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*Extraordinary Females in Three Species
of Formica, with Remarks on Mutation
in the Formicidæ.*

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Article XXVIII. — EXTRAORDINARY FEMALES IN
THREE SPECIES OF FORMICA, WITH REMARKS
ON MUTATION IN THE FORMICIDÆ.

By WILLIAM MORTON WHEELER.

The three species of *Formica* described in the following paper were all taken within a radius of thirty miles of Colorado Springs, Colorado, during the past summer. They agree in presenting certain very unusual characters in the females, although the corresponding workers and males deviate but little from the ordinary species of *Formica*. Even a superficial study of the workers shows that they are all to be assigned to the *rufa* group, and were this sexual phase alone known, one would be tempted to regard them merely as subspecies or varieties of *F. rufa*. Fortunately we are not bound still further to complicate this well-known circumpolar species by including under it the three Colorado forms, since the females and, to some extent also, the workers and males display characters of undoubted specific value.

The first species, *F. ciliata* Mayr, has hitherto been known only from isolated female specimens.¹ Emery, in his revision of the North American *Formica*,² erroneously regarded it as perhaps belonging to the *pallide-fulva* group. It departs from all known species of the genus in its singular pilosity and, to a lesser degree, in the yellow color of the whole body. The female of the second species, *F. oreas* n. sp., is remarkable in coloration and to some extent also in pilosity, especially in that of the antennal scapes. In coloration it resembles the female of *ciliata* as well as that of *F. dakotensis* Emery. The third species, *F. microgyna* n. sp., is remarkable on account of the diminutive size of the females, which are actually smaller than the largest workers, a condition quite unknown among the normal females of any other species of *Formica*.

¹ Mayr, G. Die Formiciden der Vereinigten Staaten von Nordamerika. Verh. zool. bot. Ges. Wien, 1886, pp. 419-464.

² Emery, C. Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. Zool. Jahrb., Abth. f. Syst., Bd. VII, 1893, pp. 633-682, Taf. 22

I subjoin descriptions of all three sexual forms of each of the three species, together with some ethological field notes. At the end of the paper I have added a few remarks on the significance of the aberrant female characters.

Formica ciliata Mayr.

Worker (fig. 1.—Length, 3–8 mm.

With the habitus of *Formica rufa* subsp. *obscuriventris* Mayr. Mandibles 8-toothed. Clypeus broadly rounded in front, hardly produced in the middle, strongly carinate its entire length. Head, excluding mandibles, fully as broad as long; occipital border slightly concave, especially in large individuals; posterior corners rounded; sides distinctly converging anteriorly, cheeks rather long. Joints 1–4 of antennal funiculus decidedly more slender and somewhat longer than joints 5–10. Thorax resembling that of *F. rufa*; mesoepinotal constriction pronounced, basal surface of epinotum flattened, horizontal, forming a decided angle with the slightly concave declivity. Petiole in profile rather thick at the base, with a thin edge; its anterior surface distinctly convex, the posterior flattened; seen from behind, the scale is produced upwards in the middle in the form of a blunt point, sides rounded.

Mandibles finely and densely striated. Whole body opaque, except the frontal area and clypeus and, in the largest workers of some colonies, also the whole head, which are more or less shining. Head, thorax, petiole, and gaster very finely shagreened.

Hairs yellow, those on the clypeus and mandibles rather coarse, on the former projecting forward. Upper surface of head naked; lower surface with a few erect hairs. Thorax covered with erect hairs, except the mesonotum, mesopleuræ, and basal epinotal surface, which are naked. Petiole below and along edge of scale with a fringe of short hairs, also with a few hairs on its anterior and posterior surfaces. Gaster invested with short, rather dense grayish yellow pubescence in addition to numerous uniformly distributed, suberect, and subobtuse hairs, which are hardly longer on the terminal segments than elsewhere. Antennæ delicately and inconspicuously pubescent. Legs with sparse pubescence; coxæ and flexor surfaces of tibiæ and tarsi with prominent hairs.

In the largest workers the head, thorax, and petiole are rich yellowish red, the mandibles and clypeal sutures deeper red. Gaster brown. anal segment, and often also the base of the first segment and the venter, yellow. Antennæ and legs reddish yellow, the funiculus toward the tip, the coxæ, femora, and often also the tibiæ, dark brown. The smallest workers usually have the posterior portion of the head, dorsal surface of thorax and of petiole clouded with black or dark brown.

In some small specimens the whole body excepting the mandibles and anterior portion of the head, is uniformly infuscated.

Female (Fig. 1, — Length, 6–8 mm. Mandibles 8-toothed. Clypeus with broadly rounded anterior border, not produced, indistinctly carinate. Antennæ rather slender. Head, excluding the mandibles, hardly longer than broad, decidedly narrower in front than

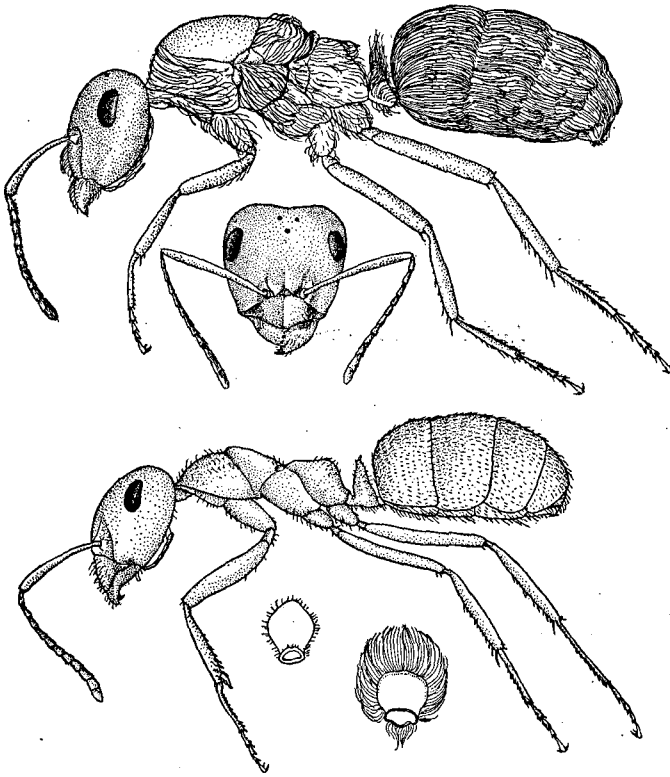


Fig. 1. *Formica ciliata* Mayr. Female (deâlated) and worker in profile; head of worker (frontal view); petiole of worker and female from behind. This and the following figures are all drawn to the same scale.

behind, occipital border nearly straight. Thorax rather small, somewhat narrower than the head. Petiole broadly rounded above, scale not produced in the mid-dorsal line as in the worker; posterior and anterior surfaces as in the worker, edge sharp.

Mandibles subopaque, striato-punctate. Body and appendages smooth and shining, especially the head, mesonotum and scutellum, which are very glabrous.

November, 1903.]

Pilosity remarkable, consisting of very long, golden yellow hairs, which have a tendency to curl at their ends. These hairs are absent on the upper surface of the head, the mesonotum, and legs, excepting the coxæ. They are long and conspicuous on the mandibles and clypeus, on the latter scattered over the disc and also arranged in a row along the anterior border. Lower surface of head with appressed long hairs. Remainder of body, excepting the nude portions above mentioned, covered with long woolly hairs, which are very prominent on the petiole, around the edge of which they form a conspicuous fan (Fig. 1, e). On the gaster they are very long and abundant, appressed, overlapping, and curled at their extreme ends, so that this region of the body appears opaque, in marked contrast to the head and mesonotum. Antennæ and legs covered with delicate, inconspicuous pubescence, flexor surfaces of fore femora with flexuous hairs, corresponding surfaces of middle tibiæ each with a single row, hind tibiæ with two rows of stiff hairs.

Rich reddish yellow throughout; only the following regions being infuscated or blackened: terminal half of funiculus, metanotum and adjacent portion of scutellum and the alar insertions. Wings uniformly grayish hyaline; veins and apterostigma more yellowish gray, the latter not very conspicuous.

Male. — Length, 6.5–8 mm. Mandibles sharply pointed, edentulous. Head very short, very broad behind the eyes, very narrow in front, occipital border straight. Clypeus strongly carinate. Maxillary palpi 5-jointed. Thorax robust, broader than the head. Petiole thick, convex anteriorly, more flattened posteriorly, border very blunt, evenly rounded both in profile and when seen from behind. Gaster rather broad, with flattened dorsal surface. Genitalia of the usual size.

Whole surface of body and appendages opaque, the former finely shagreened; dorsal surface of gaster with a slight silky lustre.

Body, legs, and antennæ covered throughout with short grayish hairs and pubescence. Eyes hairy.

Deep black. Genitalia pale yellowish, tipped and bordered with black. Wings grayish hyaline, of a little deeper tint than in the female. Veins and apterostigma black.

Described from numerous females, males, and workers taken from several colonies during the latter half of July (13th to 28th). These colonies were all found in the Ute Pass about Manitou or between Manitou and Colorado City on sunny mountain slopes at an altitude of 7000–8000 feet. The nests resembled those of small colonies of *F. rufa*. Sometimes a colony occupied several small mound-nests close together and

consisting of vegetable débris collected by the ants. At other times the nests were under stones banked about their edges with débris (like the colonies of *F. rufa* subsp. *difficilis* in the New England hills). The largest nest was found July 17 near Red Rock Cañon opposite the Garden of the Gods. It was a débris mound built around the stem of an *Opuntia*, and measured 40 by 60 cm. in diameter and 5-10 cm. in height. In it were found hundreds of workers, dozens of females, and a few males. The pugnacious workers behaved like the workers of *F. rufa*.

Formica oreas, n. sp.

Worker (Fig. 2). — Length, 4.5-7 mm. With the habitus of *F. rufa* subsp. *obscuriventris* and very similar to the worker of *F. ciliata*, but differing in the following characters: When seen from behind, the petiole, though variable, is usually rounded above or even somewhat depressed in the middle. Some individuals, however, have a blunt median projection; in profile the anterior surface is distinctly convex, the posterior flattened or even somewhat concave, its edge rather sharp. Depth of mesoëpinotal constriction also variable, being considerable in some and not very conspicuous in others. In some individuals the basal and declivous surfaces of the epinotum form almost a right angle with each other.

Body opaque; mandibles, clypeus, frontal area, and front of head somewhat shining.

The pilosity also resembles that of the *ciliata* worker, but is more general, more abundant, and silvery white instead of yellow. Upper and lower surfaces of head, petiole, mesonotum, and mesopleuræ, as well as the remainder of the thorax, with numerous short, erect hairs. These hairs are conspicuously long on the ocellar region. Antennal scapes as well as the legs with prominent, suberect hairs. On the gaster the short, suberect hairs are less conspicuous than in *ciliata*, so that this region appears more uniformly grayish on account of the dense pubescence. Hairs on the terminal segments longer and more slender.

In color the following differences may be observed: legs, especially middle and hind pairs blacker, bases and tips of femora and of tibiæ red; fore coxæ much less infuscated than the posterior pairs. Gaster black, with clear reddish yellow anal segment. Smallest workers much less infuscated on the dorsum than the smallest *ciliata* workers. In some of these minors the vertex, pro- and mesonotum are each blotched with black; but in others the head and thorax are almost immaculate.

Female (Fig. 2). — Length, 7.5-9 mm. Robust, and with the stature of the typical *Formica* females. Mandibles 8-toothed. Cly-

peus convex, rounded in front, indistinctly carinate. Head, excluding the mandibles, as broad as long, sides converging anteriorly, posterior corners prominent, rounded, occipital border nearly straight. Thorax nearly as broad as the head, robust. Petiole broad, compressed anteroposteriorly; in profile faintly convex in front, flattened

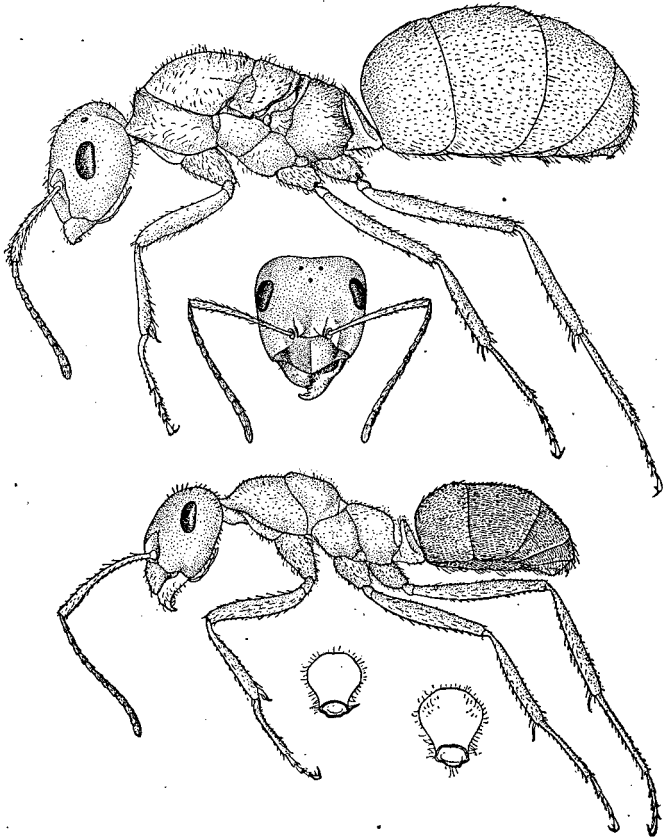


Fig. 2. *Formica oreas* n. sp. Female (decalated) and worker in profile; head of worker (frontal view); petiole of worker and female from behind.

behind; seen from behind, the rather sharp border is depressed and horizontal in the middle and truncated on the sides. Gaster and legs of the usual conformation.

Mandibles striatopunctate, subopaque. Body and appendages smooth and shining, especially the upper surface of the head, mesonotum, and scutellum, which are highly glabrous.

Entire insect covered with delicate erect or suberect silvery white hairs, which fail to conceal the ground color as in *ciliata*. These hairs are conspicuous on the antennal scapes, legs, and gaster, less abundant on the front of the head and on the mesonotum, at least in some specimens.

Color rich yellowish red; only the following regions infuscated or black: mandibular teeth, anterolateral borders of clypeus, thoracic sutures, alar insertions, metanotum, adjacent border of scutellum, posterior border of each gastric segment, palpi, articulations of legs, and terminal half of funiculus. Wings uniformly gray, veins and apterostigma sordid yellow.

Male. — Length, 7 mm. Mandibles with a short, acute terminal and three distinct basal teeth. Maxillary palpi 5-jointed, slender. Head small, cheeks rather concave, postocular region less prominent than in the male *ciliata*. Thorax robust, through the alar insertions decidedly broader than the head. Petiole thick at base, but ending above suddenly in a very thin edge in the middle. Seen from behind, the border is horizontal and depressed in the middle, obliquely and somewhat concavely truncated on either side. Gaster compressed dorsoventrally. Genitalia moderately large.

Body opaque, finely shagreened. Mesonotum, scutellum, and gaster above slightly lustrous.

Whole insect, including the appendages, covered with rather dense gray hairs. These are longest and suberect on the head, thorax, and petiole, more reclinate on the gaster, short and subappressed on the antennæ and legs. Eyes distinctly hairy. Gaster, moreover, delicately gray pubescent.

Deep black; genitalia, tips of trochanters, knees, basal portions of first and second tarsal joints, reddish yellow. Wings like those of the female, except that the apterostigma is more deeply infuscated.

Described from many workers and females and a single male taken from two colonies in the Ute Pass, Colorado. One of these colonies, containing the sexual forms, was found July 26 at Woodland Park (8500 ft.), well up in the Pass. The colony occupied several nests in an open, sunny place under some large stones, the edges of which were banked with vegetable débris collected by the ants. The other colony, containing workers only, was found near Manitou at a lower altitude, under otherwise similar conditions.

***Formica microgyna*, n. sp.**

Worker (Fig. 3). — Length, 3.5–6.5 mm. With the habitus of a small *Formica rufa*. Mandibles 8-toothed. Clypeus rounded in

front, not produced in the middle, carinate its entire length and with uneven surface. Maxillary palpi rather long. Head, excluding the mandibles, somewhat longer than broad even in the largest workers. Cheeks long, subparallel, occipital border not excised; antennæ like those of the preceding species and *F. rufa*. Mésoëpinotal constriction very distinct, epinotum more rounded than in either of the preceding species, its dorsal and declivous surfaces of about equal length, the former convex, the latter slightly concave in profile. Petiole narrow and thick, with a sharp edge, convex anterior and flattened posterior face; seen from behind, the edge varies from evenly rounded or even somewhat produced upward in the middorsal line to subdepressed or concave. Gaster and legs as usual.

Body, including mandibles and clypeus, opaque, legs faintly lustrous. Frontal area shining.

Entire insect, including appendages, covered with microscopic gray pubescence, densest and most distinct on the gaster. Hairs pale yellow, erect, and, except on the mandibles, distinctly clavate with obtuse tips. These hairs are placed rather far apart on the clypeus, on the front of the head, where they form four longitudinal rows as far back as the ocelli, on the thoracic dorsum, coxæ, border of petiole, and surface of the gaster. On the last they are particularly conspicuous on account of their equidistant arrangement and contrasting color. They are readily rubbed off. A few of these hairs are occasionally present on the lower surface of the head, but entirely absent in most specimens. Anterior border of scape with a row of delicate, suberect, tapering hairs and a row of similar hairs on the flexor surface of each tibia.

Head, thorax, and petiole deep yellowish red, mandibles and clypeus somewhat darker. In small workers, the front, vertex, thoracic dorsum, and petiole are spotted with black. Gaster black, only the anal region yellowish. In the largest workers the legs are red throughout, in intermediates the femora and tibiæ are brownish, in the smallest workers the infuscation extends also to the coxæ. Antennæ red, funiculus more or less infuscated toward the tip.

Female (Fig. 3). — Length, 4–4.5 mm. Mandibles 8-toothed; clypeus and head resembling those of the worker; thorax distinctly narrower than the head. Petiole narrow, thick at the base, both its anterior and posterior surfaces alike convex, dorsal border rather sharp; seen from behind variable, in some specimens evenly rounded, in others somewhat produced upward in the middorsal line. Gaster and legs of the usual shape.

Body subopaque, very finely shagreened; gaster and anterior portion of head faintly shining. Mandibles striatopunctate. Frontal area shining.

Whole insect, including the antennæ and legs, covered with delicate white hairs, which are longer and more abundant than in the worker, and nowhere clavate or obtuse. These hairs are conspicuously long

and suberect on the frontal and lower surfaces of the head, on the thorax, petiolar border, gaster, antennal scapes, and legs. In addition to these hairs the body and appendages are invested with microscopic white pubescence.

Head, thorax, petiole, and legs dull, reddish yellow. Mandibular teeth, funiculi, a blotch covering the ocellar region, a large antero-

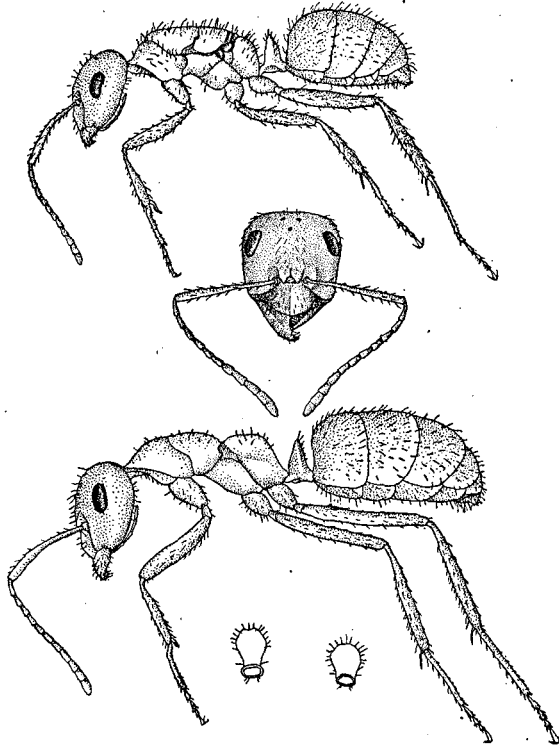


Fig. 3. *Formica microgyna* n. sp. Female (decalated) and worker in profile; head of worker (frontal view); petiole of worker and female from behind.

median mesonotal, two elongate parapsidal blotches, alar insertions, metanotum, and more or less of the adjacent portion of the scutellum, fuscous. In some specimens the clypeus, frontal region, coxæ, and pleuræ are infuscated. Gaster black, anal segment and more or less of the base of the first segment, brownish yellow. Wings whitish hyaline, veins and stigma brown, the latter conspicuous.

Male.—Length, 5–5.5 mm. Mandibles slender, edentulous,

pointed. Maxillary palpi 5-jointed. Head rather short, broad behind the eyes, narrow in the region of the cheeks. Eyes large and prominent. Clypeus distinctly carinate anteriorly, its border somewhat reflected. Antennæ slender. Thorax broader than the head, rather robust, mesonotum conspicuously flattened just in front of the scutellum. Petiole very thick with obtuse and broadly rounded upper surface. Genitalia rather slender.

Subopaque; frontal area, anteromedian suture of mesonotum, parapsidal furrows, paraptera and upper surface of gaster, smooth and shining. Mandibles coarsely punctate near the tips, finely striated toward the base.

Body and appendages clothed with microscopic grayish pubescence, which is sparse and visible only in certain lights. Hairs covering the body and appendages delicate, sparse, suberect, of an indistinct grayish color. Eyes naked.

Deep black; legs and genitalia dirty yellow; coxæ, femora, tibiæ, and terminal tarsal joints more or less infuscated. Wings like those of the female.

Described from many workers and females and a single male. Six colonies of this species were found in different localities about Manitou and Cheyenne Cañon, Colo. (July 10 to 30). In three of these I took the diminutive females in considerable numbers. They varied but little in size and were all normal in structure. When the nests were disturbed, they were as timid as the workers were pugnacious. The nests were all under single stones or clusters of stones, the edges of which were banked with vegetable débris collected by the workers. A single incipient colony, under a small stone in South Cheyenne Cañon, was found to contain about twenty workers, a few worker cocoons, and a gynandromorph, which had a female head, male gaster, and the thorax and petiole male on one side and female on the other.

I have also found the following distinct variety of the above species:

***Formica microgyna* var. *rasilis* var. nov.**

All three sexual phases averaging somewhat larger than the typical form (worker: 4-6.5 mm.; female, 5-5.5 mm.; male, 6-6.5 mm.). The worker and female have the antennal scape, lower surface, and posterior corners of head, and the legs, excepting for the row of hairs on the flexor surfaces of the tibiæ, entirely naked. Hairs on the clypeus, thorax, and petiole much less numerous. Frontal area opaque.

In the female the black blotches on the head and thorax are indistinct or entirely lacking, even in mature specimens, and the hairs on the head, thorax, petiole, and gaster are thick, clavate, and obtuse, instead of tapering as in the female of the typical form. In the male the mandibles are decidedly broader than in *microgyna* s. str., and furnished with three distinct basal teeth. Paraptera opaque, legs more deeply infuscated. Suberect hairs on lower surface of head, and on legs sparse or entirely lacking. External genital valves broader and blunter at their tips.

This variety appears to be commoner and more widely distributed than the typical form and occurs in more populous colonies. These live under stones, and may occupy separate nests covering an area of a square meter or more. Between July 11 and August 21, I found, in all, thirteen of these colonies in the neighborhood of Manitou (Red Rock Cañon, Williams Cañon, Ute Pass), between Broadmoor and Cheyenne Cañon, and on Pike's Peak. The largest colony, found in Cheyenne Cañon July 20, contained many males and several dozen of the diminutive females. Some of the latter were deálated and in all probability were the mother queens of the colony. Three of the colonies deserve special mention: First, a colony taken at Woodland Park (8500 feet) July 26, contained only workers, which were clearly intermediate between the true *microgyna* and the var. *rasilis*, as the antennal scapes and legs were beset with a few suberect hairs. Second, a colony taken on Pike's Peak, August 4, at an altitude of 11,500 feet, very near timber-line, differed from the colonies taken at lower altitudes in the deep infuscation of the head and thorax even in the largest workers. Third, a colony taken at Broadmoor, August 8, was mixed with workers of a small variety of *Formica fusca*, near *subsericea*. The two species were living together in such perfect amity (synclerobiosis) that I at first mistook them for a colony of *F. sanguinea* with slaves.¹

The anomalous character of the three *Formica* females above described, especially of *F. ciliata* and *microgyna*,

¹ Since this paper was sent to press I have received from Mr. R. V. Chamberlin numerous females and workers of *F. microgyna* var. *rasilis* collected near Salt Lake, Utah. They differ from the Colorado specimens in the duller and more brownish color of the head, thorax, and petiole.

seems to be brought nearer our comprehension, if we consider it in connection with another Formicid with equally unusual females, namely, *Lasius latipes*, recently studied by Mr. J. C. McClendon and myself.¹ This ant has females of two different kinds which occasionally occur in the same colony. One of these is such as we should expect to find after an examination of the females in the other species of the genus *Lasius*. The other is a most unusual form, with greatly dilated legs and peculiar pilosity. The female which conforms most closely to the generic type we have styled the α -, the extreme form the β -female. In Colorado, during the past summer, I happened on what I take to be α -, and β -females of another *Lasius* (*L. niger* var. *neoniger*). In the same colony of this species I found two kinds of females differing greatly in the length of the wings and not connected by intermediate forms. The majority of females had very long wings (9 mm.), but in a number of individuals of the same stature these appendages were so short that their tips did not reach beyond the gaster (5 mm.). The former are probably to be regarded as α -, the latter as β -females. Another American ant, in which the normal female is in all probability a β -form, is *Stenamamma* (*Aphenogaster*) *tennesseense*. This female departs remarkably in its small size, glabrous surface, and peculiar epinotal spines from the females of all the other known species of the genus. Here, as in *Formica ciliata* and *F. microgyna*, we may suppose that the α -form has become extinct, or, at any rate, has not yet been seen. Mr. McClendon and myself preferred to regard the occurrence of α - and β -females in *L. latipes* as a case of dimorphism. This involves no contradiction with the following clearer definition of my views.

Since reading the admirable work of de Vries,² and especially after some correspondence on this matter with my friend, Prof. Carlo Emery of Bologna, I am strongly inclined to see all these cases of dimorphism in the light of the mutation theory. The β -females would then seem to be striking

¹ Dimorphic Queens in an American Ant (*Lasius latipes* Walsh). *Biol. Bull.*, Vol. IV, No. 4, March, 1903, pp. 149-163

² Die Mutationstheorie. Leipzig, Veit & Co. Vol. I, 1901, Vol. II, 1903.

mutations or saltations of relatively recent phylogenetic origin, which in some species (*L. latipes* and *neoniger*) may continue to exist side by side with the primitive (α -) form. Or the α -form may be a reversional or atavistic occurrence in colonies that normally bring forth only β -forms.¹ In species like *F. ciliata*, *microgyna* and *Stenammina tennesseense* the α -form has not yet been seen. *Formica oreas* may also be included in the same category, though the female of this species is less extreme,—hardly more so, in fact, than the female of *F. dakotensis*.

A discussion of the more general question as to how far the species, subspecies, and varieties of the Formicidæ show evidence of having arisen by mutation instead of continuous variation would require more space than can be given in this article. In my opinion, the mutation theory not only plausibly indicates how the species, subspecies, etc., have arisen in this group of insects, but also throws light on the development of caste or polymorphism within the confines of the single species. It is difficult, however, with the means at our command, accurately to separate the phenomena of trophic variability from those of mutation proper, as I shall endeavor to show in a future paper.

¹ Similarly the peculiar wingless, or "ergatoid" males of *Formicoxenus*, *Anergates*, etc., may be regarded as β -males, *i. e.*, as saltatory aberrations or extreme mutations from the normal winged type, which has been suppressed in the phylogeny. It should also be noted that the different ergatoid females of forms like *Leptothorax emersoni* are not continuous variations, but mutations which differ from one another by the presence or absence of whole characters — *e. g.*, ocelli, thoracic sclerites, etc., at the same time that they exhibit true variations, *i. e.*, differences in dimensions.