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## STUDIES ON MYRMECOPHILES. III. MICRODON.

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Few insects have occasioned more perplexity in the minds of entomologists than the species of *Microdon*, or, more accurately speaking, than the larvæ and pupæ of *Microdon*, for no tyro in entomology could fail to recognize the imagines as Syrphid flies. So repeatedly have even experienced observers been deceived by the singular elliptical larvæ and puparia, that the history of the genus is unusually instructive. The adult flies have been described under a variety of generic names: *Microdon* (Meigen, 1803), *Aphritis* (Latreille, 1805), *Ceratophya* (Wiedemann, 1830), *Chymophila* (Macquart, 1834), *Dimeraspis* (Newman, 1838), *Mesophila* and *Ubristes* (Walker, 1849 and 1856), and, to add to the confusion, Conrad, in 1842, described a genus of Silurian bivalves under the name of *Microdon*. The larva of the common European species, *M. mutabilis*, was first seen by von Heyden, who in 1823 described and figured, but refrained from naming it. He says that he does not believe it to be "the larva of an insect (perhaps a species of fly) for its whole organization, especially the structure of its mouth-parts, is too different from that of any insect larva" known to him. So he concludes that "it is much more probably a mollusk, but if such be the case, it must constitute a new and extraordinary genus." The following year (1824) von Spix found the larva of the same species of *Microdon*, and believing it to be a slug, named it *Scutelligera amerlandia*. Thereupon von Heyden published a second paper on the creature and dubbed it *Parmula cocciformis*, for the joy of naming things was as great in the early decades of the nineteenth century as it is to-day. The name *cocciformis* seems to have suggested to Burmeister (1839) that the creature was the "larva of a *Coccus* living on oaks"; at any rate, he enumerates it among the *Coccidæ*. The same year Schlotthauber presented to the German naturalists assembled at Pyrmont a carefully written paper with illustrations to prove that the organisms described by von Heyden and von Spix as mollusks, were really the larvæ of *Microdon mutabilis*. Unfortunately this paper was never published; a brief reference in Oken's "Isis" of 1840 being apparently the only record of its contents. In 1845 Elditt



endeavored to make good this loss to science in an excellent article on the metamorphosis of the insect. But the resemblance of the larval *Microdon* to a naked mollusk has continued to breed new generic names down to the present day. Prof. T. D. A. Cockerell calls my attention to a recent article by Simroth (1907), in which he describes what is evidently the puparium of a *Microdon* or of some allied Syrphid genus, from Cape Flats, South Africa, as a new genus and species of slug (*Ceratoconche schultzei*) to be placed "between the genera *Testacella* and *Apera*." Simroth actually interprets the posterior tubercle of the puparium as a vestigial shell! There is apparently no reason why unusual *Microdon* larvæ and pupæ, as fast as they are brought to light in various parts of the world, should not become the types of futile genera of naked mollusks, at least till the millennium arrives, when naturalists no longer itch to attach a name to everything that swims within their ken.

The genus *Microdon* embraces about 70 described species, and seems to be cosmopolitan in its distribution. Many of the species, however, are highly variable and have been but little studied, so that it is impossible at present to give more than a general account of their number, range and habits. According to Schiner (1864) and Verrall (1901), there are only three or four species in Europe. Aldrich (1905) enumerates 28 from North America. Lea (1893) has found the larvæ of a form, which he calls *M. variegatus*, in New South Wales. Simroth, as we have seen, has described the puparium of a South African species, and several have been recorded from South and Central America and Madagascar (Sharp, 1899; Wasmann, 1894).

The larval and pupal stages of these singular insects are found only in the nests of ants, wasps and termites. Wasmann (1890) seems to be the only author who has seen them in wasp nests. In his list of myrmecophiles and termitophiles (1894) he mentions their occurrence also in the termitaria of Madagascar and Brazil. Most frequently, however, both in temperate and tropical regions, the larvæ and puparia are found living with ants. In these stages the insects are gregarious, as a rule, so that several may be seen clinging to the walls of the galleries and chambers. They seem to live indifferently in nests in the soil, under stones, under the bark of trees or in the cavities of branches. The larvæ, while young or partially grown, often inhabit the deeper recesses of the nests, but when they reach maturity and are ready to pupate, they emigrate to the surface



and are then found near or at the entrances. They creep very slowly, with a wave-like motion of the flat and viscid ventral surface, which so closely resembles the foot of a slug, and keep the fringed border of the body in close contact with the surface over which they are moving. The anterior end, however, is occasionally raised for a few moments. At such times one may see the small pointed head of the larva moving about uneasily under the fringed border as if in search of food. What this food is, has not been determined, Laboulbène (1882) surmised that it might be the ant larvæ, but I am inclined to believe that it is the minute pellets of food, which, after their moisture has been extracted, are ejected from the hypopharyngeal pockets of the worker ants. These pellets are scattered about the nest, especially about the superficial galleries, and though hard and dry, must contain considerable nutriment. They are probably eaten not only by the *Microdon* larvæ but also by many other synœketes (*Clytra*, *Coscinoptera*, etc.).

The larvæ of the common European and North American *Microdons* are usually of a dirty white or drab color, with yellow or brown fringes of hair-like processes around their creeping sole, and a prominent, heavily chitinized tubercle near the posterior end. Usually no traces of segmentation are to be observed in their elliptical bodies, but in some adult larvæ of *M. tristis*, just before pupation and after their upper surfaces had been dried by exposure to the air, I have been able to discern in certain lights a distinct division of the body into seven or eight subequal segments. When the time for pupation arrives the larva remains stationary on its creeping sole, contracts somewhat, becomes harder and more convex and of a deeper brown color. The reticulations or markings, with which the upper surface is sometimes ornamented, become more pronounced, and a pair of short tubercles or protuberances make their appearance near the anterior end in addition to the single respiratory tubercle at the posterior end.

I am convinced that there is but one annual brood of these insects, at least in temperate regions, and that the larvæ, after passing the winter in the ant-nest, pupate in April or May. The flies hatch early in June and are much less active than other Syrphidæ. They are most frequently taken in sweepings in meadows or rather low grounds. During July young larvæ may be found in the nest and these mature by autumn. I believe, therefore, that Mann (1882) must be mistaken when he claims to have seen several specimens of



*Microdon globosus* issuing from a hole in the woodwork of a house and infers that they had been hibernating in this retreat.

The habits of the European *Microdons* have been studied by a number of entomologists: Bertkau (1889), Bignell (1891), Elditt (1845), Gadeau de Kerville (1884), Laboulbène (1882), Mayet (1882), Poujade (1883*a*, 1883*b*), Schenck (1852), Verhoeff (1892), Wasmann (1891, 1894), Wissmann (1848), and others. Of the two common species, *M. mutabilis* L. and *M. devius* L., the former is cited by Wasmann as occurring in the nests of *Formica rufa*, *fusca* and *rufibarbis*, and of *Lasius niger*, *brunneus* and *flavus*, the latter in nests of *F. fusca*, *sanguinea* (with *fusca* slaves) and *L. fuliginosus*.

So far as I am able to ascertain, but one of our numerous North American species, *M. tristis* Loew, has been bred from the puparium. Packard (1869) does, indeed, figure a puparium and fly which he refers to *M. globosus* Fabr., from a specimen taken by Sanborn at Andover, Mass., but I have recently examined the specimen, which is in the Museum of Comparative Zoölogy, and find it to be without doubt a puparium of *tristis*. Lintner (1885) reproduced Packard's figure and description, which he also erroneously attributed to *globosus*. Both the Museum of Comparative Zoölogy and that of the Boston Society of Natural History contain specimens of *tristis* mounted on the same pins with the puparia from which they were reared. During May, 1907, Mr. W. T. Davis reared the flies from a lot of twenty-four *tristis* puparia which I found at Newfoundland, N. J., in a nest of *Formica schaufussi*, and during the spring of 1908 I reared a number from puparia found at Bronxville, N. Y., and Paterson, N. J. In both of these localities the host ant was *schaufussi*. My collection also contains specimens of the adult insects and puparia taken in the following localities and with the following ants: Manchester, N. J., with *Formica* (species undetermined); Colorado Springs, with *F. rufa obscuripes* Forel (July); Colebrook, Conn., with *F. difficilis* var. *consocians* Wheeler (June 30); South Harpswell, Maine, with *F. sanguinea aserva* Forel (July). There are puparia of *tristis* in the Museum of Comparative Zoölogy from Loon Lake, Washington; Binghamton, N. Y., and Boston, Mass. (Henshaw).

In 1906 I published a few notes on some larvæ of *tristis*, one of which lived in an artificial nest of *F. consocians* from July 7 till September 10. On the former date I found three young larvæ in a nest of this ant at Colebrook, Conn., together with some empty



puparia from which the flies must have escaped during the previous spring. The ants resented my interference by moving to a new nest. On July 25 I found two more partly grown larvæ in the deserted formicary, but these were weak and emaciated. This shows that the *Microdons* do not accompany the ants when they move, and that the presence of the latter is essential to the well-being of the former. The emaciated condition of the abandoned larvæ is easily accounted for, if they feed, as I believe they must, on the ejected hypopharyngeal castings of their hosts.

The larva of *M. tristis* (Fig. 1) is 8–10 mm. long, opaque, pale, dirty brown or dark drab above and lighter beneath. The border is brown and striated and bears a simple fringe of short, flattened and pointed hair-like processes. The convex dorsal surface is covered with a coarse reticulum consisting of pale gray, cord-like elevations, which converge toward the anterior end and the posterior tubercle. On closer examination the convex surface is seen to be divided into five

subequal areas by four longitudinal strips which are rather free from reticulations. The posterior tubercle is short, robust, rounded, opaque, yellow, and covered with minute papillæ of the same color as the reticulum on the dorsal surface. This tubercle is surmounted by the two reniform anal stigmata, which are sometimes connected by a bridge. They are dark brown and shining.

The puparium is of the same size as the adult larvæ, but more convex and dark brown in color. Its sculpture is like that of the larva, but there are two prothoracic tubercles, each less than twice as long as broad, slightly diverging and somewhat obliquely truncated at their tips, which are shining and covered with minute papillæ.

The following additional observations on *tristis* were made during the past spring. April 19 I found a flourishing colony of *F. schaufussi* under a large flat stone in a sloping pasture at Bronxville, N. Y. The nest contained twelve adult larvæ and twelve puparia of *tristis*, all attached to the smooth earthen walls of the galleries either at their entrances or not more than 3 cm. below the surface of the soil. In

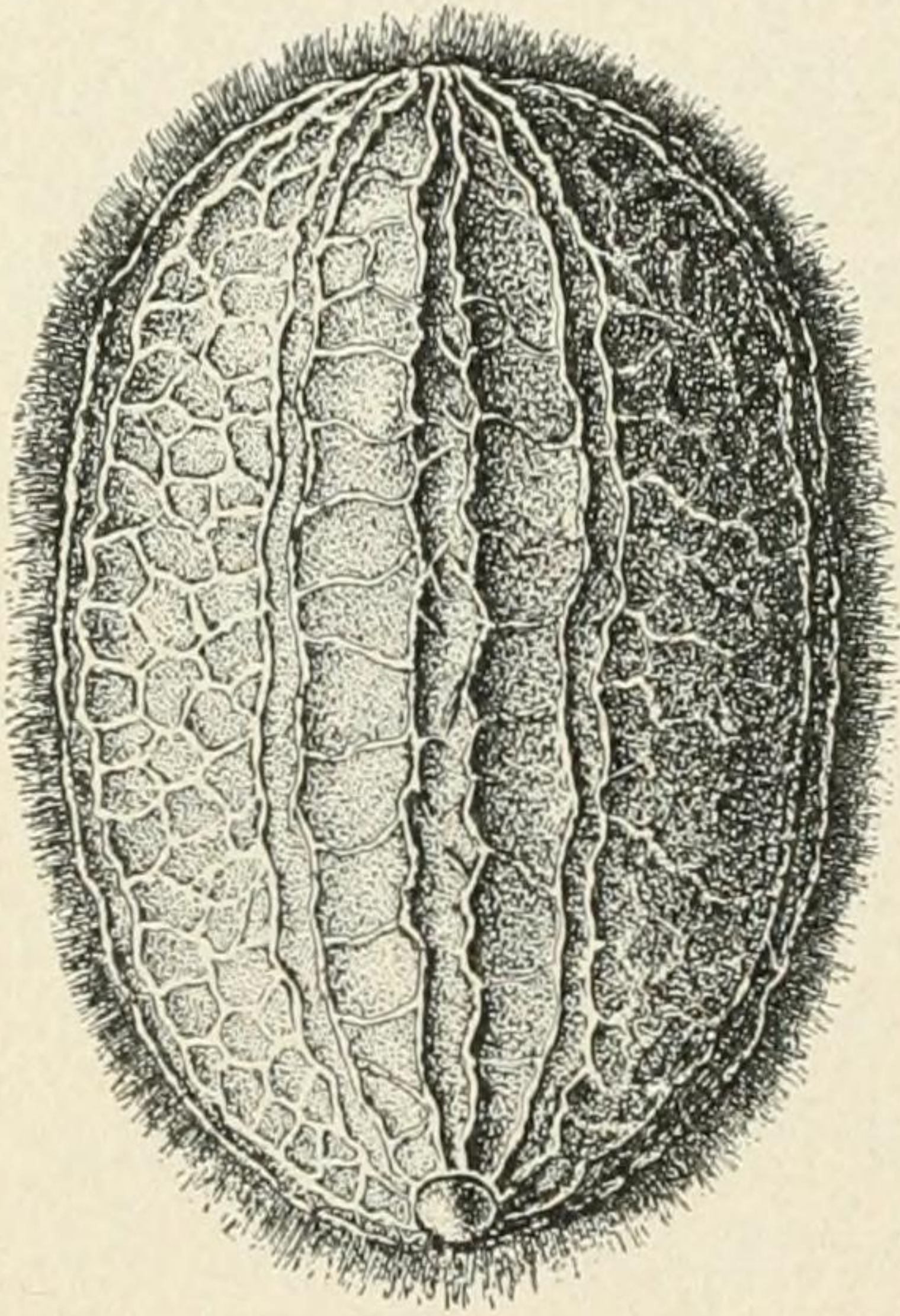


FIG. 1. — Larval *Microdon tristis* Loew; dorsal aspect.  $\times 6$ .



the flat superficial chambers there were also several of the earthen cases of *Coscinoptera dominicana* containing pupæ. Part of the *schaufussi* colony was confined in a Fielde nest together with the *Microdons* and the *Coscinoptera*. The ants paid no attention to either of these insects. By April 22 all the *Microdon* larvæ had attached themselves to the glass floor of the nest and had pupated. May 15 and 16 ten of them hatched, and eight of them hatched on May 20; the six remaining failed to develop. The flies emerged by breaking off the cover formed by the tripartite anterior third of the dorsal portion of the puparium and were at first of a dull drab color. Their bodies were moist and their covering of pile was glued to the chitinous surface. While in this stage they walked about among the ants without being noticed or, at any rate, without being molested. After a few hours, or sometimes much sooner, their wings had expanded and were folded over each other on their backs, their integument had acquired the adult metallic coloration and the pile had dried and become conspicuous. They remained very quiet except when rudely touched. Then they emitted a loud humming sound, but without moving their wings. This peculiar behavior has also been noticed by Bignell (1891) in *M. mutabilis*. The humming attracted the ants, which at once seized the defenseless creatures by the legs or wings and drenched them with formic acid. This killed them almost instantly. After seven had been dispatched in this manner, I removed the others from the nest in order to save them. These observations show very clearly that the adult *M. tristis* is treated with pronounced animosity even by ants among which for many months it has been tolerated with indifference as a larva and as a pupa. It is probable that the migration of the full-grown larvæ to the entrances of the nest and their pupation in the superficial galleries are an adaptation to making it as easy as possible for the adult flies to escape to the open fields without being noticed by the ants. All of my flies hatched at night and I believe that this must be the time of emergence also out of doors. The nights in May are apt to be cool, so that the ants would be in a torpid condition or huddled together in the lower chambers of the nest, and would not molest the flies while they were expanding their wings and perhaps even mating and ovipositing in the nest. In several instances, as in the case of the *F. consocians* nest mentioned above, I have found empty puparia in nests containing partially grown *Microdon* larvæ. This would indicate that the flies are apt to oviposit in the



very nests in which they have passed their larval and pupal stages. Verhoeff (1892), however, has seen the adult flies hovering about and apparently attempting to oviposit among the ants on the outside of the nest.

*M. tristis*, like other members of the genus, is highly variable in size and coloration. To some extent this variability may be geographical, since this species is known to range from the Mackenzie River to Virginia and from Maine to Washington and Oregon. Williston (1886) describes a var. *ruficrus* from Connecticut and regards *M. cothurnatus* Bigot from Oregon as being merely a variety of *tristis*. I have found still another variety which cannot be due to geographical causes, since it was bred from one of the twenty-four puparia taken in the *schaufussi* nest described above. The puparium from which it emerged was indistinguishable from the others, but the adult insect was covered with rich orange-yellow pile, whereas the seventeen other specimens had the pale yellow or silvery pile of the typical *tristis*. I have seen two other specimens of this orange variety in the American Museum of Natural History. Both of these were collected by Mr. W. Beutenmuller, one at Grant's on the Indian River, Fla., the other in sweepings with several specimens of the typical *tristis* and *globosus* in low ground at Katonah, N. Y. (June 4-14). This singular variety suggests a number of questions: Does it indicate that *M. tristis* is dichromatic like certain species of birds? Or is it a mutant? And if a mutant, is it an adaptation to more intimate symbiotic relations with the ants? In other words, does the orange-yellow pile have the same significance as the trichomes of the true myrmecophiles (symphiles), and would its possessor be more amicably treated by the ants than the typical *tristis*? I could, perhaps, have answered this last question, had not my specimen died soon after leaving its puparium.

*M. globosus* Fabr. and *M. fuscipennis* Macq., two other North American species not uncommon in collections, have not yet been bred from their puparia. I have seen a larva and puparium which are quite unlike the corresponding phases of *tristis* and probably belong to one or the other of these species. The larva measures 8-11 mm. It is opaque, pale brown above and lighter beneath. The dorsal surface is smooth and not covered with reticulations, but in dried and alcoholic specimens may be vermiculately wrinkled from contraction. The border has two fringes of golden yellow hairs, separated by a rather broad space crossed by sparse transverse ridges.



The more dorsal fringe consists of very delicate, short, curly hairs, while the ventral fringe is borne on a diaphanous striated lamina and is made up of flattened hairs, with long, slender, flexuous tips. The anterior border of the body is distinctly notched in the middle. The posterior tubercle is very long (1.7 mm.), with a ring-like groove around its base, and terminates in a pair of short blunt processes, each of which bears one of the anal stigmata. The whole surface of the tubercle is somewhat shining and finely rugulose.

The puparium measures 11 mm. It is smoother, more convex and somewhat darker brown than the larva. The anterior tubercles seem to be replaced by a pair of large, broadly elliptical discs or spots, representing less heavily chitinized areas of the puparial wall.

Larvæ and puparia of this description were found in a nest of *F. fusca* var. *subsericea* at Fort Lee, N. J., during April. I have some larvæ also from two localities in Massachusetts, collected in nests of the same ant by Mr. A. P. Morse and Mr. A. C. Burrill, and there are in the Museum of Comparative Zoölogy several specimens taken in the same state by Mr. E. A. Samuels.

We may conclude from the foregoing account that the typical and most frequent hosts of *Microdon* in the north temperate zone are the species of *Formica*. In tropical and subtropical regions, however, where this genus of ants is absent, the hosts belong to different and often to very diverse genera. Wasmann (1894) mentions *Camponotus hildebrandti* as the host of a *Microdon* in Madagascar. I have given an account (1901) of the larva of another undetermined species from the nest of *Pseudomyrma mexicana*, one of the fiercest of our American ants, and Brues (1903) has described and figured a very peculiar puparium, which probably belongs to a genus allied to *Microdon* and was taken in California by Prof. H. Heath in the nest of a very small black Myrmicine ant, *Monomorium minutum* Mayr. I find no mention of the species of ants with which the other recorded tropical and subtropical *Microdons* have been taken. We should expect the Australian forms to occur in the nests of *Iridomyrmex* species, the South African forms with the larger species of *Plagiolepis*.

The relations of *Microdon* to its hosts appear in an interesting light if we compare this insect with *Cremastochilus*. The larval and pupal *Microdon* are synœketes and are usually indifferently tolerated. Occasionally, however, the ants attack them even in these stages although they are well protected by their hard skins and marginal



fringes. The imaginal insects are treated as synechthrans, or persecuted intruders, and are quite defenceless. The larval and probably also the pupal *Cremastochilus* are synechthrans, or at any rate the ants would destroy them if they did not protect themselves by hiding away in the soil. The adult beetle may become indifferently tolerated, though it seems generally to be treated with hostility. Still it is well protected by its hard armor, so that it walks about the nest with impunity like the larval *Microdon*. Thus each of these myrmecophilous genera has its Achilles heel. At first sight this seems to show a lack of adaptation in a portion of the life cycle (larval and pupal stages in *Cremastochilus*, imaginal stage in *Microdon*), but a broader view suggests that what appears as a defect is really an advantage, both to the parasite and its host, for it prevents the former from exceeding a proper numerical relation to the latter. In other words, it is better for *Cremastochilus* and *Microdon* to sacrifice individuals and thus become rather rare forms, than to over-run the colonies and seriously disturb the domestic economy of their hosts.

#### ADDENDA.

To the account of *Cremastochilus* and *Heterius* given in the former studies of this series, I would add the following notes:

During the past summer I succeeded in finding the larvæ of *Cremastochilus castaneæ* in a nest of *Formica fusca* var. *glacialis* Wheeler, at South Harpswell, Me., and in rearing the beetles. I have described the larval and pupal stages in a recent paper (The Ants of Casco Bay, Maine, With Observations on Two Races of *Formica sanguinea*, Bull. Amer. Mus. Nat. Hist., XXIV, 1908, pp. 619-645).

In my summary of the records of *Cremastochilus*, I unfortunately omitted an important paper by Wickham (On Coleoptera Found with Ants. Fifth Paper. Psyche IX, 1900, pp. 3-5). This author cites *C. harrisi* as occurring with *Formica pallidefulva nitidiventris* Emery (Lowa, May 4) and *C. saucius* and *knochii* with *Pogonomyrmex occidentalis* Cresson (*opaciceps* Mayr). *C. saucius* was taken by E. J. Oslar at Denver, Berkeley and Salida, Colo. (April 10-July 11), *C. knochii* at Berkeley (April 8) and Chimney Gulch, Colo. (June 18). Oslar is quoted as stating that the former species occurs singly in the *occidentalis* hills at all times of the year, and Wickham adds that "it is difficult to get perfect specimens of this beetle, the legs often being much mutilated supposedly by the ants, which are large and fierce creatures."



It is probable that the primary, or regular hosts of these two *Cremastochili* are to be found among the many species of *Formica* which abound within the geographical range of *P. occidentalis*, and that this latter ant is merely a secondary, or accidental host. This is indicated by the fact that I have recently received from Mr. W. Knaus a specimen of *C. knochi* taken at Stockton, Utah, by T. Spalding in a colony of a very pale form of *Formica sanguinea subintegra* Emery with *F. subpolita* slaves.

In the same paper Wickham mentions the occurrence of *Heterius brunneipennis* in the nests of *Formica fusca* var. *subsericea*, in company with *Ptomphagus parasita*.

Wasmann (The Guests of Ants and Termites, Entom. Record, XII, 1900, pp. 204, 205) publishes the following note on the common European species: "Just one word about *Heterius ferrugineus* and its allies. What seems easier at first sight than that a small Histerid, which already possesses in its oval shape a kind of protection, should force the ants to receive it as a lodger, and which would be tolerated because of its being unattackable, and that finally the ants, taking pleasure in licking it, would elevate it to the rank of a true guest. But it is not as simple as it appears. In my observation-nests I have had a number of *Heterius* for more than five years, and I have come to the conclusion that it would be better for this species to be merely tolerated. It is in truth licked by the ants, but this is not to its advantage, as the ants do not feed it. It is often in great danger. *Formica sanguinea* and *pratensis* play with it for a quarter of an hour at a time, like a cat plays with a mouse, trying to get hold of its jaws, so it is often hurt. Once a *Heterius* was so badly used by a *Formica sanguinea* that it was half killed and nearly devoured. Whilst licking the wounded beetle the ant's greed had been awakened."

In a later paper (Zur näheren Kenntniss des echten Gastverhältnisses (Symphilie) bei den Ameisen- und Termitengästen, Biol. Centralbl., XXIII, 1903, p. 207) Wasmann makes a few remarks on the adipose tissue and notices the large size of the ovarian eggs of *H. ferrugineus*. He kept a pair of these beetles for more than three years in an artificial nest, but they never oviposited and he saw neither larvæ nor pupæ.

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## NEW RHYNCHOPHORA. III.

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RHYNCHITIDÆ.

### **Eugnamptus pallidus, new species.**

Form of *collaris*, color testaceous. Head behind the eyes feebly narrowing to base; between the eyes a feeble fovea; punctuation sparse; beak carinate at middle; antennæ slender. Prothorax closely and rather coarsely punctate, with a feeble median impression. Elytra with rows of large, approximate punctures; intervals flat, with an irregular row of smaller punctures; surface as usual, clothed with semi-erect, pale hairs. Length 4 mm.

Huachuca Mts., Arizona.

The uniform pale color, the larger eyes of the male and the slender antennal joints distinguish *pallidus* from any of our other species.