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THE PHYLOGENETIC DEVELOPMENT OF SUBAPTEROUS AND APTEROUS CASTES IN THE FORMICIDAE

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It is generally admitted that each of the four groups of social insects—the social bees, social wasps, ants and termites—has had an independent phyletic origin and history and that the similarities in their habits are due to parallelism, or convergence, of which, indeed, they exhibit striking examples. In both the fertile and sterile females of social wasps and bees the wings show no signs of reduction, whereas these appendages are well-developed in the fertile females (females proper) of the great majority of ants, at least prior to fecundation, but are normally always absent in the sterile females, or workers. Paleontology proves that identical conditions have long existed in the Formicidae as a family, since they are clearly shown in the abundant and beautifully preserved ants of the Baltic amber from the Lower Oligocene Tertiary.¹

Writers also agree that the ants must be descended from certain

primitive wasps belonging to the families Scoliidae, Mutillidae and Thynnidae, but authorities differ as to which of these families should be selected as the most probable ancestors. Emery² believes that the ants arose from the Mutillidae, Forel from the Thynnidae and Handlirsch³ from the Scoliidae. But as all three families are so closely related to one another that authorities fail to assign them the same limits, the differences of opinion are after all not very pronounced.

Handlirsch⁴ advances the opinion that the ants first made their appearance during the Cretaceous, but I am inclined to seek their origin in an earlier period, during the Jurassic or possibly even as far back as the Triassic. According to Schuchert,⁵ these were periods of maximum continental emergence and aridity and would therefore present what I conceive to be the optimum environmental conditions for the development of the family Formicidae. The insects most closely related to the ants (Thynnids, Scoliids, Mutillids) are very decidedly xerothermic and hence confined to deserts or to hot sandy and gravelly situations, and the ants present a number of peculiarities which seem to indicate more or less clearly that they originally lived and developed in the same kind of a habitat. They are at the present time extraordinarily abundant in species and individuals in the desert regions of the globe (Australia, North Africa, Sonoran Regions of North America) and as a group seem to show in their inherited small average stature the stunting effects of an arid environment. The great majority of species have retained the primitively terrestrial and fossorial habit, which is an obvious adaptation to avoiding intense heat, insolation and evaporation during the summer months and the cold of nights and of the winter. The aptery of the workers and dealation in the females are closely connected with such habits. Most of the species, moreover, are decidedly petrophilous and many are exquisitely hypogaeic. The marriage flight, to which the males and females of most of the species so rigidly adhere, would seem to be a habit that had originated in open, unobstructed country. The adaptations, though numerous and intricate, to living in mesophytic and hygrophytic forests (Amazonian and East Indian rain-forests) are clearly secondary and of much more recent origin.

That the workers of ants originally possessed wings like the females is shown by the presence of minute vestiges of these organs in the larval and pupal stages⁶ and by the occasional, pathological development of very small wings in the adult. This condition occurs in the 'pterergates' found by Donisthorpe⁷ and myself⁸ in certain species of *Myrmica*, *Cryptocerus* and *Lasius*. The development of aptery, with the concomitant

simplification of thoracic structure (micronoty) so universal in the workers, is evidently a phylogenetic process, which was completed in most ant-genera before the Lower Oligocene. *Aptery* is, of course, to be carefully distinguished from *deälation*, the dropping of the wings by the female ant immediately after fecundation. Deälation is really a form of mutilation (autotomy) which has been practiced by female ants for millions of years without necessarily entailing any modification or diminution in the development of wing structures. Compared with this case of the non-inheritance of mutilations, the cases usually cited in the

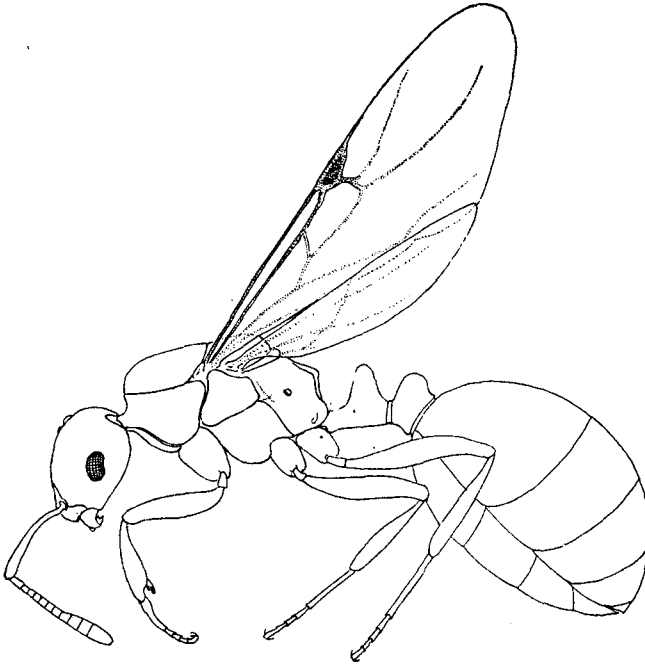


FIG. 1

Winged, macronotal female of *Monomorium rothsteini* Forel var. *humilius* Forel, lateral view.

text-books, such as circumcision and the docking of tails in mice, are insignificant, because they refer to such limited series of generations.

There are a few genera of ants, especially in the subfamily Myrmicinae, in which it is possible to trace all the transitions in thoracic structure from that of the female to that of the worker, except that, in all cases hitherto recorded, the wings show no transitions, but are perfectly developed in the typical female and entirely lacking in all the other forms of the series. Good examples are certain species of *Myrmecina* (*M. graminicola*) and *Leptothorax* (*L. emersoni*), but of all the genera

I have studied *Monomorium* is the most instructive in this connection, because at least two of its species exhibit a normal and hitherto unsuspected condition of subaptery in the female. Some years ago Forel⁴ described a *Monomorium rothsteini* from worker specimens received from Queensland, Australia, and later distinguished two varieties of it, *humilius*,¹⁰ from Tennant Creek, Central Australia and *leda*,¹¹ from northern Queensland. During December, 1914, I observed many colonies of *rothsteini* in various localities in Queensland. The workers of this species store their subterranean nests with small grass-seeds and are therefore harvesters, like the species of *Holcomyrmex*, now regarded as a subgenus of *Monomorium*. Among a lot of ants recently received from the Museum of South Australia I find a large series of cotypes of the var. *humilius* comprising 14 specimens of the female, which was unknown to Forel. This phase measures 7-7.5 mm. and has long, well-developed wings (6.8-7 mm.). In the same collection I find three series of a closely allied species; which I shall describe in another place as *M. subapterum* sp. nov. Two of the series, representing the typical form of the species, comprise numerous workers, 10 males and 10 females (5 deälated) taken by Mr. W. D. Dodd on the Harding River in North West Australia and one female and several workers taken by the same collector at Derby in the same region. The remaining series represents a color variety of *subapterum*, which I shall call *bogischi* var. nov., comprising several workers and four females (three deälated) from Point Wakefield, South Australia (G. P. Bogisch). The winged females in all three series measure 6.5-7 mm. and agree in having very small wings, measuring only 3 mm., and a distinctly smaller thorax than *rothsteini*. There are other specific differences which need not be discussed at the present time. Figs. 1 and 2, drawn to the same scale, show the differences in wing and thoracic structure between the females of the two species, corresponding to what may be called the macronotal, winged and mesonotal, subapterous types respectively (1 and 2, p. 114). The males of *M. rothsteini* and *subapterum* show no differences in the size and development of the wings, which in both are large and of the usual structure. There can be no doubt that the deälated females of two of the series of *subapterum* originally bore small wings like the nondeälated individuals. The fore wings have a singular truncated apical border, as if they had been trimmed with scissors, and this appearance is accentuated by the fact that the membranes are as thick at the border as at the base. It is certain, however, that the wings have not been reduced to their present form by the mandibles of the ants. The venation is abortive, only the submarginal vein being distinct, although the fore wings show faint

traces of the basal portions of some of the other veins. Brues¹² distinguishes three classes of vestigial wings among insects: those having essentially a pupal character, those essentially normal, except for their smaller size and less complex venation and those consisting of little more than a hollow bag, without venation. The wings of *M. subapterum* evidently belong to the second class.

In six specimens of a pale variety of *Monomorium rubriceps* Mayr (*cinctum* var. nov.) taken by Mr. Albert Koebele in Victoria, Australia, I find the following graduated series of forms connecting the subapterous female with the typical worker. One specimen (fig. 3a and b), measuring 6.5 mm. has the ocelli well-developed, the thorax rather small but with distinct mesonotum, scutellum, metanotum, paraptera and

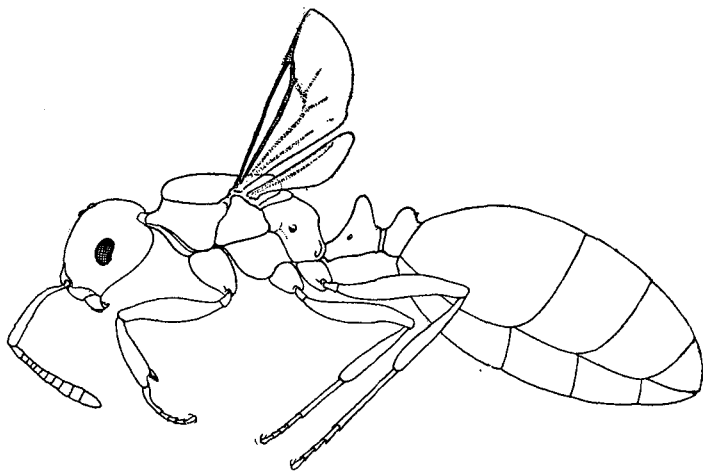


FIG. 2

Subapterous, mesonotal female of *Monomorium subapterum* sp. nov., lateral view.

tegulae, with stumps of wings and on the right side one nearly entire posterior wing. The latter is evidently vestigial, though its tip is lacking. The remaining vestigial wings have evidently been lost by deälation. This specimen is therefore a partially deälated female in a more advanced stage of subaptery than the female of *M. subapterum*. A second specimen (fig. 3c) is slightly smaller and has a similar thoracic structure, except that the tegulae and paraptera are lacking and the thorax has never borne wings. A third and fourth specimen (fig. 3d) measure 4.5–5 mm. and have small ocelli and the thorax is still more reduced and worker-like, but the mesonotum, though small and flat, is distinct and there is a visible promesonotal suture and a metanotal sclerite. The two remaining specimens, 3.5–4 mm. long (fig. 3e), are normal

workers, without distinct mesonotal and metanotal sclerites and without ocelli. The first specimen is therefore of the subapterous mesonotal type, the second is apterous and stenonotal, the third and fourth are ergatogynes. Thus the three species, *M. rothsteini*, *subapterum* and *rubriceps* together represent all the principal stages from the perfect female to the worker.

My study of the large genus *Monomorium* shows that in some species the only females are stenonotal and apterous (*M. floricola*, *carbonarium*, etc.), whereas in others they are ergatogynes (*M. venustum*, *schurri*, etc.). In still other species both winged and ergatogynic forms occur (*leae*, *dichroum*, etc.). This "morphological restlessness" of the female is evidently a survival of a condition which was once common to all ants but which has disappeared in most genera through a survival of the two extremes of the graduated series of forms, the macronotal, winged form (female proper) and the micronotal, apterous form (worker), and the suppression of all the intermediate phases. That the species of *Monomorium* should retain so complete a picture of the various stages that have led up to the development of the worker caste is not surprising when we stop to consider that the genus is one of the most primitive in the subfamily Myrmicinae. This is shown by its simple morphological characters, the present cosmopolitan distribution of its species, their dominance in the ant-faunas of regions noted for the archaic character of their biota (Africa, Southern Asia, Australia and New Zealand), and the known geological age of the genus, which is represented in the Baltic amber by two species differing but slightly from existing forms. Space forbids a discussion of a few other Formicid genera in which a similar diversity of females is known to occur. Among the ants as a family we may conveniently recognize the following female types which at the same time represent stages in the phylogenetic development of the worker:

1. The macronotal, winged female.—Most ants.
2. The mesonotal, subapterous female.—*Monomorium subapterum* and *rubriceps* var. *cinctum*.
3. The stenonotal apterous female.—Some species of *Monomorium*, *Anochetus*, *Myrmecia*, *Odontomachus hastatus*, etc.
4. The micronotal female, or ergatogyne.—Some species of *Monomorium* and *Crematogaster*, *Polyergus rufescens*.
5. The ergatoid female.—*Leptogenys*, *Acanthostichus*, *Sphinctomyrmex*, *Onychomyrmex*, *Paranomopone*. These forms grade into the 'dichthadiigynes' of the Dorylinae.

6. The gynaecoid worker.—*Ocymyrmex*, *Leptomyrmex*, *Diacamma*, *Rhytidoponera*, etc.

In this connection it is interesting to note that a series of forms between the winged female and worker closely paralleling those described in the preceding paragraphs, may be developed in ants as the result of parasitism and therefore under pathological conditions. Mrázek,¹³ Donisthorpe¹⁴ and I¹⁵ have shown that small-winged or subapterous females ('mermithogynes') are produced in *Lasius niger* by the presence

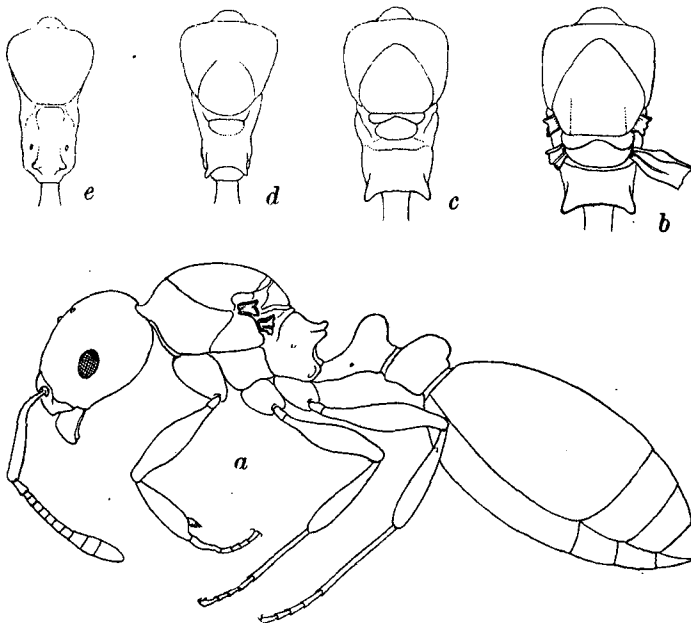


FIG. 3

Monomorium rubriceps Mayr. var. *cinctum* var. nov. a, Mesonotal, incompletely dealated, subapterous female, lateral view; b, thorax of same, dorsal view; c, thorax of stenonotal apterous female, dorsal view; d, thorax of ergatogyne (micronotal female), dorsal view; e, thorax of worker, dorsal view.

of Nematode worms (*Mermis* sp.) in the abdominal cavity, and Wasmann¹⁶ and others have demonstrated that 'pseudogynes,' i.e., forms closely resembling ergatogynes and ergatoids, are produced by the parasitism of Lomechusine beetles (*Lomechusa*, *Atemeles*, *Xenodusa*) on the ant colony as a whole. Gynaecoid workers, finally, may be developed by what really amounts to a pathological disturbance in the trophic status of the colony when it loses its queen.

Attention may also be called to a parallel tendency to aptery and micronoty in the males of certain ant-genera. Thus the male of *Sym-*

myrmica chamberlini has lost its wings, but apparently so recently that it still retains the typical male structure of the head, antennae and thorax, even to the development of the Mayrian furrows. In several other genera (*Formicoxenus*, *Cardiocondyla*, *Ponera*), however, the males have acquired the same structure of the head and thorax as the worker, so that they can be distinguished only by their genitalia and the number of their antennal joints. In one species (*Anergates atratulus*) the apterous male degenerates still further into an almost pupoidal condition.

The facts briefly presented in the preceding paragraphs seem to me to have an important bearing on the question of continuous variation *versus* mutation in the production of organic forms. In most species of ants the constant and striking structural differences between the different castes would, at first sight, suggest that such forms as the apterous females, apterous males, soldiers and workers, must have arisen as so many saltatory variations, or mutants and that they survived and secured representation in the germ-plasm, because they happened to fulfill specialized and useful functions in the life of the colony. I believe, however, that this view of the castes, at least so far as their origin is concerned, cannot be maintained, because all the available evidence points to their being merely the surviving extremes of graduated and continuous series of forms, the annectant members of which have suffered phylogenetic suppression or extinction. This is most clearly seen in the case of the soldier and worker. Only within comparatively recent time, i.e., probably since the middle Tertiary, has the originally monomorphic worker caste become polymorphic in certain genera (*Camponotus*, *Atta*, *Pheidologeton*, some species of *Pheidole*), i.e., developed a complete series of workers ranging from huge-headed major workers or soldiers (macrergates, dinergates) through intermediates of various sizes (desmergates) to small workers (micrergates). There is much evidence to show that in some genera (e.g., *Pheidole*, *Oligomyrmex*, etc.) all the forms in this series, except the dinergates and micrergates, have been suppressed, so that a marked dimorphism of the worker caste, simulating an origin of one or both of the forms by mutation, has been produced. In other genera (*Carebara*, many *Solenopsis*) the soldier form has also been suppressed, so that the worker caste has again become monomorphic through the survival of nothing but the smallest forms (micrergates) of the originally graduated series. Finally, in certain parasitic ants, (*Anergates*, *Anergatides*, *Epæcus*, *Wheeleriella*, etc.) the last traces of the worker caste have vanished, just as in several Australian genera (*Leptomyrmex*, *Rhytidoponera*, *Diacamma*)¹⁷ and the South African *Ocymyrmex*¹⁸ the

female caste has been abolished and its reproductive function transferred to gynaecoid workers, i.e., to forms differing from ordinary workers only in their ability to produce worker as well as male offspring. It is very probable that even this abolition of whole casts has been accomplished by very slow and gradual processes and not by sudden variations, or mutations.

¹ Wheeler, The Ants of the Baltic Amber, *Königsberg Schr. physik. Ges.*, 55, 1914, (1-142).

² *Zool. Jahrb. Abth. Syst., Jena*, 8, 1895, (774).

³ *Die Fossilen Insekten, Leipzig*, 1908, (p. 1283).

⁴ *Loc. cit.*, (p. 1285).

⁵ *Bull. Geol. Soc. Amer.*, 20, 1910, (427-606), and *Climates of Geologic Time, Carnegie Inst. Washington Pub. No. 192*, (pp. 263-298).

⁶ Dewitz, *Zs. wiss. Zool., Leipzig*, 30, 1878, (78-105), Pl. 5.

⁷ *British Ants*, 1915, (p. 131 and 221), Fig. 50.

⁸ *Bull. Amer. Mus. Nat. Hist., New York*, 21, 1905, (405-408), 1 pl.; *Ants, etc.*, 1910, (p. 99), Fig. 63.

⁹ *Rev. Suisse Zool.*, 10, 1902, (444).

¹⁰ *Ibid.*, 18, 1910, (27).

¹¹ *Ark. Zool.*, 9, 1915, (71).

¹² *Biol. Bull.*, 4, *Woods Hole, Mass.*, 1903, (180).

¹³ *Acta Soc. Ent. Bohemiae*, 5, 1908, (139-146), 4 figs.

¹⁴ *British Ants* 1915, (p. 220), Fig. 47.

¹⁵ *J. Exper. Zool.*, 8, 1910, (421), Fig. 7.

¹⁶ *Zs. wiss. Zool.*, 114, 1915, contains a full bibliography of the author's papers on the *Lomechusini*.

¹⁷ Wheeler, *Boston, Proc. Amer. Acad. Arts Sci.*, 51, 1915, (257).

¹⁸ Arnold, *Ann. S. Afric. Mus.*, 14, 1916 (195).