

Photo 2. Epinotum and petiole of *T. schneideri* from the Pyrenees (a, c) and *T. kutteri* (b, d).

Photo 1-2: from Tinaut, A., 1990; Spixiana.

"AntWiki.org.", for *Anergates*.

"Wheeler, W. M., 1908, "Comparative ethology of the European and North American ants." *Journal für Psychologie und Neurologie*, vol. 13, p. 404-435, pl. III-IV."

"Wheeler (1908) described *atratum* queens and males he found in nest during a 1907 visit to Europe. Not only does his account provide insights about this ant's biology, it is also an interesting account of Wheeler collecting, and experimenting with, ants with Forel."

"On only one occasion was I fortunate enough to find a colony of this rare, workerless parasite. June 6, at 2 P. M., while collecting near Vaud, in the very meadow in which Forel as a young man made many of his classical observations for the "Fourmis de la Suisse", I discovered a medium-sized *Tetramorium caespitum* colony from which female *atratum* were escaping in considerable numbers. The nest was around the roots of a plantain (*Plantago major*) and the females issued one by one from the entrances, climbed the leaves to their tips, and flew away in all directions over the sun-lit grass. At 3.30 P. M. Prof. Forel joined me and we excavated the nest with great care. It contained besides the obese mother queen of *atratum* and several hundred *Tetramorium* workers, more than a thousand winged queens, a few hundred of the wingless, pupa-like males, several pupae and a few larvae of the parasitic species. In the galleries of the nest dozens of couples were united in the act of mating. The *Tetramorium* workers picked up the single males and hurried away with them, but they paid little attention to the females. The colony was placed in a bag and on the following day used for experiments on *Tetramorium* colonies in Prof. Forel's garden at Chigny. On opening the bag the next morning, I found several of the *atratum* in copula, but most of the females had either lost their wings or were ready to drop them at the slightest touch. Eight *Tetramorium* colonies that had large nests with multiple craters in the paths of the garden, were selected, and the females were placed near them, one at a time, on the ground. In all cases when they were placed within a few centimeters of the openings, they entered the nest almost immediately; when placed at a greater distance they wandered about demurely till they found an opening and then at once crept into it. Seven of the nests were thus entered by numbers of the queens without creating the slightest excitement among the *Tetramorium* workers. These merely stopped when they happened to meet a female, seized her by the wings, thorax or pedicel, but at once dropped her and went about their work. In no case was one of the queens injured. In three of these colonies they were seized by single workers and carried into the nest as fast as I could set them on the craters. Both males and females were placed near the openings of one of the nests. The males were seized with signs of keen interest and some animosity, to judge from the way in which the workers bent their gasters forward and tried to sting the helpless creatures. They were not killed, however, but carried a few decimetres from the nest and thrown away, sometimes from the top of a pebble or lump of earth. This was being done while other workers were carrying the females into the nest. One vigorous colony exhibited a different behaviour. All the parasites, both male and female, were at once seized, pulled about by the legs, wings and antennae and then carried away and dumped on the ground at some distance from the nest. In this instance several of the parasites of both sexes were injured so that they could not walk. Strange *Tetramorium* workers placed on any of the nests above mentioned were suddenly pounced upon and killed. These observations show that the *atratum* queens are, as a rule, treated with great lenity and even carried into the nests, but that the males are rejected. They also show that certain colonies are positively hostile to both sexes of the parasites. In all cases, however, the behaviour of the *atratum* queens was very uniform: they sought and entered the *Tetramorium* nests as if these belonged to them, offered no resistance when seized and, when roughly handled, merely curled up and feigned death. The experiments were continued throughout the morning. With the gradually increasing temperature towards noon the *Tetramorium* workers became more numerous and active outside their nests but their treatment of the *atratum*, which I was continually giving them, remained the same. Late in the afternoon the experiments were repeated with two of the colonies which during the morning had been entered without protest by a number of

the parasitic queens. The workers were out in a multitude, excavating and dragging in insect food. When male, female or pupal *atratum* were placed on these nests, the males and pupae were promptly seized and thrown away and the females were also seized, but less promptly, and also rejected. Some of the latter that had managed to enter the nests were brought out and dumped at a distance of several decimetres from the entrances. I watched the nests for some time and although a few of the females were not brought out, I am, of course, unable to state whether they were subsequently adopted, killed in the galleries or ejected. It appears, therefore, that the acceptance of *atratum* by the *Tetramorium* under natural conditions is not as immediate as the observations of Adlerz and Wasmann on artificial nests would lead one to suppose. The fact that *atratum* is so rare an ant, although its sporadic colonies produce enormous numbers of females in regions inhabited by myriads of *Tetramorium* colonies, shows that permanent adoption is not easily effected."

"Wheeler remarks in a footnote that Forel assessed the colonies in his garden the following year. He found sexual pupae of *Tetramorium* in every nest, showing that none of the queens had successfully been adopted into the colonies."

"Wheeler, W. M., 1909, "Observations on some European ants." Journal of the New York Entomological Society, vol. 17, p. 172-187."

"Wheeler (1909) described finding two *Tetramorium* nests with *atratum* about 1 km south of Zermatt, Switzerland "at an altitude of about 1,620 m., on the warm western slope of the Matter valley"

"August 13. A large *Tetramorium* colony under half a dozen rather large, flat, contiguous stones arrested my attention, because it, contained several hundred larvae, all of the same size and of a peculiar gray color, unlike the gleaming white larvae so abundant in the other colonies of this ant. On scrutinizing the superficial chambers of the nest more closely, I saw four fine, dealated *atratum* queens in the peculiar, obese or physogastric condition, which this alone of all European ants is able to attain. Three of these queens were close together under the centre of one of the stones, the other was in a similar position under an adjacent stone. It was quite clear then that the gray larvae were the offspring of these queens, and from their size it was evident that they were mature and nearly or quite ready to pupate. Of course, there were besides only *Tetramorium* workers in the colony and none of their larvae. I do not know whether other observers have noticed the singular uniformity in the age and development of the larvae of *atratum*. It is very striking, though it is what we should expect, for the life of the *atratum* colony must be of short duration, since it cannot exceed that of its sterile host, the *Tetramorium* workers. It is, indeed, quite possible that the whole development of the *atratum* colony does not require more than a year, or, at any rate, that the queens of this species become physogastric, owing to the rapid and enormous development of their ovaries, and begin to lay within a few months after entering the *Tetramorium* colony, and that the brood matures by the following summer. Owing to the altitude at which this colony was found (about 1,600 m.), the maturity of the brood must have been greatly delayed and probably would not have hatched till the latter part of August or early in September."

"August 14. In the same locality but lower down the slope and less than a hundred meters from the Matter, I detected a second colony, which, however, was small and depauperate and was living under a single small stone. This colony, too, contained a number of the grey larvae, which, as in the preceding case, were all of the same size and partly adhering by means of their hooked, dorsal hairs to the lower surface of the stone. The nest also contained a number of large root aphids of both sexes and in all their developmental stages. After careful search I found the obese *atratum* queen, but she was dead and somewhat shrivelled, and her thorax had been separated from her gaster."

"Wheeler then goes on to offer some advice about how one might find *Tetramorium atratum*:"

"As collectors are always interested in the various parasitic ants that live with *Tetramorium*, I may here introduce a few suggestions that may aid them in detecting infested colonies. In the first place, it is advisable to concentrate one's attention on a locality in which *Tetramorium* colonies are unusually abundant. In the second place, the collector should examine the nests at the height of the breeding season, that is, during June and July at the lower, and early in August at the higher altitudes, when the normal colonies contain larvae and pupae of all three phases. He may safely pass over at once all colonies containing the larger, male and female larvae and pupae of the *Tetramorium*, as such colonies do not contain *atratum* and concentrate his attention on the colonies which at first glance appear to contain only workers and worker brood of the *Tetramorium*."

"The presence of uniformly developed, grey larvae may be taken to indicate the occurrence of *atratum*, if its presence is not already conspicuously indicated by the numerous imaginal brood of small black females and sordid yellow, nymphoid males. With a good pocket lens the *atratum* larva may also be recognized by its peculiar hairs. I give a figure of a larva from one of the nests described above, and also of a mature worker larva of *Tetramorium* for comparison. It will be seen that though both larvae possess pairs of long anchor-tipped dorsal hairs, the head of the *atratum* larva is naked, and its short dorsal and ventral hairs are much more densely and compactly branching, while the longer hairs are serrate and not branched at their tips like the homologous structures of the *Tetramorium* larva. The anchor-tipped hairs with sigmoid basal flexure are used in both species for fastening the larvae to the lower surfaces of stones, the roots of plants and the walls of the galleries and chambers of the nest."

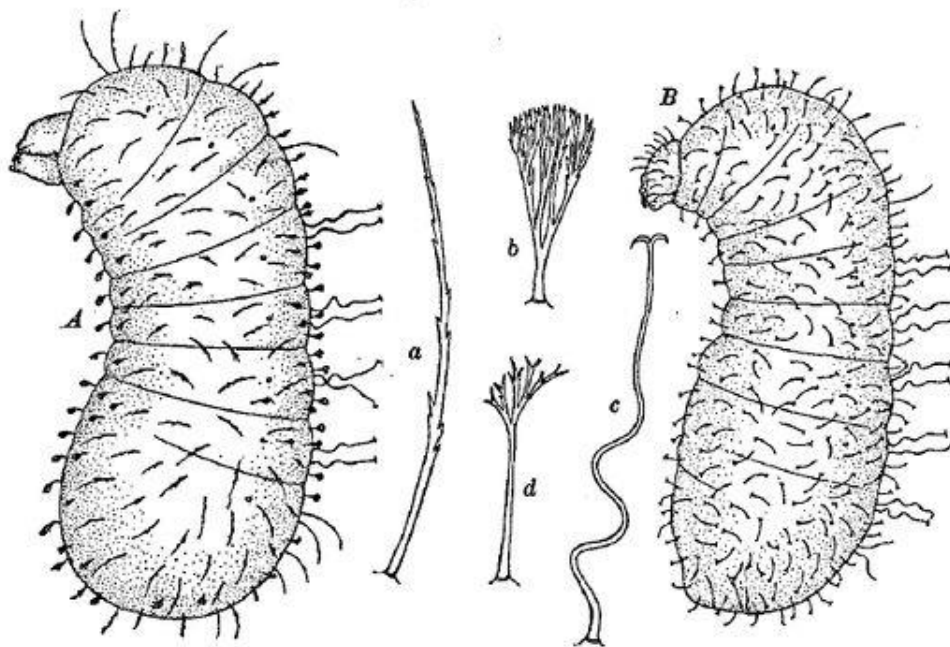


FIG. 2. A, adult larva of *Anergates atratulus*; a and b, long, serrate and short, branching hair of same, more highly magnified; B, adult worker larva of *Tetramorium cespitum*; c and d, long, anchor-tipped, dorsal hair and short, branching hair of same, more highly magnified.

Fig. 2: from Wheeler, W. M., 1909; New York Entomological Society.