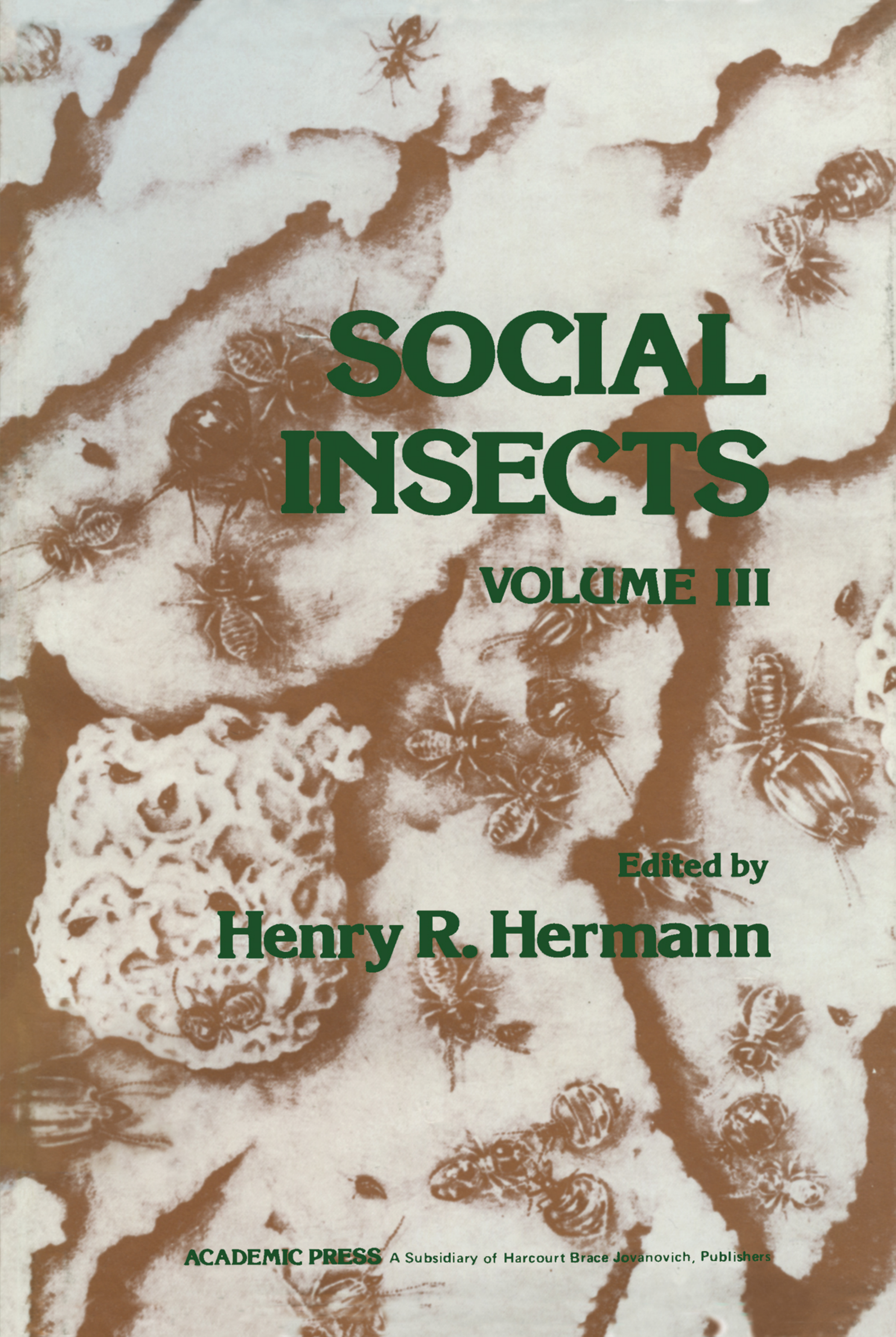

SOCIAL INSECTS

VOLUME III

Edited by

Henry R. Hermann

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Volume III

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Edited by HENRY R. HERMANN

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To My Wife, Lisa,
and Son, Brad

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Preface

Chapter 1 of this volume represents the culmination of discussion on social insect phenomena in this four-volume treatise, and leads into subsequent chapters on the biology of the groups of eusocial Insecta themselves.

As portrayed in Chapter 1, insect symbionts represent a very complex group of organisms of quite diverse habits. Knowledge of the number of symbiotic species and their unusual associations with eusocial insects is staggering—hence the very lengthy treatment. Nonetheless, new symbionts are still being recognized almost daily, and the relationships are increasingly fascinating.

The remainder of this volume is dedicated to the Apidae, including the Apinae (Meliponini and Apini) and the Bombinae. As pointed out in Volume I, Chapter 3, by Carpenter and Hermann, the patterns of social behavior in the Apidae are considerably more diverse than in the Vespidae, as well as in the Formicidae. The bees obviously have developed eusociality independently many times, and eusociality in the bees has reached its climax in the Apidae. Since social behavior is found in other groups of bees as well, especially in some Halictidae and Anthophoridae, the reader is invited to peruse Volume II, Chapter 3, by Eickwort, to round out the picture of sociality in the bees in general.

Henry R. Hermann

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1

The Social Insects' Bestiary

DAVID H. KISTNER

SOCIAL INSECTS, VOL. III

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I. INTRODUCTION

A. Definition of Terms

Symbionts of social insects are usually called myrmecophiles, termitophiles, melittophiles, or sphecophiles depending upon whether they are found with ants, termites, bees, or wasps, respectively. The terms, as they are used in the literature, merely denote that an insect is usually found in association with its host. They do not imply anything about whether the relationship is facultative or obligatory or anything about the specificity. However, as more is known about the relationships of the arthropods involved, casual relationships can usually be excluded from the category and they then imply some sort of symbiosis. The origins of the terms are quite interesting. Myrmecophile is the oldest, first appearing in English literature in the late 1800s and transferring quite naturally into American English. Termitophile was used quite freely in the German literature as early as 1857 (Kraatz, 1857) but it did not appear in English literature until the American, Schwarz (1889), introduced it. Mellitophile and sphecophile were introduced into English by Wheeler (1928) and they have not found their way yet into standard English dictionaries.

A myrmecophile (or other symbiont) is said to be integrated into the ant colony (or other colony) if it interacts with the ants so that the ants accept it into their society. This is in contrast to other myrmecophiles which may never achieve integration into the ant society but which may, nevertheless, live in the nest and exploit its natural resources. Such myrmecophiles are said to be nonintegrated. These definitions are greatly expanded and illustrated in Chapter 8 of Volume I of this series.

Integration may be effected by the use of chemical cues or by tactile mimicry. These concepts are also expanded and illustrated in Volume I of this series. Tactile mimicry when used to effect social integration is called Wasmannian mimicry (Rettenmeyer, 1970). The meaning of Wasmannian mimicry was expanded by Kistner and Jacobson (1975) to include all mimicry of social releasers. Thus integration by the use of pheromones could also be a form of Wasmannian mimicry if the chemical mimicked a pheromone which functioned as a normal social releaser among members of the social insect colony.

Such mimicry is still controversial among students of social insects, some of whom believe that tactile mimicry is the result of selection by predators outside the social insect society. Social insects tend to be avoided by predators, since most have stings, can emit noxious substances, or have powerful mandibles. Thus a symbiont might escape predation by its resemblance to undesirable prey. If this is true, then ant mimicry or termite mimicry would be a form of Batesian mimicry. Undoubtedly, elements of Batesian mimicry function in the New World army ant societies where some myrmecophiles such as *Ecitophya* and *Ecitomorpha* habitually accompany their *Eciton* hosts on raids. Where color changes throughout the range of *Eciton burchelli* Westwood, the color of the species of *Ecitomorpha* and *Ecitophya* varies accordingly. The color of other myrmecophiles found with the same hosts which do not comingle on raids does not vary. Thus form and texture of *Ecitophya* and *Ecitomorpha* are probably aspects of Wasmannian mimicry, permitting acceptance by the ants, whereas color, which would be meaningless to the ants with their limited eyesight, would be a form of Batesian mimicry directed at outside predators such as the numerous ant birds who are attracted to the ant columns primarily to pick up insects which are flushed out by the ants (Willis and Oniki, 1978).

The foregoing types of phenomena are stressed in this chapter, however, any interesting aspects of social biology of the symbionts are reviewed even if they do not presently fit into any existing conceptual framework. It is only by keeping unexplained phenomena in the forefront that new concepts emerge. Absent from this discussion are concepts such as amical selection and symphilic instincts which were elaborated by Wasmann (1920, and elsewhere). These concepts have been laid to rest many times, most thoroughly by K. Hölldobler (1948), so that there is no need to resuscitate them here. The concept of Wasmannian mimicry does not need these erroneous props.

B. Scope of the Chapter

In Chapter 8 of Volume I of this treatise, the social and evolutionary significance of myrmecophiles and termitophiles was discussed. Data organized around such themes are necessarily selective and tend to give the impression that far fewer foreign insects inhabit the nests of social insects than are actually there. The purpose of this chapter is to review the social biology of all the groups of Arthropods found with the social insects. The mere presence of a foreign insect in a nest of social insects is a biological fact, but these myriads of facts are not reviewed unless something else is known about the interaction of the foreign insect with its hosts. There is a great need for a catalog of the social insect symbionts by host but this is not the format in which to do it.

To my knowledge, the only previous attempts to do this were by Escherich (1909) and Donisthorpe (1927). Escherich's essay was limited to guests of termites, while Donisthorpe's book was limited both to guests of ants and geographically limited to the United Kingdom. Wilson (1971) gave an adumbrated table in which he briefly reviewed some of the biology. All other monographs are limited to single taxonomic groups often found with far more limited hosts (Seevers, 1957, 1965). So many new discoveries have been made since the early 1900s that the time is propitious, if not overdue, for a general biological survey of the guests of social insects.

II. ARTHROPODS OTHER THAN INSECTS

A. Mites

Mites are among the most frequent guests of social insects. They are usually phoretic but some are clearly ectoparasites. Rettenmeyer (1962a), over a period of 6 years, examined 12,566 associates of army ants, of which 8000 or 64% were mites. A more extensive examination of individual neotropical army ants for phoretic or ectoparasitic arthropods showed that at least 95% of all arthropod guests are mites (C. W. Rettenmeyer, personal communication).

Mites were reported as phoretic upon ants in one of the earliest studies of myrmecophiles (Janet, 1897a). In his pioneering work, Janet showed that *Antennophorus uhlmanni* Haller rode on the underside of the head of *Lasius mixtus* Nylander with its elongated first legs directed forward (Fig. 1). In this position, it moved among other ants without incident. If the *Antennophorus* fell off the body of the ant, it walked along with its normal legs and at the same time tested the air with the long antenniform legs. When a *Lasius* passed by, it climbed aboard and resumed its normal position which is effected by adhesive pads on the walking legs.

Janet goes on to say that *Antennophorus* arranges itself symmetrically on the host. If one mite is on the ant (the majority of observations), it is on the underside of the head. If more than one is present, the next two go on the abdomen, one to a side, where they direct their antenniform legs backward. The mites exhibit a preference for newly enclosed workers with one such ant having seven mites. The workers first attempt to remove the mites but seem to give up after several unsuccessful trials. That the mites eat food passed from one worker to another was proven by Janet by coloring the ants' food with Prussian blue and then detecting the dye inside the mites. The antenniform appen-

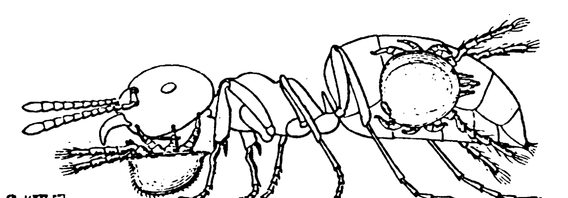

Fig. 1. *Antennophorus uhlmanni* in their normal position on a worker of *Lasius mixtus*. (From Janet, 1897a.)

dages, waved at the ants, have been interpreted as mimicking the ants' begging behavior. Mites attached to the gaster obtain their food by soliciting from nearby or passing ants.

The genus *Antennophorus* is found with many species of *Lasius* in Europe, (Bernard, 1968) and has been captured in America with *Acanthomyops* and *Lasius* (Wheeler, 1910b). Wheeler (1910b, 1928) suggests that the reduced eyes of the subterranean *Acanthomyops* helps the mites in their begging subterfuge. Observations similar to those of Janet were made by Park (1932) of *Antennophorus wasmanni* Wheeler associated with *Lasius aphidicola* Walsh in the United States. Antennophorids have also been taken from a nest of the stingless bee, *Trigona amalthea* (Oliv.), in Colombia (Salt, 1929).

Macrochelidae have recently been captured in the nests of *Odontotermes kibarensis* (Fuller) near Caiei, Angola, by A. de Barros Machado (personal communication). There they ride principally on the dorsal surface of the heads of worker termites (Fig. 2). We have observed them on the same species of termite near Cacula, Angola, and never saw more than one mite per termite. When disturbed, the mites crawled about on the surfaces of other parts of the workers, but they always resumed their favored position on the head soon thereafter. The workers gave no hint that the mites were detected, whether they were on their heads or elsewhere. Macrochelids have been cap-

Fig. 2. Uropodine mites riding (arrows) on the heads of worker termites, *Odontotermes* sp. (Original figure by A. de Barros Machado.)

tured only with this one species of *Odontotermes,* in spite of intensive field efforts with many other species.

The behavior of mites associated with New World army ants has been studied extensively by Rettenmeyer (1961d). This was partially reviewed and illustrated in Volume I of this treatise. At least three families are unique to these ants. The Circocyllibanidae are phoretic on the mandibles head, thorax, and gaster of adult workers. They have also been observed riding upon larvae and have been found rarely on adult males and queens (Elzinga and Rettenmeyer, 1976). This family is only found with ants of the genera *Eciton* and *Labidus*. Their concave ventral surface permits close attachment to such parts as the mandibles and head. In contrast, the Coxequesomidae have different morphologies which permit attachment to the antennae or coxae of the ants. *Planodiscus* sp. (family Planodiscidae, Fig. 8, p. 359 in Volume I of this treatise) are confined normally to the undersides of the meso- and metatibiae of the ants (Rettenmeyer, 1961a; Elzinga and Rettenmeyer, 1970). These tibiae are groomed by other legs while the protibia are groomed through the mandibles of the ants. The close resemblance of the surface of the mite to the tibial surface and its interpretation as an example of Wasmannian mimicry have already been noted in Volume I of this treatise. The functions of the holdfast mechanism of *Planodiscus* and those of other mites have been further studied by Elzinga (1978). Other mesostigmatid mites have been reported as phoretic upon fungus growing ants [*Cyphomyrmex rimosus* Spinola and *Atta cephalotes* (L.)] by Weber (1972). One species *Garmania* (?) sp. fed upon fungus.

Other mites found with the New World army ants are true ectoparasites such as the Macrochelid, *Macrocheles rettenmeyeri* Krantz, which feeds on hemolymph from the arolium of the hind leg of its host, *Eciton dulcius* Forel. The ant actually walks upon it while it is in this position. Less spectacular ectoparasites, such as *Cillibano comato* Leon (Uropodidae) insert their chelicerae into the gasters of their *Lasius* hosts (Janet, 1897b) and feed upon hemolymph, while other Uropodidae, such as *Urodiscella philoctena* Trous., attach to the strigils (pectinate appendages) of the foretibiae where they are thought to be scavengers upon materials cleaned off the body of the ants by the use of the strigil. Many other Uropodidae have been recovered from ant nests (Bernard, 1968) where they are considered as primarily scavengers; from termite nests (Hirst, 1927) where they are also considered as scavengers, although one species was phoretic on the antenna of *Glyptotermes xantholabrum* (Hill); and from the nests of *Ceratina metallica* Smith (Gordh and Barrows, 1976). Uropods frequently attach by stalks to their host (Gordh and Barrows, 1976) which remain after the mites drop off. These were shown to be sucker shaped processes by scanning electron microscopy by Sokolowski and Wisniewski (1975), who also showed that a large percentage of ants had been so infected. Phillipsen and Coppel (1978) showed that *Urobovella formosana*

P. & C. is phoretic upon *Coptotermes formosanus* Shiraki in that the deutonymphs attach by anal pedicels to the abdominal dorsa of both workers and soldiers.

Gamasidae reported from the nests of ants (Bernard, 1968) and from the nests of stingless bees (Salt, 1929) are phoretic but their food habits are not known. One species (*Sphaerolaelaps holothytroides* Leon) found with *Lasius* sp., was studied by Donisthorpe (1927) who believed that it ate pellets ejected from the infrabuccal pockets of the ants. Skaife (1955) reported *Termitacaris cuneiformis* as phoretic on the soldiers and workers of *Amitermes hastatus* (Haviland).

Laelaptidae have been found with ants (Donisthorpe, 1927; Rettenmeyer, 1961a), with stingless bees (Salt, 1920), with halictid bees (Eickwort, 1966), and with a colletid bee (Roberts, 1971). *Hypoaspis myrmecophilus* (Berl.) is occasionally antennated by ants which carry them to safety when the nest is disturbed. It is common in nests of *Lasius mixtus, L. flavus* Linné, *Formica fusca* Linné, and *Tetramorium caespitum* (*L.*) where it feeds on the immature stages of other mites. *Laelaspis equitans* Mich., also found with *Tetramorium* is able to jump from one ant to another while the ants are in motion. *Laelaspis dubitatus* Hunter (1964) is known from nests of *Aphaenogaster* in Georgia, while *L. brevichelis* H. is phoretic on adults and larvae of *Crematogaster* (*Acarocoelia*) *lineolata* (Say) in Kansas. *Oolaelaps oophilus* Wasmann lives among the egg masses of many species of *Formica* where it is reported to eat the secretions of the ants' salivary glands which are deposited over each egg. By soaking dead ant bodies with carmine stain, it has been shown that *Cosmolaelaps cuneifer* Mich., also found with many hosts, is a scavenger that feeds on dead ants. This stain was recovered from the intestines of the mites subsequent to feeding. Adult *Hypoaspis* sp. were reported from the nests of bulldog ants by Gray (1974).

Salt (1929) reported the following six species of Laelaptidae from the nests of stingless bees (see tabulation below).

Mite species	Host
Meliponaspis debilipes Vitzthum	*Trigona (Meliplebeia) africana tanganyikae* Strand
Hypoaspis meliponacrum Vitzthum	*Melipona interrupta* var. *salti* Schwarz
Trigonholaspis salti Vitzthum *Trigonholaspis columbianum* Vitzthum *Trigonholaspis trigonarum* Vitzthum *Trigonholaspis amaltheae* Vitzthum	*Trigona amalthea*

Hypoaspis was found moving over the nest structures, particularly the pollen pots while the four species of *Trigonholaspis* were found parasitizing bee pupae inside the cells. These were abundant over the comb and only rarely found on the pollen and honey pots.