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Apterous females and shift of dispersal strategy in the *Monomorium salomonis*-group (Hymenoptera: Formicidae)

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The assumption that a number of apterous females belonging to the *Monomorium salomonis*-group are socially parasitic or inquilinous is reviewed and discarded. An hypothesis is presented which postulates that the development of aptery in females of this group is associated with a shift in dispersal strategy in the species involved. Morphological modifications connected with this process are outlined and possible consequences discussed.

Introduction

The large *salomonis*-group of the ant genus *Monomorium* is remarkable in that it contains a number of species in which the reproductive females are strikingly modified away from the pattern normally seen in such ants. These females are apterous and the species involved exhibit a serial morphological reduction of the flight sclerites, from the usual full complement down to an almost worker-like condition of the alitrunk.

In the past such forms, when discovered, were automatically treated as socially parasitic, being regarded as temporary social parasites or more commonly as workerless inquilines which had taken over the colony in which they were found. Strangely there was no direct evidence for this assumption of social parasitism in such females; the mere fact that they showed anatomical specialization by wing loss and reduction of the flight sclerites was enough to have them assumed to be inquilinous.

Following the custom of the early part of this century, socially parasitic forms, whether genuine or assumed, were automatically described as separate species and were very frequently placed in separate genera. In the *M. salomonis*-group this resulted in the erection of several spurious genus-level names which were created especially to hold such odd forms. The synonymizing studies of Brown and Wilson (1957), Ettershank (1966) and Espadaler (1982) have since sunk these names into the synonymy of *Monomorium*, but in large part have not suggested any alternative to the presumed socially parasitic lifestyles of the species involved, although both Brown and Wilson and Espadaler challenged the assumption of social parasitism in these species.

Interestingly, a few females of *salomonis*-group species are confirmed workerless inquilines (*santschii* (Forel), *wroughtoni* (Forel)) but in these the females retain their wings and have a full complement of flight sclerites, as is the case in other confirmed inquilines from other species-groups of *Monomorium*, such as *hospitum* Viehmeyer, *inquilinum* DuBois, *pergandei* (Emery) and *talbotae* DuBois.

By the early 1950s five species had been described from apterous (assumed inquilinous) females in that section of *Monomorium* now referred to as the *salomonis*-group, these assumed inquilines occupying the now-synonymized genus-level names

Epixenus Emery and *Xenhyboma* Santschi. Each of these females had been found either alone or in numbers within nests containing numerous perfectly ordinary *salomonis*-group workers. In all cases, because of the peculiar appearance of the female, it had been tacitly assumed that the female was not the rightful occupant but had usurped the position of the original reproductive female of the colony and was hence a workerless inquiline within a nest of host workers. Questions concerning the whereabouts of the 'genuine' females of these colonies, which were never found (that is, every time a colony of one of the presumed host workers was discovered it always had 'parasitic' females in it), and concerning how such apterous parasitic females could possibly achieve dispersion to fresh host colonies, were apparently never asked.

Brown and Wilson (1957) cast grave doubt on the supposed parasitic nature of many of these forms, demolished the logic which until then had rather weakly supported *Epixenus*, and went on to suggest that at least some of these odd females were in fact the normal reproductive form of the workers with which they were found. More recently Tohmé and Tohmé (1979) and Espadaler (1982) have also shown or deduced that these oddly apterous females are indeed the genuine reproductive females of the nests in which they are found, and are not inquilines. A taxonomic revision of the Afrotropical fauna of *Monomorium* by the present author, which is now in progress, has unearthed several more species where apterous females are produced by members of the *salomonis*-group.

Thus to date some 13 members of the *salomonis*-group are known which produce apterous females, and all indications point away from these forms being socially parasitic. To replace the social-parasitism theory an hypothesis is presented below which links the production of apterous females to a basic shift in the dispersal strategies of the species concerned.

Hypothesis

Apterous females, when developed in the *Monomorium salomonis*-group, indicate a change in dispersal strategy from mating flight followed by claustral nest founding to autoparasitism followed by colony fission.

Discussion of hypothesis

The vast majority of *salomonis*-group species produce seasonal swarms of alate females which undergo a mating flight and then shed their wings and initiate new colonies claustrally. However, in *M. pharaonis* (L.), a species belonging to a small complex which is peripheral to the core-species of the *salomonis*-group, the mating flight has been entirely abandoned. Although alate females are produced they mate and shed their wings within the parent colony, without ever venturing outside. This process, whereby new females either do not leave the parent colony or return to it immediately after mating, is termed autoparasitism. The polygynous colony thus produced by the autoparasitic process then undergoes fission when the population of the colony reaches a critical density. Despite repeated fissions mature colonies usually maintain several reproductive females.

Morphologically and ethologically it is only a small step from the strategy adopted by *pharaonis* to one in which the females, which never leave the nest to mate, never develop wings. In fact, another species of the *pharaonis*-complex, *dichroum* Forel, is known to produce apterous females in which the alitrunk retains nearly the full complement of flight sclerites. An Afrotropical species, *rufulum* Stitz, apparently produces both alate and apterous females, the latter matching the former except for the

lack of wings and some other slight modifications of the alitrunk. A full complement of alitrunk sclerites is present in the apterous female of *rufulum*.

The females of species which have adopted autoparasitism plus colony fission, and which have achieved an apterous condition because of it, are constrained evermore to this dispersal strategy; the mating flight is obviously irretrievably lost. The morphology of such apterous females then gradually becomes more specialized to exploit the apterous condition. Primarily this involves a diminution in size and reduction in number of the now useless flight sclerites, resulting in a female in which the alitrunk is very worker-like in overall appearance but still larger than that of the conspecific worker.

Such apterous forms are presently known from the following species of the *salomonis*-group: *advena* Brown & Wilson (= *andrei* Emery), *algiricum* (Bernard), *biroi* (Forel) (this is a preoccupied name for which no replacement has been proposed, see Brown and Wilson, 1957), *dichroum* Forel, *grassei* (Tohmé & Tohmé), *hesperium* Emery, *libanicum* (Tohmé & Tohmé), *medinae* Forel (= *mystes* Santschi), *minor* Stitz, *opacior* Forel, *rufulum* Stitz, *syriacum* (Tohmé & Tohmé), *venustum* (Smith).

Of the names included in Brown and Wilson (1957), *guineense* (Bernard) is omitted here as it does not belong to the *salomonis*-group, and *creticum* (Emery) is omitted as it is based on a male. It is possible that some of these 13 species may be capable of producing both alate and apterous females, although this has been proved only in *rufulum* where the apterous form is very similar to the alate; this species may just be making the transition from the one dispersal strategy to the other. Other species which at present are only known to have alate females may prove also to have some capability to produce apterous forms. Only detailed investigation in the field can confirm or disprove this supposition, but it seems reasonable to assume that the more worker-like the apterous female becomes the less likelihood there is of alate forms being produced as well. Three basic grades may be postulated within the *salomonis*-group.

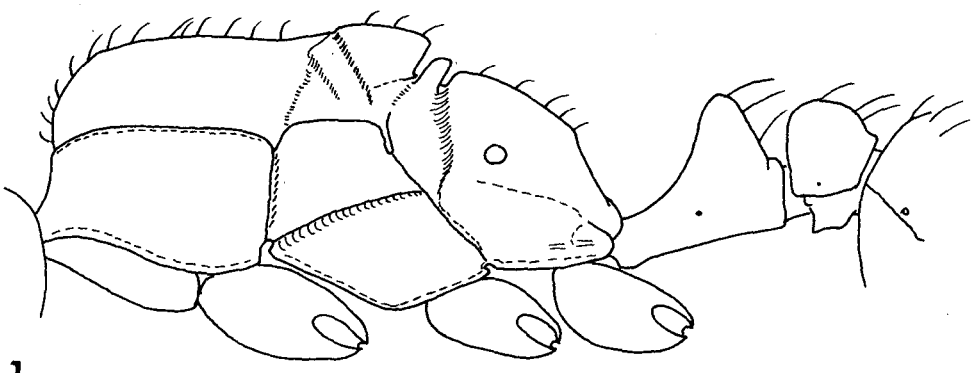
First, species in which all known females are alate and which apparently always undergo a mating flight followed by claustral nest founding (the vast majority of *salomonis*-group members, including the common species *afrum* André, *albopilosum* Emery, *bicolor* Emery, *junodi* Forel, *salomonis* (L.), *subopacum* (Smith)).

Second, the transitional forms such as *pharaonis* where all females produced are alates but are autoparasitic, mating within the parent colony, and *rufulum* where the females may be alate or apterous; whether the alate forms of *rufulum* are autoparasitic is not known.

Third, those species in which all females, as far as is known, are apterous and which found new colonies only by autoparasitism followed by colony fission. (It should be pointed out that the development of aptery in these females does not constitute an apomorphy delimiting a holophyletic lineage, as species from several different complexes of related forms are involved.)

Among the apterous species listed several stages in a morphoclinal reduction in the alitrunk sclerites, both in size of individual components and in number of sclerites represented, is discernable. These reductions and their postulated order of occurrence are:

(1) Retention of all flight sclerites seen in normal female but the wings not developed, the wing-roots sealed by overgrowths of cuticle. Alitrunk of normal female form but usually the mesoscutal dorsal outline slightly concave or saddle-shaped (fig. 1).
(2) Axillae fuse to mesoscutum, first partially then totally.



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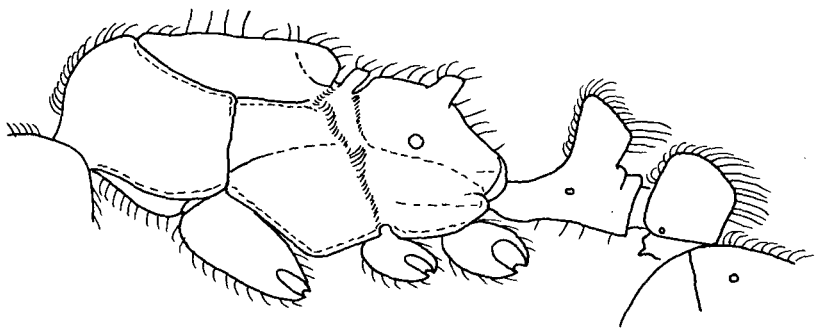

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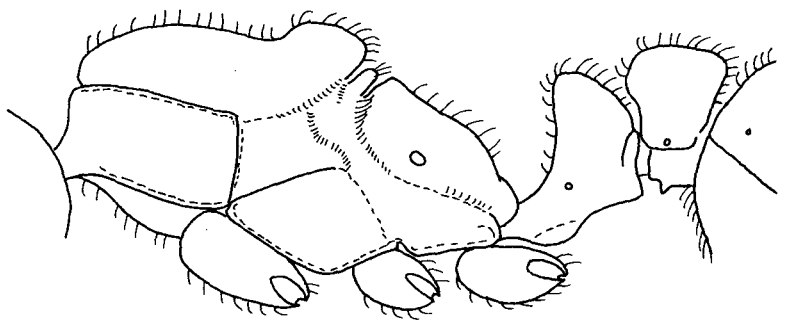

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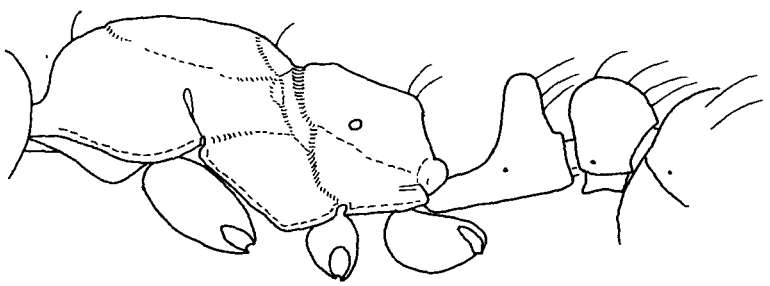

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FIGS 1–4. *Monomorium* apterous females, alitrunk profiles of: 1, *rufulum*; 2, *hesperium*; 3, *medinae*; 4, *advena*.

(3) Reduction in size of mesonotum and corresponding increase in size of pronotum so that the latter comes to form part of the dorsal alitrunk when viewed in profile (figs 2, 4).
(4) Mesoscutellum fuses to mesoscutum, first partially then totally (figs 1–3).
(5) Disappearance of metanotum as a separate dorsal sclerite (fig. 4).
(6) Promesonotal suture obliterated on dorsal alitrunk and lateral sutures of mesonotum reduced or effaced (fig. 4).

The distribution of these characters among the eight species of apterous females available for examination is as follows:

	Character number					
	1	2	3	4	5	6
opacior	+					
rufulum	+					
venustum	+	+				
medinae		+		+		
minor		+	+	+		
hesperium		+	+	+		
dichroum		+	+	+		
advena		+	+	+	+	+

From descriptions the females of *algiricum, biroi, grassei, libanicum* and *syriacum* appear to have an alitrunk structure similar to that of *advena* or slightly less or more reduced. The reduction in complexity of the alitrunk is accompanied in some species, especially the more extremely simplified forms, by a reduction in size of the eyes towards the relative size seen in the workers, and a gradual disappearance of the ocelli.

Consequences of changing dispersal strategy

Given that the majority of *Monomorium salomonis*-group species utilize a mating flight followed by claustral colony founding as their dispersal technique, what are the advantages and disadvantages to abandoning this system in favour of autoparasitism followed by colony fission, and what reasons can be advanced for why such a change in strategy should be inaugurated? Obviously, while the biology and ecology of the species involved remains unknown only speculation on the possible advantages and disadvantages can be put forward, but the following suggestions seem reasonably sound at the present time.

Advantages to adopting autoparasitism followed by colony fission include:

(1) New females mate within the safety of the parent colony.
(2) Newly mated females are maintained within the parent colony and are not exposed to the massive predator pressure which accompanies those sexual forms undergoing a mating flight; in consequence they escape the great loss of reproductive potential inherent in this system.
(3) As a consequence of (2), the colony needs to expend less energy on production of reproductive females because the survival potential of those which are produced is very high.
(4) Mated females leaving the parent nest to found new colonies can be accompanied by workers and brood when the parent colony undergoes fission; this increases the survival chances of the new colony as a whole.

(5) Adoption of a colony fission strategy means that areas relatively rich in nest sites and good resources can be colonized quickly.
(6) The presence of more than one reproductive female (polygyny) in the nest means that the death of one female does not dictate that the colony will die out.

Disadvantages connected with the loss of the mating flight include:

(1) The distance of spread of new females from any parent nest is relatively short.
(2) Inhospitable areas cannot be crossed easily by apterous forms and hence populations will tend to be relatively restricted.
(3) Changes in the environment in the immediate vicinity of the colonies may lead to complete destruction of all nests of a given locality. Loss of alate females means that reproductives cannot easily leave the area to attempt colonization elsewhere.

As for why the mating flight should be abandoned and a system of autoparasitism and colony fission adopted, some partial answers may perhaps be gleaned from the list of advantages given above. In particular advantages (2) and(3) may prove very important, as the production of masses of new females each year absorbs an enormous amount of the energy available to a colony. In regions where food may be relatively sparse the production of a few females with high survival potential may represent a marked advantage over squandering the colony's energy resources in the production of swarms of alates, most of which are doomed to end as a meal for some predator. Support is lent to this suggestion by the fact that most species of the *salomonis*-group which have evolved apterous females live in arid to semi-desert zones such as rocky oceanic islands, the margins of the Sahara, Namib and Kalahari deserts, and the dry southern and eastern shores of the Mediterranean.

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