Article XXIX. — SOME NEW GYNANDROMORPHOUS ANTS, WITH A REVIEW OF THE PREVIOUSLY RECORDED CASES.

By WILLIAM MORTON WHEELER.

In the following paper six new gynandromorphous ants are described. The study of these and of the previously recorded cases among the Formicidæ and other insect groups has been greatly facilitated by a perusal of the recent review by Dalla Torre and Friese of all the Hymenopterous gynandromorphs known up to 1899. In the hope of bringing the subject to the notice of American students, I have included an English résumé of the known cases among the Formicidæ, as these singular anomalies are certainly most frequently found and therefore most easily studied among the insects of this family. Of the 80-odd known Hymenopterous gynandromorphs recognized by Dalla Torre and Friese ('99), 19 are ants. Two of these cases, however, are spurious. Their No. 20, *Myrmica lævinodis*, recorded by Cooke ('82) is the same as case No. 19, previously recorded by Smith ('74), and the *Ponera punctatissima* (Case No. 24) is a normal ergatoid male and not a gynandromorph.[1] Omitting these two cases, therefore, and adding the six described in this paper, we have 23 Formicid gynandromorphs, *i. e.*, nearly a third of the total number of Hymenopterous cases. Of these, 15 are honey bees (*Apis mellifica*) and comprise a number of individuals. The explanation of the high percentage of cases contributed by this one species is, of course, perfectly obvious. Similarly the relatively very large proportion of ant gynandromorphs may be readily accounted for. The Formicidæ are not only of all insects, but probably of all animals, the most abundantly represented by individuals, and this greatly increases the chances of finding such anomalies among collected material. And the fact that ants live in communities of workers which are so devoted to their young that they help them to emerge from their cocoons and to divest themselves of their

[1] See Emery '95, pp. 293, 295.

pupal envelopes, readily accounts for a greater survival of adult anomalies among these than among the non-social Hymenoptera and other insects. It is, in fact, rather surprising that the gynandromorphs of so many non-social insects should be able to run the gauntlet of their various ecdyses and metamorphoses and reach maturity. This, perhaps, implies a considerable degree of muscular coördination in these often very asymmetrical creatures.

Dalla Torre and Friese ('99, pp. 92, 93) have adopted the following classification of gynandromorphs:

GROUP I.

Lateral Gynandromorphs (*i. e.*, differing in sexual characters on the two sides).

1. Left side male, right side female.	a. Head alone.
	b. Thorax alone.
2. Left side female, right side male.	c. Abdomen alone.
	d. Head and Thorax.
3. Decussating, now male on the left, now male on the right, etc.	e. Head and Abdomen.
	f. Thorax and Abdomen.
	g. The whole body.

GROUP II.

Transversal Gynandromorphs (*i. e.*, differing in sexual characters dorso-ventrally).

1. Dorsally male, ventrally female.	a. Head alone.
	b. Thorax alone.
	c. Abdomen alone.
	d. Head and Thorax.
2. Dorsally female, ventrally male.	e. Head and Abdomen.
	f. Thorax and Abdomen.
	g. The whole body.

GROUP III.

Frontal Gynandromorphs (*i. e.*, differing in sexual characters antero-posteriorly).

1. Anteriorly male.	a. Head alone.
	b. Head and Thorax.
2. Anteriorly female.	c. Thorax of one, Head and Abdomen of other sex.

GROUP IV.

Mixed Gynandromorphs (combining the peculiarities of the above groups, *i. e.*, lateral, transversal and frontal intermingled).

1. Left side male.
2. Left side female.
3. Anteriorly male.
4. Anteriorly female.
5. Dorsally male.
6. Dorsally female.
7. Decussating.

In certain respects, this classification is as good as any that can be devised at the present time. Perhaps another group should have been established to include cases of *blended* gynandromorphs, such as, *e. g.*, anomalies which have the form of one sex with the color, sculpture or pilosity of the other, since the four groups above given include only *mosaic* gynandromorphs.[1]

Apart from this omission, the classification suffers, moreover, from certain defects that become very obvious as soon as we attempt to consign a given gynandromorph to one of the groups. It is then seen that, strictly speaking, nearly all of these anomalies belong to the fourth group. Pure lateral hermaphrodites are extremely rare, since the majority of cases thus designated exhibit some mingling, or, at any rate, some deviation of the external sexual characters from any conceptual scheme like the above. In tabulating 65 of the known Hymenopterous gynandromorphs, Dalla Torre and Friese find 38, or somewhat over half the cases, belonging to the first, nearly one quarter (16) to the third, and the remaining quarter (18 cases) to the fourth group. Only a single gynandromorph, a honey bee described by Menzel (**'62a**), can be included in group II (*sub.* 1). Hence all the remaining divisions of this group are purely conceptual and empty. Another difficulty is encountered in the detailed classification of cases belonging to the fourth group. If we adopt the classification of Dalla

[1] From a remark on p. 29 of Dalla Torre and Friese's paper, concerning Tosi's case of a female *Chalicodoma muraria* with male coloration, I infer that the authors do not regard cases of this kind as gynandromorphs, but I would maintain that differences in pilosity and sculpture at least are clearly morphological and cannot therefore be lightly set aside.

Torre and Friese in a loose and provisional sense, we find that the Formicidæ, like other Hymenopterous families, present examples of the first, second and fourth groups.

It is, of course, necessary to distinguish accurately between gynandromorphs and hermaphrodites, since both kinds of sexual organs are not necessarily present in all gynandromorphs (*e. g.*, in the case of *Leptothorax obturator* described below). In the great majority of the recorded cases, the nature of the correlation of internal with external sexual characters is absolutely unknown. It is not even certain that a definite correlation exists. The dissection of the smaller Hymenoptera (especially ants) is so difficult and uncertain that one is tempted to refrain from it and to preserve the specimen on account of its rarity, rather than run the risk of destroying it and of obtaining no satisfactory knowledge of its sexual anatomy. Furthermore, gynandromorphous specimens are often accidentally found only after they have been carded or preserved for a long time in strong alcohol. The recorded correlations of external with internal sexual characters, even in insects as large as gynandromorphous honey bees, are contradictory, and may have been influenced to some extent by the expectation of finding hermaphroditic conditions.

Six Gynandromorphous Ants.

1. **Formica microgyna** *Wheeler.*

Fig. 1.

A mixed frontal and lateral gynandromorph; the head being almost purely female, the gaster male, the thorax, petiole and legs male on the left, female on the right side. The specimen is a callow.

Head that of a female, slightly asymmetrical above, owing to the left eye being somewhat larger and more prominent than the right. Apart from some of the coloring, this is the only male character in the head. The mandibles, antennæ, palpi and other mouth-parts are perfectly normal and symmetrical, except that the left antennal scape is somewhat more slender than the right. Thorax symmetrical except in the region of the paraptera and scutellum, where the right side is somewhat

impressed and defective. Left half of petiole low and rounded, exactly as in the male, right half higher and with a sharper border to the scale, as in the female. Gaster male in form and structure. External genitalia those of a normal male, symmetrical, except that the terminal segments are turned somewhat to the left. Legs male on the left side,

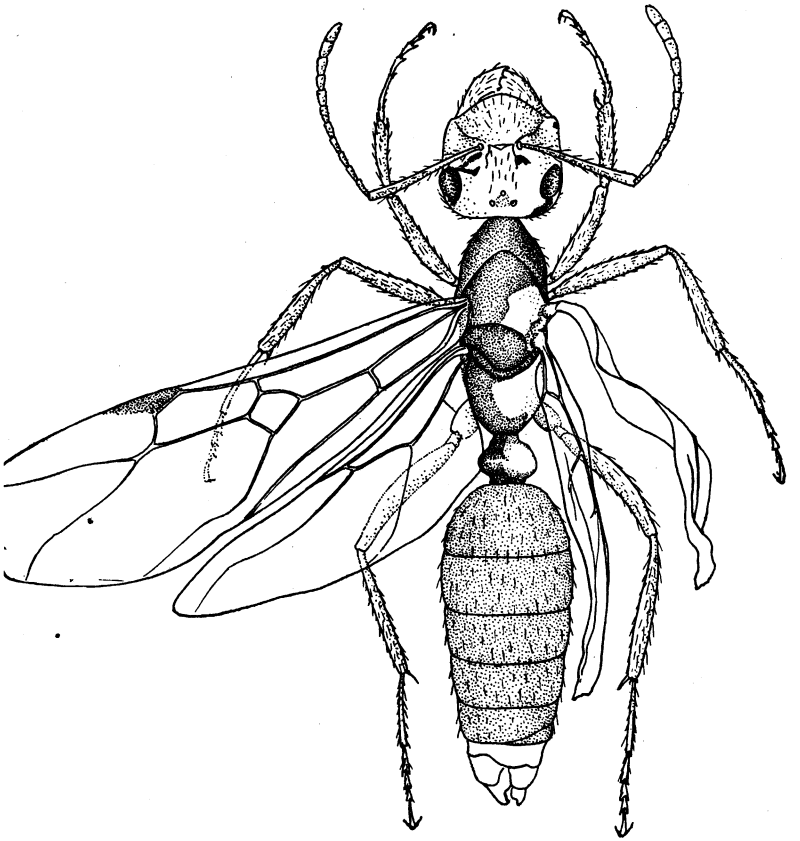

Fig. 1. *Formica microgyna* Wheeler. Gynandromorph; male and female.

female on the right, but hardly differing in length on the two sides. The sexual differences between the legs of the two sides are seen in the more slender tibiæ and smaller strigil on the left side. Left wings normal, right wings smaller and dishevelled, apparently in correlation with the defective thoracic region on which they are inserted.

The coloration of the specimen is peculiarly striking. The head is

pure yellow. Teeth of mandibles and ocellar area infuscated as in the normal female. There is a peculiar, black, V-shaped spot between the left frontal carina and the left anterior orbit, a small black spot at the left posterior orbit, another at the outer border of the right frontal carina, one near the right anterior corner of the head, and a broader, oblique, black band extending from the right posterior orbit to the union of the head with the prothorax. On the lower surface there is a slender black band extending from near the insertion of the right mandible to the posterior edge on the same side. Antennal scapes yellow, somewhat infuscated towards their tips, funiculi and palpi black. Thorax black with the exception of the following regions, which are yellow, the boundary lines between the two colors being very sharp: a large irregular spot on the right posterior corner of the mesonotum, a blotch of similar shape and dimensions on the right mesopleuræ, involving the episternum, another large blotch covering the whole right half of the epinotum except its inferior portion. Left half of petiole black, right half yellow, except the postero-inferior portion, which is also black. The line of color demarcation is median and coincides with the difference in structure of the right and left halves of the petiole. Gaster black, with yellow, somewhat infuscated genitalia as in the normal male. In certain lights the right basal portion of the first gastric segment is seen to be suffused with yellow. Legs infuscated, more heavily on the left (male), than on the right (female) side; articulations yellow. Coxæ black on the left side, infuscated on the right, where the anterior surface of the fore coxa is largely yellow. Wings whitish, the left pair with veins and stigma colored more like those of the female than the male.

Whole body opaque, except the upper surface of the gaster which is lustrous as in the male. The hairs on the head and antennal scapes are exactly as in the normal female, the pile and pubescence of the thorax, petiole, gaster and legs as in the male, except for the yellow (female) blotch on the right side of the mesonotum which bears stiffer hairs like those of the normal female. The remaining yellow blotches are bare.

Length 5.75 mm.

This specimen was found moving about clumsily among a few small workers in an incipient colony of *F. microgyna* in Cheyenne Cañon near Colorado Springs, Colo., July 20, 1903. *F. microgyna*, as I have shown in a previous paper ('03), differs from all the known species of the genus in the remarkably small size of the female. This may, perhaps, facilitate the development of anomalies like the one described above, because the male and female are so nearly of the same size.

2. **Polyergus rufescens** *Latr.* subsp. **lucidus** *Mayr.*

This case is somewhat dubious. It is a female with well-developed wings but an extremely small head, hardly half as broad as the head of the normal female and only about two thirds as broad as that of the worker. The antennæ are very short. So far as its form is concerned, the head could be described as that of a very small worker, but the coloring is decidedly blackish and the surface is somewhat more coarsely shagreened than the head of the worker or female. In these particulars the specimen approaches the male type.

Taken near Colorado City, Colo., Aug. 18, 1903, in a flourishing colony of *Polyergus lucidus* with *Formica nitidiventris* as slaves. The nest contained many males and females of the *Polyergus*, but the above was the only anomalous specimen found.

3. **Stenamma (Aphænogaster) fulvum** *Roger* subsp. **aquia** *Buckley* var. **piceum** *Emery.*

FIG. 2.

A nearly complete lateral gynandromorph; male on left, worker on right side. Callow.

Head and antennæ symmetrical, of the worker type. Ocelli absent, but eyes larger and more prominent and antennal scapes shorter than in the normal worker. Funiculus 13-jointed on the left (hence male), 12-jointed on the right, but with the last joint incompletely divided into two, so that the antennæ, like the eyes, present male characters on both sides. Left mandible small, like that of the male, right large, like that of the worker. Thorax asymmetrical, male on the left side, with mesonotum, scutellum, metanotum, remnants of dishevelled wings, and on the epinotum a blunt projection as in the normal male; on the right side the thorax is like that of the typical worker except that the metanotum is distinct. The prominent worker spine is present on the right side of the epinotum. Petiole and postpetiole symmetrical, somewhat intermediate in shape between the worker and male, but much more rounded and thicker set than in either of these sexual phases. Gaster asymmetrical, evidently worker on the right, with broad base, and male on the left, with the greatest breadth nearer the middle. There are five distinct segments as in the male. External genitalia represented only by the left half of the male organs,

but the cerci are present on both sides. No trace of a sting can be seen. Legs of the left side male throughout, long and slender; those on the right side decidedly shorter, of the worker type.

Sculpture of the head differing from that of the worker in having comparatively few clean-cut, longitudinal rugæ, which do not anastomose as in the worker. Interrugal spaces smooth and shining instead of opaque and punctate as in the worker. In its more shining surface the head approaches the male, in the presence of the rugæ, the worker type. The thorax and pedicel are sculptured like the male on the left side and are therefore rather smooth and shining, whereas the right side is rugose and less shining like the corresponding regions in the worker. Gaster shining throughout.

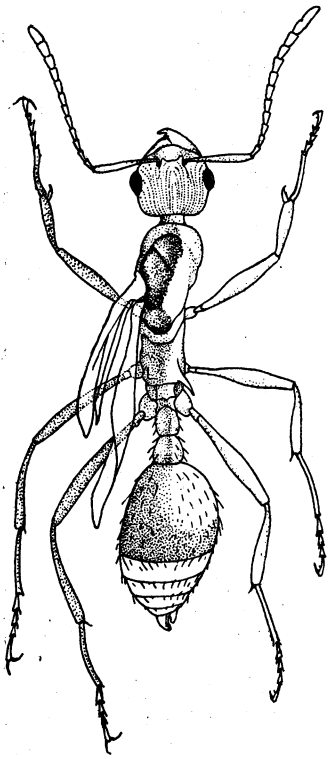

Fig. 2. *Stenamma fulvum* Roger subsp. *aquia* Buckley var. *piceum* Emery. Gynandromorph; male and worker.

Body sordid yellow, *i. e.*, like that of a callow worker, but with the male regions blackened as follows: rugæ of head, which stand out like black lines on a yellow background, left lower surface of head, the left half of the thorax, petiole, postpetiole, first gastric segment and the legs of the left side. The pigment is deepest in the thorax in front of the metanotum. On the right (worker) side the normally intense color of the posterior portion of the first gastric segment is represented by a blackish cloud.

Hairs on the whole head and right half of the remainder of the body like those of the worker, on the left half like those of the male.

Length, 4 mm.

The lateral gynandromorphism is very distinct in this specimen in nearly all parts except the head. In the latter region characters of the two sexes are blended, except in the mandibles, since the eyes, antennæ, sculpturing and coloration of the head show evidence of the male characters extending to

the right, and worker characters to the left side, with nearly perfect bilateral symmetry.

This specimen was kindly given me by Miss Adele M. Fielde, who sent me the following note concerning its capture: "It was found in one of my artificial nests here in the laboratory at Wood's Hole, Mass., Aug. 25, 1903, and must have been recently hatched. Fearing it might be torn by other ants, I at once bottled it in 95 % alcohol. One side was jet black. It seems that the color of this side has lessened in the alcohol. The other side was the usual color of callow *Stenamma piceum*. The nest in which I found it contained queens and workers that had been there a year, but I had lately put in newer ants and a quantity of pupæ from the old wild colony. This ant was probably hatched from the pupæ lately introduced." Miss Fielde also alludes to this specimen in a note at the end of her latest paper (**'03,** p. 624).

4. **Stenamma (Aphænogaster) fulvum** *Roger* subsp. **aquia** *Buckley* var. **piceum** *Emery*.

FIG. 3.

This insect is a normal worker apart from the head, which is intermediate in size between that of the male and worker. The eyes are much larger and more prominent than those of the worker, the one on the left distinctly larger than the one on the right. There are three well-developed ocelli on the vertex. The mandibles are of the worker type but the right one is clearly broader than the left. The antennæ are much shorter than those of the worker though both are 12-jointed;

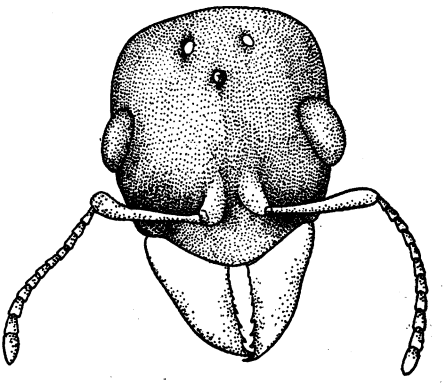

Fig. 3. *Stenamma fulvum* Roger subsp. *aquia* Buckley var. *piceum* Emery. Head of gynandromorph; male and worker.

the right scape is somewhat bent and distorted towards its apical end, which is incrassated, like the corresponding portion of the left scape. The sculpturing of the cephalic surface is also intermediate between that of the worker and the male. It is opaque and densely punctate like the male but with distinct indications of the longitudinal, reticulate rugæ of the worker. I regard the specimen as exhibiting gynandromorphism of the blended type in the head only. In certain respects the specimen resembles the above described *Polyergus lucidus*.

Received from Father Jerome Schmitt, O.S.B., who found it near St. Vincent, Pennsylvania, during the summer of 1901.

5. **Leptothorax obturator** *Wheeler.*

FIG. 4.

Incomplete lateral gynandromorph ; male on left, worker on right side ; head largely, gaster entirely of the worker type.

Head somewhat asymmetrical; the left eye being a little larger than the right, the left half of the clypeus smaller than the right half and separated from it by a deep notch. Left mandible distinctly smaller than the right but similar to it in other respects. Right antenna that of a normal worker; left antenna distorted, with the number of joints (12) peculiar to the worker; its scape only half as long as the right scape, bent toward its distal end; first funicular joint globose and therefore more like that of the male than the worker. Vertex with two ocelli, the left lateral, which is the larger, and the anterior unpaired ocellus, which is much smaller. Thorax nearly symmetrical, that of a male as far back as the paraptera which form a transverse band of uniform width just back of the mesonotum. Behind this region the thorax is decidedly asymmetrical, being male on the left side with a small abortive scutellum, half of the mesonotum and a nearly normal epinotum; worker on the right side with the epinotal spine blunter and more indistinct than in the normal worker. Petiole and postpetiole somewhat asymmetrical, very nearly of the worker type. Gaster purely worker, with well-developed, perfectly normal sting. Legs on the left side entirely male, with slender femora, tibiæ and tarsi; on the right side entirely of the worker type, with femora incrassated in the middle, stout tibiæ and larger strigil. Wings absent on right (worker) side; present on left (male) side, but somewhat dishevelled. When spread out in water the fore wing was found to have a peculiar claw-shaped process on the stigmatic border. Veins, owing

to their pale color, indistinct and difficult to trace, as they are in the wings of normal individuals.

Whole surface of head and pedicel and right half of epinotum sculptured like the worker; symmetrical anterior portion of thorax and left epinotum like the male. Gaster smooth and shining like that of the worker.

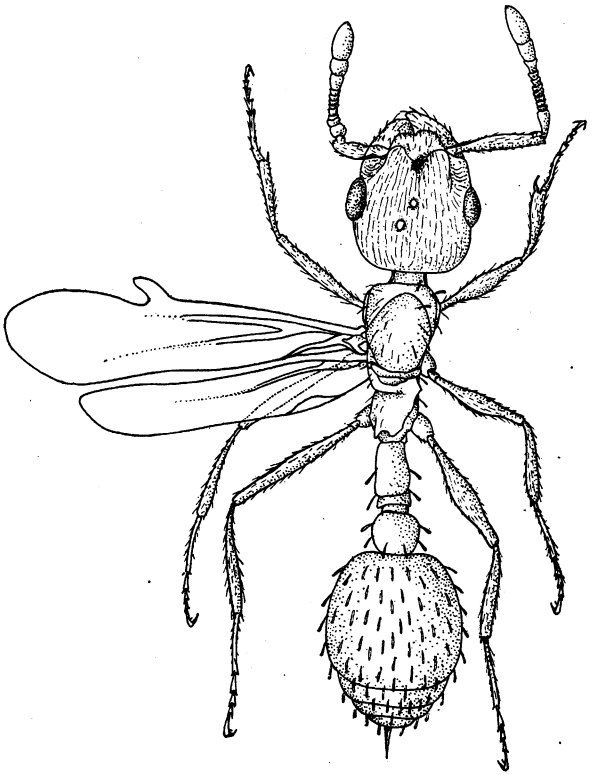

Fig. 4. *Leptothorax obturator* Wheeler. Gynandromorph; male and worker.

Head, petiole, postpetiole, gaster and right half of epinotum beset with the erect, clavate, white hairs so characteristic of the worker. Male portions of thorax with a few scattered, tapering hairs.

Black; mandibles, articulations of legs, lower portion of thorax and pedicel and basal joints of antennal funiculi, yellowish. Wings whitish hyaline.

Length, 2.4 mm.

This specimen was found at Austin, Tex., in a normal col-

ony of *Leptothorax obturator* that had been taken from a live oak gall (produced by *Holcaspis cinerosus*) and transferred to an artificial nest. It hatched Nov. 28 and was seasonally out of place in the colony, since the winged forms of this *Leptothorax* normally make their appearance only during April and May. The gynandromorph lived for several days in the nest and was fed and cared for by the workers. Its movements were very awkward, owing, without doubt, to the differences in the structure of the legs on the two sides of the body, the abortive left antenna and wings.

A former pupil, Miss Margaret Holliday, accomplished the difficult feat of dissecting the reproductive organs from the gaster, which was only .75 mm. in length. These organs were those of a normal worker: two slender ovarian tubules, one on either side. The one on the right side contained a rather large egg in the lowermost follicle. The vagina, sting and poison apparatus were quite normal. No traces of testes could be found, though the organs were carefully stained and mounted in balsam. Hence the specimen was not hermaphroditic.

6. **Epipheidole inquilina** n. gen. et n. sp.

FIG. 5.

A nearly perfect lateral gynandromorph ; left side male, right side female. Mature.

Head very asymmetrical; left half small and clearly that of a male, with large eye, normal male antenna (13-jointed) and very small mandible, with only one basal tooth; right half much larger, female, with normal female mandible (with three large basal teeth) and antenna (12-jointed). Left ocellus large, of the male type; right small, of the female type, the anterior unpaired ocellus intermediate in size between the two. Thorax rather robust, symmetrical, except in the epinotal region where the spine is of the male type (short and pointed) on the left side, of the female type (stout, laterally compressed and very blunt) on the right side. Petiole and postpetiole nearly symmetrical, intermediate between those of the male and female. Gaster somewhat asymmetrical basally, being broader on the right (female) than on the left (male) side. Terminal segments and genitalia turned to the left and slightly twisted. Five segments are clearly discernible. Genitalia asymmetrical, represented by the male valvules

of the left side, the penis and one cercus. There is no visible trace of a sting. The legs are male on the left, female on the right side, differing little in length. The sexual difference is seen only in the larger strigil and the somewhat stouter tibiæ and femora on the right side. Wings perfectly normal, alike on the two sides.

Left side of head opaque, right finely longitudinally rugose, as in the female. Left mandible smooth, impunctate; right with coarse piligerous punctures. Mesonotum, paraptera and scutellum shining, intermediate in character between the male and female. Pronotum,

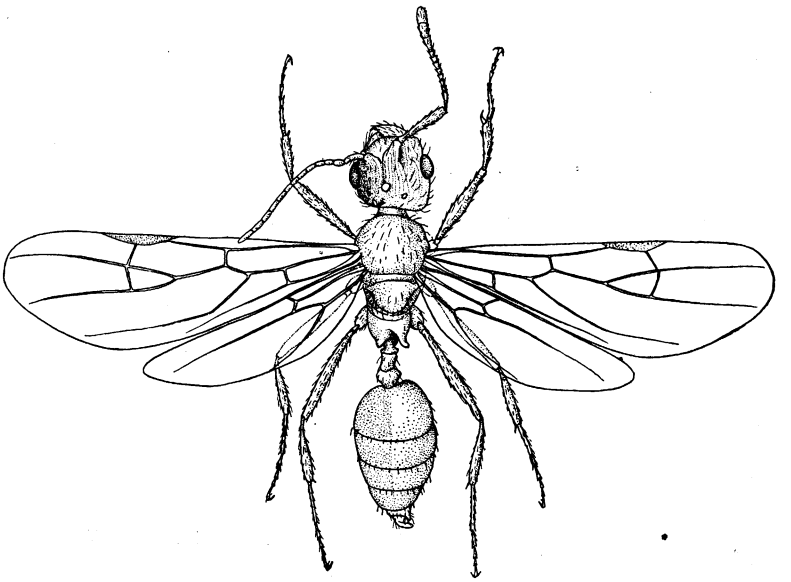

Fig. 5. *Epipheidole inquilina* n. gen. et n. sp. Gynandromorph ; male and female.

pleuræ and epinotum on left side finely reticulate-punctate (male), on the right more coarsely reticulate-rugose as in the female. Petiole and postpetiole subopaque, finely reticulate-punctate, except dorsal surface of postpetiole, which is smoother. Gaster glabrous, shining.

Hairs on the left half of the body like those of the male, long, slender and tapering; on the right half stouter, and distinctly obtuse or even clavate at their ends, as in the female. Hairs on the antennæ and legs short and appressed as in both sexes.

Left side of head and ocellar region black, like the head of the male; left mandible pale yellow; right mandible, clypeus and right anterior portion of head reddish brown gradually becoming darker on the posterior corner. Thorax reddish brown, the left (male) half being

distinctly darker than the right (female) half. Pleuræ on both sides paler than the dorsum. Pedicel and gaster reddish brown, left half of latter distinctly darker than the right half. Gastric incisures, genitalia, mandibles and legs pale brownish yellow. Wings grayish hyaline, veins and stigma yellow, the latter not very conspicuous.

Length, 3 mm.

This interesting species, of which a full description will be published in a forthcoming paper, was found during the past summer in three different nests of *Pheidole pilifera* Roger var. *coloradensis* Emery, near Colorado Springs, Colo. It is, in all probability, a parasitic species, like *Anergates* and *Epœcus*, and, like these forms, has no workers. Another very distinct new species, apparently of an allied genus and also without workers, occurs as a parasite in the nests of *Pheidole ceres* n. sp., in the same territory.

The above described gynandromorph was found together with several normal males and females in a *Ph. coloradensis* nest at Broadmoor, Aug. 11. The mother queen of the parasitic colony had a very abnormal gaster, the basal segments being greatly inflated and containing the telescoped and somewhat distorted terminal segments. This fact is suggestive in connection with Menzel's discovery (*vide infra*, p. 679) that the queen bee that produced so many gynandromorphs in the Eugster hive had an abnormal abdomen.

Formicid Gynandromorphs Described by Previous Authors.

1. Tischbein ('51, p. 295, and '53, Taf. III, figs. 2, 2*a*, 2*b*,) and Klug ('54, pp. 102, 103). *Formica sanguinea* Latr.

Fig. 6.

Nearly complete lateral gynandromorph; male on left, worker on right side. In the head, the left mandible, outer third of clypeus, antenna, eye, median and lateral ocellus, are male, though the black coloring also covers the smaller right ocellus. Remainder of head red (worker). Thorax and petiole male on left, worker on right, the line of division being median on the dorsal surface, and the structure of the meso-, meta- and epinotum correspondingly asymmetrical. Left half of thorax black, right half red, sharply divided above; on the ventral

surface the dividing line is median only on the prothorax but passes outside the middle and hind coxa on the male side. Petiole sharply divided into a black male (left) and a red female (right) half. Gaster black, with a large red blotch on the right side at the base of the first segment. The pilosity and sculpture of the left side are male, those of the right, worker. External male genitalia are present on the left side and the anal sternite is present only on this side. Remaining

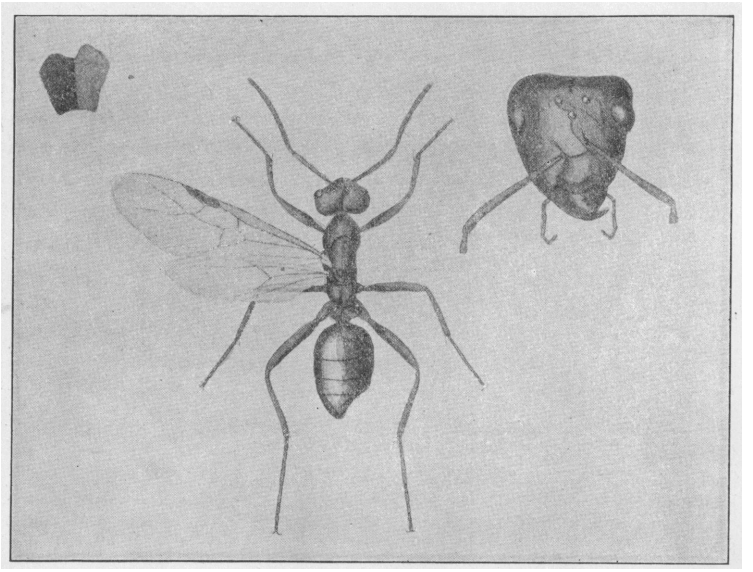

Fig. 6. *Formica sanguinea* Latr. Gynandromorph; male and worker; dorsal view of entire insect, with petiole and head. (After Tischbein.)

organs of this region "quite malformed." All the legs, and the coxæ of the male side, are red and hence of the worker type. Wings of the male side of normal size, but their veins and stigma are paler and hence more like those of the female. There are, of course, no wings on the worker side.

2. Roger ('57, pp. 15–17, Taf. I, fig. 2). *Tetramorium simillimum* (Smith) Mayr (= *Tetrogmus caldarius* Roger).

Fig. 7.

Lateral gynandromorph; male on left, worker on right side. In the head the left mandible, eye and antenna, median and left lateral ocellus and the sculpture and color of the left side, are male, the

remainder of head of the worker type. In the thorax the left (male) side is very convex, the right (worker) side flat. Left side black and more strongly sculptured than the right. Wings had been present on male side as shown by their stumps. Legs of left side slender, nearly

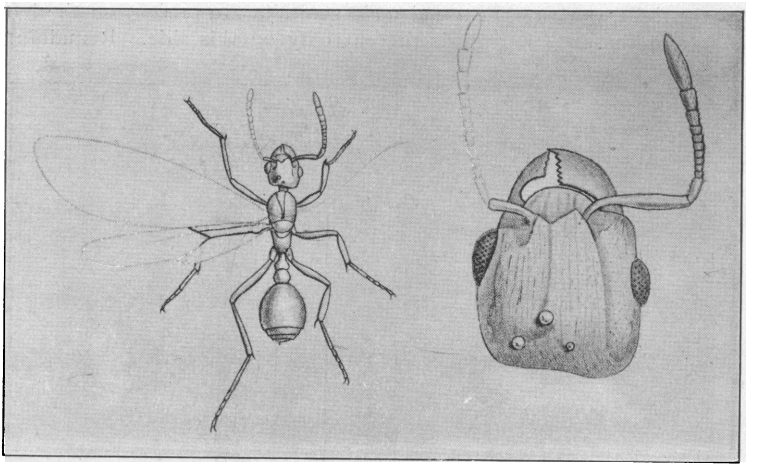

Fig. 7. *Tetramorium simillimum* (Smith) Mayr. Gynandromorph, male and worker. Entire insect with head more highly magnified. (After Roger.)

twice as long as those on the worker side. Petiole, postpetiole and gaster apparently of the worker type, though the tip of the gaster had been broken.

3. MEINERT ('60, p. 331). *Tetramorium simillimum* (Smith) Mayr (=*Myrmica caldaria* Roger).

Mixed frontal gynandromorph. Head male, thorax and abdomen female, with the exception of the thoracic dorsum which resembles the corresponding portion of the male in color and sculpture.

4. MEINERT ('60, p. 327). *Myrmica lobicornis* Nyl.

Mixed frontal gynandromorph. Head female in size; thorax and external genitalia, as well as the color and sculpture of the body, male Wings intermediate between those of the two sexes.

5. FOREL ('74, p. 142.) *Myrmica ruginodis* Nyl.

Frontal gynandromorph. Body perfectly symmetrical. It is rather a male, as the gaster has five segments in addition to the petiole and postpetiole and the external genitalia are male. The epinotum

has only two tubercles instead of spines, but the eyes are much smaller than those of the male, and hence more like the female. The head is also a little larger than the head of a male, but both its form and color are intermediate between the two sexes. Antennæ 13-jointed as in the male, but in color and form recalling the antennæ of the female. There are also two distinct red bands on the anterior portion of the mesonotum, which are never found in the male. Sculpture of head and epinotum more rugose and less shining than in the male.

6. FOREL ('74, p. 140). *Formica exsecta* Nyl.

Incomplete lateral gynandromorph. Worker, with some portions of the left side male. Stature of ordinary worker. Male portions: a longitudinal black band under the head, left half of pronotum, a large V-shaped, black blotch on mesonotum, a black protuberance (scutellum?) and vestiges of alar articulations. All the rest worker. Epinotum malformed.

7. FOREL ('74, p. 141). *Formica rufibarbis* Fabr.

Mixed gynandromorph, *i. e.*, with male and female characters mingled on the two sides. Halves of head identical, but of such a character that it is impossible to say whether they are male or female; in form the head is exactly intermediate between the two sexes. Both antennæ 13-jointed as in the male, but scapes too long in proportion to funiculi for this sex. Mandibles indistinctly denticulate, particolored reddish black and brown, intermediate between male and female, as are also the size and conformation of the eyes and ocelli. Whole head more robust than that of the male, smaller than that of the female; black (hence male). Thorax indeterminate; right half of epinotum yellowish red, left half black, whereas the right half of the scutellum and petiole is black, the left half reddish yellow; hence the epinotum is female on the right, male on the left side; whereas the scutellum and petiole are male on the right and female on the left. Since in the normal female the thorax is more or less red or black according to individual variation, and has the same form as that of the male, in which it is almost entirely black, it is impossible to determine the sex of these parts. The three pairs of legs are symmetrical, yellowish and have rather the form of the female. The wings, being the same in both sexes, are indeterminate in the gynandromorph. Gaster apparently female, globular, very small, with five segments, excluding the petiole. Anus round, encircled by hairs as in the female, but it opens above into a transverse, eciliate slit, situated between the hypopygium and pygidium as if forming a second anus. The anus proper is cut into the hypopygium. This gynandromorph was taken flying with copulating males and females

of its own species and hence must have exhibited the reproductive instinct. Dissection was not successful, but nevertheless exhibited the following points: Poison vesicle very distinct, almost normal, but short, thick-set and with small pulvini. On the left of the stomach was a perfectly normal ovary, with tubules full of eggs of the normal form but very small. On the right, rather near the middle and superficially placed, there was a peculiar little organ, evidently vestigial, but of unknown significance, perhaps the remains of the testis. Accessory gland of the poison apparatus very large but flattened and abortive. Near the cloaca there were some vestigial chitinous appendages (male genital valves?). Alimentary canal partly abortive. On the whole the genitalia were much atrophied; their female nature on the left was certain, but doubtful on the right.

8. FOREL ('74, p. 140). *Formica truncicola* Nyl.

Mixed gynandromorph, the characters of the two sexes being very intimately and irregularly intermingled. Right half of head entirely female, left half male, but incompletely. Left mandible smaller than right, 7- instead of 8-toothed (the male mandible is edentulous); left antenna 12-jointed, but the 12th joint is half divided (the male has 13 joints). Thorax red, blotched with black, predominantly female, but somewhat male on the left side. Externally the gaster appears to be male, with six segments (not counting the petiole); external genitalia male, quite alike on the two sides. Dissection showed perfectly normal, bilaterally symmetrical male organs. Beneath these the structures were confused, though an ovary, smaller than that of the normal female, but larger than in the worker, was isolated. Like the female ovary, it had a number of tubules, each containing numerous eggs, but all were very small and immature. Another organ, in all probability a vestigial poison-sac, was isolated. This does not exist in the male. Hence the specimen was a true hermaphrodite, with two entirely normal testes and at least one almost normal ovary.

9. FOREL ('74, p. 142). *Polyergus rufescens* Latr.

FIG. 8.

Approximately lateral gynandromorph, worker and male. Head red, worker throughout, except for a black (male) blotch on the right under side. Prothorax entirely worker. Right fore leg a little larger than the left. Mesothorax, epinotum and petiole worker on the left and male on the right side, the demarcation being very sharp and in the median line. Male side of thorax somewhat atrophied, but nevertheless with a vestigial half scutellum and metanotum, a perfect fore and a dishevelled hind wing. Middle and hind leg worker on the left, male on the right side. Three anterior gastric segments divided, both dorsally and ventrally, along the median line into a male right and a

worker left half. Ventral laminæ of the same configuration on the two sides. But the right half of the second tergite is fused not only with the corresponding left half but also with the left half of the third tergite; the two latter are therefore separated from each other only as far as the median line. The left half of the third tergite thus separated, ends toward the middle in a rounded edge. Externally the fourth and fifth segments are entirely male, with nearly normal sternites and tergites. There is a very small sixth segment, partly defective on the left side, composed of a pygidium (tergite) and a hypopygium (sternite). External genitalia entirely male, paired, of the ordinary size, consisting of the three plates and the three pairs of external valvules, exactly as in the normal male. Dissection showed the probable occurrence of a small poison-sac opening into the cloaca to one side of the rectum, but without distinct pulvini. The vagina was almost normal and received on the left a normal oviduct terminating in a normal worker ovary of six or seven tubules containing eggs. On the right was a perfectly normal vesicula seminalis opening below into the vagina and ending anteriorly in a vas deferens. The latter terminated in front, in a very complex organ comprising on one side several distinct ovarian tubules with eggs and on the other a thick, irregular, granular appendage, probably a vestigial testis.

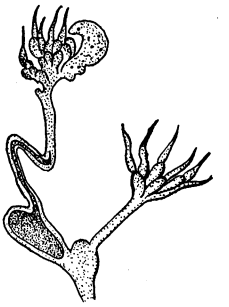

Fig. 8. Reproductive organs of hermaphroditic and gynandromorphic *Polyergus rufescens* Latr. Ventral view. To the left ovary and testis with vas deferens and vesicula seminalis; to the right ovary with oviduct. (After Forel.)

This specimen is of considerable interest, as it was captured carrying a larva of *Formica rufibarbis* and participating with normal workers of its own species, in a slave-making raid. This proves, according to Forel, that the intelligence of ants has its seat in the brain. Even the female of *Polyergus* does not exhibit such instincts. The head of the individual above described was completely worker and the remainder of the body, though to a considerable extent male, had no effect in counteracting the normal worker instincts.

10. FOREL ('74, p. 139). *Polyergus rufescens* Latr.

FIG. 9.

Approximately lateral gynandromorph. Right half of head almost exactly like that of the male (black); left half worker (red); the former with a very short mandible, an enormous eye, and an antenna with

short scape and long funiculus; left side with a large, falciform mandible, very small eye and worker antenna. Demarcation between black (male) and red (worker), sides extremely sharp and nearly median. Nevertheless the anterior ocellus is completely on the male side; it is very large like the right ocellus, whereas the left ocellus is small (worker type). Pronotum worker, except for two black spots on the right side. Mesonotum worker on the left and male on the right side, which has dishevelled wings and a small scutellum. There are, of course, no traces of wings on the left side. Epinotum and petiole worker, with the exception of some black (male) blotches on the right side. Right legs partly male; left legs worker. Externally the gaster is entirely worker. Stature that of a worker. Observed alive in an artificial nest in which it lived for two weeks. The movements of the right and left mandibles were perfectly coördinated. The specimen was not dissected.

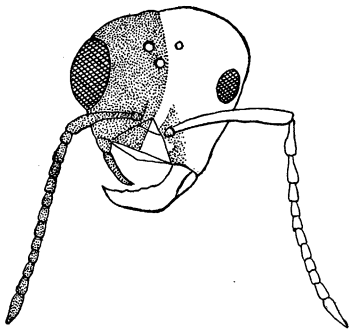

Fig. 9. *Polyergus rufescens* Latr. Head of gynandromorph; male and worker. (After Forel.)

11. Smith ('74, p. 147) and Cooke ('82, p. 30). *Myrmica lævinodis* Nyl.

"It combines characters of the male, female and worker: the right side is entirely worker, on the left side the head is female, hence we see an ocellus and antenna exhibiting the characters of the female; but the left side of the thorax is certainly male and consequently the mesothorax has, in front, a deeply-impressed oblique line — in an ordinary male of this species there are two such lines which form a V-shaped space, which is not found in either the female or the worker — the metathorax on the left side, is destitute of the spine which characterizes both the female and the worker, the legs on the same side are all male, being longer and much more slender than those of the other sexes."

12. Adlerz ('86, p. 82). *Leptothorax tuberum* Fabr.

Incomplete lateral gynandromorph. Right side exclusively worker, left partly male and partly worker. Left half of head male, pronotum worker, mesonotum, paraptera, scutellum and mesopleuræ male; metanotum and epinotum worker; legs male with worker coloring. Petiole and postpetiole between male and worker, but left side darker

like that of the male. Gaster as in the worker, but on left side of tip with an incomplete sternite representing the seventh segment of the male. There is a projecting, irregular penis, with its genital valves so abortive on the right side as to be recognizable only with difficulty. At the right of the penis is a rather irregular sting. Internal male genitalia represented by two vesiculæ seminales, the somewhat larger left one receiving a vas deferens which is not represented on the right side. There were no testes. Below and to the right of the male genitalia an ovary was found, consisting of one large and two small tubules, of which only the large one contained a mature egg in the lowest follicle. This ovary was connected with an oviduct which opened into a vagina. No traces of the poison gland or vesicle were found.

13. WASMANN ('90, p. 299). *Myrmica lævinodis* Nyl.

A mixed gynandromorph, male and worker, with only the color of the head like that of the worker and the ocelli much smaller and more closely aggregated than in the male. In all other respects the specimen was a normal male.

14. WASMANN ('90, p. 298). *Myrmica scabrinodis* Nyl.

Approximately lateral gynandromorph with left half of the body almost entirely that of a worker, whereas the right half is that of a normal male. Left (worker) half of head larger than the right, opaque, coarsely and longitudinally rugose, with a large yellowish red blotch above, sharply delimited on the right side as far as the middle of the face, extending back on the left to the middle of the side of the head as far as the first third of the superior orbit, and anteriorly to the antennal insertion, which is encircled by a black ring. Mandibles, antennæ and left half of clypeus yellowish red, the remainder of the head black. Right half of head smaller, more finely longitudinally furrowed and therefore more shining (male). Right eye larger (male), left smaller (worker). Ocellus lacking in that portion of the vertex corresponding to the left side of the head (worker). The two remaining ocelli are present, the median lying rather accurately on the boundary of the black side of the head, but still entirely on that side. Right mandible male in size, shape and number of teeth, but reddish yellow (worker), whereas normally the male mandibles are reddish yellow only at their tips. Left, much more robust, mandible entirely worker. Antennæ both alike, 13-jointed, almost purely male, but very short and sparsely hairy in contradistinction to the long, abundant pilosity of the normal male antennæ in *Myrmica scabrinodis*. They are also lighter in color, being almost uniformly reddish yellow as in the worker.

15. PERKINS ('91, p. 123). *Stenamma westwoodi* Westw.

Approximately lateral gynandromorph. Left side worker, right side male, gaster apparently worker. "*Left half:* Head red, with darker cloud reaching from vertex to eye. Mandible very large, with 7 teeth. Antenna 12-jointed, testaceous, with pale hairs, first joint of flagellum longer than next two together; these and the following joints much wider than long; apical joint very large and stout, as long as two preceding; scape very long and bent, as long as many joints of flagellum. Eye small. Mesothorax red. Second node of petiole lighter. Abdomen from middle line testaceous brown. Legs shorter and thicker.

"*Right half:* Head dark brown. Mandible small (the ant being carded I cannot clearly make out the form of the right mandible). Antenna 13-jointed, dark, thin, with pale hairs; first joint of flagellum stouter than next, but subequal to it; the following joints all much longer than wide; apical joint as long as on left side, but not nearly so stout; scape short and straight, only about as long as two joints of flagellum, and *per se* barely half the length of that of left side. Eye larger; more than twice the size of the other, and much nearer to the base of antenna. Mesothorax dark, laterally with two rough projections, apparently tegulæ. Second node of petiole darker. Abdomen from middle line dark brown. Legs longer and thinner.

"The form of the abdomen, so far as I can make out in this specimen (set on card), is that of the worker. The shape of the mesothorax is unsymmetrical bilaterally. Length, about 3 mm."

16. FOREL ('92, pp. 268–270, pl. xvi). *Azteca instabilis* Smith.

FIG. 10.

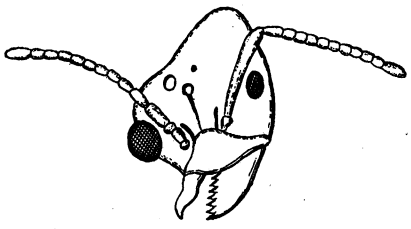

Fig. 10. *Azteca instabilis* Smith. Head of gynandromorph; male and female. (After Forel.)

Lateral gynandromorph; male on the right, female on the left, at least as far back as the gaster. The latter is somewhat corneous and entirely male. Head clearly divided down the middle, except the median ocellus which is male. The small male mandible is entirely without teeth. External genitalia entirely male. Thorax narrow, legs on the male side slender, those of the female side more robust.

17. KLAPÁLEK ('96, xxviii, pp. 1–4, 2 Figs.). *Camponotus ligniperdus* Latr.

FIG. 11.

Incomplete lateral gynandromorph, worker and male. Body much distorted, differently colored on the two sides. Head very irregular; clypeus oblique; left mandible large, 5-toothed as in the worker, right small, as in the male. Left antenna worker, right male. Left eye apparently somewhat larger than right; only two ocelli, the anterior on the middle line, the other on the right side. Pro-, meso- and epinotum asymmetrical; left side without vestiges of wings, right with small stumps. Petiolar node like that of male. Gaster in front on left side much broader than on the right; left half of gastric segments with many more hairs than the right, where they are either entirely lacking (first and third segments) or very spare. Sixth and following segments entirely as in the male, the last bearing the external, completely developed male genitalia. Joints of left stouter than those of the right legs. Left mandible and anterior portion of head reddish brown, remainder of head blackish brown; left half of thorax, scutellum and first gastric segment yellowish brown, right half and remaining segments blackish brown, genital segments grayish yellow. Klapálek concludes that the specimen is a lateral gynandromorph, with the left side (excluding the sixth and succeeding gastric segments) worker, the right side male. The dorsal line of separation is accentuated in the head, clypeus and gaster by a fine furrow, elsewhere by a difference in coloration. The division is

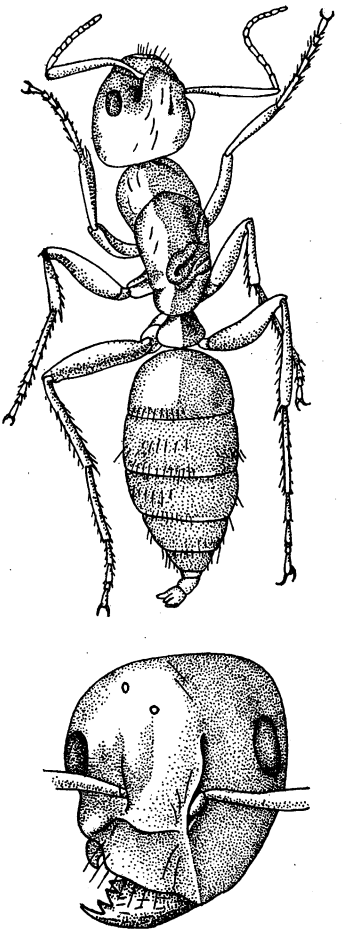

Fig. 11. *Camponotus ligniperdus* Latr. Gynandromorph; male and worker. Entire insect and head of same. (After Klapálek.)

completely median, even on the ventral surface till it turns to the left to terminate on the fifth gastric segment external to the left half of the sixth, so that the sixth and following segments are completely male, thus disturbing the symmetry of the two halves of the body.

Theoretical Considerations.

Up to the present time, all attempts to offer a hypothetical explanation of gynandromorphism among insects in general, and ants in particular, have proved to be unsatisfactory. This was inevitable, since any such explanation must necessarily rest on more general hypotheses concerning the determination of sex and the significance of fertilization. Moreover, all the leading hypotheses from those of Dönhoff ('60) down to that of Boveri ('02), have centred about the gynandromorphous honey bees. This was unfortunate because it was inevitable that the question should be complicated by the Dzierzon hypothesis of the origin of male bees from parthenogenetic, of worker and queen bees from fertilized eggs. The Dzierzon hypothesis in its strict formulation has never been fully demonstrated [see *e. g.*, Pérez ('78)]. Its tacit extension to the ants has recently received a severe blow in the researches of Reichenbach ('02), who has shown that the workers of *Lasius niger* may lay parthenogenetic eggs and that these may develop into workers instead of males, as the Dzierzon theory demands. And quite recently Mrs. A. B. Comstock has independently obtained the same results in queenless artificial colonies of *L. niger*, var. *americanus* (*in litteris*). It is probable that in ants, as in the bees, the males normally make their appearance only at certain seasons and it is quite possible that they may arise either from parthenogenetic or fertilized eggs, their sex depending on other conditions. It is clear that both males and females of many insects presenting occasional gynandromorphs of the very same character as those of the honey bee must develop from fertilized eggs. And, furthermore, there are plenty of cases in which parthenogenetic eggs give rise to females instead of males (viviparous Aphides, Phyllopoda, etc.). I conclude from these facts first, that we must endorse von Buttel-Reepen

('03) when he maintains that we are not yet justified in applying apicultural theories to the social wasps, ants and termites, since all of these groups may follow different laws in sex and caste determination; and second, that we would do well to regard parthenogenesis and sex-determination as independent problems, just as it is an obvious advantage to distinguish accurately between the phenomena of sex and those of heredity. If we accept von Lenhóssek's hypothesis ('03) of sex determination in the egg previous to fertilization, there can be no question concerning the truth of this assertion.

With these considerations in mind, we are prepared to undertake a brief critical study of some of the leading hypotheses of gynandromorphism. Dönhoff ('60) appears to have been the first to seek for the causes of this singular phenomenon when he advanced the two following suppositions to account for the structure of a frontal gynandromorph of the honey bee:

"1. It is probable that the egg, from which this animal developed, contained two yolks, one of which was fertilized, the other not. In the one yolk a drone had begun to develop, in the other a worker. Both eventually fused to form a single animal.

"2. According to the Dzierzon theory of the origin of drones from unfertilized eggs, the developmental process will admit of a simpler explanation. The egg, namely, contains the male individual potentially, the spermatozoon the female egg. The development of all animals consists in the fusion of the spermatozoon with the germ of the egg. In the development of the bee the spermatozoon-germ predominates, so that in fertilization this (female) element develops. In the present case both have developed, but so incompletely that the germ of the spermatozoon has given rise to the head and thorax, the germ of the egg to the abdomen of the insect."

These paragraphs may be restated in modern cytological phraseology, thus:

1. The gynandromorphous bee may have originated from two eggs, matured in a single ovarian follicle and enclosed in the same chorion. The eggs fused just before or after fertiliza-

tion, but only the female pronucleus of the egg nearest the micropyle united with a male pronucleus derived from one of the spermatozoa that had entered the egg while it was passing the orifice of the receptaculum seminis.

2. The animal in question may have arisen from a single egg in which the female and male pronuclei did not unite to form a cleavage nucleus, but each independently underwent cleavage and gave rise to the embryonic nuclei. The descendants of the male pronucleus gave rise to female, those of the female pronucleus to male organs of the adult gynandromorph.

It is evident that both suppositions are built on the Dzierzon hypothesis and suffer from this dubious support and from the fact that they are really applicable to gynandromorphs of the social Hymenoptera only. Nevertheless, as I shall show in the sequel, it is possible to give Dönhoff's views a more acceptable meaning.

Wittenhagen ('61) and Menzel ('62) advance no less than seven hypotheses to account for honey bee gynandromorphs. Some of these can be eliminated as they deal with such conceptions as "hohe Potenzierung der männlichen Wesenheit" of the egg, etc., as well as conditions peculiar to bees, and consequently inapplicable to gynandromorphs in general. Two of Menzel's hypotheses, however, are still worthy of consideration:

1. Gynandromorphs may be produced by disturbances in the even tenor of the developmental process. Hence the origin of local defect, which expresses itself in certain portions of the body as male characteristics.

2. Temporary disturbances in the care of the brood, perhaps in the whole economy of the hive.

In other words, the sexual mosaic of the body may be the result of local inhibition of growth or uneven distribution of nutriment to the tissues during embryonic or post embryonic development.

Later, after investigating the famous Eugster hive, which had produced great numbers of gynandromorphous bees (87 of which were dissected by von Siebold!), Menzel ('65) came to

the conclusion that some malformation of the internal reproductive organs of the queen must be responsible for the production of these anomalies.[1]

He suggests that the egg may have passed the opening of the receptaculum so slowly or in such a position that the spermatozoa entered too late and were thus unable to bring about a complete feminization of the egg. In certain respects this view is an adumbration of Boveri's recent hypothesis.

Von Siebold's hypothesis ('64) that gynandromorphous bees are the result of an inadequate number of spermatozoa entering the egg, may be rejected, since we now know that even during normal polyspermy only a single spermatozoon fuses with the female pronucleus. In fact, if polyspermy is at all concerned in the production of gynandromorphs, the very opposite of von Siebold's hypothesis would be more probable, as shown by Boveri.

In the concluding paragraphs of his recent remarkable paper on "multipolar mitoses," Boveri ('02, pp. 86, 87) advances the following hypothesis to account for gynandromorphous development:

"When a bee is a drone on the right side and a worker on the left, the right half has developed as a parthenogenetic, the left as a fertilized egg; the right, therefore, like an egg containing only maternal, the left like one containing both kinds of chromosomes. On the basis of this consideration, and since it has been possible to show that in the sea-urchin egg we can produce asymmetries of a definite kind by means of unequal chromatin combinations in different regions of the egg, the conclusion is inevitable that the cause of insect asymmetries that consist in a mosaic of male and female parts, must be sought in nuclear differences. And in the case of purely symmetrical hermaphroditism under discussion, we cannot have recourse to dispermy, but to some other abnormal distribution of the chromatin, such as I have found in sea-urchin eggs, where one of the half blastomeres contains only maternal, the other mingled male and female chromosomes, and hence,

[1] *Confer* the observation recorded on p. 666 concerning the malformation of the queen *Epipheidole inquilina*.

if the cause lies in the chromatin, the very thing that must be postulated for hermaphroditic bees. Owing to the peculiar conditions under which the bee develops, the occurrence of this anomaly is obviously greatly favored, inasmuch as i appears possible that the egg nucleus may undergo cleavage even before its copulation with the sperm nucleus, owing to its parthenogenetic propensities, so that the sperm-nucleus may chance to fuse with one of the cleavage nuclei. This fusion could even be delayed till later cleavage stages, and polyspermy — which is known to occur in the bee — might bring about the copulation of sperm-nuclei with certain derivatives of the egg-nucleus and not with others. In this manner might arise such manifold mixtures of male and female characters, as have actually been observed."

This passage clearly shows that Boveri is in essential agreement with previous authors in accepting the Dzierzon hypothesis and the view of sex determination which it implies. In discarding this portion of the hypothesis as perhaps inessential and inapplicable to many cases of gynandromorphism, I have no desire to dissent from the fundamental conception of my esteemed friend and teacher. This fundamental conception, which implies that the peculiar chromosomal constellation of the nuclei in a given organ of the body is responsible for the peculiar characters of that region, is too well substantiated by the brilliant experimental work of Boveri and others, to be lightly set aside. This view readily accounts for hereditary phenomena like those of blended and mosaic hybridism. It may also be used to explain not only the mosaic characters of hermaphrodites and gynandromorphs (which, as we have seen, are not necessarily the same) but may be extended, with modifications, to cases like the "Hahnenfedrigkeit" of senile hen birds, the viragoism of aged women, to pathological cases like "mental hemaphroditism" and sexual inversion in human beings, and to the effects on the soma of castration, injury to the gonads, etc. Some of the latter cases are, perhaps, traceable to ontogenetic or trophic changes affecting the chromosomal characters in different parts of the body. Of course, the theory of internal secretions is not precluded in these cases.

Returning to the insect gynandromorphs, I would restate the various possible causes in the spirit of Boveri's hypothesis, as follows:

1. A gynandromorph may, perhaps, arise from a pair of eggs which have fused, like zur Strassen's giant eggs of *Ascaris*, to form a single egg with two egg-nuclei (Dönhoff). These eggs may have been of different sex originally (v. Lenhóssek) or may become different through the non-fertilization of one nucleus and the fertilization of the other (Dönhoff, Boveri).

2. It is possible that the egg nucleus of a single egg may either undergo cleavage prematurely or receive the spermatozoa too late, so that in cases of polyspermy, so general in insects, the resulting cleavage nuclei may unite with different sperm-nuclei, or in part develop parthenogenetically, thus giving rise to different chromosomal constellations in the cells that ultimately go to form different parts of the body (Boveri).

3. It is conceivable that the somatic peculiarities of unisexual gynandromorphs at least, may be the result of trophic disturbances during the postembryonic, *i. e.*, larval or pupal development (Wittenhagen, Menzel). These disturbances may, perhaps, be analogous to those which cause viragoism, "Hahnenfedrigkeit," etc., in other animals, and may depend on pathological changes in the chromosomal conditions of certain tissues.

Two peculiarities in the development of the normal insect egg are obviously favorable to the formation of both mosaic and blended gynandromorphs: First, polyspermy, which would favor the conditions mentioned in the second hypothesis (Boveri); and second, the syncytial nature of the egg in its cleavage and preblastodermic stages. The latter condition permits of a free migration of the cleavage nuclei to different parts of the egg and the consequent development of mixed or blended characters. On the other hand, the absence of such migration or its limitation, would readily lead to the more definite cases of frontal, transversal and lateral gynandromorphism.

In conclusion we may say that however valuable the above

suppositions may be as working hypotheses, we can have no genuine understanding of gynandromorphism till this anomaly can be produced experimentally. This will probably be a difficult task to accomplish in insects, owing to the impossibility of fertilizing their eggs artificially and the difficulty of studying the nuclear phenomena. On the other hand, in the lower invertebrates, where all this is feasible, the secondary sexual characters are very feebly developed. Possibly the lower vertebrates (fishes, *e. g.*) may afford better opportunities for such experimental studies.

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