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THE PHORESY OF ANTHEROPHAGUS.¹

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August 16, 1919, while collecting Hymenoptera near Colebrook, in northwestern Connecticut, I observed a worker humble-bee (*Bombus vagans*) behaving in an erratic manner on the flowers of a golden-rod. The insect was standing with straightened legs on the tips of its tarsi and repeatedly attempting to insert its proboscis into the flowers, but did not succeed because a small red beetle was firmly attached by its mandibles to the tip of the right maxilla and the tongue. The beetle, which proved to be a female of the Cryptophagid *Antherophagus ochraceus* Mels., did not release its hold in the cyanide jar, so that I am able to show it in its original position in the accompanying figure (Fig. 1). I failed to find any record of such behavior in our American Antherophagi (*ochraceus*, *convexulus* and *suturalis*), but a perusal of the accounts of the closely allied European species (*nigricornis*, *silaceus* and *pallens*) yields a satisfactory explanation of the peculiar activities described above.

In 1896 Lesne called attention to a number of small insects that habitually ride on larger insects. To this phenomenon he applied the term "phoresy" and showed that it is distinguished from ectoparasitism by the fact that the portee does not feed on the porter and eventually dismounts and has no further relations with the latter. The following year (1897) Charles Janet studied the known cases of phoresy somewhat more comprehensively, expanded the concept and distinguished no less than six different categories:

(1) Cases like that of the small flies of the genus *Limosina* which ride on the dung-beetle, *Ateuchus*, and represent phoresy in its typical form as conceived by Lesne.

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 162.

(2) Cases in which the portee is conveyed to the nest of the porter, like the triungulin larvæ of certain beetles (*Sitaris*, *Meloe*, etc.) and the triungulinids of the Strepsiptera.

(3) Cases like a few myrmecophilous beetles (*Thorictus*) which attach themselves to the antennæ of ants for the purpose of accompanying them on their peregrinations.

(4) Cases like the mites of the genus *Antennophorus* which are not only carried but fed by the ants. These and the cases under (3) might be referred to ectoparasitism.

(5) Indirect phoresy, as exhibited by certain mites that cling to the surfaces of ant larvæ and pupæ which are in turn transported by the ants.

(6) The cases of ants that carry in their mandibles their own young, other members of the colony or guests.

In 1911 Banks published a valuable list of some 17 cases of phoresy collected from the literature, and several others have been recorded by Warner (1903), Brues (1917a, 1917b) and Rabaud (1917). Among the cases cited by these authors are those of certain small parasitic Hymenoptera which attach themselves to the abdomens of Orthoptera or to the wings of Mantoidea in order to be on hand to oviposit in the eggs of their porters. Such cases really represent a seventh category of phoresy.

Among the cases cited by Lesne and Janet and apparently overlooked by Banks, is *Antherophagus*, which attaches itself to the legs, mouthparts or antennæ of humble-bees for the purpose of being transported to their nests. The earliest observation of this habit seems to have been made by the British Coleopterist T. J. Bold. This author's two references to *Antherophagus* (1856 and 1871) were kindly sent me from London by my friend, Mr. Horace Donisthorpe, after I had vainly endeavored to find them in the Boston libraries. The first reference runs as follows: "Mr. Smith, in his admirable work on British bees, records the finding of *Antherophagus glaber* in the nest of *Bombus deshameilus*. This season I met with an instance of the manner in which such insects may be transported thither. When hunting *Bombi* in September last, the peculiar motions of a neuter of *B. sylvarum* attracted my attention: it was clinging to a thistlehead, and wriggling and twisting its legs about in all directions. On getting hold of it I found that a large specimen of *Antherophagus nigricornis* had

seized the tarsus of a hind leg between its jaws, and was holding on like grim Death. I put both into my bottle, and the *Antherophagus* retained its hold until both were killed by the fumes of the laurel." The reference of 1871 is to this same find and occurs

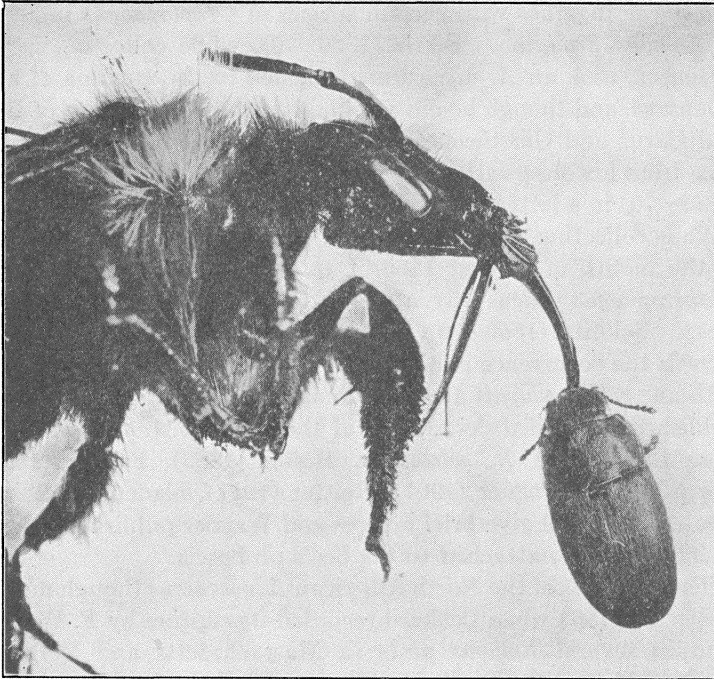


Fig. 1. *Antherophagus ochraceus* Mels. attached to proboscis of *Bombus vagans* Sm.

on page 60 of Bold's "Catalogue of the Insects of Northumberland and Durham."

Redtenbacher (1858) records having taken three adult *A. nigricornis* in a humble-bee's nest, together with a number of larvæ, which very probably belonged to the beetle. In 1863 Carus and Gerstaecker published the following note on the genus *Antherophagus*: "The species live on flowers, attach themselves to humble-bees and permit the latter to transport them to their nests, probably for the purpose of oviposition; at any rate, small

larvæ resembling those of *Cryptophagus* are sometimes found among the beetles in the nests of humble-bees." Eichhoff (1866) after examining several *Bombus* nests states that *A. nigricornis* was nearly always present and that single specimens of *silaceus* and *pallens* occurred in the same situations. Gorham (1869) captured *A. pallens* together with certain species of *Cryptophagus* in a nest of *Bombus pratorum*. Perris (1869-'70), while collecting in the Pyrenees, took an *A. nigricornis* attached to the antenna of a *B. montanus*, and though he did not know of the observations of Bold and Carus and Gerstaecker he nevertheless drew the same inference from his observations as the two German authors. Bugnion (1869-'70) in a letter to Perris recorded the following observation: "While collecting at Angeiades (alt. 1900 m.) in the Alps of Vaud, in the month of August 1866, I took a *Bombus* which had an *Antherophagus pallens* Oliv. attached to its proboscis by the mandibles." Seidlitz (1869-'70), commenting on Perris' observations, records the occurrence in a museum collection of three *Bombi* each with an *Antherophagus* attached to an appendage. In 1875 Perris published a detailed description of the larva of *A. silaceus* taken from the nest of *B. sylvarum*. Hoffer (1883), Fowler (1889), Sharp (1899), Wagner (1907), Reitter (1911), Sladen (1912) and Reuter (1913) all give brief notices and Wagner publishes a figure of *A. nigricornis* attached to the bee's proboscis.

The accounts of the North American *A. ochraceus* though meager go back to 1864 when Packard recorded its capture by F. W. Putnam in several *Bombus* nests in Massachusetts and Vermont. Packard figured the beetle in this paper and the beetle and larva in two of his well-known books (1872, 1873). J. B. Smith (1909) and Blatchley (1910) mention the occurrence of *A. ochraceus* on various flowers and the former notes its occurrence in *Bombus* nests. Casey (1900) in his taxonomic revision of the Cryptophagidæ says nothing about the habits of the beetle, though he makes the following significant remarks on the genus (p. 87): "This is one of most isolated genera of the family and contains by far the largest species, *Haplolophus* being the only other which approaches it in this respect. The emargination of the clypeus, very deep in the male but feeble in the female is apparently a unique character in the family," etc.

The observations recorded at the beginning of this paper to-

gether with Packard's show that our species are very similar in habits to their European cousins. Though possessed of well-developed wings and able to fly about and take up their position on flowers, *Antherophagus* does not seek out the *Bombus* nests but compels the bee to carry it to the place in which its eggs and larvæ are to develop. As Sharp says, "we must presume that its senses and instincts permit it to recognize the bee, but do not suffice to enable it to find the bee's nest." The structure of the mandibles and the peculiar notch in the clypeus are clearly adaptations to firmly grasping the more or less cylindrical joints of the bee's appendages, and the red color of the integument and investment of golden yellow hairs, so very suggestive of conditions in many myrmecophilous beetles, may account for the fact that the *Antherophagi* live unmolested in the *Bombus* nests.

The feeding habits of the adult and larval *Antherophagus* seem not to have been actually observed by any of the authors mentioned in the preceding paragraphs. Packard (1864) believed it "probable from the fondness, which these insects manifest for the sweets of flowers, that they visit the nests of the bees for the purpose of consuming the honey stored up within them." In 1873, however, he inferred that the beetle "probably feeds upon the wax and pollen," a statement which seems to have been suggested by the generic name given by Latreille. The views of the various authors concerning the feeding habits of the larva are, with one exception, practically unanimous. Perris (1875) says: "The larvæ of *Antherophagus* probably play the same rôle in the humble-bee nests as do *Cryptophagus pubescens* and *scanicus* in the nests of wasps. I do not believe that they devour the honey stored up by the bees or that they attack the bee larvæ, not one of which showed the slightest lesion; I am convinced that they live on the feces of the inhabitants and that they are, properly speaking, merely scavengers." In the same paper he calls attention to the larva of *Cryptophagus dentatus* Herbst which lives under chestnut bark in company with the larva of *Dryocætus villosus* and feed on its excrement. Lesne (1896) states that the *Antherophagus* larvæ "live as mutualists rather than as commensals in the *Bombus* nests." In contrast with this rather vague and colorless statement, Wagner (1907) paints a lurid picture of the activities of the beetle and its larvæ. After describing the transportation of the beetle on the

bee's proboscis, he continues: "The humble-bee evidently feels decidedly uncomfortable if she does not actually suffer pain. She crawls over the combs of the nest, extrudes her proboscis and makes a series of movements for the purpose of getting rid of her burden, but in vain. Other bees come up, 'affectionately' palpate her with their antennæ and pass on without the slightest attempt to help their 'comrade,' without the feeblest movement towards assisting her to ward off the dangerous enemy. And dangerous the beetle certainly is for from the eggs it lays hatch larvæ which, by destroying both the wax and the cocoons, will cause enormous devastation in the nest." It is difficult to estimate how much of this is observation and how much is imagination. Subsequent writers return to the opinion of Perris and regard the *Antherophagus* larvæ as harmless scavengers. Thus Reitter (1911) asserts that they "probably live on the excrement of the inhabitants of the nest" and Reuter (1913) that they "live on all sorts of refuse." Sladen (1912), who has a very intimate knowledge of the humble-bees and their nest-mates, classifies the *Antherophagi* "among the smaller and less important inhabitants of humble-bees' nests." We may conclude, therefore, that the larvæ of these beetles are in all probability merely scavengers in the *Bombus* nests and hence closely resemble the larvæ of *Cryptophagus* in habits as well as structure.

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