A NEW MYRMECOPHILE FROM THE MUSHROOM GARDENS OF THE TEXAN LEAF-CUTTING ANT.[1]

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On the 10th of April last, with the assistance of Messrs. A. L. Melander and C. T. Brues, I excavated a large nest of leaf-cutting ants (*Atta fervens* Say), situated in a piece of woodland a quarter of a mile from the University of Texas. The large burrows, nearly an inch in diameter, were found to extend down to a depth of from three to five feet and to open into large chambers, some of which were fully ten inches across and five to eight inches high. A few of these chambers were traversed by the roots of a large cedar, in the shade of which the ants had dug their formicary. Descending into the pit we had dug, and braving the attacks of tens of thousands of infuriated ants, we soon discovered the objects of our search — the mushroom gardens heaped up on the floor, or, more rarely, enveloping, as aërial or "hanging" gardens, the roots that extended across the chambers.

The gardens were hastily extracted — I say hastily because putting one's hand into one of these chambers is like grasping the handles of an electric machine, so valiantly do the ants defend their property. The material, reeking with an odor like that of stale honey, was placed in large glass jars. These had to serve as artificial nests, as nests of the Lubbock and Janet pattern were obviously not suited to these aberrant ants. By the following day the ants had completely rebuilt their gardens on the bottoms of the jars.

These gardens proved to be very similar to those so carefully described and figured by Möller[2] for several South American species of Atta (*A. discigera* Mayr., *A. hystrix* Latr., *A. coronata*

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, No. 9.

[2] *Die Pilzgärten einiger südamerikanischer Ameisen.* Jena, Gustav Fischer, 1893.

Fabr., and *A. Mölleri* Forel). Möller has described how the ants cut and bring the large pieces of leaves into their cellars, then cut them into smaller fragments, and finally com-

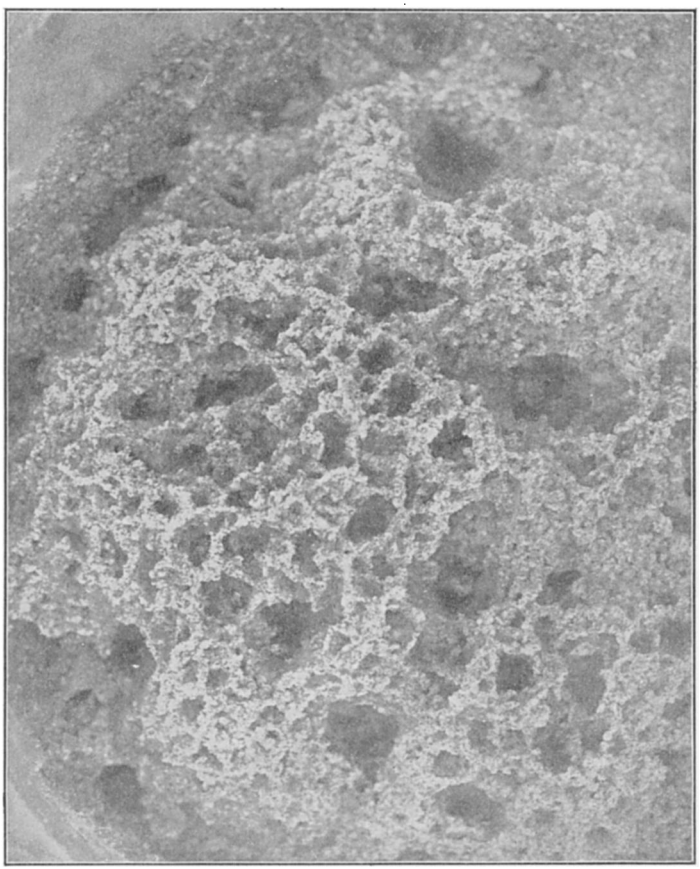

FIG. 1. — Mushroom garden of *Atta fervens* Say.

minute these still further till they form a flocculent greenish-brown pulp.[1] This pulp is heaped up and soon becomes invaded

[1] *Atta fervens*, like other species of the genus, is not fastidious in its choice of the material to be used as a soil for its gardens. Almost any vegetable substance will answer this purpose. In October, 1899, I saw a colony busily engaged collecting caterpillar excrement which had dropped from the overhanging foliage of a large sycamore. Several months later I found a large colony near the same spot marching in long procession, conveying big grains of cracked corn which

by the mycelium of a fungus (*Rozites gongylophora*). The mycelium is kept aseptically clean — *i.e.*, free from all other species of fungi and even from bacteria — and induced to grow in an abnormal way by bringing forth minute swellings which

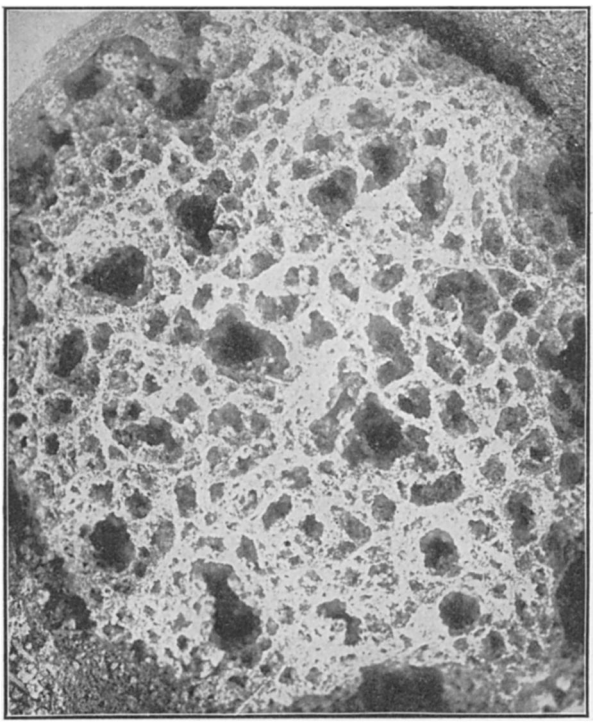

FIG. 2. — Mushroom garden of *Atta fervens* Say.

constitute the only food of the ant colony. Möller likens these swellings to the "Kohlrabi" of the German kitchen gardens.

they had filched from a mill near their nest. Sometimes they prefer to collect seeds or young flower-buds. In winter, when the leaves have fallen from all the trees except the live oaks and cedars — trees which the Attas avoid, probably because the leaves offer too much resistance to their mandibles — they garner the young leaves of the sorrel and lupine. At such times, especially when the landscape is flooded with the brilliant Texan sunshine, one may, perhaps, not inappropriately compare the ant procession with a procession of "Sunday-school children carrying banners" (McCook, On the Architecture and Habits of the Cutting Ant of Texas (Atta fervens), *Proc. Acad. Nat. Sci. Phil.*, pp. 33–40, 1879).

More recently Forel has studied the habits of two other species (*Atta cephalotes* L. and *A. sexdens* L.) in Colombia.[1] He seems to have given some attention to the rôle performed by the different casts of worker ants — casts which are also represented in our *Atta fervens* — in this process of collecting and comminuting the leaves and in cultivating the mushroom. At p. 31 he says: "The largest workers (soldiers) triturate the leaves and defend the nest. They draw blood when they bite. The indigenes are said to use these insects for closing wounds. They induce them to bite the two lips of the wound and thereupon sever the bodies from the heads, which then serve as a suture. The medium-sized workers cut the leaves from the trees, while in the nest the workers of the minim cast are forever clipping the threads of the mycelium of the Rhozites, which then develops the 'Kohlrabi,' on which the ants feed."

The shape of a mushroom garden is that of a discoidal sponge. On its upper surface the ants pile up the flocculent vegetable débris, threaded in all directions with fungus hyphæ, in the form of thin, vertical, anastomosing plates, so that as much surface as possible is exposed to the atmosphere of the chamber. This atmosphere must contain a great amount of carbon dioxide and a very small amount of oxygen. The peculiar appearance of the surface of two large gardens is shown in the photographs (Figs. 1 and 2, about ¼ the natural size). Although these gardens of *Atta fervens* closely resemble those of the South and Central American species observed by Möller and Forel, I have seen fit to figure them, both because Möller's work is out of print and may not be readily accessible to the reader, and because, to my knowledge, the gardens of our Texan leaf-cutter have not been figured heretofore. The ants leave several tubular or funnel-shaped openings (clearly shown in the figures), varying in diameter, and extending down into some chambers excavated in the base of the vegetable mass. In these chambers lives the huge queen of the colony, — an insect nearly an inch long, — the newly fledged males and virgin queens, together with the larvæ, pupæ, and attendant ants.

[1] *Biologia Centrali-Americana Hymenoptera.* Formicidæ (1899–1900), pp. 31 *et seq.*

The whole mushroom garden swarms with workers, representing all the different casts so characteristic of the genus Atta. The big-headed soldiers — like "Brownie" police officers — stalk about slowly over the surface of the comb, descending from time to time into the interior, as if to make sure that the great family is properly attending to its multifarious occupations, while thousands of minims keep moving about through the meshes of the mycelium, weeding the garden. In the presence of these varied activities and instincts one has a feeling of regret that all "anthropomorphism" is now to be banished from the study of ant life, and that we are asked to look at all this elaborate division of labor as nothing but an agglomeration of machine-like "reflexes."[1]

It is natural to suppose with Wasmann[2] that the vast amount of comminuted and decomposing vegetable matter collected by the leaf-cutting ants as a soil, or culture medium for the growth of their mushroom diet, would form a most favorable resort for a great number of myrmecophiles. Nevertheless, comparatively few of these symbiotic animals have been taken up to the present time. Besides the amphisbænians, which, though often found in the nests of the tropical Attas,[3] may not even be myrmecophagous, I find mention of comparatively few species in the literature. These include the following histerid beetles taken in the nests of *Atta fervens* in Mexico and enumerated in Wasmann's very useful *Verzeichnis*[4]: *Philister rufulus* Lewis, *Hister* (?) *costatus* Mars, *Reninus Salvini* Lewis, and *Carcinops* (?) *multistriata* Lewis. Belt[5] saw a species of "Staphylinus" in the Atta nests of Nicaragua, and Wasmann[6]

[1] See Bethe, Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben, *Arch. f. d. gesam. Physiologie*, Bd. lxx (1898), pp. 15–100, Taf. I u. II, 5 text-figs.; and Bethe, Noch einmal über die psychischen Qualitäten der Ameisen, *ibid.*, Bd. lxxix (1900), pp. 39–52.

[2] Die Ameisen- und Termitengäste von Brasilien, *Verhandl. d. k. k. zool. bot. Gesell.*, pp. 2–46, Wien, Jahrg. 1895.

[3] See Bates, *The Naturalist on the River Amazons*, London, 1876, pp. 51 and 52; Brent, Notes on the Œcodomas, or Leaf-Cutting Ants of Trinidad, *Amer. Nat.*, vol. xx (1886), pp. 123–131, No. 2; and Wasmann, *loc. cit.*, p. 9.

[4] *Kritisches Verzeichnis der myrmekophilen und termitophilen Arthropoden.* Berlin, Felix Dames, 1894.

[5] *A Naturalist in Nicaragua*, p. 84.

[6] Die Ameisen- und Termitengäste von Brasilien, *loc. cit.*

mentions two species of Aleochara and an Atheta found in the entrances to the nests of *Atta sexdens* L. at San Paolo, Brazil.

This short list of myrmecophiles led us to sift with considerable care the gardens of the nest we excavated. The result was a single species of myrmecophile, but this appeared in considerable numbers — more than seventy specimens being taken from three of the large gardens — and proves to be a cockroach (Blattid) of very small size and peculiar structure. With the exception of four males and two females, all the specimens are immature. The species appears to be undescribed, and as it does not belong to any genus of which I can find an account, I propose to describe it as the type of a new genus under the name of *Attaphila fungicola*.

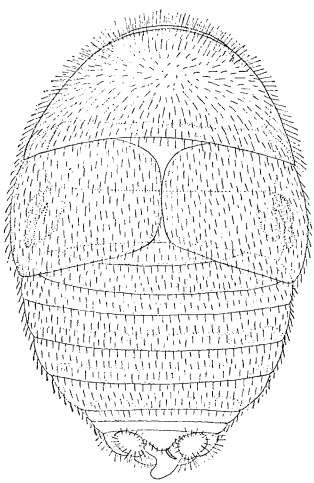

FIG. 3. — *Attaphila fungicola* n. sp., male, dorsal aspect.

In the artificial nests above mentioned the little cockroaches were frequently seen moving in and out of the tubular perforations in the vegetable mass. Occasionally one of them would mount a huge soldier that was slowly patrolling the surface of the garden, and ride about on its back or enormous head for minutes at a time. The ant did not appear to be in the least annoyed by this performance, nor did any of the other ants pay the slightest attention to the cockroaches when they were encountered in the passages. It is probable that Attaphila, like the ants, feeds on the modified hyphæ of the fungus. This is indicated by the fact that the intestines of several dissected specimens contained a whitish substance which may be the remains of the masticated mycelium. If this supposition proves to be correct, the relationship between the ants and the cockroaches is of a peculiar character. It is, in fact, a kind of myrmecoclepsy, or thieving. As the cockroaches eat the fungus cultivated by the ants for their own consumption, this kind of myrmecoclepsy may be said to differ from the typical form

exhibited by the Thysanuran Lepismina and the mite Antennophorus. In these cases, as Janet has shown in an excellent paper,[1] the guest steals some of the liquid food while it is passing from the mouth of one ant (*Lasius umbratus mixtus* Nyl.) to that of another.

Before passing to a more detailed description of Attaphila, attention may be called to a few of its structural and taxonomic peculiarities:

1. Up to the present time a genus of diminutive crickets (Myrmecophila) has comprised the only known myrmecophiles

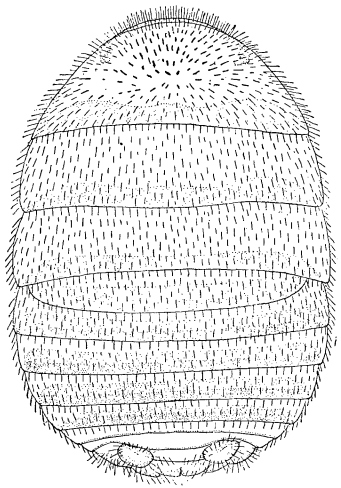

FIG. 4.

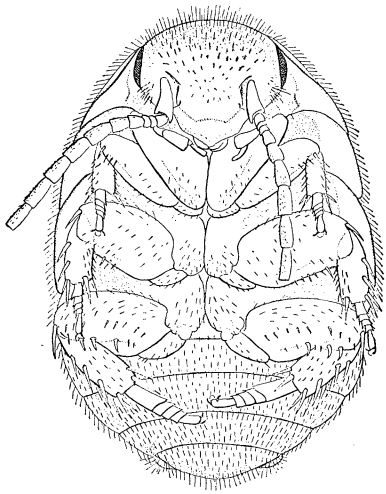

FIG. 5.

FIG. 4. — *Attaphila fungicola* n. sp., female, dorsal aspect.
FIG. 5. — *Attaphila fungicola* n. sp., female, ventral aspect.

in the great Orthopteran order.[2] With Attaphila a genus belonging to a very different family, the Blattidæ, must be added to the long list of insect myrmecophiles. Considering that there is no family of Orthoptera apparently so well fitted to enter into symbiotic relations with ants, it is rather surprising to find that other myrmecophilous Blattidæ have not been discovered, especially in the tropics, where the family is rich in species.

[1] *Études sur les fourmis, les guêpes, et les abeilles.* Note 13, Sur le Lasius mixtus, l'antennophorus Uhlmanni, etc., pp. 1–58, 16 figs. Limoges, 1897.

[2] For an account of the habits of one of the species (*M. nebrascensis* Bruner) the reader may be referred to an article in *Psyche* (1900).

2. While the Orthoptera, as a rule, are large or medium-sized insects, both Myrmecophila and Attaphila are so far below even the average stature of insects of this order that we must conclude either that they have become reduced in size secondarily in adaptation to their present habitat and companionship, or that they were originally diminutive species, and, for that very reason, better able to enter into symbiotic relationship with the ants. The latter alternative seems to be the more probable.

3. The eyes of Attaphila are vestigial in both sexes. This is indicated by their very small size, the greatly reduced number of their facets, and their irregular orbits (Fig. 6). There are scarcely more than seventy ommatidia in either eye, whereas, according to Miall and Denny,[1] there are about eighteen hundred in the eye of the common cockroach (*Periplaneta orientalis*), and some other species have even larger eyes, and therefore, in all probability, a still greater number of ommatidia. The vestigial condition of the eyes in Attaphila is of interest because it shows that the insect has become thoroughly adapted to living in the dark. It is, in fact, a truly cavernicolous form, living in caves constructed by its emmet hosts. The reduction of the eyes has not, however, proceeded so far as in another diminutive cockroach, *Nycticola Simoni*, which is known to inhabit caves in the Philippine Islands.

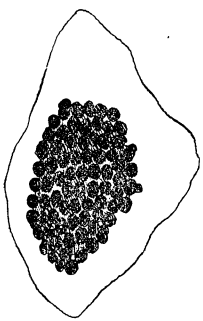

FIG. 6.—*Attaphila fungicola* n. sp., eye of adult male.

4. Additional evidence of the lifelong confinement of Attaphila to the chambers of the ants' nest is seen in the extremely rudimental condition of the tegmina and wings in the adult male, and the complete absence of these structures in the adult female. There can be no doubt that the specimens figured (Figs. 3–5) were mature, as the testes of the male contained ripe spermatozoa, and the ovaries of the female contained large, elliptical white eggs. The oötheca of this form must be an

[1] *Studies in Comparative Anatomy.* III. The Structure and Life History of the Cockroach, p. 99. London, 1886.

interesting object, if the species actually produces one. My specimens were taken too early in the year, as shown by the great number of immature individuals, so that I am unable to make any statements concerning the breeding habits.

5. It is a singular fact that in every one of my specimens of Attaphila the antennæ are incomplete, so that I cannot ascertain the full number of joints. There seems to be only one explanation of this, *viz.*, that the antennæ have been clipped off by the ants, either by the minims, which are continually trimming the fungus hyphæ, or by the large workers, which cut up the pieces of leaves brought in by the medium-sized workers. It is easy to understand how an insect like a cockroach, living in the midst of thousands of ants which are continually opening and closing their scissor-like mandibles, should be certain sooner or later to have its long antennæ cropped. One wonders how the tarsi of the cockroach escape the same treatment. The human habit of cropping the tails of horses and the ears and tails of dogs may be said to be remotely paralleled by the leaf-cutting ants when they inadvertently clip the antennæ of their household insects. The treatment to which the cockroaches are subjected in the nests of *Atta fervens* — a treatment which they have probably undergone for ages — suggests an interesting problem for those who may still believe in the inheritance of mutilations.

The number of antennal joints that escape the scissors of the ants varies in forty-five specimens, in which they were counted on both sides, from three to eleven. In seventeen of these specimens the number of joints is the same in both antennæ, the variations being: 7–7, 8–8, 9–9, and 10–10. In twenty-one cases the two antennæ differ by only a single joint, the variations being: 7–8, 8–9, 9–10, 10–11. In seven specimens the discrepancy between the two antennæ is greater, being 3–9, 5–7, 5–9, 7–9. Thus in thirty-eight out of forty-five specimens the cropped antennæ are very nearly or quite symmetrical. I am unable to explain this singular condition, which can hardly be a mere coincidence. It is probable that in this symmetrical and cropped form the antennæ of the Attaphila are more like those of the ant, and as they are kept

in constant vibration, they may on that account more readily simulate the "antennal language" of the host insects. This, however, would be the result, not the cause, of the symmetrical clipping.

6. Judging from the stumps which remain, the antennæ of Attaphila differ considerably in structure from those of other Blattidæ known to me. The joints are relatively much larger and longer, and therefore of a more generalized or embryonic type than those seen in the nymphs and adults of other species. Can this somewhat hypertrophied condition be the result of the continual clipping to which these organs are subjected?

7. The structure of its antennæ suggests that a more extended comparison of Attaphila with other Blattidæ may assign it a peculiar, if not unique, taxonomic position. On this matter my limited acquaintance with the insects of this family hardly qualifies me to write.

The following is a more detailed description of the myrmecophile that is the subject of the foregoing general remarks.

ATTAPHILA FUNGICOLA, NOV. GEN. ET NOV. SP.

Male (Fig. 3). — Length, 3–3.5 mm. Color: amber yellow; antennæ, tibiæ, tarsi, pleuræ, tegmina, and overlapping portions of terga and sterna of the thoracic and abdominal segments more brownish. Body about twice as long as broad, glabrous, covered with rather evenly distributed short, yellowish hairs. Head scarcely projecting beyond the anterior margin of the pronotum, so that only its posterior edge is visible when the insect is seen from above. Epicranium and front broad, smooth, without any traces of the λ-shaped suture and fenestræ. Labrum not bilobed, but obtusely pointed, extending a little beyond the acute, tridentate mandibles. Labial palpi scarcely half as robust as the maxillary palpi. Eyes very small, with irregular orbits, occupying the extreme lateral portions of the head and separated by a considerable distance from the antennal foveæ. Antennæ incomplete in all the specimens, both nymphs and adults; first joint rather stout, somewhat longer than the second to fifth joints taken

together ; joints six to eleven of gradually increasing length, but little narrower than the basal joint. Pronotum evenly rounded in front, considerably broader than the meso- and metanota, and as long as both of these regions taken together. There is a brown spot on either side above the eye. Tegmina rhomboidal, without traces of nervures, covering and extending somewhat beyond the meso- and metathoracic segments, and meeting for a short distance in the mid-dorsal line. Wings very small, vestigial, completely covered by the tegmina and exhibiting only very feeble traces of nervures. Abdominal segments short and broad, the first concealed, considerably narrower than the succeeding segments ; terga of seventh and eighth without hairs and lighter in color than the preceding segments ; tergum of ninth segment, forming the lamina supra-analis, subtriangular, not more than one and one-half times as broad as long, rounded behind, and fringed with a few hairs. Cerci very short, not longer than broad, ovoidal, one-jointed, covered with radiating hairs except over an elongate, glabrous area on the upper surface. Subgenital plate small, rounded and smooth, projecting beyond the supra-anal lamina and turned to the left. Above the subgenital plate lies a pointed, spine-like projection (penis ?), which turns to the right side. Stylets apparently absent. Legs short, flattened, the pairs increasing in length from before backwards ; tips of the fore femora far from reaching the pleural edges of the prothorax, those of the hind pair just reaching the lateral edges of the abdomen. All the femora furnished with spines on their lower surfaces. Tibiæ, especially the middle and hind pairs, with robust spines on their extensor edges and at their tips. Tarsi short, flattened, second to fourth joints oblique ; fifth joint provided with a distinct arolium between the claws.

Female (Figs. 4 and 5). — Length 3.25–3.5 mm. Differs from the male in the following characters : Body much broader and more rounded behind ; meso- and metathoracic segments without tegmina or wings, but with broad pleural flaps, so that these segments are slightly wider than the prothorax, though their antero-posterior diameter is only about half that of the large pronotum. Posterior edges of the lamina supra-analis

notched in the middle. Cerci with a very clearly circumscribed, linear white spot on the dorsal surface. Subgenital plate large, nearly as long as broad, evenly rounded behind.

Nymph. — Length, 1.5–3 mm. Resembling the female, except in the smaller size and the distinctly lighter color.

COLEBROOK, CONN., August 20, 1900.