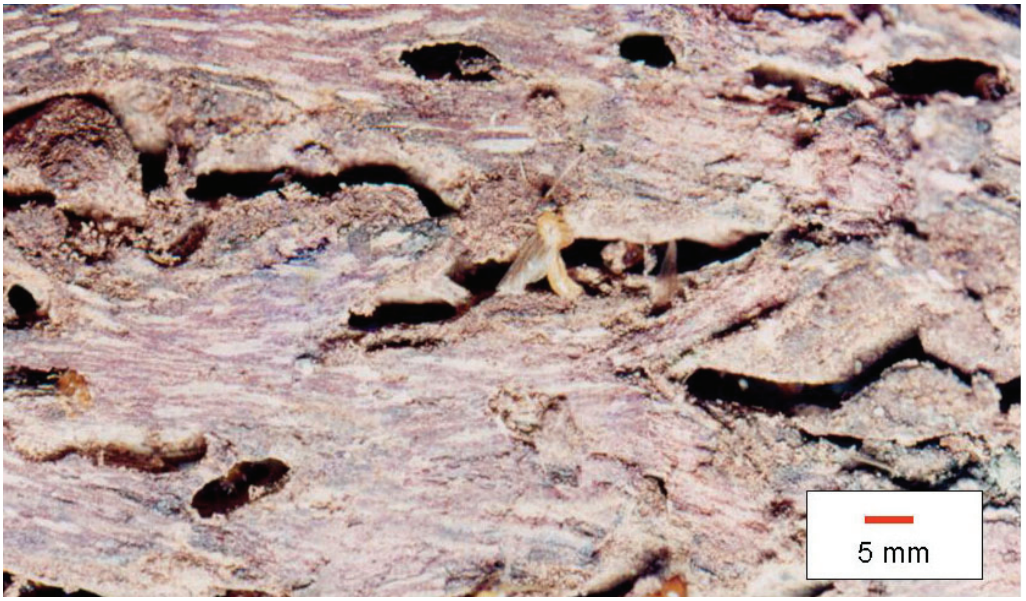

FIG. 3. Exposed tunnels of *M. beccarii* in bark of *L. praemorsum.*

FIG. 4. Gallery of *M. beccarii* with live population of *Morganella* sp., Lamto, Ivory Coast.

TABLE 1. Published records of *Melissotarsus* species, their associated Diaspididae species and host plants in the Afrotropical and Madagascar regions, listed chronologically by date of discovery of the association.

Country	***Melissotarsus* spp.**	**Diaspididae species**	**Host plants**	**Reference**
Ivory Coast	*Me. beccarri* Emery	*Morganella pseudospinigera* Balachowsky	*Bridelia* sp., *Bauhinia* sp. *Piliostigma thoningii*	Delage-Darchen et al. 1972
Ivory Coast	*Me. beccarri* Emery	*Aspidiotus* sp.	*Cynometra* sp.	Delage-Darchen et al. 1972
South Africa	*Me. emeryi* Forel	*Morganella conspicua* (Brain)	*Leucospemum praemorsum*	Prins et al. 1975
South Africa	*Me. beccarri* Emery	*Andaspis formicarum* Ben-Dov	*Ficus capensis*	Ben-Dov 1978
Burundi	*Melissotarsus* sp.	*Morganella* sp.	*Mangifera indica*	Ben-Dov & Matile-Ferrero 1984
Congo	*Melissotarsus* sp.	*Melanaspis* sp.	*Mangifera indica*	Ben-Dov & Matile-Ferrero 1984
Saudi Arabia	*Me. emeryi* Forel	Not recorded	*Tamarix* sp.	Collingwood 1985
Cameroon	*Me. weissi* (Santschi)	*Morganella pseudospinigera* Balachowsky	*Mangifera indica*	Dejean and Mony 1991, Mony et al. 2002
Cameroon	*Me. beccarri* Emery	*Diaspis* sp.	*Dacryodes edulis*	Dejean and Mony 1991, Mony et al. 2002

TABLE 1 (continued). Published records of *Melissotarsus* species, their associated Diaspididae species and host plants in the Afrotropical and Madagascar regions, listed chronologically by date of discovery of the association.

Country	***Melissotarsus* spp.**	**Diaspididae species**	**Host plants**	**Reference**
Madagascar	*Me. insularis* Santschi	*Melanaspis madagascariensis* Mamet	Euphorbiaceae, *Euphorbia antso* *Euphorbia stenoclada* *Hilsenbergia croatii* *Leptadenia madagascariensis* *Pachypodium geayi*	Ben-Dov, 2010
Madagascar	*Me. insularis* Santschi	*Melissoaspis fisheri* Ben-Dov	undetermined	Ben-Dov 2010
Madagascar	*Me. insularis* Santschi	*Melissoaspis fisheri* Ben-Dov	undetermined	Ben-Dov 2010
Madagascar	*Me. insularis* Santschi	*Melissoaspis reticulata* Ben-Dov	*Albizia* sp. *Boscia longifolia*	Ben-Dov 2010
Madagascar	*Me. insularis* Santschi	*Morganella conspicua* (Brain)	*Boscia longifolia* *Casuarina equisetifolia* *Fernandoa madagascariensis* *Leptadenia madagascariensis* *Maytenus linearis*	Ben-Dov 2010
Madagascar	*Me. insularis* Santschi	*Morganella formicaria* Ben-Dov	*Azima tetracantha* *Grewia cyclea* *Rinorea greveana* *Salvadora angustifolia*	Ben-Dov 2010

Diversity of the *Melissotarsus* and the Diaspididae species

The four ant species of the genus *Melissotarsus* and their geographic distribution in Africa and Madagascar are listed in Table 1. Seven named species of Diaspididae, and 4 unnamed species have been found (see Table 1) to live in association within galleries of these *Melissotarsus* species. These armoured scale insects belong to the two major sub-families, namely Aspidiotinae and Diaspidinae, of the family Diaspididae.

Host plants

The association of *Melissotarsus* ants with species of armoured scale insects has been recorded so far from 23 species of dicotyledonous trees that belong to 15 different families, as follows: Anacardiaceae: *Mangifera indica*. Apocynaceae: *Pachypodium geay, Leptadenia madagascariensis.* Bignoniaceae: *Fernandoa madagascariensis.* Boraginaceae: *Hilsenbergia croatii*. Brassicaceae: *Boscia longifolia.* Burseraceae: *Dacryodes edulis*. Casuarinaceae: *Casuarina equisetifolia*. Celastraceae: *Maytenus linearis*. Euphorbiaceae: *Bridelia ferruginea, B. micrantha, Cynometra megalophylla, Euphorbia sp., E. antso, E. stenoclada*. Fabaceae: *Albizia* sp., *Piliostigma thoningii.* Malvaceae: *Grewia cyclea*. Moraceae: *Ficus capensis.* Proteaceae: *Leucospermum praemorsum.* Salvadoraceae: *Azima tetracantha, Salvadora angustifolia.* Violaceae: *Rinorea greveana*.

Discussion and Conclusions

The trophobiotic interrelationships between ants and species of hemipteran insects has been comprehensively described and reviewed by Nixon (1951), Way (1963), Wilson (1971), Ben-Dov (1990) and by Gullan (1997). In as much as scale insects (Coccoidea) were concerned these reviews indicated that until the 1970's the association was recorded only with honeydew-producing scale insects, such as members of the families Coccidae, Kerriidae, Margarodidae and Pseudococcidae.

Since the early 1970's, many observations have provided growing evidence that close and direct relationships also exist between ants and armoured scale insects, family Diaspididae, coccoids which do not eliminate honeydew (see Ben-Dov 2010, and Table 1). These relationships have been observed so far only in Africa and Madagascar between 11 species of Diaspididae, and ant species that belong to the genus *Melissotarsus* Emery (Formicidae, Myrmicinae, Melissotarsini).

The association might be generalized as follows:

1. It takes place between populations of armoured scale insects that infest, develop and reproduce within galleries constructed by *Melissotarsus* ants in live bark of the host plants.
2. The armoured scale associates within the ant galleries are without the normal diaspidoid scale covers.
3. The *Melissotarsus* ants are uniquely adapted to live in galleries. The workers walk with their mesothoracic legs pointing upwards in contact with the ceiling of the galleries. Workers taken out of the galleries and placed on a flat surface will stagger.
4. The Diaspidoid partners involve members of the two largest (in terms of species diversity) sub-families of the Diaspididae, namely Aspidiotinae and Diaspidinae.
5. The association is widely-distributed in Africa and Madagascar (see Table 1).
6. These associations were recorded from 23 species of host plants, belonging to 15 dicotyledonous families. It was not recorded from monocotyledons, nor from palm trees; See 'host plants' above.

The absence of the normal diaspidoid scale covering in armoured scales when living in the galleries of the ants is the most unusual or 'puzzling' feature, for which the

following hypotheses are suggested: i. The diaspidids have become highly adapted to an association with certain ant species and no longer secrete a scale cover. Indeed, four Diaspididae species, namely *Andaspis formicarum*, *Melissoaspis fisheri, Melissoaspis reticulata* and *Morganella formicaria* are so far known only from populations that lack this cover. On the other hand, several species have been recorded both from 'scale-less' populations as well as from populations that possess normal diaspidoid scale cover, namely, *Morganella conspicua*, *Morganella pseudospinigera,* and *Melanaspis madagascariensis*. ii. The individuals of all of these diaspidid populations are excreting the waxy material from their pygidial glands, but the wax is continuously collected by the *Melissotarsus* ants, consequently preventing the scale formation. Prins et al. (1975) observed the workers of *Melissotarsus emeryi* moving within population of *Morganella conspicua,* scanning both surfaces of the pygidium with their mouthparts. It is very likely that the workers were collecting the waxy excretion during this process. iii. A chemical effect is exerted by the ants which interferes with or inhibits the regular process of scale formation. Staal (1975) reported that juvenile hormone and insect growth regulators inhibited scale formation in the Diaspididae, causing abnormalities.

Armoured scale insects can only disperse as first-instar crawlers, becoming sessile at later stages. Therefore, the establishment of a Diaspidoid population within the galleries might be realized only if the crawlers moved into or have been introduced to the galleries. Based on current knowledge of this mutualism, we speculate that the ants appear to be a major active participant. The ants introduce the armoured scale insects into their galleries, maintain and control their populations. Ben-Dov (1978) suggested that the scale insects are eaten by the ants. Mony et al. (2007), based on their observations, confirmed this interpretation. The Diaspidoid partner is confined to a closed habitat in which the ants almost entirely control and maintain its population. The benefit to the armoured scale insects appears to be mainly, if not only, the protection from natural enemies.

It is suggested here that the mutualism have evolved over much wider territories in the Afrotropical region, between *Melissotarsus* species and many more Diaspididae species. It will be found wherever the trophobiotic requirements and the ecological conditions are suitable for both partners, the ants and the Diaspidids.

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Συμβίωση μυρμηγκιών του γένους *Melissotarsus* και κοκκοειδών εντόμων στην Αφρική και τη Μαδαγασκάρη: Κατανομή, φυτά ξενιστές και βιολογία

Y. BEN-DOV[1] ΚΑΙ B.L. FISHER[2]

[1]*Department of Entomology, Agricultural Research Organization, The Volcani Center, P.O. Box 6, Bet Dagan, 50250, Israel*
[2]*Department of Entomology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA*

ΠΕΡΙΛΗΨΗ

Είδη μυρμηγκιών του γένους *Melissotarsus* Emery είναι διαδεδομένα στην Αφροτροπική περιοχή (τρία είδη *M. beccarii* Emery, *M. emeryi* Forel και *M. weissi* Santschi) καθώς και ένα είδος στην Μαγαδασκάρη (*M. insularis* Santschi). Τα μυρμήγκια όλων αυτών των ειδών δημιουργούν τις στοές τους σε ζωντανό ξύλο διαφόρων δικοτυλήδονων δένδρων, κοντά στο φλοιό. Τα μυρμήγκια διατηρούν εντός των στοών πληθυσμούς διαφόρων ειδών κοκκοειδών εντόμων της οικογένειας Diaspididae. Στην παρούσα εργασία παρουσιάζεται μια ανασκόπηση πάνω στη γεωγραφική κατανομή της παρατηρούμενης συμβίωσης των ειδών μυρμηγκιών του γένους *Melissotarsus* και των δέκα ειδών κοκκοειδών εντόμων της οικογένειας Diaspididae, καθώς και των φυτών ξενιστών όπου παρατηρείται η συμβίωση. Η οικολογία της παρατηρούμενης συμβίωσης συζητείται καθώς και τα πιθανά οφέλη που προκύπτουν για τα είδη που συμβιώνουν.