

MOSAICS AND OTHER ANOMALIES AMONG ANTS

BY

WILLIAM MORTON WHEELER



Now, by two-headed Janus,
Nature hath framed strange fellows in her time.

The Merchant of Venice.

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TO THE MANES
OF
AUGUSTE FOREL

FOREWORD

The manuscript of this book was brought by Professor Wheeler to the Press but a few days before his death. With characteristic generosity he had associated with his own name that of his student, Dr. Neal Weber, as co-author.

Dr. Weber, however, has felt that inasmuch as absence from Cambridge prevented him from playing much part in the preparation of the manuscript, he would prefer that it should stand under Professor Wheeler's name alone. Thus he has made a very real sacrifice and paid the highest tribute to a beloved teacher. His desire that this book should be a monument to Professor Wheeler's memory without any division of credit merits this record of appreciation.

Dr. F. M. Carpenter also is to be thanked for his painstaking revision of the proofs and checking of the bibliography.

THOMAS BARBOUR

Museum of Comparative Zoölogy

Cambridge, Mass.

August 2, 1937

PREFACE

During the year 1935 Dr. Neal Albert Weber, while holding a National Research Fellowship and pursuing his investigations at the Imperial College of Tropical Agriculture in Trinidad, B. W. I., collected the entire personnel of two large ant colonies which contained unprecedented numbers of anomalous individuals. In one of these colonies, belonging to a large Cryptocerine, *Cephalotes atratus quadridens* DeGeer, there were more than 4000 remarkable gynandromorphs, or female-male mosaics, which will be described in a future publication. The present volume deals with the other colony, which is that of a fungus-growing (Attine) ant, *Acromyrmex octospinosus* Reich. It contains only 164 anomalous individuals, but fifty-three of these are of unusual interest both because they are quite unlike any previously observed among ants or indeed among any other social insects and because they enable us to decide between two theories of caste determination which have baffled and divided the students of ants for more than half a century.

Since these anomalies happened to appear in an ant that is also of considerable interest to the animal behaviorists and economic entomologists, we have included a number of observations on its fungus-growing habits and those of other members of the Attine tribe. This seemed the more timely because Dr. Weber was able to supply new data and considerations from his observations and experiments in Trinidad, British Guiana, and Venezuela. To the principal paper there is appended a revision of the known non-mosaic ant anomalies, because these appear in a new light as a result of the studies of the *octospinosus* anomalies.

We wish in conclusion to express our indebtedness to Miss Eleanor Bartlett for assistance in preparing specimens for study and to Miss Barbara Polk for carefully typing the manuscript.

W. M. W.

Biological Laboratories
Cambridge, Mass.
February 10, 1937

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MOSAICS AND OTHER ANOMALIES
AMONG ANTS

PART I

DISTRIBUTION, HABITS, AND NORMAL CASTES OF ACROMYRMEX

The ants of tropical America are very numerous both in species and individuals. Though they constitute the dominant component of the richest insect fauna in the world, only two of their tribes, comprising the highly insectivorous legionary or army ants of the genus *Eciton*, and the parasol, leaf-cutting, or fungus-growing ants of the genus *Atta*, exhibit behavior patterns sufficiently striking to attract the attention of the most casual observer. The *Attas* are so injurious to both wild and cultivated plants that they are known to the inhabitants of Latin America by a variety of local names.¹ Their huge earthen craters and the interminable processions of their velvety, red-brown, spiny, big-headed workers, carrying erect in their jaws pieces of green leaves or flowers — “like Sunday-school children carrying banners,” as Rev. H. C. McCook once remarked — are so frequently encountered in the open forests, in the savannahs, or even in the gardens of the cities as to contribute a characteristic note to the Neotropical landscape. Certain somewhat smaller species, with one of which the present volume chiefly deals, were assigned by the eminent Austrian entomologist, Gustav Mayr, to the genus *Acromyrmex*. These, owing to their similar habits, are often confused with the true *Attas*. Of the genus *Atta*, however, only seven species and as many subspecies and varieties are known, whereas *Acromyrmex*, including

¹The name most widely employed for species of *Atta* in Middle America seems to be “hormiga arriera.” In some parts of Panama “bachaca” is applied to *A. cephalotes* L. and the allied *columbica* Forel; in Trinidad *cephalotes* is commonly called “bachac”; in Venezuela *cephalotes* and *A. sexdens* are termed “bachaco” and in British Guiana these two species are known as “cushi,” “cuschi,” or “acushi”; in British Honduras *cephalotes* is named “wee-wee”; and in Guatemala *cephalotes* and *A. mexicana* F. Smith are called “zampopos” or “zompopos.” In Mexico *A. mexicana* has numerous local names: “cuatalata” in the state of Morelos, “chancharra” in Guanajuato, “chicantana” in Oaxaca, “mochoma” in Chiapas, and “sonteta” in some other localities. Common names for *A. sexdens* L. in Brazil are “saúva,” “saúba,” “mineira,” and “carregadeira.” According to Bruch, *A. vollenweideri* Forel is known in Argentina as the “hormiga isaú.” The common name for *A. insularis* Guérin in Cuba is “bibijagua.”

PART I

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its subgenus *Moellerius*, possessing nearly the same geographical distribution — from southern Arizona and southwestern Texas to Patagonia (Chobut) — is represented by no less than eighty-seven known forms (twenty-four species, twenty-six subspecies, thirty-seven varieties). The several remaining genera of Attine ants are known only to the interested specialist because their diminutive and very timid species form colonies of few individuals and nest in concealed situations.

The species of *Acromyrmex* resemble those of the genus *Atta* in having strongly polymorphic workers, but the largest individuals (*maximae*) are smaller and structurally less profoundly modified, so that they do not as in *Atta* constitute a distinct soldier caste. The *Acromyrmex* colonies, moreover, are less populous, and their nests, which are either excavated in the soil, with or without crateriform entrances, or composed of a mass of vegetable detritus above ground, are not only smaller than *Atta* nests but contain fewer chambers and fungus-gardens.

Forel, in the "Biologia Centrali-Americana" (1899), and Santschi more recently (1925) in his summary of the habits of *Acromyrmex*, state that the nest contains only a single fungus chamber, with a single garden built up on its floor. This is true of several but not of all of the species. As long ago as 1893, Moeller, in an important paper, described the nests of four species of *Acromyrmex sens. str.* in Santa Catharina, Brazil. He found that three of these, *disciger* Mayr, *hystrix* Latreille, and *coronatus* Fabricius (= *subterraneus* Forel), have only a single large chamber and garden, but that there are several in some nests of *moelleri* Forel. Forel (1899) states that *moelleri* does not nest in the earth, "but in some natural cavity such as occurs under bark or in dry leaves, and excavates neither chambers nor galleries." According to Gallardo (1916), the nest of *A. ambiguus* Emery consists of a mound of dead leaves a meter in diameter and contains at a depth of 30 cm. several fungus chambers "pas trop grandes." The nest of another Argentinian species, *A. lundi* Guérin, which has been studied by Berg (1890), Lynch-Arribalzaga (1910), and Bruch (1921), usually makes a single large chamber in the soil, but its construction seems to be preceded by the establishment of a few small fungus chambers. Bruch (1928) has shown that *A. aspersus* F. Smith does not make a special nest but places its gardens, of which there are several, in cavi-

ties among rocks, and that *A. lobicornis* Emery var. *pencosensis* Forel excavates a small superficial chamber and at a lower level a large chamber which may contain a garden more than 40 cm. in diameter. Bruch (1916, 1921, 1928) has also described and published beautiful photographs of the nests of three species of Moellerius. Of these, *M. heyeri* Forel has only a single garden, but *M. fracticornis* Forel var. *joergensenii* Forel, *M. silvestrii* Emery, and its var. *bruchii*, excavate several small chambers and build in each a pendent fungus garden, like some primitive Attines of the genera *Mycetosoritis* and *Trachymyrmex*.

Some species of *Acromyrmex* heap up great masses of dead leaves and other vegetable debris on the trunks or branches of trees or between their buttresses, occasionally several feet above the ground. I examined a few of these nests, the work of *A. hystrix* Latr. (Santschi), near Kartabo, British Guiana. One of them, of a flattened oval shape, was fully 4 feet long and nearly 2 feet wide and was placed on a large horizontal branch about 35 feet above the forest floor. Only one large chamber with its garden was found in each of these nests.

Observations made by Dr. Weber on several species of *Acromyrmex* indicate that nests with multiple gardens are by no means infrequent even in species which normally have but one. Thus a nest of *A. coronatus globoculis* Forel, which he found near Forest Settlement on the Mazaruni River, British Guiana, contained more than five gardens. Four nests of *A. hystrix* exhibited the following peculiarities: One, under a mass of debris at the base of a clump of palms in the Orinoco Delta and at high tide surrounded by water, at low tide by mud, contained several gardens, of which only three were examined. A second nest, built in a mass of aerial roots near the Oko River, a tributary of the Cuyuni, in British Guiana, was 174 cm. high, 150 cm. wide, and 75 cm. deep and contained about a dozen gardens (Plate I, above). A third nest in the Orinoco Delta was 2.3 meters above the ground in a mass of moss, humus, and epiphytic roots between two *Manicaria* palm trunks. It contained only a single sessile garden 15 cm. high and 10 cm. wide. The fourth nest, observed near Forest Settlement, was at the base of a bromeliad growing a few meters above ground on a prostrate log and contained several gardens. Other nests of *A. hystrix* with a single garden like those which I saw near Kartabo were also encountered. *A. octospinosus* also occasionally has more than one garden. A nest of this description,



PLATE I. Above, a large nest of *Acromyrmex hystrrix* Latr. in section, showing numerous small fungus gardens; Oko River, British Guiana. Below, normal nest of *A. octospinosus* under a log, with a single fungus garden; Galeota, Trinidad. The card measures 5 x 3 inches.

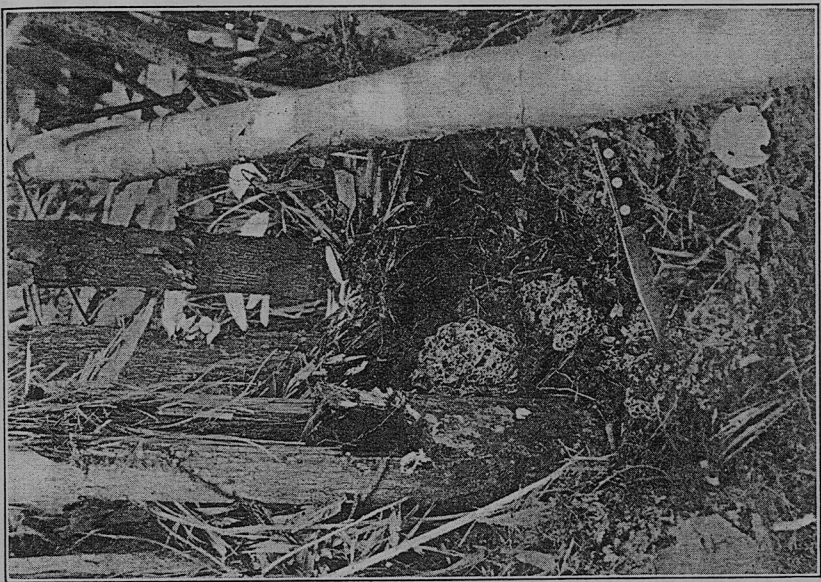


PLATE II. Left, sectioned nest of *A. (Moellerius) balzani* Forel, var., with two fungus gardens connected by a perpendicular gallery; Llanos of Venezuela. Right, section of nest of *A. hystrix* with two of the many large fungus gardens; Orinoco Delta, Venezuela. The knife in the foreground is ten inches long.

found in Trinidad near the Imperial College of Tropical Agriculture, extended over an area of 65 x 75 cm. and from only 5 cm. below the surface of the soil to 40 cm., and contained six gardens. Another nest of the same species was in a most unusual situation, as it occupied a mass of humus and epiphytic roots more than six meters above the ground in a palm (*Attalea spectabilis* Mart.) A nest of *A. (Moellerius) balzani* Forel var. encountered in the llanos of Venezuela, north of Ciudad Bolívar, contained two gardens and the beginning of a third (Plate II, left).

Although it was easy to identify the Trinidad colony collected by Dr. Weber in 1935 as belonging to *A. octospinosus* Reich, the earliest member of the genus to be described (1793) and therefore accepted as the genotype, there has been some doubt regarding the identity of the typical form of this species. For this reason I have been led to study all the *octospinosus* material in my collection and to present the results in an appendix to this paper (Appendix A). This seemed to be justified also by the rather summary discussion of *octospinosus* in the two revisions of *Acromyrmex* by Emery (1905) and Santschi (1925). Reich's type specimens came from Cayenne, but the species has since been found to have a wide range, extending from northern Mexico (Chihuahua) to the equator and including also Cuba among the Antilles. And since it seems to be as variable as many of the other species of the genus, it is possible to recognize several local races, or choriomorphs. In 1894 Forel described the Trinidad form from all three castes as a distinct species, *A. guentheri*, but later (1899) synonymized it with the typical *octospinosus*, an interpretation which has been accepted by both Emery and Santschi. Forel also described (1899) a var. *echinator* from Panama and Costa Rica, and more recently Crawley (1921) has added a var. *pallidus* from British Guiana. Now the specimens collected not only by Dr. Weber but also by all previous collectors in Trinidad are referable to Crawley's variety, which has also been taken recently by Dr. Weber in Venezuela. *A. pallidus* and *guentheri* are, therefore, in our opinion, not only synonymous but the same as the typical *octospinosus*.

The nests of *octospinosus* exhibit unusual variation in adaptation to the sites in which they are made. A few colonies of the subspecies *echinator* which I examined in 1923 and 1924 at Frijoles and on Barro Colorado Island, in the Panama Canal Zone, were nesting

above ground, either between the buttresses of large trees or in logs. In both cases there was only a single large fungus garden in a chamber surrounded by a mass of vegetable detritus. Numerous colonies of *echinator* observed in Costa Rica and Guatemala, however, had nests in the ground provided with crateriform entrances. The nests of the typical *octospinosus* in Trinidad have been described by Urich (1895) and Forel (1899). According to Urich, "this species is a regular plague in gardens, even those situated in the heart of the town. They do not form such large colonies as do the preceding ones [*Atta sexdens* L. and *cephalotes* L.], but they form small nests from $1\frac{1}{2}$ to 1 cubic foot in clayey soil which they excavate, but they readily avail themselves of any suitable crevices in the masonry of buildings, under woodwork, and when once lodged there are very difficult to get rid of. Their mushroom garden is constructed in the same way as [that of] *A. cephalotes*, but presents a more compact appearance." Urich found that in artificial nests the largest workers not infrequently produce eggs and brood, and that the females, which often lose their wings without any marriage flight, may work as hard as the workers and engage in such occupations as cutting and carrying leaves. The behavior of a colony of these ants sent by Urich to Forel, while he was residing in Zurich, is briefly described in the "Biologia Centrali-Americana" (Forel 1899).

A. octospinosus seems to be the only *Acromyrmex* occurring in Trinidad. According to Dr. Weber, it is the commonest and most conspicuous Attine ant on the island and nests freely both in the ground and in rotted stumps. It shows great adaptability, nesting in open fields as well as in the forest. It often makes a disk-shaped crater opening, but this may be dispensed with and the excavated soil carried some distance away, so that the opening is an inconspicuous hole beside a rock, tree, or herb. Owing to its abundance and its habit of cutting the leaves of cultivated plants, such as cassava, orange, grapefruit, and papaya, *A. octospinosus* is of considerable economic importance. The long files of its workers, each carrying a leaf section or a bright piece of a flower or fruit, are a familiar sight along the fields in Trinidad.

Dr. Weber has supplied from his notebooks the following data on the aberrant colony described in the sequel. It was found on the rainy afternoon of May 5, 1935, in a cocoa and coffee plantation

up the Tucuragua River, a tributary of the Tacarigua, on the slope of the Northern Range, at an altitude of 300 feet. The nest was on the north side of a road cut in a perpendicular bank. The single comparatively firm and compact fungus garden, nearly as large as a man's head, was situated in a chamber only four inches from the surface of the bank and was partly suspended from roots and partly

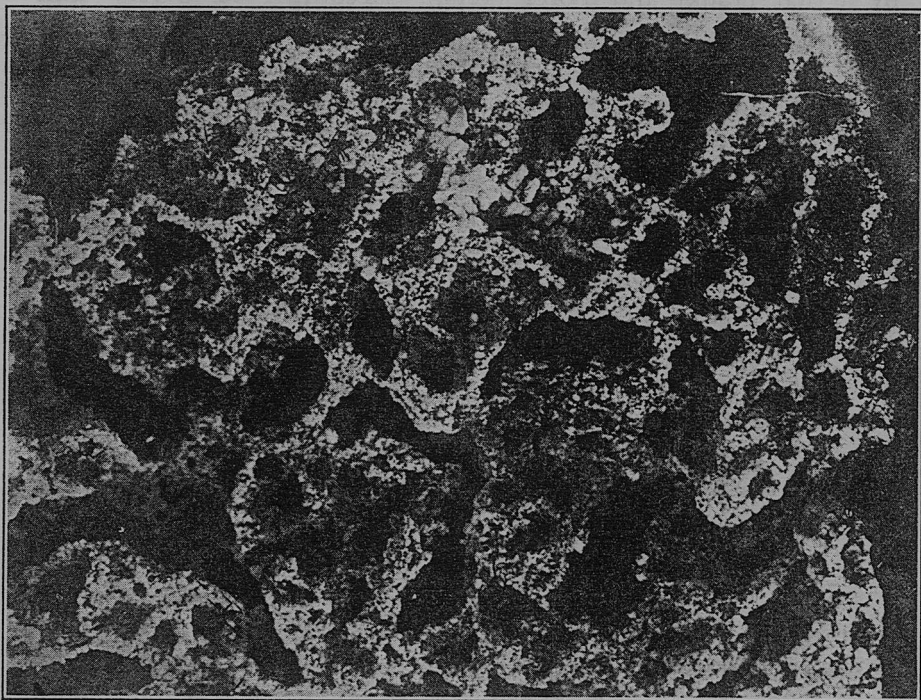


FIGURE 1. Portion of the single fungus garden of the aberrant *Acromyrmex octospinosus* colony in its original site, viewed from above. Larvae and pupae below; natural size.

supported at the base by small stones, between which the ants had removed the soil, thus providing free drainage (Fig. 1). A portion of the garden with many pupae of sexual forms and many males just past the callow stage was collected and placed in an observation nest in the laboratory of the Imperial College of Tropical Agriculture at 8.15 P.M. By the following morning the ants had completely reconstructed their garden and had incorporated in it some bread which

had been placed in the arena. They were carrying water to the nest in order to bring the humidity up to normal. This behavior, observed many years ago by Miss Adèle M. Fielde in our northern *Aphaenogaster fulva*, is also exhibited by *Atta* workers. The females, which were much less numerous than the males, took refuge in the garden as soon as it had been rebuilt (Fig. 2). It was noticed that some of the maxima workers were much darker than the bulk of the population.

This colony fragment was kept under observation from May 6 to August 7. During this period the ants kept their garden in excellent shape, using bread, boiled yam and cassava, orange rind, flowers, leaves, and papaya fruit. The colony behaved precisely like other *octospinosus* colonies kept under observation at the same time. Since Dr. Weber was concentrating his attention on the fungus-growing behavior of the insects, his notes contain references to only a few of the more conspicuously anomalous individuals. On May 14 one of two mature gynandromorphs (Fig. 7c) was seen to escape into the arena of the nest and persistently attempt copulation with several workers (!), without, however, extruding its genitalia. On May 15 the other gynandromorphs (Fig. 7e) was seen to attempt copulation with a worker minima (!).

On May 25 the entire laboratory colony, which was in a very flourishing condition and had enlarged its garden by collecting pieces of leaves and other vegetable matter, was carefully examined. All the sexual pupae had become adult and only a few larvae and worker pupae remained in the nest. Apparently none of the females had oviposited since the establishment of the colony in the laboratory, because there was very little brood and no eggs. On the succeeding days several females, mostly dealated or with abnormal wings, were observed wandering around the arena.

On the morning of June 18, when the original site of the colony was revisited, it was found that the ants had taken the remains of the garden demolished May 5 and had moved them to a new nest 1.8 meters up the road. Nearly all the reconstructed garden with its population was collected. There were at this time several Phorids (*Diploneura cornuta* Bigot) and other flies in the garden, but their relations to the ants could not be ascertained. When the collected material was combined with the fragment of the colony that had been kept in the laboratory since May 5, it was found that several

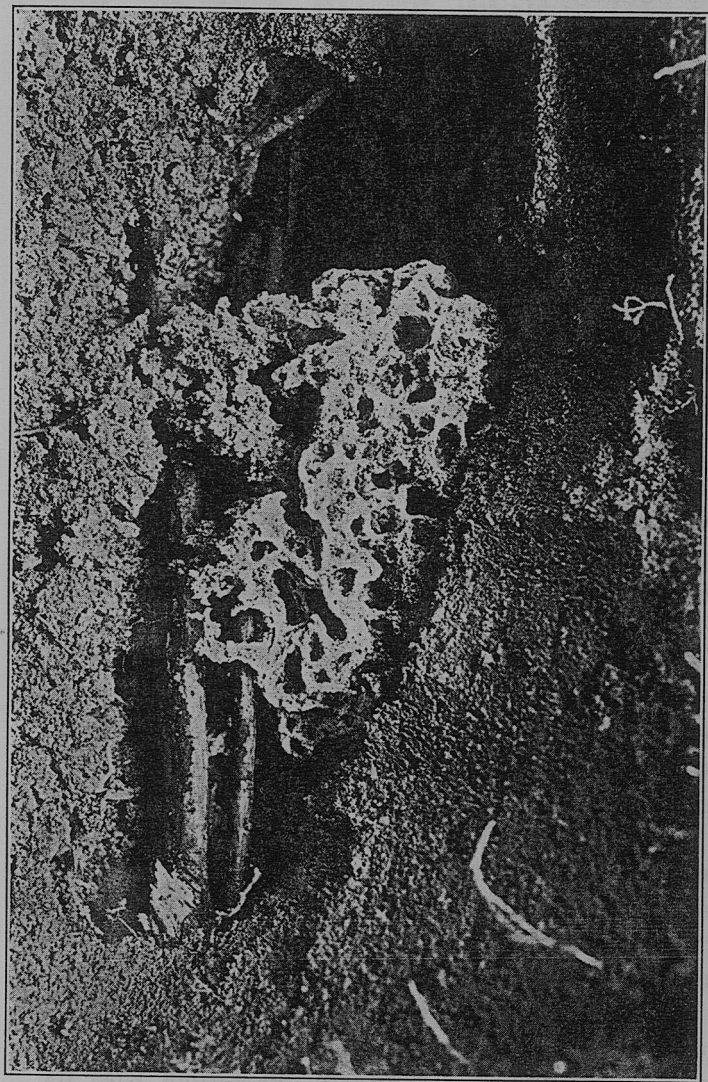


FIGURE 2. Photograph of the fungus garden of the aberrant *octospinosus* colony taken June 18, 1935, after it had moved to a new site. The garden is partly suspended from horizontal roots. About one half natural size.

additional dealated females had been acquired and that the workers of the later treated those of the earlier collection as aliens, though the members of both groups tolerated one another while foraging together on the laboratory table.

On August 7, when Dr. Weber was preparing to leave for British Guiana, the entire colony with its fungus garden was carefully preserved in alcohol and later turned over to me for study. This colony was undoubtedly several years old and, as will be seen from the foregoing account, at the very height of its annual breeding period in early May.

The entire preserved colony comprises 8174 individuals, each of which has been carefully examined. The various castes are represented by the following numbers of specimens:

Normal individuals:

Workers 7166
Winged females 175
Dealated females 11
Males 660

Anomalies:

Mutant females 6
Mutant workers 100
Gynergates 46
Diploergate 1
Gynandromorphs 10

The anomalies, therefore, comprise a little more than 2 per cent of the whole population, which probably amounted originally to about 9000, if allowance be made for individuals absent from the nest while the two collections were being made and for the escape of a few individuals from the artificial nest.

Before taking up the series of anomalies it will be necessary to introduce brief descriptions of the normal workers, female, and male of *octospinosus* to serve as a basis for comparison. The workers from a continuous series from very small to large individuals, a series that may be divided for greater convenience of description into majors, mediae, and minors, measuring respectively 6 to 8 mm., 4 to 5.5 mm., and 2.3 to 2.5 mm. The number of individuals of each of these subcastes varies inversely as their size, the majors constituting 13.5 per cent, the mediae 30.3 per cent, and the minors 56.2 per cent of the total worker population.² The majors and some mediae collect and

²It is the belief of Dr. Weber that a larger proportion of minor workers are produced in artificial nests, maintained for a long time, than in the natural state. In the laboratory it has been found repeatedly that the specialized major workers of *Acro-*

comminute the leaf fragments, which serve as the substratum of the fungus garden, while some mediae and the more numerous minors, as in the even more highly polymorphic species of *Atta*, confine themselves to the delicate indoor tasks of weeding the fungus mycelium which produces the kohlrabi-like food bodies, or bromatia, on which both the adult and larval members of the colony subsist. These indoor members of the colony prepare bits of the leaf fragments brought into the nest for imbedding in the garden. A bit of green leaf, roughly one or two millimeters in diameter, is rotated between the mandibles of a worker, or several workers may operate at opposite sides of the same fragment. As it is rotated the fragment is squeezed so that the periphery is finely scored and the juices exude. Now comes an important part of the procedure which seems to have been overlooked by previous investigators. After the fragment has been reduced to a juicy mass, the worker carefully places it at the tip of the gaster and defecates an amber fecal droplet on it. This treatment is given not only to all green leaf fragments but also to dried leaves and miscellaneous vegetal material, and is the final stage before the ant imbeds it in the fungus garden. Experiments to be described in a subsequent paper by Dr. Weber show that the role of the substratum is largely passive, affording mainly a convenient framework for the nutritive fecal droplets and the mycelium which grows on them. Thus it is that the ants of various genera (e.g., *Cyphomyrmex*, *Sericomyrmex*, *Mycetophylax*, *Myrmicocrypta*, *Atta*), including *Acromyrmex*, frequently use in nature slivers of wood and even skeletons of other insects. While the growing mycelium may break down the vegetal substratum to a certain extent, it appears that the fecal droplets of the ants afford most of the needed nutriment. A cycle is thus set up which is theoretically endless — the ants feeding on a fungus which in turn grows on the excrement of the ants.

In the following descriptions attention is especially directed to the structural and sculptural characters of the head, because the modifications in all but one of the anomalous specimens are confined exclusively to this region of the body.

The major worker is shown in profile without the legs in Figure

myrmex and *Atta* die off much earlier than the smaller castes. The percentage in the above figures is therefore probably low for major and high for minor workers under natural conditions.

3a, the dorsal aspect of its head in Figure 3b. In the largest individuals (maximae) of this subcaste the head, without the mandibles, is about 2.3 mm. long and 2.7 mm. wide. The frontal carinae are expanded anteriorly as large subquadrate lobes and continued pos-

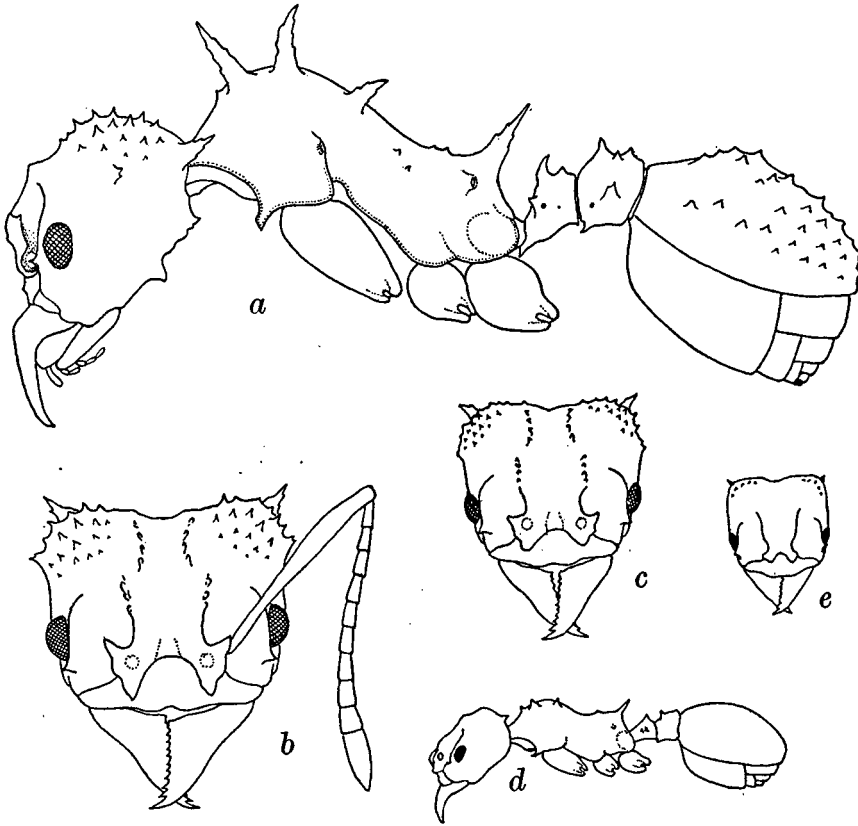


FIGURE 3. *Acromyrmex octospinosus*. a, major worker in profile; b, head of same, dorsal aspect; c, head of media worker; d, minor (minima) worker in profile; e, head of same.

teriorly as subparallel and eventually divergent tuberculate ridges. On the vertex there are two similar but more approximated rows of tubercles (vertical carinae). The posterior corners are beset with a variable number of small, acute, and sometimes apically bidentate tubercles and are produced backward and upward as a pair of short,

acute, crenate spines or teeth. Just behind the moderately large, subspherical eyes the sides of the head are smooth and either flat or feebly concave. These postocular areas terminate posteriorly at the postocular tubercles, which though often poorly developed are a diagnostic character separating the subgenus *Acromyrmex* from the subgenus *Moellerius*. Each eye is bounded medially by a preocular carina which curves inward posteriorly towards the frontal carina of the same side and terminates anteriorly in a small, acute tooth. Thus a shallow, posteriorly open scrobe is formed on each side between the preocular and frontal carina. The antennae are eleven-jointed, with the first funicular joint not thicker than the immediately succeeding joints. The color of the worker major is pale ferruginous or brownish-yellow; the media and especially the minor (Fig. 3*c, d, e*) are usually darker. The spines and tubercles decrease in size and number with the size of the body till they become very short and poorly developed in the minimae, which measure only 2.3 to 2.5 mm. The width of the head in proportion to its length also diminishes and the eyes become smaller and less convex. Moreover, the surface of the body, which is opaque in the majors and mediae, becomes smoother and somewhat shining in the minimae.

The normal female (Fig. 4*a* and *b*) is a decidedly larger and bulkier insect than the largest worker. It measures 10 to 11 mm. and is of a much darker color, being rich castaneous brown. The wings (omitted in the drawing) are 11 to 12 mm. long and deeply infuscated, especially along their anterior borders. The posterodorsal surface of the postpetiole, the lateral borders of the first gastric segment, and a longitudinal streak in its middorsal groove are black or brownish-black. The head resembles that of the major worker but is decidedly broader in proportion to its length (3 x 2.3 mm.), without the mandibles. The ocelli are small, the posterior pair placed at the sides of the short carinae of the vertex, the eyes considerably larger than in the major worker, the antennal scapes proportionately shorter and stouter, the preocular carinae and their teeth coarser and blunter, and the tubercles on the posterior corners of the head larger and less acute. The surface of the head differs also from that of the worker in being rugulose, with the rugules longitudinal between the frontal and vertical carinae, diverging on the posterior corners and concentric in the scrobes. There is a similar but coarser sculpture on the thorax; the

first gastric segment is feebly shining or glossy, with fine longitudinal striae on its dorsal surface.

The male (Fig. 4c-f) measures 8 to 9 mm. and resembles the female in the shape of the thorax and abdomen, but the thorax

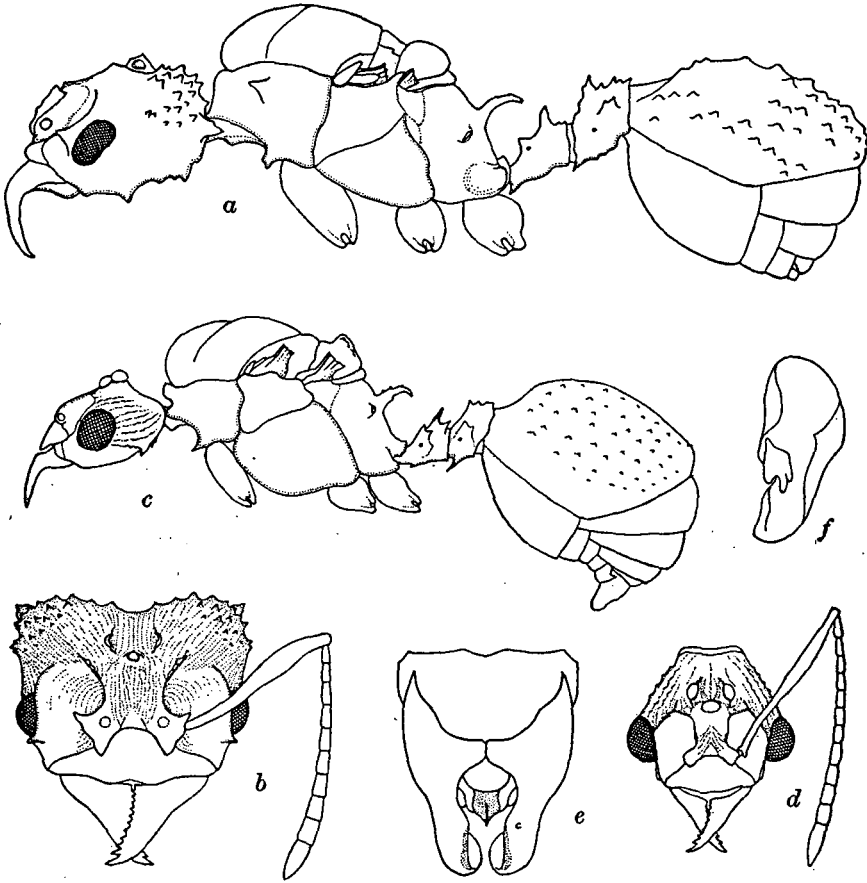


FIGURE 4. *Acromyrmex octospinosus*. a, female in profile with wings and legs removed; b, head of same, dorsal aspect; c, male; d, head of same; e, genitalia, dorsal aspect; f, volsella, mesial aspect.

possesses notaulices, the legs are slender, and the head is small — only 1.8 mm. wide through the eyes and 1.6 mm. long without the mandibles — and of a very different shape from that of the worker and female. The mandibles are much smaller, narrower and thinner, the

eyes and ocelli much larger and more convex, the antennae long, slender, and thirteen-jointed, with the first funicular joint distinctly stouter than the immediately succeeding joints. The scrobes are not open behind as in the worker and female but closed by angulate carinae, and the preocular carinae are delicate and lack anterior teeth. The posteriorly converging sides of the head behind the eyes are loosely and longitudinally rugulose, with series of small acute tubercles along the rugules, the front with chevron-like rugules. The body is of a sordid yellowish-brown color, the head darker brown posteriorly. There is a dark brown streak on each side of the mesonotum, and the middorsal streak of the first gastric segment is narrow, faint, or even absent. The wings, which measure 8.5 to 9 mm., are as deeply infuscated as in the female. The genitalia (extruded) are shown in Figure 4*e* and *f*.

PART II

THE ANOMALIES OF ACROMYRMEX OCTOSPINOSUS

The 660 normal males recorded on page 13 are very constant in structure and coloration. They exhibit, of course, appreciable differences in size and in the proportions of the head and other parts of the body, but these differences fall well within the normal limits of variability. The same statement holds good of the 175 winged, or virgin, females, most of which are mature. We believe that all or nearly all of the eleven normal, dealated and therefore fecundated females are the mothers of the 7162 yellowish-ferruginous workers, the 660 males, and the 175 winged females,³ but the six remaining females, listed under "anomalies," represent three distinct mutations, which may be briefly described as follows:

(1) A *rugose mutation* is represented by a single dealated female which had died and had been consigned to the refuse heap before the

³ The *Acromyrmex* colony is founded by a single fecundated female and is therefore of the primary haplometrotic type, but in subsequent years with the growth of the population several of her daughters may be retained in the nest as complementary queens, so that the colony becomes secondarily pleometrotic.

colony was preserved. This insect, which is dark brown or castaneous like the normal females but has a distinctly broader head, a rougher, more strongly rugose integument, and opaque gaster, we take to be the mother of the 100 major and media workers which contrast with the much more numerous normal, yellowish-ferruginous worker population in being dark brown or blackish and in having a distinctly rougher, subpunctulate, and somewhat more pilose integument.

(2) A *pale, spotted mutation* represented by one dealated and two winged females, which are yellowish-ferruginous like the normal workers but have the head, thorax, legs, and gaster dotted or spotted with black. The dots, at least on the head and gaster, are confined to

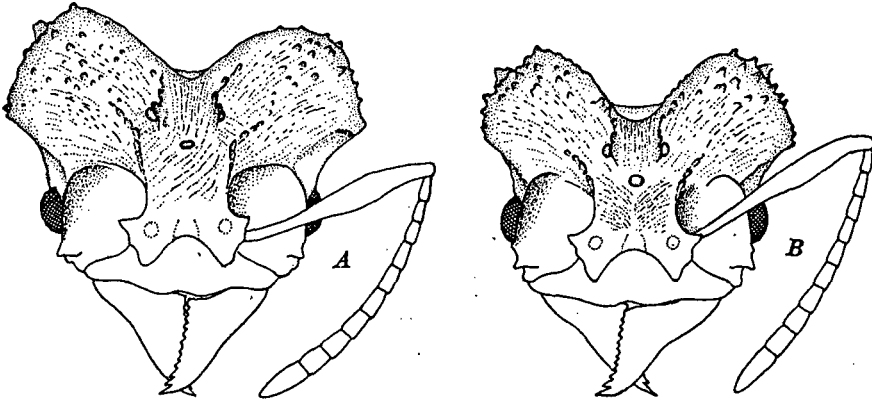


FIGURE 5. *Acromyrmex octospinosus*. A, head of scrobiculate mutant female; B, head of winged female, daughter of A.

the tubercles, the spots are small and mostly confined to the pleurae. The two winged females, of which one has well-developed, the other abortive wings, are apparently daughters of the dealated mutant. A single large worker which exhibits the same maculation may perhaps be regarded as the last survivor of this female's worker progeny of a former season.

(3) Much more interesting than the preceding anomalies is what may be called the *scrobiculate mutation*. It is represented by one dealated and one winged female, both of which are somewhat smaller than normal individuals. Since, as we shall show, there are good reasons to assume that the dealated female is the mother not only of the winged female but also of the ten gynandromorphs and the forty-

six gynergates, it will be advisable to give a more detailed description of these two mutants. Their thoraces, abdomens, and legs are those of perfectly normal females, but their heads (Fig. 5A and B) are remarkable in exhibiting the following twelve peculiarities not observable in any of the normal females nor in the two preceding mutations.

(a) Although the thorax, abdomen, and legs are yellowish-feruginous as in the spotted mutation, the head is more or less fuscous or blackish, at least posteriorly. This color contrast enables one to recognize these mutant females and their gynandromorphous and gynergate progeny at a glance.

(b) The head, which measures 3.3 x 2.6 mm. and 3 x 2.5 mm. in the two females respectively, is remarkably expanded posteriorly compared with the head of the normal female.

(c) The occipital border is deeply excised in the middle.

(d) Hence the posterior corners are more narrowly rounded, more lobular, and more convex than in the normal female, so that the head may be described as bilobed or cordate.

(e) The vertical carinae and the posterior tuberculate extensions of the frontal carinae are decidedly coarser and more prominent.

(f) The antennal scrobes are somewhat deeper or more excavated.

(g) The preocular carinae and their anterior teeth are decidedly coarser.

(h) The posterior incurving ends of the preocular carinae and lateral branches of the frontal carinae unite or overlap to form arcuate carinae (scrobal arches) which close the scrobes posteriorly.

(i) The postocular triangles are very distinct, concave, and bounded mesially by branches of the preocular carinae.

(j) The integument of the head is more uneven and more irregularly and sparsely rugose than in the normal female.

(k) The occipital tubercles are more rounded and less regularly arranged.

(l) There is a tendency to suppression of the minute hooked hairs on the occipital tubercles of the normal female and worker (not shown in any of the drawings).

The combination in the same individuals of all these deviations from the normal structure and coloration of the *octospinosus* female shows that we are dealing with a complex or cumulative mutation not

strictly comparable with the many simple mutations described by the geneticists. It is difficult, therefore, to account for the anomaly without additional material and especially without data derived from experimental breeding. This is apparent from a consideration of the two most conspicuous peculiarities of the mutation, the cordate shape of the head and the presence of the arcuate carinae which close the antennal scrobes posteriorly. Turning to an examination of other Attine ants for the purpose of ascertaining whether any of them exhibit similar peculiarities, we find that neither occurs in the females or workers of any of the known species of *Acromyrmex sens. str.*, though there is an approach to this condition in *A. laticeps* Emery. A similar cordate head, however, is exhibited by species of the subgenus *Moellerius*, for example by *M. versicolor* Pergande of northern Mexico, southern Texas, and Arizona (Fig. 6a), *M. striatus* Roger of the Argentine (Fig. 6e), and especially *landolti* Forel of Colombia and Venezuela (Fig. 6i). The only other Attini which have a somewhat similar though much more convex head are the largest workers or soldiers of *Atta*. Since the subgenus *Moellerius* seems to be more primitive than *Acromyrmex sens. str.*, we may perhaps regard the scrobiculate mutant as a reversion to a phylogenetically older head form.

A review of the various genera of Attini shows that the scrobal arches are a feature of sporadic occurrence. In the highest genus, *Atta*, there are no traces of them in any of the castes, and in no known *Acromyrmex* do they occur in the female or worker. As previously stated, they are well developed in the male of *A. octospinosus* and we find them also in the same sex of *A. aspersus* F. Smith and *A. (Moellerius) striatus* Roger (Fig. 6g). Emery, however, does not figure them in any of the males of ten species of the genus depicted in his monograph of 1905, but he may have overlooked them in some of the forms. In *Mycetosoritis hartmani* Wheeler the arches are present in all three castes but indistinct in the females and workers; in *Trachymyrmex* they are distinct in the males of some species (*septentrionalis* McCook, *intermedius* Forel, and *arizonensis* Wheeler) but absent in others (*jamaicensis* Ern. André, *relictus* Borgmeier, and *urichi* Forel). In *Sericomyrmex* they are absent in the females and workers and in all probability also in the male, but specimens of this sex were not available for study. Among the other more primitive genera,

which differ from *Atta* and *Acromyrmex* in having monomorphic workers and small females, live in small colonies, and practice simpler forms of fungus culture on substrata sometimes consisting of insect

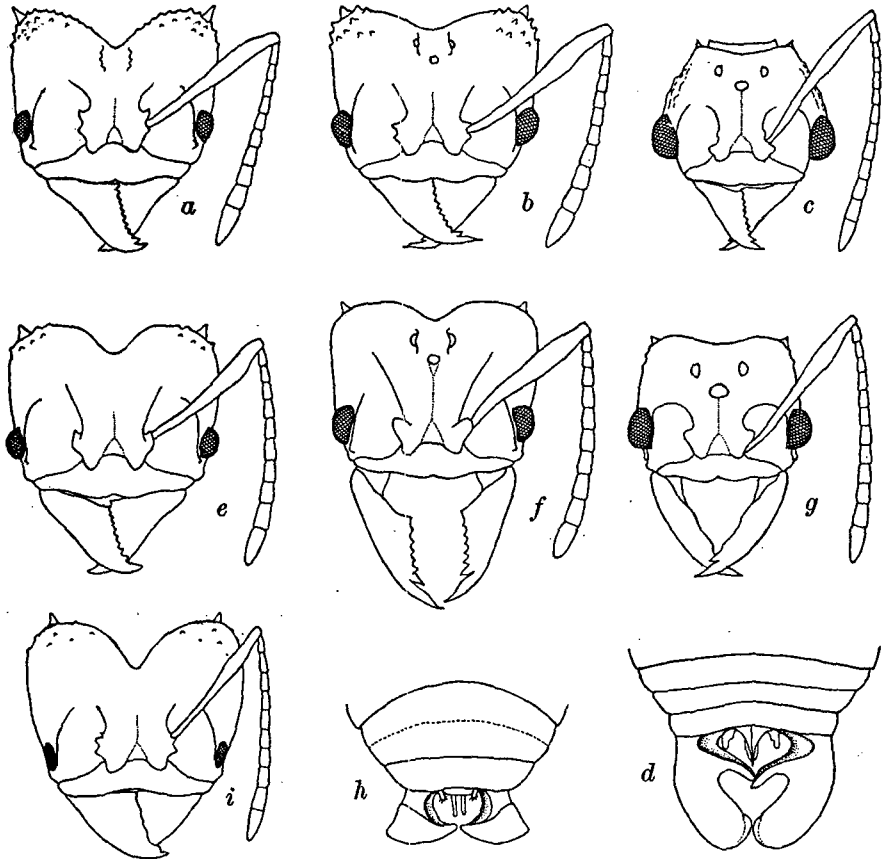


FIGURE 6. *a*, head of worker of *Acromyrmex* (*Moellerius*) *versicolor* Pergande; *b*, head of female; *c*, of male; *d*, genitalia of male, dorsal aspect; *e*, head of worker of *A. (M.) striatus* Roger; *f*, head of female; *g*, head of male; *h*, genitalia of same, dorsal aspect; *i*, head of worker of *A. (M.) landolti* Forel.

excrement, we find the scrobal arches absent in all three castes of *Mycetophylax*, *Myrmicocrypta*, and *Mycocephurus*. In *Cyphomyrmex* they are absent in *rimosus* Spinola and related forms but well developed in all castes of *auritus* Mayr, *strigatus* Mayr, *olitor* Forel, *paniscus* Wheeler, *foxi* Ern. André, *bigibbosus* Emery, *flavidus*

Pergande, *salvini* Forel, and *wheeleri* Forel. In the females and workers of these species, however, the arcuate closure of the scrobes is at the extreme, somewhat auriculate, posterior corners of the head. Most of the species of *Apterostigma* lack the scrobal arches, but they are present in all three castes of *A. urichi* Forel. It would seem, therefore, that the scrobal arches of the mutant female are not new but ancient structures which crop out sporadically in the males alone or in both sexes as vestiges of structures that are well developed in the females and workers of all the *Cryptocerine*, a tribe remotely related to the putative ancestors of the *Attini*.

The fact that scrobal arches are present in the normal male of *A. octospinosus*, though absent in the males of several allied species, might suggest that we are concerned with a male character that has been transferred to the mutant female, but such an interpretation seems improbable because, as we hope to show in the general discussion (p. 51), the female is decidedly the more variable and genetically the more dominant and progressive sex among ants as among the other social *Aculeates*. It is less difficult, therefore, to point to female characters that have been acquired by the male of the same species than to adduce examples of the acquisition of male characters by females. In the case of *A. octospinosus* and the few other species of the genus in which the scrobal arches still persist in the male, they may be regarded as a conservative character that has become phenotypically latent in the normal female and worker.

The ten gynandromorph offspring of the scrobiculate mutant female (Fig. 5A) are not ergatandromorphs, or male-worker, but male-female mosaics (gynandromorphs proper). In each of them the female component is confined to the head, and the body is that of a perfectly normal male, except in one specimen, which has abnormal genitalia. The heads of the ten specimens, drawn to the same scale, are represented in Figure 7A–J. It will be seen that they form a series ranging from very broad-headed to narrow-headed individuals. The last individual, J, has a head differing from that of the normal male (Fig. 4d) only in its somewhat greater width and in having the sides behind the eyes more convex. This is the individual possessing abnormal genitalia (Fig. 8). The left volsella is replaced by a slender, curved spine-like sclerite, representing, perhaps, a portion of the female sting, but the cerci are both present though very

asymmetrical in position. This individual, *J*, and two others, *C* and *E*, are the only fully mature individuals in the series. The two latter are the individuals which Dr. Weber observed in the attempt to copulate with workers in the artificial nest (see p. 11). The remain-

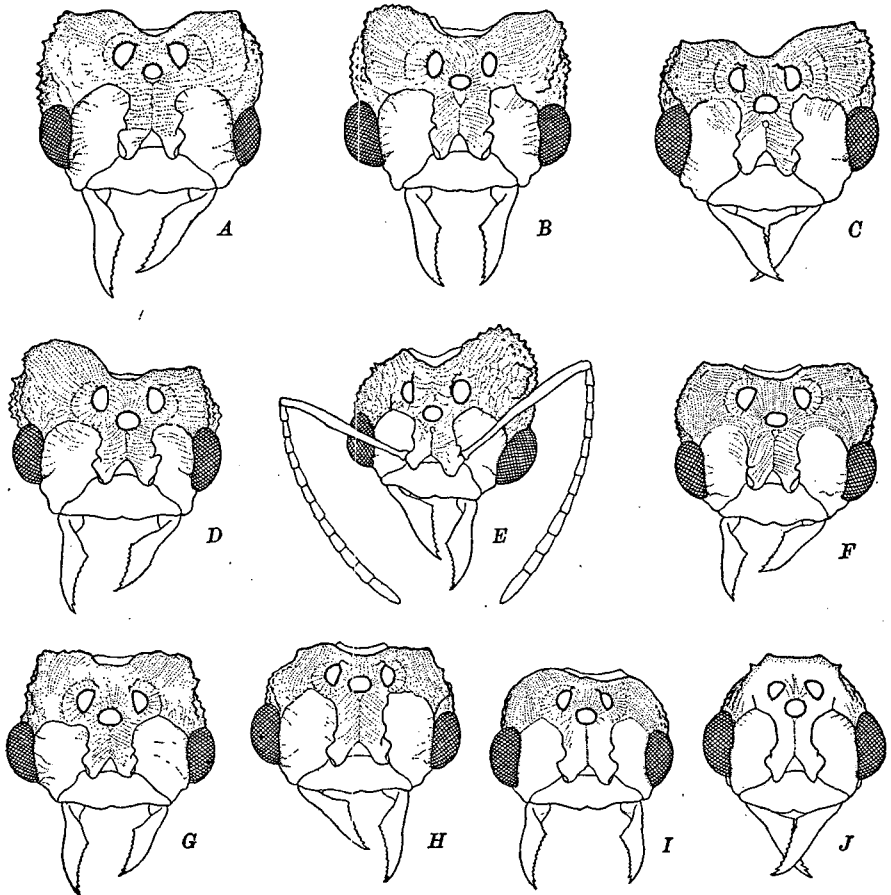


FIGURE 7. Heads in dorsal aspect of ten gynandromorphs of *Acromyrmex octospinosus*. For explanation see text.

ing seven specimens, *A*, *B*, *D*, *F*, *G*, *H*, *I*, are all callows which had died and had been buried in the refuse heap before the colony was preserved. Two of them, *A* and *I*, had lost both antennae, and the left antenna of two others, *D* and *G*, was missing. Since the antennae when present are uniformly of the normal thirteen-jointed male type, there

is no reason to suppose that the missing antennae were not of the same structure. The wings are perfectly developed in all the specimens, except *A*, which has been dealated. Since this happens to be the most feminized specimen in the series, the workers may have mistaken it for a female and clipped off its wings, or the individual may have had impulses sufficiently feminine to dealate itself.

Like the maternal mutant (Fig. 5*A*) and her daughter (Fig. 5*B*), all the gynandromorphs have the head of a distinctly brown color contrasting with the yellowish-ferruginous of the remainder of the

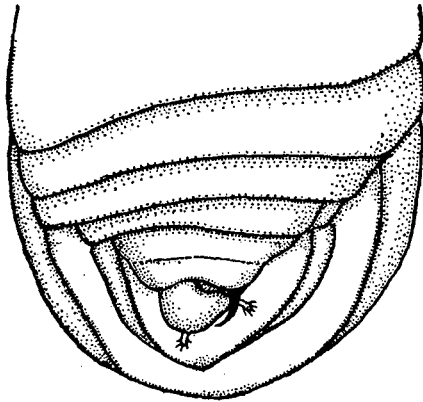


FIGURE 8. Ventral aspect of gaster of gynandromorph *J*, showing asymmetrical genitalia (male on right, female on left side).

body. Nine of them (all except *E*) are clearly anteroposterior mosaics, in which the female characters, and especially the great widening of the vertex, so unmistakably like the corresponding regions of the mother mutant and her daughter, are confined to the postocular region, whereas the anterior portion of the head, comprising the eyes, ocelli, frontal carinae, antennae, and mandibles, are male. In *D* and *I*, however, the left half of the head is noticeably less developed than the right behind the eyes. In *I* the greater tendency to segregation of masculinization on the left side is shown in the much smaller size of the left than of either the right or median ocelli, since each of the latter represents a fusion of a male and a female ocellus. *E* is of particular interest, because the postocular segregation of the

male and female components in the two halves of the head is more complete. In this specimen, therefore, which is, so far as its head is concerned, nearly a complete lateral gynandromorph, the left eye, ocellus, and antenna are much larger than the corresponding organs on the right side. This enlargement, again, is obviously due to the additive effect of the two sexual components in the anterior region of the head, which is strongly male in all of these gynandromorphs.

In most of the specimens the scrobal arches, which are at or near the transverse boundary between the female and male regions, are more or less angulate on one or both sides and therefore more as in the male, but on both sides in *D* and on the right side in *B* the arch is semicircular and hence of the maternal type. In *F* the connection between the frontal and preocular carina on each side is interrupted as in the normal worker and female. The sculpture of the posterior portion of the head, though very irregular as the result, apparently, of growth disturbances in the pupal hypodermis, nevertheless resembles the more regular sculpture of the mutant and normal females except in *E* and *J*. In the former the rugules are peculiarly reticulate, in the latter like those of the normal male. In nearly all the specimens the antennal scrobes are more or less irregularly, transversely wrinkled along the preocular and frontal carinae, a condition not seen in any of the normal males and females. This wrinkling would seem to be due to some mechanical stress and necessity for mutual adjustment in the pupal integument between the narrow male anterior and broad female posterior portions of the head. In some specimens, as on the left side in *E* and on one or both sides in *A*, *B*, *C*, *D*, and *F*, there are distinct vestiges of the anterior tooth of the preocular carina, a character which is absent in the normal male (Fig. 2*d*).

The gynandromorphs briefly described in the preceding paragraphs are interesting because they are the first examples of such anomalies to be found among the Attine ants and because of their number. Up to the present time sixty-one ant gynandromorphs have been described by various observers, but only two of them at most, and most frequently only one, have been taken in a single colony. In no instance, however, was the entire population of any of these gynandromorph-producing colonies carefully examined. Of course, the more than 4000 sex mosaics of *Cephalotes atratus quadri-*

dens, still to be described from a single colony also collected in Trinidad by Dr. Weber, is most exceptional, because this number far exceeds that hitherto observed in any animal species either under natural conditions or as the result of breeding experiments in the laboratory.

Of much greater theoretical significance than the gynandromorphs is the series of forty-six gynergates, or female-worker mosaics, and a single individual which may be called a diploergate because we regard it as a major and media worker mosaic. With the exception of a single poorly developed gynergate described by Tulloch (1932) and considered below (p. 42), no anomalies of this description have ever been recorded.⁴ The forty-seven specimens, all of which were found in the fragments of the fungus garden, had died some time before the colony was preserved. This was indicated by the extensive decomposition or complete disappearance of the soft tissue in their bodies, and even of the whole or part of the retinal pigment. All the forty-six gynergates possessed normal yellowish-ferruginous thoraces, abdomens, and legs, indistinguishable from those of major workers measuring 6.5 to 7.5 mm. or more rarely of large mediae measuring 5 to 5.7 mm., but the head was in every case dark brown or blackish, so that it was easy to recognize and separate them from the normal workers. The antennae, one or both of which had been retained by nearly all the specimens, were of the usual eleven-jointed worker or female type.

From this series of forty-six specimens, all of which vary in the configuration of the head, though their bodies are quite uniform except for slight differences in size, twenty-five have been selected for illustration in Figures 9*H-I*, 10*J-Q*, and 11*R-Y*. The whole series may be divided roughly into three groups which, like the gynandromorph series, show transitions from more or less symmetrical anteroposterior to very asymmetrical right and left segregation of the worker and female characters:—

⁴ The term "gynergate" was independently coined by Gösswald (1932, p. 151) in the same year as its introduction by Tulloch for a mosaic female-worker anomaly of *Myrmecia aberrans*. The German investigator, however, applied it to the ergatogynes of *Solenopsis fugax*. The anomalous specimen of *Aphaenogaster fulva* var. *picea* Emery which I described and figured in 1903 (p. 661) may be a gynergate or possibly a mixture of all three castes. The head alone is affected, the body being normal as in all but one of the Acromyrmex anomalies.

(1) This group comprises five very similar specimens, of which only one is figured (Fig. 9A). They are like the normal major workers of *octospinosus* in having a quite symmetrical head, but it is distinctly broader and more deeply excised behind, more narrowed anteriorly, with distinctly infuscated integument, and the preocular carinae are stronger and have stouter anterior teeth. In three of the specimens the scrobes, though open behind, are more concave and the occipital corners are more convex and rounded. In none of the five, however, are there any traces of scrobal arches. The tubercles on the occipital corners are acute or bicuspidate and frequently bear hooked hairs (omitted in the drawings) as in the normal major worker. In these specimens, therefore, the maternal characters are feebly but unmistakably manifested, especially in the posterior portion of the head.

(2) This group, which is much larger and more heterogeneous than the preceding, comprises thirty-six specimens, of which nineteen are figured (Fig. 9B-I, Fig. 10J-O and Q, and Fig. 11R-U). In many of them the posterior portion of the head is quite symmetrical (B, C, F, G, M, J) though the occipital lobes are more like those of the mutant mother, with much deeper median incision than in group 1. In others (L, M, N, O, Q) the maternal character of these lobes is even more pronounced. All the specimens have much more concave scrobes than A, the scrobal arches are complete or nearly complete, and the posterior continuations of the frontal carinae, the vertical carinae, the postocular triangles, and the occipital tubercles are unmistakably of the maternal type (matroclinous). It will be observed that in a number of these specimens (C, D, E, F, H, I, K, O, Q, R, S, T, U, V) the mandibles differ very appreciably in size, the larger being of the female, the latter of the worker type. Hence, as a rule, the larger mandible belongs to the more voluminous half of the head (G, J, O, Q, R, S, T, U). Moreover, the eye on the female side is apt to be distinctly larger than that on the worker side (N, O, Q, R, S), and the same is true of the antennae. The heads in this second group have a peculiar shriveled appearance and their surfaces are rough and very irregularly rugose as if the chitinous surface had contracted on hardening after the pupal stage. This is probably due to a disturbance of the young hypodermis in the pupal stages even more pronounced than in the gynandromorphs. In numerous

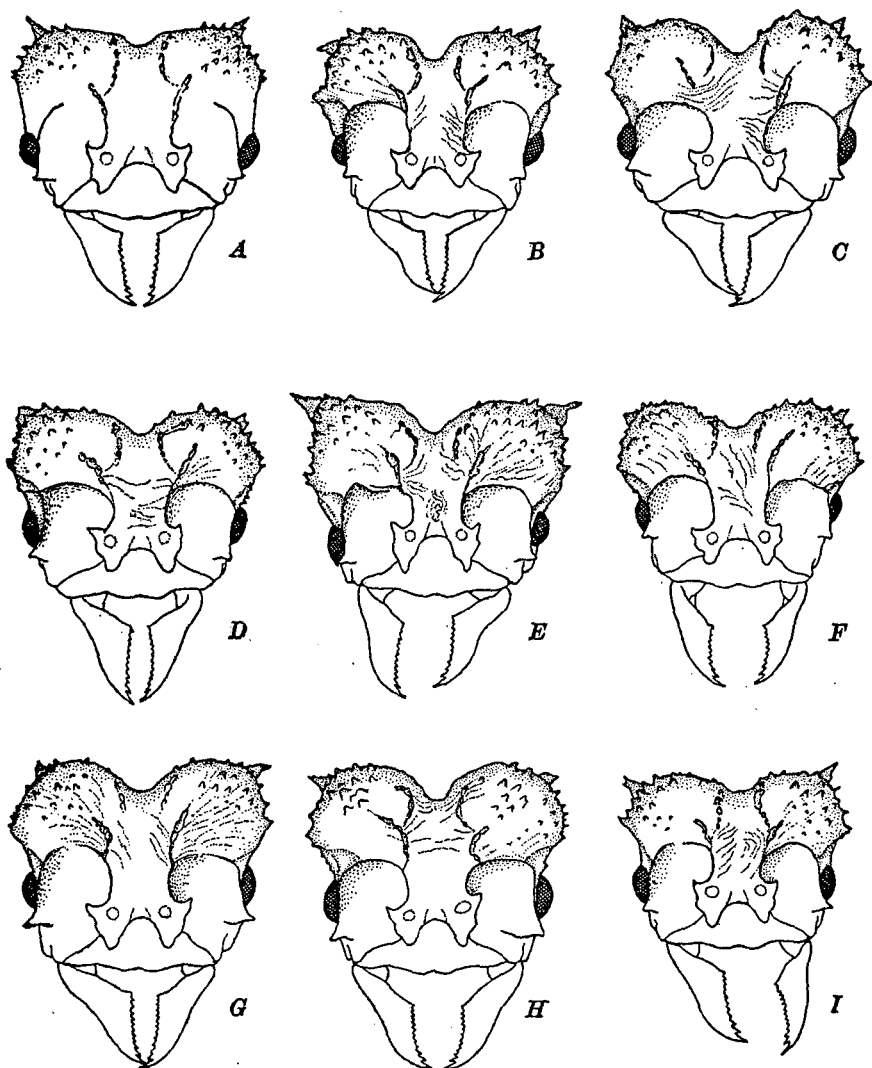


FIGURE 9. Heads of nine gynergates, dorsal aspect. For explanation see text.

instances the preocular carinae are not only coarse, but have very large anterior teeth, one or both of which may be prolonged mesially as transverse, accessory carinae crossing the scrobes (*H, K, L, M, O, Q, T*). In a few specimens, even when one half of the head is distinctly more voluminous than the other, the clypeus may be strongly asymmetrical (*R, S, T, U*). These specimens exhibit a condition in which the posterior portion of the head is clearly matroclinous on both sides, but is anteriorly more clearly worker (ergatoclinous) on the shorter side. This is seen most strikingly in *R, S*, and *T*, which have the scrobal arch interrupted and therefore more worker-like on the smaller, left side. Some cases, nevertheless, have the interrupted scrobal arch and larger mandible on the same side (*E, G, I*).

(3) This group, though comprising only five specimens (*P, V, W, X, Y*), is unusually interesting, because the head is extremely asymmetrical, with a small purely worker side, with posteriorly open scrobe, small mandible, antenna (as shown, e.g., in *X*), and eye, and the corresponding structures of the purely female side much larger. The occipital tubercles of the two sides are also clearly characteristic of the worker and female, with hooked hairs only on the acuminate tubercles of the worker side. Four of these specimens (*V, W, X, Y*) are rendered even more conspicuous by having the black pigment (shown by stippling) confined to the female side and leaving the smaller worker side yellowish-ferruginous like the thorax, abdomen, and legs. These specimens are, therefore, very distinct lateral mosaics, strictly comparable with gynandromorph *E* (in Fig. 7), except that the male component is replaced by a worker component.

The head of the single diploergate is shown in Figure 11Z. This specimen is a young, entirely unpigmented callow with the body of a large media. It was regarded at first as belonging to the third group of gynergates on the assumption that it was too young to have developed any pigment on the larger, left, female side of the head, but it seems more probable that the absence of pigment is due to this side's being that of a major worker combined with a worker media component on the right. Although the left postocular triangle might seem to indicate that the specimen is a gynergate, the posteriorly open scrobe, the character of the occipital tubercles, and the absence of irregular rugae on the same side indicate that we are actually dealing with a true major-media mosaic. This interpretation is supported

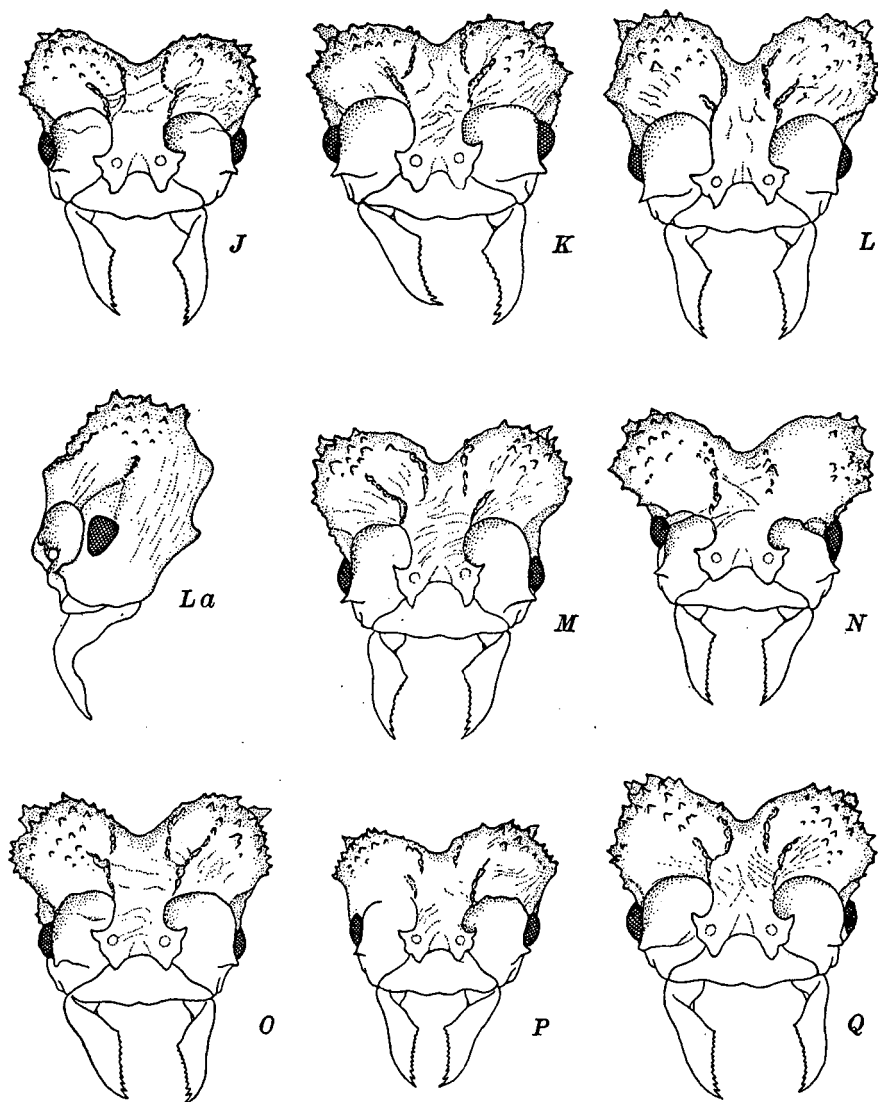


FIGURE 10. Heads of eight gynergates. *La*, lateral aspect; all others dorsal.
For explanation see text.

also by the fact that it is the only one of the forty-seven specimens that has the mandibles closed. That this is not a merely accidental or chance occurrence, as it might seem to be, is shown by the following considerations. The mandibles of ants are always open during the pupal stage, but after emergence they are kept closed, except when in use, and as a rule the insects die with closed mandibles. We must assume, therefore, that in all of the forty-six gynergates the divarication of these appendages was due to an inability to close them, and we must, of course, trace this inability to some defect in the mandibular musculature. Since the powerful flexor muscles which close the mandibles are attached to the inner surfaces of the occipital lobes of the cranium, and the much feebler extensor muscles which open the mandibles are attached to the gular apodeme in the anteroventral portion of the head, we can see why in the mosaics coöordinated movement of the jaws would be impossible, since in the anteroposterior mosaics the flexors would be of the female and the extensors of the worker type, and in the lateral mosaics each of the two pairs of muscles would be partly female and partly worker. Although complete inability to close the mandibles would not necessarily result from this bisexuality of the muscles, it would at once follow from abnormal histological structure of the flexors alone. That this actually existed in the gynergates is indicated by the great external asymmetries and irregularities of the integument of the posterior portion of the head. The matter could not be investigated, unfortunately, because of the decomposition of the tissues in the preserved specimens. Owing to their inability to close their mandibles the mature gynergates had to retain them in the open pupal position. This would account for the fact that these anomalous individuals died soon after reaching maturity. They are really lethal forms, useless to the colony because unable to cut and transport the leaf-materials for the substratum of the fungus garden and incapable of feeding on the bromatia.⁵ Closure of the mandibles in the single

⁵ This statement may require qualification. According to my earlier observations (1925, p. 159) on colonies of the Panamanian *Sericomyrmex amabilis* Wheeler, kept in artificial nests, the workers do not use their mandibles, but their maxillae, in cropping the fungus bromatia. If *octospinosus* feeds in the same manner, the gynergates and gynandromorphs should be able to feed unless, as seems very probable, at least in individuals with anteriorly asymmetrical head, their maxillary muscles are also incapable of normal coöordination. Observations made by Dr. Weber on many species belonging to a number of Attine genera in Trinidad and British Guiana support the foregoing

diploergate was possible, however, because of the less profound differences between the major and media worker in the volume and structure of the mandibular muscles and the lesser incompatibility between the other tissues in the right and left halves of the head. The gynandromorphs, of which eight of the ten specimens represented in Figure 7 have open mandibles, probably owed their early lethality to the same causes as the gynergates.

Another point of interest is the absence of the female ocelli in the gynergates. Though these organs are very small in the normal female of *octospinosus* (Fig. 2*b*), they are normal, nevertheless, in her winged daughter (Fig. 3*B*), and we should expect to find them at least in some of the gynergates. Yet we have failed to detect in any of them even the most minute traces of ocelli. Their complete absence may be imputed either to the histological disturbance of the pupal integument in the region of the vertical carinae or to a strong ocellus-inhibiting factor (perhaps hormonal?) in the worker component of the mosaic. That the latter is the more probable explanation seems to be indicated in many of the known ergatandromorphs in which the lateral male ocellus is completely blotted out or reduced in size like the anterior ocellus when the lateral worker component extends to the middorsal line of the head.

The occurrence of such anomalies as the gynergates is so unusual and their close mosaic resemblance to the gynandromorphs is so surprising as to upset widely accepted views concerning the origin of the latter. It is generally assumed that the gynandromorphs of the Hymenoptera develop from fertilized eggs, and various hypotheses have been framed to account for the nuclear determination and eventual distribution of their sexual components. We must obviously assume as the result of the observations recorded in the preceding paragraphs a similar nuclear and developmental mechanism for the gynergates, but this necessarily implies a genetic determination of the two female castes in the egg. Moreover, this early determination must also be attributed to the subcastes of the worker,

observations on *S. amabilis*. Hyphae are kept down more by attrition than by clipping, and the mandibles are not used, and in fact are of such a configuration that they cannot be used effectively by the major workers unless they stand on their heads. When feeding on a bromatium the ant, with closed mandibles, may abrade the surface of the mass as it lies in the fungus garden, or the bromatium may be picked up and rotated between the mandibles and fore tarsi while it is being abraded by the tongue.

if we are correct in interpreting the single diploergate as a major and media worker mosaic. We are, perhaps, concerned with a number of polyploid forms, but this is a matter which must be left to the decision of the cytologists and geneticists. A problem equally obscure and intriguing is presented by the strict limitation of the mosaic characters to the cephalic region, except in the single gynandromorph, *J* (Figs. 7 and 8), in which the genitalia are also involved. This limitation, which is characteristic of many of the described gynandromorphs, is most striking in the more than 4000 cases of these anomalies in *Cephalotes*, because in fully 95 per cent of them the male component is confined to the head. The processes responsible for this peculiar segregation present interesting problems in development and will be discussed at length in a future paper.

The portion of the *octospinosus* colony consisting of the scrobiculate mutant mother, her winged daughter, the gynandromorphs, gynergates, and diploergate, is of unusual significance also from another point of view. The unmistakable transmission of the mother's singular head form to all but a few of her progeny, and the lethal character of most of them, seem to throw an unexpected light on certain possibilities in the evolution of the workerless parasitic ants. In the third part of this paper we have undertaken a consideration of this question in connection with the long-smoldering controversy concerning the determination and differentiation of the castes and intercastes in the Formicidae as distinguished from the social wasps and bees. This is, of course, an undertaking of considerable scope, even with the suppression of much of the material that has been repeatedly reviewed by the author and others, and the omission of all specially genetic considerations—for which our observations provide no adequate data, since they were not and, indeed, could not be controlled by experimental breeding. The concluding part of the paper, therefore, is rather voluminous, but we believe that myrmecologists will find in it suggestions of several novel problems not unworthy of more intensive investigation.

PART III

GENERAL CONSIDERATIONS

The long controversy between those who maintain that the dimorphism of the female sex in the social Aculeates or the emergence of a normally sterile, in addition to a fertile, female caste⁶ is due merely to differential larval feeding (trophogenic) and those who maintain that this dimorphism is already predetermined in the eggs from which they develop (blastogenic) cannot be completely composed till biologists have found an escape from the older, more comprehensive environment-*versus*-heredity *impasse*. This appears to be obvious from the following factual statements and inferences from morphology, ethology, and phylogeny:

- (1) The ants, like the bees, are merely a peculiarly specialized group of wasps.
- (2) A worker caste has developed independently in each of the three groups of Aculeate Hymenoptera (wasps, bees, ants).⁷
- (3) This caste, at least in the ants, has been remarkably stable and highly specialized since Pretertiary times.

⁶ We are designating the two castes simply as "female" and "worker," and are therefore restricting the use of the former term throughout this paper to the fertile as distinguished from the normally sterile female or worker. The terms "feminized" and "feminization" refer to the influence of the female as a distinct genotype on the other castes. "Ergatized" and "ergatization" are suggested as corresponding terms for the influence of the worker. "Queen," while useful as a designation for the fertile mother queen of a colony, is objectionable on account of its inept anthromorphic connotations and was long ago discarded by the taxonomists. The term "neuter" for worker, in general use at a time when this caste was supposed to be sexless, is now rare except in popular writings.

⁷ Although this statement applies to the wasps and bees, it is not improbable, as I have previously suggested (1928), that the differentiation of the two forms of female, winged and apterous, actually preceded the social stage in the phylogenetic development of the Formicidae. If, as is usually conceded, the ancestors of the ants were Scolioid wasps, the recent discovery by Denis (1930) of two forms of female, one winged and one apterous, in the European *Myzine tripunctata* Rossi, is very significant. (The pronounced "antigeny" or sexual dimorphism of the species of *Elis* is another ant-like character.) The condition in other Scoliidae, in which the female is monomorphic and winged, may be due to phylogenetic suppression of the apterous female, and the retention of this form in the Mutillidae, Methocidae, Thynnidae, etc., may have been accompanied by the loss of the winged female. If the dichthadiigyne of the Dorylinae is really only a highly specialized worker (see Appendix B, p. 85) we have even within the family Formicidae an analogous phylogenetic retention of the apterous and a loss of the winged female.

- (4) A worker caste can develop only in a social environment.
- (5) In the wasps and bees all the available observational and experimental evidence favors the trophogenic as opposed to the blastogenic origin of dimorphism.
- (6) The mosaic character of the anomalies described as gynergates in the preceding pages cannot be explained as due to differential feeding in the larval stages.

From these statements we seem to be justified in drawing the following conclusions:

- (1) Certainly in some, and probably in all ants the essential characters of the worker caste cannot be due to larval feeding.
- (2) The caste, which could have arisen in the remote past only in response to a very special social environment and can still maintain itself only in such an environment, has somehow become genotypic.

Since the advocates of a thoroughgoing trophogenic explanation of the castes may regard the gynergates as unimportant, because they are monsters or "freaks," so rare and exceptional that they have only recently come to light, it will be advisable to continue the discussion with special attention to the nurse-brood relationship, which is, of course, the *punctum saliens* of the whole controversy. Not only are the female and worker castes of social wasps and bees very feebly differentiated compared with their analogues among the ants, but the pattern of the nurse-brood behavior, or what I have elsewhere called the "threptic environment," is certainly much simpler, more stable, less intimate, and therefore more amenable to experimental investigation than in the ants. Since in the wasps and bees the larvae are reared in stationary cells, the behavior of the nurses is limited to feeding, whereas the ant nurses add to this office the cleansing of the young from the egg stage to emergence from the pupa and their transportation to suitable sites in response to adverse changes of temperature and moisture and when other dangers impend. Moreover, much greater versatility is exhibited by the ant nurses in the selection and methods of administration of the larval food, a versatility which ranges from merely placing pieces of mutilated insects, crushed seeds, or malaxated tufts of fungus bromatia within

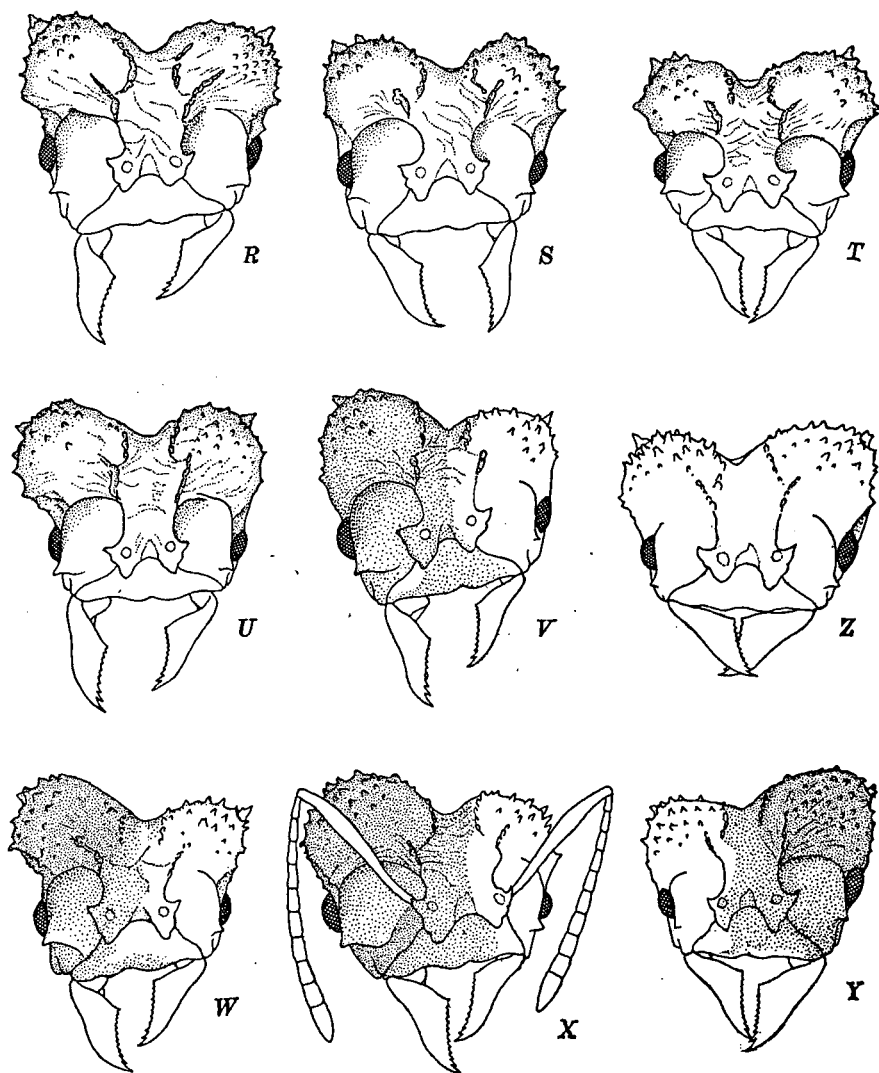


FIGURE 11. Heads of eight gynergates (R-Y) and one diploergate (Z), dorsal aspect. For explanation see text.

reach of the larval mouth parts (Ponerinae, harvesting Myrmicinae, Attini) or the insertion of ejected infrabuccal pellets of refuse into a special pocket beneath the larval mouth parts (Pseudomyrminae),

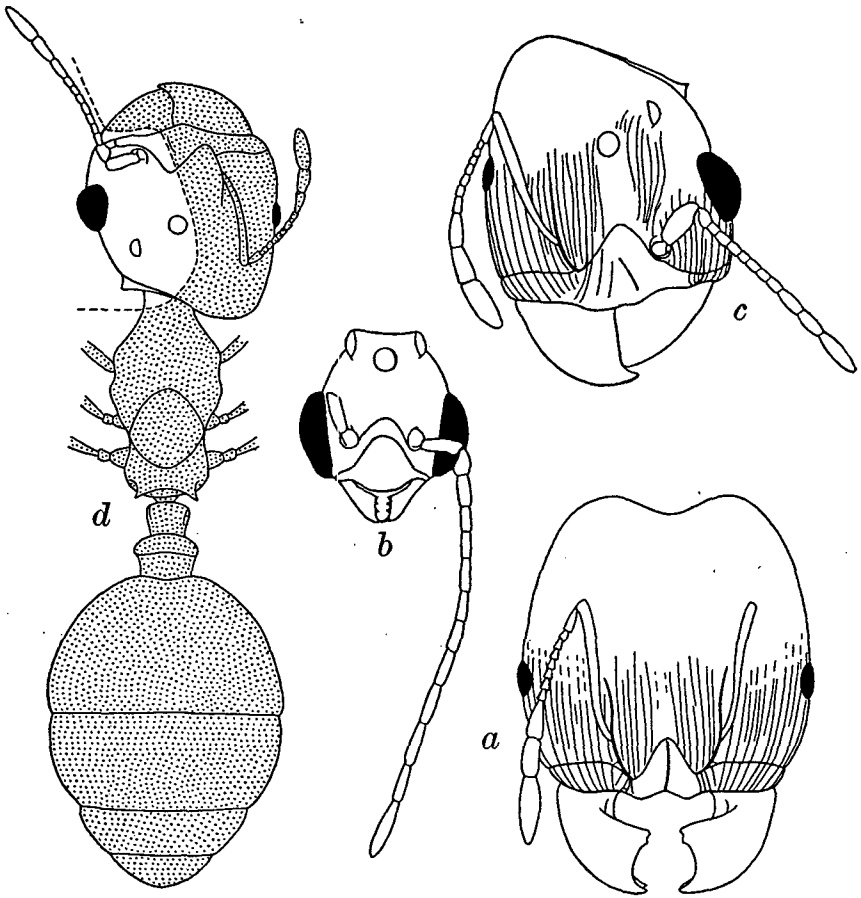


FIGURE 12. *a*, head of normal soldier of *Pheidole pallidula* Nyl.; *b*, head of male; *c*, head of dinergatandromorph; *d*, body of latter, showing extent of soldier (stippled) and male (unstippled) components. (After A. Vandel.)

to a careful administration *per os* of liquid food regurgitated from the nurse's crop (Dolichoderinae, Formicinae, many Myrmicinae). The ant nurses, therefore, enjoy a much closer tactile and trophallactic acquaintance with their charges in all their stages than the worker-

nurses of the wasps and bees. The trophogenic hypothesis, which seems to have been established for these insects, may seem at first sight to gain additional support from this greater intimacy of the nurse-brood relationships in ants, but the blastogenist might argue with equal plausibility that the ant nurses, owing to their more protracted and closer acquaintance with and more versatile responses to their charges, may be able to detect the prospective female or worker potencies in the eggs, perhaps as very delicate chemical stimuli, and thus be enabled to regulate more precisely the quality and quantity of food required for a consonant development of the larvae. Probably, furthermore, the treatment of the larvae is guided throughout their development by the expressions of their voracity or appetites and their changing metabolic states (writhing, "pouting," chemical composition of exudates, secretions, fat body, etc.). It must be admitted, however, that the brood relationship in ants is so elaborate, the difficulties of submitting it to controlled experimental investigation so great, and observations of it so productive of conflicting "explanations," that the controversy concerning the determination of the castes in these insects has persisted with little change for many years. This is shown by the attitudes of the two very eminent myrmecologists, Emery and Forel. Although both were thoroughly conversant with all the relevant facts established during their lifetimes, Emery nevertheless remained an intransigent trophogenist throughout his career, and Forel, though he wrote less on the subject, was as thoroughly convinced that the castes are determined in the egg. During the past thirty years I have remained "on the fence" (1907, 1910) in this controversy, with an increasing inclination to drop off on the blastogenic side, as shown in the following passage from one of the chapters on polymorphism in my "Social Insects" (1928):

If my contention is correct that polymorphism originated and developed independently in the various groups of social insects, and if, as seems probable, they are of very different geological age, we should expect the castes which first arose as functional, i.e., behavioristic and physiological results of a division of labour, and only gradually acquired their morphological differentiation, to differ with respect to their hereditary determination in the germ plasm. While there seems to be little doubt that in the two recent groups, the social wasps and bees, the feebly differentiated queen and worker castes develop from eggs of the same kind, it

is more probable that in the two more ancient groups, the ants and termites, the pronounced fertile and sterile castes may be blastogenic. The latter statement may not apply to the soldier caste, which is evidently of very different age in ants and termites.⁸

The fact that in many ants there is in addition to the female-worker dimorphism a di-, tri-, or even tetramorphism of the worker caste adds to the complications of the trophogenic *versus* the blastogenic hypothesis. Are we to suppose that each of the worker subcastes, namely the soldier, major, media, and minor worker, is predetermined in the egg? This seems improbable at first sight for the following reasons:

(1) The polymorphism of the worker is evidently a much more recent phylogenetic development than the dimorphism of female and worker.

(2) In most ant genera the worker is monomorphic and the di- and polymorphism of this caste has developed independently and only in certain tribes or genera.

(3) In some cases of dimorphism (soldier-worker proper) the differences between the two subcastes are pronounced and very stable as, e.g., in nearly all of the species of the huge genus *Pheidole*. In many others, however, the largest and smallest subcastes of workers are connected by a graded series of intermediates as in nearly all social wasps, thus exhibiting a condition most plausibly attributable to mere quantitative larval feeding.

(4) We might contend, therefore, that trophogenic determination may occur in some species and blastogenic determination in others, or in other words that the polymorphic ants as a whole may be in various stages of a shifting of environmentally acquired subcaste characteristics to the germ plasm.

One of the arguments which have been advanced in favor of the blastogenic hypothesis is the occurrence of two kinds of sex mosaics, the ergatandromorphs and the gynandromorphs proper, accord-

⁸ Vandel (1930a), who also favors the blastogenic hypothesis, has published an admirably succinct account of polymorphism in the Formicidae. Although the explanation of the intercastes as examples of a variable feminization occurred to me independently as a result of my study of the *octospinosus* anomalies, it was a pleasant surprise on reperusing Vandel's paper to find that he had already detected feminization in the mermithergates of *Pheidole* and had thus been able to correct my former interpretation (1928a) of these anomalies. (See also Appendix B, p. 76.)

ing to the worker or female character of the non-male component. In 1919 I described a third kind of gynandromorph, in the Philippine *Camponotus (Colobopsis) albocinctus* Ashm., as a dinergatandromorph, because the mosaic consisted of soldier and male components. Emery, however, did not accept this interpretation, but regarded the soldier component, without sufficient evidence in our opinion, as being that of a female. If there is still any doubt about the composition of this mosaic, there can be none in regard to a very striking dinergatandromorph of the common European *Pheidole pallidula* Nyl., recently discovered by Vandel (1931). In this specimen the body is that of a normal soldier, the left half of the head, a small area at the base of the left mandible, and the left side of the neck are male (Fig. 12). The normal soldier of *Pheidole* is so characteristic and so very different from the worker and female that there can be no difference of opinion in regard to the interpretation of this mosaic, as there was in the case of *albocinctus*. After considering the latter, Santschi added the following remarks, which evince an attempt at a trophogenic explanation of the female and worker components of gynandromorphs:

Thus the question of the determination of the sexes seems to me to require revision. If the larvae receive a special food according to their caste, what is there to prevent the nurse workers being aware of the sex of the egg or of the young larva and of thereby being stimulated to modify the food to be administered instead of determining the sex by this means and on their own initiative? On the other hand, one may also contend that the larvae which hatch [from the egg] as gynandromorphs may still be determined as ergatandromorphs and dinergatandromorphs by alimentary castration, like the ordinary workers and soldiers, without any determinants necessarily existing in the germ. The problem would be elegantly solved by the discovery of a dinergatogynomorph in which discrete female parts alternated with worker or soldier parts. But I am not aware that such a combination has ever been observed, and this negative result rather favors the alimentary hypothesis. This hypothesis cannot be impugned by pointing to the existence of ergatogynes, which are intermediates between workers and females and present all intergradations, because their existence can be as readily explained by mixed alimentation as by the presence of attenuated sexual or subsexual determinants.⁹

⁹ While Santschi thus regards the fact that gynergates had never been seen up to the time of the publication of his paper as favoring the trophogenic hypothesis, Vandel (1930a) employs the same argument to support the blastogenic hypothesis. He says: "Santschi (1920) maintains that the absence of ergatogynomorphs or of dinergatogynomorphs favors the trophogenic theory. But such anomalies should not exist. In fact,

Since no one has attempted to explain sex differentiation in the Hymenoptera by feeding, Santschi's repeated use of the word "sex" instead of "caste" is confusing, to say the least. The citation has been introduced because a true gynergate corresponding to Santschi's "dinergatogynomorph" was actually described some years later (1932). This was a specimen of the most primitive of all known ants, *Myrmecia* (*Promyrmecia*) *aberrans* Forel, from New South Wales, which had been standing in my collection for many years till it was discovered by Tulloch while he was making a comparative study of the Formicid thorax. He describes the specimen as follows:

The right half of the insect has characteristics of the female while the left half has those of a worker. In the head the structure of the opposite sides appears to be quite typical of their respective castes, but the lateral margin of the right (female) side is distinctly concave and the posterior corner angular while the left (worker) side is convex and the posterior corner broadly rounded. The right eye is slightly larger than the left, and the clypeus is prolonged further forward on the right side than on the left. Structural characteristics peculiar to the component forms are prominent in the thoracic region. The structure of the right (female) side indicates that this specimen once bore two vestigial wings. The anterior one has been broken off (its position indicated by an insertion) but the hind one is still retained in the specimen. The structures which accompany wings are present. The parascutal ridge and the transcutal suture are present in their usual positions. The plate covering the metathoracic spiracle may be noted as well as the upper plate of the metapleuron. The left side of the thorax is distinctly that of a worker. No trace of wings or their accompanying structures can be detected. The large metathoracic spiracular plate, a characteristic of all workers of this genus, is in its usual position. The metapleuron is fused completely with the propodeum. In the dorsal aspect of the thorax, it will be noted that the right side appears to be large and swollen. This is probably due to the presence of wing muscles. A vestige of a scutellum distorted toward the right side may be seen in the specimen as well as a portion of a distinct metanotum. In the abdominal region the node presents an asymmetrical appearance. The right side is longer and its corners more angular than the left side, so that each side is typical of its respective caste.

gynandromorphism arises from disturbances produced at the moment of fecundation. The portion of the germ derived from the 'fecundated blastomeres' will be female, that derived from the 'parthenogenetic blastomeres' will be male. There should be no ergatogynomorphs unless it be conceded that the gynandromorph is derived from two accidentally fused eggs; but this interpretation is at present abandoned." That neither investigator should have used such negative evidence to support a biological hypothesis is proved by the existence of gynergates in *A. octospinosus*.

That Tulloch was fully aware of the theoretical significance of the specimen is apparent from the last sentence of his paper: "From the finding of this ant, therefore, it would appear that the trophic hypothesis of caste determination may have to be discarded in favor of the blastogenetic hypothesis." The specimen is clearly a lateral gynergate differing from our *octospinosus* gynergates in the extension of the mosaic characters to the thorax and pedicel of the abdomen. It is much less striking than our gynergates because the monomorphic worker of *aberrans* is very similar to the female. The female of this ant is not actually known, but apart from its possible subaptery, must be very similar to the females of the other subgenera of *Myrmecia* (*Myrmecia sens. str.* and what Emery called *Pristomyrmecia*). We have called our worker-female mosaics gynergates, but they might have been called gynodiner gates, because their worker component is in most cases that of the major.

It is clear, then, that just as in the gynandromorphs a female or a worker component may combine as a discrete entity with a male component, so also in the gynodiner gates, or gynergates, soldier or worker components may behave independently in forming a mosaic with the female component. Moreover, the single diploergate of *octospinosus* shows that mosaics consisting of major and media worker components may exist. If, therefore, we regard the gynandromorph as a germinally predetermined mosaic we must adopt an analogous interpretation for the subcastes, at least in certain species of ants. A few of Emery's observations are very suggestive in this connection, because they indicate that anomalies occur in which three different components may be combined in the same individual. In 1924 he described and figured two frontal, or anteroposterior, gynandromorphs of the European *Myrmica ruginodis* Nyl. (Fig. 13), which he interpreted as ergatogynes with male genitalia. They represent, therefore, a fourth kind of gynandromorph ("ergatogynandromorph") which is significant if, instead of adopting the usual interpretation of the ergatogyne as merely an intergrade or *Zwischenform* between the female and worker, we regard it as a feminized worker, or blended rather than mosaic gynergate (see the discussion on ergatogynes, p. 82). Of the two specimens represented in Figure 13, *a* is distinctly more worker-like, or less feminized, than *b*.

Another anomaly described and figured by Emery as early as 1894

belonged to the common East Indian *Pheidologeton diversus* Jerdon (Fig. 14). It had the head of a soldier and a body which he interpreted as that of a pseudogyne, but which is obviously that of an ergatogyne, as will be seen by comparing Figures 13 and 14. Here we have a combination of soldier, worker, and female in the form of an imperfect mosaic if we interpret the ergatogynous component as a blended

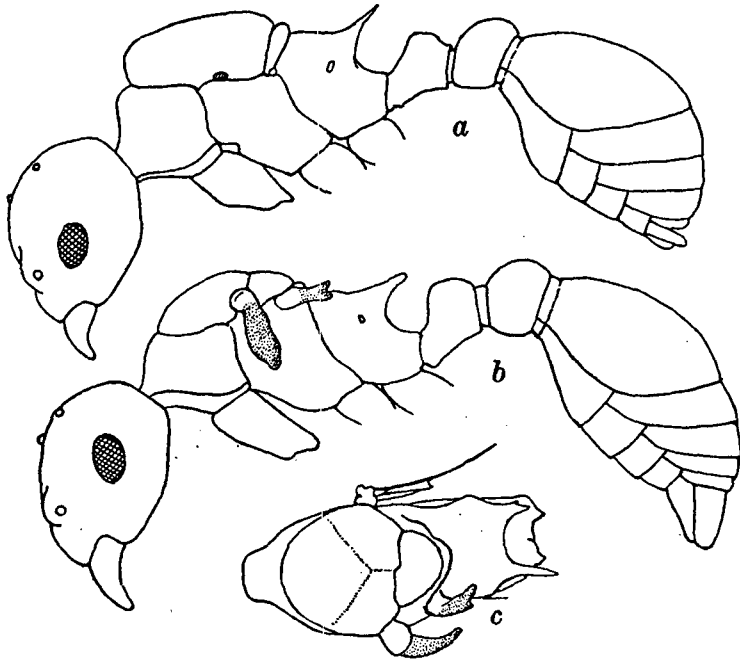


FIGURE 13. *Myrmica ruginodis* Nyl. a, ergatogynandromorph in profile; b, another specimen with the thorax more male and vestiges of wings; c, thorax of same, dorsal view. (After C. Emery.)

gynergate. As will be shown in the subsequent discussion, the specimen may be interpreted as a dinergatogyne, or hyperfeminized soldier, because the thorax is essentially that of the normal soldier of *diversus* (Fig. 14c), but with the homologous sclerites, and especially the mesonotum and scutellum, more voluminous.

An adequate account of the outcropping of worker di- or polymorphism in the family Formicidae would fill many pages. Since it happens that the single sharply differentiated tribe Attini illustrates the phenomena in a particularly striking manner, we confine our re-

marks to this one group, a procedure the more relevant to our argument because the gynergates which suggested our discussion were observed in a species of Attine ant. *Proatta*, a Malayan and Indonesian

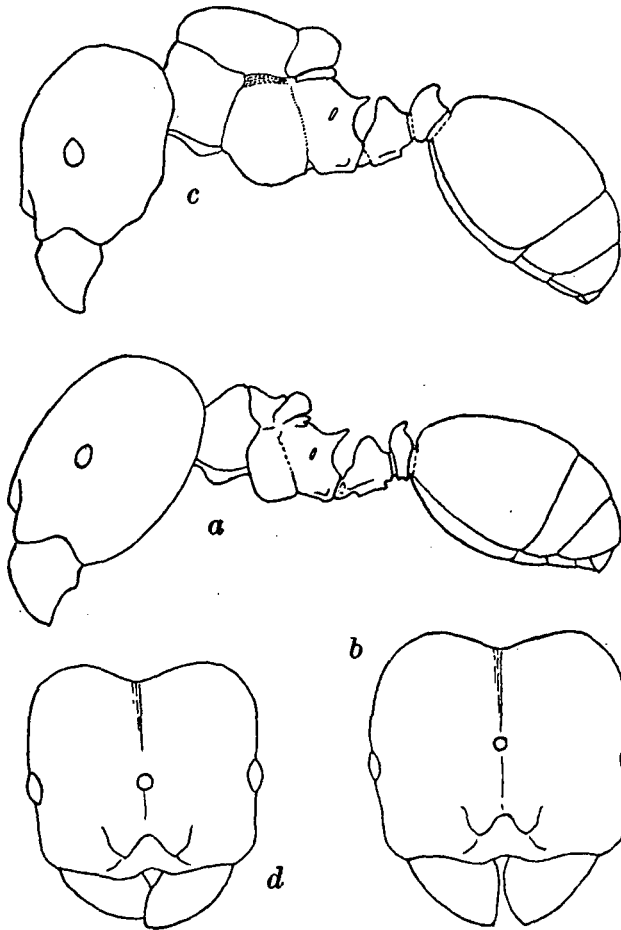


FIGURE 14. *Pheidologeton diversus* Jerdon. *a*, normal soldier in profile; *b*, head of same, dorsal aspect; *c*, dinergatogyne in profile; *d*, head of same, dorsal aspect. (After C. Emery.)

genus, which Forel and Emery include among the Attini, is here excluded from consideration, because only its worker and male castes have been seen and nothing is known concerning its habits. The remaining genera, which are exclusively American, fall naturally into the following four categories:

(1) Primitive genera: *Apterostigma*, *Sericomyrmex*, *Mycocepurus*, *Myrmicocrypta*, *Cyphomyrmex*, *Mycetarotes*, *Mycetophylax*, *Mycetosoritis*, and *Trachymyrmex*. In these the three castes are of nearly the same size, the workers are monomorphic, and the species, colonies, and nests are small. Each nest contains only one or a few fungus gardens.

(2) The single genus *Acromyrmex*, with the subgenus *Moellerius*. Its females are decidedly larger than the workers, which are roughly trimorphic. The species, colonies, and nests are larger, and the fungus gardens, though single or few in number, are larger than in group 1.

(3) The single, highly specialized genus *Atta*. Its females are very large compared with the workers, which are tetramorphic, comprising large differentiated soldiers and three intergrading subcastes of workers as in *Acromyrmex*. The species, however, average larger, form much more populous colonies, and have very extensive nests with numerous large fungus gardens.

(4) *Pseudoatta*, a parasitic genus, comprising a single species, *Ps. argentina* Gallardo, which completely lacks the worker caste and has homomorphic females and males.

Forel and Emery agree that the tribe Attini is descended from the Dacetini, the two tribes being connected by the genera *Stegomyrmex* and *Proatta*. Emery believes that the existing genera of Attini represent at least three divergent lines of evolution. Forel was so impressed by the structural and ethological peculiarities of the tribe that he regarded it as constituting a special section of the subfamily Myrmicinae, the Mycetomyrmicinae. Though Emery denied it this status in the "Genera Insectorum" (1921), he nevertheless placed it at the head of the subfamily. This is evidently its natural position if due weight be given to the very high specialization, both morphological and behavioristic, of all the species. Though the establishment and care of the fungus gardens, to which all the Attini except the parasitic *Pseudoatta* are devoted, is astonishingly complicated, the feeding habits of both the adults and larvae are much simpler than those of many less specialized ants, because each species cultivates only a particular species of fungus and under normal conditions has no other diet. The bearing of this fact on the trophogenic hypothesis of caste determination is apparent when we consider that the larvae of all stages are scattered through the gardens and like the adults subsist only on the bromatia, or hyphal swellings. These bromatia,

which since the publication of Moeller's paper (1893) have been supposed to be artificially induced by the workers, are, according to Dr. Weber's recent observations and experiments, a natural growth of the fungus.

The observations recorded in the literature on the feeding of the larvae are, unfortunately, neither numerous nor precise. The earliest and fullest observations were made by Tanner (1892) on *Atta cephalotes* L. in Trinidad and are here cited *in extenso*:

The larvae are usually placed on the top of the nest [fungus garden] and are constantly attended by the smallest workers — the nurses — who separate them into divisions according to their size. At first it seemed a mystery how these minute grubs could be fed so systematically, knowing that each individual larva was only one among so many, yet certain it was that all were attended to. Further observations showed that nature had provided most efficiently for them for food when they required it. This the larvae do by pouting their lips; on this notification of their requirement the first nurse who happens to be passing stops and feeds them. The nurses are continually moving about among them with pieces of fungus in their mouths ready for a call for food. The nurses feed the minute larvae by merely brushing the fungus across their lips, showing that the spores [*sic!*] alone are sufficient for its food at that period of its life. But it is not so when the larvae have increased so much in size that the pout can be seen without a glass, for then the whole piece, after having been manipulated by the nurse's mandibles into a ball in the same manner as the leaves are served when they are first brought into the nest, is placed in its throat; and if that is not sufficient, the pout continues, when the next one and even the next passing proceeds with the feeding, till the pout is withdrawn, showing that it is satisfied. No further notice is then taken of it by the feeders, until it again asks for a meal by pouting later in the day.

This account of larval feeding in the most highly specialized group of Attini differs from my earlier observations (1925) on *Sericomyrmex amabilis* Wheeler on Barro Colorado Island, Panama. The queen of this very primitive species scatters her eggs among the fungus and its substratum in her immediate vicinity. Some time after the larvae hatch they are carried by the workers to other parts of the garden and placed in contact with fresh masses of the fungus. Since the workers were never observed in the act of administering bromatia to the larvae, it was inferred that the latter merely reach out and crop the food that is within reach of their mandibles.

During 1935 Dr. Weber was able to make a number of observations in Trinidad and British Guiana on the care and feeding of the brood in *Atta cephalotes*, *A. sexdens*, and *Acromyrmex octospinosus* colonies. The eggs, larvae, and pupae of *cephalotes*, roughly classified by the workers according to size, are kept in the most flourishing portion of the gardens. Tanner's statement concerning the feeding of the young larvae with spores is incorrect, of course, because these fruiting bodies are not produced by the fungus. He also failed to notice that the workers also often feed one another and their larvae with regurgitated food. The workers roll masses of bromatia between their mandibles before placing them in the mouths of the pouting larvae. Dr. Weber noticed that one larva, which was lying on its back, on receiving the pellet of bromatia, worked its mandibles in and out with a piston-like movement while at the same time moving its labrum up and down. Eating, as in the adult, is a process of attrition and a lapping up of the juices exuding from the crushed bromatia. On another occasion, a worker minima was seen to be rotating a mass of bromatia between its mandibles and fore tarsi. It then walked over to a plump larva whose mouth parts were extruded ("pouting"), as it rested on its back, and placed the pellet over its mouth. The larva ate with the piston-like movement of its mandibles and after consuming the pellet within two or three minutes, worked its mouth parts a moment longer before becoming quiet. A third larva had at the side of its mouth a mass of food which it seemed to be unable to masticate, though it worked its mandibles and labrum. A worker media came up and regurgitated to it assiduously, directing its tongue and palpi to the corner of the larva's mouth opposite to the bromatial pellet. The regurgitation continued for thirty seconds, after which the worker passed on. In another *cephalotes* colony the workers for several days kept a worker and a soldier larva, which were much larger than the remainder of the brood, in the same or in separate cells of the garden and gave them special care. They unquestionably received more attention than the small larvae, either from more workers or from more frequent feeding by the same workers. The more conspicuous "pouting" of these larger larvae, which is perhaps accompanied, as it is in the larvae of the social wasps, by the emission of some trophallactic secretion, probably tends to attract more of the passing workers and may thus account

for the more frequent feeding. (Compare nestling birds, among which when one is accidentally fed more than the others it soon outstrips them in vigor and can beg for food more effectively.) On April 17, 1935 Dr. Weber installed in an observation nest a portion of a large *cephalotes* colony that was rearing its huge sexual larvae. The workers had defended these larvae too well when the nest was exposed, swarming over them and holding on to the larvae with their mandibles, so that the integument of nearly all was cut in many places. By April 21 only one was left, the rest shriveling up as the result of the workers' lapping up their juices through the cuts in their integument. This larva was fed with bromatia in the same manner as the worker larvae and similarly rested on its back. It pupated May 3 and the imago emerged May 31. This account of *cephalotes* recalls Emery's observations (1918) on *Pheidole pallidula*, the soldier, male, and presumably also the female larvae of which are more assiduously fed (in this case by regurgitation only) than the worker larvae. Larval feeding in an *A. sexdens* colony kept under observation in British Guiana was found to be precisely the same as in *cephalotes*, and the observations made by Dr. Weber on *A. octospinosus* in Trinidad, though less numerous than those on *cephalotes*, show nevertheless that the feeding of the brood is very similar. A larva of *octospinosus* that was resting on its back was seen to receive a pellet of bromatia from the worker, to hold it in its mouth with the mandibles, and to eat it by abrading the surface while occasionally rotating it, without breaking off pieces.

All the preceding observations relate to larval feeding in well-established colonies of Attine ants. It is doubtful, however, whether the colony-founding mother feeds the larvae of her first brood in the same manner. This seems improbable because the fungus of the incipient garden which grows from the mother's ejected infrabuccal pellet, as was demonstrated for *Atta sexdens* by H. von Ihering and J. Huber, for *A. cephalotes* by Goeldi, and for *Moellerius heyeri* by Bruch, is a pure mycelium on which the bromatia do not develop till after the first brood of workers has emerged and taken over the cultivation of the garden. Furthermore, the females of *Acromyrmex*, and especially of *Atta*, are such gigantic creatures compared with the just-hatched larvae that it is difficult to see how the mother can feed them either by regurgitation or with sufficiently minute pellets of fungus. It is more probable that the larvae of the incipient colony eat the

mycelium directly and that larval feeding in this very early phase of colony development may really represent an ancient phylogenetic stage which persists throughout the life of the colony in *Sericomyrmex* and other primitive genera. One of the brief notes made by Dr. Weber seems to support this assumption. On May 6, 1935 he captured a female *Acromyrmex octospinosus* that had taken her nuptial flight after 10 P.M. on the preceding day. When she was installed in a small artificial nest she established her fungus garden in the manner described by the investigators above mentioned for the species of *Atta* and *Moellerius*, and in it deposited a number of eggs. All of these she devoured, but on June 17 she laid an egg from which a minute larva hatched on June 19. When observed it seemed to be feeding on the fungus, as its ventral surface was curved into the mass of hyphae.

While the various observations above reported show that larval feeding in the Attine ants may be differential in the sense that the differences in the mere body bulk of the various castes and subcastes probably depend on the quantity of food administered and this in turn on the intensity of the appetites of the larvae, there is no indication of a qualitative diversity in the pabulum sufficient to account for the pronounced morphological diversity of the adults, since even the food regurgitated by the workers consists of the expressed juices of the bromatia. And even if we assume that the regurgitated or malaxated bromatial food may be mixed with minute quantities of some growth-promoting or form-determining enzyme, it is very difficult to imagine how in an average colony, comprising its host of — to all appearances — rather desultory nurses, clear-cut caste differences in the progeny could result; and the origin of the gynergates would still remain inexplicable. It may not be a mere coincidence, therefore, that with a single exception all of the known anomalies of this description have appeared in an otherwise normal colony of Attine ants, in which the food of both larvae and adults is so monotonously uniform.

The peculiarities of the mutant scrobiculate female of *A. octospinosus* and her mosaic offspring have a bearing not only on the question of caste and subcaste determination, but also on another matter which has not been adequately elucidated in the myrmecological literature. We allude to the predominance of the female as compared with the male and worker in the hereditary transmission of the species and caste characteristics. This predominance is obvious in the

octospinosus gynandromorphs and gynergates, which are clearly feminized males and workers, but its significance has not been fully appreciated in many other anomalies, because they happen to be quite symmetrical in bodily structure and their female and male or female and worker components are fused or blended instead of forming mosaics. The blends of female and worker, especially, seem to have been too hastily interpreted as mere "intermediates" between the two castes and to owe their origin to mixed feeding (see Santschi, *supra* p. 41, Donisthorpe, 1929) or to failure or perversion of the normal brood-behavior of the worker nurses (Wasmann). Though much less dominant than the female, the worker, too, may transmit its characters to the male. This ergatization of the male is easily possible, of course, because many and perhaps most of the males produced in ant colonies are the sons of workers rather than of the mother, or queen. We here briefly review the simpler and better known examples of feminization and ergatization of the male, reserving for subsequent treatment the more numerous but more obscure cases of feminization of the worker.¹⁰

In some ants the feminization of the male involves whole regions of the body, in others only particular organs. Thus in the Attini, of which *Acromyrmex* may serve as a typical example, the antennal scapes, the mandibles, thorax, and abdomen, excepting the genitalia, are decidedly feminized as compared with the homologous parts in the males of other Myrmicinae. (Compare *A* and *E* in Fig. 4.) Examples of a more local and really mosaic feminization are furnished by certain other ants in which the funicular joints of the antennae, which are normally twelve in the male, as in most Aculeate Hymenoptera, are reduced to eleven or ten, the most frequent numbers in the female. This reduction occurs in a whole subfamily, the Pseudomyrmecinae, in which the head, thorax, and abdomen of the male seem also to be feminized, and likewise in a few scattered genera belonging to other subfamilies. The mandibles of the male, which are often poorly developed or vestigial, may also show feminine characters. Santschi

¹⁰ It is very difficult to find instances of masculinization of the female. The only case we have met with is certainly spurious because it is contrary to the principle that an organ that has completely disappeared during phylogeny is never redeveloped. Emery believed that the female of the primitive ancestral ants was apterous, like the female Mutillids and Thynnids, and that the wings had been reacquired by the females of all the subfamilies of existing ants, except the Dorylinae.

(1906) has called attention to the mandibles of the male *Polyergus*, which are falcate like those of the female, though they are not used as in that sex for piercing the heads of other ants. A peculiar feminization of the male mandibles occurs also in a few species of *Moellerius*. In the female of the Arizonan *M. versicolor* Pergande (Fig. 8B) the apical tooth of each mandible is greatly elongated, but the mandibles of the male (Fig. 8C) are of the usual simple type; but in the Argentinian *M. silvestrii* and *striata* (Fig. 8E), in which the apical tooth of the female is even longer than in *versicolor*, the male (Fig. 8F) has acquired this character, with a concomitant reduction of the other teeth and a loss of the angle between the apical and basal mandibular borders.

Even more pronounced feminization of the males occurs in many of the anergatic, or workerless, parasites (Anergates, *Epoecus*, *Bruchomyrma*, *Wheeleriella*, etc.). The male closely resembles the female not only in the number of its antennal joints but also in the size, shape, sculpture, and color of the body. In *Bruchomyrma acutidens* Santschi (Fig. 15) the very long antennal scapes and even the peculiar neck-like constriction of the occiput of the female recur in the subapterous male. The workerless parasite *Pseudoatta argentina* (Fig. 16) is particularly interesting in this connection because it happens to be an Attine ant. It was originally described by Gallardo (1916) from two females and a male, the latter taken in a colony of *Moellerius balzani* Emery. His conjecture that *Pseudoatta* is a workerless parasite was confirmed by Bruch (1928), who found it in considerable numbers and on several occasions in colonies of *Acromyrmex lundii* Guérin and demonstrated its parasitism by bringing about its adoption by strange workers of the host species in artificial nests. Gallardo in 1928 added some interesting notes on the mating of *Pseudoatta*, which had also been observed by Bruch. The males and females copulate at the entrance of the *Acromyrmex* nest, so that there is no nuptial but only a dissemination flight of the females. Gallardo noticed that the "entrances of the nest are guarded by the minima workers of the *Acromyrmex*, which prevent the exit of the sexual forms except when they are *in copulâ*. As soon as a couple issues from the entrance the female rids herself of the male, sometimes violently, and marches quickly and decidedly to some elevated point from which she takes flight." Gallardo called attention to the

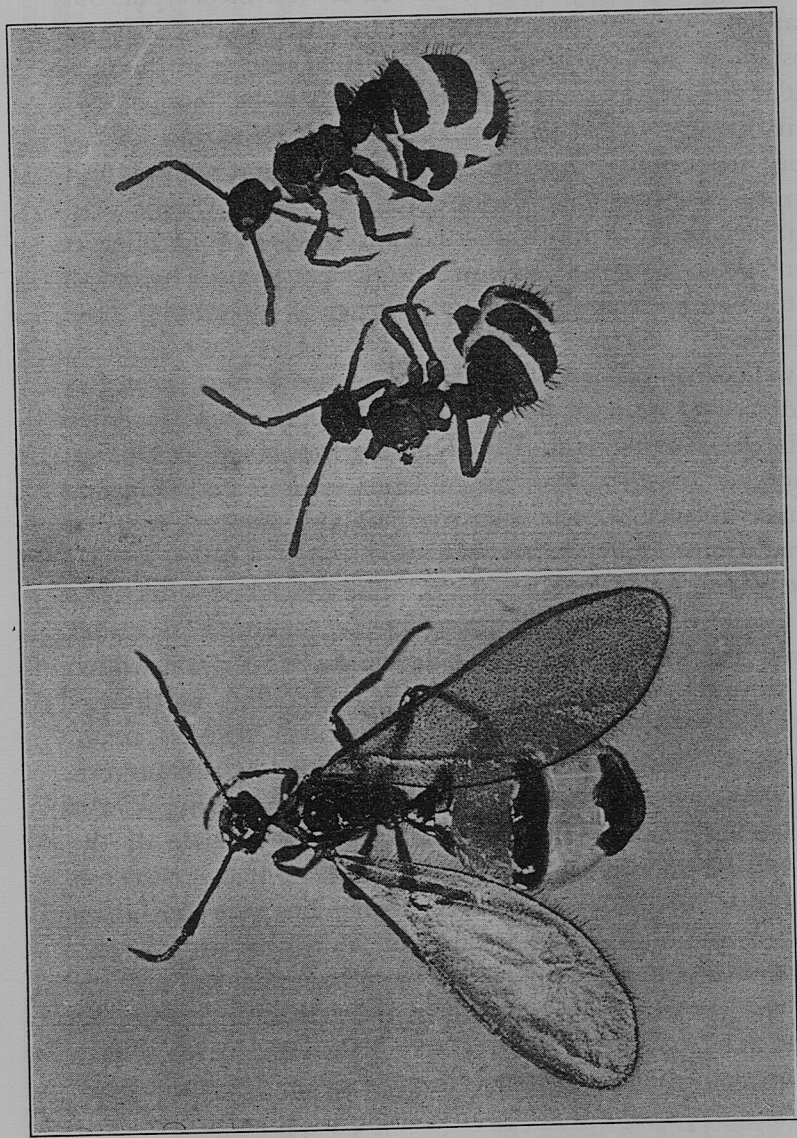


FIGURE 15. Winged female of *Bruchomyrma aculidens* Santschi, with developed ovaries, and two of the subapterous males. (After Carlos Bruch.)

close similarity between the male and female *Pseudoatta* in size, form, sculpture, color, and number of antennal joints (eleven). In his opinion the genus is most closely related to *Myrmicocrypta*, but Emery regarded *Cyphomyrmex* as its nearest ally. Examination of five females and a male received from Dr. Bruch results in the conviction that *Pseudoatta* is, as we should expect it to be, most closely related to its host genus, *Acromyrmex*. Though the surface of the body of both sexes of the parasite is very smooth and shining and therefore unlike that of any of the species of *Acromyrmex sens. str.*, we find a similar sculpture in certain species of *Moellerius (striatus)* and *Atta (vollenweideri, laevigata, mexicana)*. The larvae of *Pseudoatta*, moreover, are described by Bruch as resembling those of *Acromyrmex*.

Some twenty-five species of anergatic, or workerless, parasites have been described from all the continents except Australia. They are all small, rare, very sporadically occurring forms, mostly belonging to monotypic genera. Their resemblance to their hosts suggests that they have arisen, like the parasitic bees and workerless social wasps, as mutations either of their present host or of allied species of the same genus (see Wheeler, 1919). The described workerless ants can be arranged in a series of increasing "degeneration" or rather specialization, beginning with only slightly modified species in which both sexes are fully winged (*Pseudoatta*, *Wheeleriella*), or in very exceptional cases apterous (*Crematogaster atitlanica* Wheeler 1936), and ending with species in which the male alone is subapterous (*Bruchomyrma*) or even apterous (*Anergates*). Various hypotheses have been advanced to account for the complete absence of the worker caste in all the species. Some have suggested that it died out gradually because its role was taken over by the host workers which rear the brood produced by the parasitic female. Emery (1910) assumed on the basis of the trophogenic hypothesis that the original workers of the parasite were actually converted into females by being overfed as larvae by the host workers. An alternative hypothesis for the disappearance of the worker caste is suggested in the sequel.

The workerless parasites have been considered at length not only because they have highly feminized males but also because some light seems to be shed on the method of their origin by the mutant *octospinosus* female and her offspring. If, instead of receiving the

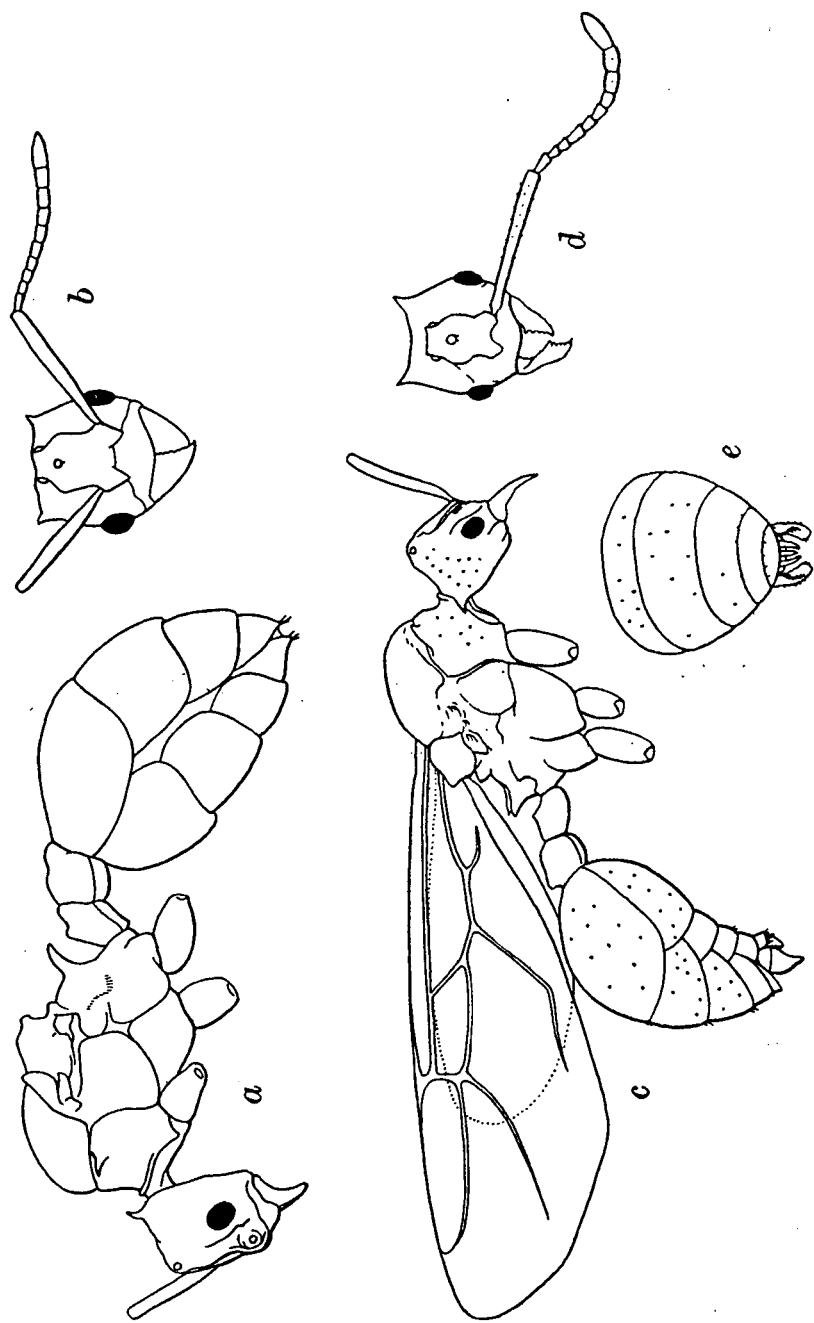


FIGURE 16. *Pseudoatta argentina* Gallardo. *a*, female in profile with wings removed; *b*, head of same, dorsal aspect; *c*, male in profile; *d*, head of same, dorsal aspect; *e*, tip of gaster with genitalia, dorsal aspect. (After Gallardo.)

whole *octospinosus* colony, I had received for examination only a fragment of it comprising a number of the normal brownish-feruginous workers, one or both of the female mutants, and one or more of the symmetrical gynandromorphs (Fig. 7A, F, or G), neither I nor any other myrmecologist who had seen the specimens would have hesitated to regard the mutant females and the gynandromorphs as the two sexes of a new species of workerless parasite. Owing to the strongly feminized head, the gynandromorph with its perfectly male body and genitalia would at once be taken to be the normal and only male of the species. The resemblance of the mutant female, her daughter, and her symmetrical gynandromorphic offspring to the normal sexual castes of a workerless parasite is the greater because the mutant mother was fertile and at least two of the gynandromorphs were able to attempt copulation with workers. The preceding interpretation would have to be abandoned if a few of the normal males or females of *octospinosus* had been included in the imagined fragmentary collection, because the host colony of a workerless parasite loses its mother and never produces males and females. And, of course, the finding of the mutant female's worker offspring in the colony (the gynergates) shows at once that we are not dealing with a workerless parasite. The fact, however, that all the worker offspring (the gynergates and the diploergate) were non-viable, or lethal, is, perhaps, suggestive of one of the processes whereby the worker caste may have been eliminated in the anergatic parasites, especially if we suppose that in some of the species, owing to abnormal chromosomal conditions in eggs destined to become workers, the lethal factors might be activated at a much earlier ontogenetic stage, such as that of the egg or young larva.¹¹

¹¹ Emery's trophic explanation of the disappearance of the worker caste in the anergatic ants is much less satisfactory than it appears at first glance. As Vandel (1930a) remarks, "this disappearance cannot be explained so simply. If it is a mere matter of nutrition, it is surprising that we fail to witness the reappearance from time to time of some worker that has hatched from a poorly nourished larva. And especially is it difficult to account for the existence, in a single genus such as *Epimyrma* of closely related species, some of which possess while others lack workers." In fact the known species of this South European genus, *E. kraussi*, *foreli*, and *gösswaldi*, possess workers, while *E. vandeli*, *ravauxi*, and possibly also *corsica*, are workerless. Gösswald (1930a, 1933) has shown that the worker personnel of *gösswaldi* is poorly represented, as it is in *Strongylognathus testaceus*, a parasite of *Tetramorium caespitum*. He accepts the blastogenic hypothesis and suggests that the workers of the anergatic species have disappeared simply because this caste was no longer reared by the host workers (*Leptothorax tuberosus*).

There are reasons for believing that other mutants have become temporary social parasites or slave-makers, but in these cases the females must have retained the ability to produce normal worker offspring. In a paper published as long ago as 1903 I conjectured that the unusual females of three of our North American species of *Formica* (*ciliata*, *oreas*, *microgyna*) arose as mutants.¹² Later these ants were shown to be temporary social parasites. It is interesting to note in this connection that several other species belonging to the genera and subgenera *Bothriomyrmex*, *Aphaenogaster*, *Dendrolasius*, *Chthonolasius*, and *Acanthomyops* all have aberrant females and have been shown to have the same habits. Most of them have peculiarly modified heads not unlike the head of the *octospinosus* mutant in being broad or subcordate posteriorly and therefore able to accommodate more powerful muscles and enabling their possessors to kill or decapitate the mother queens of the colonies which they invade. In the obligatory slave-makers (*Polyergus*, some species of *Strongylognathus*) the head is not thus modified, but the mandibles are sickle-shaped and are used for piercing the head of the host queen.¹³ We are inclined to conclude, therefore, that the females of the workerless, temporary, and slave-making parasites have all arisen as mutations, many of them with peculiarly modified heads or mandibles, that at least some of the workerless forms may have lost their workers because they were lethal in the egg or larval stages, and that the temporary parasites and slave-makers retained their workers because their females could produce viable offspring of that caste. Of course, much more must have been necessary to complete the evolution of the parasitic species, because each of them is characterized also by an

¹² Unfortunately, I reversed this opinion in 1917 and was inclined to regard some of the anomalies as persisting fluctuant, or what are now called phenotypic variations.

¹³ This was demonstrated by Emery for *Polyergus*. In 1928 Arnoldi discovered in southeastern Russia a remarkable ant, *Rossomyrmex proformicarum*, which enslaves *Proformica nasuta* Nyl. His figures show that the worker mandibles are of the usual type (i.e., nonfalcate), though powerful, and that the head has pronounced posterior corners. No doubt the unknown female has a similar head and probably either decapitates the host queen or pierces her head before adoption by her workers.

It must not be supposed that unusual heads of the type we have been considering are universal among the parasitic ants. Though the female of *Wheeleriella* among the workerless parasites has a subcordate head, she does not decapitate the host queen, and the head of the *Pseudoatta* female is narrowed behind and that of *Bruchomyrma* is actually constricted. Moreover, many of the females of the temporary parasites, like the *Formicae* of the *microgyna* group, are very small and non-aggressive or conciliatory in their behavior towards the host species.

elaborate behavior pattern. We should have to suppose that this behavior was a gradual subsequent development, impossible in mutations of non-social insects, but by no means improbable in forms

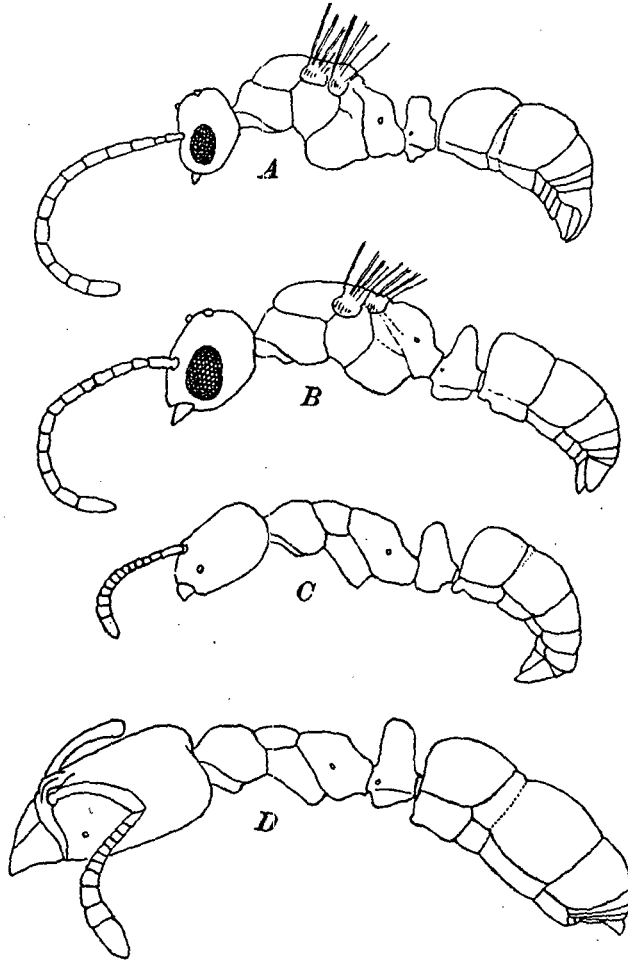


FIGURE 17. A, winged male of *Ponera coarctata* in profile; B, winged male of *P. eduardi*; C, subergatomorphic male of the same species; D, ergatomorphic male of *P. punctatissima*. (After C. Emery.)

that live and develop in such a protective, tolerant, and fostering environment as that of the ant colony.

The cases of ergatization of male ants, though rare, are much more striking than the cases of feminization because, as a general

rule, the male, apart from its primary sex-characters, antennae, and usually smaller size, resembles the female more closely than it does the worker. Only four genera of minute species present examples of ergatization ("ergatomorphism"), namely, *Ponera* and *Cardiocondyla*, which comprise non-parasitic forms, and *Symmyrmica* and *Formicoxenus*, which are monotypic genera of guest ants. In most of the numerous species of *Ponera* the male is of the normal winged type (Fig. 17A), but in five species, *punctatissima* Roger, *ergatandria* Forel, *mina* Wheeler, *ragusai* Emery, and *opaciceps* Mayr, the males are pale, wingless, myopic creatures, so much like the workers in form that they can in some cases be distinguished only by their genitalia (Fig. 17D). In some of these species (*ragusai*, *opaciceps*) the antennae have retained the original thirteen joints of the normal male, though their scapes have lengthened, but in others (*punctatissima*, *mina*, *ergatandria*) the number has been reduced to that of the worker and female (twelve). A single species, *eduardi* Forel, is known to have dimorphic males, one form (Fig. 17B) being of the normal winged type, the other (Fig. 17C) being wingless but possessing thirteen-jointed antennae with short scapes and therefore less extremely ergatomorphic than the males of the *punctatissima* group. Very similar conditions obtain in *Cardiocondyla*. Some species (*emeryi* Forel, certain subspecies of *nuda* Mayr) seem to have only normal winged males, others only wingless ergatomorphic males (*stambuloffi* Forel (Forel 1892a, 1892b), *elegans* Emery (Menozzi 1918)) and still others (*batesi* Forel var. *nigra* (Santschi 1907)) both forms of males. In our North American *Symmyrmica chamberlini* Wheeler the male has the head, thorax, abdomen, and antennae of a normal male but is wingless; in the European *Formicoxenus nitidulus* Nyl. the male is almost indistinguishable from the worker, except in the genitalia and more curved antennal funiculi.¹⁴

¹⁴ Forel (1908) has described ergatomorphic males of *Technomyrmex albipes* F. Smith taken by Donisthorpe from colonies accidentally introduced into Kew Gardens. These specimens, which are smaller than the normal winged males of the species, had a narrow, humped thorax like that of pseudogynes, without wings or alar articulations and with workerlike epinotum, but the genitalia were those of the normal male. According to Donisthorpe (1927) these anomalies were "sometimes abundant with the winged form." Perhaps they were really ergatandromorphs.

Dr. Bequaert has called our attention to a species of social wasp from the Carolinas, *Vespula squamosa* Drury, the male of which is clearly ergatized though the worker characters are only those of size and coloration. In his paper of 1931 he remarks that this wasp "is unique, not only in the subfamily Vespinae, but among all social Diplop-

There is every reason to assume that these various ergatomorphic males arose as mutations. They are, in fact, as Forel and Emery long ago maintained, merely anteroposterior gynandromorphs which have managed to survive as the sole, or as accessory, functional males of their respective species. In these minute, weak ants, which form very small colonies, and the marriage flights of which must often be a hindrance rather than an aid to the meeting of the sexes, it seems to have been advantageous to possess wingless males that could mate with their sisters in the nest soon after their emergence from the pupae. The same advantages accrued, of course, in the case of the wingless or subapterous males of the workerless parasites (Anergates, Bruchomyrma, Anergatides). That the ergatization of the male may extend also to its behavior was shown by Santschi (1907), who saw an ergatomorphic male of *Cardiocondyla nuda mauritanica* Forel transporting the larvae to safety when the nest was disturbed. It would be interesting to ascertain whether the even more highly ergatized males of *Ponera* also have acquired the behavioristic peculiarities of the worker.

Turning now to the anomalies that exhibit a feminization of the worker we are confronted with a more difficult task of interpretation. The word "feminization" here seems inappropriate because the worker is already a female, though wingless, with greatly simplified thorax and rudimental ovaries. We are using the term, however, not with reference to the external characters, which were the only ones used to illustrate the feminization and ergatization of the male, but as referring more particularly to the ovaries, which are still capable of development and of becoming as highly functional as they are in the female. As will be seen from the diagram (Fig. 18), there are at least twenty-five different anomalies that may be interpreted more or less satisfactorily as modified females or workers. These may be divided into two categories, the parasitogenic and the non-parasitogenic. The former, nine in number, with italicized

tera for the extraordinary dimorphism of the sexes. While worker and male are very similar, the queen is so different in size and color pattern that for a long time its true identity was not even suspected. Intermediate examples, which in most social Diplop-tera connect the fertile queens with the sterile workers, are not known in *V. squamosa*." A similar pronounced size dimorphism of the female and worker occurs in the closely allied *V. sulphurea* Sauss. of the Western United States, but there is not the same striking color difference between the female on the one hand and the worker and male on the other.

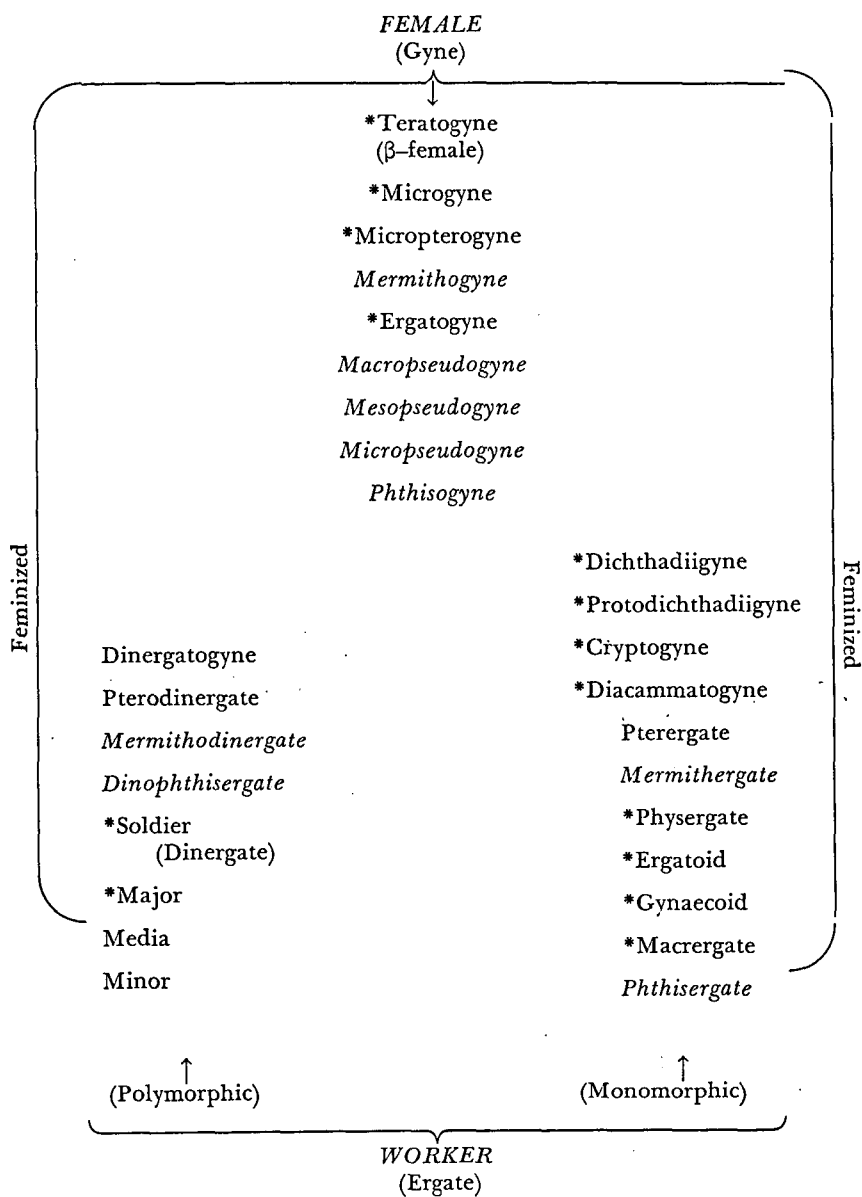


FIGURE. 18. Diagram of non-mosaic female, worker, and soldier anomalies. The italicized names are those of parasitogenic forms, the asterisked names of forms that may function as fertile females. For explanation see text and Appendix B.

names in the diagram, are produced either by the infection of individual larvae with Mermis or Chalcidoid parasites or by infestation of the colony as a whole with Staphylinid beetles of the tribe Lomechusini. These anomalies have, of course, a pathological but no genetic significance. The seventeen non-parasitic anomalies are very diverse. Some of them are aberrant but normally functioning forms such as the soldiers, or females, like the teratogynes, microgynes, micropterogynes and ergatogynes, which may function as normal or complementary mothers in the colony; others have the appearance of being intermediate in structure between the normal female and worker of the species. The latter are the "blended gynergates" referred to on page 43, which Wasmann designated "Zwischenformen" (1890) and I termed "intercastes" (1928). It is these forms which Santschi, Donisthorpe, and others have adduced in support of the trophogenic hypothesis.

In 1890 Wasmann recorded the occurrence of a continuous series of forms connecting the female with the worker in colonies of *Leptothorax acervorum* and *Formicoxenus nitidulus* Nyl. Later Miss Holliday (1903) described a similar series in *Leptothorax emersoni*, and Stumper (1918, 1921) confirmed Wasmann's observations on *Formicoxenus*. In all these ants the entire series comprises normal winged females, microgynes, various ergatogynes, and ergatoids, and these seem to pass over gradually into the macrergates and normal workers. Miss Holliday's and Stumper's figures show, however, that besides the sudden absence of wings in the ergatogynes, there is also a perceptible gap in thoracic structure in the series between the smaller ergatogynes and the ergatoids, or ocellate workers. The series seems, in fact, to comprise two series, one of females, with loss of wings and increasing simplification of the thorax, the other of workers which increase in size and acquire ocelli. In other words, the semblance of a single graduated series seems to be produced by a recessive structural simplification of the females and a progressive increase in size and ovarian development (feminization) of the workers. Some confirmation of the correctness of this interpretation is provided by recent experiments of Ezhikov (1934). He states that

when we subjected to hunger the larvae of ants destined to be females (*Camponotus*, *Myrmica*) at different moments of their development, we never were able to obtain forms transitional between the queen ant and the

worker, but either real fertile females, perhaps somewhat reduced in size, or else typical working individuals. Following particularly the fate of the ovaries, we did not meet a single case of a transitional ovary's being produced; at best it was possible to distinguish in the rudiments of the ovaries which had taken the direction of developing into ovaries of workers, feeble signs of their transformation out of rudiments of ovaries of females. In nature, also, transitional forms between females and workers in ants represent frequently, by the structure of the separate organs, either typical females or else workers. . . . The definite character of the reaction and the difficulty with which transitional forms seem to appear in ants speak in favor of the opinion that in this group peculiar modes of feeding, if in general such really exist, can have but an auxiliary role, as compared to the capacity of reaction belonging to the organism itself.

In addition to the worker series, there is, starting from the major worker in those species of ants in which the worker caste is di- or polymorphic, a third independent series. The major worker and especially the soldier, which is really a monstrous major worker that has become a normal member of the colony with a useful, specialized function, are distinctly feminized, especially in the structure of the thorax and head and possibly also in the development of the ovaries. Two unusual anomalies, the pterodinergate which I described (1905) in *Cryptocerus aztecus* Forel, and the dinergatogyne, described by Emery (1904, see Fig. 14) in *Pheidologeton diversus*, show an even greater feminization of the soldier. Unfortunately, owing to the fact that the species with well-developed soldiers are almost exclusively tropical or subtropical, we have little knowledge of the development of their ovaries. Certain observations suggest, nevertheless, that the soldiers of some species may not only have functional ovaries but may on occasion actually usurp the reproductive role of the females.

Two objections may be made to the contention that we are dealing with three discrete series or groups of anomalies instead of a single series connecting the normal female and worker castes. First, it may be urged that the female anomalies gradually approximate to the worker type and may therefore be regarded as progressively ergatized forms. Apart from the consideration that there can be no ergatization of the female in the genetic sense in which we are employing the term, because the worker ant is unable to produce females and is therefore precluded from transmitting its characters to this

caste, we can as plausibly interpret the non-parasitic female anomalies as a series of increasingly recessive mutations. That the smaller and simpler ergatogynes may closely resemble the ergatoids and workers in the number and size of their thoracic sclerites is admitted but does not affect the argument, because in many species of Ponerinae and Camponotinae the normal workers may have these sclerites distinctly developed, though the females and workers differ greatly in other respects. Second, it may be urged that the presence of vestigial wings in the pterergates, pterodinerghes, and diacammalogynes effaces our distinction between female and worker. This argument loses its force when we consider that, as Dewitz showed many years ago, vestiges of wings are normally present in the worker larvae. The presence of small veinless wingpads in the adult pterergate does not prove, therefore, that these anomalies have arisen from female eggs but only that they are feminized workers, that is, gynergates, in which the larval wing-vestiges have persisted as more enlarged appendages in the adult.

In the diagram (Fig. 18) the anomalies are arranged roughly according to their structural complexity, with the female series extending downwards from the normal winged form towards the worker, the worker and soldier series upward towards the female. Since we believe that each of the nonparasitogenic anomalies has arisen as an independent mutation, not once only but repeatedly and in the most diverse genera, we cannot regard the different forms as derived from one another. It will be noticed that the monomorphic worker series admits of an interesting alignment beginning with the gynaecoid, which is merely a normal worker that develops its ovaries as an adult and replaces the mother of the colony after she has been removed by accident or death, and ending with forms like the cryptogynes, diacammalogynes, pseudodichthadiigynes, and dichthadiigynes, which, after completely usurping the function of the winged female, are now the only fertile females of their respective species. That this must have occurred during the very early phylogenetic history of the Formicidae is shown by the fact that all these forms occur only in the most primitive subfamilies, the Ponerinae, Cerapachyinae, Dorylinae, and Leptanillinae. As many years have passed since the various female and worker anomalies have been reviewed, we planned to include an account of them in this third

part of our paper, but owing to its excessive length it seemed preferable to relegate the data collected from the literature to an appendix (Appendix B), which may be consulted by the interested reader.

If we are justified in regarding all the nonparasitogenic anomalies as mutations that keep recurring in various species and occasionally survive and reproduce their kind, more extensive investigations in this field may yield results of considerable theoretical importance. But in collecting material the myrmecologist should not, as heretofore, confine himself to the study of samples of a colony, but preserve the entire population, preferably at the height of its breeding season, and devote more attention to the mutations of the females and males. After such studies have been made of whole colonies of other species, the *octospinosus* colony may not seem to be so exceptional as the observations recorded in this paper might seem to imply. They suggest, at any rate, that the obstacles to experimental breeding of ants in the laboratories may not be as formidable as we have been inclined to believe, especially as there are several species of ants like *octospinosus* and the workerless parasites in which mating may occur in the nest instead of during the nuptial flight. The study of entire colonies is important also because the ant colony is an organism, as I suggested in 1911 and as Eidmann (1926, 1935, 1936) has recently maintained. Morphological, physiological, and ecological investigations of fragments of colonies are, therefore, necessarily inadequate, like similar investigations of defective individual organisms. From an organicist or holistic point of view, an ant's structure and reactions are significant not only as those of an individual element of the colony, but also as an expression of the constitution and behavior of the colony as a whole. Thus, without the potential background, so to speak, of the entire colony, of which all the workers possess rudimental ovaries capable of being stimulated to further development by abundant feeding, such fertile anomalies in the worker series as the cryptogynes and dichthadiigynes could not have developed, and they could not have survived and replaced the winged females without the peculiar behavioristic environment provided by the colony as a whole.

APPENDICES

APPENDIX A

TAXONOMIC NOTES ON *ACROMYRMEX* *OCTOSPINOSUS* REICH

Though *octospinosus* was the first of the numerous species of *Acromyrmex* to be described and was therefore selected as the genotype, its treatment in the general myrmecological literature and even in the admirable monographs by Emery (1905) and Santschi (1925) is meager and inadequate compared with the treatment of many of the other species of the genus. This neglect is due partly to the inadequacy of the original description of the species and partly to its confusion for many years with *A. hystrix*, described by Latreille (1802) from the same locality. The history of the original description of *octospinosus* was correctly presented by Emery as early as 1891. It was Olivier and not Reich who first described the ant in 1792, on page 122 of a paper on a collection of miscellaneous insects made by Le Blond in Cayenne and sent to the Society of Natural History of Paris. Olivier's paper was not consulted by Emery, but I have succeeded in finding in the library of the Museum of Comparative Zoölogy a copy of the first volume of the "Actes de la Société d'Histoire Naturelle de Paris," in which it was published. Ten species of "Formica" are recorded as collected by Le Blond, five of which were previously known and named, and five of which were given brief Latin diagnoses, but were not named. Reich, a year later (1793), as Emery has shown, selected the latter five, copied Olivier's diagnoses, and gave them specific names in the first volume of the "Magazin des Thierreichs," also a rare work, of which there is a copy in the library of the Philadelphia Academy of Sciences. One of the five species named by Reich was *Formica octospinosa*, which Olivier had described as follows: "*Formica fusco-ferruginea, capite thorace multispinosus, abdomine multotuberculato. Caput magnum spinis tuberculisque plurimis armatum. Thorax octospinosus. Abdomen tuberculatum.*" Since this diagnosis applies to almost any of the species of *Acromyrmex*, it is not surprising that most authors have referred their specimens to the more adequately but subsequently described *A. hystrix* of Latreille. Both Emery and Forel always believed *hystrix* to be a mere synonym of *octospinosus*, but Santschi (1925) is emphatically of the opinion that they are distinct species and that *hystrix* is really the form described by Forel (1904) as *emili*:

The type of this species [*hystrix*] described by Latreille has unfortunately disappeared, but the description he gives of it actually enables me to recognize

it as clearly applying to *Acromyrmex emili* Forel and not to *A. octospinosus* Reich. In fact, Latreille states that the inferior spine of the pronotum is "menue, très aiguë, perpendiculaire au corps," a character peculiar to *A. emili* and not to *octospinosus*, in which this spine is blunt and flattened. Furthermore, the whole description applies in detail (stature, color, etc.) to *emili*. This species, like *octospinosus*, has no traces of the median spines of the pronotum, which is not the case in the other allied large species.

Although I am not completely convinced of the precise identity of either Reich's or Latreille's species, I adopt Santschi's interpretation because it relieves us of still further complicating the nomenclature by introducing a new name for Reich's very inadequately described species. It should be noted, however, that the large workers of what we take to be his species vary greatly in size and coloration, and that the inferior pronotal forms are more frequently than has been supposed neither obtuse nor flattened, but narrow and acute as in *hystrix* and other species of *Acromyrmex*. The character by which *octospinosus* and *hystrix* (= *emili* Forel) can at once be distinguished is the presence of paired carinae or tubercles on the base of the epinotum in the former and their complete absence in the latter.

Acromyrmex octospinosus octospinosus Reich

It follows from Santschi's interpretation that the form of *octospinosus* inhabiting the north coast of South America and the island of Trinidad is to be regarded as the typical form of the species. All three castes of this form have been figured and briefly described in the first part of this paper. The major worker is small compared with some of the other subspecies, the thoracic spines are shorter and stouter, the inferior pronotal spines are less obtuse and flattened, and the tubercles on the head and abdomen are less developed. There are also distinct differences in the sexual castes, as will be shown in the sequel. This typical form was long ago (1894) redescribed by Forel from Trinidad specimens of all three castes as *A. guentheri*, and more recently (1921) Crawley redescribed workers of this same form as var. *pallidus* from British Guiana. His very brief description is confined to the color of some pale workers, but Santschi (1925), who has seen cotypes of *pallidus*, adds the following structural details which prove their identity with the Trinidad form (*guentheri* Forel):

It is a smaller variety than the type of the species. Besides its paler color, it is also distinguished by the inferior pronotal spine, which is less distinctly flattened and less blunt at the tip. There are also between the lateral pronotal spines two small, widely separated tubercles, which are less indicated in the type. The dorsal surface is more or less pruinose.

Santschi accepted *pallidus* as a valid variety because he was unaware that he was actually dealing with specimens of the typical *octospinosus*. There is in this form considerable variation, owing, apparently, to very

slow maturation. In the same colony, as, for example, in the one collected by Dr. Weber, the large workers may vary from pale yellow (callows) through yellowish-ferruginous (young adults) to ferruginous brown (the "*fusco-ferruginea*" of Olivier). These fully mature specimens may eventually acquire also a bluish bloom. Similar color variations are seen in colonies of the other subspecies of *octospinosus* and of other species of *Acromyrmex* (e.g., *A. coronatus*), so that varieties based exclusively on this character are invalid.

The known range of typical *octospinosus* may be gleaned from the following locality records:

French Guiana: Cayenne (Le Blond), type-locality ♀

Surinam: Courantyne R. 4°50' N. Lat. ♀ (N. A. Weber)

British Guiana: Issororo (Bodkin) ♀ Oronoque R. 2°41' N. Lat. ♂ (N. A. Weber)

Venezuela: La Moka (F. Meinert); Puerto Cabello ♀, Macuto ♀ Caracas ♂, Curiapó, Curiapó Island and Barrancas, Orinoco R. ♀, Barrancas (N. A. Weber) ♀

Trinidad (Günther, M. F. W. Urich, A. Forel, H. D. Chipman) ♀ ♀ ♂; Port of Spain (W. M. Wheeler, A. Busck) ♀ ♀; Monserrat (A. Busck) ♀; Gasparee Island (R. Thaxter) ♀; Tucaragua River and Maracas Valley, Northern Range ♀ ♀ ♂; Galeota Point ♀, Foothills north of Tunapuna ♀, Guayaguayare Bay, Trinity Hills Reserve ♀, St. Augustine ♀, Patos and Monos Islands, Gulf of Paria, San Fernando, Pitch Lake, Macqueripe Bay, Point Radix (N. A. Weber)

Acromyrmex octospinosus echinatio Forel

The major workers of this subspecies, originally described as a variety, measure 7–9 mm. and average, therefore, larger than those of the typical form. The spines of the occiput and thorax are more slender though rather short, those on the epinotum being straight and erect as in the typical form and shorter than the declivity. The inferior pronotal spines are broad, flattened, and blunt at the tips also in the mediae. The tubercles on the posterior corners of the head, the pedicel, and the gaster are more developed and subspiniiform, and some of those on the sides of the head are distinctly curved forward. The larger tubercles on the first gastric segment are more or less definitely arranged in two median longitudinal and on each side in two obliquely transverse rows, leaving a narrow, etuberculate, concave, middorsal area. The sculpture of the larger workers is feeble as in the typical form, but the minimae are distinctly smoother and more shining. The coloration shows the same variations as in the typical form.

The female is also somewhat larger than the same sex of the type, the body and wings of the same color, except that the first gastric segment lacks the dark brown or black middorsal streak and borders. The occipital, superior pronotal, and epinotal spines are longer and

stouter, and the tubercles on the first gastric segment are much coarser, with more marked linear arrangement. On each side at the posterior third of the first segment the tubercles are massed to form a distinct prominence or projection.

The male differs from the male of the typical form in the shape of the head, its postocular portion being decidedly broader and more convex, with the sides less converging posteriorly and the occipital border broader and more rectilinear. The ocelli, especially the posterior pair, are much smaller. The carinae closing the scrobes behind are straight and transverse, and not angulate, and the preocular carinae are continued back to the posterior corners of the head as a pair of denticulate ridges. The tubercles on the pedicel and first gastric segment are decidedly larger and more numerous and the epinotal spines are somewhat stouter.

Mexico: Montezuma en Chihuahua (T. D. A. Cockerell) ♀

Guatemala: Senahú en Vera Paz; El Reposo and Zapote (Champion) ♀ ♀; Tsanjuyú, Panajachel, and Sololá, Lake Atitlán (W. M. Wheeler) ♀; Trece Aguas, Alta Vera Paz (Barber and Schwarz) ♀, in cacao plantations

Costa Rica: Volcán de Irazú 6000–7000 ft. (H. Rogers) ♀; El Higuito, near San Mateo (P. Biolley) ♀; Carrera Nacional, 4650 ft. (P. P. Calvert) ♀; San Carlos (Schild and Burgdorf) ♀; San José (W. M. Wheeler) ♀; Port Limón (F. C. Paulmier) ♀; Liberia (A. Alfaro) ♀

Panama: Bugabá, Volcán de Chiriquí (Champion) ♀; Barro Colorado Island, Frijoles, Ancon, Las Sabanas, Taboga Island (W. M. Wheeler) ♀ ♀ ♂; Tres Rios Plantation (J. O. Tschokke) ♀; Balboa Heights (J. Zetek) ♀

Colombia: Rio Frio (P. J. Darlington) ♀

Ecuador: Guayaquil (F. Buchwald, C. T. Brues, F. X. Williams) ♀

I have not seen specimens of this subspecies from Montezuma, Chihuahua. Since specimens from this extreme northern limit of the range of the species may be varietally or subspecifically different from the Central American specimens and since the only Mexican material I have seen is from Yucatan and represents a distinct subspecies, I suggest that the Volcan de Chiriquí, Panama, be regarded as the type locality of *echinator*. Montezuma is so near the Rio Grande that we may expect the form recorded from Northern Chihuahua to occur in southwestern Texas.

Acromyrmex octospinosus inti subsp. nov.

Worker major. Length 6.5–7 mm. Smaller than the worker major of *echinator*, with more slender occipital and thoracic spines, the lateral pronotal not longer than the anterior mesonotal spines, the posterior mesonotal spines very short, the epinotal spines as long as the declivity of the epinotum, directed more backward, and feebly, sigmoidally curved. Inferior pronotal spines narrow, pointed, not flattened. Lobes of frontal carinae larger than in the typical *octospinosus* and the subsp. *echinator*,

more erect and with their posterolateral angles distinctly prolonged and rounded at the tip. Carinae on the base of the mesonotum inconspicuous, reduced to a pair of small tubercles. The pair of tubercles between the lateral pronotal spines very minute. Tubercles on the occipital corners of the head acute and rather long but few in number, those on the abdomen as in *echinator*, but less numerous and less regularly arranged on the first gastric segment. Integument very smooth but opaque; antennal scrobes finely and concentrically rugulose. Hairs, especially on the head and thorax, much less abundant than in typical *octospinosus* and subsp. *echinator*. Rich ferruginous, antennae scarcely darker; anterior border of clypeus and external borders of mandibles red, the apical border and teeth black.

Described from four specimens taken by Prof. C. T. Brues at San Bartolome, Peru.

Acromyrmex octospinosus volcanus subsp. nov.

Worker major. Length 8–9.5 mm. Larger than the subspecies *echinator*, with decidedly longer legs, the hind femora measuring 5 mm. instead of 4 mm. as in the largest specimens of *echinator*. Occipital and thoracic spines very stout at base; lateral pronotal nearly twice as long as the anterior mesonotal pair; posterior mesonotal pair very short; epinotal pair straight, erect, much shorter than the epinotal declivity; inferior pronotal spines thick and blunt. Tubercles of head and abdomen as in *echinator*, but those on the first gastric segment less numerous and without arrangement in a distinct transverse row on each side. There are no tubercles between the lateral pronotal spines. Surface rougher and more distinctly reticulated than in any of the preceding subspecies; scrobes and sides of head sharply rugulose, posterior portion of head and thorax generally with numerous, sparse, piligerous points or minute tubercles. Hairs black, longer, and more conspicuous than in *echinator*. Color much darker, varying from deep ferruginous or castaneous to black, usually with the pleurae, tips of thoracic spines, pedicel, sides of gaster, legs, and antennae somewhat paler and more reddish than the remaining parts. Mandibles red with black borders. Head and thorax of some of the specimens with a glaucous coating through which the spines, tubercles, and piligerous points project.

Described from seven specimens taken by C. W. Dodge at the Finca Hamburgo, on the Volcán de Barba, Costa Rica.

This is the largest form of the species, easily recognized by its long legs, coarse sculpture, and unusual coloration.

Acromyrmex octospinosus ekchuah subsp. nov.

Worker major. Length 6–7 mm. Very similar to *echinator* but smaller. Occipital and thoracic spines proportionally longer; lateral pronotal pair distinctly longer than the anterior mesonotal pair; inferior pronotal spines

narrow, slightly flattened, in some specimens acute; posterior mesonotal spines well-developed; basal carinae of epinotum very prominent, bituberculate; epinotal spines curved, as long as the declivity, directed backward. Tubercles on head and abdomen even more developed than in *echinator*. Though less numerous on the head, some of the lateral tubercles are very long and spine-like. There is a pair of small but very distinct tubercles between the lateral pronotal spines. Linear arrangement of tubercles on the first gastric segment often indistinct, the tuberculate prominence on each side at the posterior third of the segment more developed than in *echinator*. Sculpture, coloration, and pilosity as in that subspecies.

Described from numerous specimens collected by Prof. A. S. Pearce in the following caves in Yucatan: Puz Cave, Oxkutzab; Gongora Cave, Oxkutzab; Tiz Cave; San Bulha Cave, Merida; Xkyc Cave, Calcehtok; Luchil Cave, Tixcacal.

This subspecies is named after the ancient Mayan god of travel and cacao plantations.

Acromyrmex octospinosus cubanus subsp. nov.

Worker major. Length 7-8 mm. Very similar to *ekchuah* but nearly as large as *echinator* and differing only in the slightly more rugulose head and thorax, the even more backwardly directed epinotal spines, the more conspicuous tuberculate prominences at the sides of the first gastric segment, and the more uniform and regularly distributed tubercles on its dorsal surface. The inferior pronotal spines are narrow, usually acute, and not flattened.

Described from six specimens from Cojimar, Cuba (W. M. Wheeler, C. F. Baker), and three from Camoa, Havana (G. Aguayo). Emery referred specimens of this subspecies taken in Cuba by De Saussure to *echinator*.

The specimens from Cojimar are rich ferruginous brown, those from Camoa dark brown, with very slightly paler mandibles and appendages and with a bluish bloom on the body. The very close relationship of this subspecies to *ekchuah* is zoögeographically interesting because it suggests a direct derivation of the Cuban form from the Yucatan form. Another Cuban Attine ant, the large leaf-cutter *Atta insularis* Guérin, also restricted to Cuba among the Antilles, is similarly most closely related to *A. mexicana* F. Smith, which ranges over Mexico and Guatemala. Emery regarded *insularis* as a mere subspecies of *mexicana*.

APPENDIX B

A REVISION OF THE KNOWN NON-MOSAIC FEMALE AND WORKER ANOMALIES OF ANTS

Our knowledge of the anomalies of female and worker ants has grown very slowly. The first anomaly to be recognized was the ergatoid of *Polyergus rufescens* described and figured by Pierre Huber (1810, p. 251, Plate 2, Fig. 1). Forel (1874, p. 137), in his memorable work on the ants of Switzerland, cited three groups of anomalies, or 'intermédiares entre ♀ et ♂,' which he designated by the symbol ♀ ♂ and distinguished from "the monstrosities properly so called and from the hermaphrodites [our gynandromorphs and ergatandromorphs] by the complete symmetry of their organs." Of these intermediates he clearly described what we now call the ergatoids (Huber's "femelles aptères"), the pseudogynes, and the microgynes, but did not give them technical names. In his study of the Swedish ants, Adlerz (1886) encountered these same anomalies and published the earliest figures of the pseudogynes of *Formica sanguinea*.

During the last decade of the nineteenth and the first decade of the present century the anomalies and particularly the pseudogynes acquired a more general interest because they were cited by Weismann (1894, 1920) in his speculations on the germ plasm and in his controversy with Herbert Spencer. At that time Wasmann (1890, 1895, 1897) began to investigate the anomalies of ants and especially the pseudogynes, of which he published an elaborate account in 1909. In his paper of 1890 he recognized six classes of anomalies ("Zwischenformen") and in 1895 gave them special names. These are the ergatoid females (Huber's "femelles aptères"), the gynaecoid workers, the macroërgates, the pseudogynes, the microgynes (Forel's "petites femelles") and the "ergatogyne Mischformen." During the same period also, Emery (1894, 1894a, 1906, 1906a, 1907, 1910) and Forel (1895, 1904) discussed the bearing of these and certain other anomalies on the blastogenic and trophogenic origin of the female and worker castes. In a paper of 1908 and in my ant-book of 1910, sixteen aberrant forms were defined, but four of these, the macrogyne, micrergate, desmergate, and pterergate, should not be included among the anomalies because they are obviously normally recurring variations, or phaenotypes, traceable to deficient or abundant larval feeding. For the same reason the macrergate and gynaecoid should not be included, but I have retained them in the diagram (Fig. 18) because the former seems to represent an incipient stage in the development of the feebly feminized major worker and the latter a similar stage in the development of the ergatoid, cryptogyne, diacamatogyne, pseudodichthadiogyne, and dichthadiogyne, which have supplanted the winged female in several genera.

Emery saw little advantage in naming all the various anomalies, but now that so many of them have come to light the task of naming, defining, and classifying them can be no longer avoided. Definition, especially, is necessary because the loose employment of such terms as "ergatoid," "ergatomorph," and "ergatogyne" is causing considerable confusion in the taxonomic literature. The Greek names suggested are often long and awkward, but English equivalents would be even more cumbersome. While the list of anomalies given below seems to be complete to date, there are probably omissions among the cited examples, but a search through the entire literature for additional instances would consume much time and yield little. Probably, too, some of the categories which I have distinguished and named will be differently interpreted, "lumped," or even discarded by future investigators, but — *feci quod potui, faciant meliora sequentes*.

I. PARASITOGENIC ANOMALIES

(1)–(3). *Mermithergate*, *mermithodinergate*, *mermithogyne*. These anomalies are produced by Mermithid Nematodes in the gasters of workers, soldiers, and females of various ants belonging to the three subfamilies, Ponerinae, Myrmicinae, and Formicinae. I originally designated the infested worker and soldier of *Pheidole* as a "macroërgate" (1901), but as this term had been used by Wasmann (1895) for a different anomaly (see p. 83), I substituted "mermithergate" in 1907. The infested female of *Lasius* was called a "mermithogyne" by Mrázek in 1908. Vandel (1930b) has introduced the term "mermithostratiotes" for the mermithized soldier of *Pheidole*, but "mermithodinergate" is here suggested as more consonant with the names of the other soldier anomalies. "Mermithophore" (incorrectly "mermitophore"), employed by Escherich (1908) and some other German authors, is perhaps worth adopting as a general term for all the mermithized castes.

William Gould (1747, p. 63) was the first to find Mermithids in *Lasius flavus* females and to call attention to their lethal effect.¹ Since 1901, when I first found the mermithized specimens of the Texan *Pheidole commutata*, I have repeatedly referred to them and have described similar anomalies in several other ants, but have never been able to examine large series of any one species. It is not surprising, therefore, that some of my interpretations of these anomalies have been shown to be inadequate or untenable by two admirable investigators, Vandel (1927, 1930, 1930a, 1930b, 1934) and Gösswald (1929, 1930, 1932), who have had the good fortune to discover considerable areas in France and Bavaria in which the ant colonies

¹"Among other Incidents that tend to lessen and destroy Ant-Flies, it is observable that abundance of them are demolished by a white and long Worm, which is often met within their Bodies. You may frequently take three from the Insides of the large, but seldom more than one from a small Ant-Fly. These Worms lie in a spiral Form, and some of them may be extended Half an Inch."

were heavily infested with *Hexameris* sp., *Allomeris myrmecophila* Baylis, and probably other species of the old genus *Mermis*. Vandel has examined more than three hundred mermithized *Pheidole pallidula*, and Gösswald has listed more than twenty mermithized species. The latter found that in some colonies as many as 80 per cent of the individuals were mermithized, and that the parasites are therefore important agents in the extermination of their hosts.

The very young Mermithids enter either the larval or adult ant. Gösswald believes that entry is through the mouth and both he and Vandel are of the opinion that the young infected ant larvae always die before pupation. Vandel maintains that even in the case of the mermithodiner gates of *Pheidole* the young *Hexameris* enter the late larva or even the prepupa. The character of the modification manifested by the adult ant depends, therefore, on the caste of the infested larva. Gösswald has also discovered mermithized males, or mermithaners, of *Aphaenogaster subterranea*, *Myrmica scabrinodis*, *Lasius niger*, *alienus*, and *flavus*, but these are not modified. In all the infested workers, soldiers, and females the gaster is apt to be noticeably swollen, and in most species this is the only modification produced by the parasite. The mermithogynes of *Lasius* are usually brachypterous, with smaller heads and thoraces than the uninfested females, but the mermithogynes of the myrmicinae and Ponerinae show only an enlargement of the gaster. In the mermithized workers of *Camponotus* and of the large Neotropical Ponerinae, and in the soldiers of *Pheidole*, the head is small and more or less feminized and may possess one or more ocelli. As Vandel has shown (1930b), it was my failure to interpret this fact correctly that led me to adopt an untenable trophogenic explanation of these anomalies in my paper of 1928. I subjoin a list of the worker, soldier, and female ants now known to be parasitized by Mermithids.

Mermithergates: *Ectatomma tuberculatum* Olivier (Emery 1890, Wheeler 1930) and its var. *punctigerum* Emery (Wheeler 1930); *Paraponera clavata* Fabr. (Emery 1904); *Pachycondyla fuscoatra* Roger (Emery 1904), *striata* F. Smith (Strelnikov 1928); *Neoponera villosa inversa* F. Smith (Emery 1890, 1904; Wheeler 1928); *Odontomachus haematoda* L. (Emery, 1890, 1904, originally described as *O. microcephalus*); *chelifer* Latr. (Emery, 1890, 1904, originally described as *O. leptcephalus*); *Myrmica laevinodis* Nyl. (Vandel 1930b, Gösswald 1930, 1932), *ruginodis* Nyl., *rugulosa* Nyl., *scabrinodis* Nyl., and *schencki* Emery (Gösswald 1930); *Aphaenogaster subterranea* Latr. (Gösswald 1930); *Pheidole pallidula* Nyl. (Vandel 1926, 1927, 1930, 1930b); *Solenopsis fugax* Latr. (Gösswald 1929, 1932; Vandel 1930b); *Leptothorax acervorum* Nyl. (Gösswald 1930, 1932), *tubereum* Fabr., its subsp. *unifasciatus* Latr., *interruptus* Schenck, its var. *nigriceps* Mayr, and a var. near *nigriceps* (Gösswald 1930, 1932); *Tetramorium caespitum* L. (Gösswald 1932); *Plagiolepis pygmaea* Latr. Vandel 1930b); *Camponotus herculeanus* L. (Finzi 1930); *C. (Tanaemyr-*

mex) *pompejus cassius* Wheeler (Wheeler 1922); *consobrinus* Erichs. (Wheeler 1933); *punctulatus minutior* Forel (Wheeler 1929); *C. (Myrmothrix) abdominalis stercorarius* Forel (Wheeler 1933); *C. (Myrmophyma) claripes piperatus* Wheeler (Wheeler 1933); *Lasius niger* L., *alienus* Först., and *flavus* Deg. (Gösswald 1930, 1932); *Formica rufa pratensis* Deg., *sanguinea* Latr., *fusca* L., and *rufibarbis* Fabr. (Gösswald 1930, 1932).

Mermithodinergates: *Pheidole absurda* Forel (Emery 1890, 1904); *commutata* Mayr (Wheeler 1901, 1907, 1928); *pallidula* Nyl. (Wasmann 1909a, 1910, described as a new parasitic ant, *Ph. symbiotica*; Menozzi 1921; Vandel 1926, 1927, 1930, 1930b; Wheeler 1928); *gouldi* Forel (Wheeler 1928); *opaca* Mayr var. near *incrustedata* Forel (Wheeler 1928); *susannae articolor* Forel (Wheeler 1928).

Mermithogynes: *Myrmecia forficata* Fabr. var. *rubra* Forel (Wheeler 1933); *Aphaenogaster subterranea* Latr. (Gösswald 1932); *Myrmica scabrinodis* Nyl., *schencki* Emery *rugulosa* Nyl. and *laevinodis* Nyl. (Gösswald 1930, 1932); *Epimyrma gösswaldi* Menozzi (Gösswald 1930); *Lasius alienus* Först. (Mrázek 1908; Crawley and Baylis 1921; Donisthorpe 1921, 1927, 1927a; Gösswald 1929, 1930, 1932; Ezhikov 1934); *niger* L. (Gösswald 1932); *neoniger* Emery (Wheeler 1910a); *americanus* Emery (Wheeler 1928, Sturtevant 1931); *flavus* Deg. (Gould, 1747; Crawley and Baylis 1921; Gösswald 1930, 1932, Ezhikov 1934); *brevicornis* Emery (Wheeler 1928; *umbratus* Nyl. (Emery 1924).

(4)–(6). *Phthisergate*, *phthisodinergate*, *phthisogyne*. The first and last of these terms were suggested in my paper of 1907 for the pupal anomalies of *Pheidole* species attacked by the ectoparasitic larvae (*planidia*) of Eucharid Chalcidoids of the genus *Orasema*. Reëxamination of my figures shows that some of the infested prepupae were those of soldiers. These, therefore, may be designated as “phthisodinergates.” Male prepupae are also occasionally attacked and were therefore mentioned as “phthisaners” in 1907. Since the *Orasema* larvae attach themselves to the neck or thorax of their host, perforate the skin, and feed on the body juices, the anomalies, though symmetrical, have very small, shrunken heads and thoraces and eventually perish before reaching maturity.

Species of *Orasema* seem to be numerous and widely distributed in the Southwestern States, Middle America, and the Antilles. I have taken *O. viridis* Ashm. with *Pheidole instabilis* Emery in Texas, *O. wheeleri* Ashm., with *Ph. ceres* Wheeler and *O. coloradensis* Ashm. with *Ph. vine-landica* Forel in Colorado. In all these cases phthisergates were found in the nests and in *Ph. instabilis* also similar anomalies of the other castes. Mann (1914) has taken *O. tolteca* Mann in nests of *Ph. vasliti* Pergande var. *acolithua* Wheeler in Mexico and other species of *Orasema* in *Pheidole* nests in Lower California. Recently Dr. W. von Hagen sent me from the Galapagos Islands a portion of a colony of *Ph. williamsi* Wheeler infested with a small undescribed *Orasema* near *viridis*. There were several phthisergates among the brood. But *Orasema* also parasitizes other small

Myrmicine ants. I have taken *O. coloradensis* with *Solenopsis molesta validiuscula* Emery in Colorado, and Mann (1918) has recorded *O. minutissima* Ashm. from a colony of *Wasmannia auropunctata* Roger which was nesting in a hollow twig in Cuba. Clausen (1923) published a fine account of the life history of the Japanese *Schizaspidia tennicornis* Ashm., which is allied to *Oreasema* and parasitizes *Camponotus japonicus* Mayr. He figures a larva attached to a normal male pupa of the ant. Unlike *Oreasema*, *Schizaspidia* seems to produce no modifications of the pupae of any of the castes.

(7)–(9). *Micropseudogyne*, *mesopseudogyne*, *macropseudogyne*. The term "pseudogyne" was first given by Wasmann in 1895 to certain peculiar anomalies which sometimes occur in considerable numbers in colonies of *Formica sanguinea* and other species of *Formica* infested by Staphylinid beetles of the genera *Lomechusa*, *Atemeles* and *Xenodusa*. The larvae of these beetles devour the ant larvae, but the adults, which have tufts of golden, secretion-diffusing hairs (trichomes) on their abdomens, are fed and cherished by the ants. In 1909 Wasmann distinguished three classes of pseudogynes: micro- and mesopseudogynes, which are small or medium-sized, with very convex or humped mesonotum but without wings, and macropseudogynes, which resemble the normal females in size but have a broader and more convex mesonotum and short or vestigial wings. All of these anomalies have the appearance of abortive females and were supposed by Wasmann to have arisen from attempts on the part of the workers to convert female larvae into workers (meso- and micropseudogynes), or worker larvae into females (macropseudogynes). He devoted many years to the study of the beetles and the anomalies, but the origin of the latter is still an unsolved problem. Although it is generally agreed that the presence of pseudogynes in the colonies of certain ants, especially *Formica sanguinea* and *F. incerta*, must be due to *Lomechusine* infestation, the occurrence of pseudogynes in species never parasitized by the beetles shows that the same or very similar anomalies may be produced by other agencies.

The specimens of *Myrmica sulcinodoides* Emery and *schencki* Emery cited in my paper of 1907 as pseudogynes I now regard as ergatogynes. The following is a list of the ants, all members of the single subfamily Formicinae, in which these anomalies are known to occur:

Formica sanguinea Latr. (Forel 1874; Adlerz 1886; Wasmann 1895, etc.; Donisthorpe 1927; Gösswald 1932; subsp. *rubicunda* Emery (Muckermann 1904); subsp. *subintegra* Emery (Wheeler 1907); *rufa* L. (Forel 1874, Donisthorpe 1927); var. *rufopratensis* Forel (Gösswald 1932); *pratensis* Deg. (Wasmann 1895, etc.); *obscuripes melanotica* Emery (Wheeler 1907); *truncicola integra* Nyl (Wheeler 1907); *fusca* L. (Wasmann 1895, etc.; Gösswald 1932); *rufibarbis* Fabr. (Forel 1874); *neorufibarbis* Emery (Wheeler 1907); *cinerea* Mayr var. *neocinerea* Wheeler (not previously recorded); *schaufussi* Mayr var. *incerta* Emery (Wheeler

1907); *Camponotus* (*Tanaemyrmex*) *vicinus nitidiventris* Emery (Hollday 1903); *C. (Myrmobrachys) senex* Fabr. (Emery 1900); *C. igneus*? (Emery 1905, in Baltic amber); *Prenolepis henschei* Mayr (Wheeler 1904, in Baltic amber); *imparis* Say (not previously recorded).

II. NON-PARASITOGENIC ANOMALIES

A. *Anomalies of the Female*

(10). *Teratogyne*. This term is suggested for a few exceptional super-female forms which I have frequently referred to as "β-females" (Wheeler and McClendon 1903, Wheeler 1910, etc.). They occur as the regular winged females in the colonies of two of our North American ants, *Lasius (Acanthomyops) latipes* Walsh and *murphyi* Forel, and in the Japanese *L. (Dendrolasius) spathepus* Wheeler, but are so unlike the females of all other species of *Lasius* that they seem to belong to quite different genera. In fact, when Mayr first saw the *latipes* teratogyne he regarded it as the type of a new genus, *Acanthomyops*, and only later noticed that its worker was a *Lasius*. The two American teratogynes have a thick, elongate head, thorax, and gaster, thick, nodiform petiole, very broad and flat femora and tibiae, short basitarsi, clavate antennal scapes, and very pilose integument. The teratogyne of *spathepus* has a broad, subcordate head, thick petiole, and long legs, with the basitarsi as well as the femora and tibiae dilated and flattened. The female of *Bregmatomyrma carnosus* Wheeler of Borneo seems also to be a teratogyne, but its worker is unknown. The habitus of all four forms suggests that they arose as fertile polyploid mutations. The colonies of *latipes* not infrequently contain another type of winged female which I have called the "α-female," intermediate in structure between the teratogyne, or β-female and the female of *L. (Acanthomyops) claviger* Roger. I suggested in 1903 that this α-female might be a hybrid between *latipes* and *claviger*, and Tanquary (1911) has suggested that it might be a hybrid between *latipes* and *L. (A) interjectus* Mayr. It would not be necessary, however, to regard the α-female as a hybrid if the cytologist were able to demonstrate from a study of the eggs and larvae that it is a tetraploid, and the teratogyne an octoploid mutation. *Latipes* and *murphyi* are almost certainly temporary social parasites of *Lasius americanus* and *neoniger*, and *spathepus* is in all probability a parasite of one of the Japanese varieties of *L. (Chthonolasius) umbratus* Nyl.

(11). *Microgyne* (Wasmann 1895). The microgyne may be defined as a winged female of very small size but otherwise of normal structure. Such individuals, which sometimes are colored like the workers, occur as occasional anomalies, as complemental females in colonies containing normal mothers, or as the only type of female of their species. As occasional anomalies or as complemental females they have been recorded for the following ants:

Neoponera villosa inversa F. Smith (Emery 1904); *Stenammas westwoodi* Westw. (Forel 1874); *Myrmica scabrinodis* Nyl. (Adlerz 1886); *laevinodis* Nyl. (Forel 1874, Wasmann 1895, Donisthorpe 1927, Gösswald 1932), *ruginodis* Nyl. (Wasmann 1895); *Manica rubida* Latr. (Forel 1874); *Lepthorax acervorum* Nyl. (Forel 1874, Adlerz 1886, Wasmann 1895); *muscorum* Nyl. (Adlerz 1886); *emersoni* Wheeler (Holliday 1903); *tuberculum* Fabr. (Adlerz 1886); subsp. *unifasciatus* Latr. (Gösswald 1930a); *Formicoxemis nitidulus* Nyl. (Adlerz 1886; Wasmann 1895; Stumper 1918, 1921 etc.); *Plagiolepis pygmaea* Latr. (Reichensperger 1911); *Formica fusca* L. (Wasmann 1895, Donisthorpe 1927); *Formica pallidefulva nididiventris* Emery (Holliday 1903).

The microgynes of *Plagiolepis pygmaea* cited by Reichensperger are particularly interesting because they represent a transition to the forms in which the only females of the species are microgynes. The two specimens which he found were less than half as long as the normal female and not larger than the largest workers. They were both dealated and each was the sole mother of a colony. They must have been fecundated as they laid eggs from which workers developed. Reichensperger believes that these females represent "eine Neubildung und Abzweigung von der Art *pygmaea*," i.e., according to our interpretation, a fertile mutation. The stage in which the large, normal female is completely replaced by the microgyne has been reached in several of our North American ants, notably in the *microgyna* section of the genus *Formica* comprising *difficilis* Emery and the species which I have described as *microgyna*, *nepitula*, *adamsi*, *impexa*, *morsei*, and *nevadensis*. The females of some of these species are actually smaller than the largest workers. Microgynes are also the only females of *Aphaenogaster tennesseensis* Mayr and *treatae* Forel, of *Lasius* (*Chthonolasius*) *umbratus minutus* Emery, and of the European *L. (C.) carniolicus* Mayr. All of these forms are temporary social parasites. Among tropical ants I may mention a minute Pheidole (*Ph. nanodes* sp. nov.) of which I found three colonies nesting in hollow twigs in British Guiana. This species possesses females no larger than its soldiers and but little larger than its workers.

(12). *Micropterygine*. This name is suggested for certain anomalies, which, like the microgynes, may occur either as complemental females in colonies possessing normal macropterous females or as the only females of the species. Though somewhat smaller, they have a thorax of the normal female type, but narrower and with very small or vestigial, deciduous wings. Such anomalies are numerous and variable in size in the nests of the Congolese *Viticicola tessmanni* Stitz (Wheeler 1922), but constant in the Central American *Tapinoma ramulorum* Emery and its subspecies (Wheeler 1934) and *T. litorale* Wheeler var. *cubaënsis* Wheeler (Weber 1934). In *T. ramulorum* the female may be said to be distinctly dimorphic, since the micropterygine is not only smaller and paler but has a more rectangular head than the macropterous female. As the only

females of their respective species I have found micropterogynes in two Australian ants, *Monomorium* (*Parholcomyrrex*) *subapterum* Wheeler (1917) and an undescribed *Stigmacros*.

(13). *Ergatogyne*. The anomalies which I include in this category require more accurate definition. Wasmann's "ergatogyne Mischformen" (1895), Miss Holliday's "ergatoids" (1903), and especially Forel's "ergatomorphe Weibchen" (1904) comprise too many different forms and even some worker anomalies like the ergatoids *sens. str.* (*vide infra*). I suggest that the term "ergatogyne" be confined to the females which are apterous or possess mere abortive stumps of wings, have somewhat larger eyes than the worker, vestigial ocelli, and a thorax of the female type with distinct mesonotal, metanotal, and scutellar sclerites. This anomaly may vary considerably in the same species or colony in the size both of the body and the thoracic sclerites. It may be precisely like the winged female, except in lacking the wings (e.g., *Crematogaster atitlanica*) or it may differ from the ergatoid only in having a more feminine thorax (most species of *Lobopelta*). It may occur as a rare or frequent anomaly in colonies possessing alate females, or it may be stabilized as the only fertile female of the species.

Ergatogynes have been recorded as occasional anomalies or as occurring in the same colonies with normal females of *Plectroctena minor* Emery (Wheeler 1922); *cristata* Emery (1899), and *latinodis* Santschi (Santschi 1924); *Ponera coarctata pennsylvanica* Buckl. and *P. opaciceps* Mayr (Holliday 1903); *eduardi* Forel (Forel 1904); *Myrmica sulcinodoides* Emery and *schencki* Emery (Wheeler 1907); *Manica rubida* Latr. (Forel 1874); *Solenopsis fugax* Latr. (Gösswald 1932); *Monomorium* (*Notomyrmex*) *rubriceps cinctum* Wheeler (Wheeler 1917); *M. (Xeromyrmex) venustum* F. Smith and *M. (Lampromyrrex) orientale* Mayr (Emery 1898); *Crematogaster (Orthocrema) froggatti* Forel (Forel 1902); *sordidula* Nyl. (Forel 1874); *Leptothorax acervorum* Nyl. (Wasmann 1890, 1895); subsp. *canadense* Prov. (Holliday 1903); *emersoni* Wheeler (Holliday 1903); *tuberculatum unifasciatum* Latr. (Gösswald 1932); *Formicoxenus nitidulus* Nyl. (Adlerz 1884, 1886; Wasmann 1890, 1895; Stumper 1918, 1927, etc.; Gösswald 1932); *Myrmecina graminicola* Latr. (Emery 1916).

In the following species ergatogynes have replaced the winged females as the sole mothers of the colonies: *Champsomyrmex coquereli* Roger (Wasmann 1897); all the known species of *Lobopelta* except *langi* Wheeler (1923), which has well-developed wings; *Monomorium minutum ergatogyna* Wheeler (1904), *carbonarium ebeninum* Forel, and *floricola* Jerdon (Wheeler 1905); *Crematogaster (Apteroocrema) atitlanica* Wheeler (1936). The female *Lobopelta ergatogyna* Wheeler (1922) of the Congo, though wingless, has a well-developed female thorax and is therefore intermediate between *langi* and the other species of the genus.

B. Anomalies of the Monomorphic Worker

(14). *Macrergate* ("Macroërgate," Wasmann 1895). This was defined by Wasmann as a worker which approaches the female only in its abnormally large size, but in other respects, even in the size of the gaster, resembles the normal worker. In some cases the head is unusually large, so that in ants with monomorphic workers the macrergate might be regarded as a forerunner of the major worker. Macrergates are not uncommon in the colonies of many species of ants. They are cited in the literature as occurring in the following Myrmicinae: *Solenopsis fugax* (Gösswald 1932); *Myrmica scabrinodis* and *ruginodis* (Wasmann 1895); *Leptothorax emersoni longispinosus*, *curvispinosus*, and *obturator* (Holliday 1903); *Myrmecina graminicola* var. *striatula* (Emery 1916).

(15). *Gynaecoid* (Wasmann 1895). This is an individual differing from the ordinary worker only in the greater development of its ovaries. When colonies lose their queen she is often replaced by one or more of these individuals which become fertile through abundant feeding by their sister workers. Wasmann observed the development of single gynaecoids in motherless colonies of *Polyergus rufescens*, *Formica sanguinea*, and *F. rufibarbis* in artificial nests, and I have seen the emergence of gynaecoids of *P. lucidus* under similar conditions. Donisthorpe (1927) mentions gynaecoids of *Leptothorax acervorum*, and more recently Gösswald (1933) has observed such individuals in colonies of *L. tubercum unifasciatus* and *nigriceps* parasitized by the small Myrmicine ant *Epimyrma gösswaldi* Menozzi. The hitherto recorded offspring of gynaecoids have always been males, but Gösswald found those of his *Leptothorax* workers to be workers! We must conclude, therefore, either that these offspring were the result of unobserved matings with males or that the *Leptothorax* workers are able to produce workers parthenogenetically. In either case the observations are very significant in connection with several of the anomalies considered in the following paragraphs.

(16). *Ergatoid* (Wasmann 1895; "ergatomorphes Weibchen," in part, Forel 1895; "ocellate worker," Holliday 1903). The ergatoid, like the gynaecoid, is a fertile worker larger than the normal worker or even as large as the female of the species, and its ovaries, instead of beginning to grow during the imaginal stage, seem to be highly developed at the time of emergence from the pupa. It is, therefore, as Wasmann said, a "true queen in the guise of a worker." The thorax is of the worker type, the gaster usually is voluminous, and ocelli are often present. Ergatoids occur either as "sports" or, more frequently, as complementary queens in the following species:

Myrmica sulcinodis Nyl. (Wasmann 1895); *Monomorium andrei* fur Forel (Forel 1894); *sahlbergi* Emery (Emery 1898); *M. (Xeromyrmex) dichroum* Forel and *schurri* Forel (Forel 1902); *M. (Notomyrmex) howense* Wheeler (Wheeler 1927); *Leptothorax emersoni* Wheeler (Hol-

liday 1903); *tuborum unifasciatus* Latr. (Gösswald 1930); *Formicoxenus nitidulus* Nyl. (Donisthorpe 1927, Gösswald 1927); *Symmyrmica chamberlini* Wheeler (1904); *Harpagoxenus americanus* Emery (Sturtevant 1927); *sublaevis* Nyl. (Meinert 1891, Adlerz 1896, Viehmeyer 1906); *Crematogaster (Orthocrema) biroi* Mayr. var. *smythiesi* Forel (1911); *minutissima* Mayr (Holliday 1903); *Polyergus rufescens* Latr. (Huber 1870, Forel 1874, Wasmann 1895, Gösswald 1932); *breviceps* Emery and *lucidus* Mayr (Wheeler); *Rossomyrmex proformicarum* Arnoldi (1928). In the following ants ergatoids seem to replace the normal females: *Cerapachys (Parasyscia) peringueyi* Emery (Emery 1895a); *Eusphinctus steinheili* Forel and *hackeri* Wheeler (Wheeler 1918); *Plectroctena mandibularis* F. Smith, *relicta* Menozzi, and *conjugata* Santschi (Santschi 1924); *Paranomopone relicta* Wheeler (Wheeler 1915a), *Anochetus ghilianii* Spinola (Wasmann 1895), *Leptomyrmex erythrocephalus venustus* Wheeler, and *nigriventris tibialis* Emery (Wheeler 1934).

(17). *Physergate*. This term is proposed for the peculiar large workers detected by Emery (1896) in colonies of the Chilean *Brachymyrmex giardi* Emery and described as "large individuals with distended abdomen and regarded by me as soldiers with well-developed ovaries capable of producing eggs, but as having mainly the function of honey reservoirs." I have seen very similar forms among specimens of *B. minutus* Forel from Colombia. Emery regarded these anomalies as soldiers, erroneously I believe, because their thorax is stouter, with more distinct articulations, than that of the worker proper. In *Stigmacros termitoxenus* Wheeler (1936) from Western Australia the functional female of the colony is obviously a physergate and the replete workers are "plerergates." The latter, as in other ants (*Myrmecocystus*, *Prenolepis*, *Plagiolepis*, etc.), are merely normal workers with greatly distended crops and abdomens.

(18). *Pterergate* (Wheeler 1905). This is merely a worker with perfectly ergatomorphic thorax but with vestigial wings. I have seen a few examples of this very rare anomaly from a single colony of *Myrmica scabrinodis* Nyl. Donisthorpe (1927) mentions a pterergate of the same species and one of *Lasius flavus* Deg., and Ezhikov (1934) one of a *Myrmica* sp., with well-developed ovaries. A specimen of *Technomyrmex albipes* F. Smith, described and figured by Emery (1924), is the only other example of this anomaly known to me.

(19). *Diacammatoogyne*. I propose this name for the workers of the Ponerine genus *Diacamma*, of which winged females have never been seen (Emery, Forel, Wheeler 1915). In 1922 Chapman and I showed that the males of *Diacamma* copulate with the workers, and that this caste has therefore usurped the reproductive function. In 1934 Tulloch found that the workers throughout the genus possess very minute, deciduous fore wings, which had been overlooked by previous observers. He infers that

the entire absence of the usual winged female and the presence of vestigial wings among the workers suggests the possibility that a general suppression of the female phase has resulted in the production of a group of individuals in which the usual differentiation into the fertile winged and sterile wingless castes has failed to take place. If such has been the case, it is highly probable that all the workers are fertile and able to carry on the reproductive activities of the colony. The evidence given by Wheeler and Chapman would appear to indicate that only one individual was selected to carry on these activities at a time.

The males of *Diacamma*, which are nocturnal and are therefore frequently taken at lights, probably either mate with their sister workers soon after they emerge from the pupae or enter strange colonies to mate with their workers.

(20). *Cryptogyne*. This name may be applied to several genera of ants of which no differentiated females are known to exist and in which the males must mate with individuals indistinguishable from ordinary workers. These genera, with one exception, are all Ponerinae and include *Rhytidoponera*, *Streblognathus*, *Dinoponera*, *Leptogenys sens. str.* and *Stenomymex*. The exception is the Myrmicine genus *Ocymymex*, which is confined to South Africa. In all these genera, as in *Diacamma*, the entire worker population of the colony seems to be feminized, probably as an adaptation to peculiar mating habits, since the nuptial flight, so prevalent among other ants, is completely suppressed.

(21). *Protodichthadiigyne*. I have introduced this term for a highly fertile form intermediate between the ergatoid and dichthadiigyne. Smaller and less specialized than the latter, it is essentially a very robust worker, with large ovaries and gaster, and functions as the only female in the species of *Acanthostichus* (Emery 1895a, Bruch 1934) and *Eusphinctus* (e.g., *E. (Nothosphinctus) manni* Wheeler, 1918) among the Cerapachyinae, in *Onychomymex mjöbergi* Forel and *doddi* Wheeler (Wheeler 1916), and *Megaponera foetens* Fabr. (Arnold 1915) among the Ponerinae.

(22). *Dichthadiigyne* ("femelle dichthadiiforme" and "*dichthadioide*" Emery). This huge, wingless, and highly fertile form functions as the sole female of the colony in all ants of the subfamilies Leptanillinae and Dorylinae, comprising the genera *Leptanilla*, *Dorylus*, *Aenictus*, *Eciton*, *Cheliomymex*, and *Aenictogeton*. It might be described as a monstrous protodichthadiigyne, with the thorax simple and ergatomorphic, except in *Eciton sens. str.*, in which it is furnished with peculiar processes. The eyes are vestigial or absent, the mandibles falcate, the petiole often resembling that of the male, the gaster enormous with very large ovaries (many ovarioles) and specialized hypopygium. It is altogether more probable that this singularly specialized female has arisen by further development (intensified feminization) of the ergatoid or protodichthadiigyne than by transformation of the winged female. The

ergatoid, protodichthadiigyne, and dichthadiigyne thus represent so many phylogenetic stages in what Forel (1895) implied when he said that "ergatomorphism is undoubtedly a phenomenon of convergence, caused by the giving up of the nuptial flight and a resort to a purely subterranean mode of life." The absence of the nuptial flight is universal of course in all Leptanillinae and Dorylinae, and all species of Leptanilla and many of Dorylus, Eciton, and Aenictus are wholly or partly subterranean.

C. Anomalies of the Soldier.

(23). *Dinergate* (Soldier). It is difficult to study the soldiers of such genera as Eciton *sens. str.*, Pheidole, Pheidologeton, Oligomyrmex, Acanthomyrmex, Cyathomyrmex, Atta, Zatapinoma, Machaeromyrma, and Colobopsis without acquiring the conviction that they are monstrous forms of mutational origin which could survive only in a peculiar social environment. This conviction is deepened by the further consideration that they are obviously specialized major workers which have arisen independently in genera with polymorphic workers. They are lacking in four whole subfamilies, the Leptanillinae, Pseudomyrmecinae, Cerapachyinae, and Ponerinae, rare in the Dorylinae, Dolichoderinae, and Formicinae, and numerous only in certain often unrelated genera of Myrmicinae. It is also interesting to note in connection with the mosaic anomalies of *Acromyrmex octospinosus* that the soldiers are characterized mainly by modifications confined to the head and mandibles, and that these parts usually exhibit a distinct feminization, which, incidentally, is also apparent even in the major workers of many species. As previously stated, the feminization may, perhaps, also involve a greater development of the ovaries, but this is a matter for further investigation, as is also the question as to whether the soldier may actually usurp the reproductive function in motherless colonies.

(24). *Pterodinergate*. This term is proposed for the soldier analogue of the pterergate. Only one example of this anomaly is known to me, a soldier of *Cryptocerus aztecus* Forel with vestigial fore wings (Wheeler 1905). The body is that of a perfectly normal soldier, but the symmetrical, veinless winglets indicate feminization.

(25). *Dinergatogyne*. I have given this name to the anomaly described and figured by Emery (1904) in *Pheidologeton diversus* Jerdon, which seems to be a combination of soldier and ergatogyne (see p. 44 and Fig. 14).

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