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Vol. XXIII, 1907.

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ERRATA.

Page 287, line 25, for PODICIPETIDÆ read PODICIPITIDÆ.
" 294, " 18, for autonymic read tautonymic.
" 295, " 32, for 1840 read 1855.
" 297, " 4 from bottom, for Gray (1840) and by elimination read the founder.
" 305, " 8, " " for Sharp read Sharpe.
" 306, " 9, " " for 189 read 187.
" 308, " 10, for *fisheri* read *fischeri*.
" 312, " 2, from bottom, for 1840 read 1855.
" 317, bottom line, for *Anucylocheilus* read *Ancylocheilus*.
" 323, line 13, for **Dendragopus** read **Dendragapus**.
" " " 14, " *Dendragopus* read *Dendragapus*.
" 327, " 21, " *Zenaidura* read *Zenaida*.
" 334, " 24, " Latham read Pennant.
" 237, " 7, " *Pyrhula* read *Pyrrhura*; also on p. 238, lines 9 and 11 from bottom.
" 348, " 7 from bottom, for 1852 read 1859.
" 350, " 5, for CABANIS read HARTLAUB.
" 367, " 18, " *Xipholema* read *Xipholena*.
" 371, " 8 from bottom for *Motacilla* read *Muscicapa*.
" 373, " 22, for 1848, i, 98, read 1847, i, 323.
" 375, " 13, " 17 read 77.
" " dele line 14 and insert: 2 congeneric species. Type, *C. stellaris* Licht., as designated by Gray in 1855.
" 440, " 23 and 32 for Tomochic read Temochic.
" 442, lines 13 and 14, for limestone schists, read limestone and schists.

BULLETIN

59. 57, 96: 11.51

Article I. — THE POLYMORPHISM OF ANTS, WITH AN
ACCOUNT OF SOME SINGULAR ABNORMALITIES
DUE TO PARASITISM.

By WILLIAM MORTON WHEELER.

PLATES I–VI.

The study of sex determination among organisms — a subject obviously
included under the greater problem of the origin of variation, since sexual
dimorphism is the most striking and constant form of intraspecific variability
both in animals and plants — and the related but much more restricted prob-
lem of polymorphism, have of late attracted the attention of many biologists.
A perusal of some of the literature bearing on these subjects, however, has
convinced me that the simplicity of the questions involved may have been
overestimated.   That this is especially true of polymorphism as manifested
in the social insects, will, I believe, be evident from a consideration of the
facts recorded in the following paper.   At any rate, it will not be a difficult
task to show that we are still very much in the dark concerning the funda-
mental causes of the differentiation of one sex into several distinct phases,
and, while it may be urged that the problem of polymorphism as it is pre-
sented by the social insects, may be more complicated than that of sex, on
purely a priori grounds the opposite view would seem to be the more prob-
able, for polymorphism is undoubtedly not only a more restricted phenome-
non but one of much more recent phylogenetic and ontogenetic development,
and hence presumably dependent on conditions both more specialized and
more amenable to observation and experimentation.   While the observa-
tions recorded in this article suggest both the need of experiment and some
of the points at which the problem is open to this method of investigation,

they indicate with equal force that the causes of polymorphism may be so recondite as to give little encouragement to the crude physiological methods at present available.   In other words, much water will have to flow through the biological mill before we possess sufficient knowledge of the physiological chemistry of such small organisms as the insects, to enable us to determine the exact nature of the subtle influences that decide whether an ant or bee shall become a queen or a worker.

The following observations relate to some of the unusual or pathological individuals occasionally found in ant colonies, and referable, with more or less probability, to trophic disturbances induced by specific parasites.   The inferences from these cases have a value approaching those derived from experiment, since the phenomena make their appearance only under very definite circumstances.

PART I. OBSERVATIONS.

1. THE PARASITISM OF ORASEMA AND OTHER CHALCIDIDÆ ON ANTS.

A. *Orasema viridis Ashmead.*

This beautiful Chalcidid is abundant in Texas in the nests of *Pheidole kingi* André subsp. *instabilis* Emery, but only from May to September.   For this reason I failed to notice it till May 25, 1903, about six weeks before I moved from Austin to New York, although during my four years' residence in Texas I had examined hundreds of *instabilis* nests during the autumn, winter, and early spring months.   I was so much impressed with the peculiar behavior of the *Orasema* and the ants that I devoted to the subject every available moment of the short remainder of my sojourn in Texas, but the necessary preparations for my departure, the intense heat, which sets in during the month of May, and a peculiar misunderstanding of the conditions under which the *Orasema* develops, seriously interfered with the progress of my work.   It was only after I had left Texas that the study of preserved material led me to what I believe to be a correct interpretation of the life history of the insect.

Before describing the *Orasema* and its development it will be necessary to say something about the host.   *Ph. instabilis* is a common ant in central Texas and certain parts of Mexico, at least as far south as the State of Morelos, where I have taken it near Cuernavaca.   It forms populous colonies which prefer to nest under stones in sunny places.   In central Texas

it is often found in bottom lands and waste places where the soil is rich and supports an open growth of grasses and especially of Crotons (Croton texensis and C. monanthogynus). It is a harvesting species and stores the flat chambers of its nests with innumerable seeds collected from all the plants in the neighborhood. Like other harvesting ants, however, it does not confine itself to a vegetable diet, but eagerly seizes on any insect food that may fall in its way.

In common with other members of the great genus Pheidole, instabilis presents four phases known as the soldier, worker, female and male respectively. The soldier is 4–4.5 mm. long. The shape and extraordinary proportions of its head are shown in Plate I, Fig. 1, and Plate V, Fig. 63 o. Its gaster is black and shining, the mandibles and clypeus are dark brown, the remainder of the head, thorax and appendages reddish brown.

The head is subopaque and elaborately sculptured as shown in the figure. The worker (Pl. I, Fig. 7, and Pl. V, Fig. 63 c) is only 1.5–1.8 mm. long. It is shining throughout, and of a dark brown or black color with yellowish appendages. The female (Pl. I, Fig. 8 and Pl. V, Fig. 63 a), which measures 5.5–6 mm., is dull black, with the legs, antennæ, mandibles and anterior half of the head yellow. The wings (removed in the specimen figured) are yellowish hyaline with pale veins. The male (Pl. I, Fig. 9 and Pl. V, Fig. 63 e) is a much smaller and more graceful insect than the female, measuring only 4–4.3 mm. Its head and gaster are black, its thorax and appendages sordid yellow, the former with pale sutures. Its wings resemble those of the female.

While instabilis agrees with its congeners in having the four phases just described, it differs from all except à small group of North American species of Pheidole in presenting in every well-developed colony a series of individuals intermediate in size, structure, and sculpture between the soldier (Pl. I, Fig. 1) and the worker (Pl. I, Fig. 7). This series, which is very complete in large colonies, is represented in Plate I by a few selected individuals (Pl. I, Figs. 2–5 and Pl. V, 63 r). The occurrence of such intermediate forms, though well-known in some other genera of ants, like Solenopsis and Camponotus, is so unusual in the genus Pheidole as to call for the special explanation which I shall attempt to give in the sequel. It is also an interesting fact that the organs are not always reduced in size in strict correlative proportions as we descend the series of intermediate individuals from the soldier to the worker. As shown in Plate I, Figs. 5 and 6, for example, the antennal scape may be of the same length in two individuals which differ considerably in the size of the head. Or, again, as shown in figure 4, the scape may be longer in one individual than in others with larger (Pl. I, Fig. 3), or smaller heads (Pl. I, Figs. 5 and 6).

The acme of the colonial activities of *Ph. instabilis* is attained during
the latter part of May and the first weeks of June. Then the nest is full
of eggs, larvæ, pupæ, and callows of all the castes and presents a bewildering
appearance, owing to the fact that the brood is not assorted according to
ages, as in many ants, but lies jumbled together in the different chambers
and galleries. The functions of the workers and soldiers are clearly dis-
tinct. The former are far and away the more numerous, and notwithstand-
ing their diminutive size, may be said to manage the affairs of the colony.
They collect the seeds and dead insects and drag them to the nest. They
excavate the galleries, feed the brood and carry even the huge female larvæ
and pupæ from chamber to chamber and assist the callows in escaping from
their pupal envelopes. The soldiers act as carvers, or trenchers of the
tough insects and hard seeds brought in by the workers. Their powerful
mandibles admirably fit them for this office and for guarding the nest.
They are often seen to form a stationary cordon about the brood and the
callows in the chambers. They are never seen to eat the seeds or insects
which they cut up for the other members of the colony but are fed on liquid
food regurgitated by the workers. They are very stolid and inactive, very
rarely leave the nest and never assist in carrying the larvæ and pupæ about.
Their heads are so large in proportion to their bodies that, when dropped
on their backs on a smooth surface like that of glass or polished wood, they
are often unable to right themselves and may die standing on their heads.
The intermediates are much more active and may be seen to leave the nest,
collect food, carry larvæ and, in short, perform all the duties of the workers
which they approach in their smaller size and smoother sculpture.

The larvæ of all the castes are provided with several pairs of flexuous,
anchor-tipped dorsal hairs, by means of which they may be temporarily fixed
to the earthern walls of the chambers or to the rough surfaces of the stone
covering the nest. While in this position they are fed by the workers with
bits of crushed seeds or insect fragments in the same way as the larvæ of the
Ponerine ants. At least the younger larvæ of the males and females, how-
ever, appear to be fed largely, if not exclusively, with regurgitated liquid
food.

Ph. instabilis is very common at Austin in the bottom and along the
banks of a small limestone cañon, known as Shoal Creek. There, during
May and June, 1903, I found a great number of colonies. Several of them
were confined in artificial nests of the Fielde pattern and one was kept
under observation till the latter part of September. I also preserved whole
colonies in alcohol after killing them in water heated to 80° C.

Fully half of the colonies examined were found to contain the peculiar
parasites which Dr. W. H. Ashmead has kindly identified for me as *Orasema*

viridis Ashm., a Chalcidid fly originally described from specimens collected at large by Mr. E. A. Schwarz near San Diego, Texas.

The genus *Orasema*, which belongs to the subfamily Eucharinæ, was originally established by Cameron on *O. stramineipes* from Panama, in the 'Biologia Centrali-Americana'.[1] According to Ashmead,[2] this genus is characterized by the possession of 10-jointed antennæ in both sexes, and in having the right mandible two-toothed, the left with a single tooth, and both mandibles acute and falcate at their tips. The genus appears to be largely restricted to tropical and subtropical America but extends somewhat further north in the western than in the eastern portion of the United States.

The female *O. viridis* (Pl. I, Fig. 10, and Pl. V, 63 *m*) measures 2.5–3· mm. and is deep metallic green with the clypeus and thoracic dorsum more golden and the gaster blue or violet. The head, thorax and petiole are uniformly and densely punctate, the gaster very smooth and shining. The legs are honey-yellow, excepting the middle portions of the femora, which are metallic green, and the terminal tarsal joints, which are black. The antennæ are black, with the basal joints yellow, as are also the mandibles, tongue, and palpi. The wings are very clear and iridescent. The epinotum and scutellum together form a rounded cone through which the thorax reaches a greater vertical diameter than it does elsewhere. The male (Pl. I, Fig. 11, and Pl. V, Fig. 63 *n*) is distinctly smaller than the female (2.3–2.5 mm.) and differs in having a much longer petiole, a much shorter and smaller gaster, and longer and thicker antennæ, with the basal joints black instead of yellow.

On opening a large *instabilis* nest a dozen or more of these superb insects may be seen lying on their sides or creeping about among the ant-brood (Pl. V, Fig. 64). It is also easy to recognize their pupæ, white when young or nearly ready to hatch, of a dull blue-green color when mature, scattered among the larvæ and pupæ of their hosts. Such nests present a splendid appearance, reminding one of a jewel casket in which the sapphires and emeralds are represented by the *Orasema*, the pearls by the larvæ and pupæ, the opals by the iridescent wings of the parasites and of the male and female ants, the garnets and bits of jet by the glistening black and red seeds and the red heads and black bodies of the soldiers.

As soon as the nest is disturbed, the workers seize the *Orasemœ* and their pupæ and, even at the risk of neglecting their own brood and callows, carry them bodily to a place of safety. In artificial nests this great fondness for the *Orasema* may be witnessed at one's leisure. The adult parasites are not only carried about and continually licked and fondled, but are also fed

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[1] Vol. I, 1883–1900, pp. 104, 105, pl v, fig. 20, pl. vi, fig. 18.
[2] Classification of the Chalcid Flies or the superfamily Chalcidoidea. Mem. Carnegie Museum, No. 4, 1904, pp. ix, 225–551, pll. xxxi–xxxix.

by regurgitation as if they were workers. They usually submit to these effusive attentions passively, but at times they may be seen to struggle and disengage themselves from the embraces of their hosts. When fully mature both sexes of the *Orasema* become highly phototropic and endeavor to escape from the dark nest to the open air and sunshine. The ants, however, redouble their attentions and carry them back to the dark chambers. Although usually aided by the workers in hatching from their pupæ, the *Orasemæ* themselves often remove the pupal envelopes from their antennæ by rubbing them with their fore legs, and, though fed by the ants, they sometimes visit and partake of the sugar in artificial nests. They spend much of their time in lying on their sides among the ant larvæ and pupæ. While the workers thus appear to be infatuated with their beautifully sculptured and brilliantly colored parasites, the latter are not sufficiently hypocritical to feign any interest in their hosts. They are, in fact, interested only in the ant brood and, as I shall show, only in a certain portion of the brood.

As several successive broods of *Orasema* pupæ appeared and hatched in my artificial nests, I was sure that the larval stages must also be present. These stages, it would seem, should be readily detected, but for a long time I was completely misled in my search for them, and even after I had found them, I was deceived by their appearance. This arose partly through certain prepossessions based on analogy with what I had read about other Chalcidids, and partly through the confusion produced by the high degree of polymorphism in the *Pheidole*. As nearly all Chalcidid larvæ are internal parasites in other larvæ, I was under the impression that the *Orasemæ* also start their life cycle within the larvæ of their hosts, and certain peculiarities in the *Orasema* larvæ merely tended to strengthen this prepossession. The great number of larval and pupal forms of the ant added to my confusion, especially as some of their larvæ differed in shape according to their feeding. Thus for a time I regarded certain small, spherical, sexual larvæ, fed with regurgitated liquids, as the young larvæ of *Orasema*. It was not till after I had left Texas and had nothing but preserved and stained material at my disposal that I succeeded in gaining a clear idea of the early larval stages of the parasite.

I have not seen the eggs of *O. viridis* after oviposition, but only the very young larvæ. Dissection of the female shows that, as we should expect in a parasite, the eggs are extremely numerous and minute. The mother insect, when she comes to oviposit, exercises a very careful selection among the ant brood. In the first place she has nothing to do with the *instabilis* larvæ but directs her attention to the pupæ. In the second place she selects, as a rule, only the pupæ of the soldiers, males, and females. The small worker pupæ would not furnish sufficient food for her larvæ. In the third place she selects

only pupæ at the very critical moment when they have just been stripped of their larval skin by the workers and are, therefore, little more than semipupæ, for obviously at this moment the cuticle is thinner and will be more easily pierced by the young *Orasema* larva than during the preceding or succeeding stages. And in the fourth place, she does not lay her eggs at random anywhere on the body of the semipupa but carefully selects one of four regions near the head. Usually she places the egg on the sternal surface just beneath the still very short, incurving legs of the semipupa but occasionally it is placed on the back of the neck between the head and the prothoracic segment, or on the right or left side of the neck beneath the corresponding prothoracic leg. These regions would seem to be singularly appropriate, both because the cuticle of the semipupa is extremely thin and readily punctured by the parasitic larva at these points, and also because the egg or resulting larva, especially when it is covered with the overlapping appendages of the semipupa, is not so readily brushed or licked off by the *instabilis* workers. I believe that the danger of detaching the egg is very great and this, together with the other special requirements above enumerated, may account for the fact that comparatively few of the great number of *Orasema* eggs ever complete their development.

Further reflection shows still greater appropriateness in the time and place selected for oviposition by the mother *Orasema*. In the sexual semipupæ of *instabilis*, and especially in those of the soldiers, the small anterior end of the body is destined to grow very rapidly and to undergo extraordinary changes in structure. For this purpose carefully elaborated liquid substances of a very high nutritive value are suddenly propelled into the anterior portion of the body of the semipupa, which therefore appears tense, clear, and transparent in this region, while the abdominal region is full of opaque, nonmetabolized fat cells. The parasitic larva is thus situated from the first at a point where it has ready access to a rich food supply and is able to grow with surprising rapidity.

The instinct that leads the mother *Orasema* to oviposit with such precision is not, however, infallible. As the number of soldier and sexual pupæ in an *instabilis* colony is always very limited compared with the number of worker pupæ, the *Orasema*, impelled, apparently, by the need of getting rid of her eggs, sometimes oviposits on the latter, although even in such cases also, she chooses the cervical and sternal region. The interesting consequences of this instinct aberration will be considered in a later paragraph.

Several of the youngest *Orasema* larvæ seen are represented in Plate II, Figs. 30–35. They are extremely small — less than .1 mm. in length — and of a dark brown color. The head is distinct and furnished with short,

acute mandibles; the body consists of a number of sharply marked segments, of which the anterior are longer and broader, the posterior smaller and often telescoped into one another so that it is difficult to ascertain their exact number.   There are probably three thoracic and ten abdominal segments. The terminal segment bears a pair of hair-like cerci.   Were it not for the absence of legs, these larvæ might be regarded as campodeiform and likened to the youngest stages of such parasites as the Stylopidæ and Meloidæ. Several of my preparations show these larvæ attached to the necks of worker semipupæ or pupæ, as represented in Plate II, Fig. 13.   Twice I have seen a pair of these larvæ attached symmetrically on the sides of the same pupa. In other cases they were found on the nuchal or sternal surfaces.

So different are these minute, sharply segmented and dark brown larvæ from those of other Chalcidid larvæ, of which I have seen descriptions or figures, that I should never have regarded them as belonging to the life-cycle of *O. viridis*, had I not seen stages like those represented in Plate II, Figs. 14 and 15.   These figures represent semipupæ of *instabilis* soldiers with undoubted *Orasema* larvæ .3 mm. in length attached, in the one case to the sternal surface between the pro- and mesothoracic segments, in the other to the nuchal surface.   In Plate II, Fig. 14, the larva has its long axis at right angles to that of its host; in Fig. 15 the parasite and host are similarly oriented.   The dark brown segments of the younger larva are represented in both cases by dark bands on a yellowish white background.   The cerci have disappeared.   The larvæ have plunged their mandibles into their host and have begun to absorb its juices, and this has led to a separation of the more heavily chitinized sclerites and great expansion of the intervening membranes.

Succeeding stages in the growth of these larvæ are shown in Plate II, Figs. 16, 17 and Plate V, Fig. 66.   All of these represent female semipupæ of *instabilis*, and in each the *Orasema* larva, which is attached as in Fig. 14, has attained a length of .7–.9 mm.   In Plate II, Fig. 17, which is drawn from a stained and mounted specimen, the parasite is somewhat shrunken through dehydration and clearing, but in Fig. 16, from an alcoholic specimen, the skin of the larva is smooth and tense.   The fact that all traces of the dark bands have disappeared is probably due to the intervention of an ecdysis between this stage and the one represented in Figs. 14 and 15.   It was stages like Figs. 16 and 17, which were first seen in my artificial nests and led me to an erroneous interpretation.   The parasite in this stage was yellowish and semitransparent, while the semipupa to which it was attached was opaque, waxy white and more or less shriveled.   The larva, moreover, seemed to make its appearance very suddenly, and this, coupled with the fact that the ants kept licking it till its surface glistened with saliva, led me to

suppose that it had reached its full growth within the ant-larva and was just breaking through the integument on the nuchal or sternal side. I saw the workers, which evinced the greatest interest in this phenomenon, pull the larva away from the semipupa and throw aside the latter, now reduced to a sickly mass, though still retaining enough of the contents of the abdomen and of its original form to be recognizable as a pupa, notwithstanding the fact that the head, as shown in Fig. 16, was much smaller than in the corresponding stages of the nonparasitized soldiers and females.

Shutting my eyes to the correct interpretation of the above stages as indicating that the larva was ecto- instead of entoparasitic, I stained and mounted *in toto* whole series of soldier and female larvæ and young pupæ in the hope of finding the *Orasema* larvæ prior to their eruption. This search proved, of course, to be futile, and I was baffled until I accidentally found the crucial stages represented in Plate II, Figs. 13 to 15.

The growth of the parasite, after it has plunged its mouthparts into the integument of its host, must be extremely rapid. I doubt whether the stages above described require more than a couple of days for their completion. Such rapid growth, however, is not surprising when we consider the accessibility and high nutritive value of the food on which the larva subsists.

As soon as the full-grown *Orasema* larva has been separated from its prey, it begins to pupate. Occasionally the ants are either unable or neglect to detach the parasite. In such cases, two of which are shown in Plate II, Figs. 18 and 19, the larva begins to pupate *in situ*. It undergoes an ecdysis in which it is undoubtedly assisted by the workers, and then appears as a short, thick-set semipupa, slightly constricted just in front of the middle of its body. Another ecdysis seems to follow almost at once, leaving the semipupa covered with a peculiar envelope studded with large blisters, or pustules. These are arranged segmentally in regular rows along each side of the body but are absent in the middorsal and midventral regions. I am unable to assign any function to these singular organs, which in *O. viridis* disappear with the semipupa stage. On focussing through the pustulate envelope the semipupa is seen to present the appearance of Fig. 20 (Pl. II). The imaginal head, with its large eyes and antennæ, is embedded in a hood-like prothoracic mass; the legs and wings are clearly indicated. A little later the pustulate envelope is shed and the complete, pure white pupa of the *Orasema* is seen enclosed in a thick membrane (Pl. II, Fig. 22) which, in the intersegmental regions of the abdomen, is thrown into prominent transverse welts. The color, which now gradually deepens, becoming first blackish and then metallic green, is dimmed by the rather opaque, white pupal envelope (Pl. II, Fig. 23). Soon after this stage is reached, the

insect hatches.   The changes from the stage represented in Fig. 21 to that
of Fig. 23 can hardly require more than three or four days.   If this and my
estimate concerning the rate of development in the earlier stages is correct,
we must suppose that *O. viridis* completes its entire life-cycle, from the egg
to the imago, in less than a week or ten days.   Similarly rapid developments
are known to occur in other Chalcidids, as I infer from the following
statements in an interesting paper published some years ago by Howard[1] :
"Ratzeburg has shown that in Europe *Pteromalus puparum* occupied on one
occasion from June 11 to July 14 to undergo its entire transformation from
egg to adult — thirty-seven days; but in this country Webster has recorded
an instance (Insect Life, I, 225) in which the eggs of the same parasite were
laid August 9, the adult insect developing August 27 — seventeen days later.
Hubbard has noted (Fourth Report U. S. Ent. Com., p. 103) that the' egg
of *Aletia xylina* gives forth the adults of *Trichogramma pretiosa* on the
seventh day after it was stung by its parents.   *Euplectrus comstockii* has
been shown by Schwarz to develop from egg to adult in Alabama in mid-
summer in seven days."

    There can be little doubt that in a state of nature the male and female
Orasemæ leave the nest very soon after hatching and mate in the open fields.
This is indicated by their strong positive phototropism.   The fertilized
females then seek out fresh *Pheidole* nests in which to lay their eggs.   In
one of my artificial nests, however, which was kept from June 19 to Septem-
ber 20, three successive broods of *Orasema* were noted, the last disappearing
about a week before the latter date.   In this case, unless the offspring arose
from parthenogenetic eggs, the males and females must have mated in the
nest.   Both in this and other cases it was found that the adult *Orasemæ*,
after they had remained in the nest for several days, were killed and dis-
membered by the workers, as though the parasites had at last been recog-
nized as predatory aliens.   This slaughter, however, may have been due
to other causes, since the workers also killed and dismembered their own
females and ultimately reared only workers and intermediates, probably
because these required less nourishment.   Such conditions point to a
deterioration of the colony and are frequently observed in artificial nests
inadequately furnished with food.   Similar behavior on the part of workers
may be seen in other species of ants when the food supply becomes insuffi-
cient or is no longer palatable.   Under these circumstances I have seen
Camponotus ferrugineus workers kill and dismember their soldiers and
Myrmica brevinodis workers do away with their males.

    Before concluding this account of the relations of *O. viridis* to *Ph.*

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[1] The Biology of the Hymenopterous Insects of the Family Chalcididæ.   Proceed. U. S.
Nat. Mus., XIV, 1892, pp. 567–588.

instabilis, it will be necessary to return to the worker semipupæ on which the *Orasema* occasionally deposits her eggs. In such cases the young larvæ of the parasite must be very inadequately fed and probably soon die and fall off, leaving their hosts in a depleted condition but still able to pass on to the pupal stage. Now in all the nests infested with *Orasema*, and only in these, I have found a number of peculiar pupæ like those represented in Plate II, Figs. 24–26 and Plate V, Fig. 65 *s*, and differing from the normal worker pupæ (Fig. 27) in several important characters. They are smaller, of a waxy white color, with more decided intersegmental constrictions and are broad behind and very narrow anteriorly. The head is remarkable for the very small size of the brain and eyes and the situation of the latter on distinct stalks. The mandibles, too, are abortive. The resemblance of the head to depleted female pupæ, like the one represented in Fig. 16, is very striking. The thorax is extremely slender and the gaster has a high fold on each side, and in balsam preparations (Pl. II, Fig. 26 and Pl. V, Fig. 67 *i*) is seen to contain a number of large urate masses in the *corpus adiposum*. In many specimens the gaster is concave ventrally, with its tip turned upward and forward. Although these singular pupæ are carefully cleaned by the workers and kept with the normal individuals, they never succeed in hatching. After lying in the chambers for many days without even acquiring a deeper color of the body or pigment in the eyes, they are either carried to the refuse heap or eaten by the workers. I am convinced that these extraordinary pupæ, which may be called *phthisergates*, have arisen from worker semipupæ that have had part of their juices sucked out by *Orasema* larvæ, so that only enough formative material was left to produce pupæ with very defective head and thorax and hence quite unable to develop as far as the imaginal instar. It is interesting to note that these microcephalic, microphthalmic, and stenonotal characters represent merely greater diminution of the similar characters of the normal workers as compared with the more macrocephalic, macrophthalmic, and eurynotal soldiers and females. The theoretical bearings of these conditions will be considered in the latter part of this article. The depleted semipupæ of the *instabilis* females and males, which like the phthisergates are incapable of further development, may be called *phthisogynes* and *phthisanērs* respectively.

In this connection the question naturally suggests itself: are the intermediates between the *instabilis* workers and the soldiers due to similar depletion in their semipupal stages? In other words, do the intermediates arise from soldier semipupæ that have been partially exhausted by *Orasema* larvæ prematurely torn from their hosts by the workers? I am inclined to answer this question in the negative, for reasons to be given in the sequel.

After finding *O. viridis* so common in the nests of *Ph. instabilis* I was

naturally led to look for it in the company of other Texan species of *Pheidole*. This search soon revealed the fact that the parasite can make its home also with other ants of this enormous genus.   June 16, I found a single female *viridis* in a flourishing colony of *Ph. dentata* Mayr at Alice, Texas, which is only about ten miles east of San Diego where the types of the parasite were originally captured by Schwartz.   *Ph. dentata*, it should be noted, is a carnivorous species with sharply separated soldier and worker castes, as represented in Plate III, Figs. 37 and 38.   June 21, I again found at New Braunfels, Texas, a colony of this same *Pheidole* containing a few female pupæ of *O. viridis*.   In this colony, which was kept for some weeks in an artificial nest, four phthisergates made their appearance.   One of these is represented in Plate II, Fig. 28.   They differed considerably in form from the *instabilis* phthisergates and had slightly pigmented eyes.   These organs, however, as well as the head and thorax were notably reduced as compared with those of the normal worker pupa, which is essentially like that of *instabilis* (Pl. III, Fig. 27).

A little later in the month (June 24), I came upon a colony of a hitherto undescribed *Pheidole* (*Ph. sciophila* sp. nov.), containing a number of imagines and pupæ of *O. viridis*.   This ant, like *Ph. dentata*, has no forms intermediate between the soldiers and workers.   It is a rare species, nesting under stones in rather damp, shady places in the vicinity of Austin.   These observations prove that *O. viridis* is not confined to a single host ant but has international relations with a number of species of the genus *Pheidole* in central and southern Texas.   It may be expected to occur also in the nests of *Ph. crassicornis*, *Ph. hyatti*, *Ph. morrisi*, etc.   Still another observation goes to show that the parasite is not confined to Texas, but is also probably widely distributed through Mexico.   In my collection there is a female specimen of *O. viridis* taken August 4 at Tuxpan, in the state of Jalisco, by Mr. J. F. McClendon.   As this specimen was found in a bottle containing a mixed lot of ants comprising three species of *Pheidole*, besides some species of other genera, I am unable to refer it to a particular host.

B.   *Orasema coloradensis Ashmead.*

During August, 1903, while collecting ants in Colorado, I came upon a second species of *Orasema*, which Dr. Ashmead has identified for me as *O. coloradensis*, in the nests of two very different species of ants.   One of these is a larger and usually darker form of a small *Solenopsis*, which I take to be *S. molesta validiuscula* Emery, the other *Pheidole vinelandica* Forel.

O. coloradensis (Pl. I, Fig. 12 and Pl. V, Fig. 68 *m*) is of about the same size as *O. viridis*, but is readily distinguished by its longer, lower, and

smoother thorax, and less prominent scutellum and epinotum. In coloration it is like the Texan species, except that the thorax is less golden above and the mesopleuræ are more shining. In the male the petiole is shorter and the tibiæ are more or less infuscated. The mature pupæ of the two species are very readily distinguished by the character of the last pupal envelope. In *coloradensis* (Pl. IV, Figs. 53 and 54) this is pustulate like the semipupal envelope of *viridis,* the pustules appearing on the abdomen as dilatations in the transverse intersegmental welts above described for *viridis.* Then, too, the pupal skin of the Colorado species has a series of large pustules extending along the middorsal line of the epinotum and abdomen and about the front of the pronotum where they are completely absent in *viridis.*

O. *coloradensis* was first noticed August 3, in a colony of *S. validiuscula* (Pl. V, Fig. 68) at Manitou. The ants with their brood were confined in a bottle for the purpose of rearing some of their numerous male and female pupæ. The tiny workers were seen to spend much time shampooing an adult female *Orasema.* Later other females and a few males hatched in the nest and were cared for by the ants like members of their own species. In the course of a few days two of the *Orasemæ* were found dead on the refuse heap, one having been decapitated and shorn of its legs and wings. This led me to wonder whether the *Solenopsis* workers which are themselves parasitic and feed on the larvæ and pupæ of other much larger ants of the genera *Formica, Myrmica, Cremastogaster,* etc., are quicker than the species of *Pheidole* to recognize the *Orasemæ* as aliens after they have been reared. August 11, while collecting near Broadmoor, south of Colorado Springs, I found two more infested *Solenopsis* colonies. This *Solenopsis* was paler than the form taken at Manitou, and in this respect approached the typical *molesta.* In one of these colonies I counted twenty pupæ and adult *Orasemæ.* At the same time I noticed that there were very few male and female pupæ of the ant. The other colony, which contained nearly as many of the parasites, was living in cleptobiosis with a large colony of *Formica ciliata* Mayr. As *S. molesta* has only one form of worker, and this of minute size compared with the males and females and since, moreover, the males and females of O. *coloradensis* are of about the same size as the corresponding sexes of the ant, I infer that the larvæ of the parasite must feed exclusively on the sexual forms, while the tiny workers enjoy complete immunity from their attacks.

In the same locality in which I saw the *Solenopsis* nests above described, and on the same day, I found two colonies of *Pheidole vinelandica* containing the same species of *Orasema.* One of these colonies was taken alive and placed in a Fielde nest. A careful examination of the worker brood revealed the presence of a single phthisergate with somewhat pigmented eyes and

very similar in shape to those of *Ph. dentata* above described.   This phthiser-
gate had neither hatched nor changed its appearance by August 29 — 15.
days later.   It eventually disappeared (eaten by the workers?).   The
colony was kept for several weeks but as no second brood of *Orasema*
appeared, it was abandoned.   August 20 I found near Beaver Ranch, south-
east of Colorado Springs, a third infested *vinelandica* colony.   This two was
kept in an artificial nest, but the observations revealed nothing that has not
been recorded for *Ph. instabilis* and *O. viridis.*   According to Forel, *Ph.*
vinelandica occasionally produces intermediates between the typical soldiers.
and workers, but although I have collected many colonies of this ant in
different parts of the United States, I have seen only the typical soldiers.
and workers.

The foregoing observations prove that *O. coloradensis*, like *O. viridis,*
does not confine its depredations to a single host ant.   It may be said to be
even more catholic in its habits, since it not only infests a species of *Pheidole*
but also attacks ants belonging to the very different genus *Solenopsis.*   The
number of colonies observed was not sufficient to show which of these genera
represents the original and more frequent host, but, judging from analogy
with *O. viridis* and the next species to be considered, there can be little
doubt that this is *Ph. vinelandica.*   *O. coloradensis* probably occurs also in
the nests of *Ph. pilifera* var. *coloradensis* and *Ph. ceres*, both common ants
in the neighborhood of Colorado Springs and other localities of about the
same altitude.

C.   *Orasema wheeleri Ashmead.*

A third species of *Orasema*, which Dr. Ashmead will describe as *O.*
wheeleri, was found July 14, 1902, on Keesy's Ranch at Fort Davis, Texas,
in the nest of *Pheidole ceres* Wheeler.   This ant is a small, dark colored
species which makes obscure nests in the shade of the cotton-woods (*Pop-*
ulus fremonti) and garners the woolly seeds of these trees.   The *Ora-*
sema was seen in only one of the nests, and though about a dozen pupæ
were found among the ant brood, only a single mature specimen, which
happened to be a female, could be secured.   It measures 2.7 mm. and
closely resembles *O. viridis*, especially in the shape of the scutellum and
epinotum, but the thorax is broader and stouter.   The last pupal envelope,
like that of *viridis*, is without pustules, though it has strong intersegmental
welts in the abdominal region.

I have examined many colonies of *Ph. ceres* near Fort Davis and in
various Colorado localities without finding any intermediates between the
soldiers and workers.   In the single colony infested with *O. wheeleri*, how-

ever, there were several of these annectant forms. As this could hardly be a mere coincidence, we must assume that there is some connection between the existence of intermediates and the presence of the parasites.

D.   Other Chalcidid Ant-Parasites.

From the observations recorded in the above paragraphs we may safely conclude that the remaining *Orasema* species, of which quite a number have been described by Cameron, Howard, and Ashmead, are parasitic on ants and have life-cycles analogous to that of *O. viridis*. Still other genera, however, of the enormous family Chalcididæ, contain ant-parasites and these, though very imperfectly known, may be passed in review before I proceed with an account of a very different type of parasitism. For the sake of convenience we may distinguish three groups of cases, first the ant-parasites of the sub-family Eucharinæ exclusive of *Orasema*, second those belonging to other subfamilies, and third, the cases too imperfectly known to be referred to any particular genera.

Among students of the Chalcididæ the opinion seems to have been gaining ground that the Eucharinæ, which according to Ashmead's recent synopsis (l. c. pp. 266–270) comprise some 25 genera, are largely, if not exclusively ant-parasites. Ashmead says that in this group "are found some of the most singular looking and wonderfully shaped Chalcids known, the structure of the thorax, and particularly of the scutellum, being most wonderfully and curiously modified and developed; and this development, in connection with the brilliant metallic green and blue colors of its members, makes the group the most striking and attractive of any in the subfamily. Some of the species are now known to be parasitic upon ants and probably the whole group attacks these insects. In temperate regions the family is poorly represented, but in tropical countries, where ants most abound and flourish in enormous colonies, these insects are not rare and seem to have reached a very highly specialized development." This extraordinary specialization, which at once reminds us of that obtaining in other highly myrmecophilous and termitophilous groups, like the Paussidæ among beetles and the Termitoxeniidæ among Diptera, etc., is clearly shown in the figures of some of the more striking Eucharine genera reproduced in this article (Pl. IV, Figs. 56–62).

The first to describe a Eucharine parasite on ants was Forel.[1] On opening the huge cocoons of one of the Australian bull-dog ants (*Myrmecia forficata*) he found several metallic green and coppery pupæ about a cm. long, which a year later were described and figured by Cameron[2] as those

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[1] Un parasite de la Myrmecia forficata Fabr.   Extr. C. R. Soc. Ent. Belg., I Fev. 1890, 3 pp.
[2] Hymenopterological Notes. Mem. Lit. Phil. Soc. Manchester (4), IV, 1891, pp. 182–194. 1 pl.

of *Eucharis myrmeciæ*. These pupæ, according to Forel, were "couvertes d' aspérités et de boursoufflures," probably analogous to the pustules above described for the pupa of *Orasema*. He concluded that the *Eucharis* attacks the *Myrmecia* larvæ, but after what I have said of *Orasema* it is more probable that the Chalcidid attacks the semipupa or pupa of the ant after the cocoon is spun and encloses both host and parasite.

In the same paper in which the *Eucharis* is described, Cameron describes a member of another genus, *Chalcura bedeli*, which was taken in nests of the Algerian *Myrmecocystus viaticus*.

Wasmann in his 'Verzeichniss', published in 1894,[1] cites as the only Chalcidids known to occur with ants the two preceding species described by Cameron and a *Chalcura* sp. which was "bred from cocoons of *Formica rufa* at Prag (Polak)."

Another Chalcidid belonging to the subfamily Eucharinæ and closely related to the preceding, was accidentally detected in some alcoholic material of *Camponotus ligniperdus* var. *novæboracensis* Fitch, collected August 12, 1904, on a bare slope of the Porcupine Mountains in northern Michigan by Mr. Otto McCreary and sent me for identification by Dr. Charles C. Adams. Two of the worker cocoons, measuring respectively 6.5 and .7 mm., were found to contain pupal parasites, which Dr. Ashmead has identified for me as *Pseudochalcura gibbosa* Provancher. In one of the cocoons, represented in Plate II, Fig. 29, there were two pigmented and therefore nearly mature pupæ, lying face to face near the anterior pole, while the remains of the ant pupa, which they had consumed, were crowded against the black meconial spot at the posterior pole. The other cocoon contained four unpigmented pupæ. It would seem that the Chalcidid larva must attach itself to the *Camponotus* larva and wait till it has spun its cocoon, before devouring the host. As the ant is an unusually large species compared with the parasite, several of the latter can obtain sufficient nourishment even from a single worker and need not, like *Orasema*, attack the still larger intermediate, soldier, and female brood.

I have received with some miscellaneous ants (*Formica fusca* var. *neorufibarbis*, *Myrmica brevinodis*, etc.) collected by Mr. H. Viereck, on the summit (11,000 ft.) of the Las Vegas Range, New Mexico, a single male specimen of a *Eucharis* (Pl. IV, Fig. 62), which is in all probability an ant parasite, although I am unable to refer it to its precise host.

In the discussion following a paper read several years ago by Ashmead before the Entomological Society of Washington,[2] Howard called attention

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[1] Kritisches Verzeichniss der Myrmekophilen und Termitophilen Arthropoden. Berlin, 1894.
[2] Notes on the Eucharids found in the United States. Proc. Ent. Soc. Wash., II, 1890–92, pp. 354–358.

to the fact "that in the collection of St. Vincent Chalcids sent to Professor Riley from Cambridge University there is a specimen of *Kapala furcata* Fabr. which bears in its jaws a medium sized red ant." Events have shown that Howard was probably correct in supposing this peculiar Chalcidid to be an ant parasite. Dr. O. F. Cook informs me that he has bred a specimen of an allied genus, *Isomeralia coronata* Westwood (Pl. IV, Figs. 58 and 59), from a cocoon of the Guatemalan kelep (*Ectatomma tuberculatum* Oliv.), and Dr. Ashmead tells me that in his opinion *Kapala floridana* (Pl. IV, Figs. 56 and 57) is probably parasitic on the Florida harvester (*Pogonomyrmex badius* Latr). He also assures me that the type of *Pseudometagia schwarzi* was taken in an ant-nest near Washington, D. C.

To the foregoing observations on Eucharinæ I am able to add some notes on a parasite belonging to another subfamily of Chalcididæ. As stated on p. 2, I failed to find *Orasema* in nests of *Pheidole instabilis* except during the summer and late spring months. At other seasons I often took a species of the subfamily Asaphinæ, namely, *Pheidoloxenus wheeleri* Ashmead (Pl. III, Fig. 36), an exquisite little Chalcidid which runs about in the dense throng of *Pheidole* workers like one of their number. It is not easily detected, as it resembles the workers in its small size (1 mm.) and in being subapterous or practically wingless. Its head is very wide, with a concave occiput and 9-jointed antennæ inserted near the oral border. These appendages are very robust, and have a club-shaped funiculus terminating in a broad flat joint. The epinotum is very short, the wings are represented only by the tegulæ and minute vestiges of the alar membranes. The surface of the body is smooth and shining. The head is deep metallic blue, with green cheeks and yellow mandibles; the antennæ are yellow at the base, with the large apical and adjacent transverse joints black. The thorax is green with golden reflections, the epinotum more blue green, the tegulæ violet. The abdomen is metallic green with a broad violet band across the posterior portion of each of the basal segments. The legs are fuscous, with yellow knees, tarsi and trochanters.

I have not been able to learn anything concerning the development of this insect. According to Ashmead the vast majority of Asaphinæ are parasites "upon plant lice, Aphididæ, and upon the bark lice, Coccidæ," but this cannot be the case with *Pheidoloxenus* since this insect is a regular myrmecophile, and *Ph. instabilis* does not, like our northern species of *Lasius*, cultivate aphids and coccids in its nests. During the autumn and winter months I have occasionally seen the *instabilis* workers carrying small pink larvæ about in the chambers. These were certainly not a portion of the ant brood, but whether they were the larvæ of *Pheidoloxenus* or not, I have been unable to determine. On one or two occasions I have seen as many as six or eight

of the little Chalcidids in a single nest.   A careful search will probably show that they are even more abundant.

In the literature I find the following scattered references to Chalcidid ant-parasites:

Fritz Müller, according to Sharp,[1] mentions a South American Chalcidid which attacks the larvæ of *Azteca instabilis* in its nests in the Cecropia trees. When the parasite pupates it suspends itself, by its posterior end, from the walls of the chambers like a butterfly chrysalis.

Wasmann[2] cites an observation of Brauns who found a Chalcidid in one of the nests of a South African subspecies of *Pheidole megacephala*.   When the nests were disturbed the workers were seen to carry the parasites, which probably devour the brood, to a place of safety.

A larva found by Rupertsberger attached to a large *Myrmica* larva, and mentioned by Wasmann in his 'Verzeichniss' (*l. c.*, p. 169) as possibly an Ichneumonid, was probably a Chalcidid.

Perhaps no single group of parasitic insects has greater surprises in store for the future investigator of habits and development than the Chalcididæ. This is indicated not only by the fragmentary materials collated in the preceding paragraphs, but more especially by the splendid researches of Bugnon,[3] Marchal,[4] and Silvestri,[5] on the extraordinary polyembryony of the Encyrtinæ.   These and future researches in the same direction may be expected to bring about many radical changes in the present taxonomy of the enormous family Chalcididæ.

2.   THE PARASITISM OF MERMIS IN ANTS.

Five years ago (June 3, 1901), I found at New Braunfels, Texas, on a shady hill that slopes to the lovely sources of the Comal River, two medium-sized colonies of *Pheidole dentata* var. *commutata* Mayr.   They were under stones about sixty feet apart.   One contained ants of the typical dark variety of the species, while both the soldiers and workers of the other colony were decidedly paler.   On lifting the stones my attention was arrested by several very large and conspicuous individuals with huge gasters, moving about among the workers and soldiers of normal dimensions.   Unfortunately I failed to preserve any living specimens at that time but collected instead a

[1] Cambridge Natural History.   Insects, Vol. I, 1895, p. 550.
[2] Die Psychischen Fähigkeiten der Ameisen.   Zoologica, Heft 26, 1899, pp. 1–132, Taf. i–iii.
[3] Recherches sur le Développement postembryonnaire, l'anatomie et les mœurs de l'Encyrtus fuscicollis.   Recueil Zool. Suisse, V, 1891, pp. 435–534, pl. xx–xxv.
[4] Recherches sur la Biologie et le Développement des Hyménoptères Parasites.   I, La Polyembryonie Spécifique ou Germinogonie.   Arch. Zool. Expér. (4), II, 1904, pp. 257–335, pl. ix–xiii.
[5] Sviluppo dell' Ageniaspis fuscicollis (Dalm.) Thoms.   Rendic. R. Accad. Lincei, XV, 1906, pp. 650–657.

number of specimens in alcohol. These were described in a paper published during the autumn of 1901.[1] In this paper the huge workers were called macroërgates, but for reasons presently to be given they may be more aptly designated as mermithergates.

Plate III, Figs. 37–40 represent, drawn to the same scale, the dorsal view of the soldier and worker, which in *Ph. commutata* are not connected by intermediates, and the dorsal and lateral views of a large mermithergate. The length of normal workers does not exceed 3 mm. Many of them are scarcely more than 2.5–2.8 mm., which was the length of Mayr's type specimens from Florida. The largest mermithergates, however, measured fully 5 mm., while the smaller ones varied from 4 to 4.5 mm. Thus the volumes of the normal workers and the extreme mermithergates, had they been of the same shape, would be in the ratio of 27 to 225, but the gasters of the latter were so enormously distended that the ratio must have been 27 to at least 300. In other words, the large mermithergates were some twelve times as large as the normal workers. They were even larger than the soldiers, which measure about 4 mm., though in this case, owing to the great size of the head in the latter caste, the difference is less conspicuous. The largest mermithergates differ from both soldiers and workers in usually possessing three ocelli, of which the anterior is the largest, and resemble the soldiers in the structure of the thorax (Pl. III, Fig. 39).

Examination of one of these extraordinary individuals, even with a good pocket lens, reveals the cause of the great enlargement of the gaster. Through its distended intersegmental membranes the coils of a parasitic worm may be distinctly seen. My friend Professor T. H. Montgomery, to whom I sent a few of the mermithergates, writes me that the parasite is a species of *Mermis*. Its exact location among the ant's viscera, *i. e.*, whether it occupies the lumen of the enormously distended ingluvies, or lies in the body cavity outside of the alimentary tract, is not easily determined. From careful dissection of a single large specimen (the one represented in Pl. II, Fig. 39) I concluded that the *Mermis* lies within the ingluvies, or crop. In this specimen the head of the parasite extended forward through the postpetiolar and into the petiolar segment, and thus occupied the attenuated neck of the crop and the most favorable position for securing the ingurgitated food of its host. The fat-body and reproductive organs seemed to have disappeared completely and the walls of the enormously distended crop were practically in contact with the walls of the gaster. The large mermithergate shown in Figs. 39 and 40 contained only a single closely convoluted *Mermis*, which was fully 50 mm. long, or ten times the length of the ant. One

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[1] The Parasitic Origin of Macroërgates among Ants.   Amer. Naturalist, XXXV, Nov. 1901, pp. 877–866, 1 fig.

individual, dissected by Professor Montgomery, contained two somewhat smaller parasites, together with many of their eggs. I have seen specimens containing as many as six and eight parasites. The specimens dissected by Professor Montgomery were "either fully mature or in what von Linstow[1] calls the second larval stage, which is, however, really the immature stage."

While it is certainly somewhat singular that a species of *Mermis* should occur in ants, even greater interest attaches to the cases under discussion, on account of the manifest effects of the parasite on its host. The fact that all the mermithergates are of huge size as compared with the normal workers is remarkable, for, on first thought, one would certainly expect an animal infested with such large parasites to be stunted, or, at any rate, below the average stature of the species. This paradoxical condition of the mermithergates of *Ph. dentata* is easily understood, however, when we make due allowance for certain peculiarities in the behavior of ants. In the first place, it is obvious that the parasite must enter the body of the ant while she is still a larva. This was proved by the fact that two of the large mermithergates were callows, one of them still very soft and pale yellow, the other with harder integument but without the deep coloration of the mature workers. Such huge parasites could scarcely have made their appearance in ants so recently escaped from their pupal envelopes. But even if there had been no callows among the mermithergates, the truth of the above statement. would still be patent, both because the mermithergates were all infested while none of the normal workers were found to contain parasites, and because the structure of an ant is, of course, fixed in the pupal stage and cannot be subsequently increased to the dimensions of the insects under consideration.

It is evident, furthermore, that the larger stature, which is very apparent not only in the distended gaster of the mermithergates, but also in all the other parts of the body, can have its origin only in an unusually large amount of food consumed during the growth period of larval life. Now *Ph. commutata* is exclusively carnivorous and feeds at least its older larvæ with pieces of insect food. The workers cannot, therefore, accurately regulate the amount of food consumed by each larva, and it must be possible for larvæ infested with parasites, and hence presumably endowed with a more voracious appetite, to consume a greater quantity and hence produce larger pupæ and imagines than unparasitized individuals. If this inference is correct we must suppose that the stimulus to the increased feeding, *i. e.* the appetite, which results in the larger stature of the mermithergate, resides

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[1] Das Genus Mermis. Arch. f. mikr. Anat., LIII, 1898, pp. 149–168, Taf. viii.

in the larva and cannot be accurately controlled by the worker ants. The theoretical bearings of these considerations will be postponed to a subsequent portion of this article.

Two years later (June 21, 1903), on revisiting New Braunfels I found on the very same hill slope two more colonies of *Ph. commutata* containing mermithergates. On this occasion every effort was made to secure the entire personnel of the colonies in a living condition. One colony, confined in too small a bottle, died before I reached my home, the other was successfully transferred to an artificial nest. On examining the asphyxiated colony I found it to consist of many female larvæ and pupæ, a few soldier and several worker larvæ and pupæ, and a dozen mermithergates which varied considerably in size from individuals but little larger than the workers and without ocelli, to huge individuals like those taken two years previously. These large mermithergates possessed ocelli, a thoracic structure like the soldiers and a rich red color like the females. Three pupal mermithergates were also found but their gasters were not distended. The earth of the nest contained two free *Mermithes*.

The personnel of the living colony comprised six adult and three pupal mermithergates, a winged and several pupal females, and a number of larval, pupal and adult workers and soldiers. All of the pupal mermithergates, like those in the asphyxiated colony, had the gaster in proper proportion to the remainder of the body, so that they appeared to be merely gigantic worker pupæ. One of these hatched June 24, the two others July 2. As soon as they had hatched, their gasters began to enlarge rapidly and in the course of a few days the coils of the *Mermis* became visible through the distended pellucid membranes between the widely separated segmental sclerites. Evidently the parasites were present but of very small size in the pupæ and grew very rapidly during the callow stages of their hosts while the chitinous investment of the gaster was still soft and distensible. This sudden growth of the parasite is probably due to the rich and abundant food with which the recently hatched callow is supplied by her sister workers.

This colony of *Ph. commutata* was kept under observation till August 12. Of the nine mermithergates which it contained, three had died by June 27, and three more by July 19, while the nest was being transported in my hand luggage from Texas to Colorado. Of the surviving three, two died July 25 and 30 and the last August 12. Hence, at least one of these parasitized ants must have lived fully six weeks in the imaginal stage. In all of these cases the *Mermis* died within its host and both were carried to the refuse heap by the workers. One of the dead mermithergates had burst and the loops of the parasite protruded. In a state of nature it probably escapes from its host at this or an earlier stage, and enters the soil for the purpose

of laying its eggs. Or the eggs may, perhaps, be discharged into the alimentary tract of the ant and escape with its excrement. It is not difficult to conceive how they may find their way into the young larva. They may adhere to the body of the workers till gathered up by their strigils or tongues and transferred to the buccal pocket. Thence they could be fed inadvertently to the larvæ, either with the regurgitated liquid food or with pieces of insects that had been malaxated and distributed by the workers.

The living mermithergates were easily studied in my artificial nest and exhibited several interesting peculiarities in their behavior. On exposure to the sunlight they hurried, like the females, to the dark chamber, thereby evincing a much higher degree of negative phototropism than the workers and soldiers. They never carried the brood, although even the soldiers were seen to do this occasionally. They never fed the larvæ, workers or females, and, had earth been present in the nest, it is very probable that they would never have shown any inclination to excavate. They never visited the manger of the nest but were fed exclusively by regurgitation. As befitted animals containing such enormous parasites they were in a chronic state of hunger. It was impossible at any time to uncover the nest without finding one or more of them either being fed by a worker or eagerly begging for food. And as soon as one was offered food, three or four of them would rush up and put out their tongues for a share of it. Once I saw a single worker trying to feed five of her huge parasitized sisters simultaneously. While imbibing their food the mermithergates stridulated, either continuously or at regular intervals. Sometimes they were so impatient to be fed that they would hold down a worker's head with their large fore feet and compel the little creature to regurgitate. Under these circumstances the larvæ must have been poorly fed, for the insatiable mermithergates continually intercepted the workers on their way from the manger to the brood chamber. The mermithergates in my artificial nest may have been massacred or starved by the workers and did not die merely as a result of parasitism for when the food supply becomes insufficient the tiny *Ph. commutata* workers, like those of *Ph. instabilis,* probably rid the colony of voracious and nonproductive mendicants, even when these belong to their own species. Apart from their chronic hunger, the mermithergates exhibited no abnormal traits of behavior directly attributable to parasitism. They ran about with as much alacrity as the workers and soldiers. Their other peculiarities, such as their strong negative phototropism, their dependence on regurgitated food, and the absence of the foraging instinct, like their large size, their ocelli and rich red color, may be regarded as female or soldier traits.

Mermithergates occur also, I believe, in two other Texan ants belonging

to the genus *Cremastogaster* (*C. minutissima* Mayr and *C. victima missouri-ensis* Pergande). Both are small honey-yellow species which nest under stones in shady places. From a colony of *minutissima* taken June 3, 1901, in the very same locality at New Braunfels as the parasitized colonies of *Ph. commutata*, I took three large workers which were described and figured by Miss Holliday as ergatoid females.[1] 'These measured 4.3–5 mm. whereas the normal workers of this species do not exceed 2 mm. They had small ocelli and greatly enlarged gasters, and though no parasites were found in them, it is not improbable that they contained young specimens of *Mermis* that may have been overlooked when Miss Holliday made her dissections for the purpose of ascertaining the condition of the ovaries.

In a lot of *C. victima missouriensis* collected by Miss Augusta Rucker at Paris, Texas, I have recently found four individuals resembling the *minutissima* mermithergates described by Miss Holliday. They measured 3.2 and 4.5 mm. respectively, although the normal workers measure only 2–2.5 mm. None of these mermithergates has ocelli. In the two largest specimens the gaster is very voluminous but seems to contain no parasites, and the mesonotum is unusually large and convex, so that the thorax resembles that of a pseudogynic *Formica*.

Recourse to the literature shows that Emery had seen mermithergates in certain Central American and South American ants as early as 1890. In his paper on a collection of these insects from Costa Rica he describes and figures two odd specimens of *Pheidole absurda* Forel from Alajuela.[2] They measured 7.25–7.75 mm., although the normal worker of this species measures only 2.75–3 mm. They had huge, elongated gasters, vestiges of ocelli, and a thorax similar to that of the soldier, but in the shape of the head they resembled the worker caste. He did not observe that they were parasitized but regarded them as "parthenogenetic females." In the same paper, and from the same locality, he also described three specimens of *Odontomachus hæmatodes* with a huge gaster and a minute ocellus, as possibly a new variety (var.? *microcephalus*).[3] In this connection he mentions three other similar cases: an *O. chelifer* (var.? *leptocephalus* Emery) from Rio Grande do Sul, a *Neoponera villosa inversa* from Venezuela, and another tropical American ant, *Ectatomma tuberculatum*. In all of these cases the great volume of the gaster was naturally attributed to an unusual develop-ment of the ovaries.

Since reading my paper Emery has reëxamined his specimens and finds

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[1] A Study of Some Ergatogynic Ants. Zool. Jahrb. Abth. f. Syst., XIX, 4, 1903, pp. 311, 312, 16 figs.

[2] Studii sulle Formiche della Fauna Neotropica. Boll. Soc. Ent. Ital. Ann., XXII, 1890, p. 49, pl. v, figs. 10 and 11.

[3] Emery calls attention to the fact that this form of *hæmatodes* had been previously seen by Roger.

that in all of them the enlargement of the gaster is due to *Mermis* parasites.[1]
In addition to the above mentioned forms he also describes mermithergates
in *Pachycondyla fuscoatra* from Bolivia, and in the well-known South Amer-
ican *Paraponera clavata.*

Both Emery (*l. c.*, p. 591) and Wasmann[2] object to my applying the
name macroërgates to the *Pheidole* workers parasitized by *Mermis.* The
latter author, who coined this term, applies it to "abnormally large workers
with normal development of the gaster," and in another place,[3] to "individ-
uals which approach the females abnormally in the size of the body, but in
other respects (even in the development of the gaster) are normal workers."
I am quite willing to be corrected, but it should be pointed out that the gaster
in the adult pupæ of the mermithergates of *Ph. commutata,* and probably
also of the other species, is normal in its proportions, the enlargement being
confined to the imaginal instar. It is merely a mechanical dilatation such
as is seen in the repletes, or plerergates of the honey ants (*Myrmecocystus*)
and in Wasmann's "gynæcoid workers," which are merely workers whose
ovaries contain mature eggs. Although the dilatation in these different
cases is due to the difference in the contents of the gaster (liquid food, ovaries
or parasites) the morphological results are the same. Even had the objection
to the use of the term macroërgates been based on the presence of the ocelli,
it would not have been greatly strengthened, for these may be absent in
specimens to which the term would seem to be applicable. In my opinion
it may be permissible to distinguish three classes of macroërgates, namely:
macroërgates proper (as defined by Wasmann), mermithergates, and
plerergates.

Emery adds to his observations an interesting hypothesis. He says (pp.
601–603): "I believe that the singular microcephaly of the worker ants
infested with *Mermis* may be attributed to a general law of growth of the
ant-body and perhaps also of the insect body in general.

"We must assume with Wheeler that the parasitic nematode enters the
ant larva and has already attained a considerable size before its metamor-
phosis. As long as the larva retains its cylindrical, spindle, or clavate shape,
the worm, no matter whether it is injurious to the growth and development
of the larva or not, will have only a slight influence on the external form.
But as soon as the constriction appears at the anterior end of the abdomen
during the preparation for the pupal stage, and the whole worm is relegated
to the latter region, the defective nutrition of the larva makes itself felt in

[1] Zur Kenntniss des Polymorphismus der Ameisen. Zool. Jahrb. Suppl., VII, 1904, pp.
587–610, 9 figs.
[2] Ameisenarbeiterinnen als Ersatzköniginnen. Mittheil. d. schweiz. entomol. Ges., XI, 2,
1904, p. 67.
[3] Die ergatagynen Formen bei den Ameisen und ihre Erklärung. Biol. Centralbl., V, 1895,
p. 606.

the anterior region, and especially in the head, while the abdomen is unduly expanded by the worm. Since the thorax of the normal worker, as a por-tion of the body already reduced to a minimum, is incapable of further diminution, it remains unchanged. In the head, however, the results of imperfect nutrition are more strongly felt; there is no longer sufficient sub-stance to form the powerful muscles that go to move the mandibles, so they remain small, and with them the muscle-containing occipital portions of the head are unable to acquire their normal proportions. Hence the char-acteristic narrowing in the posterior region of the head.

"The explanation of the appearance of the ocelli and the greater devel-opment of the eyes in the parasitized microcephalæ seems to me to present more serious difficulties. It might be supposed that, owing to the small development of the occipital region of the cranium, a greater quantity of ectodermal substance had remained over and thereby established more favorable conditions of space and nutriment for the formation of the eyes. and ocelli. Unfortunately, the preservation of the dry specimens did not permit an accurate anatomical study of the organs contained in the cranium. I feel certain, nevertheless, that we are here dealing with something like a general law.

"The effect of the parasite on the formation of the body, and especially of the head, is not always equally intense: the extent of this effect depends. on the relations of the size of the worm to that of the ant. The larger the worm, and hence the greater the volume of the abdomen of the ant, the greater the aberration in the head. For this reason *Pheidole* shows the greatest alteration, then come the two species of *Odontomachus* and *Pachy-condyla fuscoatra*, then *Neoponera inversa*, and finally *Paraponera*; in this. gigantic ant the increase in the abdomen had no appreciable influence on the shape of the head."

This adaptation of Roux's 'Kampf der Teile in Organismus' to the mermithergates seems very plausible at first sight, but on closer examina-tion it proves to be less satisfactory as an explanation of the phenomena. It would seem to be necessary to reach some definite conclusion, first, as to the morphological relations of the mermithergates to the normal castes of the species, and, second, as to which parts of the mermithergates are enlarged at the expense of other parts. In the case of *Pheidole* there are three possible answers to the first question: the mermithergates may represent small-headed, *i. e.*, defective soldiers; second, they may be very defective females, and third they may represent excess development of the worker caste. Emery rejects the third possibility, and while considering the two others, is inclined to regard the mermithergates as having arisen from soldier larvæ in which the gaster has appropriated the nutriment of the head region so.

that the latter is greatly reduced in size.   This interpretation, which derives its plausibility from the soldier-like structure of the thorax in the parasitized *Pheidole absurda*, is equally applicable to *Ph. commutata*.   Emery is, however, unable to account satisfactorily for the appearance of the ocelli and larger eyes.   The case of *Pheidole* is certainly complicated by the existence of a soldier caste.   Both in the Ponerine ants studied by Emery (*Odontomachus, Neoponera, Paraponera*, etc.), and in the species of the Myrmicine *Cremastogaster* above described, this caste does not exist, and hence the mermithergates may be only excess developments of the worker, or defective developments of the female.   Although in these cases I believe that the former alternative is the more probable, at least in some of the species, the question can hardly be settled without much additional material.

Emery takes it for granted that the gaster is an excess development, because it is so greatly enlarged in the adult mermithergates.   But I have shown that in the pupæ in *Ph. commutata*, at least, the gaster is proportionally no more developed than any other part of the body.   Hence we cannot conclude that the head is small because the gaster is large.   We must rather suppose that the whole body exhibits excessive and uniform growth, and this must, of course, mean a uniform distribution of the metabolized nutriment in the larva.[1]   It would seem, therefore, that the mermithergates, if they really arise from soldier larvæ, retain small heads because the parasites and not the abdominal tissues appropriate the substances which in the normal soldier go to form the cephalic region.   This is indicated by the fact that the head of the soldier does not develop till the semi-pupal stage, when the pellucid cephalic substances may be seen rapidly accumulating in the previously slender anterior region.   This explanation, which resolves itself into a very obvious struggle between the larva and its parasite and not between the parts of the larva, will also account for the smaller heads in the Ponerine mermithergates.   In all cases the pupa tends to become a well-proportioned whole.   It is evident that this tendency is very different from an unequal struggle of the various body regions with one another, since it implies a uniform distribution of the available nutriment.   It implies, moreover, defect developments in the head, in the case of the soldier larvæ. The failure to develop the huge head of the soldiers in *Pheidole* mermithergates is in all probability due to the suppression of a very recently acquired character by the parasite, since there is every reason to suppose that the soldier caste among these and other ants is of much less phylogenetic antiquity than the worker.   This seems to be clearly indicated in the ontogene-

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[1] Dr. T. H. Montgomery informs me that crickets (*Gryllus abbreviatus*) infested with *Mermis* or with *Paragordius varius* are apt to be larger than uninfested individuals.   The enlargement is not confined to the abdomen but also affects the other regions of the body as in mermithergates.

tic development of colonies of *Pheidole, Camponotus,* etc., for in these only small-headed workers are at first produced by the queens. Here scarcity of food produces almost the same results as parasitism — namely microcephaly. At the same time that the tendency to produce a well-proportioned pupa suppresses the recently acquired macrocephalic characters of the species, it may be conceived to encourage the development of certain ancient phylogenetic characters like the ocelli and larger eyes. This is especially the case in the *Pheidole* larva for two reasons: first, because the mermithergates of these ants probably approach more nearly the ancestral stature of the workers, since it is very probable that the *Pheidole* workers have undergone a reduction in size during the phylogeny of the genus, and second, because the larva, notwithstanding its parasites, nevertheless succeeds in accumulating more formative substance than is necessary for the production of a normal worker.[1]

On the basis of the above interpretation, which I would substitute for Professor Emery's, an interesting comparison may be instituted between the mermithergates of *Pheidole commutata* and *absurda* on the one hand, and the phthisergates of *Ph. instabilis* on the other. In the former cases the parasitic *Mermis,* situated in the abdomen of the larval ant, appropriates to its own growth the substances that will later be required to increase the volume of the pupal and imaginal head. In the latter case, the ectoparasitic *Orasema* larva, situated just behind the head of the semipupal ant, intercepts and extracts the head-producing substances as they flow forward from the abdominal region into the anterior end of the body. In both cases the result is a pathological microcephaly, extreme and peculiar in the moribund pupal phthisergates of *Ph. instabilis,* much less pronounced but persisting into the imaginal stage in the less seriously parasitized *Ph. absurda* and *commutata.*

Emery has called attention to the interesting fact that all the known mermithergates occur among American ants. They occur moreover in species peculiar to the tropical or subtropical portions of the New World. This would seem to indicate that the single or several species of *Mermis* which produce this anomaly in ants are of rather circumscribed distribution. The genus *Mermis,* however, seems to be cosmopolitan, judging from von Linstow's recent revision of the group (*l. c.*). He records species from Europe, Turkestan, Madagascar, Southwest Africa, New Zealand, United States, Costa Rica, and Brazil. Some of the species, like the European *M.*

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[1] The effects of the parasitic *Mermis* on the host are not confined to mere mechanical distortion and the withdrawal of nutriment. There is much evidence to show that both Nematodes and Cestodes secrete toxic substances that have a positive and far reaching effect on the tissues of their hosts. In this connection see: von Fürth, Vergleichende Chemische Physiologie der Niederen Tiere, Jena, 1903, pp. 308–310, and Faust, Die Tierischen Gifte, Braunschweig, 1906, pp. 223–228.

albicans von Siebold and *nigrescens* Duj., are well known parasites in several
insect hosts, although no ants are recorded among the number.

3. THE PARASITISM OF THE LOMECHUSINI.

Our knowledge of the extraordinary myrmecophilous beetles of the
Staphylinid tribe Lomechusini is largely due to the indefatigable researches
of the Jesuit Father E. Wasmann.   Beginning in 1886 and continuing to
the present time, these researches comprise a series of more than thirty
papers.[1]   The work has been taken up more recently by Viehmeyer in
Germany and by Father Muckermann in Wisconsin.   My own observations,
which are still very fragmentary but not without interest, will be recorded
after reviewing the work of the authors just mentioned.

A.   *The European Lomechusa and Atemeles.*

The ethology of the Lomechusini is succinctly summarized by Wasmann
in the following paragraphs:[2]

"The *Lomechusa* group, embracing the palearctic genera *Lomechusa*
and *Atemeles* and the nearctic genus *Xenodusa*, contains, from an ethological
point of view, the most interesting and at the same time the largest of the
true ant-guests (symphiles) of the arctic region.   These Staphylinids, which
belong to the subfamily Aleocharinæ, are treated by the ants like their own
kith and kin, live in antennary communication with them, are cleaned and
licked and occasionally also carried about; they are fed from the mouths
of their hosts, although they are also able to eat independently and frequently
devour the ant-brood.   The ants are especially attracted to these beetles on
account of the prominent tufts of yellow hairs on the sides of their abdomen
which are licked by the host with evident satisfaction.   Not only do these
beetles themselves live as guests among the ants, but the same is also true of
their larvæ.   The larvæ of *Lomechusa* and *Atemeles* are reared by the ants
like their own brood; they are licked, fed with regurgitated food and, before
pupation, covered or embedded in cells like their own larvæ.   When the
nest is disturbed they are carried by the ants to a place of safety in preference
to their own larvæ and pupæ.   The predelection of the ants for these adopted
larvæ is all the more remarkable because they are the worst enemies of the
ant-brood and consume enormous numbers of the eggs and larvæ of their
hosts.   This brood parasitism, in fact, causes the development of abortive
individuals intermediate between the female and worker castes, and these

[1] Twenty-five of these papers, down to 1902, are cited by Wasmann himself at the end of a
twenty-sixth contribution entitled: Neue Bestätigungen der Lomechusa-Pseudogynen-Theorie.
Verhandl. deutsch. Zool. Ges., 1902, pp. 107–108; the remaining bibliography may be found
among the cards of the Concilium Bibliographicum.
[2] Zur Biologie und Morphologie der Lomechusa-Gruppe.   Zool. Anzeig., No. 546, 1897,
pp. 463–465.

intermediates, which I have called pseudogynes, gradually bring about a degeneration of the parasitized colonies.

"Within the *Lomechusa* group an important ethological difference obtains between *Lomechusa* and *Atemeles,* inasmuch as the former is homœcious, *i. e.,* the species of this genus have each but a single host (a species of *Formica*), in whose company they complete their whole life-cycle; whereas the *Atemeles* are heterœcious, since as adult beetles they live with *Myrmica rubra* and a species of *Formica,* but have their larvæ reared only by the latter. The fact that *Lomechusa* has only a single host explains the more highly developed *passive* stage of its symphily. This is evident from the one fact among others that the beetle is more affectionately treated by its normal hosts and is fed, not like an ant, but more like an ant-larva. The heterœcious character of the *Atemeles,* which are compelled twice during their life time to change their normal hosts, once in the spring when they migrate for reproductive purposes from *Myrmica* to *Formica,* to have their larva reared by the latter, and once in the summer or autumn, when they migrate from *Formica* to *Myrmica* for the purpose of hibernating, enables us to explain the greater *active* perfection of their symphily, their greater initiative towards the ants, and the closer imitation of their behavior. The last peculiarity is especially apparent in that they do not, like *Lomechusa, Claviger,* and *Amphotis,* beg the ants for food merely by stroking them with their antennæ, but also raise their fore-feet after the manner of ants, and stroke the cheeks of the regurgitating hosts. On this account they are treated by their normal hosts like ants and not like ant-larvæ."

Five species of *Lomechusa* and a greater number of species and varieties of *Atemeles* have been described. Of these *L. strumosa* is the best known. It is exceedingly rare in England,[1] but appears to be more abundant in certain parts of the continent, especially in Holland and Luxemburg, where Wasmann has been carrying on his investigations. Its normal host is the blood-red slave-maker (*Formica sanguinea*), though very rarely it may be found in the nests of *F. rufa* and *pratensis.*

In the present article we are mainly concerned with the pseudogynes mentioned in the above quotation. Wasmann has subjected these individuals, which were well known to Forel[2] and Adlerz,[3] to a searching examination, and describes them as follows:[4]

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[1] According to Donisthorpe (Record of Capture of Lomechusa at Woking with Formica sanguinea. Entomologist, XXXIX, July, 1906, p. 163), only three specimens have been recorded from England. Besides the one referred to in his article, one was "taken by Sir Hans Sloane on Hampstead Heath in 1710, the other found by Dr. Leach in the mail-coach between Gloucester and Cheltenham."
[2] Les Fourmis de la Suisse. Zürich, 1874, p. 138.
[3] Myrmecologiska Studier. II Svenska Myror och deras Lefnadsförhållanden, Bihang. Svenska Vet. Akad. Handl., XI, No. 18, 1886, p. 76.
[4] Die ergatogynen Formen bei den Ameisen, *l. c.,* p. 612.

"Morphologically these pseudogynic workers may be characterized as an abortive combination of the thoracic structure of the female with the stature and gastric development of the worker; they impress one as frustrate workers, that have borrowed a female thorax. Their size, according to my observations, which extend over materials from a great number of colonies, is rarely greater than that of the average normal workers of the same colony, often considerably less. The head and gaster are small, the former, in its relatively small dimensions, more like that of the female than the worker. The ovaries are, if anything, more feebly developed than in the ordinary workers. The mesonotum is hunched, disproportionately large compared with the pro- and epinotum, and is usually relatively higher than in the female. In many specimens the scutellum is large and separated off by a transverse suture from the mesonotum. The postscutellum [metanotum], on the contrary, is barely indicated, although in some individuals it forms a distinct narrow strip, while the scutellum is not separated off in front, but instead divided into two halves by a longitudinal line which is lacking in the female." Wasmann has found the pseudogynes most frequently in the nests of *F. sanguinea*, more rarely with *F. rufa, pratensis* and *fusca*. When they occur they often make up from 5–7% of the personnel of the colony, more rarely as much as 20%. "The coloration of the pseudogynic workers is almost without exception paler than that of the normal workers. This is especially true of the thorax; the color of the head, however, is often darker than in the normal workers of the same colony, and corresponds to the darker head of the female. The slight color variation in the pseudogynic *sanguinea* is explained by the fact that in this species the female and worker are very similarly colored. Conditions are different in *F. rufa* and *pratensis*. Here the color of the pseudogyne, although generally more like the darker tint of the female, is much more variable. In some fully mature individuals it is paler than in the palest workers of the same colony....All pseudogynes are, as Forel observed, cowardly and indolent. Not one of them attempted to bite me while I was plundering their nests, though I often knelt near them for hours while sifting out the myrmecophiles. The very opposite was true of the normal workers, which defended themselves with fury. The pseudogynes act as if they regarded themselves as frustrate existences. In several of the observation nests of *F. sanguniea* kept in my room, they neither took part in excavating the earth nor in nursing the brood; they did more running about, however, than the females. Their vitality seems to be feebler than that of the normal workers, for none of them managed to survive a captivity of several months, although some were callows and the remainder of the colony was in a prosperous condition."

Transitions between the pseudogynes and the normal workers on the

one hand, and normal females on the other, are of very rare occurrence. Wasmann [1] has, however, seen one colony in which "all possible transitions between normal workers and females were represented. The pseudogynes of this colony may be divided according to their stature into micropseudogynes, mesopseudogynes and macropseudogynes. Among the mesopseudogynes there are numerous transitions to the workers, but never with vestiges of wings; among the macropseudogynes there are ergatoid and gynæcoid forms, of which the former sometimes bear distinct vestiges of wings on the relatively short, narrow mesothorax, while the latter often possess perfectly developed but rather short wings on the exceedingly broad mesothorax, and in addition similar posterior wings on the metathorax. The latter forms may be designated as macronotal, brachypterous females, in contradistinction to the normal stenonotal, macropterous females."

As Wasmann's researches progressed he became more and more impressed with the fact that the parasitism of the Lomechusini and the occurrence of the pseudogynes stood in a causal relation to each other. A five years' statistical study of 410 colonies of *Formica sanguinea* near Exäten in Holland finally led him to maintain the following theses: [2]

"a. The regions in which pseudogynes occur always coincide with *Lomechusa* regions.

"b. The colonies containing pseudogynes are always the centers of *Lomechusa* regions.

"c. Pseudogynes are never found in *sanguinea* colonies outside the *Lomechusa* regions.

"d. In colonies in which *Lomechusa* lives merely as a beetle (*i. e.*, in the imaginal instar), pseudogynes are never developed, but only in such as have for years been rearing the larvæ of *Lomechusa*."

These results were found to hold good also for other European localities. He found, moreover, a similar causal connection between the occurrence of pseudogynes of *F. rufa* and the beetle *Atemeles pubicollis*, *F. rufibarbis* and *A. paradoxus*, *F. fusca* and *A. emarginatus*. In the case of *Atemeles*, of course, the pseudogynes are restricted to the ants among which its larvæ are reared and do not occur in the *Myrmica* colonies with which it merely hibernates. The *Formica* colony is therefore analogous to the definitive host of diœcious, non-social parasites like the tapeworm, while the *Myrmica* colony corresponds to the temporary host of this entozoon.

As early as 1895 [3] Wasmann undertook to explain the origin of the

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[1] Ueber ergatoide Weibchen und Pseudogynen bei Ameisen. Zool. Anzeig., No. 536, 1897, p. 252.
[2] Neue Bestätigungen der Lomechusa-Pseudogynen-Theorie. Verhandl. deutsch. Zool. Gesell., 1902, p. 100.
[3] Die ergatogynen Formen, etc., *loc. cit.*

pseudogynes. Previous authors had been inclined to regard them as cases
of atavism, *i. e.*, as reversions to the primitive female form (Adlerz) or as
blastogenic anomalies, *i. e.*, as due to some peculiarity in the structure of
the egg and hence referable to hereditary factors (Weismann, Forel). Was-
mann, however, took the view that they "are probably due to a post-embry-
onic sistence in the development of the typical female form, and arise from
larvæ which were originally destined to become females, but had already
passed the stage of wing-formation and had then been converted into
workers."   He conceives this deflection in the normal development to take
place in the following manner:[1]

"The normal mating period of *Lomechusa strumosa*, according to my
observations, is from the middle of May to the middle of June. Usually
the *Lomechusa* larvæ are to be found in the *sanguinea* nests only after this
period. At the very time when the *Lomechusæ* begin to lay their eggs,
sanguinea begins to lay a number of fertilized eggs which are to produce
workers. Both among these and the young larvæ of the worker generation
the *Lomechusa* larvæ, as I have observed, make terrific havoc. I have
noticed that their food often consists almost exclusively of these eggs and
young larvæ, and that in the course of a few days a single *Lomechusa* larva
can devour a great number of them. I have seen some of the larger *Lome-
chusa* larvæ attack and devour several ant larvæ 4–5 mm. in length, one
after another, although the *Lomechusa* larvæ in this stage are usually fed
from the mouths of the ants. As there may be as many as several dozen
Lomechusa larvæ in a single nest, the greater portion of the first annual
worker generation may be destroyed in the course of a few weeks, for the
parasites are extremely voracious and grow on the average almost a milli-
meter in length a day, and attain their definitive development (11 mm.)
from the egg to the adult larva (and that at rather low temperatures in my
observation nests) in 12 to 13 days. Hence there must arise a very per-
ceptible and sudden falling off in the development of the worker generation
and the ants endeavor to make good this deficiency by converting into workers
all the available larvæ of the immediately preceding generation, that were
originally destined to become females.

"Another factor, secondary in importance, however, compared with
those above mentioned, confirms the tendency of the ants to transmute
the female larvæ into workers, namely the extraordinarily rapid growth of
the *Lomechusa* larvæ. On this account the workers lavish the care, which
would otherwise be devoted to the female larvæ, on the *Lomechusæ* instead,
for these impress the ants as being most admirable offspring. This in turn

[1] Die ergatogynen Formen, etc., *loco cit.* p. 632.

leads to a neglect of the female larvæ. (It is the counterpart of the rearing of the young cuckoo in the nest of the white-throat!) As a matter of fact, the *Lomechusa* larvæ are the first to be rescued when the nest is disturbed. In general it may be said (according to my observations, in part previously published) that whenever I placed *Lomechusæ* in strange *sanguinea* nests, the presence of the beetles themselves often led to a neglect of the brood, and more especially of the large female larvæ."

It will be observed that Wasmann's view, which he styles a theory, rests on several inferences of very different degrees of probability. He may be said to have demonstrated that pseudogynes result from the parasitism of *Lomechusa* and *Atemeles* on various species of *Formica*. His further contention that the pseudogynes are not of blastogenic origin but arise from normal female larvæ that have developed under abnormal conditions, must also be granted; especially as it has recently received experimental confirmation from Viehmeyer.[1] This investigator removed an aged *sanguinea* queen from her colony which had for some years been producing pseudogynes, owing to the presence of *Lomechusa* larvæ, and caused her to be adopted by a new set of fifty unusually fine workers from an uninfested colony. Her eggs under the changed conditions developed into larvæ that gave rise to normal workers. This, of course, proves that the pathogenic conditions cannot have their origin in the queen or in her ova. Wasmann has since published a similar experiment.[2] Two *sanguinea* females belonging to a colony from Exäten and containing many pseudogynes were given slaves (*F. rufibarbis*) from Luxemburg colonies that had never been infested with *Lomechusa* and *Atemeles*. During four consecutive years the offspring of these females developed only into normal workers.

Up to this point Wasmann's hypothesis seems to rest on firm foundations, but as much cannot be said of his explanation of the pseudogynes as the abortive results of a belated attempt on the part of the workers to transmute female larvæ into workers. He here steps on debatable grounds. It seems to me that he has come nearer the truth in that portion of the quotation above cited where he calls attention to the neglect of the female larvæ by their nurses, for it is natural to suppose that these neglected larvæ would be able to pupate and produce pseudogynes without any active intervention on the part of the workers such as the administration of a particular kind or quantity of nourishment. The great variation in stature among normal *Formica* workers on the one hand, and among females on the other, shows that there must be wide limits of larval stature within which spontaneous pupation

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[1] Experimente zu Wasmann's Lomechusa-Pseudogynen-Theorie. Allgem. Zeitschr. f. Entom., IX, 1904, pp. 334–344.
[2] Ameisenarbeiterinnen als Ersatzköniginnen, etc., *loc. cit.* p. 69.

is easily possible; and there is no occasion to suppose that this may not occur among larvæ intermediate in size between those of the workers and females. The only apparent objection to this view is one which undoubtedly occurred to Wasmann himself and led him to suppose that the nurses actively transmute the female larvæ into workers, namely, the fact that the stature of the pseudogynes is usually below, and often considerably below, that of the largest workers. This, however, may be due to purely physiological causes resident in the larvæ themselves, for these would suffer starvation as a result of the ants' infatuation with the *Lomechusa* larvæ and hence lose much of their substance (water and fat) by oxygenation during the period previous to pupation and subsequent to the inhibited histogenetic changes that have already progressed beyond the worker stage. Under these circumstances pupation would wear the aspect of a regenerative or regulatory process analogous to that which leads the isolated blastomeres of the sea-urchin and other animal ova to develop into complete but more or less abortive and diminutive larvæ.

The chief advantage of such an explanation lies in the elimination of an appeal to special instincts such as would be implied by an endeavor on the part of the worker ants to restore one portion of the colony — the vanishing worker personnel, at the expense of another portion—the annual supply of virgin females. Such an endeavor, though itself of the nature of a colonial regeneration or regulation, is not improbable, but on the principle of *entia non sunt multiplicanda præter necessitatem*, does not seem to be necessary to an explanation of the phenomena. On general biological principles we should expect moribund ant colonies to take the opposite course and hasten the development of the sexual forms as the most appropriate method of insuring the survival of the species and thereby the production or rejuvenation of colonies. The explanation above suggested has, moreover, the advantage of being applicable to other cases besides the pseudogynes of *Formica*. While treating of *Pheidole instabilis* (p. 3) I called attention to the occurrence in that ant and in a few allied species belonging to the Sonoran province, of a series of intermediates, or *desmergates*, as they may be called, connecting the typical worker (*ergate*) and soldier (*dinergate*) castes. As these desmergates are perfectly normal I could not regard them as the result of *Orasema* parasitism like the phthisergates, phthisogynes, and phthisanērs. Moreover, similar intermediates are of regular occurrence in species of several other genera (*Eciton, Dorylus, Solenopsis, Azteca, Camponotus*, etc.) where parasitism as an explanation is out of the question. In all of these cases the desmergates probably arise from larvæ that have been neglected by the ants after having been enabled to grow and develop beyond the typical worker stage. That such neglect

should often occur is not surprising when we stop to consider that much of
the time and energy of the workers of an ant community are consumed
in other duties besides feeding the brood, such as foraging, excavating,
cleaning one another, etc.   Then, too, the rate of reproduction is enormous
and must often out-run the available food supply, which itself is by no means
constant.   The very slow development of ants in their larval stages is evi-
dence of slow metabolism, and as this cannot be due to low temperatures,
at least during the summer months, we must suppose that long periods of
enforced fasting or positive starvation not infrequently intervene in the lives
of larval ants.   Still further conditions which may, perhaps, conduce to the
same result may be found in the apparent absence of a very definite and well
organized system of feeding the enormous brood, and the fact that this
important function is frequently entrusted to the presumably more or less
inexperienced callows.

B.   The North American Xenodusa.

The Lomechusini are represented in North America by the single genus
Xenodusa.   Our best known species is *X. cava* Leconte (Pl. III, Fig. 41),
a deep red beetle, 5–6 mm. in length, with slender legs and antennæ and
tufts of golden hairs (trichomes) on the abdomen, which is concave above,
like the thorax, and turned up at the tip.   This species, which is so closely
allied to the European forms that it has been placed successively in the genera
Atemeles and *Lomechusa*, is stated by Wasmann to be "ziemlich häufig"
in the United States, but it has certainly proved to be decidedly rare in
my own experience and that of several coleopterists of my acquaintance.
Messrs. W. Beutenmüller and C. Schäffer, who have given much attention
to our beetles, tell me that they have never taken it, and there is only a
single poorly preserved specimen in the large collection of the American
Museum.   There may, of course, be localities in which the insect is as com-
mon as *Lomechusa strumosa* in continental Europe, but if such exist, they
have not yet been discovered or divulged.

Leconte, who in 1865 first described *X. cava* under the name of *Ate-
meles cavus*, stated that he had never taken the insect and did not know its
host.[1]   Some years later, according to McCook,[2] he succeeded in taking it in
the mounds of *Formica exsectoides* in the Alleghenies of Pennsylvania and in
the nests of *F. rufa* (?) in various localities.   This latter datum, however, is
negligible, since the species of the *exsecta* and *rufa* groups in this country
had not at that time been clearly differentiated.

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[1] New Species of North American Coleoptera.   I.   Smiths. Miscell. Coll., No. 167, 1863, p.
30.

[2] Mound-making Ants of the Alleghenies, their Architecture and Habits.   Trans. Am. Ent.
Soc., VI, 1877, pp. 253–296, pl. i–vi.

Blanchard in 1879,[1] described in a brief note the capture of some 50 specimens of *X. cava* in a large colony of black ants, which could only be *Camponotus herculeanus pennsylvanicus* De G., in a white oak near Tyngsboro, Massachusetts. The word "recently" occurring in this note, which was dated May 1, shows that the *Xenodusæ* must have been taken during the winter or early spring and that they were hibernating with the *Camponotus*. Hamilton, who published a good list of American myrmecophilous beetles in 1888,[2] had apparently never taken *Xenodusa*, as he cites only the records of Leconte and Blanchard. Schwarz, in 1890,[3] mentions the insect as occurring with *C. pennsylvanicus* and *C. ligniperdus* var. *novæboracensis* (=*pictus* Forel) on his own authority and that of Leconte, Pergande, and Hubbard. Wickham,[4] also records it as occurring with *C. novæboracensis* at Iowa City, Iowa.

In a recent paper Muckermann,[5] has inaugurated a slight advance in our knowledge of the habits of *Xenodusa*. Aug. 23, 1900, he succeeded in finding it in the vicinity of Prairie du Chien, Wisconsin, in a nest of *novæboracensis*, and during October of the following year he found within a hundred feet of this nest a colony of *Formica sanguinea rubicunda* containing a number of pseudogynes. The circumstances indicated a causal connection between the occurrence of the pseudogynes and the parasites very similar to the connection established in Europe by Wasmann for the heterœcious *Atemeles*. It must be expressly stated, however, that Muckermann did not find *Xenodusæ*, either as adults or larvæ, in the *rubicunda* nest. And to my knowledge no one has yet taken the beetle in colonies of any of the Amercan forms of *sanguinea*.

Up to the present time I have been able to find *X. cava* only in two localities: Rockford, Illinois and Colebrook, Connecticut. These are, to be sure, the very localities in which I have collected ants most carefully. The following is the only observation made at Rockford: August 5, 1902, I took two fine specimens of *X. cava* from a large and flourishing colony of *C. novæboracensis* in an old log completely riddled with the galleries of the ants. Neither *Xenodusa* larvæ nor pseudogynes were seen. The nest was well stocked with *Camponotus* larvæ and pupæ in all stages and also contained several fine winged females. There were many *rubicunda* nests in the immediate vicinity but no pseudogynes were to be found among their inhabitants.

[1] Bull. Brooklyn Ent. Soc., II, 1879, p. 4.
[2] Catalogue of the Myrmecophilous Coleoptera, with Bibliography and Notes. Canad. Entom., XX, 1888, No. 5, p. 164.
[3] Myrmecophilous Coleoptera Found in Temperate North America. Ent. Soc. Wash., I, No. 4, 1890, p. 243.
[4] Further Notes on Coleoptera found with Ants. Psyche, VII, 1894, p. 80.
[5] *Formica sanguinea* subsp. *rubicunda* Em. and *Xenodusa cava* Lec. Ent. News, Dec. 1904, pp. 339–341, pl. xx.

My observations in Colebrook were more extensive and were all made on nests occurring on the slopes of three adjacent hills, which, for present purposes, may be designated as the eastern, middle and western hill, covering a strip of territory about a mile and a half long and a quarter of a mile wide, or less than half a square mile. Late in August, 1900, I found a few *Xenodusæ* in two large *novæboracensis* colonies on the middle hill. These colonies were essentially like the one seen at Rockford, except that neither contained winged females. My remaining observations relate to a very different ant, *Formica schaufussi* var. *incerta* Emery, which forms many colonies on the Colebrook hills. This ant, as I have shown in former articles,[1] is the normal temporary host of *F. difficilis* var. *consocians* Wheeler. The following observations show that it is also the host of *X. cava*. I may mention incidentally that, although *F. rubicunda* and its var. *subintegra* are very common in the same territory, I have never been able to find the beetle in any of their nests.

F. incerta first impressed me as being a probable host of *Xenodusa* in 1904, when I began to notice pseudogynes in a number of the colonies. August 13 to 24 of that year I took pseudogynes from seven colonies on the eastern and middle hills. Five of these colonies each contained only a few of the abnormal insects, but two, which seemed to be incipient colonies, contained unusually small, pale workers together with numerous pseudogynes of the same dimensions. One of the latter colonies, taken August 25 also contained a diminutive but perfectly developed female (microgyne). This colony was kept in an artificial nest till September 16. The numerous pseudogynes behaved in all respects like normal workers. They fed one another, carried the cocoons away when the nest was illumined, etc. In another colony that was used for some experiments with *F. consocians*, two pseudogynes, which had hatched late in August, 1904, lived till April 9 of the following year, and this notwithstanding the fact that one of them had much crippled antennæ and had to be fed and cared for by the normal workers during the whole period.

A remarkable colony was found during the early morning of August 13. The preceding night had been unusually cold so that the ants were still very inactive and I was able to capture the entire personnel. It consisted of the following: a single deälated female, to all appearances the mother of the colony; 8 perfectly normal winged females; 46 normal workers; 2 larvæ; 193 pseudogynes, and 12 pseudogyne pupæ. In this colony, therefore, nearly 80% of the personnel were pseudogynes! In size these averaged like

[1] A New Type of Social Parasitism among Ants. Bull. Am. Mus. Nat. Hist. XX, 1904, pp. 347–375; and On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-making Species. *Ibid.*, XXII, 1906, pp. 33–105.

the workers, and were of the same color, except that a number of them had traces of the black antero-median and parapsidal blotches of the female on the mesonotum. They had a perfectly normal appearance, as the enlargement of the mesonotum led to less distortion and inelegance of profile than in pseudogynic *F. sanguinea* and *rufa*, since in *incerta*, which belongs to the *pallide-fulva* group, the thorax, even of the normal worker, is unusually long. Traces of the scutellum and metanotum were rarely present in any of the specimens, so that the only difference between these and normal workers was the greater prominence of the mesonotum. The extent of this modification may be clearly seen by comparing Plate III, Fig. 42, which represents a large typical worker, and Figs. 43 and 44, which represent pseudogynes from the same colony and drawn under the same magnification.

On finding these pseudogynes I was convinced that an examination of the *incerta* nests earlier in the season would reveal the presence of *Xenodusa*. Accordingly, on revisiting Colebrook during July of the following year (1905) I set to work to look for the beetle and its larva. July 1, I found under a stone on the middle hill a small colony of *incerta* containing about 75 normal workers, a few worker pupæ and larvæ, and 6 larvæ which, from their resemblance to Wasmann's figure of the *Lomechusa* larva[1] could at once be recognized as those of *X. cava*. The legs, however, seemed to be much longer and the body more slender and more concave above. They were clinging to the lower surface of the stone covering the nest. I transferred them to an artificial nest together with as many of the ants as I could capture. The larvæ associated themselves with the brood which the ants had collected in the cavities of the damp sponge in the dark chamber of the nest. They walked about but little and very clumsily as their legs seemed to be incapable of much movement at the strongly flexed articulation between the femora and tibiæ. They were frequently seen in the act of begging the ants and one another for food. At such times they raised their fore feet and stroked the head of the ant or fellow larva. Although the ants usually responded very willingly to this solicitation, the liquid food thus received seemed to be insufficient, for one morning I saw one of the *Xenodusa* larvæ seize and devour an ant larva about 3 mm. in length. On July 7 two of the *Xenodusa* larvæ had disappeared (eaten by the ants?) and the remaining four had become somewhat inactive after having grown appreciably during their week's confinement in the artificial nest. Fearing that the ants might devour the remaining parasites, and concluding from their size that they must be nearly ready to pupate, I removed them from the nest and embedded them in some earth. This proved to be disastrous as I had not taken the precau-

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[1] Die Moderne Biologie und die Entwicklungstheorie.   2 Aufl., Freiburg i. Br., 1904, p. 223, fig. 30.

tion to sterilize the earth which must have contained some predacious insect. At any rate, I could find no traces of the larvæ when I carefully examined the earth several days later.

This brief but interesting glimpse of the larval life of *Xenodusa* led me to examine all the *incerta* nests I could find in the hope of obtaining more of the parasites. Although I failed to secure any more of the larvæ, I was rewarded July 14 by finding a mature *Xenodusa* in a small colony on the western hill. This colony had a depauperate appearance and comprised only about 50 workers, two deälated females and a few worker pupæ. It contained no pseudogynes.

These observations, made, as I have stated, within an area of less than a square mile, prove that the larvæ of *X. cava* are reared by *F. incerta* during the latter part of June and the first weeks of July, and that the adult beetle may be found as early as the middle of the latter month. During August, however, the *Xenodusæ* are found only with *C. novæboracensis*. That they pass the winter with ants of this species is indicated by Blanchard's note cited above. It is probable therefore that *X. cava* is heterœcious like the European *Atemeles*, as Wasmann surmised,[1] but instead of a Myrmicine and a Camponotine host, both hosts in the American species are Camponotine ants.

The occurrence of pseudogynes late in the autumn in so many of the *incerta* nests agrees well with Wasmann's theory that these anomalous forms are the result of Lomechusine parasitism, but there are several facts connected with this occurrence which seem not to be in full accord with his theory. A colony like the one above described, which contained nearly 80% of pseudogynes together with several normal winged females, was not encountered by Wasmann in his study of the *sanguinea* colonies. He never found more than 20% and usually the number did not exceed 5%. He says, moreover:[2]

"According to this theory the pseudogynes arise from converted female larvæ; from which follows, first, one ought to find no recently hatched normal females, or at least very few of them, in the same colony with recently developed pseudogynes, since the female larvæ of the respective generation have been changed into workers as far as possible; second, the number of pseudogynes in a single colony must not surpass the number of normal females which they represent. I do not hesitate to subscribe to both of these conclusions. The former, at least according to my own observations, is actually substantiated, since I cannot remember ever to have found recently developed females associated with recently developed pseudogynes. At

[1] Zur Biologie der Lomechusa-Gruppe. Deutsche ent. Zeitschr., 1897, Heft II, p. 275.
[2] Die Ergatogynen Formen, *loc. cit.*, p. 635.

first sight the second conclusion seems not to be justifiable. For how is it to be reconciled with the occurrence of as many as 20% of pseudogynes in a single nest? We must not, however, lose sight of the fact that the usual percentage of pseudogynes does not surpass that of the winged females, which may occur in a colony of *Formica sanguinea* or *rufa*, and that it certainly does not surpass the maximum which, according to my observations, may reach 5% in many *sanguinea* colonies. Now the pseudogynes do not leave the nest but remain in it, whereas the normal females escape at the time of the nuptial flight; hence it is only necessary that the conversion of larvæ into pseudogynes should be repeated for several generations and several years, to raise the number of these individuals to 20%." Wasmann also states that it is nearly always the same *Formica* colonies that are found to contain *Lomechusa* and *Atemeles* year after year. These considerations, however, fail to throw any light on the above described colony of *F. incerta* with its enormous number of pseudogynes associated with winged females and so small a number of workers. For if *X. cava* hibernates with *C. novæ- boracensis* it does not seem probable that it would return year after year to the same *incerta* nest, when there are hundreds of nests of this ant in the immediate neighborhood. Then, too, *incerta* colonies, unlike those of *sanguinea*, *rufa*, and *fusca* are very small, rarely comprising more than about 500 individuals, and could not even survive to raise *X. cava* year after year if the larvæ of this beetle are as destructive to the brood as the larvæ of *Lomechusa* and *Atemeles*. But this wholesale destruction would seem to be necessary, according to Wasmann's view, to bring about the conversion of female larvæ into pseudogynes. Moreover, if the pseudogynes are as short-lived as Wasmann supposes, how can they accumulate to any great extent in a single colony? And finally, how can a colony of *incerta* of the size of the one above described produce as many as 213 females in a single season? These considerations lend probability to the view that Wasmann's theory may require some emendation when we come to have a fuller knowledge of the habits of *Xenodusa*.

F. *incerta* and *rubicunda* are not the only North American ants that are able to produce pseudogynes. In going over my collection I find that I have mounted a number of these anomalous individuals with the normal workers from nests of the following ants:

1. *F. rufa integra* Nyl.

(a) A single pseudogyne taken several years ago by Mr. J. Angus at West Farms, now a part of New York City.

(b) A couple of callow pseudogynes collected July 8, at West Chester, Pennsylvania, by Mr. J. C. Bradley.

(c)   Five pseudogynes which hatched in an artificial nest from cocoons taken August 1, 1905, from a very large colony at Colebrook, Connecticut. None of these is larger than a small or medium-sized worker of *integra*, but they all have the thorax clouded with black, although this subspecies differs from other forms of *rufa* in the absence of any infuscation of the head and thorax even in the smallest workers.

2.   *F. rufa obscuriventris* Mayr. var. *melanotica* Emery.

During August, 1903, a number of cocoons of this ant were taken from a large and flourishing colony at Rockford, Illinois, and placed in an artificial nest containing *Polyergus rufescens breviceps* Emery with *F. cinerea* var. *neocinerea* Wheeler as slaves.   The cocoons were at first neglected and finally carried by the workers to the refuse heap.   On opening them I found in each a perfectly formed pseudogyne that must have died when very nearly ready to hatch.   Some of these were as small as the smallest, but the majority were as large as the average *melanotica* workers.   In two specimens, represented in Plate IV, Figs. 50–52, the thorax is seen to be more like that of the queen than in the pseudogynes of *F. incerta*.

3.   *F. fusca* var. *neorufibarbis* Emery.

A single pseudogyne taken in Salt Lake County, Utah, by Mr. C. V. Chamberlin.   In this specimen, which is smaller than the average worker, the dark thoracic blotches of the female are clearly indicated.

4.   *F. sanguinea rubicunda* var. *subintegra* Emery.

(a)   Two pseudogynes taken August 8, 1903, near Colorado Springs, Colorado, from a colony containing *F. fusca* var. *argentata* Wheeler as slaves.

(b)   A single pseudogyne from a small colony taken August 13, 1903, in Cheyenne Cañon, Colorado.   The slaves in this colony belonged to *F. argentata* and *F. subpolita* Mayr.

If we accept Wasmann's theory of the constant association of Lomechusini and pseudogynes, we must believe either that the single species, *X. cava*, breeds in the nests of several of our species of *Formica*, or that this name covers several closely allied species of *Xenodusa*, each with its normal host, but as yet undistinguished by coleopterists.   Wasmann's description of different varieties of *X. cava* [1] may, perhaps, be regarded as supporting

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[1] Revision der Lomechusa-Gruppe.   Deutsch. ent. Zeitschr., 1896, pp. 244–256.

the latter alternative. But there is still another possibility which I cannot regard as altogether precluded in the present state of our knowledge, namely, that Wasmann's theory may be too concisely formulated, and that pseudo-gynes may occasionally be produced even in colonies that have never been infested with Lomechusini. This would, indeed, be very probable if, as I have supposed, the pseudogynes arise from female larvæ that have been merely neglected by their nurses at a particular stage of development.

Even more fragmentary than our knowledge of *X. cava* is our knowledge of the other species of the genus. Wasmann recognizes three additional species from North America: *montana* Casey[1] from California, *caseyi* Wasm. from Colorado,[2] and *sharpi* Wasm. of Mexico.[3] Many years ago Walker described from Vancouver an *Atemeles reflexus*[4] which is probably the same as *X. cava*, and Fall[5] has recently described from southern California a *Lomechusa angusta*, which is a *Xenodusa* and may prove to be a synonym of Wasmann's *X. caseyi*, the smallest of our species.

The ethological notes accompanying the descriptions of these various species are very brief. According to Schwarz,[6] *X. montana* has been taken in the nests of *Camponotus lævigatus* F. Smith, an ant which hardly descends below 6,000 feet in the Rocky Mountains and Sierras, and P. M. Wirtner, O. S. B., according to Wasmann,[7] has taken this same beetle in the nests of *Formica subpolita* in Colorado. *X. montana* seems, therefore, to be heterœ-cious like *X. cava*. Father Wirtner also took the type of *X. caseyi* in the nest of *F. subpolita*. *X. sharpi* was found in a nest of *Camponotus auricomus*. One of the type specimens of *X. angusta* was taken by Dr. A. Fenyes "with ants in a large oak gall." It is probable that these ants belonged to some form of *Camponotus marginatus* as this is, according to my observations, the commonest and most widely distributed ant nesting in oak galls in the southwestern States. If this is the case, and if, as I suspect, *X. angusta* is the same as *X. caseyi*, this species would seem to be heterœcious like *X. cava* and *montana*.

Whether there are any *Xenodusæ* that are regularly or even occasionally monœcious with species of *Camponotus* cannot be decided at the present time. Wasmann entertains this possibility because pseudogynes of this genus have been described, and their existence would *ex hypothesi* require the rearing of *Xenodusa* larvæ by *Camponotus*. Emery has described a

[1] Descriptions of North American Coleoptera, I. Bull. Calif. Acad. Sci., II, 1886–87. p. 202, 203.
[2] Eine neue Xenodusa aus Colorado mit einer Tabelle der Xenodusa-Arten. Deutsch. Ent. Zeitschr., 1897, II, p. 273, 274.
[3] Revision der Lomechusa-Gruppe, *l. c.*
[4] In Lord, The Naturalist in Vancouver Island and British Columbia, II, 1899, p. 317, 318.
[5] List of the Coleoptera of Southern California. Occas. Papers. Calif. Acad. Sci., VIII, 1901, pp. 219, 220.
[6] Myrmecophilous Coleoptera, etc., *loc. cit.*, p. 246.
[7] Zur Biologie der Lomechusa-Gruppe, *loc. cit.*, p. 275.

pseudogyne of a variety of *C. senex* Fabr. from Bolivia,[1] and Miss Holliday[2] has called attention to a couple of pseudogynes of *C. maculatus vicinus* Mayr. var. *nitidiventris* Emery collected by Professor Harold Heath at San Jose, California. Very recently Emery has discovered a pseudogyne of *C. igneus* (?) in the Baltic amber.[3] In another place[4] he has described what he regards as a pseudogyne of a Myrmicine ant, *Pheidologeton diversus*, of India. I figure some specimens of two different varieties of *Myrmica rubra* (*sulcinodoides* and *schencki*) which have a thoracic structure that may properly be called pseudogynic (Pl. IV, Figs. 45 and 46, 48 and 49) when compared with that of the normal worker (Fig. 47). The mesonotum is distinct and unusually convex, and there are clear traces of scutellar and metanotal sclerites. Some specimens (Fig. 45) bear vestiges of wings like those of the pterergates. As there is little probability that such forms are due to Lomechusini, it has been suggested that other parasites may be responsible for their production. I am inclined to believe that they arise occasionally even in uninfested colonies. If it be true that these anomalies as well as the above described pseudogynes of *Formica* arise from neglected immature female larvæ, it should be possible to produce them artificially by separating such larvæ from their nurses for several days. During the coming summer I hope to take up some experiments with this end in view.

4. THE COMMENSALISM OF METOPINA.

The parasitic insects considered in the preceding sections of this article are of more than usual interest because they produce certain effects noticeable both in the structure and behavior of their Formicid hosts. While all these effects are wrought through a withdrawal of nourishment from the developing larvæ, each natural group of parasites adopts a different method. Thus the ectoparasitic *Orasema* larva extracts important juices from the body of the *Pheidole* larva directly and with great rapidity, thereby reducing its host to a mere skin, which, though still able to pass on to the pupal stage, no longer possesses sufficient substance or vitality to reach the imaginal stage. The *Mermis* larva develops much more slowly within the alimentary tract of the ant larva and appropriates a portion of the food before it has been metabolized and converted into living compounds of high morphogenic potential. Finally, the presence of the Lomechusini within the *Formica*

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[1] Intorno al Torace delle Formiche. Boll. Soc. Ent. Ital., XXXII, 1900, p. 17 (of extract), fig. 14.
[2] Some Ergatogynic Ants, *loc. cit.*, pp. 313–315, fig. K.
[3] Deux Fourmis de l'Ambre de la Baltique. Bull. Soc. Ent. France, Année 1905, No. 13, p. 189, fig. 2.
[4] Zur Kenntniss des Polymorphismus, *loc. cit.*, p. 605–608, figs.

nest leads to a withholding of the necessary food from the larvæ, or, if Was-mann's view be adopted, at least to a withholding of the proper kind of food.

All of the above insects are ravenous parasites which ultimately destroy their hosts either individually or as communities. The insect to be described in the following paragraphs is much more benign, for if it surreptitiously appropriates some of the food that has been given to the larval ant, the amount it consumes seems to cause no serious inconvenience to its host. It is conceivable, however, that the presence of this commensal in great numbers might lead to very appreciable disturbances in the trophic status of a colony. The insect is a little Dipteron fly, whose larval and pupal stages I described in a paper published some years ago.[1] At that time I was unable to breed the imago and could only state that it was in all probability one of the Phoridæ. During the late autumn of 1901 Mr. C. T. Brues succeeded in rearing the adult insect from some larvæ which I gave him. He has since described it as *Metopina pachycondylæ.*[2] Much of my former account is here reproduced in a slightly altered form, together with an enlarged photograph (Pl. V, Fig. 69) of the larvæ and pupæ of both host and commensal.

On October 27, 1900, 1 made a short excursion to Mt. Barker, which is hardly more than an hour's walk from the university at Austin, Texas. The woods about the base and on the slopes of the elevation are favorite nesting grounds for the large black Ponerine ant, *Pachycondyla harpax* Fabr. In October this ant is rearing its second brood of larvæ and pupæ, having completed the education of its first brood during June and July.[3] Wishing to continue some observations on the habits of *Pachycondyla*, I dug up one of the largest colonies I could find and carried it home in a bag. On transferring it to a Lubbock nest I took the census of the colony and found it to comprise 25 worker ants, 13 cocoons, 8 mature larvæ, 7 immature larvæ, and a packet of eggs. While counting the larvæ, which are shaped like the well-known cucurbitaceous product known as the "crooked-necked squash," and covered with hairy tubercles, I noticed that six of the largest and one of the smallest presented an unusual appearance. Each of these seemed to wear about its neck a huge collar — a kind of Elizabethan ruff — consisting of a curled larva (Pl. V, Fig. 69 x). That this could not be another ant-larva was apparent from a moment's examination. In all cases it almost completely encircled the ant-larva in the region of the first abdominal, or in some cases the metathoracic, segment. The posterior end

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[1] An Extraordinary Ant-guest. Am. Naturalist, XXXV, 1901, pp. 1007–1016, 2 figs.
[2] A Monograph of the North American Phoridæ. Trans. Am. Ent. Soc., XXIX, No. 4, 1903, p. 384.
[3] For an account of the habits of this ant, see my paper, A Study of Some Texan Ponerinæ, Biol. Bull., Vol. II, No. 1 (Oct. 1900), pp. 1–31, figs. 1–10.

was provided with a kind of disk, which adhered so tightly that both larvæ could be killed in alcohol without separating. The collar-like larva was broad behind the middle, but tapered anteriorly to a very slender thoracic region and head provided with small jaws (Fig. 69 *z*). These were supported by a chitinous frame-work of such characteristic structure as to show that the adult form must be a true Dipteron. The very smooth and tense integument, which was armed with some short, hooked bristles, was very transparent, so that the peristaltic movements of the viscera were clearly visible.

As soon as the ants had been transferred to the Lubbock nest they were given a number of young larvæ of *Camponotus maccooki* var. *sansabeanus* Buckley. These they soon proceeded to malaxate with their mandibles, twirling the morsels about in the meantime with their fore legs and lapping up the exuding juices with their tongues. Finally they deposited the crumpled and pulpy remains of the *Camponoti* on the trough-like ventral surfaces of their larvæ, which had been previously placed on their backs in a rough chamber dug in the earth of the nest. This chamber was immediately under the glass roof-pane, so that further developments could be closely observed with a pocket lens. Each ant-larva at once stretched forth its head eagerly and began to devour the viands with which it had just been provided. At the same moment the Dipteron larva, too, as if sniffing the odor of the fresh food, unwound its tapering neck from the ventral surface of its host, and without shifting the attachment of its posterior end, at once plunged its mandibles into the food. Under the lens both larvæ could be seen greedily dining side by side till the last particle of *Camponotus* larva had been consumed or prematurely removed by the worker ants.

When the ant-larvæ were huddled close together, a collar-like larva was sometimes observed to reach over and help itself from the food supply of a neighbor; but even when thus compelled to crane its neck to the utmost, it never shifted the attachment of its caudal end. Sometimes when there was no food within reach it would tweak with its sharp little jaws the sensitive hide of a neighboring ant-larva, till the latter squirmed with pain. It would sometimes even tweak its own host, as if to make it wriggle and perhaps thereby incite the worker ants to bring a fresh supply of provisions.

The following day two living myriopods (*Lithobius*) were placed in the nest. During the morning hours they were killed by the *Pachycondyla* workers, shorn of their many legs, cut up into pieces of convenient length, malaxated, and fed to the larvæ as on the preceding day. And again I was able to witness the strange banquet — the dwarf reaching down from the shoulders of the ogre and helping himself from the charger formed by the trough-like belly of his host. The same observation was repeated on sev-

eral consecutive days. Pieces of various ant-larvæ, beetle-larvæ, *Lithobius,*
Scutigera, Oniscus,— all were served up to the ant-larvæ and partaken of
with great relish by the Dipteron larvæ as well. There could be no doubt
that the latter were true commensals,— perhaps the most perfect commen-
sals, in the original meaning of the term, to be found in the whole animal
kingdom!

As one of the smallest *Pachycondyla* larvæ, scarcely one-fourth grown,
bore a very small Dipteron larva, it is, perhaps, safe to say that the ant-larva
acquires its commensal at a very early age. The two then grow up together,
so that there is always a certain relation between the two kinds of larvæ —
large *Pachycondyla* larvæ bearing large commensals, and *vice versâ.* The
worker ants lick and cleanse the commensals at the same time that they are
caring for their own larvæ. This is usually done after meals. Since,
during this operation of cleansing, the ants spend no more time over the
commensals than they do on a similar area of the body surface of their own
larvæ, it would seem that they are not even aware of the existence of the
commensals. To these nearly blind ants, which must rely almost exclu-
sively on their senses of smell and touch, the larvæ bearing commensals,
if distinguished at all from individuals without these satellites, would prob-
ably be perceived merely as having unusually protruding necks. But
there is nothing to indicate that these insects are really capable of perceiving
such differences in their environment.

On the 5th of November I obtained satisfactory evidence that the *Meto-*
pina larva is not obliged to remain always with the same *Pachycondyla*
larva. During the night one of the large larvæ had moved and attached
itself to the first abdominal segment of an ant larva which already bore a
commensal around its metathoracic segment. The two larvæ were oriented
in opposite directions, *i. e.,* with their heads reaching around opposite sides
of their host. Subsequently one of these commensals moved to an unoccu-
pied *Pachycondyla* larva. I was not present when the change occurred,
nor was I able to determine whether it was the originally stationary or the
adventitious larva that moved. Although this observation makes it certain
that the *Metopina* larvæ can shift their position from one host to another,
I am convinced, nevertheless, that they must do this with great reluctance
and only under urgent circumstances, such as extreme hunger, the death
of the larva to which they are attached, or, perhaps, when fully mature and
about to pupate.

As the days passed, the mature ant-larvæ spun their brown cocoons
(Pl. V, Fig. 69 *u*) one by one, and one by one the mature commensals dis-
appeared. Did they also pupate and for this purpose conceal themselves
in the soil of the nest? Or had the ants at last detected the villains and

converted them into food for the larvæ which had not yet pupated? Or did they stick to their hosts and pupate within the cocoons? In order to ascertain, if possible, the true state of affairs, I transferred the whole colony to a fresh nest and examined the soil of the old nest with great care. There were no traces of the missing commensals. The only remaining resource was to open the cocoons. Several of the cocoons which had been taken with the nest October 27 had hatched, but by November 10 there were still thirteen cocoons in the nests, as several of the larvæ had pupated in the meantime. Five of these were opened, and in two, which contained semi-pupæ of *Pachycondyla* and were, therefore, of recent formation, commensals were found! Having shared the table of their host, they had come to share its bed as well. The *Metopina*, too, had pupated after the manner of its kind — forming a puparium; *i. e.*, instead of spinning a cocoon like the ant larva, the dead larval skin, somewhat shriveled and contracted, was used as an envelope, and within this the pupa proper was formed.

This puparium, represented in Plate V, Fig. 69 *v*, is from 2.25 to 2.5 mm. long and clearly of the cyclorhaph type. It is elliptical, much flattened dorso-ventrally, especially along the edges, which are thin and hyaline and almost alate. The brownish dorsal surface is thrown into delicate and irregular transverse wrinkles. Anteriorly, in the thoracic region, there is a pair of short black respiratory tubes. The ventral surface is very glabrous and distinctly paler than the dorsal surface.

Subsequently, several other cocoons were opened and two more were found to contain the puparia of commensals. In all four cases the puparium was invariably located in the caudal pole of the cocoon, just to one side of the black blotch of ejecta deposited by the ant-larva before becoming a semipupa. At this point the puparium was immovably stuck to the wall of the cocoon by means of its smooth ventral surface. Its anterior end was directed towards the cephalic pole. As there is always considerable space, especially at the posterior pole, between the walls of the cocoon and the enclosed ant-pupa, the much flattened fly puparium did not in the least crowd its host.

It would be interesting to know what the commensal larva is doing while the ant-larva is weaving its cocoon. Does it move about to avoid the swaying jaws of the spinning larva? Or does it take up its position from the first at the posterior end of the larval ant and there remain motionless while the posterior pole of the cocoon is being completed? It is very difficult to answer these questions. The fact that the posterior poles of all the cocoons containing puparia were somewhat distorted, being broader, more obtuse, and more irregular than the normal cocoons, would seem to indicate that the ant-larva may modify this end of its cocoon for the better accom-

modation of the commensal. I am inclined to believe, however, that the distortion may be produced by the *Metopina* larva while attaching itself just before pupating to the newly woven and still plastic cocoon.

Reflection shows that the position of the puparium in the posterior pole of the cocoon, though the reverse of the position of the larval commensal with respect to its larval host, is the only one which can be maintained by the commensal with perfect safety. Like other ants, the *Pachycondyla* leaves its cocoon through a rent in the anterior pole. This rent is certainly made by the mandibles of the hatching ant, and it is possible that the callow insect may succeed in making its way out of the cocoon without any assistance from the workers. I have hitherto failed, however, to surprise one of these ants in the act of hatching. But even if the obstetrical aid of the workers is necessary, as it is in the more highly specialized Camponotinæ, any position for the commensal puparium, except at the posterior pole of the cocoon, might be fatal, for the struggling jaws and legs of the emerging ant and the jaws of the assisting ants would certainly be very liable to cut into so delicate an object attached to the anterior or median walls of the cocoon.

At this point my first set of observations on the *Metopina* ended. The Phorid puparia were kept for several weeks in what I supposed to be the proper conditions of warmth and moisture, but to my intense disappointment they failed to hatch. During the autumn and winter frequent and diligent search was made for more of the commensals in all the *Pachycondyla* nests I could find, but in vain. Finally, during the latter part of May of the following year, I discovered in a very different locality two *Pachycondyla* nests which contained a few *Metopina* larvæ. This discovery proved that the Phorid is double-brooded like its host. But the larvæ were very small and attached to such very young ant-larvæ that I despaired of being able to raise them in my artificial nests as far as the imaginal stage. The search for *Pachycondyla* nests containing *Metopinæ* was again renewed in the fall. Two colonies were found, and from one of these Mr. Brues succeeded in rearing several of the imaginal flies. These measure 2 mm. in length, are black with yellowish brown legs and antennæ and clear, hyaline wings. As yet *M. pachycondylæ* is the only known North American species of the genus.

It is not difficult to imagine the circumstances under which the *Metopina* hatches and manages to lay its eggs in the same or other *Pachycondyla* nests. Undoubtedly the ant is the first to hatch and to leave the cocoon. Now very soon after this occurs, the useless cocoon is always carried by a worker and placed on the refuse heap, which in the natural nest is often almost entirely made up of the empty cocoons of from one to several broods of ants, and lies in a rather dry and well-ventilated spot immediately beneath the

stone covering the nest. Along with the cocoon is carried the *Metopina* puparium still adhering to the wall at its unopened posterior end. Thus after a privileged existence as free pensioner and bedfellow to a generous host, it is unwittingly carried away in the worn-out bedclothes and consigned to the family rag pile. Here the small and very active Dipteron hatches, leaves by the wide-open front door of the cocoon, and, after mating, either returns to lay a few eggs in the galleries of its former host, or flies away to oviposit in some other *Pachycondyla* nest. Thus the simple fact that the *Metopina* hatches later than the ant renders it unnecessary for the fly to possess some peculiar means of perforating the tough wall of the cocoon, and also accounts for the position of the puparium in the posterior pole, where it would be completely concealed from the workers even after the escape of the callow ant.

In conclusion attention may be directed to certain particulars of special interest in connection with the life history of the *Pachycondyla* commensal: First, the peculiar habits of the Phorid show clearly that the Ponerine method of feeding the larvæ with comminuted insects is not only the typical but the only method employed by these ants, for such a commensal would certainly starve if the *Pachycondyla* larvæ were carefully fed like the larvæ of *Camponotus* and *Formica*, by regurgitation of liquid from the mouths of the workers. The Phorid profits by a peculiarity in the behavior of its host, and thereby demonstrates — by one of Nature's experiments — that *Pachycondyla harpax* does not feed its young by regurgitation. Second, in the peculiar symbiotic relationship existing between the Phorid and the ants, the adaptations are all on the side of the former, whereas the latter pursues its ancient and well-established mode of life uninfluenced by and apparently in complete ignorance of the very existence of its little guests. Even the distortion of the cocoon may be entirely due, as I have suggested, to the activity of the *Metopina*. These strikingly unilateral adaptations are probably to be explained on the ground that the Phorid is so careful and conservative of the life and welfare of its host. The small amount of food consumed by the little commensals can hardly be a serious drain on the provisioning instincts of the Ponerinæ, at least under ordinary conditions. The larvæ bearing the commensals were certainly as large and healthy as any others in the nest, and produced perfectly normal pupæ, which in the cases observed all lacked the imaginal disks for the wings and were therefore of the worker type.

PART II. CONCERNING THE POLYMORPHISM OF ANTS.

There is a sense in which the term polymorphism is applicable to all living organisms, since no two of these are ever exactly alike.[1]   But when employed in this sense, the term is merely a synonym of 'variation', which is the more apt, since polymorphism has an essentially morphological tinge, whereas variation embraces also the psychological, physiological, and ethological differences between organisms.   In zoölogy the term polymorphism is progressively restricted, first, to cases in which individuals of the same species may be recognized as constituting two or more groups, or castes, each of which has its own definite characters or complexion.   Second, the term is applied only to animals in which these intraspecific groups coëxist in space and do not arise through metamorphosis or constitute successive generations.   Cases of the latter description are referred to 'alternation of generations' and 'seasonal polymorphism.'   And third, the intraspecific groups which coincide with the two groups of reproductive individuals existing in all gonochoristic, or separate-sexed Metazoa are placed in the category of 'sex' or 'sexual dimorphism.'   There remain therefore as properly representing the phenomena of polymorphism only those animals in which characteristic intraspecific and intrasexual groups of individuals may be recognized, or, in simpler language, those species in which one or both of the sexes appear under two or more distinct forms.

As thus restricted polymorphism is of rare occurrence in the animal kingdom and may be said to occur only in colonial or social species, where its existence is commonly attributed to a physiological division of labor.   It attains to its clearest expression in the social insects, in some of which, like the termites, we find both sexes equally polymorphic, while in the others like the ants, social bees, and wasps, the female alone, with rare exceptions, is differentiated into distinct castes.   This restriction of polymorphism to the female in the social Hymenoptera, with which we are here especially concerned, is easily intelligible if it be traceable, as is usually supposed, to a physiological division of labor, for the colonies of ants, bees, and wasps are essentially more or less permanent families of females, the male representing merely a fertilizing agency temporarily intruding itself on the activities of the community at the moment it becomes necessary to start other colonies.   We may say, therefore, that polymorphism among social Hymenoptera is a physical expression of the high degree of social plasticity and efficiency of the female sex among these insects.   This is shown more specifically in two

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[1] The term is used in this sense by Waxweiler, for example, in his admirable 'Esquisse d'une Sociologie,' Brussels, 1906, pp. 141–143.

characteristics of the female, namely the extraordinary intricacy and ampli-
tude of her instincts which are thoroughly representative of the species, and
her ability to reproduce parthenogenetically. This, of course, means a
considerable degree of autonomy even in the reproductive sphere. But
parthenogenesis, while undoubtedly contributing to the social efficiency of the
female, must be regarded and treated as an independent phenomenon,
without closer connection with polymorphism, for the ability to develop
from unfertilized eggs is an ancient characteristic of the Hymenoptera and
many other insects, which made its appearance among the solitary species,
like the Tenthredinidæ and Cynipidæ, long before the development of social
life. Moreover, polymorphism may occur in male insects which, of course,
are not parthenogenetic. That parthenogenesis is intimately connected with
sexual dimorphism, at least among the social Hymenoptera, seems to be
evident from the fact that the males usually if not always develop from unfer-
tilized, the females from fertilized eggs.

While the bumble-bees and the wasps show us the incipient stages in the
development of polymorphism, the ants as a group, with the exception of a
few parasitic genera that have secondarily lost this character, are all com-
pletely polymorphic. It is conceivable that the development of different
castes in the female may have arisen independently in each of the three
groups of social Hymenoptera, although it is equally probable that they
may have inherited a polymorphic tendency from a common extinct ancestry.
On either hypothesis, however, we must admit that the ants have carried
the development of female castes much further then the social bees and wasps,
since they have not only produced a wingless form of the worker, in addition
to the winged female, or queen, but in many cases also two distinct castes
of workers known as the worker proper and the soldier. Some systematists
have, therefore, appropriately separated them from all other Hymenoptera
as 'Heterogyna.'

Different authors have framed very different conceptions of the phyloge-
netic beginnings of social life among the Hymenoptera and consequently also
of the phylogenetic origin and development of polymorphism. Thus Her-
bert Spencer evidently conceived the colony as having arisen from a con-
sociation of adult individuals. I infer this from his remarks on the origin
of the amazon colony in his well-known reply to Weismann:[1] "Some variety
of them [the amazon ants] led to swarm — probably at the sexual season —
did not disperse again as soon as other varieties. Those which thus kept
together derived advantages from making simultaneous attacks on prey
and prospered accordingly. Of descendants the varieties which carried

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[1] A Rejoinder to Professor Weismann. Contemp. Review, Sept. 1893, p. 14.

on longest the associated state prospered the most; until, at length, the associated state became permanent. All of which social progress took place while there existed only perfect males and females." Although Spencer is particularly unfortunate in selecting a parasitic ant like the amazon (*Polyergus rufescens*) on which to hang his hypothesis, there are a few facts which would seem to make his view applicable to other social Hymenoptera. Fabre [1] once found some hundreds of a species of solitary wasp (*Ammophila hirsuta*) huddled together under a stone on the summit of Mt. Ventoux in the Provence at an altitude of about 5,500 feet, and Forel [2] found more than fifty deälated females of *Formica rufa* under similar conditions on the Simplon. I have myself seen collections of a large red and yellow *Ichneumon* under stones on Pike's Peak at an altitude of more than 13,000 feet, and a mass of about seventy deälated females of *Formica fusca* var. *gnava* Buckley apparently hibernating after the nuptial flight under a stone near Austin, Texas. I am convinced, however, that such congregations are either entirely fortuitous, especially where the insects of one species are very abundant and there are few available stones, or, that they are, as in the case of *F. rufa* and *gnava*, merely the result of highly developed social proclivities and not a manifestation of such proclivities in process of development.

A very different view from that of Spencer is adopted by most authors. They regard the insect society as having arisen, not from a chance concourse of adult individuals but from a natural affiliation of mother and offspring. This view which has been elaborated by Marshall [3] among others, presents many advantages over that of Spencer, not the least of which is its agreement with what actually occurs in the founding of the existing colonies of wasps, bumble-bees and ants. These colonies pass through an ontogenetic stage which has all the appearance of repeating the conditions under which colonial life first made its appearance in the phylogenetic history of the species — the solitary mother insect rearing and affiliating her offspring under conditions which would seem to arise naturally from the breeding habits of the nonsocial Hymenoptera. The exceptional methods of colony formation seen in the swarming of the honey bee and in the temporary and permanent parasitism of certain ants, are too obviously secondary and comparatively recent developments to require extensive comment. The bond which held mother and daughters together as a community was from the first no other than that which binds human societies together — the bond

[1] Souvenirs Entomologiques. I, 3 ed., 1894, pp. 187, 188, 196 *et seq.*
[2] Fourmis de la Suisse, p. 257.
[3] Leben and Trieben der Ameisen. Leipzig, 1889, pp. 3–6.

of hunger and affection so beautifully described in the famous lines from Schiller's " Die Weltweisen " :

> Einstweilen, bis den Bau der Welt
> Philosophie zusammenhält,
> Erhält sie [Natur] das Getriebe,
> Durch Hunger und durch Liebe.

The daughter insects in the primitive colony became dependent organisms as a result of two factors: inadequate nourishment and the ability to pupate very prematurely.   But this very ability seems to have entailed an incompleteness of imaginal structure and instincts which in turn must have confirmed the division of labor and thus tended to perfect the social organization.

Before further discussing the problems suggested by this view of the origin of the colony and the general subject of polymorphism, it will be advisable to pass in review the series of different phases known to occur among ants.   This review will be facilitated by consulting the diagram on Plate VI, in which I have endeavored to arrange the various phases so as to bring out their morphological relations to one another.   The phases may be divided into two main groups, the normal and the pathological.   In the diagram the names of the latter are printed in italics.   The normal phases may again be divided into primary or typical, and secondary or atypical, the former comprising only the three original phases, male, female, and worker, the latter the remaining phases, which, however, are far from all having the same status or frequency.   The three typical phases are placed at the angles of an isosceles triangle, the excess developments being placed to the right, the defect developments to the left, of a vertical line passing through the middle of the diagram.   The arrows indicate the directions of the affinities of the secondary phases and suggest that those on the sides of the triangle are annectant, whereas those which radiate outward from its angles represent the new departures with excess and defect characters.

1. THE TYPICAL, ATYPICAL AND PATHOLOGICAL PHASES OF ANTS.

(1)   The *male* (anēr) is far and away the most stable of the three typical phases which are found in all but a few monotypic and parasitic genera of ants.   This is best shown in the general uniformity of structure and coloration which characterize this sex in genera whose female forms (workers and queens) are widely different; *e. g.*, in such a series of cases as *Myrmecia, Odontomachus, Cryptocerus, Formica, Pheidole*, etc.   In all of these genera the males are very similar, at.least superficially, whereas the workers and females are very diverse.   The body of the male ant is graceful in form, one might almost say emaciated.   Its sense-organs (especially the eyes and antennæ), wings and genitalia are highly developed; its mandibles are

more or less undeveloped and in correlation with them the head is por-
tionally shorter, smaller and rounder than in the females and workers of
the same species.   Even when the latter phases have brilliant or metallic
colors, as in certain species of *Macromischa* and *Ectatomma*, the males are
uniformly red, yellow, brown or black.   Yet notwithstanding this monotony
of structure and coloration, the male type may present the following inter-
esting modifications.

(2)   The *macranēr* is an unusually large form of male which occasion-
ally occurs in populous colonies.

(3)   The *micranēr*, or dwarf male, differs from the typical form merely in
its smaller stature.   Such forms often arise in artificial nests.

(4)   The *dorylanēr* is an unusually large male form peculiar to the
driver and legionary ants of the subfamily Dorylinæ (*Dorylus* and *Eciton*).
It is characterized by its large and peculiarly modified mandibles, long
cylindrical gaster and singular genitalia.   It may be regarded as an aberrant
macranēr that has come to be the typical male of the Dorylinæ.

(5)   The *ergatanēr*, ergatomorphic, or ergatoid male resembles the
worker in having no wings and in the structure of the antennæ.   It occurs
in the genera *Ponera*, *Formicoxenus*, *Symmyrmica*, and *Cardiocondyla*.
In certain species of *Ponera* (*P. punctatissima* and *ergatandria*) and in
Formicoxenus nitidulus the head and thorax are surprisingly worker-like,
in other forms like *Symmyrmica chamberlini* these parts are more like those
of the ordinary male ant, while *P. eduardi* shows a more intermediate devel-
opment of the head with a worker-like thorax.   Forel,[1] has recently shown
that the ergatanēr may coëxist with the anēr, at least in one species of *Po-
nera* (*P. eduardi* Forel).   In other words, this ant has dimorphic males.

(6)   The *gynæcanēr*, or gynæcomorphic male occurs in certain parasitic
and workerless genera (*Anergates* and *Epæcus*) and resembles a female
rather than a worker form.   The male of *Anergates* is wingless, but has
the same number of antennal joints as the female.   In *Epæcus* both sexes
are very much alike and both have 11–12-jointed antennæ.[2]

(7)   The *phthisanēr* is a pupal male which in its late larval or semipupal
state has its juices partially exhausted by an *Orasema* larva.   This male is
too much depleted to pass on to the imaginal stage.   The wings are sup-
pressed and the legs, head, thorax, and antennæ remain abortive.

(8)   The *female* (gynē), or queen, is the more highly specialized sex
among ants and is characterized, as a rule, by her large stature and the
more uniform development of her organs.   The head is well developed and

[1] Dimorphisme du Mâle chez les Fourmis.   Ann. Soc. Ent. Belg., XLVIII, 1904.
[2] For an account of the ergatandric and gynæcandric forms see Emery, 'Zur Kenntniss
des Polymorphismus der Ameisen,' Biol. Centralbl., XXVI, 1906, pp. 624–630, 4 figs.

provided with moderately large eyes, ocelli, and mandibles; the thorax is large (macronotal) and presents all the sclerites of the typical female Hymenopteron; the gaster is voluminous and provided with well developed reproductive organs. The wings and legs are often relatively smaller than in the male.

(9)   The *macrogyne* is a female of unusually large stature.

(10)   The *microgyne*, or dwarf female, is an unusually small female which in certain ants, like *Formica microgyna* and its allies, is the only female of the species and may be actually smaller than the largest workers. In other ants, like certain species of *Leptothorax* and *Myrmica* microgynes may sometimes coëxist in the same nests with the typical females.

(11)   The *β–female* is an aberrant form of female such as occurs in *Lasius latipes*, either as the only form or coëxisting with the normal female which is then called the *a*-female. In this case, therefore, the female is dimorphic. The *β*-female is characterized by excess developments in the legs and antennæ and in the pilosity of the body.

(12)   The *ergatogyne*, ergatomorphic, or ergatoid female, is a worker-like form but with large eyes, ocelli, and a thorax more or less like that of the female, but without wings. Such females occur in a number of species of ants. They have been seen in *Myrmecia, Odontomachus, Anochetus, Ponera, Polyergus, Leptothorax, Monomorium*, and *Cremastogaster*. There is nothing to prove that they are pathological in origin. In fact, in *Monomorium floricola* and certain species of *Anochetus* they seem to be the only existing females. In other cases, like *Ponera eduardi*, as Forel has shown, they occur with more or less regularity in nests with normal workers. They occur also under similar conditions in colonies of the circumpolar *P. coarctata*, and probably also among other species of the genus.

(13)   The *dichthadiigyne*, or dichthadiiform female is peculiar to the ants of the subfamily Dorylinæ. It is wingless and stenonotal, destitute of eyes and ocelli, or with these organs very feebly developed, and with a huge elongated gaster and extraordinary, voluminous ovaries.

(14)   The *pseudogyne* has been sufficiently characterized in the preceding pages as a worker-like form with enlarged mesonotum and sometimes with traces of other thoracic sclerites of the female, but without wings or very rarely with wing vestiges.

(15)   The *phthisogyne* arises from a female larva under the same conditions as the phthisanēr, and differs from the typical female in the same characters, namely absence of wings, stenonoty, microcephaly and microphthalmy. It is unable to attain to the imaginal instar.

(16)   The *worker* (ergates) is characterized by the complete absence of wings and a very small (stenonotal) thorax, much simplified in the structure of its sclerites. The eyes are small and the ocelli are usually absent or,

when present, extremely small. The gaster is small, owing to the undeveloped condition of the ovaries. A receptaculum seminis is usually lacking, and the number of the ovarian tubules is greatly diminished.[1] The antennæ, legs and mandibles are well developed.

(17) The *gynæcoid* is an egg-laying worker. It is a physiological rather than a morphological phase, since it is probable that all worker ants when abundantly fed become able to lay eggs. Wasmann[2] observed in colonies of *Formica rufibarbis* that a few of the workers became gynæcoid and functioned as substitution queens. In colonies of the Ponerine genus *Leptogenys* (including the subgenus *Lobopelta*), and probably also in *Diacamma* and *Champsomyrmex*, the queen phase has disappeared and has been replaced by the gynæcoid worker.

(18) The *macrergate* is an unusally large worker form which in some species is produced only in populous or affluent colonies (*Formica*, *Lasius*).

(19) The *micrergate*, or dwarf worker, is a worker of unusually small stature. It appears as a normal or constant form in the first brood of all colonies that are founded by isolated females.

(20) The *dinergate*, or soldier is characterized by a huge head and mandibles, often adapted to particular functions (fighting and guarding the nest, crushing seeds or the hard parts of insects), and a thoracic structure sometimes approaching that of the female in size or in the development of its sclerites (*Pheidole*).

(21) The *desmergate* is a form intermediate between the typical worker and dinergate, such as we find in more or less isolated genera of all the subfamilies except the Ponerinæ, *e. g.*, in *Camponotus*, some species of *Pheidole*, *Solenopsis*, and *Pogonomyrmex*, *Azteca*, *Dorylus*, *Eciton*, etc. The term might also be employed to designate the intermediate forms between the small and large workers in such genera as *Monomorium*, *Formica*, etc.

(22) The *plerergate*, 'replete,' or 'rotund,' is a worker which in its callow stage has acquired the peculiar habit of distending its gaster with stored liquid food ('honey') till this portion of the body is a large spherical sac and locomotion becomes difficult or even impossible. This occurs in the honey ants (some North American species of *Myrmecocystus*, some Australian *Melophorus* and *Camponotus*, and to a less striking extent in certain species of *Prenolepis* and *Plagiolepis*).

(23) The *pterergate* is a worker or soldier with vestiges of wings on a thorax of the typical ergate or dinergate form, such as I have described in certain species of *Myrmica* and *Cryptocerus*.[3]

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[1] Adlerz's often-cited statement that the ovarian tubules are completely lacking in the workers of *Tetramorium cæspitum* seems to me to require confirmation. These organs may be easily overlooked in dissecting such small ants. The study of stained sections of adult pupal workers would probably yield more satisfactory results.

[2] Ameisenarbeiterinnen als Ersatzköniginnen, *loc. cit.*

[3] Worker Ants with Vestiges of Wings. Bull. Am. Mus. Nat. Hist., XXI, 1905, pp. 405–408, pl. xiv.

(24)   The *mermithergate*, which has been described in detail in the pre-ceding pages, is an enlarged worker, produced by *Mermis* parasitism and often presenting dinergate characters in the thorax and minute ocelli in the head.

(25)   The *phthisergate*, which corresponds to the phthisogyne and phthisanēr, is a pupal worker which in its late larval or semipupal stage has been attacked and partially exhausted of its juices by an *Orasema* larva.   It is characterized by extreme stenonoty, microcephaly and microphthalmy, and is unable to pass on to the imaginal stage.   It is in reality an infra-ergatoid form.

(26)   The *gynandromorph* is an anomalous form in which male and female characters are combined in a blended or more often in a mosaic manner.

(27)   The *ergatandromorph* is an anomaly similar to the last but having worker instead of female characters combined with those of the male.[1]

2.   THE VIEWS OF SOME PREVIOUS AUTHORS ON POLYMORPHISM.

In their attempts to explain polymorphism authors have not, of course, taken all of the above enumerated phases into consideration, but have been content to include only the typical and perhaps a few of the atypical and pathological phases.   And it is clear that if the main phases could be ac-counted for, the rarer and less important deviations would present few dif-ficulties.   I shall endeavor to show, however, that some of these singular forms may shed at least a few rays of light on the problem of polymorphism.

The social insects have held an important place in discussions of evolution and heredity ever since Darwin called particular attention to these animals in the eighth chapter of the 'Origin.'   In later years they assumed even greater prominence in the controversies between the Neolamarckians and Neodarwinians concerning the efficacy of natural selection.   This was unavoidable, for polymorphism would seem to be of such a nature as to afford a test of the validity of any hypothesis bearing on the inheritance or noninheritance of acquired characters as well as of any hypothesis concern-ing the rôle of preformation, or epigenesis, in the development of organisms. As it will be impossible in this place to present a detailed history of the subject or to dwell on all its wider implications, I shall confine myself mainly to the views which were championed by Weismann and Herbert Spencer respectively in their well-known controversy in the 'Contemporary Review',

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[1] For an account of the known cases of this and the preceding anomaly among ants see my paper: 'Some New Gynandomorphous Ants, with a Review of the Previously Described Cases.' Bull. Am. Mus. Nat. Hist., XIX, 1903, pp. 653–683, 11 figs.

and have been maintained with more or less modification by zoölogists down to the present time.[1]

In order to make his explanation of polymorphism conform with the remainder of his hypothesis of heredity, Weismann is compelled to assume, not only a set of germ-plasmic determinants for each of the sexes in ordinary sexual dimorphism, but a double set for the female in the social Hymenoptera and a double set for each sex in the termites. At least four sets must also be postulated for ants with differentiated worker and soldier castes. This is evident from the following quotation:[2]

"So when instead of dimorphism, there is polymorphism, when, for instance, the females of a species are similarly distinguished among themselves, and occur in two forms, this results, according to my idea, from the double determinants becoming triple determinants. If there were workers among the butterflies, and if these showed red color on the part of the wing that is blue in the male and brown in the female, there would always be three representative determinants present at a definite part of the extremely elaborate and highly complicated germ-plasm; but only one of these would become active during the development of the egg and sperm-cell concerned, and would produce the patch of brown or blue or red scales in the wing.

"According to this theoretical representation, every part of the body that is differently formed in the males, females and workers is represented in the germ-plasm by three corresponding determinants but in the development of the eggs, never more than one of these attains to value — i. e., gives rise to the part of the body that is represented — and the others remain inactive.

"Thus, then, the metamorphosis of the body parts of the workers of ants and bees will have to be considered in connection with the fact that the males and females whose germ-plasm contains favorable variations of the determinants of the workers have a better prospect for the maintenance of their successors than others which showed less favorable variations of such determinants. The process of selection is the same as if the matter at issue were the attainment of favorable adaptations in the body of the sexual forms; for in both cases it is, as I have once before said, not really the body that is

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[1] The papers called forth by this controversy are here cited in the order of their publication: Spencer: 'The Inadequacy of "Natural Selection",' Contemp. Rev., Feb. and March, 1893, pp. 153–166, 439–456; 'Professor Weismann's Theories,' ibid., May, 1893, pp. 743–760; Weismann: 'The All Sufficiency of Natural Selection,' ibid., Sept., 1893, pp 309–338; Spencer: 'A Rejoinder to Professor Weismann,' ibid., Dec. 1893, pp. 893–912; 'Weismannism Once More,' ibid., Oct. 1894, pp. 592–608. Weismann has also repeated or elaborated his views on the polymorphism of the social insects in the following works: 'Das Keimplasma. Eine Theorie der Vererbung.' Jena, Gustav Fischer, 1892, pp. 494–498; 'The Effect of External Influences upon Development,' Romanes Lecture, London, Henry Frowde, 1894, pp. 29–48; and 'Vorträge über Descendenz-theorie,' Jena, Gustav Fischer. 2 Bd. pp. 101–118. For an aftermath of the Spencer-Weismann controversy see also the discussion of the subject in 'Natural Science,' IV, 1894, by Ball (Neuter Insects and Lamarckism, pp. 91–97), and Cunningham (Neuter Insects and Darwinism, pp. 281–289).
[2] The All-Sufficiency, etc., loc. cit., pp. 326, 327.

selected, but the germ-plasm from which the body develops. The difference is this: in the one case the survival in the struggle for existence depends on characters and variations of the body of the individual; in the other, only on the character of a certain kind of descendant — the worker. If the ant state were composed of individuals connected together like a colony of poly-pes or *Siphonophoræ*, a process of selection by which only the workers were changed would be within easier reach of our imagination, as these would then, in a manner, be only *organs*, just like the snaring-threads, the swim-ming bells, and the gastric tubes of the *Siphonophoræ*. As these do not reproduce, and accordingly can only vary by selection of the egg or germ-plasm from which the whole colony is formed, so in the case of the ant-colony, or rather state, the barren individuals or organs are metamorphosed only by selection of the germ-plasm from which the whole state proceeds. In respect of selection the whole state behaves as a single animal; the state is selected, not the single individuals; and the various forms behave like the parts of one individual in the course of ordinary selection."

It must be admitted that this hypothesis is boldly and clearly conceived and its author's knowledge of myrmecology and melittology is only surpassed by the adroitness with which he compels the facts to tally with his assump-tions. Nowhere in Weismann's work are both the strength and the weak-ness of his elaborate architectonics of the germ-plasm more apparent than in this attempt to explain the complicated and adaptively correlated organi-zation of the sterile worker as the result of a single mechanical factor, natural selection, acting on constellations of fortuitous determinants in the germ-plasm of the fertile female.

Spencer, too, seeks a mechanical explanation of the purposeful adapta-tions of the worker, though this is utterly at variance with the fundamental teleological spirit of the Lamarckian view which he elsewhere advocates. He starts out with the social wasps (*Vespa*), some species of which present an uninterrupted series of transitional forms between the small sterile worker and the large fertile female, or queen. He calls attention to the abundant evidence to show that these arise progressively and in close depend-ence on the food supply of the colony, so that the sterility and dwarfing of the workers are manifestly caused by insufficiency of food during their larval stages. He then proceeds to extend this same explanation to the ants, although these insects differ from the wasps in presenting great morphologi-cal differences between the workers and females. After considering the African driver ants which have highly polymorphic workers, he goes on to say: "In contrast with this interpretation, consider now that of Professor Weismann. From whichever of the two possible suppositions he sets out, the result is equally fatal. If he is consistent, he must say that each of these

intermediate forms of workers must have its special set of 'determinants,' causing its special set of modifications of organs; for he cannot assume that while perfect females and the extreme types of workers have their different sets of determinants, the intermediate types of workers have not. Hence, we are introduced to the strange conclusion that besides the markedly distinguished sets of determinants there must be to produce these intermediate forms, many other sets slightly distinguished from one another — a score or more kinds of germ-plasm in addition to the four chief kinds [namely for the male, female, soldier, and worker]. Next comes an introduction to the still stranger conclusion, that these numerous kinds of germ-plasm, producing these numerous intermediate forms, are not simply needless but injurious — produce forms not well fitted for either of the functions discharged by the extreme forms: the implication being that natural selection has originated these disadvantageous forms! If to escape from this necessity for suicide Professor Weismann accepts the inference that the differences among these numerous intermediate forms are caused by arrested feeding of the larvæ at different stages, then he is bound to admit that the differences between the extreme forms, and between these and perfect females, are similarly caused. But if he does this, what becomes of his hypothesis that the several castes are constitutionally distinct, and result from the operation of natural selection? Observe too that his theory does not even allow him to make this choice; for we have clear proof that unlikenesses among the forms of the same species cannot be determined this way or that way by differences of nutrition. English greyhounds and Scotch greyhounds do not differ from one another so much as do the Amazon-workers [soldiers] from the inferior workers, or the workers from the queens. But no matter how a pregnant Scotch greyhound is fed, or her pups after they are born, they cannot be changed into English greyhounds: the different germ-plasms assert themselves spite of all treatment. But in these social insects the different structures of queens and workers are determinable by differences of feeding. Therefore the production of their various castes does not result from the natural selection of varying germ-plasm."

If we omit the portion of Spencer's argument in which he postulates the dysteleological character of the intermediates, or desmergates, as I have called them — a probably erroneous assumption, since there is every reason to believe that individuals embodying varying combinations of the worker and soldier traits may be just as useful to the colony as the soldiers and workers themselves — the position taken in the above quotation seems to be unassailable. But when Spencer comes to deal with the crucial problem, namely the marvelous, purposeful coadaptation of organs in the sterile workers, he fails as signally as Weismann, for no one familiar with the habits

.and taxonomy of ants can regard his attempts to trace such specialized .structures and instincts as those of the amazon slave-makers (*Polyergus*) to inherited presocial acquirements as seriously invalidating Weismann's .argument. As I shall show in the sequel, however, Spencer presents a vague adumbration of facts which have since come to light and easily dispose of the portion of Weismann's argument relating to the amazons.

Weismann returns to the charge in his Romanes lecture and asserts that he cannot look upon Spencer's view "as a correct one in the sense implied. It is certainly true that bees have it in their power to cause a larva to become .a queen or a worker according to the manner in which they feed it: it is ·equally true of all animals that they reproduce only feebly or not at all when badly and insufficiently nourished: and yet the poor feeding is not the ·*causa efficiens* of sterility among bees but is merely the stimulus which *not ·only results in the formation of rudimentary ovaries, but at the same time .calls forth all the other distinctive characters of the workers.* It appears to me to be doubly incorrect to look upon the poor nourishment as the actual ·cause; for such a view not only confuses the stimulus with the real cause, but also fails to distinguish between an organ that becomes rudimentary .and one that is imperfectly developed. Moreover the fact is overlooked that the ovaries of the workers are actually rudimentary organs: a great proportion of their really essential parts have disappeared, while only a .small remnant is retained."

Weismann goes farther and maintains that he has disproved Spencer's view experimentally. He reared two lots of blow-fly larvæ (*Musca vomi- .toria*), one on poor the other on abundant food, and obtained imaginal flies differing greatly in size but with the reproductive as well as the other ·organs normally developed even in the smallest individuals. The latter on being well fed, mated and produced normal young. He concludes as follows from this experiment: "By comparing the result of this experiment with the known facts as to bees, the difference in the behavior of the two ·organisms is made clear. In the case of bees a distinct degeneration of the ·ovaries and various accessory organs of reproduction takes place in conse- ·quence of poor nourishment; while in flies the whole reproductive apparatus is formed quite as perfectly when the nourishment of the larva is deficient .as when it is ample. There is even no delay in the maturing of the eggs, .as shown by the fact that the first batch was laid at exactly the same time .as in the case of the flies arising from normally fed larvæ.

"It might, however, be said that flies and bees are very different organ- isms, and therefore react differently to external influences. This is quite ·true, and is exactly what I wish to be acknowledged. My experiments ·with the flies were merely meant to show that all insects, even though they

may resemble bees in some respects, do not react in a similar way to the bee to meagreness of nutrition, and that accordingly *this mode of reaction is a characteristic of bees*: — it is a new acquisition, and was not possessed by the ancestors of these insects."

The views of the more active European myrmecologists, Emery, Escherich, Forel and Wasmann, are in close accord with those of Weismann, but there are some significant departures, especially in Emery's view, which approaches that of Spencer. Emery gives this summary of his position in a paper on the origin and development of the worker among ants:[1] "The theory which I have attempted to carry out in hypothetical form, is based on the assumption, that the production of the worker depends on the instinctive art of breeding workers, and that the origin of the worker caste is to be attributed more to a difference in the quality, the differentiation of several kinds of workers more to the quantity of the food. From the latter process I would not, of course, exclude the possible play of qualitative factors; their intervention is, indeed, probable in specific cases, such as, *e. g.*, in the *Melissotarsus beccarii*, which I have described, and which has two kinds of workers of the same size but with heads of a different form.

" *The peculiarities in which the workers differ from the corresponding sexual forms are, therefore, not innate or blastogenic, but acquired, that is somatogenic.* Nor are they transmitted as such, but in the form of a peculiarity of the germ-plasm that enables this substance to take different developmental paths during the ontogeny. Such a peculiarity of the germ may be compared with the hereditary predisposition to certain diseases, which like hereditary myopia develop only under certain conditions. The eye of the congenitally myopic individual is blastogenetically predisposed to short-sightedness, but only becomes short-sighted when the accommodation apparatus of the eye has been overtaxed by continual exertion. Myopia arises, like the peculiarities of the worker ants, as a somatic affection on a blastogenic foundation.

"With this assumption the problem of the development of workers seems to me to become more intelligible and to be brought a step nearer its solution. The peculiarities of the Hymenoptera workers are laid down in every female egg; those of the termite workers in every egg of either sex, but they can only manifest themselves in the presence of specific vital conditions. In the phylogeny of the various species of ants the worker peculiarities are not transmitted but merely the faculty of all fertilized eggs to be reared as a single or several kinds of workers. The peculiar instinct of rearing workers

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[1] Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen. Biol. Centralbl., XIV, 1894, pp. 58, 59.

is also transmitted, since it must be exercised by the fertile females in establishing their colonies."[1]

In other words, Emery supposes that the germ-plasm of the social insects is characterized by a peculiar sensitivity which makes it amenable to the different influences to which it is subjected in the fostering environment of the colony. This view, as I shall endeavor to show in the concluding paragraphs of this article, is worthy of more attention than it has received. It was rejected by Weismann in his Romanes lecture on the ground that typical organs like the wings, ovarian tubules, spermatheca, etc. could not disappear from the worker by any ontogenetic, but only by a phylogenetic process, but his argument is based on what is known to occur in other animals and necessarily fails to apply to animals which, like the social Hymenoptera, seem to be unique in presenting the very conditions Emery has been trying to explain.

Wasmann[2] accepts Weismann's view of the determinants and the function of nutrition as a mere stimulus, but he rejects his view that natural selection alone can account for the adaptive structures and instincts of worker ants.

Forel in his 'Fournis de la Suisse' (p. 440, 441, *nota*) accepts the Darwinian view of the origin of the worker caste by natural selection acting on a primitive differentiation of the female into fertile and sterile forms in the sphere of instinct before definite morphological differentiation sets in. In a recent paper[3] he is inclined to side with Weismann and to lay considerable stress on the effects of natural selection and the struggle for existence in producing variation and polymorphism as opposed to the internal factors.

Escherich,[4] has given a valuable review of the subject of polymorphism among ants, without, however, clearly defining the general issues. His own view is apparently in complete accord with that of Weismann.

Marchal, as the result of his splendid work on the habits of the social wasps,[5] has given the following suggestive discussion of polymorphism along the lines suggested by Spencer and Emery: "At the beginning of the social state the infertility of the first brood of progeny produced by the mother gradually became established. This infertility was the result of the necessarily insufficient nourishment distributed by the queen among her too numerous offspring, and the eggs in the ovaries of the young females could not mature, first, because the reserve substances (adipose tissue)

[1] For a fuller account of Emery's views, see his article ' Le Polymorphisme des Fourmis et la Castration Alimentaire.' Compt. Rend., 3me. Congr. Internat. Zool., Leyde (Sept. 1895), 1896, pp. 395–407.
[2] Die ergatogynen Formen, etc., *loc. cit.*, p. 638.
[3] Ueber Polymorphismus und Variation bei den Ameisen. Zool. Jahrb., Suppl., VII, 1904, pp. 571–586.
[4] Die Ameise. Schilderung ihrer Lebensweise. Braunschweig, 1906, pp. 45–54.
[5] La Reproduction et l' Evolution des Guêpes Sociales. Arch. Zoöl. Expér. et Gén., 3. ser., IV, 1896, pp. 1–100, 8 figs.

stored up in the larva were insufficient, and second, because immediately after hatching, the young females had to devote themselves to the care of the numerous larval colony, and especially to the *function of nursing*, which, as we have shown experimentally, prevents the maturation of the eggs. The mother being relieved of the care of feeding the larvæ and having over the workers the advantage of ovaries swollen with eggs, while the other females at the time of hatching contained only immature germs, continued to lay to the exclusion of the other females, whose nutricial functions kept them in a condition of sterility.

"At the end of the year, however, owing to the greater length of the imaginal than of the larval period, and also on account of the diminution in the egg laying of the queen or owing to her disappearance, the adult colony came to surpass the larval colony sufficiently in numbers to permit the later broods to receive and store up the reserve food which is indispensable to the maturation of the eggs. Hence these later broods alone would be able to hibernate and reproduce the species during the following spring. Only these individuals, therefore, should be regarded as representing the stirp from which all the future individuals proceed, the others being naturally eliminated from the genealogical tree.

"This single fact, namely, that only the individuals reared at the end of the season participate in the direct lineage of the different generations, suffices to account for a modification in the germ-plasm of the species; for *without even adducing the specific instinctive dispositions* which would later be acquired by natural selection, the conditions of nurture, and in particular those of nourishment, which control the development of the animal till the end of the year, depart from the mean of the variable conditions of nurture to which the evolving presocial insect was submitted. Under the influence of this modification acting as *external conditions*, constantly and always in the same manner, a new physicochemical constitution of the germ-plasm must necessarily arise and a new direction of development be opened up, namely, that which leads to the queen type.

"If the preceding theory be granted, the realization of the worker type becomes equally comprehensible. As long as there is no perceptible variation in the constitution of the germ-plasm, the worker will differ from the queen only in slight quantitative morphological variations, depending essentially, as we have demonstrated, on the phenomena of nutrition. This is the case in *Polistes* and less obviously in certain species of wasps (*Vespa*) which present an uninterrupted series of forms connecting the worker and queen types.

"But as soon as a perceptible modification of the germ-plasm intervenes, matters cease to be the same. The egg laid by a queen in the spring, like

all the eggs which she lays, contains, of course, this germ-plasm which has been modified by the autumnal régime and therefore presents all its modifications. Now the conditions under which it is called upon to pursue its development are not the same as those of the autumn, to which its germ-plasm has been exclusively habituated during a very long series of generations. This germ-plasm whose fixed constitution is adapted to a precise method of development in a given environment according to the queen type, and has been determined by the conditions to which it has been subjected for a great number of generations, finds itself in this particular egg suddenly emancipated from these modifying conditions and subjected to altogether new ones. What may we expect it to produce? If the modifications to which it finds itself submitted are too severe, it must perish; if, on the contrary, they are compatible with its evolution, it must proceed with its development as well as it can, like an animal constrained to develop under abnormal conditions. It is evident that the latter alternative alone is to be considered, since the former would lead to the extinction of the species. Now it is easy to see that this second alternative is nothing more nor less than a case of *experimental dichogeny.*"

In a later paper Marchal [1] aptly designates the suppression of the functional activity of the ovaries through the nursing, or nutricial habits of the workers as *nutricial castration.* He has shown that by eliminating the queen from the *Vespa* colony as many as a third of the workers become fertile. A similar result is brought about by a suppression or merely by a temporary suspension of the egg-laying of the queen. This can be due, as he maintains, only to abolition of the nursing function and the appropriation by the workers of the food which under normal conditions they would feed to the larvæ.

Marchal's view differs from that of Weismann in postulating a homogeneous germ-plasm and in rejecting representative units like the ids, determinants, etc. He regards the "differentiation" of the queen as due to the direct action of external conditions, especially of nourishment, and the differentiation of the workers as belonging to a class of phenomena, "which, if not essentially understood, are nevertheless known in their manifestations, namely *teratogenesis* and *dichogeny.*" Although this view is very similar to those of Spencer and Emery, the conception of nutricial castration seems to me to represent a valuable addition and I shall revert to it. [2]

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[1] La Castration Nutricial chez les Hymenopterès Sociaux. Compt. Rend. Sec. Biol., 5 Juin 1897, 2 pp.

[2] Nutricial castration (from *nutrix,* a nurse) must be distinguished from 'alimentary castration' (Emery, Le Polymorphisme, etc., *loc. cit.*), although both are responsible for the infertility of the worker. Through alimentary castration the development of the reproductive organs is inhibited in the larva and pupa, and this inhibition is maintained in the adult by the strong

The various extracts above quoted show very clearly that previous authors have been impressed by very different aspects of the complicated phenomena of polymorphism, and that each author has emphasized the aspect which seemed the most promising from the standpoint of the general evolutionary theory he happened to be defending. Escherich has recently called attention to two very different ways of envisaging the problem; one of these is physiological and ontogenetic, the other ethological and phylogenetic. As these furnish convenient captions under which to continue the discussion of the subject, I shall adopt them, and conclude with a third, the psychological aspect, which is certainly of sufficient importance to deserve consideration.

3. The Ontogenetic and Physiological Aspects of Polymorphism.

While the ontogeny of nearly all animals is a repetition or reproduction of the ontogeny of the parent, this is usually not the case in the social Hymenoptera, since the majority of the fertilized eggs do not give rise to queens but to more or less aberrant organisms, the workers. And as these do not, as a rule, reproduce, the whole phenomenon is calculated to arouse the interest of both the physiologist and the embryologist. The former, concentrating his attention on the reactions of the animal to the stimuli proceeding from its environment, is inclined to study its later stages as determined by the reactions to such stimuli, without regard to any internal or hereditary predetermination or disposition, while the embryologist seeks out the earliest moment at which the organism may be shown to deviate from the ontogenetic pattern of its parent. If this moment can be detected very early in the development he will be inclined to project the morphological differentiation back into the germ-plasm and to regard the efforts of the physiologist as relatively unimportant if not altogether futile. Now in his study of the social insects the embryologist is at a serious disadvantage, since he is unable to distinguish any prospective worker or queen characters in the eggs or even in the young larvæ. Compelled, therefore, to restrict his investigations to the older larvæ, whose development as mere processes of histogenesis and metamorphosis throws little or no light on the meaning of polymorphism, he is bound to abdicate and leave the physiologist in possession of the problem.

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nursing instincts which prevent the workers from appropriating much of the food supply of the colony to their individual use. In many of the higher animals also (birds, mammals) reproduction is inhibited by the exercise of the nutricial function. A third method of inhibiting or destroying the reproductive function is known to occur in the ' parasitic castration ' of certain bees and wasps (*Andrena, Polistes*) by Strepsiptera (*Stylops, Xenos*, etc.). See Perez, Des Effets du Parasitisme des Stylops sur les Apiaires du Genre Andrena. Actes Soc. Linn. Bordeau., 1886, 40 pp. 2 pll. Westwood (Notice of the Occurrence of a Strepsipterous Insect Parasitic on Ants, discovered in Ceylon by J. Nietner, Trans. Ent. Soc. London (2), V, 1861, pp. 418–420) has also described a Strepsipteron (*Myrmecolax nietneri*) which in all probability produces this form of castration in certain Formicidæ.

The physiologist, in seeking to determine whether there is in the environment of the developing social Hymenopteron any normal stimulus that may account for the deviation towards the worker or queen type, can hardly overlook one of the most important of all stimuli, the food of the larva. At first sight this bids fair greatly to simplify the problem of polymorphism, for the mere size of the adult insect might seem to be attributable to the quantity, its morphological deviations to the quality of the food administered to it during its larval life. Closer examination of the subject, however, cannot fail to show that larval alimentation among such highly specialized animals as the social insects, and especially in the honey-bees and ants, where the differences between the queens and workers are most salient, is a subject of considerable complexity. In the first place it is evident that it is not the food administered that acts as a stimulus but the portion of it that is assimilated by the living tissues of the larva. In other words, the larva is not altogether a passive organism, compelled to utilize all the food that is forced upon it, but an active agent capable, at least to a certain extent, of determining its own development. And the physiologist might have difficulty in meeting the assertion, that the larva utilizes only those portions of the proffered food which are most conducive to the specific predetermined trend of its development. In the second place, while experiments on many organisms have shown that the quantity of assimilated food may produce great changes in size or stature, there is practically nothing to show that even very great differences in the quality of the food can bring about morphological differences of such magnitude as those which separate the queens and workers of many ants.[1]

These more general considerations are reinforced by the following inferences from the known facts of larval feeding:

1. There seems to be no valid reason for supposing that the morphogeny of the queens of the social Hymenoptera depends on a particular diet, since with the possible exception of the honey and stingless bees, to be considered presently, they differ in no essential respect from the corresponding sexual phase of the solitary species. In both cases they are the normal females of the species and bear the same morphological relations to their males quite irrespective of the nature of their larval food. Hence, with the above mentioned exception of the honey and stingless bees, the question of the morphogenic value of the larval food may be restricted to the worker forms.

2. Observation shows that although the food administered to the

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[1] Emery (Le Polymorphisme, etc., *loc. cit.*) has called attention to the importance of the assimilative powers of the ant larva itself, quite irrespective of the quantity and quality of the food administered by the nurses — a very obscure physiological phenomenon, but not without analogies in other animals and especially in plants, which may assume a dwarfed habitus under apparently very favorable trophic conditions. The production of 'high' and 'low' males in Scarabæid and Lucanid beetles seems to be of the same nature.

larvæ of the various social insects is often very different in its nature, even in closely related species, the structure of the workers may be extremely uniform and exhibit only slight specific differences. Among ants alone we find the larvæ fed with a great variety of substances. Thus the Attii feed their larvæ on fungus hyphæ, the harvesting species of *Pheidole, Pogonomyrmex,* etc., on seeds, the Ponerinæ and many Myrmicinæ on pieces of insects, and most Dolichoderinæ and Camponotinæ supply their young with regurgitated liquid food. According to Dahl,[1] the larvæ of at least one species (*Camponotus quadriceps*) feed on the pith of plants. The quality of the food itself cannot, therefore, be supposed to have a morphogenic value. And even if we admit what seems to be very probable, namely, that a salivary secretion — possibly containing an enzyme — may be administered by some of these ants at least to their younger larvæ, the case against the morphogenic effects of qualitative feeding is not materially altered, as we see from the following considerations:

3. In incipient ant-colonies the queen mother takes no food often for as long a period as eight or nine months, and during all this time is compelled to feed her first brood of larvæ exclusively on the secretions of her salivary glands. This diet, which is purely qualitative, though very limited in quantity, produces only workers and these of an extremely small size (micrergates).

4. In the honey-bees, on the other hand, qualitative feeding, namely with a secretion, the so-called "royal jelly," which according to some authors (Schiemenz) is derived from the salivary glands, according to others (Planta) from the clylific stomach of the nurses, does not produce workers but queens. In this case, however, the food is administered in considerable quantity, since it is not provided by a single starving mother, as in the case of the ants, but by a host of vigorous and well-fed nurses. Although it has been taken for granted that the fertilized egg of the honey-bee becomes a queen as the result of this peculiar diet, the matter appears in a different light when it is considered in connection with von Ihering's recent observations on the stingless bees (Meliponidæ) of South America.[2] He has shown that in the species of *Melipona* the cells in which the males, queens, and workers are reared are all of the same size. These cells are provisioned with the same kind of food (honey and pollen) and an egg is laid in each. Thereupon they are sealed up, and although the larvæ are not fed from day to day as in the honey-bees, but like those of the solitary bees subsist on stored provisions, this uniform treatment nevertheless results in the production of

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[1] Das Leben der Ameisen im Bismarck-Archipel, Friedländer u. Sohn, 1901, p. 31.
[2] Biologie der stachellosen Honigbienen Brasiliens. Zool. Jahrb., Abth. f. Syst., XIX, 1903, pp. 179–287, 13 pll., 8 text-figs.

three sharply differentiated castes. On hatching the queen *Melipona* has very small ovaries with immature eggs, but in the allied genus *Trigona*, the species of which differ from the *Meliponæ* in constructing large queen cells and in storing them with a greater quantity of honey and pollen, the queen hatches with her ovaries full of ripe eggs. These facts indicate that the large size of the queen cell and its greater store of provisions are merely adaptations for accelerating the development of the ovaries. Now on reverting to the honey-bee we may adopt a similar explanation for the feeding of the queen larva with a special secretion like the "royal jelly." As is well known, the queen honey-bee hatches in about sixteen days from the time the egg is laid, while the worker, though a smaller insect and possessing imperfect ovaries, requires four or five days longer to complete her development. That the special feeding of the queen larva is merely an adaptation for accelerating the development of the ovaries is also indicated by the fact that this insect is able to lay within ten days from the date of hatching.[1] If this interpretation is correct the qualitative feeding of the queen larva is not primarily a morphogenic but a growth stimulus.

5. The grossly mechanical withdrawal of food substances already assimilated by the larva, as in the case of the *Pheidole instabilis* parasitized by the *Orasema* described in the first part of this article, produces changes of the same kind as those which distinguish the worker ant from the queen, *i. e.*, microcephaly, microphthalmy, stenonoty, and aptery. This case is of unusual interest because the semipupa, after the detachment of the parasite, seems to undergo a kind of regeneration and produces a small but harmonious whole out of the depleted formative substances at its disposal. What is certainly a female or soldier semipupa takes on worker characters while the worker semipupa may be said to become infra-ergatoid as the result of the sudden loss of formative substances. These observations clearly indicate that the normal worker traits may be the result of starvation or withholding of food rather than the administration of a particular diet.

6. The pseudogynes of *Formica* admit of a similar interpretation if it be true, as I have maintained (p. 33) that they arise from starved female larvæ. Here, too, the organism undergoes a kind of regeneration or regulation and assumes the worker aspect owing to a dearth of sufficient formative substances with which to complete the development as originally planned.

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[1] Cheshire (Bees and Bee-keeping. Scientific and Practical, 2 vols.) gives a different interpretation of the rapid growth of the queens. On p. 244, Vol. I, he regards the acceleration as the result of selection, since the first queen to hatch destroys her unhatched sisters. Hence the more rapidly the insect develops the greater her chances of survival. In another place (Vol. II, pp. 320, 321), however, he regards this individual advantage as a social disadvantage, since the toleration of several queens would greatly increase the number of workers and thereby strengthen the colony. My view refers not so much to the acceleration of the development of the queen as to that of her ovaries. It is evident that this, too, may be expressed in terms of advantage to the colony, since it enables the queen to lay very soon after the marriage flight.

7.   In the preceding cases, as I have shown in the first part of this article, the ants undergo a peculiar structural modification as the result of tolerating parasites that bring about unusual perturbations in the trophic status of the colony.   When ants themselves become parasitic on other ants a similar perturbation results, but in these cases the morphological effects are confined to the parasitic species and do not extend to their hosts.   This must be attributed to the fact that the parasitizing species live in affluence and are no longer required to take part in the arduous and exacting labors of the colony.   Under such circumstances the inhibitory effects of nutricial castration on the development of the ovaries of the workers are removed and there is a tendency for this caste to be replaced by egg-laying, gynæcoid individuals or by ergatogynes, or for it to disappear completely.   These effects are clearly visible in nearly all parasitic ants.   In the European *Tomognathus sublævis,* for example, the only known females are gynæcoid workers.   In the American *Leptothorax emersoni,* as I have shown,[1] gynæcoid workers and ergatogynes are unusually abundant while the true females seem to be on the verge of disappearing.   Among the typical amazon ants (*Polyergus rufescens*) of Europe, ergatogynes are not uncommon.   In *Strongylognathus testaceus* the worker caste seems to be dwindling, while in several permanently parasitic genera (*Anergates, Wheeleria, Epœcus, Epipheidole* and *Sympheidole*) it has completely disappeared.   Only one cause can be assigned to these remarkable effects — the abundance of food with which the parasites are provided by their hosts.

8.   In the Ponerinæ and certain Myrmicinæ, like *Pheidole, Pogonomyrmex,* and *Aphænogaster,* the larvæ are fed on pieces of insects or seeds, the exact assimilative value of which as food can neither be determined nor controlled by the nurses.   And while they may perhaps regulate the quantity of food administered, it is more probable that this must fluctuate within limits so wide and indefinite as to fail altogether to account for the uniform and precise morphological results that we witness in the personnel of the various colonies.   Moreover, accurate determination of the food supply by the workers must be quite impossible in cases like that of the *Pachycondyla* larva attended by the commensal *Metopina* which surreptitiously consumes a portion of the proferred food.

9.   The intimate dependence of the appearance of the different castes of the social insects on the seasons may also be adduced as evidence of the direct effects of the food supply in producing workers and queens.   The latter are reared only when the trophic condition of the colony is most favorable and this coincides with the summer months.   In the great major-

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[1] Ethological Observations on an American Ant (Lepthorax Emersoni Wheeler), Arch. f. Psych. u. Neurol., II, 1903, p. 6.

ity of species only workers and males are produced at other seasons. Here, too, the cause is to be sought in the deficient quantity of food rather than in its quality, which is, in all probability, the same throughout the year, especially in such ants as the fungus-growing Attii and the seed storing Myrmi-.cinæ.

While these considerations tend to invalidate the supposition that qualitative feeding is responsible for the morphological peculiarities of the worker type, they are less equivocal in regard to the morphogenic effects of quantitative feeding. Indeed, several of the observations above cited show very clearly that diminution in stature and, in pathological cases, even reversion to the worker form may be the direct effect of underfeeding. To the same cause we may confidently assign several of the atypical phases among ants, such as the micrergates, microgynes, and micranērs, just as we may regard the macrergates, macrogynes, and macranērs as due to overfeeding. These are, of course, cases of nanism and giantism, variations in stature, not in form. Similarly, all cases in which, as in certain species of *Formica, Camponotus, Pheidole*, etc., the workers or desmergates vary in size, must be regarded as the result of variable quantitative feeding in the larval stage. Here we are confronted with the same conditions as Weismann observed in the blow-flies and which entomologists have noticed in many other insects. Such variations are of the fluctuating type and are therefore attributable to the direct effects of the environment. The soldier and worker, however, differ from the queen in the absence of certain characters, like the wings, wing-muscles, spermatheca, some of the ovarian tubules, etc., and the presence of other characters, like the peculiar shape of the head and mandibles. In these respects the sterile castes may be regarded as mutants, and Weismann's contention that such characters cannot be produced by external conditions, such as feeding, is in full accord with de Vries's hypothesis. His further contention, however, that they must therefore be produced by natural selection need not detain us, since it is daily becoming more and more evident that this is not a creative but an eliminative principle. It is certain that the very plastic social insects, like the ants, have developed a type of ontogeny which enables them not only to pupate at an extremely early period of larval life, but also to hatch and survive as useful though highly specialized members of the colony. It is quite conceivable that this precocious pupation may be directly responsible for the complete suppression of certain organs that require for their formation more substance than the underfed larva has been able to accumulate. At the same time it must be admitted that a direct causal connection between underfeeding on the one hand and the ontogenetic loss or development of characters on the other, has not been satisfactorily established. The conditions in the termites,

which are often cited as furnishing proof of this connection, are even more complicated and obscure than those of the social Hymenoptera. While Grassi and Sandias,[1] and Silvestri,[2] agree with Spencer in regarding the feeding as the direct cause of the production of the various castes, Herbst,[3] who has reviewed the work of the former authors, shows that their observations are by no means conclusive; and Heath[4] makes the following statement in regard to his experiments on Californian termites: "For months I have fed a large number of termite colonies of all ages, with or without royal pairs, on various kinds and amounts of food — proctodæal food dissected from workers or in other cases from royal forms, stomodæal food from the same sources, sawdust to which different nutritious ingredients had been added — but in spite of all I cannot feel perfectly sure that I have influenced in any unusual way the growth of a single individual."

This rather unsatisfactory answer to the question as to whether quantity or quality of food or both, have an ergatomorphic value, has led some investigators to seek a solution along more indirect lines. Thus O. Hertwig and Herbst suggest that the morphogenic stimulus may be furnished by some internal secretion of the reproductive organs. This, too, is possible, but owing to our very imperfect knowledge of the internal secretions, even in the higher animals, we are not in a position either to accept or reject this suggestion.

More tangible is Emery's attempt[5] to explain the worker characters as the result of a struggle among the parts of a prematurely metamorphosing insect. He has not been led into the invisible battle of the ids and determinants on which Weismann recently constructed his hypothesis of germinal selection,[6] but is content with a struggle between the larger regions of the body and between their various organs. This point of view was suggested by his study of the mermithergates. He is of the opinion that "the same law of growth which determines the proportions of the head and gaster in the *Mermis*-infested workers (see pp. 24, 25 *antea*) obtains also in normal ants. I designate it as the "law of opposition between head and gaster" and would state it as follows:

"While the imago is developing within the full-grown ant larva, what is needful for the structures essential to the life of the organism is first emphasized, especially for the digestive and reproductive organs contained in the gaster; the formation of the external shape of the head, and especially of

[1] Costituzione e Sviluppo della Società dei Termitidi. Catania, 1893, 150 pp., 5 pll.
[2] Operai ginecoidi di Termes, con osservazioni intorno l' origine delle varie caste nei Termitidi, Real. Accad. Lincei, X, sér. 5, 1901, pp. 479–484.
[3] Formative Reize in der Tierischen Ontogenese, Leipzig, Arthur Georgi, 1901, pp, 20–24.
[4] The Habits of California Termites. Biol Bull. IV, Dec. 1902, pp. 62–23.
[5] Zur Kenntniss des Polymorphismus, etc., *loc. cit.*, p. 603.
[6] On Germinal Selection. Religion of Science Library. Open Court Publ. Co., Chicago, 1896.

the mandibles and of the muscles which are to move them, is regulated according to the amount of formative substance remaining. Perhaps phylogenetic factors also enter into this process and, with the absence of sufficient substance, also phenomena of atavism in the form of a certain stress on the phylogenetically older structures.

"As a result of these processes we find that when one of two metamorphosing larvæ has a large abdomen its head will be relatively smaller than that of the other, because there remains a relatively smaller amount of larval food substance."

Towards the end of his paper (pp. 608, 609) Emery still further elaborates this view and concludes with the following remarks: "The determination both of the relative size of the various regions of the body and of the individual organs to one another may be regarded as a struggle among the parts (Kampf der Theile) of the organism. In the metabolic insects, in particular, this struggle may be divided into two periods:

"During the first period, which may be of long duration, food supplies are accumulated in an indifferent manner as the larval fat-body while at the same time the rudiments of the imaginal organs arise and prepare themselves for the struggle.

"During the second period the struggle among the rudiments actually sets in and must be particularly acute in cases where the store of food is meager on account of underfeeding of the larva. The struggle will be decided in favor of the rudiments which are capable of most vigorously appropriating the nourishment.

"To this struggle is due the regular type of polymorphism as it is exhibited by worker ants in its definite relations to the volume of the body. But before this struggle takes place, the result is already decided, because the ability of the individual imaginal rudiments to attract the larval food reserves has been determined. We may therefore assume that during the first period, by a process still completely unknown, there is a determination of the growth energy of the individual imaginal rudiments which, in the second period, will struggle for the possession of the limited supply of larval food. We may further assume that during the first period, through the relations of the imaginal rudiments to one another and to the amount of larval food substances, the type of the individual, whether female, worker, pseudogyne, etc., as well as its size, is determined. These peculiarities, however, do not manifest themselves till the second period.

"*As trophic polymorphism the polymorphism of the female sex in ants is a function of the distribution of the nutritive substances accumulated during larval life, a distribution which in turn is determined by the struggle among the imaginal rudiments.*"

In commenting on this hypothesis of a struggle of the parts in connection with the mermithergates, I have already shown (p. 26) that it is inapplicable to the cases which first suggested it. This does not, however, disqualify it as a possible explanation of the normal worker forms. It does, indeed, appear to give us an insight into the possible conditions of development in the starved larvæ from which the workers arise and suggests interesting problems for the experimentalist. Still it is incomplete and like the other views considered in the preceding paragraphs, fails to account for the highly adaptive structure of the worker.

There lurks, perhaps, in Emery's hypothesis a suggestion of a widespread notion that there is something monstrous, teratological or hypertelic, about the workers and especially about the soldiers of the social insects. This is more explicitly stated in the above-quoted passages from Spencer and Marchal (pp. 60, 65). The latter, in fact, regards the rearing of the sterile forms as a kind of experimental teratogeny. Such an impression is very natural, for the soldiers of many ants and termites certainly exhibit developments of the head and mandibles unlike anything found in other insects. And it is not impossible that these castes may have orginally made their appearance as teratological developments. But that they are such at the present time is very improbable, since we find that they are not only normal and all-important constituents of the colony, but have become exquisitely adapted to particular functions. Wherever the habits of the soldiers have been carefully studied it has been found that their singular and apparently hypertrophied structures have a very definite function. Thus it has been shown that the peculiarly truncated heads of the *Colobopsis* soldiers are used as "animated front-doors" in closing the circular entrances to the galleries of the nest, that the colossal crania of the *Pheidole* soldiers accommodate the huge muscle-masses of the jaws which in turn are used in cracking hard seeds and the tough integument of insects, and that the peculiar sickle-shaped mandibles of the soldiers of *Myrmecocystus bombycinus* are used for carrying the voluminous pupæ.[1] It is very probable that in termites the singular heads of the nasute and mandibulate soldiers will be found to be similarly adapted to special functions in the economy of the colony. At any rate we are not justified in regarding such structures as hypertelic or teratological till we know more about the habits of the species in which they occur.

We may conclude, therefore, that while the conception of the worker type as the result of imperfect nutrition is supported by a considerable volume of evidence, we are still unable to understand how this result can take

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[1] See Escherich, Die Ameise, *loc. cit.*, p. 46.

·on so highly adaptive a character. Such a concise effect can hardly be due to manifold and fluctuating external causes like nutrition, but must proceed from some, more deeply seated cause within the organism itself. Of course, the difficulty here encountered is by no means peculiar to polymorphism; it confronts us at every turn as the all-pervading enigma of living matter. Whether we shall fare better by approaching the subject from a different point of departure remains to be seen.

4. THE PHYLOGENETIC ASPECT OF POLYMORPHISM.

An intensive study of the structure and habits of ants must inevitably lead to a certain amount of speculation concerning the phylogenetic devel-·opment of their colonies. That these insects have had communistic habits for ages is clearly indicated by the fact that all of the numerous existing species are eminently social. There can be little doubt, however, that they arose from forms with habits not unlike those we find today in some of the solitary wasps, such as the Bembecidæ, or in the remarkable South African bees of the genus *Allodape*.[1] Unlike other solitary wasps, the females of *Bembex* may be said to be incipiently social, since a number of them choose a nesting site in common and, though each has her own burrow, coöperate with one another in driving away intruders. *Bembex* has also taken an important step in the direction of the social wasps not only in surviving the hatching of her larvæ, but also in visiting them from day to day for the pur-pose of providing them with fresh insect food.[2]

At a very early period the ants and social wasps must have made a fur-ther advance when the mother insect succeeded in surviving till after her progeny had completed their development. This seems to have led nat-urally to a stage in which the young females remained with their mother and reared their progeny in the parental nest, thus constituting a colony of a number of similar fertile females with a common and indiscriminate interest in the brood. This colony, after growing to a certain size, became unstable in the same way as any aggregate of like units, and must soon have shown a differentiation of its members into two classes, one of individuals devoted to reproduction and another class devoted to alimentation and pro-tection. In this division of labor only the latter class underwent important somatic modification and specialization, while the former retained its prim-

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[1] I infer this from a brief account (*in litteris*) of two species of these insects, recently received, together with specimens of their extraordinary larvæ, from Dr. Hans Brauns of Cape Colony.
[2] Interesting accounts of the habits of this insect have been published by Fabre (Souvenirs Entomologiques. Prem. Sér., Paris, Chas. Delagrave, 1 éd., 1879; 3 éd., 1894, pp. 221–234); Wesenberg-Lund (Bembex rostrata, dens Liv og Instinkter. Ent. Meddel. Kjöbenhavn, III, 1891, pp. 19–44; English résumé in Psyche, VII, p. 62); and Geo. W. and Elizabeth G. Peck-ham, On the Instincts and Habits of the Solitary Wasps. Wis. Geol. Nat. Hist. Surv., Bull. No. 2, 1898, pp. 58–72.

itive and more generalized characters. It is more than probable, as I.
shall attempt to show in the sequel, that this differentiation was manifested:
in the sphere of instinct long before it assumed morphological expression.
The social wasps and bumble bees are practically still in this stage of soci-
ogeny. The ants, however, have specialized and refined on these conditions.
till they not only have a single marked alimentative and protective caste
without wings[1] and lacking many other female characters, but also in some
species two distinct castes with a corresponding further division of labor.
Both in the phylogeny and the ontogeny these characters appear as the
result of nutricial castration.

If the foregoing considerations be granted the biogenetic law may be
said to hold good in the sociogeny of the ants, for the actual ontogenetic
development of their colonies conforms not only to the purely conjectural
requirements of phylogeny but also with the stages represented by the va-
rious extant groups of social insects. It is clear that we cannot include the
honey-bee among these groups, since this insect is demonstrably so aberrant
that it is difficult to compare it with the other social insects.

Comparison of the different genera and subfamilies of ants among them-
selves shows that some of them have retained a very primitive social
organization, and with it a relatively incomplete polymorphism, whereas
others have a much more highly developed social life and a greater differ-
entiation of the castes. Such a comparison coupled with a study of the
natural relationships of the various genera as displayed in structure, shows
very clearly that the advance from generalized to highly specialized societies.
did not follow a single upward course during the phylogeny, but occurred
repeatedly and in different phyletic groups. And since the complications.
of polymorphism kept pace with those of social organization, we may say
that the differentiation of the originally single worker caste into dinergates,
or soldiers on the one hand and micrergates, or small workers, on the other,

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[1] Emery (Zur Kenntniss des Polymorphismus, etc., *loc. cit.*, pp. 628, 629) has recently restated
his opinion that the females of the primitive ants were wingless, like the workers of existing
species, and acquired wings during the phylogeny, an opinion to which he was led by deriving
the ants from Mutillid-like ancestors. McClendon and I (Dimorphic Queens, etc., *loc. cit.*, p.
161, 162) dissented from this view on the ground that there is no known case among insects of
a reacquisition after loss of these organs. Emery replies that they have not been lost but still
exist in the germ-plasm of the female Mutillid, since she produces males with perfect wings.
He believes that the wings of existing female ants are an inheritance from the male. The possi-
bility of such an inheritance cannot, of course, be disputed, but when the matter is so largely
conjectural, the simpler hypothesis maintained by McClendon and myself seems preferable. It
is certainly easier to believe that both Mutillids and ants are derived from a common ancestor
with both sexes winged, and that the wings were retained by the worker ants, as they are still
in the social bees and wasps, till these castes had been definitely established, than to assume a
loss followed by a reacquisition of these organs in the queens. Moreover, there is no known
case in which an organ has been completely transferred to the opposite sex. Even cases like
the vestigial mammæ of mammals and the antlers of the female reindeer are best explained as.
characters once equally developed and functional in both sexes. (See Lydekker, The Deer of
all Lands, London, Rowland Ward, 1898, p. 10). The ergatoid and gynæcoid characters of
male ants referred to by Emery, may indeed be inherited from the workers and females respec-
tively, but they are modifications of well-developed and functional organs of the male. This.
case is therefore not strictly comparable with the transfer of whole organs like the wings with.
their complicated musculature, venation, etc., from one sex to the other.

has been repeated in remotely related genera. In some genera (*Stenamma* sens. str., *Leptothorax*) there are also indications of a lapsing of highly specialized into simpler conditions by a kind of social degeneration. In its extreme form this manifests itself as a suppression of castes and a consequent simplification of polymorphism. Beautiful illustrations of this statement are furnished by the parasitic species that have lost their worker caste. But there are also cases in which the queen caste has been suppressed and its functions usurped by workers.

Not only have these greater changes been effected and fixed during the phylogenetic history of the Formicidæ, but also many subtler differences such as those of stature, coloration, pilosity and sculpture. And although such differences belong to the class of fluctuating variations and are usually supposed to have a greater ontogenetic than phylogenetic significance, they are undoubtedly of great antiquity and must therefore be regarded as more important than many of the minor morphological traits.

Emery was the first to call attention to a number of peculiar phylogenetic stages in the development of stature among ants.[1] We find by comparison with the male, which may be regarded as a relatively stable and conservative form, that the cospecific females and workers may vary in stature independently of each other. The following are the stages recognized by Emery, with some additions of my own:

1. In the earliest phylogenetic condition which is still preserved in the ants of the subfamily Ponerinæ and in certain Myrmicinæ (*Pseudomyrma, Myrmecina*, etc.), the workers are monomorphic and of about the same size as the males and females.

2. The worker becomes highly variable in stature from large forms (dinergates, or maxima workers) resembling the female, through a series of intermediates (desmergates) to very small forms (minima workers, or micrergates). This condition obtains in the Dorylinæ, some Myrmicinæ, (some species of *Pheidole, Pheidologeton, Atta*), Camponotinæ (*Camponotus*) and Dolichoderinæ (*Azteca*).

3. The worker becomes dimorphic through the disappearance of the desmergates, so that the originally single, variable caste is now represented by two, the soldier (dinergate) and worker proper. We find this condition in certain Myrmicinæ and Camponotinæ (*Cryptocerus, Pheidole, Acanthomyrmex, Colobopsis*, etc.).

4. The soldier of the preceding stage disappears completely, so that the worker caste again becomes monomorphic but is represented by individuals very much smaller than the female. Such individuals are really micrergates.

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[1] Die Entstehung und Ausbildung der Arbeiter bei den Ameisen, *loc. cit.*, pp. 55, 56.

This condition is seen in certain Myrmicine genera, especially of the tribe Solenopsidii (*Carebara, Erebomyrma, Diplomorium*, most species of *Solenopsis*, etc.).

5. The worker form disappears completely, leaving only the males and females to represent the species, which thus returns to the condition of sexual dimorphism seen in the great majority of insects and other Metazoa. This occurs in the parasitic ants of the genera *Anergates, Wheeleria, Epœcus, Sympheidole* and *Epipheidole*.

6. In certain species the workers remain stationary while the female increases in size. This is indicated by the fact that the worker and male have approximately the same stature. Such a condition obtains in certain Myrmicinæ (*Cremastogaster*), Camponotinæ (*Lasius, Prenolepis, Brachymyrmex*, the North American species of *Myrmecocystus*), and Dolichoderinæ (*Iridomyrmex, Dorymyrmex, Liometopum*).

7. The worker caste remains stationary while the female diminishes in size till it may become even smaller than the large workers. This occurs in certain parasitic species of North America, like *Aphœnogaster tennesseensis* among the Myrmicinæ, and among the Camponotinæ in the species of the *Formica microgyna* group (*F. difficilis, nevadensis, impexa, montigena, nepticula*).

8. The female phase disappears completely and is replaced by a fertile, or gynæcoid worker form. This occurs in the Myrmicine *Tomognathus sublœvis*, in certain Ponerine genera like *Leptogenys* (including the subgenus *Lobopelta*), and probably also in *Diacamma* and *Champsomyrmex*. The conditions in *Acanthostichus* and certain Cerapachyi (*Parasyscia peringueyi*) indicate that the dichthadiigynes of the Dorylinæ may have arisen from such gynæcoid workers instead of from winged queens.

9. The female shows a differentiation into two forms (*a*- and *β*-females) characterized by differences in the structure of the legs and antennæ, in pilosity and coloration (*Lasius latipes*), or in the length of the wings. (macropterous and micropterous females of *L. niger*). The macrocephalic and microcephalic females of *Camponotus abdominalis* and *confusus* described by Emery[1] may also be regarded as *a*- and *β*-forms. In this series of stages, one to five represent changes in the worker caste while the female remains relatively stationary, whereas stages six to nine represent the converse conditions. Stages one to four probably succeeded one another in the order given, but stage five may have arisen either from the first or fourth. The sixth to ninth stages must, of course, be supposed to have developed independently of one another.

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[1] Le Polymorphisme des Fourmis, etc., *loc. cit.*, pp. 400, 401.

The stature differences described in the above paragraphs are in most if not all cases, highly adaptive. This is clearly seen in such forms as the Indo-African *Carebara*, the huge, deeply colored females of which are more than a thousand times as large as the diminutive, yellow workers. This ant dwells in termite nests where it occupies chambers connected by means of tenuous galleries with the spacious apartments of its hosts. The termites constitute a supply of food so accessible and abundant that the workers are able to rear enormous males and females, while they themselves must preserve their diminutive stature in adaptation to their clandestine and thievish habits. Similar conditions are found in many species of the allied genus *Solenopsis*, which inhabit delicate galleries communicating with the nests of other ants on the larvæ and pupæ of which they feed. In one species of this genus (*S. geminata*) however, which leads an independent life and feeds on miscellaneous insects and seeds, the worker caste is still highly polymorphic.

Another interesting case of adaptation in stature is seen in the ants of the *Formica microgyna* group. The females of these species are temporarily parasitic in the nests of other *Formicæ* and are therefore relieved of the labor of digging nests for themselves and rearing their first brood of larvæ. On this account they need not store up large quantities of food, so that the nourishment which in nonparasitic species goes to produce a comparatively few large females may be applied to the production of a large number of small females. This latter condition is necessary in parasitic species which are decimated by many vicissitudes before they can establish themselves successfully among alien hosts. I have already emphasized the adaptive significance of the disappearance of the worker caste among permanently parasitic species like *Anergates*, *Wheeleria*, etc.

There are several cases in which the worker and female differ greatly in color, pilosity, or sculpture, and in such cases either caste may be conservative or aberrant according to ethological requirements. Thus in certain temporary parasites like *Formica ciliata, oreas, montigena, dakotensis,* and *difficilis*, the female is aberrant in one or more of the characters mentioned, while the cospecific worker retains the ancestral characters of the same caste in the closely allied forms of *F. rufa*. The same condition is seen in a very different ant, *Aphænogaster tennesseensis*, as the result of similar parasitic habits. In all of these species the females alone have developed myrmecophilous characters, like the long yellow hairs of *F. ciliata*, or the mimetic coloring of *F. difficilis*, which enable them to foist themselves on allied species and thus avoid the exhausting labor of excavating nests and rearing workers.

The foregoing observations indicate that in their morphological charac-

ters the worker and female of the same species have advanced or digressed in their phylogeny, remained stationary or retrograded, independently of each other. The same peculiarity is also observable in species with distinct worker and soldier castes. It thus becomes impossible even in closely related species of certain genera, like *Pheidole*, to predict the characters of the worker from a study of the cospecific soldier or *vice versâ*. And while adaptive characters in stature, sculpture, pilosity and color must depend for their ontogenetic development on the nourishment of the larvæ, it is equally certain that they have been acquired and fixed during the phylogeny of the species. In other words, nourishment, temperature, and other environmental factors merely furnish the conditions for the attainment of characters predetermined by heredity. We are therefore compelled to agree with Weismann that the characters that enable us to differentiate the castes must be represented in the egg. We may grant this, however, without accepting his conception of representative units, a conception which has been so often refuted that it is unnecessary to reconsider it in this connection. Far preferable appears to be the view of the constantly increasing number of biologists who conceive the adult characters to be represented in the germ as dynamic potencies or tensions rather than as morphological or chemical determinants.

Having touched upon this broader problem of heredity it will be necessary to say something about the inheritance or non-inheritance of acquired characters, especially as Weismann and his followers regard the social insects as demonstrating the non-transmissibility of somatogenic traits. In establishing this view and the all-sufficiency of natural selection to which it leads, Weismann seems to me to have slurred over the facts. While he admits that the workers may lay eggs, and that these may produce male offspring capable of fertilizing females, he nevertheless insists that this is altogether too infrequent to influence the germ-plasm of the species. I venture to maintain, on the contrary, that fertile workers occur much more frequently in all groups of social insects than has been generally supposed. As this fertility is merely a physiological state it has been often overlooked. Marchal (*vide ante*, p. 65), has shown how readily the workers of the social wasps assume this state, and the same is true of honey bees, especially of certain races like the Egyptians and Cyprians (*Apis mellifica-fasciata* and *cypria*). In the hives of these insects fertile workers are either always present or make their appearance within a few days after the removal of the queen. In the termites fertile soldiers have been observed by Grassi and Sandias (*l. c.*), and fertile workers by Silvestri (*l. c.*). Among ants fertile, or gynæcoid, workers occur so frequently as to lead to the belief that they must be present in all populous colonies. Their presence is also

proved by the production of considerable numbers of males in old and queen-less colonies. In artificial nests Wasmann,[1] Miss Fielde[2] and myself have found egg-laying workers in abundance.

As the males that develop from worker eggs are perfectly normal, and in all probability as capable of mating as those derived from the eggs of queens, we are bound to conclude, especially if we adopt the theory of heredity advocated by Weismann himself, that the characters of the mother (in this case the worker) may secure representation in the germ-plasm of the species. Weismann is hardly consistent in denying the probability of such representation, for when he is bent on elaborating the imaginary structure of the germ-plasm he makes this substance singularly retentive of alteration by amphimixis, but when he is looking for facts to support the all-sufficiency of natural selection the germ-plasm becomes remarkably difficult of modification by anything except this eliminative factor. Certainly the simplest and directest method of securing a representation of the worker characters in the germ-plasm would be to get them from the worker itself that has survived in the struggle for existence, rather than through the action of natural selection on fortuitous constellations of determinants in the germ-plasm of the queen.

If we grant the possibility of a periodical influx of worker germ-plasm into that of the species, the transmission of characters acquired by this caste is no more impossible than it is in other animals, and the social insects should no longer be cited as furnishing conclusive proof of Weismannism. Weismann undoubtedly deserves lasting credit for his accurate distinction of blastogenic and somatogenic characters, and for having rid biological science of a multitude of crude conceptions concerning the inheritance of the latter. Even the many investigators, who, like Boveri,[3] Delage,[4] Pauly,[5] Plate,[6] Rignano,[7] and Semon,[8] still believe in the transmissibility of acquired characters, show the effects of Weismann's clarifying and critical efforts.

Plate[9] attempts to overcome the difficulties presented by the normal sterility of the worker by supposing that the distinguishing characters of this caste arose prior to their inability to reproduce. He recognizes the following stages in the phylogeny of the social insects:

"1. The presocial stage with but a single kind of male and female.

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[1] Parthenogensis bei Ameisen durch Künstliche Temperaturverhältnisse.   Biol. Centralbl., XI, 1891, pp. 21–23.
[2] Observations on the Progeny of Virgin Ants.   Biol. Bull., IX, 1905, pp. 355–360; Temperature as a Factor in the development of Ants, *ibid.*, IX, 1905, pp. 361–367.
[3] Die Organismen als Historische Wesen.   Wurzburg, 1906.
[4] L' Hérédité et les Grands Problèmes de la Biologie Générale.   2 ed., Paris, C. Reinwald, 1903.
[5] Darwinismus und Lamarckismus.   München, Ernest Reinhardt, 1905.
[6] Ueber die Bedeutung des Darwin'schen Selectionsprincips und Probleme der Artbildung. 2 Aufl., Leipzig, Wilh Engelmann, 1903.
[7] Sur la Transmissibilité des Charactères Acquis.   Paris, Felix Alcan, 1906.
[8] Die Mneme als Erhaltendes Prinzip im Wechsel des Organischen Geschehens.   Leipzig, Wilh. Engelmann, 1904.
[9] Ueber die Bedeutung des Darwins'schen Selectionsprincips, etc., *loc. cit.*, p. 73–75.

"2. The social stage with but a single kind of male and female. The peculiarities in nesting, caring for the brood, and the other instincts were already developed during this stage.

"3. The social stage with one kind of male and two or several kinds of females, which were all fertile, but in consequence of the physiological division of labor became more and more different in the course of generations. The division of labor took place in such a manner that the sexual functions passed over primarily to a group A,· while the construction of the nest, predatory expeditions and other duties devolved mainly on another group of individuals (B) which on that account used their reproductive organs less and less.

"4. The present stage with one kind of male, a fertile form of female, which arose from group A, and one or several kinds of sterile females, or workers (group B).

He thus assumes that the differentiation into sterile and fertile forms did not take place till stage 3, and, if I understand him correctly, not till after "the races had become differentiated morphologically." This view, as Plate admits, resembles Spencer's (p. 59). The two views, in fact, differ merely in degree, for the underlying contention is the same, namely that sterility is one of the most recently developed characters among the social insects. There can be little doubt, however, that the smaller adaptive characters, for example those of the females of certain *Formicæ* above mentioned, must have made their appearance in the fourth stage of Plate's scheme. The view which I have advocated differs from Plate's in admitting that even in this stage the workers are fertile with sufficient frequency to maintain a representation of their characters in the germ-plasm of the species. Conclusive evidence of the presence or absence of such representation can be secured only by experimental breeding and especially by hybridizing the male offspring of workers of one species (a), with females of another (b) that has workers of a different character. Under these conditions some of the characters of a should make their appearance in b. The most favorable genera for such experiments would probably be *Myrmica, Formica,* and *Lasius,* in all of which there are species, subspecies, and varieties with distinctly characterized workers while the corresponding males and females are sufficiently alike to make hybridization seem feasible.

5. The Ethological and Psychological Aspects of Polymorphism.

In the foregoing discussion attention has been repeatedly called to adaptation as the insurmountable obstacle to our every endeavor to explain polymorphism in current physiological terms. Of course, this is by no means a peculiarity of polymorphism, for the same difficulty confronts us in every

biological inquiry. Adaptation, conceived as a phylogenetic process, and its ontogenetic counterpart, accommodation or regulation, are not only the central problems of all biology, but they constitute the proper field of ethology.[1]   Emery,[2] and Waxweiler regard ethology as at bottom merely external physiology. The former defines it as treating of "the *ensemble* of phenomena whose physiological analysis has not yet been accomplished and is not even possible at the present time." This implies that when the analysis has been accomplished, ethology will be merged into physiology. Such a view is in my opinion open to discussion, since ethology also embraces the behavior, *i. e.*, the instinctive and intelligent actions by means of which organisms adapt or accommodate themselves to their environment and must be to that extent psychological. Hence there is opportunity for considerable difference of opinion in regard to the ultimate fate of ethology. Authors who believe that psychology will resolve itself into physiology will agree with Emery, whereas those who believe that biology will become increasingly psychological and metaphysical — and the number of these seems to be increasing — will predict that ethology will ally itself more closely with the mental sciences.

This dual possibility depends, of course, on two ways of envisaging the problem of adaptation. Those who view it from the physical (*i. e.*, mechanical), antiteleological and Neodarwinian standpoint, repudiate any attempt to substitute psychological terms in biological explanation, and assign as their reason for this course the existence of a psycho-physical parallelism. On the other hand, those who view the problem from the vitalistic, teleological and Lamarckian standpoint, turn to psychical manifestations like the will, with which we as acting subjects are perfectly familiar, as yielding a more adequate and satisfying insight into the phenomena. These different standpoints have been recently presented in violent contrast to each other in two works on adaptation by Detto[3] and Pauly.[4]

At first sight it may be difficult to understand why allusion should be made to these abstruse and very general matters in the discussion of a special subject like polymorphism. Reflection shows, however, that the social insects make a consideration of these matters necessary, since these organ-

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[1] An excellent discussion of the scope and problems of this science has been recently published by Waxweiler (Esquisse d'une Sociologie, *loc. cit.*, p. 29 *et seq.*). He has shown that Is. Geoffroy Saint Hilaire, in 1854, first introduced the term 'ethology' for the subject which Hæckel in 1866 designated as 'œcology' in his 'Generelle Morphologie.' The term 'bionomics' employed by Lankester, Baldwin, Gulick and others, is of course, of still more recent date. 'Ethology' therefore, not only has priority, but it is also more apt than the other terms that have been suggested. It will probably come into general use among English and American zoölogists, now that it has been adopted in such works as the 'Zoölogical Record.'

[2] Ethologie, Phylogénie et Classification. Comptes Rendus du 6 Congrès internat. Zool., Berne, 1904.

[3] Die Theorie der directen Anpassung und ihre Bedeutung für das Anpassungs-und Descendenzproblem. Jena, Gustav Fischer, 1904.

[4] Darwinismus und Lamarckismus, *loc. cit.*

isms are far and away the most plastic and adaptable and psychically the most richly endowed of all the lower animals. I use this term "psychically" advisedly, for, like Forel and Wasmann, I find myself utterly unable to accept the views of Bethe, Uexküll, and others, who regard the social insects as mere reflex machines. Nor have I the slightest hesitation in substituting psychological terms wherever physical terms are inadequate, as I am by no means convinced of the cogency of the hypothesis of psychophysical parallelism and the epistemological restrictions to which it is supposed to bind the investigator. If I am not greatly mistaken, psychophysical parallelism has of late received some pretty rough treatment at the hands of more than one eminent psychologist.[1]

As the type of polymorphism with which I have been dealing has been developed by psychically highly endowed social insects, it cannot be adequately understood as a mere morphological and physiological manifestation apart from the study of instinct. This has been more or less distinctly perceived by nearly all writers on the subject. However various their explanations, Spencer, Weismann, Emery, Forel, Marchal, and Plate all resort to instinct. Emery, especially, has seen very clearly that a worker type with its peculiar and aberrant characteristics could not have been developed except by means of a worker-producing instinct. In other words, this type is the result of a living environment consisting of the fostering queen and workers which instinctively control the development of the young in so far as this depends on external factors. Only under such conditions could a worker caste arise and repeat itself generation after generation. This caste may be regarded as a mutation, comparable with some of De Vries's *Œnothera* mutations, but able to repeat and maintain itself for an indefinite series of generations in perfect symbiosis with its parent form, the queen, because notwithstanding its relative infertility, it can be put to very important social use. Among ants this social use not only pervades the activities of the adult worker but extends even to the more inert larval stages. Thus the latter represent a rich and ever-fresh supply of food that can be devoured whenever a temporary famine overtakes the colony. In certain species, like the East Indian *Œcophylla smaragdina* and the South American *Camponotus senex,* the larvæ are put to a more humane use as spinning machines for constructing the silken nest inhabited by the colony. These examples also illustrate the purposive manner in which an organism can satisfy definite needs by taking advantage of ever-present opportunities.

In the lives of the social insects the threptic, or philoprogenitive instincts are of such transcendent importance that all the other instincts of the species,

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[1] See, *e. g.,* Busse, Geist und Körper. Leipzig, Dürr'sche Buchhandlung, 1903; and Binet, L'Âme et le Corps. Paris, Ernest Flammarion, 1905.

including, of course, those of alimentation and nest-building, become merely tributary or ancillary. In ants, especially, the instincts relating to the nurture of the young bear the aspect of a dominating obsession. The very strength and scope of such instincts, however, renders these insects more susceptible to the inroads of a host of guests, commensals and parasites. besides the parasitic larvæ of Chalcidids, Lomechusini and *Metopina* described in the first part of this article, there are many adult beetles and other insects on which the ants lavish as much or even more attention than they do on their own brood. And when the ants themselves become parasitic on other ants, it is always either for the sake of having their own brood nurtured, as in the temporarily and permanently parasitic forms, or for the purpose of securing the brood of another species, as in the slave-making, or dulotic species.

The philoprogenitive instincts arose and were highly developed among the solitary ancestral insects long before social life made its appearance. In fact, social life is itself merely an extension of these instincts to the adult offspring, and there can be no doubt that once developed it reacted rapidly and powerfully in perfecting these same instincts. It is not so much the fact that all the activities of the social insects converge towards and center in the reproduction of the species, for this is the case with all organisms, as the elaborate living environment developed for the nurture of the young, that gives these insects their unique position among the lower animals. A full analysis of the threptic activities would involve a study of the entire ethology of the social insects and cannot be undertaken at the present time. Nevertheless the bearing of these instincts on the subject of polymorphism can hardly be overestimated and deserves to be emphasized in this connection.

All writers agree in ascribing polymorphism to a physiological division of labor among orginally similar organisms. This is tantamount to the assumption that the phylogenetic differentiation of the castes arose in the sphere of function before it manifested itself in structural peculiarities. Although this view implies that the female, or queen, was the source from which both the instincts and structures of the worker were derived, it has been obscured by an improper emphasis on the instincts of the honey-bee, in which the female is clearly a degenerate organism, and on certain specialized instincts, supposed to belong exclusively to worker ants like the slavemakers (*Polyergus* and *Formica sanguinea*). We have therefore to consider, first, the instincts of the queen and, second, any evidence that may go to show that instinct-changes precede morphological differentiation in the phylogeny of the species.

It is evident that the social insects may be divided into two groups according to the instinct rôle of the queens. In one group, embracing the

social wasps, bumble-bees, ants and termites, the female is the complete prototype of her sex. Even in the slave-making ants, as I have shown in a former article,[1] she manifests in the founding of her colonies all the threptic instincts once supposed to be the exclusive prerogative of the worker caste. These may be called the primary instincts. After the colony is established, however, and she no longer needs to manifest these instincts, she becomes a mere egg-laying machine and her instincts undergo a corresponding change. These may now be designated as secondary instincts. She thus passes through a gamut of instincts successively called into activity by a series of stimuli which in turn arise in a definite order from her changing social environment. The workers, however, are capable of repeating only a portion of the female gamut, the primary series. In gynæcoid individuals there is also a tendency to take up the secondary series, but in most workers this has been suppressed by countless generations of nutricial castration. The social insects of this type may be called *gynæcotelic*, to indicate that the female has preserved intact the full series of sexual attributes inherited from her solitary ancestors. In these the primary and secondary series were simultaneous or overlapped completely, in the gynæcotelic social insects they are extended over a longer period of time and overlap only in part, as social life permits the extension of the secondary long after the primary series has lapsed into desuetude. It will be seen that the division of labor which led to the spacial differentiation of like females into workers and queens is clearly foreshadowed in the consecutive differentiation of instincts in the individual queen.

The second group of social insects is represented by the honey-bees and probably also by the stingless bees (Meliponidæ). In these insects only the secondary instincts are manifested in the queen, while the worker retains the primary series in full vigor and thus more clearly represents the ancestral female of the species. This type may therefore be called *ergatotelic*.[2]

The suppression of the primary instincts in the queen honey-bee was undoubtedly brought about by a change in the method of colony formation. When the habit of swarming superseded the establishment of colonies by solitary queens, as still practiced by the gynæcotelic insects, the primary instincts of the female lapsed into abeyance or became latent. This change took place so long ago that it has had time to express itself in the structure of the queen honey-bee as compared with the worker (shorter tongue and wings, feebler sting, degenerate structure of hind legs, etc.).

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[1] On the Founding of Colonies by Queen Ants, etc., *loc. cit.*

[2] The distinction of gynæcotelic and ergatotelic types corresponds with Cook's "principles of matriarchy and ergatarchy" (The Social Organization and Breeding Habits of the Cotton-protecting Kelep of Guatemala. U. S. Depart. Agric., Bull. Entom., Tech. Series No. 10, 1905, p. 34). These terms are objectionable because they imply an erroneous, not to say anthropomorphic, conception of governing or ruling on the part of the queen or workers.

The first of the following examples, which seem to indicate the occurrence of instinctive prior to morphological differentiation, shows at the same time how the ergatotelic type of the honey-bee arose from the gynæcotelic type of the social wasps and bumble-bees.

1.   The queens of certain species of *Formica* (*F. rufa, exsectoides*, etc.) are no longer able to establish colonies without the coöperation of workers. The common method of colony formation among these insects is by a process of swarming like that of the honey-bee: a certain portion of the colony emigrates and founds a new nest with one or more of the queens. When this method is impracticable the young queen seeks the assistance of an allied species of *Formica* (*F. fusca*), the workers of which are willing to perform the same function as those of her own species in rearing her brood.   In *F. rufa* and *exsectoides* there is nothing in the stature or struc- ture of the queen to indicate the presence of these parasitic instincts, but, in many of the allied species like *F. ciliata, montigena, microgyna*, etc., the colonies of which are smaller and no longer swarm, or do so only to a very limited extent, the queens have become more dependent on the workers of other species of *Formica* and have developed mimetic characters or a dwarf stature to enable them to enter and exploit the colonies of alien species.

2.   In many ants the callows, or just-hatched workers, confine them- selves to caring for the larvæ and pupæ and do not exhibit the foraging instincts till a later period.   But even the adult workers may perform a single duty in the colony for long periods of time, if not indefinitely.   Thus Lubbock,[1] and Viehmeyer,[2] have observed in certain nests of *Formica* that only certain individuals forage for the community.   The latter has also noticed that certain other individuals, indistinguishable morphologically from their sister workers, stand guard at the nest entrances.   In other genera, like *Camponotus, Atta, Pheidole*, etc., with species that have des- mergates, the morphological differentiation between foragers and guardians is still unsettled.   It becomes completely established, however, in certain genera and species with the suppression of the desmergates.   A remark- able example of division of labor without corresponding structural differ- entiation is seen also in the above-mentioned *Œcophylla*, an ant which inhabits nests of leaves sewn together with fine silk.   According to the observations of Dodd[3] and Doflein,[4] when the nests are torn apart the monomorphic workers separate into two companies, one of which stations itself on the outside of the nest, draws the separated leaves together and

[1] Ants, Bees, and Wasps.   Revised ed., New York, Appleton & Co., 1894, pp. 45–47.
[2] Experimentelle Untersuchungen, etc., *loc. cit.*, p. 336.
[3] Notes on the Queensland Green Tree Ant (*Œcophylla smaragdina* Fab.?).   Victor. Natural., XVIII, 1902, pp. 136–140.
[4] Beobachtungen an den Weberameisen (*Œcophylla smaragdina*), Biol. Centralbl., XXV, 1905, pp. 497–507, 5 figs.

holds them in place with the claws and mandibles, while the other moves the spinning larvæ back and forth within the nest till the rent is repaired with silken tissue.

3. An interesting case is presented by the honey-ants (*Myrmecocystus melliger* and *mexicanus*). All the workers of these species, though variable in size, are structurally alike. Among the callows, however, and quite independently of their stature, certain individuals take to storing liquid food, as I have found in my artificial nests of the latter species, and gradually in the course of a month or six weeks become repletes, or plerergates. Except for this physiological peculiarity, which gradually takes on a morphological expression, the plerergates and ordinary workers are indistinguishable. We must assume, therefore, that the desire to store food represents an instinct specialization peculiar to a portion of the callow workers. There can be no doubt that as our knowledge of the habits of ants progresses many other cases like the foregoing will be brought to light.

It may be maintained that in these cases physiological states must precede the manifestation of the instincts, and that these states, however inscrutable they may be, are to be conceived as structural differentiations. There is undoubtedly much to justify this point of view. The elaborate sequence of instincts in the queen ant, for example, is accompanied by a series of physiological changes so profound as to be macroscopical. After the loss of her wings, the wing muscles degenerate and the fat-body melts away to furnish nourishment for the ovaries, which in the old queen become enormously distended with eggs as the breeding season approaches. Such changes would seem to be amply sufficient to account for the changing instincts. As I have shown,[1] mere artificial dealation at once alters the instincts of the queen, probably through a stimulus analogous to that which leads to the atrophy of a muscle when its nerve is severed, and in the case under consideration leads to the degeneration of the wing-muscles and to changes in the ovaries.

In the mermithergates and pseudogynes described in the first part of this paper, the aberrant instincts may be referred to peculiar physiological states. Similarly nutricial castration itself, considered as an instinct, may be said to be the result of the physiological state of hunger. There is indeed every reason to suppose that the worker, both in its ontogenetic and phylogenetic development, is through and through a hunger-form, inured to protracted fasting. Miss Fielde has shown,[2] that the workers of *Camponotus americanus* may live nearly nine months without food, which is as long

[1] On the Founding of Colonies, etc., *loc. cit.*, p. 103.
[2] Tenacity of Life in Ants. Biol. Bull., VII, No. 6, Nov. 1904, p. 300; and *ibid.*, Temperature in the Development of Ants, *loc. cit.*, p. 366.

as the much larger and more vigorous queens are known to fast while estab-
lishing their colonies.   The larvæ of ants, too, are known to remain alive in
the nests for months without growing.   And even when food is abundant
the workers appropriate very little of it to their individual maintenance but
distribute it freely among their sister workers, the brood and queen.   It
is not improbable, moreover, that the single instinct peculiar to work-
ers, the instinct to leave the nest and forage, is the direct result of a chronic
state of hunger.

Undoubtedly such physiological states are neither more nor less mysteri-
ous than those of man and the higher animals, in which they are universally
recognized as leading to changes in the instinctive and emotional life of the
individual.   We may not only concede the existence of physiological states
in the above and many other cases, but we may also admit that this conces-
sion is favorable to the hypothesis of psychophysical parallelism.   On look-
ing deeper into the matter, however, we find that our knowledge of the
physiological states, and especially of their precise connection with the
instincts, is extremely vague and unsatisfactory.   Furthermore, we are com-
pelled to confess that even the simplest physiological reaction, the simplest
reflex depending on the simplest of physiological states, such as the general
irritability of all living matter, still involves a non-mechanical or teleologi-
cal and therefore a psychological factor, to the understanding of which the
hypothesis of psychophysical parallelism contributes nothing.   The inter-
pretation of organic behavior as the result of "trial and error" seems to have
a value in indicating that the teleological factor is a blind activity groping
for the means with which to supply an organic need.   But not only is this
conception borrowed from psychology but it is thoroughly teleological, since
the eventual selection and retention on the part of the organism of the par-
ticular mode of reaction best suited to supply its needs, is incapable of a
mechanical explanation.   Of course, 'teleology' as applied to biological
phenomena must not be understood in the sense of an altruistic or external
teleology like the 'design' of theologians but is, as Pauly has shown,[1] an
immanent and egotistical principle capable of great simplification in the
lower biological units like the cells, without losing its essentially pur-
posive character.

Driesch,[2] in his attempt to establish the autonomy of the vital processes on
the basis of regulatory phenomena in ontogeny, says: "A special problem
which is calculated to lead to a parallelism between the instincts and on-
togeny, may be briefly mentioned in conlcusion: the course of ontogeny may

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[1] Darwinismus and Lamarckismus, *loc. cit.*, pp. 15–22.
[2] Die "Seele" als Elementarer Naturfaktor, Leipzig, Wilhelm Engelmann, 1903, p. 26.

be interfered with, but it regulates itself; and from the study of just such regulations important insight has accrued to morphology. Will it also be possible to bring about regulations in instinctive processes? No definite answer can be given to this question at the present time." He goes on to say that if they should prove to be capable of such regulations, the instinctive reactions would present further evidence of the autonomy of living organisms.

It seems to me that there are, especially in the social insects, a few facts which point to such regulations in the sphere of instinct. When, for example, the firstling brood is removed from a queen ant that has just manifested her primary series of instincts, she will proceed to rear another brood, although under normal circumstances she would pass on to the purely secondary series of reactions. In this case the absence of a colony acts as a stimulus to produce a highly adaptive regulation, which is equivalent to a regeneration of the colony. If on the other hand the queen ant, wasp, or termite is removed from her colony, some of the remaining workers themselves become gynæcoid and function as substitutional queens, or in bees raise a new queen. A similar regulation of the personnel of the colony is also apparent in other cases, as when strange queens are adopted or the numerical proportions of the different castes are regulated. If we accept Wasmann's view of the production of pseudogynes in *Formica* nests infested with Lomechusini, the conversion of queen larvæ into workers would be a splendid example of regulation. Such facts point to instinct as offering evidence as important as that of ontogeny in support of a vitalistic conception. And even if my interpretation of the pseudogynes as the result of simple neglect and starvation be accepted, we still have an interesting case of regulation, for the pseudogynes of *Formica*, like the phthisergates of *Pheidole instabilis* and the mermithergates of *Ph. commutata*, are the result of a tendency to produce a symmetrical and adaptive whole out of formative materials that have been abnormally depleted, augmented, or disturbed in the course of their development through the action of parasites.

In concluding this rather long discussion of polymorphism it is hardly necessary to point out that I have added little of constructive value apart from a few suggestions and a clearer definition of some of the problems involved in an extremely intricate subject. If I have succeeded in showing that the underlying problem is the same as that of all other biological phenomena, and that the social insects cannot be used to support any of the current mechanical conceptions of development, my object will have been achieved.

EXPLANATION OF PLATES.

PLATE I.

FIG. 1. — *Pheidole kingi* André var. *instabilis* Emery. Soldier, Austin, Texas.
FIGS. 2–6. — Series of intermediate forms (desmergates) between the soldier and
            worker of *Ph. instabilis.*
FIG. 7. — Typical worker of same.
FIG. 8. — Deälated female of *Ph. instabilis.*
FIG. 9. — Male of same.
FIG. 10. — *Orasema viridis* Ashmead. Female. Austin, Texas.
FIG. 11. — *Orasema viridis.* Male.
FIG. 12. — *Orasema coloradensis* Ashmead. Female. Colorado Springs, Colorado.

PLATE II.

FIG. 13. — Phthisergate of *Ph. instabilis* with very young *Orasema viridis* larva
            attached to the right side of the prothorax beneath the fore leg.
FIG. 14. — Soldier semipupa of *Ph. instabilis* with *O. viridis* larva in second stage
            attached to the presternal region between the first and second pairs
            of legs.
FIG. 15. — Female semipupa of *Ph. instabilis* with *O. viridis* larva in the second
            stage attached to the pronotal region behind the head.
FIG. 16. — Female semipupa of *Ph. instabilis* with *O. viridis* larva in the third
            stage attached to the presternal region.
FIG. 17. — Female semipupa of *Ph. instabilis* with nearly mature *O. viridis* larva
            (shrunken by reagents) attached to the sternal surface between the
            middle and hind pairs of legs. From a specimen mounted in balsam.
FIG. 18. — Female pupa (phthisogyne) of *Ph. instabilis* with *O. viridis* semipupa
            in the pustulate stage, still attached in the position which it occupied
            as a larva. From a specimen mounted in balsam.
FIG. 19. — Female pupa (phthisogyne) with *O. viridis* semipupa in the pustulate
            stage, still attached to the sternal region. From an alcoholic specimen.
FIG. 20. — Semipupa of *O. viridis,* viewed as a transparent object, showing the
            head, wings, and legs developing beneath the hood-like prothoracic
            mass. From a specimen mounted in balsam.
FIG. 21. — Semipupa of *O. viridis* in a more advanced stage. From a specimen
            mounted in balsam.
FIG. 22. — Pupa of female *O. viridis* just before pigmentation, showing the promi-
            nent intersegmental abdominal welts.
FIG. 23. — Pigmented pupa of *O. viridis* nearly ready to hatch.
FIG. 24. — Phthisergate of *Ph. instabilis* viewed in profile as an opaque object.
            From an alcoholic specimen.
FIG. 25. — Phthisergate of *Ph. instabilis* in ventral view to show the greatly atten-
            uated thorax, small projecting eyes, etc.

FIG. 26. — Phthisergate of *Ph. instabilis* viewed as a transparent object to show
          the urate masses in the gaster.   From a specimen mounted in balsam.

FIG. 27. — Normal worker pupa of *Ph. instabilis* in profile.   From an alcoholic
          specimen.

FIG. 28. — Phthisergate of *Ph. dentata* Mayr.   From an alcoholic specimen.

FIG. 29. — Worker cocoon of *Camponotus herculeanus ligniperdus* var. *novæboracen-
          sis* Fitch, from northern Michigan, showing an enclosed pair of pupæ
          of *Pseudochalcura gibbosa* Provancher near the anterior pole, and the
          remains of the consumed *Camponotus* semipupa applied to the black
          meconial spot at the posterior pole.

FIGS. 30–35.— Six larvæ of *Orasema viridis* in the youngest stage observed, corre-
          sponding with the one shown in Fig. 13.

PLATE III.

FIG. 36. — *Pheidoloxenus wheeleri* Ashmead.   Female, taken from a colony of *Ph.
          instabilis* at Austin, Texas.

FIG. 37. — *Pheidole dentata* var. *commutata* Mayr.   Soldier.   New Braunfels, Texas.

FIG. 38. — *Ph. commutata*.   Worker.

FIG. 39. — Mermithergate of *Ph. commutata*, drawn to the same scale as Figs. 37 and
          38; showing *Mermis* parasites in the distended gaster.   The head of
          the ant bears occelli; the thorax is shaped like that of the soldier.

FIG. 40. — Lateral view of same mermithergate.

FIG. 41.— *Xenodusa cava* Leconte, taken from a colony of *Formica schaufussi* var.
          incerta Emery at Colebrook, Connecticut.

FIG. 42. — *Formica schaufussi* Mayr. var. *incerta* Emery.   Normal worker.   Cole-
          brook Connecticut.

FIG. 43. — Pseudogyne of *F. incerta* drawn to the same scale as Fig. 42.

FIG. 44. — Pseudogyne from the same colony as Fig. 43, showing a somewhat differ-
          ent conformation of the thorax.

PLATE IV.

FIG. 45. — Pseudogyne of *Myrmica rubra brevinodis* Emery var. *sulcinodoides*
          Emery, with vestige of left fore wing, from Isle Royale, Michigan.

FIG. 46. — Thorax of same in profile.

FIG. 47. — Thorax of normal worker of *M. sulcinodoides*.

FIG. 48. — Thorax of pseudogynic *M. rubra scabrinodis* Nyl. var. *schencki* Emery,
          from Jeanette, Pennsylvania.   This specimen has minute vestiges
          of both fore wings.

FIG. 49. — Lateral view of same.

FIG. 50. — Pseudogyne of *Formica rufa obscuriventris* Mayr. var. *melanotica* Emery,
          with well-developed mesonotum, scutellum and metanotum, from
          Rockford, Illinois.

FIG. 51. — Dorsal view of thorax of same.

FIG. 52. — Pseudogyne of *F. melanotica* with more convex mesonotum, from the
          same colony as the specimen shown in Figs. 50 and 51.

FIG. 53. — Pupa of female *Orasema coloradensis* Ashm.; dorsal view showing the
   arrangement of the pustules.

Fig. 54. — Lateral view of same.

Fig. 55. — Pupa of female *Pseudochalcura gibbosa* Prov., from northern Michigan.

Fig. 56. — *Kapala floridana* Ashmead. Female, from eastern Florida. From a specimen in the United States National Museum.

Fig. 57. — *Kapala floridana*. Male, from eastern Florida. From a specimen in the United States National Museum.

Fig. 58. — *Isomeralia coronata* Westwood. Female, from Pernambuco, Brazil. From a specimen in the United States National Museum.

Fig. 59. — Lateral view of same.

Fig. 60. — *Dicœlothorax platycerus* Ashmead. Female. After Ashmead.

Fig. 61. — Scutellum of same, seen from above. After Ashmead.

Fig. 62.— *Eucharis* sp. Male, from the top of the Las Vegas Range, New Mexico (11,000 ft.).

PLATE V.

Fig. 63. — *Pheidole instabilis*; *a*, females (winged and deälated); *e*, male; *o*, soldier; *c*, workers; *r*, intermediates (desmergates); *m*, *Orasema viridis*, female; *n*, male. × 2.

Fig. 64. — Brood of *Ph. instabilis*; *a*, female larvæ and pupæ; *e*, male pupæ and semipupæ; *o*, soldier pupæ; *c*, worker larvæ and pupæ; *r*, pupæ of desmergates; *m*, *O. viridis*, adult female, *m'*, pupæ and semipupæ; *n*, male; *n'*, pupæ of same. × 3.

Fig. 65. — Brood of *Ph. instabilis*. Letters as in the preceding figure; *s*, phthisergates. × 3.

Fig. 66. — Three female semipupæ (phthisogynes) of *Ph. instabilis* bearing larvæ of *O. viridis* on their sternal surfaces. × 3.

Fig. 67. — Worker brood of *Ph. instabilis*; *c*, normal worker pupæ and semipupæ; *i*, phthisergates; *r*, intermediate (desmergatic) phthisergate. From specimens mounted in balsam.

Fig. 68. — *Solenopsis molesta validiuscula* Emery; *a*, female; *e*, male; *c*, workers; *m*, *Orasema coloradensis*, female.

Fig. 69. — Brood of *Pachycondyla harpax* Fabricius. The larvæ marked *x* each bear a larva of *Metopina pachycondylæ* Brues; *z*, detached *Metopina* larva; *v*, puparium of *Metopina*; *u*, cocoon of *Pachycondyla*.
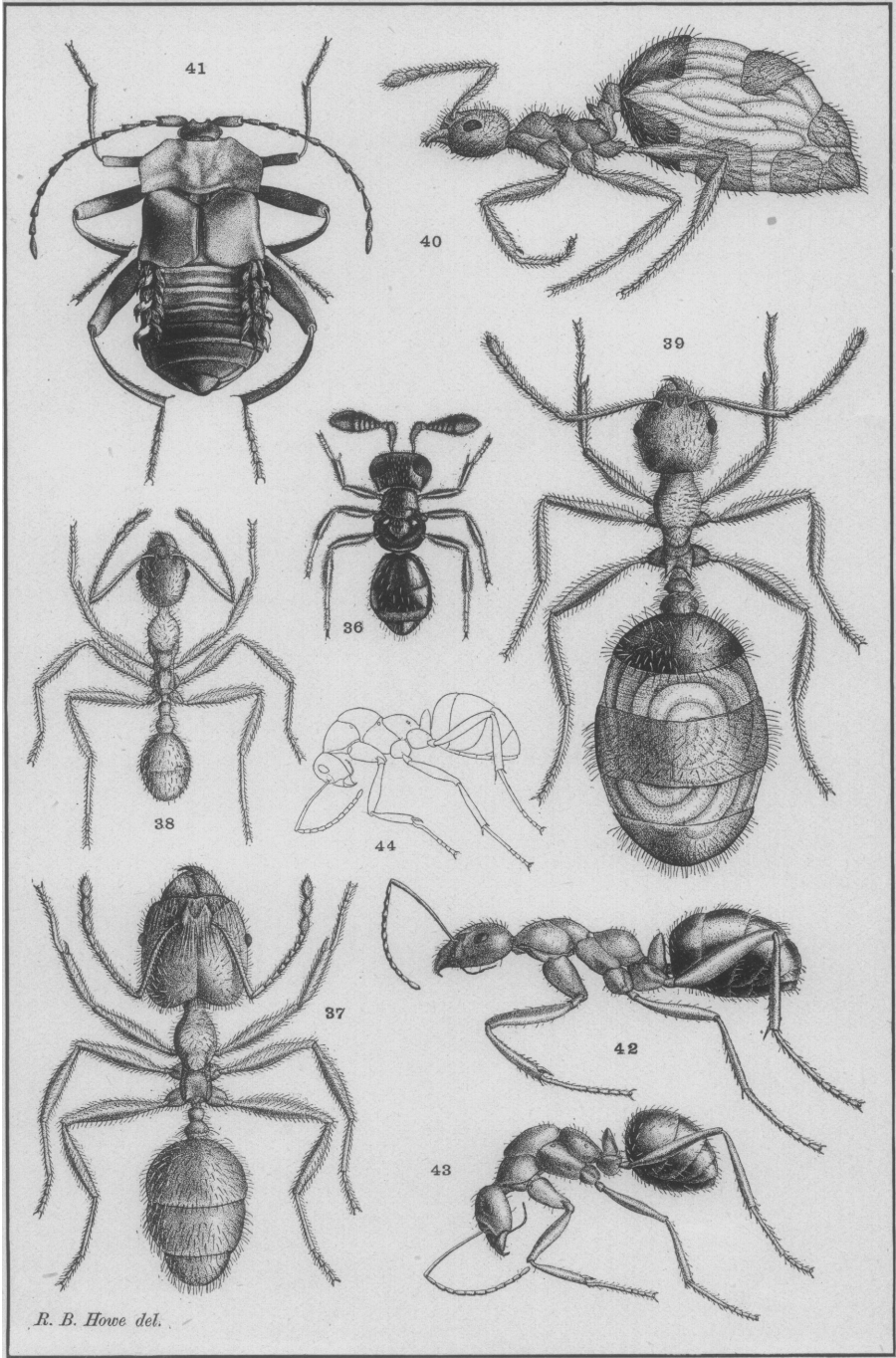
PLATE VI.

Diagram to illustrate the relationships of the typical and atypical phases of ants. The three typical phases are placed at the angles of an isosceles triangle, the excess developments to the right, the defect developments to the left of a vertical line passing through the middle of the diagram. The normal atypical phases are in ordinary, the pathological phases in italic type. The arrows indicate the direction of the affinities of the atypical phases. The phases arranged on the sides of the triangle are annectant, those radiating outward from its angles are new departures showing excess or defect characters. For definitions of the different phases see pp. 53 to 57.
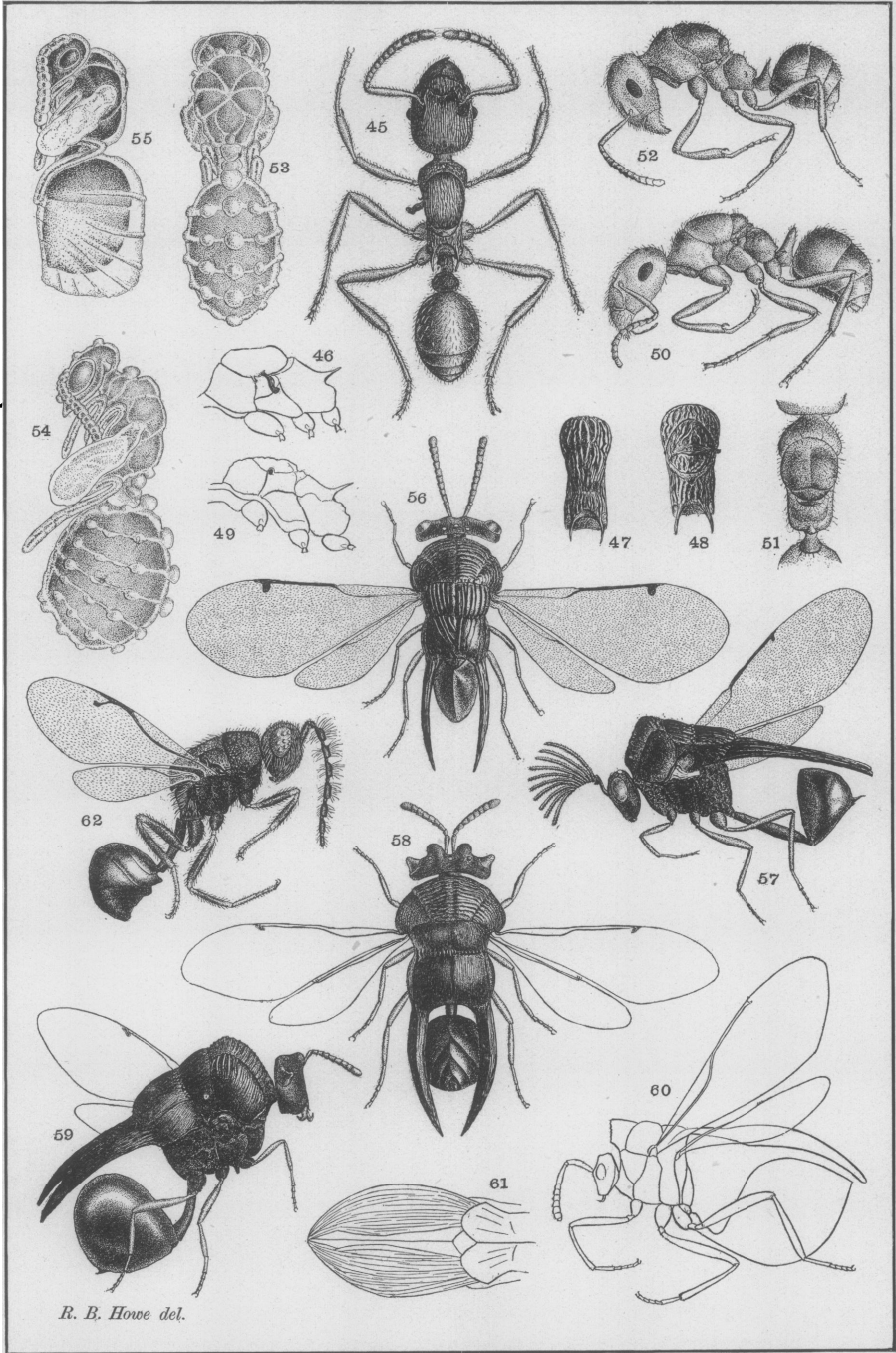
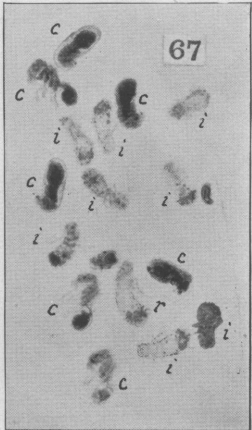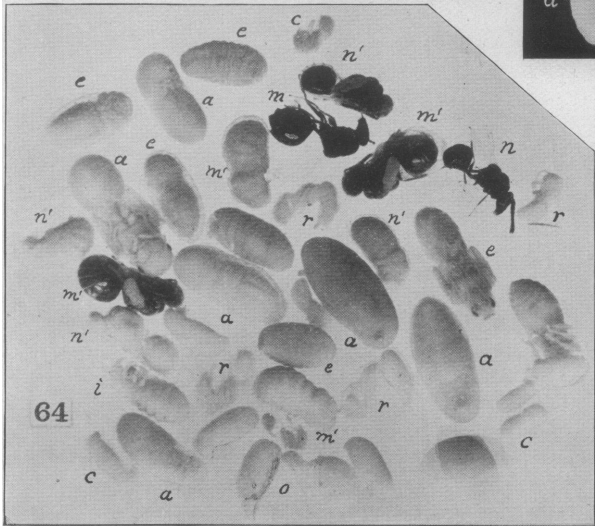R. B. Howe del.
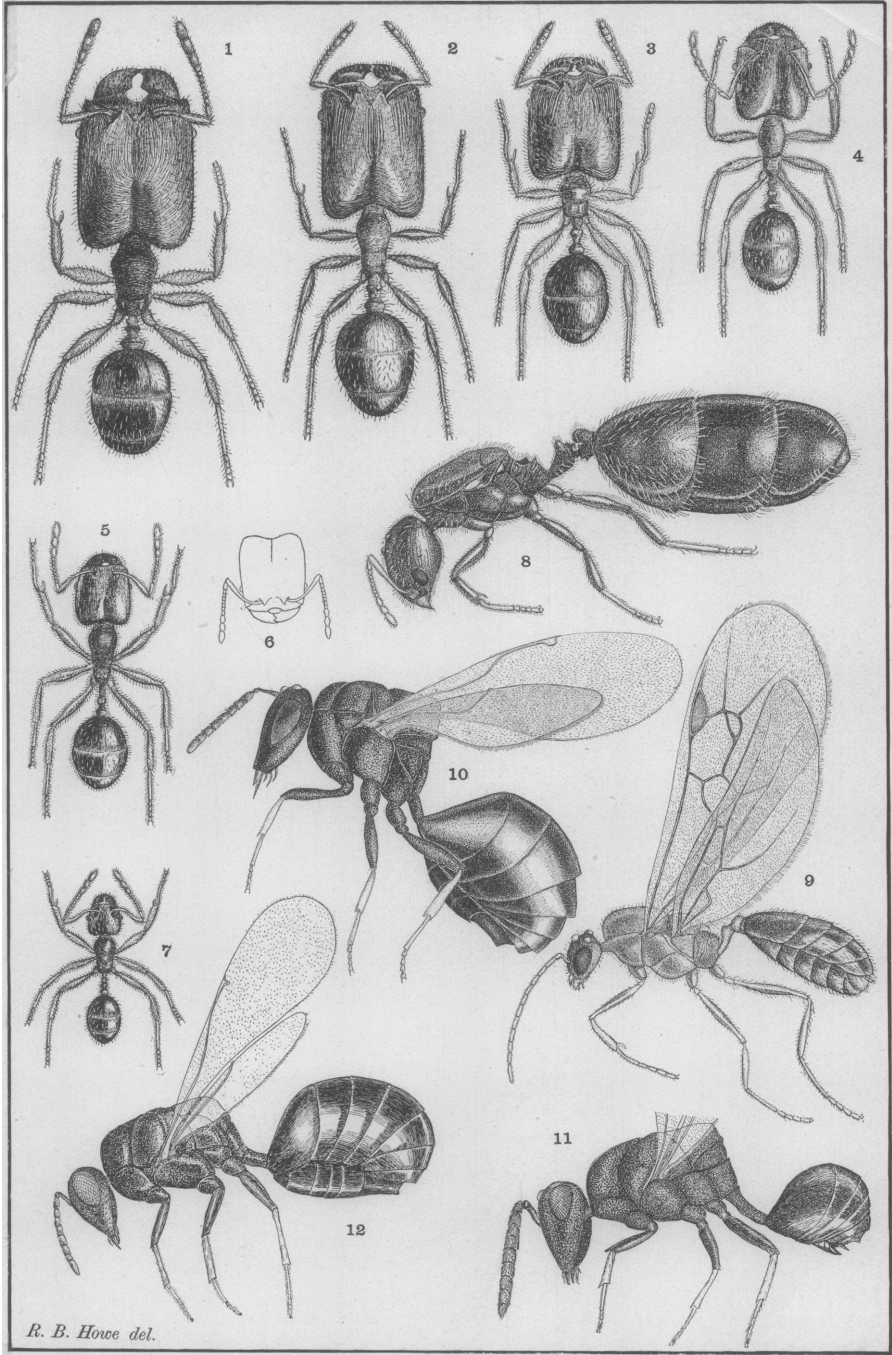
PHEIDOLE INSTABILIS AND ORASEMA.

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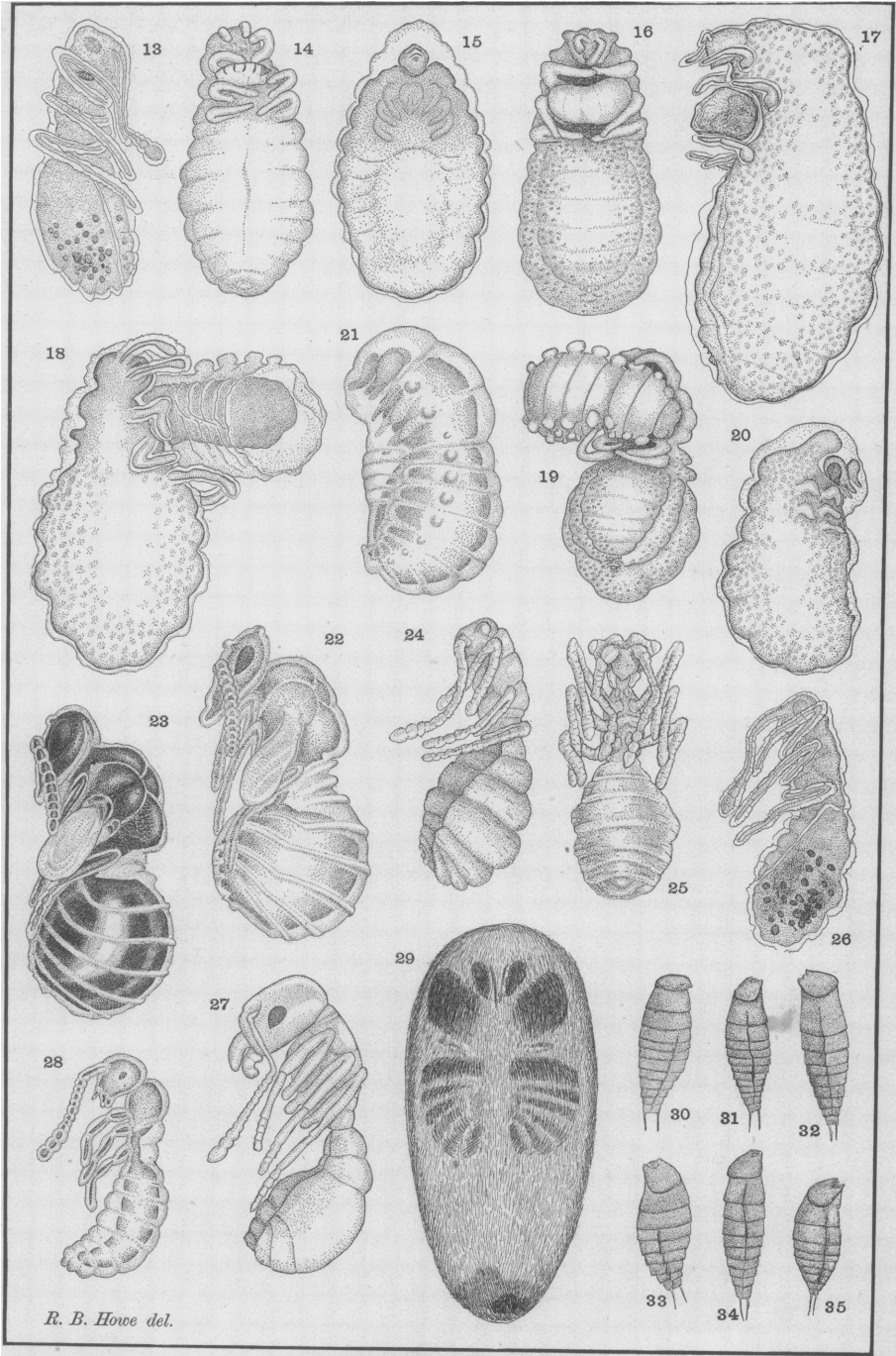
Development of Orasema

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PARASITES OF PHEIDOLE AND FORMICA.

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CHALCIDID PARASITES OF ANTS, ETC.
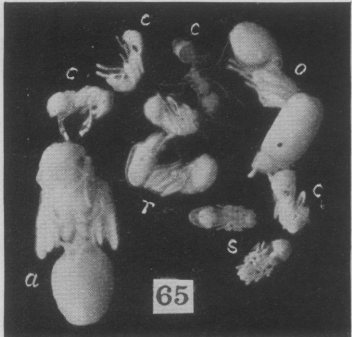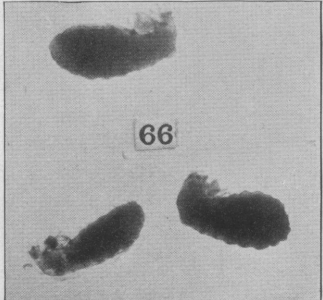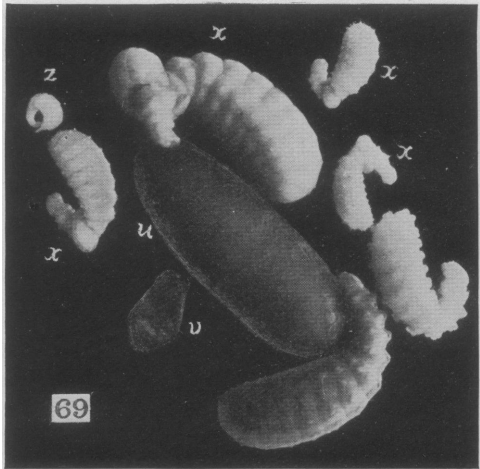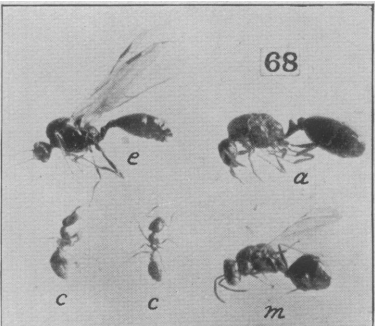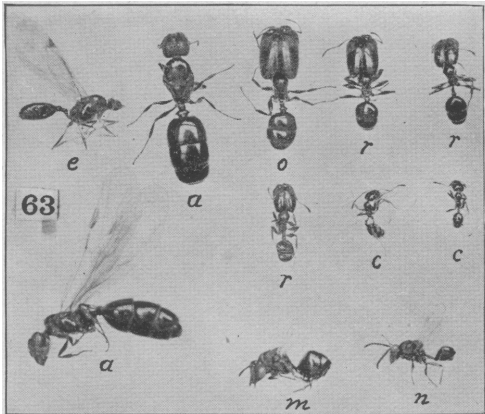
PARASITES OF PHEIDOLE, SOLENOPSIS AND PACHYCONDYLA.

Macrogyne

β-Female

Macranēr

Dorylanēr

Gynæcanēr

Gynandromorph

FEMALE
(Gyne)

♀

MALE
(Anēr)

Ergatogyne

Pseudogyne

Dichthadiigyne

Microgyne

Phthisogyne

Micranēr

Phthisanēr

Erganēr

Ergatandromorph

Pterergate

Mermithergate

Plerergate

Macrergate

Gynæcoid

Dinergate

WORKER
(Ergates)

♀

Desmergate

Micrergate

Phthisergate

The Typical, Atypical and Pathological Phases of Ants.