“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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus 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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus*, 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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus* 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 *A. atratulus*. It is very striking, though it is what we should expect, for the life of the *A. atratulus* 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 *A. atratulus* 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 *A. atratulus* 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 *Anergates atratulus*:”

"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 *A. atratulus* 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 *A. atratulus*, 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 *A. atratulus* 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 *A. atratulus* 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."

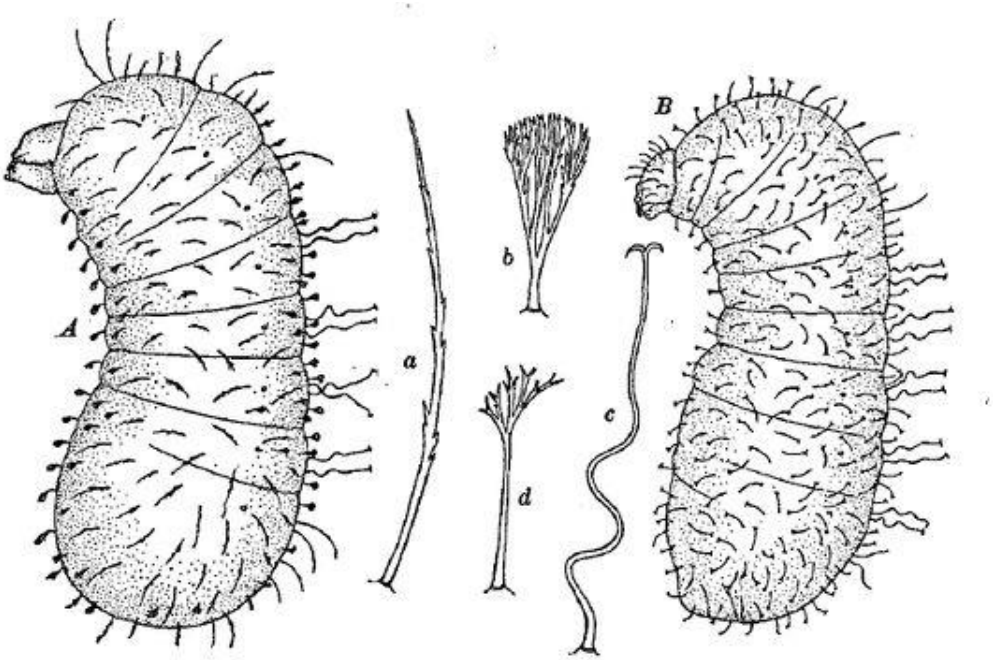

FIG. 2. *A*, adult larva of *Anergates atratulus*; *a* and *b*, long, serrate and short, branching hair of same, more highly magnified; *B*, adult worker larva of *Tetramorium cespitum*; *c* and *d*, long, anchor-tipped, dorsal hair and short, branching hair of same, more highly magnified.

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

“Wheeler, W. M., 1910.”, for *Anergates*.

“*Anergates atratulus*. -- This extraordinary ant, like the preceding, is far from common, though it is widely distributed in continental Europe. For this reason it is better known than any of the other workerless parasites. Its host is *Tetramorium caespitum*. Studies on its habits have been published by Schenck (1852), von Hagens (1867), Forel (1874), Adlerz (1886), Wasmann (1891) and Janet (1897). Both male and female are peculiarly modified. The former is 2.7-3 mm. long, of a pale, sordid yellow colour, wingless and pupa-like, with the gaster strongly curved downward at the tip. Although its legs are rather well developed, it moves very slowly and with a dawdling gait. The forelegs are furnished with strigils which are pectiniform in specimens from certain localities (Switzerland), but in those from other localities (Sweden, Holland, France) the teeth are lacking and the strigils may be vestigial or absent. Janet has shown that the mandibular glands are well developed, though the mandibles are very small and feeble. The black, winged female is of the same size as the male and has the gaster of normal dimensions, but with a longitudinal dorsal groove before fecundation. After entering the *Tetramorium* nest, however, the ovaries become greatly enlarged and the gaster expands till it becomes a flattened sphere 4 mm. in diameter, on which are seen, in the form of little plates, isolated by the enormous distention of the articular membranes, the strongly chitinized rings, which, in the virgin, constitute the whole external surface of the gaster. Both male and female have 11-jointed antennae and large ocelli, but the eyes are rather poorly developed. Owing to the apterous condition and sluggish movements of the male, mating takes place in the nest among the offspring of the same mother (adelphogamy). This can be readily observed both in natural and artificial nests. The couples are so firmly united that they can be killed, without separating, in warm alcohol. After fecundation the females fly out of the nests, so that the nuptial flight, though vestigial and unisexual in this ant, still subserves the important function of disseminating the species. *Tetramorium* colonies infested with *Anergates* contain only the workers of the host species. Adlerz and Wasmann have shown that these pay very little attention to the virgin *Anergates*, but carry the males about and lick them assiduously, and that during these operations the latter assume a characteristic, motionless attitude. Both the male and female parasites are, of course, fed by their hosts, as they are quite unable to eat independently.”

“Adlerz and Wasmann have made some experiments with a view to ascertaining the method whereby the female *Anergates* becomes associated with the *Tetramorium*. Adlerz in Sweden placed several unfertilized *Anergates* queens in a strange nest of the host species. They moved about aiming the workers as if unperceived. Nearly the same results were obtained on placing unfertilized *Anergates* in a normal colony containing a *Tetramorium* queen. He also placed several larvae, pupae and male and female imagines of *Anergates* in a normal *Tetramorium* colony which was living in an artificial nest. In every case the strangers were almost at once amicably received. Similar observations were made by Wasmann in Holland. He found that strange *Tetramorium* workers did not in the least injure the male and female *Anergates*, where as they killed without mercy a number of *Strongylognathus testaceus* males and females which he placed in the nest.”

“The experiments of Adlerz and Wasmann were not carried far enough to throw any light on the permanent adoption of the *Anergates* and the fate of the *Tetramorium* queen. It now seems probable that the latter insect is killed by her own workers soon after the colony is invaded by the parasitic queen. Since the publication of Santschi's notes on *Wheeleriella*, renewed observations on young *Anergates* queens in the presence of alien *Tetramorium* colonies, and under natural conditions, have become a desideratum. June 6, 1907, at 2 P.M., while collecting ants near Vaud, in the very meadow in which Forel as a very young man made many of his classical observations on *Formica sanguinea*, *Polyergus*, *Strongylognathus testaceus* and other species of his "Fourmis de la Suisse," I discovered a medium-sized *Tetramorium* colony from which female *Anergates* were escaping in considerable numbers. The nest was around the roots of a plantain, 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. Professor Forel joined me and we excavated the nest with great care. It contained, besides the obese mother queen of *Anergates* and several thousand *Tetramorium* workers, more than a thousand winged queens, a few hundred of the 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 Professor Forel's garden at Chigny. On opening the bag I found several of the *Anergates* 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 centimetres of the openings, they entered the nests 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 these 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 then 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 antennas, 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 *Anergates* 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 *Anergates* 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* became more numerous and active outside their nests, but their treatment of the *Anergates*, which I was continually giving them, remained the same. Late in the afternoon the experiments were repeated on 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 *Anergates* 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 soon 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 the parasites by the *Tetramorium* under natural conditions is not an immediate and simple as the observations of Adlerz and Wasmann on artificial nests would lead one to suppose. The fact that *Anergates* is so rare an ant, notwithstanding its sporadic colonies produce enormous numbers of females in regions inhabited by myriads of *Tetramorium* colonies, shows that permanent adoption is not easily effected. Were the contrary the case, *Tetramorium caespitum* would itself become a rare, if not extinct, species."

"There can be no doubt that of the seven permanent social parasites above enumerated, *Anergates* is the most specialized and degenerate. This is clearly shown in the ergatoid and nymphoid structure

of the male and the structure of the head in both sexes. All the other species agree in being in a less advanced stage, although they, too, have lost the worker caste. This loss may be said to be due to disuse, but it followed necessarily upon there duction in size of the male and female, and this condition in turn was probably initiated by the same causes that have led to the dwarfing of the queens among the temporary parasites. Forel, Lubbock and Wasmann are inclined to believe that *Anergates* represents a form that was once dulotic. Lubbock says: "In *Anergates,* finally, we come to the last scene of this sad history. We may safely conclude that in distant times their ancestors lived, as many ants do now, partly by hunting, partly on honey; that by degrees they became bold marauders and gradually took to keeping slaves; that for a time they maintained their strength and agility, though losing by degrees their real independence, their arts, and even many of their instincts; that gradually even their bodily force dwindled away under the enervating influence to which they had subjected themselves, until they sank to their present degraded condition-weak in body and mind, few in numbers, and apparently nearly extinct, the miserable representatives of far superior ancestors, maintaining a precarious existence as contemptible parasites of their former slaves. "This interpretation of *Anergates* as a very degenerate dulotic ant seems to have been suggested by the obvious dwindling of the worker caste in *Strongylognathus testaceus*, but there is nothing in the structure of *Anergates* or of any of the other workerless ants to prove that they are descended from slave-making species. More probable is the supposition that they have been derived from temporary parasites or xenobiotic forms with habits like those of *Leptothorax emersoni*. The *Anergates* or *Wheeleriella* colony differs from those of species like *Formica consocians* in reaching its complete development, that is, the stage in which the sexual offspring of the mother queen mature, in a much shorter period of time. This period must fall within the life time of the *Tetramorium* or *Monomorium* workers and can therefore hardly exceed three or four years. This acceleration of colonial development is made possible by a suppression of the useless worker caste and a dwarfing of the sexual individuals, although there is a concomitant increase in their numbers. And all of these interesting compensatory developments are necessitated in turn by the castration of the host colony, for this is what the elimination of the host queen amounts to. As this is a mortal injury to the host colony and a serious injury to the host species, it is not surprising that the intrusion of the parasites is resisted and that the latter, as Lubbock says, are "few in number and apparently nearly extinct." In other words, extreme parasitism in ants, as in other organisms, tends continually to defeat its own ends and to undermine its own existence."

Crawley, 1912, is the only one to observe, until now, the killing of a *Tetramorium* queen by its own workers. All the others go on to say that *Anergates* is adopted in a queenless *Tetramorium* colony.

“Creighton, W. S., 1950.”, for *Anergates*.

“This extraordinary workerless parasite was first described by Schenck in 1852. This observer was also the first to publish on the habits of *Anergates*. It would be hard to imagine a more remarkable set of structural modifications than those which occur in both sexes of *A. atratulus*. The virgin female possesses a deep, median sulcus on the dorsum of the gaster. After fertilization the excessive development of the ovaries separates the gastric sclerites and stretches the intersegmental membranes between them. The lateral expansion is greater than the dorsoventral stretching, with the result that the gaster of the fertile female finally assumes a shape rather like a biscuit. The separated sclerites appear like islands on the top and bottom surfaces. The structure of the male is even more aberrant. This sex is apterous and pupoidal. The body apparently never becomes fully chitinized. The gaster is curved under at the tip and provided with a disproportionally large set of genitalia. In both sexes the mandibles are poorly developed and apparently quite useless for purposes of feeding. It is no wonder that this insect has attracted much interest or that, despite its rarity, its habits have been repeatedly studied. While the significance of some of the observations is not altogether clear, there is good general agreement as to the behavior of this remarkable species. *Anergates* is a parasite of *Tetramorium caespitum*. At maturity a parasitized nest consists of a single fertile female of *Anergates*, a considerable number of *T. caespitum* workers and a large number of pupoidal males and virgin females of *Anergates*. The *T. caespitum* workers feed and care for the parasites but are particularly attentive to the males and much less interested in the females, (Adlerz 1913, Wasmann 1908). It was shown by Janet (1897) that the male of *Anergates* possesses unusually large mandibular glands and Forel (1922) supposes that the secretion from these glands is relished by the *T. caespitum* workers. Because the *Anergates* male is apterous, the nuptial flight has undergone some peculiar modifications. Copulation takes place between sisters and brothers (adelphogamy) within the confines of the nest. Mating is difficult for the clumsy, pupoidal male and is facilitated, as Forel has pointed out, (1922) by the docility of the female. After fertilization the female emerges from the nest for the nuptial flight. It is obvious that at the completion of the nuptial flight the *Anergates* female must find a nest of *T. caespitum* and gain access to it. Repeated experiments have been performed to ascertain how this is accomplished but the results have been uncertain in most cases. It is easy to show that the fertilized *Anergates* female will try to gain access to the *T. caespitum* nest. This she does by making an unobserved entry or, in many cases, by seizing the antenna of a *T. caespitum* worker who thereupon drags her into the nest. What follows next is not so clear. In the great majority of cases the *Anergates* female is killed by the *T. caespitum* workers if we may judge from experimental data. In one case, however, there has been a different result. In 1912 Crawley succeeded in getting a colony of *Tetramorium* to accept an *Anergates* female. This colony contained sexual forms of the host. At the end of a week following the introduction of the *Anergates* female to the nest, the *T. caespitum* workers had killed and cut to pieces the *T. caespitum* males and females. The introduced female of *Anergates* later showed the characteristic gastric enlargement which marks the mature queen but died without having laid any eggs. In summing up the evidence concerning this and other experiments Donisthorpe (1915) expressed the opinion that the destruction of the *Tetramorium* female by her own workers is probably the normal sequence of events following the entrance of the *Anergates* female into a *T. caespitum* colony. It is difficult to see how else the *T. caespitum* female could be eliminated, since it is unlikely that the *Anergates* female could kill her.”

“Kutter, H., 1977.”, for *Anergates*.

“***Anergates*** Forel.
Forel 1874 Les Fourmis de la Suisse: 93.
Gattungstypus und bis jetzt alleinige Art:“

“***A. atratulus*** (Schenck) Fig. 178-192.
Schenk 1852 Ver. Nat. Nassau 8: 91 Weibchen. 1861 ibidem 16: 164 Männchen.
Die flügellosen Männchen sind zwar von Schenk bereits 1852 bemerkt, nicht aber als solche erkannt, sondern mit unausgefärbten Weibchen verwechselt worden.
Arbeiterin fehlt.
Weibchen: 2,5-3 mm lg. Jungfräulich geflügelt. Schwarz mit hellen Gliedmassen. Fühler 11-gliedrig. Gastermitte mit vertiefter Längsfurche. Stachel reduziert. Als Nestmutter zeigt die *Anergates*-Königin stark ausgeprägte Physogastrie.
Männchen: 2,7-3 mm lg. Ungeflügelt. Schmutziggelb. Fühler 11-gliedrig. Beine plump, ohne resp. mit nur stark reduziertem Putzapparat am Vorderbein. Gasterende stark nach unten und vom gekrümmt.“

“Die Ameise lebt als obligatorischer Sozialparasit bei *Tetramorium*. Ihre Fortpflanzung erfolgt adelphogam. Die ungeflügelten Männchen paaren sich bereits im Muttemest mit ihren geflügelten Schwestern. Die Kolonien sind monogam d. h. dulden nur 1 fertiles, physogastres *Anergates*-Weibchen. Die Aufzucht der Brut wird völlig den Wirtsarbeiterinnen überlassen.“

“ Über die phylogenetische Abstammung von *Anergates* bestehen zwei Hypothesen. Beide Geschlechter sind stark an ihr parasitisches Leben angepasst und zeigen viele bemerkenswerte Rückbildungen resp. Umbildungen normaler Merkmale. Das Fehlen der typischen *Tetramorium*-Fûhler bei den Männchen z. B. spricht dafür, dass *Anergates* nicht von seiner Wirtsart sondern eher von *Monomorium* abstammen könnte und erst später zur Rasenameise hinübergewechselt sei. Demgegenüber scheinen die Chromosomenverhältnisse eher an jene von *Tetramorium* zu erinnern. Das Problem ist nicht gelöst.“

“*Anergates atratulus* darf überall dort, wo auch die Rasenameise *Tetramorium* vorkommt, erwartet werden. In der Schweiz vom Tiefland bis über 2200 m (Saas-Fee). Er ist bis jetzt vor allem im ganzen palaearktischen Gebiete, vornehmlich in Mitteleuropa, dann aber auch in Nordamerika nachgewiesen worden.“

“Buschinger, A., 1999.”, for *Anergates*.

“Die in Europa von den Küsten bis in die Hochalpen weit verbreitete, generell aber sehr seltene arbeiterinlose Inquiline *Anergates atratulus* lebt in Nestern zweier Wirtsarten, der Rasenameisen *Tetramorium caespitum* (Linnaeus, 1758) und *Tetramorium impurum* (Förster, 1850), wobei offenbar nur bereits weisellose Wirtsvölker parasitiert werden können. Die entsprechend kurzlebigen Völker erzeugen große Mengen an geflügelten *Anergates*-Jungweibchen und in geringerer Zahl die flügellosen, puppenartig erscheinenden Männchen. Die Kopula findet demzufolge im Mutternest statt, doch scheinen gelegentlich mehrere fertile *Anergates*-Königinnen, auch unterschiedlicher Herkunft, in einem Wirtsnest zusammen zu leben.“

The “Inquiline Syndrome.”.

Wilson, E. O. (1971, p. 374) and Hölldobler, B. K. and Wilson, E. O. (1990, p. 467) defined **the “Inquiline Syndrome”** and listed 41 characters of morphological, behavioural and life history traits that evolved convergently in inquiline social parasites (a 19 points of special interesses-list.). Not all those inquilines have all the characters but they have most of them. The ants of the genus *Teleutomyrmex* display 36 characters of the list.

Here is the list from Chapter 12 of “The Ants.”:

“1. The worker caste is lost.
2. The queen is either replaced by an ergatogyne, or ergatogynes appear together with a continuous series of intergrades connecting them morphologically to the queens.
3. There is a tendency for multiple egg-laying queens to coexist in the same host nest.
4. The queen and male are reduced in size, often dramatically so; in some cases (for example, *Teleutomyrmex schneideri*, *Plagiolepis ampeloni*, *Plagiolepis xene*) the queen is actually smaller than the host worker.
5. The male becomes “pupoid”: its body is thickened, the petiole and postpetiole become much more broadly attached, the genitalia are more externally exposed when not in use, the cuticle becomes thin and depigmented, and the wings are reduced or lost. The extreme examples of this trend are displayed by *Anergates atratulus*, *Pheidole neokohli*, and *Pheidole acutidens*.
6. There is a tendency for the nuptial flights to be curtailed, and to be replaced by mating activity among nestmates (“adelphogamy”) within or near the host nest. Dispersal of the queen afterward is very limited.
7. Probably as a consequence of the curtailment of the nuptial flight just cited, the populations of inquiline species are usually very fragmented and limited in their geographic distribution.
8. The wing venation is reduced.
9. Mouthparts are reduced, with the mandibles becoming smaller and toothless and the palps losing segments. Concomitantly, the inquilines lose the ability to feed themselves and must be sustained by liquid food regurgitated to them by the host workers.
10. Antennal segments are fused and reduced in number.
11. The occiput, or rear portion of the head, of the queen is narrowed.
12. The central nervous system is reduced in size and complexity, usually through reduction of associative centres.
13. The petiole and postpetiole are thickened, especially the latter, and the postpetiole acquires a broader attachment to the gaster.
14. A spine is formed on the lower surface of the postpetiole (the Parasitendorn of Kutter).
15. The propodeal spines (if present in the ancestral species) “melt,” that is, they thicken and often grow shorter, and their tips are blunted.
16. The cuticular sculpturing is reduced or lost altogether over most of the body; in extreme cases the body surface becomes strongly shining.
17. The exoskeleton becomes thinner and less pigmented.
18. Many of the exocrine glands are reduced or lost, a trait already described in some detail in the earlier account of *Teleutomyrmex schneideri*.
19. The queens become highly attractive to the host workers, which lick them frequently. This is especially true of the older, physogastric individuals, and it appears to be due to the secretion of special attractant substances which are as yet chemically unidentified.”

“Emery’s Rule” in its strict and its loose version.

In 1909, the entomologist/taxonomist Carlo Emery made an important generalization and noted that social parasites among insects and their hosts share common ancestry and hence tend to be parasites of species or genera to which they are closely related. Over time, this pattern has been recognized in many additional cases, and generalized to what is now known as **“Emery's rule”**. The pattern is best known for various taxa of Hymenoptera. The significance and general relevance of this pattern are still a matter of some debate, as a great many exceptions exist, though a common explanation for the phenomenon when it occurs is that the parasites may have started as facultative parasites within the host species itself (such forms of intraspecific parasitism are well-known.), but later became reproductively isolated and split off from the ancestral species, a form of sympatric speciation.

In **the “strict version”** of Emery’s rule, social parasitic species are their host’s closest relatives (a sister taxon to its host in a phylogenetic sense.), and likely evolved from their host’s lineage by sympatric speciation, or through a combination of allopatric and subsequent sympatric speciation. In **the “loose version”** of Emery’s rule, social parasites are close relatives of their host, but not sister species. Although few host-parasite pairs have been subjected to molecular phylogenetic analysis, studies to date support at least the loose version of Emery’s rule.

Good general reviews of **“Emery’s rule”**, going over all the pro and cons about the rule itself or about the two versions, you can find in Rabeling, 2020 or in Lopez-Osorio, 2020.

The “Kutter-Wilson Paradox.”.

There are only 371 known parasitic species of ants among the 14,091 extant and 770 fossil ant species. Despite their rarity, they are common in a few subfamilies like the Myrmicinae and the Formicinae, and common in temperate ants but rare in tropical ants. Why is there such a strong bias in both the taxonomic and ecological distributions of social parasites and their hosts, **the “Kutter-Wilson Paradox”**? The selective forces and ecological conditions that favour social parasitism continue to be researched and discussed. Factors like cooler temperatures and polygyny (i.e., colonies with multiple queens.) are important considerations, but cannot explain the evolution of social parasitism in all cases.

The “Kutter-Wilson Paradox” (Kutter, 1968 (“1969”) and Wilson, 1971.) was recently reviewed by Gray, Rabeling, 2023 (“2022”), on all 371 taxonomically described socially parasitic ant species (Dulosis (79 species or 21% of social parasites.), inquilinism (88 species or 24% of social parasites.), and temporary social parasitism (204 species or 55% of social parasites.).). It was surprizing to note that the results came from the dulotic species but not from the inquiline and the temporary social parasitic species (These are normal distributed around the equator.). The dulotic species are centred on the temperate and polar regions of the Northern hemisphere.