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NOTE ON THE METHOD OF COLONY FOUNDATION
OF THE PONERINE ANT *BRACHYPONERA*
(*EUPONERA*) *LUTEA* MAYR

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Introduction

The methods of colony foundation among the Ponerinae are of peculiar interest to students of the phylogeny of the Formicidae, for, as emphasized elsewhere, (Wheeler, 1900a, 1900b, 1906, 1932, 1933, Haskins, 1928, 1930, 1941, Haskins and Enzmann, 1938, Haskins and Haskins, 1950a, 1950b) careful study of this most elementary stage of social development in the socially most primitive subfamily of ants may well shed very considerable light on the manner of origin and of subsequent evolution of the social mode of living in the Formicidae. In this connection, it is of particular interest that the observations of Clark (1925, 1934a, 1938), of Wheeler (1932, 1933), and of Haskins and Haskins (1950a, 1950b) on perhaps the two most archaic and socially generalized tribes of the Ponerinae, the Myrmeciini and the Amblyoponini, have indicated that in both of them, despite wide differences in morphology, physiology, and general habitus, the methods of colony foundation are closely similar, and are of a cruder and less specialized character than in any other known ants. In both cases the young female dealates herself, before or after fertilization, secretes herself in a chamber excavated in the soil, and then leaves this chamber at more or less frequent intervals to forage in the open for nourishment to sustain first herself and later her develop-

ing brood. The brood, when mature, comprises a few workers of the smallest form of the species. The workers and the adult female continue to forage in common until the colony is well developed.

This pattern of colony foundation suggests rather forcefully the nature of social organization of the earliest semi-social ants, which must long since have become extinct, and suggests further that the development of the social habit in the Formicidae, while strikingly similar to that well understood among the social wasps and bees and attested in those groups by the existence today of contemporaneous living intermediate forms, occurred independently in evolution, and probably at a much more remote period of time. It contrasts very strongly with the evidently derived pattern of claustral colony foundation which is common among the higher ants, in which the sexual female and the workers commonly differ greatly in stature, and in which a complicated physiological mechanism has been developed leading to the deterioration of the wing musculature shortly after dealation and, probably, to the conversion of this bulky protein reserve to a suitable form to assist in the sustenance of the queen, and to provide food reserves for the developing brood. These females, which are typical in such well-known genera as *Lasius* and *Camponotus*, after flight and dealation commonly isolate themselves in closed cells, from which they never emerge to forage. Eggs are laid, larvae are reared on a diet consisting entirely of ingluvial food administered by mouth, and at maturity the young workers, and they alone, break open the cell, emerge to forage, and bring back provender to restore the depleted fat-body of the sedentary queen, which never emerges into the open air again, except occasionally very briefly under unusual circumstances connected with a shift of the nesting site.

This specialized method of colony foundation common to so many Myrmicine and Formicine ants presents obvious selectional advantages over the primitive pattern as exemplified in *Myrmecia*. The young founding female, being amply supplied with reserve food material, is far less at the mercy of seasonal and environmental hazards than is the female of *Myrmecia*. The female of *Myrmecia*, forced to forage in the open every day or two for nectar or for living prey, is constantly exposed

to dangers from predators from which the female of *Lasius* or *Camponotus* is permanently protected as soon as its first cell is constructed. Finally, even if the young queen of *Myrmecia* succeeds in overcoming the numerous environmental hazards of drought or excessive moisture, of scarcity of food-sources, and of reptilian, avian, and mammalian predators during the difficult days of colony foundation, it is quite likely to become lost or otherwise permanently separated from its nest and its first brood in the course of its extensive wanderings.

Before this advantageous specialization can have taken place in the course of Formicid evolution, however, several concomitant physiological specializations must have occurred in whole or in part, and have been at least partially perfected. One of them is the ability of the individual to regurgitate ingluvial food for the larvae, thus precluding the necessity of supplying the larvae entirely with solid nourishment which must be brought in from outside. This power of regurgitation seems to be wholly lacking in both the Myrmeciini and the Amblyoponini. A second specialization which, while not essential to the development of the claustral method of colony foundation, is exceedingly helpful to it, is the faculty of breakdown of wing-muscle tissue to form a reserve of nutriment for the female. Work is in progress to determine whether there is any indication of such a development in *Myrmecia* or in *Amblyopone*. If present at all, it is certainly not nearly so conspicuous as among the higher ants. Third, it must have been essential, before the claustral method of colony foundation could be fully established, that a considerable difference of size should have been developed between the queen and the worker forms of a given species, so that several of the latter, pupating prematurely, could be sustained from the much greater bulk of the queen, with its specialized reserve of fat-body and perhaps of transformed wing-muscle tissues.

It is clear that none of these specializations occurred suddenly in evolution, and that they must all have been closely interrelated. Concomitantly, it would be expected that the development of the claustral mode of colony foundation would have occurred gradually, as these physiological specializations progressed, manifesting itself as a growing reliance of the queen on the sustaining powers of her own tissues, and an increasing

tendency to limit foraging to more and more lengthy intervals, feeding the larvae less and less upon insect prey and more and more upon ingluvial food, until, at last, the habit of foraging disappeared altogether.

The higher tribes among the Ponerinae, especially the Ectatommini, the Odontomachini, and the Ponerini are of peculiar interest in this connection. Here two of the three requisite physiological specializations, at least, seem to be moderately developed in certain species. Considerable discrepancy of stature between the perfect female and the first-brood workers is notable in a number of species of all these tribes. The power of regurgitation, though feebly developed, has been reported for the Brazilian *Odontomachus affinis* by Borgmeier (1920), for *Ectatomma tuberculatum* by Cook (1904-5) and has been observed in *Euponera gilva harnedi* by Haskins (1931). It might be supposed, therefore, that among these higher Ponerinae, examples could be found in which the females, unusually capable of fasting, tended to supply the first-brood larvae at least partially with ingluvial salivary or regurgitated substances and only in part with captured insect food, and to forage much less frequently than the fertile females of *Myrmecia* or *Amblyopone*.

A very definite suggestion of this intermediate situation was obtained in the course of the present study with *Odontomachus haematoda*. A young female, taken immediately after the nuptial flight and dealation, isolated itself in the artificial nest in a closed cell in the typical manner reported by a number of students of this genus. In this case, however, all opportunities to obtain nourishment outside the nest were withdrawn, so that the young queen was thrown entirely on its own resources. Under these conditions, this *Odontomachus* female produced numerous eggs, hatched them, and evidently fed the resulting larvae with ingluvial food (although the process was difficult to observe) since they developed rapidly. They remained healthy for some time but, when somewhat less than one-half mature, declined slowly and eventually perished. Shortly after this, the female perished also. It had been captured on December 9, 1947, and died on March 3, 1948. Thus, although it had been unable to bring its young larvae to maturity or to establish a permanent formicary without outside nourishment, it had raised a good-sized brood through almost half the period of growth on nour-

ishment supplied by its own body and had itself survived for ninety days without food. This represented a much closer approach to the claustral condition than could be achieved among the lower Ponerinae, and it was clear that the question of the intermediate evolutionary stages in colony formation exhibited among the higher Ponerinae merited further investigation.

Perhaps the most interesting of all Ponerine ants for studies of this kind is the Australian species *Brachyponera lutea*, because of the great disparity of size and differentiation of bodily structure between the perfect females and workers, in which it is unique among the Ponerines but approaches rather closely the condition among higher ants. It might be expected that in this species, above others, a close approach to the claustral mode of colony foundation might be achieved. Accordingly, observations were undertaken in the field and in the artificial nest which are recorded herewith.

Brachyponera lutea

The genus *Brachyponera* was considered by Emery (*Genera Insectorum*) as a subgenus of *Euponera*, and exhibits close affinities with that group, and with the genus *Ponera* *s. str.* in many respects of structure and behavior. As in *Euponera*, it is composed of active ants of wide distribution, showing a remarkable degree of variability and of plasticity of habit for a Ponerine group. In the majority of forms of *Brachyponera*, as in *Euponera*, the stature of the perfect females and of the workers is rather similar. In two species, however, *B. sennaarensis* Mayr of tropical Africa and *B. lutea* Mayr of Australia, the workers are very much smaller than either sexual form. In *B. lutea* this differentiation reaches an extreme both qualitatively and quantitatively, the workers averaging but 4–5 mm. in length and being of a pale yellow to brownish coloration, while the queens attain dimensions of 10–11.5 mm., are of brownish black pigmentation, and carry so much fat-body that their form is very different from that of the workers as, indeed, from the typical form of *Ponera* or *Euponera*.

The species was first described by Mayr (1868, 1876). The extraordinary difference in stature and appearance between queens and workers caused Crawley (1918) to call the cospecificity of the described types into question. The cospecificity

has, however, been thoroughly established by studies of Clark, Wheeler, and many others.

Brachyponera lutea is nearly ubiquitous in Australia, extending from the tropics almost into the coldest areas of the continent, and from the very moist soils of the extreme southwest into comparatively dry dune or rocky regions far from the coast. In some areas it is very common. It forms rambling meshes of galleries interwoven in a complex fashion, and probably often extending well underground. These galleries are excavated by preference underneath flat stones or fallen logs, but may occasionally show open craters. The colonies are unusually populous for a Ponerine, and fully developed communities may well comprise over two thousand individuals. There seems to be good evidence that the species feeds extensively on termites, and probably also on the larvae of other ants. Frequently, but not always, it nests close to or within the mounds of various species of termites, or near other ants, not excluding *Myrmecia*. It is very probable that it commonly behaves as a facultative, primitive thief ant.

The habits of *B. lutea* have been described by Clark (1925, 1938) and particularly by Wheeler (1933) who studied the method of colony foundation in the field. During November and December of 1914 and 1931 numerous recently fecundated females were taken by Wheeler in many localities in Australia including Queensland, New South Wales, and southwestern West Australia. All of them were isolated in cells under stones and logs, and in all cases these cells, unlike those typical of *Myrmecia* females, were located so far from the edges of the overlying cover that, in Wheeler's view, it would have been difficult for the occupants to excavate galleries to the outside permitting them to emerge periodically to forage, after the manner of *Myrmecia* and *Amblyopone*. From this evidence, together with the great relative stature and the voluminous fat-body of the queen, Wheeler concluded that colony foundation occurred in the claustral fashion typical of higher ants. Since none of the females observed by him in the field had produced eggs by the end of December, however, he was unable to confirm this conjecture. In the present study, it has been possible to observe the process of colony foundation in *Brachyponera lutea* in the arti-

ficial nest from its inception until the maturation of the first brood of workers.

On January 15, 16, and 17, 1948, three isolated fertile females of *Brachyponera lutea* were taken in closed cells excavated in nearly pure sand under stones in a typical Hawkesbury sandstone area near Sydney, N. S. W. These chambers were essentially as described by Wheeler, but one of the three queens had two small worker cocoons, evidently recently spun, and a second had several nearly grown larvae in the chamber. The third was without brood. The existing brood of the two females was destroyed in order to stimulate a recapitulation of the founding process, and all three insects were isolated in artificial nests. Here they soon excavated typical closed cells, which they showed no tendency to reopen. One of the three females was lost. The other two shortly produced further eggs, which were formed into packets and carefully tended.

Drops of a dilute solution of honey were proffered to these females from time to time, and were greedily accepted when thrust within the brood-chamber, but the females did not emerge to hunt for them. No solid food was made available. As the eggs hatched, the young were fed entirely by regurgitation, and developed rapidly. At maturity, the larvae were banked with earth in the usual fashion, the cocoons were spun, were cleaned by the female, and continued to be attentively cared for. By March 15, one of the females had brought to maturity three exceedingly small cocoons and had several young larvae, while several nearly mature (though still small) larvae were present in the other cell. By the end of the month the first cocoon was hatched, the extremely small and very callow young worker being much assisted by the female in eclosion. A second cocoon was successfully hatched by the female on April 11. The young workers remained for some time in the parent chamber, which was still tightly closed, before essaying to forage for food. No assistance was given by the queen in this process, just as the queens had shown no tendency to emerge to forage during the period of growth of the young.

These observations would seem to indicate fairly conclusively the correctness of the conjectures of Wheeler, first, that feeding by ingluvial regurgitated food is the commonest if not the only method by which the young queen of *B. lutea* nourishes the first-

brood workers, in contrast to the lower Ponerines, and second, that the colony may be formed in a perfectly claustral manner in this Ponerine, as among the higher ants.

There is some indication, however, that although such perfectly claustral colony foundation can and perhaps usually does occur in *B. lutea*, the pattern may not be as firmly established as among the Formicinae or the Myrmicinae. Thus five mature but virgin females, taken from adult nests near Sydney, when artificially dealated in Lubbock nests, behaved somewhat more typically of the lower Ponerines. All of them formed cells of the usual type, and all shortly produced eggs which were kept in compact packets and carefully tended. The cells, however, were not completely closed in this series. They were, in fact, frequently opened to permit the queens to emerge and forage. These queens, in sharp contrast to those described above, excavated extensive galleries, and, although they spent considerable periods quiescent within the brood-chambers, they also spent much time foraging, and eagerly accepted both nectar and insects, taking workers of *Reticulitermes flavipes* with especial avidity. At times, the females left the nests altogether to wander for periods in the open air before returning to the galleries and eventually to the brood chambers. Although these queens persisted until June, the infertile eggs failed to hatch, and no colonies were established. This was very probably abnormal behavior, based on the infertility of the females. It is of some interest, however, since the pattern so closely approximated that of the normal pattern of the fertile females of other Ponerine species.

It may be concluded, then, that the fertile females of *Brachyponera lutea* are capable of founding their colonies in the typically claustral fashion of higher ants, isolating themselves in permanently closed cells and bringing a few very small workers to maturity on ingluvial food probably derived entirely from their own tissues. At the same time, this remarkably advanced behavior-pattern may be more labile than among the higher ants. It is evident that the females of *B. lutea* retain the capacity to actively forage under certain conditions, and, it is quite likely, may do so normally if an unusually rich supply of insect

food is present, as it might be, for example, in a termite mound. This matter remains to be confirmed.

LITERATURE

- BORGMEIER, T.
1920. Zur lebenweise von *Odontomachus affinis Guérin*. Deutsch. Ver. Wiss. u. Kunst Sao Paulo: 31-38.
- CLARK, J.
1925. The ants of Victoria (Part II). Victor. Naturalist, 42: 135-144.
1934. Notes on Australian ants, with descriptions of new species and a new genus. Mem. Nat. Mus. Melbourne, 8: 5-20.
1938. Insects of Victoria. Part I. (Ants). Victorian Year Book, 1937, 38: 7-11.
- COOK, O. F.
1904. Report on the habits of the Kelep or Guatemalan cotton-boll weevil ant. U. S. Dept. Agri. Div. Ent. Bull., 48: 15 pp.
1905. Progress in the study of the Kelep. Science N. S. 21: 552-554.
- CRAWLEY, W. C.
1918. Some new Australian ants. Ent. Rec. Jour. Var., 30: 86-92.
- HASKINS, C. P.
1928. Notes on the behavior and habits of *Stigmatomma pallipes* Halde-
mann. Jour. N. Y. Ent. Soc., 36: 179-184.
1930. Preliminary notes on certain phases of the behavior and habits of
Proceratium croceum Roger. Jour. N. Y. Ent. Soc. 38: 121-126.
1931. Notes on the biology and social life of *Euponera gilva* Roger var.
harnedi M. R. Smith. Jour. N. Y. Ent. Soc. 39: 507-521.
1941. Note on the method of colony foundation of the Ponerine ant
Brothroponera soror. Jour. N. Y. Ent. Soc. 49: 211-216.
- AND E. V. ENZMANN.
1938. Studies of certain sociological and physiological features in the
Formicidae. Ann. N. Y. Acad. Sci., 37: 97-162.
- AND E. F. HASKINS.
1950a. Notes on the biology and social behavior of the archaic Ponerine
ants of the genera *Myrmecia* and *Promyrmecia*. Ann. Ent. Soc.
Amer. (in press).
1950b. Note on the method of colony foundation of the Ponerine ant
Amblyopone australis Erichson. Amer. Mid. Nat. (in press).
- MAYR, G.
1868. Formicidae in Novara Expedition. Zool. Theil. 2: 1-119.
1876. Die Australischen ameisen. Jour. Mus. Godeffroy, 5, Heft 12:
56-115.
- WHEELER, W. M.
1900a. A study of some Texan Ponerinae. Biol. Bull. 2: 1-31.
1900b. The habits of *Ponera* and *Stigmatomma*. Biol. Bull. 2: 44-69.
1906. On the founding of colonies by queen ants, with special reference
to the parasitic and slave-making species. Bull. Amer. Mus. Nat.
Hist. 22: 33-105.
1932. How the primitive ants of Australia start their colonies. Science,
N. S. 76: 532.
1933. Colony-founding among ants, with an account of some primitive
Australian species. Cambridge, Mass., Harvard University Press.



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