Mite Faunas and Morphology of Acarinaria on Japanese and Taiwanese Large Carpenter Bees (Hymenoptera: Apidae)

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ABSTRACT

We examined structures of acarinaria and phoretic mite faunas of the large carpenter bees *Xylocopa amamensis*, *X. flavifrons*, *X. albinotum*, and *X. ogasawarensis* from Japan, and compared them with those of *X. tranquebarorum* and *X. ruficeps* from Taiwan. While the first three Japanese *Xylocopa* bees had acarinaria both on the mesosoma and on the first metasomal tergum like the common Japanese large carpenter bee, *X. appendiculata circumvolans*, *X. ogasawarensis* did not have distinctive mesosomal acarinaria. *Xylocopa tranquebarorum*, which nests in bamboo, did not have either kind of acarinarium. Of the species examined, only *X. ruficeps* had a distinctive metasomal acarinarium, which was a deep, round cavity that opened on the first metasomal tergum.

All mites except for *Dinogamasus* were collected from host's mesosoma, wing base furrows, mesosomal acarinaria and the metasomal acarinarium. We collected mites of two *Sennertia* spp. (*alfkeni*, *japonica*) and *Horstia helenae* from the Japanese bees. The Taiwanese bees also carried *Sennertia* and *Horstia* mites but probably of different species. Only *X. ruficeps* carried mesostigmatid mites (*Dinogamasus* sp.) in the metasomal acarinarium. We suggest that *Sennertia* deutonymphs are well adapted to be phoretic on the large carpenter bees with specialized body structures such as attachment organs and hook-like pretarsal claws as seen in other astigmatids phoretic on bees. In contrast, putatively beneficial mites, such as those of the genus *Dinogamasus*, have possibly been specialized to settle in the distinctive acarinaria in the course of mutualistic evolution with the host.

Key words: *Sennertia*, *Dinogamasus*, *Horstia*, *Xylocopa*, phoresy, morphological adaptation

INTRODUCTION

Since Roepke (1920) first used the term "acarinarium" to refer to a groove or cavity harboring phoretic mites, their morphologies have been documented in several taxa of Hymenoptera. For example, a number of bees (e.g. *Ctenocolletes* of Stenotritidae, several genera of Halictidae, and Xylocopinae of Apidae) and wasps (*Acarozumia*, *Seudonortonia* and *Acarodinerus* of Eumenidae) have various types of acarinaria (Eickwort, 1994; Fain, 1984; OConnor and Klompen, 2000; Soika, 1985) on their mesosoma and/or metasoma. Although in most cases the mites are only phoretic on the hosts, mutualism has often been suggested between the mites and the hosts, because the acarinaria of some bees or wasps

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look so specialized that it is difficult to think of other relationships.

Large carpenter bees of *Xylocopa* have two different kinds of acarinarium: a pair of relatively small cavities on mesosoma (hereafter called mesosomal acarinarium) as described by OConnor (1993) in *X. latipes* (Drury), and a single metasomal acarinarium on the first tergite of various sizes and shapes (e.g. *X. flavorufa* (DeGeer) and *X. latipes*) (Madel, 1974;

Fig. 1. Distribution of five Japanese (*Xylocopa appendiculata circumvolans*, *X. amamensis*, *X. albinotum*, *X. flavifrons*, and *X. ogasawarens*) and two Taiwanese (*X. ruficeps* and *X. tranquebarorum*) large carpenter bees.

OConnor, 1993). The metasomal acarinarium varies from a mere vertical fold to an invaginated chamber among the host species (Hurd and Moure, 1963). Mites of *Dinogamasus* of Mesostigmata, Cheyletidae and *Tarsonemus* of Prostigmata, and *Sennertia* and *Horstia* of Astigmata have been particularly documented as using acarinaria during phoretic activities on xylocopine bees (Eickwort, 1994; Fain et al., 1980; Lindqvist, 1998; OConnor, 1988, 1993; Putatunda and Kapil, 1988; Smiley and Whitaker, 1981).

Mites of the genus *Sennertia* are associated with large and small carpenter bees throughout the world. Most of the mites are collected from adult hosts as deutonymphs and only phoretic association has been confirmed in such examples. Only a few cases indicated that the mites were cleptoparasites and also scavengers in host nests (Alzuet and Abrahamovich, 1990; Lombert et al, 1987; OConnor, 1988; Skaif, 1952; Watmough, 1974).

Dinogamasus mites are specific to carpenter bees of subgenera including *Koptrotosoma*, *Mesotrichia* and *Afroxylocopa*, and have so far been found only in the deep metasomal acarinarium, while *Sennertia* mites stay not only in the mesosomal and metasomal acarinaria but also on other locations of a host including metasomal hair. We examined four species of Japanese and two Taiwanese large carpenter bees for phoretic mite fauna and phoretic positions. We used the results of a previous study (Okabe and Makino, 2002) on the common Japanese large carpenter bee, *X. appendiculata circumvolans* Smith and its phoretic mites for comparison. Finally, we considered how the acarinaria of those hosts might have value for the associated mites.

MATERIALS AND METHODS

We examined phoretic mites on dried specimens of four Japanese (*X. amamensis* Sonan, *X. albinotum* Matsumura, *X. flavifrons* Matsumura and *X. ogasawarensis* (Matsumura)) and two Taiwanese (*X. ruficeps* Friese and *X. tranquebarorum* (Swederus)) large carpenter bees. All specimens were loaned from the Natural Resource Inventory Center of the National Institute for Agro-Environmental Sciences (for collection data, host sexes and the number of specimens, see Appendix I). Geographical distributions of the bee species are shown in Fig. 1.

Dried bee specimens were softened in a plastic jar with wet cotton for a week at room temperature (about 20°C). We collected as many mites as possible from the following four parts of the host body: mesosoma (except wing base furrows and acarinaria), wing base furrows, mesosomal acarinaria (if they existed) and the metasomal acarinarium on the first tergum to learn distribution of each mite species on different locations on the same host (also see Eickwort, 1994). The collected mites were mounted in Hoyer's medium for identification. Idiosomal lengths of 10 *Sennertia* individuals randomly taken from each of the four body locations of every specimen were measured with an ocular micrometer under a microscope.

Because we were not allowed to dissect the bee specimens, we were not able to observe mesosomal and metasomal acarinaria in details. Only the first tergum was photographed in each species.

RESULTS

Mite faunas of the *Xylocopa* species were as follows: *Sennertia alfkeni* (Oudemans) and *S. japonica* (Oudemans) of Chaetodactylidae, and *Horstia helenae* (Oudemans) of Acaridae on all Japanese species, *X. amamensis*, *X. albinotum*, *X. flavifrons* and *X. ogasawarensis*; two (possibly undescribed) species of *Sennertia* very different from *S. alfkeni* or *S. japonica* and a few *Horstia* species on *X. tranquebarorum*; and two species of *Sennertia* similar to *S. alfkeni* or *S. japonica* on both male and female, and *Dinogamasus* sp. on female *X. ruficeps*. All bee species we examined, then, harbored at least two species of *Sennertia*. The morphology of the Taiwanese mites are described in detail elsewhere.

We found only a few individuals of *Horstia* mites (maximum 10) on each host. In every host species, some individuals had no mites but others had hundreds of *Sennertia* mites.

Table 1. Developmental states of acaritaria of bees. Mesosomal acaritaria were stated as either 1 (shallow indentation) or 2 (deeper cavity) and metasomal acarinarium was stated according to Hurd and Moure (1963) as 1 (the least developed state) to 4 (the most developed state).

	<i>X. a. circumvolans</i>	<i>X. amamensis</i>	<i>X. albinotum</i>	<i>X. flavifrons</i>	<i>X. ogasawarensis</i>	<i>X. ruficeps</i>	<i>X. tranquebarorum</i>
Mite species	<i>Sennertia alfkeni</i>	<i>S. alfkeni</i>	<i>S. alfkeni</i>	<i>S. alfkeni</i>	<i>S. alfkeni</i>	<i>Sennertia</i> spp.	<i>Sennertia</i> spp.
	<i>S. japonica</i>	<i>S. japonica</i>	<i>S. japonica</i>	<i>S. japonica</i>	<i>S. japonica</i>	<i>Dinogamasus</i>	<i>Horstia</i> sp.
	<i>Horstia helenae</i>	<i>Horstia helenae</i>	<i>Horstia helenae</i>	<i>Horstia helenae</i>	<i>Horstia helenae</i>	sp.	
Mesosomal acaritaria	2	2	2	2	1	2	1
Metasomal acarinarium	3	2	2	2	2	4	1

Fig. 2. Pictures of metasomal acaritaria of four Japanese (*X. amamensis*, *X. albinotum*, *X. flavifrons*, and *X. ogasawarensis*) and two Taiwanese (*X. ruficeps* and *X. tranquebarorum*) large carpenter bees, photographed under a stereomicroscope.

Fig. 3. Histograms of idiosomal lengths of *Sennertia* species on the mesosoma (except for the wing base furrows and mesosomal acarinaria) of four Japanese (*X. amamensis*, *X. albinotum*, *X. flavifrons*, and *X. ogasawarensis*) and two Taiwanese (*X. ruficeps* and *X. tranquebarorum*) large carpenter bees. Large mites (*S. alfkeni* on the Japanese bees and unidentified on the Taiwanese bees) are shown by bars with lines and the smaller mites having different structures from the large ones (*S. japonica* on the Japanese and unidentified on the Taiwanese) are shown with white bars.

Because of the small number of host specimens but large variation in the number of mites on them, we were not able to investigate the average number of phoretic *Sennertia* mites on each host. At any rate, we found no clear relationship between host sex and mite occurrence.

Dominant mites phoretic on the hosts were of *Sennertia*, and *Horstia* mites were sometimes found together with *Sennertia* mites. The *Horstia* mites were collected from the furrows and/or acarinaria on the specimens. Only female *X. ruficeps* had an invaginated metasomal acarinarium and possessed *Dinogamasus* and *Sennertia* mites together in it. *Xylocopa ruficeps* also had a pair of mesosomal acarinaria but only *Sennertia* mites were in them.

The number of *Dinogamasus* mites, which were only collected from the metasomal acarinarium, ranged from one to 10 on a single host. The mites sometimes were packed in the chamber so closely that it was difficult to pull out them intact. It was impossible to extract all *Sennertia* mites in the metasomal acarinarium without breaking the host, so that the exact number of mites was not counted.

The metasomal acarinarium corresponded to what Hurd and Moure (1963) called the “sulcate vertical fold of the first metasomal tergum” in a revision of the world *Xylocopa*. They recognized four character states of the structure based on the degree of development of

Fig. 4. Histograms of idiosomal lengths of *Sennertia* species on the wing base furrows of four Japanese (*X. amamensis*, *X. albinotum*, *X. flavifrons*, and *X. ogasawarensis*) and a Taiwanese (*X. ruficeps*) large carpenter bees. No mites were collected in the furrows of *X. tranquebarorum*. Legends are the same as in Figure 3.

the fold. The most developed state was the one that was found in *X. ruficeps*, and a slightly developed state (the second developed state in Hurd and Moure, 1963) was found in *X. amamensis*, *X. albinotum*, *X. flavifrons*, and *X. ogasawarensis* (Fig. 2). The groove on the first tergum of *X. tranquebarorum* represented the least developed state of the structure, which was a faint, linear depression.

It is much more difficult to recognize the mesosomal acarinarium as compared with the metasomal one, partly because they were heavily covered with hair. All large carpenter bees we examined had at least a narrow indentation on the dorsolateral position of the mesosoma, posterior to each of the wing bases. *Xylocopa ogasawarensis* and *X. tranquebarorum*, however, had no mites in the indentations.

Variations of idiosomal lengths of *Sennertia* mites found on the six host species are depicted in Figs. 3–6. Most mites collected from the mesosoma were located in dorsal and lateral hair although those on *X. tranquebarorum* aggregated both inside and outside the hairy region. In addition, idiosomal lengths of the mites showed the widest range on the mesosoma (except for the wing base furrows and the acarinarium) on most hosts (Figs. 3–6). While the mesosoma harbored larger mites (=mites with longer idiosomas) in the Japanese hosts, there was no clear tendency in the size of the mites on the Taiwanese hosts (Figs. 3–6).

The wing base furrows were very small in *X. tranquebarorum*, making it virtually impossible for mites to enter them. The furrows were similarly small in *X. ogasawarensis*

Fig. 5. Histograms of idiosomal lengths of *Sennertia* species on the mesosomal acarinaria of three Japanese (*X. amamensis*, *X. albinotum*, and *X. flavifrons*) and a Taiwanese (*X. ruficeps*) species of large carpenter bees. No mites were collected on the mesosomal acarinaria of either *X. ogasawarenensis* or *X. tranquebarorum*. Legends are the same as in Figure 3.

but they were covered with a small number of mites (Fig. 4). Larger *Sennertia* mites covered an open area of the narrow, shallow groove of the first tergum of *X. tranquebarorum*, while smaller *Sennertia* attached to the surfaces of the grooves in the Japanese bees (Fig. 6).

DISCUSSION

Morphologies of both mesosomal and metasomal acarinaria were more or less similar in *X. appendiculata circumvolans* (Okabe and Makino, 2002), *X. amamensis*, *X. albinotum* and *X. flavifrons* (Fig. 2). These four species all belong to the subgenus *Alloxylocopa* (Hurd and Moure, 1963) and are morphologically similar to each other (Hirashima and Yasumatsu, 1964). Although they show typical allopatric distributions in the Japanese mainland and the Ryukyu archipelago, there might be and/or may have been numerous occasions for these bees with a strong flying ability to invade each other's range (Yamane, 1983). Unintended, artificial introduction of nests is also possible (Yamane, 1983). These events may have allowed the introduced mites to infest indigenous hosts and establish there.

Of course, it is also possible that ancestral species of these carpenter bees had the same mite species as found today. *Xylocopa ogasawarenensis*, which is the only Japanese species of the subgenus *Koptortosoma* (but see Hurd and Moure, 1963; Yasumatsu and Hirashima,

Fig. 6. Histograms of idiosomal lengths of *Sennertia* species on the metasomal acarinarium of four Japanese (*X. amamensis*, *X. albinotum*, *X. flavifrons*, and *X. ogasawarensis*) and two Taiwanese (*X. ruficeps* and *X. tranquebarorum*) large carpenter bees. Legends are the same as in Figure 3. *Xylocopa tranquebarorum* did not have any metasomal acarinarium, but we collected mites from the surface of the first tergite.

1964), also had the same mite species that the other Japanese carpenter bees had. Although the origin of *X. ogasawarensis* has not been determined yet, its ancestor that invaded the islands (most likely by means of driftwood) might have the same mite fauna that is found there today.

The acarinarium of the Taiwanese hosts were different from those of the Japanese. We do not consider the state of the mesosomal cavity on *X. tranquebarorum* as a functional acarinarium, because it was too shallow to harbor mites; in fact, there were really no mites in it. Similarly, the metasomal groove could not be a functional acarinarium because mites did not settle in it but instead covered the surface. Distribution of idiosomal lengths of the mites on *X. tranquebarorum* was not the continuous variation represented in the other hosts (Fig. 3 & 6). This suggests that two *Sennertia* species on the host were not close relatives but possibly different species.

Only *X. ruficeps* harbored a *Dinogamasus* species, which may be an undescribed one (Lindqvist, *pers. com.*). This is because, of the *Xylocopa* species examined, only *X. ruficeps* had the invaginated metasomal acarinarium deep enough to harbor large *Dinogamasus* mites; moreover, because no other bees had such acarinarium or *Dinogamasus* mites, it might have been necessary for carpenter bees to evolve the invaginated acarinarium in order to keep the mite with them.

Dinogamasus mites may confer a benefit to the host by eating various microbes, thus maintaining hygiene in the nest (Eickwort, 1994; Madel, 1975). However, we have found no unequivocal relationship between *Dinogamasus* mites and the host at present; thus, it may be too early to conclude that the metasomal acarinarium has been developed in order to keep *Dinogamasus* mites in it.

In *X. ruficeps*, the larger of the two *Sennertia* species was collected more often around the mesosomal acarinaria than in the other *Xylocopa* bees, probably because their openings are larger than those of the other bees.

No studies have shown or suggested any beneficial effect of *Sennertia* in terms of increasing the fitness of the host. *Sennertia* mites are documented as scavengers, which may or may not be crucial for host survival or reproduction (Alzuet and Abrahamovich, 1990). On the other hand, they may be facultative cleptoparasites feeding on stored pollen (Okabe, unpublished). We presume, however, that their negative or positive effects to the host, if any, are very weak.

Sennertia alfkeni and *S. japonica* efficiently use the body structure of *X. a. circumvolans*: the larger species *S. alfkeni* harbor themselves in the hair using its pretarsal claws which adapted to hold host hairs, while the smaller *S. japonica* tend to stay in grooves and cavities. The smaller species has attachment organs like *S. alfkeni* but their claws are not large enough to hold hairs (Okabe and Makino, 2002, and in this study).

Except for the distinctive invaginated metasomal acarinarium as found in *X. ruficeps*, so-called acarinaria (various grooves or depressions) on large carpenter bees seem to be generally used by mites that are neutral in terms of host survival or reproduction. It is likely that mites such as *Sennertia* only utilize pre-existing structures on the body surface, which have evolved irrespective of symbiosis with the mites. Once the mites started to use those structures, they may have developed behavioral and morphological characters useful for phoresy. The function of “acarinaria” should be critically examined from the viewpoint of host-mite relationships.

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摘要

日本および台湾産クマバチのダニ相とアカリナリウムの形態

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日本産クマバチのアカリナリウムとハチに便乗するダニを調べ、台湾産 2 種 (*X.*

tranquebarorum, *X. ruficeps*) と比較した。キムネクマバチ、アマミクマバチ、オキナワクマバチ、アカアシセジロクマバチは、中胸の翅基部後方と腹部第1節にアカリナリウムを有したが、オガサワラクマバチには中胸のアカリナリウムがなかった。日本産クマバチには、クマバチコナダニとコガタノクマバチコナダニ、ヒメクマバチカザリコナダニが便乗していた。竹に営巣する *X. tranquebarorum* にはどちらのアカリナリウムもなく、日本産とは別種の *Sennertia* と *Horstia* が便乗していた。 *Xylocopa ruficeps* だけは腹部に大きく深いアカリナリウムを有し、 *Dinogamasus* 属の一種はこのアカリナリウムだけから発見された。コナダニは胸部や翅基部からも得られた。 *Sennertia* 属の第二若虫は付着器や大型の爪などの特殊化した形態を有し、便乗に特化していると考えられた。また、 *Dinogamasus* 属は、大型のアカリナリウムを利用するように特殊化したと考えられた。

Appendix I. Host large carpenter bee specimens examined

Xylocopa amamensis Sonan

Kagoshima, Japan: 1 ♀, Amamioshima Is., 25.IV.1969 (A. Uno leg.); 1 ♀, Koshuku, Amamioshima Is., 8.V.1987 (T. Yasunaga).
Ryukyu Is., Japan: 1 ♀1 ♂, 29.IV.1953 (T. Shiraki); 1 ♂, 1.V.1953 (T. Shiraki); 4 ♀♀, 11.V.1953 (T. Shiraki); 1 ♂1 ♀, 20. V.1953 (T. Shiraki); 1 ♂, 21.V.1953 (T. Shiraki).

X. albinotum Matsumura

Okinawa Prefecture, Japan: 1 ♀, Iriomote Is., 22.X.1971 (N. Uemura); 1 ♀, Iriomote Is., 21–22.III.1987 (I. Hattori); 1 ♂, Funadomari, Iriomote Is., 9.X.1977 (S. Yamane); Sonai, Iriomote Is., 28.VI.1973 (S. Yamaguchi); 1 ♀, Shirahama, Ishigaki Is., 3.XI.1963 (K. Iha); 1 ♀, Mt. Hanna, Ishigaki Is., 4.III.1973 (H. Hasegawa); 1 ♀, Mt. Omoto, Ishigaki Is., 26.VI.1971 (T. Aoki)

X. flavifrons Matsumura

Kagoshima Prefecture, Japan: 1 ♀, Yoron Is., 28.IV.1969 (A. Uno).
Okinawa Prefecture, Japan: Kumejima Is., 1 ♀, 10.VII.1952 (K. Sato); 1 ♂, Yomitan, Okinawa Is., 24.VI.1952 (K. Sato); 2 ♂♂, Yona, Okinawa Is., 31.III.1973 (T. Teruya); 1 ♀, Okinawa Is., 1.VII.1958 (J. Minamikawa); 2 ♀♀, Okinawa Is., 18–24.VII.1965 (K. Hayakawa);
Ryukyu Is., Japan: 2 ♀♀, 20.III.1953 (T. Shiraki); 1 ♀, 1.IV.1953 (T. Shiraki); 1 ♂, 7.IV.1953 (T. Shiraki); 10 ♂♂, 9. IV.1953 (T. Shiraki); 2 ♀♀, 9.IV.1953 (T. Shiraki); 6 ♂♂1 ♀, 11.IV.1953 (T. Shiraki).

X. ogasawarensis Matsumura

Ogasawara, Japan: 1 ♀, Chichijima Is., 1.VIII.1968 (A. Savory)

X. tranquebarorum (Swederus)

Taiwan: 1 ♀, Heito, 11.VII.1941 (K. Okamoto); 3 ♀♀, Kenting Park, Heng-chun, 8.III.1982 (S. Watahiki); 1 ♀, Kenting Park, Heng-chun, 12.III.1982 (S. Watahiki); 2 ♀♀, Kenting Park, Heng-chun, 14.III.1982 (S. Watahiki); 1 ♀, Kenting, 22.IV.1971 (N. Fukuhara); 1 ♀, Kenting, 26.IV.1971 (N. Fukuhara); 3 ♀♀, Kenting, 24–25.VI.1985 (M. Miyazaki); 1 ♀, Kuantzuling, 2.V. 1971 (N. Fukuhara); 2 ♀♀, Lien-hua Chi, 24.III.1982 (S. Watahiki); 3 ♀♀, Santimen, 28. IV.1971 (N. Fukuhara); 3 ♀♀, 18.VII.1940 (M. Kawai); 2 ♀♀, Tensiang, 16.V.1971 (N. Fukuhara); 1 ♀, Yangmingshan, 23.V.1971 (N. Fukuhara).

X. ruficeps Fries

Taiwan: 1 ♀, Chihpen, 11.IV.1971 (N. Fukuhara); 1 ♀, Kenting Park, Heng-chun, 7.III.1982 (S. Watahiki); 3 ♀♀, Kenting Park, Heng-chun, 12.III.1982 (S. Watahiki); 1 ♀, Lanyu Is., 11.IV.1971 (N. Fukuhara); 4 ♀♀, Lanyu Is., 14.IV.1971 (N. Fukuhara); 2 ♀♀, Lanyu Is., 15.IV.1971 (N. Fukuhara); 3 ♀♀, Lanyu Is., 17.IV.1971 (N. Fukuhara); 3 ♀♀, Lien-hua Chi, 24.III.1982 (S. Watahiki); 1 ♀, Taitung-Lanyu, 1.IV.1971 (N. Fukuhara); 1 ♀, Yangmingshan, 23.V.1971 (N. Fukuhara).