

The diversity and evolution of recruitment behaviour in ants, with a discussion of the usefulness of parsimony criteria in the reconstruction of evolutionary histories

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Summary

Three alternative hypotheses about the evolution of recruitment behaviour in ants, based on accounts in the literature, are compared by means of a cladistic analysis. The three hypotheses are the following: *Hypothesis 1*. Increasingly efficient recruitment behaviours exhibited by different ant species have been shaped by or are correlated with ant phylogeny. *Hypothesis 2*. Increasingly efficient recruitment behaviours represent necessary evolutionary steps independently followed during the evolution of different ant clades. *Hypothesis 3*. Differently efficient recruitment behaviours have been selected in a convergent way among different species by similar population/environmental constraints.

In a first stage of the analysis, these hypotheses have been compared in terms of parsimony (i.e. in terms of tree length = TL) of alternative cladograms based on recruitment behaviour only. The analysis gave the following results: Hypothesis 1, TL = 4; Hypothesis 2, TL = 18; Hypothesis 3, TL = 11. At least in terms of parsimony, hence, Hypothesis 1 appears to be the “best”. This hypothesis, however, cannot be retained for its total lack of congruence with current views on ant phylogeny. Among the remaining two hypotheses, Hypothesis 3 is again much (ca. 40%) more parsimonious than Hypothesis 2, but the retention index for recruitment behaviour on the relative cladogram is 0.2 as compared with 0.7 for Hypothesis 2. Practically, this implies biologically very implausible behavioural evolution indicated by very improbable ancestors for the species included in the analysis. In the case of recruitment evolution the biological credibility of each hypothesis is inversely proportional to its parsimony.

The three hypotheses on the evolution of recruitment behaviour are compared again taking into account the morphological and behavioural correlates of recruitment. The results confirm those obtained by simple cladistic analysis of behaviour alone, namely that an obligatory (i.e. neither reversible nor random) increase in recruitment efficiency has been repeatedly selected within different ant clades. Inclusion of the recruitment correlates allows, in addition, a more precise formulation of the implications of each hypothesis and a tentative test of two other alternatives deduced from the literature. Most papers dealing with recruitment assume this behaviour to be controlled by a single gland, while at least two experimental analyses show that more than one gland is likely to be involved as behavioural releaser. A cladistic approach allowed testing of the following two adaptational hypotheses: A) Synergic behavioural control by several glands, allowing shift of the dominant role from one gland to another. B) Single gland control, making improbable the replacement of one gland by another that performs the same function. The results of the analysis appear to favour alternative A slightly, though neither alternative results in implausible evolutionary paths.

It is stressed that parsimony remains the sole decisional criterion when no other criteria are available but it can by no way be preferred to the slightest trace of biological common sense.

Introduction

Recruitment of nestmates to a food source or to a new nesting site is perhaps one of the best explored behaviours among ants. Its manifestation and its biochemical and anatomical components have been subjected to several detailed analyses in a relatively wide array of species (see e.g. the review by Hölldobler, 1984a, and references therein). The main idea resulting from most reviews and comprehensive papers dealing with this subject is that "primitive" ants should be unable to recruit or able to recruit only a few individuals, whereas, more advanced ant species should have developed pheromonal and anatomical means which enable them to recruit larger numbers of individuals simultaneously. This view, in its simplicity, strongly influenced several students, but showed varying disagreement with our knowledge of ant phylogeny. Three hypotheses about the origin of the diversity of recruitment mechanisms in ants can be found in the literature. However, as more specific behaviours were analyzed, the plausibility of a hypothetical concordance between recruitment behaviour and ant phylogeny appeared to decrease. Further, opinions changed very quickly, and were sometimes formulated in a contradictory way within the same paper. These adaptational explanations were proposed before the modern cladistic principles became established, and, for this reason, they need to be interpreted to different extents in order to be tested in a logical way and are reformulated here in more precise terms. In the following text, I give a short logical reformulation of the contrasting, available hypotheses, together with some citations of papers supporting them to various degrees.

Hypothesis 1. *The evolution of recruitment behaviour recapitulates at least to some extent ant phylogeny.* This hypothesis has been formulated or used as a working hypothesis by Hingston (1928), Sudd (1959), Wilson (1959, 1971, 1975), Hölldobler (1971, 1977, 1981a), Maschwitz (1975), Cammaerts and Cammaerts (1980), and Jaffe (1984), who attempted to attribute variable extents of phylogenetic value to recruitment behaviour. The common idea is that, in the course of ant evolution, greater recruitment efficiency has been selected for in one or more steps. Stated succinctly, ant species able to recruit one single nestmate at once (tandem running) have been considered as more "primitive" than, or somehow ancestral (i.e. less specialized) to, species able to recruit simultaneously more individuals on a trail.

This hypothesis is attractively simple; however, all authors supporting it were well aware that it apparently contrasted with some facts, such as the absence of recruitment among members of supposed advanced subfamilies, like the Formicinae (e.g. *Cataglyphis*). Some resolution of this dilemma may be found in the phylogenies of the Formicidae proposed by Baroni Urbani (1989) and Baroni Urbani et al. (1992) in which the Formicinae are shown to exhibit many more plesiomorphic characters than used to be thought.

Hypothesis 2. *The different degrees of recruitment efficiency represent obligatory successive evolutionary steps for each species but they may have evolved convergently*

within supraspecific taxa. This hypothesis can be seen as a necessary refinement of Hypothesis 1, a refinement which becomes more and more necessary as more species are studied. The hypothesis has been assumed by Traniello (1977), and has been supported particularly by Hölldobler (1978, 1981 b and 1984 a: 368) and Hölldobler and Wilson (1990).

This view denies a strict correspondence between phylogeny and recruitment mechanisms. It restricts the evolutionary meaning of different recruitment types to a number of steps, still in increasing order of efficiency, necessary to explain the genesis of the most efficient recruitment behaviours, from tandem running to the raiding behaviour of army ants. The difficulty with this hypothesis lies on the fact that taxa which are polymorphic for their recruitment type must have evolved from an ancestor exhibiting the lowest rank recruitment. The presence of genera, like *Camponotus*, in which "primitive" and "advanced" recruitment mechanisms coexist could still imply – though to a lesser extent than under Hypothesis 1 – great increases in the total number of steps necessary to explain recruitment evolution and/or implausible phylogenies.

Hypothesis 3. *Differences in recruitment behaviour reflect specific adaptation mechanisms to population or environmental structure*. Although never explicitly formulated by these authors, this hypothesis could have been surmised from experimental results obtained by Bernstein (1975), Hölldobler (1976), Cammaerts (1978). These papers describe the use or non-use of a recruitment behaviour within the same species according to the changing environmental situation. The hypothesis seems to have been clearly formulated for the first time by Hölldobler (1978: 87). More recently, Oster and Wilson (1978), Traniello and Hölldobler (1984 a: 371), Deneubourg et al. (1986, 1987), Peeters and Crewe (1987), Baroni Urbani (1989), Hölldobler and Wilson (1990: 265) have used this perspective to explain difference of recruitment mechanisms observed among ants. Beckers et al. (1989) denying a significant phylogenetic meaning to ant recruitment behaviour went a step further in this direction by interpreting behaviours leading to different numeric efficiencies as straightforward responses to specific colony sizes (i. e. excluding small colonies due to young age).

The purpose of this paper is to examine the relative merits of these three competing hypotheses.

A first step of the analysis conducted in the present paper consists in an adaptational test of recruitment evolution as recently recommended by Coddington (1988). The study of recruitment behaviour, however, may permit further insights in this way of hypotheses testing, insights which may be easier to perform than while dealing with other behaviours. Recruitment, in fact, is a complex behaviour depending on a set of morphological and other correlates which, logically, can not be omitted while dealing with its evolution. Explicit consideration of these correlates – by including them in the cladistic analysis – should permit a deeper understanding of the whole phenomenon.

The majority of the pertinent literature, in addition, implicitly supports the hypothesis that recruitment behaviour is released by the products of a single gland. This idea finds its logical support in a broad set of bioassays showing how, for several species, trail following workers may be recruited to artificial trails traced by means of

an isolated gland. On the other hand, at least Robertson et al. (1980) and Cammaerts (1982) gave evidence that recruitment behaviour is likely to be not released by one glandular product only and that other glands secrete smaller amounts of pheromones also contributing to the behavioural manifestation. An explicit experimental test of these two alternative hypotheses is difficult to perform, due to the fact that complete evidence for the non-use of a gland whatever is much more difficult to gather than evidence for its use. In the present paper an attempt will be made to resolve the dilemma of single gland control versus glandular synergy in purely cladistic terms.

Materials and methods

1. Species and characters considered

In this analysis, I included 15 ant species already graphically tabulated in the review by Hölldobler (1984a), plus 7 additional ones for which the recruitment behaviour (or its absence) are well documented and which have phylogenetic positions suitable for supporting or falsifying possible phylogenetic pathways. Other ant species which have been carefully analyzed in their recruitment behaviour have not been included in the analysis because either their behaviour or systematic position or both were uninformative in this context (i.e. extending the analysis to species pertaining to the same unresolved clade and exhibiting the same behaviour would result in redundancy only); further, inclusion of additional species in the data matrix would have increased the computation time necessary to the analysis itself by an order of magnitude far beyond the possibility of any available computer.

Recruitment behaviour has been coded into 5 different steps. Their meaning should be self evident and they correspond well to those already used by Maschwitz (1975) and Beckers et al. (1989). Nevertheless, some confusion could arise from the fact that different authors sometimes used the terms "group recruitment" and "mass recruitment" with different meanings. Here I consider the following two and define these by the presence (= trail following) or absence (= mass recruitment) of a leader, i.e. of the first recruiting ant(s) on the way back to the food site together with the first recruited nestmates. An additional state for this character often mentioned in the literature, i.e. trunk trails, has not been distinguished from mass recruitment in this paper. As suggested by Jacques Pasteels (personal communication), it is likely that its difference from the latter often corresponds much more to differences in food distribution (i.e. clumped seeds for harvester ants in my own experience) than to specifically characteristic behaviours.

In addition to recruitment behaviour itself, the following 11 correlates of recruitment have been tabulated and included in the data matrix. The first 9 are morphological characters strictly related to recruitment behavior of the species considered and the last two characters are behavioural ones. They have all been coded as 0 and 1. The first 8 characters refer to glands which – except the tibial gland – are widespread if not omnipresent among ants. Coding of one or more of these glands as 0 or 1 for one ant species means not, of course, the absence or presence of the gland itself, but its use or non-use during recruitment behaviour. This corresponds to the

current view as expressed by most behavioural analyses of recruitment, but, in this context, one should not forget that at least Robertson et al. (1980) gave strong evidence that, in *Linepithema*, one gland is likely to play a dominant role in recruitment, while many more additional glands can still play a minor but essential role, and, Cammaerts (1982) showed that, in *Myrmica*, at least two, completely separate, groups of secretory cells are involved in recruitment. All sternal glands (character 2) have been tentatively coded together here as already done by Hölldobler (1984a), though their real homology remains doubtful. Character 9 (dorsal stridulatory organ) is coded according to its actual presence or absence. When present, it is arbitrarily assumed that it plays a role in recruitment as indicated by growing evidence in the literature as given by Markl and Hölldobler (1978), Maschwitz and Schönege (1983), and Baroni Urbani et al. (1988). Recruitment, in addition, seems to represent the socially "most important" behaviour in which the organ is known to be involved and the more detailed analyses of "motor display" during recruitment suggest regular use of the stridulatory organ (see e.g. Szlep-Fessel, 1970, and Baroni Urbani et al., 1988). Character 11 (motor display, i.e. a set of jerking movements and/or short zigzag runs of the recruiting ant after its return to the nest) has been considered as present in all species showing recruitment, even in the few cases in which it has not been explicitly described, because it is regarded as the necessary prerequisite for following behaviour as already suggested by Hölldobler (1971) and Szlep (1973). The potential interest of this character for the analysis lies, of course, in its presence in one of the two non-recruiting species and its absence in the other one among those considered in this paper (see the data matrix).

Tandem running recruitment and stereotyped adult transport have been arbitrarily coded as present if they have been described during nest migration, recruitment to food, or both. For the purpose of the present analysis it seems advisable to record their presence/absence even if they have not been observed during recruitment: I consider this solution preferable to the alternative of considering absent a behaviour which might have been simply not observed or reported. No semiochemical characters have been considered in this analysis because recruitment (and other) pheromones in ants are often described from glandular extracts but the role of the individual compounds in behaviour is too poorly known to allow their coding as releasers of recruitment (see review by Attygalle and Morgan, 1984).

The five recruitment types – coded here as increasing states of a single multistate character – and the species for which they have been described, together with the anatomical correlates of recruitment behaviour are given in Table 1. Coding of recruitment behaviour in this way and comparing the results obtained under different evolutionary assumptions is regarded as the main tool enabling this analysis. In fact, each different evolutionary sequence attributed to this behaviour corresponds to one of the hypotheses available from the literature and discussed here. For completeness, and in order to allow comparison with the other taxa, the table includes all known correlates of recruitment behaviour, including those reported for one taxon only, like tibial gland, rectal gland, and cloacal gland. These characters are autapomorphic in the data matrix, and, as such, cladistically uninformative. Equally autapomorphic in this context is the absence of motor display, recorded for one species only.

Table 1. Distribution of the morphological and behavioural correlates of recruitment behaviour for the 22 species considered in the present analysis, together with the pertinent source of information.

1. Janet's gland, involved in recruitment (1) or not (0); 2. Sternal glands involved in recruitment (1) or not (0); 3. Poison gland, involved in recruitment (1) or not (0); 4. Hindgut, involved in recruitment (1) or not (0); 5. Dufour gland, involved in recruitment (1) or not (0); 6. Tibial gland, involved in recruitment (1) or not (0); 7. Rectal gland, involved in recruitment (1) or not (0); 8. Cloacal gland, involved in recruitment (1) or not (0); 9. Stridulatory organ, present (1) or absent (0); 10. Stereotyped adult carrying behaviour present (1) or absent (0); 11. Motor display present (1) or absent (0); 12. Recruitment type: none (0), tandem running (1), trail laying (2), mass recruitment (3), army ants (4)

Species	Subfamily	Characters												Source of character coding (*)
		1	2	3	4	5	6	7	8	9	10	11	12	
<i>Anuretus simoni</i>	Aneuretinae	0	1	0	0	0	0	0	0	0	1	1	3	Traniello & Jayasuriya 1981
<i>Camponotus ephippium</i>	Formicinae	0	0	0	1	0	0	0	1	0	1	1	2	Hölldobler 1982b
<i>Camponotus socius</i>	Formicinae	0	0	0	1	0	0	0	0	0	1	1	1	Hölldobler 1971
<i>Cataglyphis bicolor</i>	Formicinae	0	0	0	0	0	0	0	0	0	1	1	0	Wehner et al. 1983; #11 from Szlep 1973
<i>Cerapachys turneri</i>	Cerapachyinae	1	0	1	0	0	0	0	0	0	?	1	3	Hölldobler 1982a
<i>Crematogaster ashmeadi</i>	Myrmicinae	0	0	0	0	0	1	0	0	1	1	1	2	Leuthold 1968a and 1968b; #10 from Wilson 1971
<i>Eciton hamatum</i>	Ecitoninae	1	0	0	1	0	0	0	0	0	0	1	4	Hölldobler 1984a
<i>Formica fusca</i>	Formicinae	0	0	0	1	0	0	0	0	0	1	1	3	Möglich & Hölldobler 1975
<i>Lasius fuliginosus</i>	Formicinae	0	0	0	1	0	0	0	0	0	1	1	3	Hangartner & Bernstein 1964
<i>Leptogenys chinensis</i>	Ponerinae	1	0	1	0	0	0	0	0	1	0	1	2	Maschwitz & Schönege 1983
<i>Linepithema humile</i>	Dolichoderinae	0	1	0	0	0	0	0	0	0	1	1	2	Wilson & Pavan 1959; Robertson et al. 1980; Beekers et al. 1989
<i>Monomorium pharaonis</i>	Myrmicinae	0	0	1	0	1	0	0	0	1	?	1	3	Sudd 1959; Hölldobler 1973
<i>Myrmica rubra</i>	Myrmicinae	0	1	1	0	1	0	0	0	1	1	1	2	Cammaerts 1978; #10 from Abraham & Pasteels 1980

Table 1 (continued)

Species	Subfamily	Characters												Source of character coding (*)
		1	2	3	4	5	6	7	8	9	10	11	12	
<i>Nothomyrmecia macrops</i>	Nothomyrmecinae	0	0	0	0	0	0	0	0	0	0	0	0	Hölldobler & Taylor 1983; #9 from Taylor 1978
<i>Oecophylla longinoda</i>	Formicinae	0	1	0	0	0	0	1	0	0	1	1	3	Hölldobler & Wilson 1978
<i>Onychomyrmex hedleyi</i>	Ponerinae	1	1	0	0	0	0	0	0	0	?	1	4	Hölldobler et al. 1982; #9 personal observations
<i>Orectognathus versicolor</i>	Myrmicinae	1	0	1	0	0	0	0	0	?	1	1	2	Hölldobler 1981 a
<i>Pachycondyla laevigata</i>	Ponerinae	1	0	0	0	0	0	0	0	?	?	1	2	Hölldobler & Traniello 1980
<i>Pachycondyla obscuricornis</i>	Ponerinae	1	0	0	0	0	0	0	0	1	1	1	1	Traniello & Hölldobler 1984; #9 personal observations
<i>Paltothyreus tarsatus</i>	Ponerinae	1	0	0	0	0	0	0	0	0	?	1	3	Hölldobler 1984 b
<i>Pogonomyrmex badius</i>	Myrmicinae	0	1	1	0	1	0	0	0	1	0	1	3	Hölldobler & Wilson 1970; #10 from Möglich & Hölldobler 1974
<i>Solenopsis invicta</i>	Myrmicinae	0	0	1	0	1	0	0	0	1	0	1	3	Wilson 1962

(*) Character #9, if not stated otherwise, has been coded mainly according to Markl (1973). For *Leptogenys chinensis* its presence is reported in the behavioural paper by Maschwitz & Schönegge (1983). Character #10 has been considered as present among all Formicinae and Dolichoderinae as it is usually assumed in the literature even if it has been not expressly described for all the species included in this analysis

2. *Assumptions about character evolution*

The testing of the three hypotheses resulting from literature implies some assumptions about the evolution of the behaviour under study. One of the two following possibilities has been assumed: transitions between character states in recruitment evolution have been coded as “unordered”, i.e. allowing change from any state to any other state in one step, or “irreversible”, permitting only increasing stepwise character evolution. Irreversible evolution of recruitment behaviour from less efficient to more efficient mechanisms corresponds to Hypotheses 1 and 2. Unordered evolution of different recruitment mechanisms describes the contents of Hypothesis 3 (i.e. the individual species adaptation to environmental constraints in a way independent from phylogeny).

These same different models of character evolution (i.e. unordered vs. irreversible), when applied to the correlates of recruitment, should permit a test of the dilemma between single gland control and glandular synergy. The first alternative, i.e., the single gland control can be translated in cladistic terms by assuming the use or non-use of a given gland as irreversible. The idea supporting this assumption considers unlikely that a given ant species may have recruited by using the products of a given gland, and, in the course of evolution, continued recruiting by means of another gland (i.e., once an ant species started recruiting by means of a gland, use of this gland can not be completely lost in favour of another). If more than one exocrine gland contributes to the release of recruitment behaviour, the shift of the dominant role from one gland to another without complete loss of use of the first appears much more probable. Allowing such a shift within the phylogenetic constraints corresponds to coding the morphological/behavioural correlates of recruitment as unordered.

This implies, practically, that each of the three hypotheses to be tested has been analyzed twice, once (A) with the correlates of recruitment coded as unordered and hence allowing for use or non use of a given gland in one equally probable step; this corresponds to assuming a synergic effect of more than one gland. The same hypothesis, afterwards, had been tested again (B) by assuming the evolution of the recruitment correlates to be irreversible, i.e., use or non use of a gland can be gained or lost only once as one should assume in the hypothesis that a single gland controls recruitment behaviour.

3. *Topological constraints*

The search for the most parsimonious reconstruction, in general, can not be free but, as already stated in the introduction, must take into account the most probable phylogenetic relationships of the taxa under study. Only Hypothesis 1 predicts that an increasing evolutionary complexity of recruitment behaviour alone should be consistent with the formicid phylogeny. While comparing the formicid phylogeny with the cladograms resulting from the present analysis, two levels of the classification of the species examined in this paper are regarded as realistic and satisfactorily understood: the subfamilial and the generic classification. This means

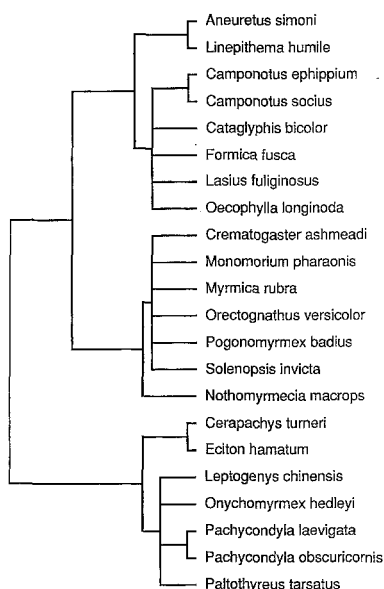


Figure 1. Partially resolved ant phylogeny inputted as phylogenetic constraint in order to test some hypotheses on the evolution of ant recruitment behaviour. In this phylogeny only generic monophyly and the presumend subfamilial relationships as described by Baroni Urbani et al. (1992) are taken into account

that only cladograms allowing species of the same genus and species of the same subfamily to cluster together have been retained. Arrangements of different genera within a subfamily or successive branching within different subfamilies have been left free because the infra-subfamilial phylogeny of ants is not yet known with sufficient certainty. This is meant to impose strict monophyly of at least the genera and of the subfamilies included in the analysis. The most probable phyletic relationships within the different ant subfamilies, however, have been recently described by Baroni Urbani et al. (1992) and they have been also included into the phylogenetic constraints. The phylogenetic constraints used for the different analyses were, hence, as shown in Fig. 1. Polytomies in this cladogram correspond to still unresolved dichotomies in the phylogeny of the species considered (Baroni Urbani et al., 1992). Since at least part of the species clustering on each polytomous branch differ in their recruitment behaviour, these polytomies can tentatively be further resolved by the following analysis of behavioural characters.

A very simple approach in comparing the three hypotheses described in the introduction consists in finding out which one is the most parsimonious one. Parsimony has been measured – as usual in cladistic analyses – in terms of the sum of the number of evolutionary steps necessary to construct the shortest possible tree(s) describing each hypothesis. This last property, i.e. the minimum number of evolutionary steps to construct a phylogeny, is a common parameter in cladistic analyses called “tree length” (see later).

In the behavioural literature, until now, the most parsimonious hypothesis has been searched for intuitively. Considering that for 22 species, as many as they are those examined here, over 2.37×10^{29} different rooted evolutionary trees with unlabeled interior nodes exist (Felsenstein, 1978a), it appears worthwhile to try the cumbersome but surely more exact approach employed here.

4. Methods of computer analysis

The cladistic analysis has been performed by PAUP, Version 3.0b (Swofford, 1989). Search of the optimal tree for Hypotheses 1 A, 1 B, and 2 A, given the high number of taxa involved, has been performed by the approximate heuristic method. Since adding constraints to the search for the shortest tree(s) greatly reduces the number of possible solutions, the optimal tree(s) for the other hypotheses have been searched for by the exact "Branch-and-bound" algorithm (Hendy and Penny, 1982) which gives the mathematical guarantee to find all optimal solutions. The character state optimization has been performed by the DELTRAN (= delayed transformation) option (Swofford and Maddison, 1987). This transformation differs from other possible ones for privileging parallelisms over reversals in evolution and I regard it as the most appropriate one while trying to describe the adaptive value of a behaviour within a phylogenetic framework.

Each set of data has been examined a second time with the CONDENSE option in order to verify the total number of evolutionary reconstructions consistent with each hypothesis, including those which are not explicitly supported by the data matrix. Congruence between the behaviour-derived phylogenies and the phylogenetic constraints has been evaluated by means of the FILTER option in PAUP, where the presumed formicid phylogeny has been used as a filter to retain potentially compatible behaviour-derived trees.

Results

A. Monothetic analysis of recruitment behaviour

Computing the most parsimonious tree(s) for the 22 species examined and assuming irreversible evolution of recruitment behaviour without phylogenetic constraints corresponds to Hypothesis 1. This leads to the construction of only one, largely polytomous, tree. Its length, as was to be expected for a single 5-states character, is of 4 evolutionary steps only, but none of the dichotomies appearing on it corresponds to those assumed by ant phylogeny. Computation of all data-compatible dichotomies under this hypothesis produced a memory overflow in a Macintosh II computer after 24 600 trees had been retained in memory without accomplishing the job. In addition, between the phylogenetic constraints and the recruitment-derived phylogeny there is complete lack of consensus.

Search of the most parsimonious tree(s) after coding recruitment evolution as irreversible but with addition of the phylogenetic constraints described in the method

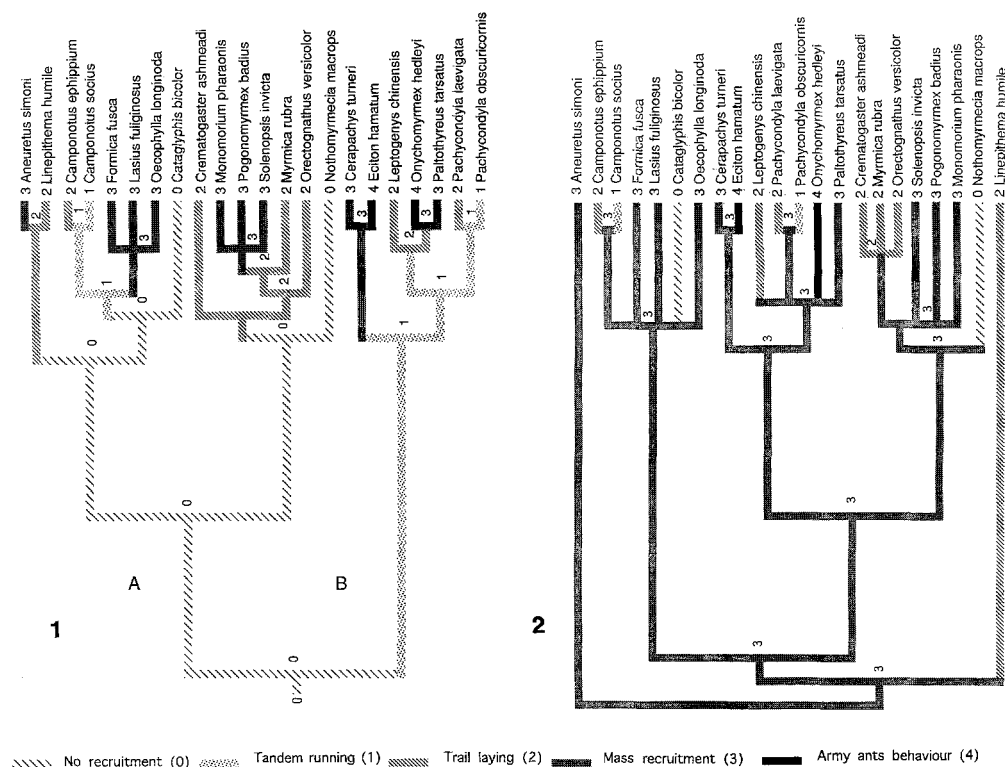


Figure 2. Most parsimonious reconstruction of the evolutionary path of recruitment behaviour according to different hypotheses discussed in the text. Optimization by delayed character transformation. The figures on the trees indicate the reconstructed states for internal nodes. The letters A and B label the two major clades referred to in the text. **2.1.** Unique partly polytomous tree accounting for the most parsimonious reconstruction of the evolutionary path of recruitment behaviour assumed irreversible and under the phylogenetic constraints (Hypothesis 2 in text). **2.2.** Most parsimonious reconstruction of the evolutionary path of recruitment behaviour assumed unordered and under the phylogenetic constraints (Hypothesis 3 in text). Strict consensus of 6 trees

chapter corresponds to Hypothesis 2. The search allows the construction of only one tree of length 18. This tree (Fig. 2.1) is better resolved than were the initially loaded phylogenetic constraints (Fig. 1), though it presents still three polytomies corresponding to four dichotomically unresolved taxa. Allowing all possible but not data-supported dichotomies to be drawn, will lead to the construction of 135 equally parsimonious trees.

Search of the most parsimonious tree as before but assuming recruitment evolution to be unordered (i.e. testing Hypothesis 3), allows the construction of 6 equally most parsimonious trees of length 10. Allowing all non data-supported dichotomies to be drawn increases the number of equivalent trees to 23 625. To better understand the meaning of this hypothesis, hence, the strict consensus tree showing only the identical portions of these trees has been drawn (Fig. 2.2). It must be noticed

Table 2. Comparison of some parameters and properties relative to the three models of recruitment evolution described in the text

	Tree length	Consistency index	Retention index
Hypothesis 1	4	1	0.333
Hypothesis 2	18	0.222	0.702
Hypothesis 3	11	0.364	0.222

that the consensus tree representing Hypothesis 3, in this case, has a length of 11, i.e. it is one step longer than the trees from which it was originally drawn.

Table 2 compares the unique partially polytomous cladograms of Hypothesis 1 and 2 with the consensus cladogram of Hypothesis 3 in terms of the following three parameters: 1. Tree length, i.e. the total number of evolutionary steps required by the character(s) employed by the analysis. 2. Consistency Index, the sum of the minimum number of steps for each character divided by the observed number of steps; the Consistency Index (C.I.) varies between 0 (= no consistency among characters) and 1 (= no homoplasy among characters). 3. Retention Index, defined as $R.I. = (g - s)/(g - m)$, where g is the greatest number of evolutionary steps which can be required by the data of any tree, s is the number of steps actually required by the tree, and m is the minimum number of steps in the data. The Retention Index is a measure of the number of equal character states which, in a given cladogram, can be retained as homologies. A greater Retention Index, hence, implies less homoplasy and, in terms of parsimony, a more plausible phylogeny.

As one can see from the table, Hypothesis 1 is definitely better than Hypothesis 2 and 3 in terms of both parsimony and consistency. Hypothesis 1, of course, is completely incompatible with our present understanding of ant phylogeny and must, hence, be rejected. Between Hypotheses 2 and 3, as one may have expected from the fact that Hypothesis 2 requires a longer tree, the Retention Index shows that Hypothesis 2 accounts better for the variation observed in recruitment, though the Consistency Index is lower.

B. Polythetic analysis including the correlates of recruitment

The results of the cladistic analysis for each hypothesis with its two sub-hypotheses (i.e. single gland behavioural control and glandular synergy) are given in Table 3.

From it one can see that coding of the data as to describe Hypothesis 1 A (i.e. recruitment irreversible and its correlates unordered) allows the construction of 112 character-justified trees vs. 1908 possible on the whole. None of them, however, is compatible with the currently accepted ant phylogeny.

Testing Hypothesis 1 B (corresponding to coding all characters as irreversible) allows construction of 312 unequivocal most parsimonious trees, vs. 18840 possible in all and, once more, none of them is compatible with the ant phylogeny.

Both variants of Hypothesis 1 which predicts a congruence between recruitment behaviour and ant phylogeny, hence, must be rejected again.

Hypotheses 2 and 3, however, have been both formulated in a way imposing them to be compatible with the formicid phylogeny and they can be compared again in terms of parsimony and of the variability accounted for. Hypothesis 3 is regularly more parsimonious than Hypothesis 2 in terms of tree length and consistency index of its individual trees (the consensus trees exhibit a slightly different behaviour), but I would reject again this hypothesis because, even including the anatomical and behavioural correlates of recruitment in the analysis, the most parsimonious reconstruction of recruitment evolution still needs the very implausible assumption of mass recruitment for the hypothetical ant ancestor (Figs. 3.1 and 3.2).

Hypothesis 2, hence, should be preferred. But, within it, hypothesis 2A (epigenetic increase of recruitment efficiency determined by synergic effect of more than one gland) and hypothesis 2B (the same evolutionary model of recruitment efficiency but controlled by one single gland), allow the reconstruction of different but substantially equally plausible pathways for recruitment evolution (Figs. 3.3 and 3.4 refer to their respective consensus trees).

Deciding which hypothesis should be preferred on the basis of the differences in Retention Index has problems: Retention Indices of individual trees (Hypothesis 2B R.I. 0.709 vs. 0.667 of Hypothesis 2A) support Hypothesis 2B, but the Retention Index of consensus trees (Hypothesis 2A R.I. = 0.654 and Hypothesis 2B R.I. = 0.618) support Hypothesis 2A.

Table 3, however, shows that the consensus tree of hypothesis 2A has the shortest tree in absolute, the second greatest Consistency Index, and the highest Retention Index in absolute. Its superiority to Hypothesis 2B in terms of parsimony and explanatory power can be better appreciated from Table 4 where the number of homoplasies (i.e. character states shared by convergence or by parallelism among the 22 species considered) is given for each hypothesis. Hypothesis 2A implies 742 cases of homoplasy and hypothesis 2B 1182, i.e. the latter needs 440 more *ad hoc* explanations for the reconstruction of the evolution of recruitment behaviour and its correlates. This difference, however, may be a mere consequence of the more rigorous evolutionary model imposed by Hypothesis 2B. Nevertheless I regard all this circumstantial evidence as simply indicative to prefer hypothesis 2A, at least at the present state of knowledge, as the most probable and the most realistic one.

Figures 4–6 give the reconstructed evolutionary pathway for 6 out of 7 informative correlates of recruitment behaviour. Use or non use of the Janet's gland is an informative character but it has been not graphically mapped since its evolutionary pathway is easy to understand: use of the gland is regularly present in all the taxa of the clade at the right of the formicid cladogram and, in addition, it appeared convergently only once more in *Orectognathus*.

Discussion

A. Monothetic analysis of recruitment behaviour

Figs. 2.1 and 2.2, however, display also the most parsimonious evolution of recruitment behaviour assumed by the two hypotheses retained for their compatibility with ant phylogeny.

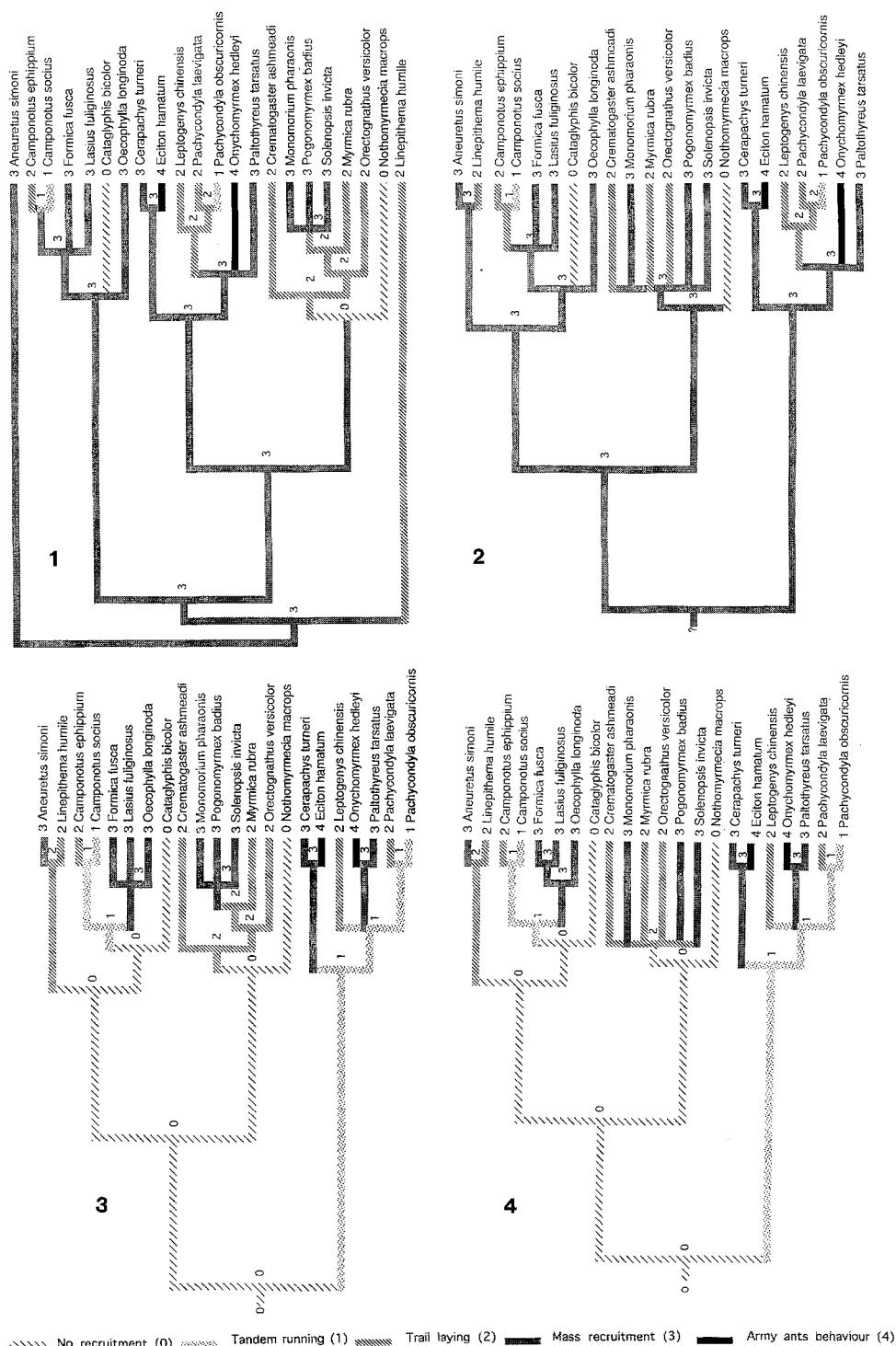


Fig. 2.2 shows that the most parsimonious reconstruction of unordered recruitment evolution assumes mass recruitment for all hypothetical ant ancestors except the common ancestor of *Crematogaster*, *Myrmica*, and *Orectognathus* which should have secondarily lost this behaviour in favor of trail laying, a character synapomorphically inherited by the three genera in question. All other known recruitment types should equally be due to secondary losses, except army ant behaviour which arose convergently in *Eciton* and *Onychomyrmex*. The latter convergence is, in my opinion, the sole credible assumption implied by this model which, hence, should equally be rejected.

From Fig. 2.1 one can see that, under the constraints of Hypothesis 2, the hypothetical ant ancestor should have been a non-recruiting animal, while the common ancestor of all ants of clade B, morphologically characterized by fused sclerites of abdominal segment III (Baroni Urbani et al., 1992), should have been able to recruit by tandem running only and this character has been maintained in the hypothetical ancestor of all Ponerinae. Recent Ponerinae show a wide array of recruitment behaviours. One species, in fact, (*Pachycondyla obscuricornis*) is still plesiomorphically capable of tandem running only, while its congener *P. laevigata* and *Leptogenys chinensis* have independently acquired the capacity of laying trails. In this clade the hypothetical ancestor of *Leptogenys*, *Onychomyrmex* and *Paltothyreus* should also have been a trail laying ant. More efficient recruitment mechanisms, like mass recruitment, are exhibited convergently by *Paltothyreus tarsatus* and by the hypothetical ancestor of *Eciton hamatum* and *Cerapachys turneri*. The latter maintained this ancestral character, while sharing of army ant behaviour among the ecitonine *Eciton* and the ponerine *Onychomyrmex* should be due to convergence as under Hypothesis 3. The clade A on the left of Fig. 2.1, corresponding to all ants with ancestrally covered antennal socket (Baroni Urbani et al., 1992) still had a non-recruiting hypothetical ancestor and non-recruiting were also the ancestors of the Aneuretinae + Dolichoderinae + Formicinae, and the ancestor of the Nothomyrmecinae + Myrmicinae. Lack of recruitment in both *Cataglyphis* and *Nothomyrmecia*, hence, should be interpreted as a plesiomorphy. The hypothetical ancestor of *Aneuretus* and *Linepithema* was a trail laying ant, as it was the ancestor of all Myrmicinae. Trail laying in *Myrmica*, *Crematogaster*, and *Orectognathus* is due to common ancestry but is shared paraphyletically by these genera, since other members of the same clade evolved mass recruitment behaviour. Mass recruitment behaviour evolved convergently also in *Paltothyreus* (Ponerinae), *Cerapachys* (Cerapachyinae),



Figure 3. Most parsimonious reconstruction of the evolutionary path of recruitment behaviour according to different hypotheses discussed in the text. Polythetic analysis taking into account 11 behavioural correlates. The figures on the trees indicate the reconstructed states for internal nodes. Optimization by delayed character transformation. **3.1.** Hypothesis 3 A (unordered evolution of recruitment efficiency determined by synergetic effect of more than one correlate). Strict consensus of 12 trees. Tree length 33. **3.2.** Hypothesis 3 B (unordered evolution of recruitment efficiency controlled by a single gland). Strict consensus of 4 trees. Tree length 46. **3.3.** Hypothesis 2 A (epigenetic increase of recruitment efficiency determined by synergetic effect of more than one gland). Strict consensus of 11 trees. Tree length 43. **3.4.** Hypothesis 2 B (the same evolutionary model of recruitment efficiency but controlled by one single gland). Strict consensus of 12 trees. Tree length 57. Further explanations in text

Table 3. Cladistic description of the three hypotheses on the evolution of recruitment behaviour and of their relative sub-hypotheses. Hypotheses 1–3 resulting from the literature have been further divided into two sub-hypotheses each: A (synergic effect of more than one gland), and B (single gland behavioural control). TL = tree length; CI = consistency index; RI = retention index

Hypothesis	Search	Individual trees				Consensus tree			
		TL	Unequivocal trees	All possible trees	CI	RI	TL	CI	RI
1 A	Heuristic	28	112	1908	0.458	0.475	62	0.19	0.42
1 B	Heuristic	32	312	18480	0.414	0.845	67	0.188	0.527
2 A	Heuristic	42	11	18	0.289	0.667	43	0.282	0.654
2 B	Branch & Bound	47	12	28	0.273	0.709	57	0.222	0.618
3 A	Branch & Bound	33	12	81	0.379	0.581	33	0.379	0.581
3 B	Branch & Bound	37	4	162	0.353	0.694	46	0.279	0.569

Table 4. Pairwise homoplasy matrices for recruitment behaviour and its correlates giving the number of common traits evolved by convergence or parallelism among the 22 species considered under the hypothesis of evolutionary increase of recruitment efficiency independent from ant phylogeny. Above the diagonal assuming a synergic effect of more than one gland, below the diagonal assuming a single gland behavioural control

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 <i>Aneuretus simoni</i>	4																					
2 <i>Camponotus ephippium</i>	4	4	2	0	6	4	6	6	0	6	4	6	6	0	10	8	4	4	2	6	8	6
3 <i>Camponotus socius</i>	2	0	0	0	2	2	4	0	2	2	4	4	4	0	2	4	4	2	2	4	4	4
4 <i>Cataglyphis bicolor</i>	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	2	2	2	2	2	2	2
5 <i>Cerapachys turneri</i>	8	6	4	2	4	4	0	0	0	4	6	4	8	0	8	4	8	0	0	0	0	0
6 <i>Crematogaster ashmeadi</i>	8	8	6	4	6	4	4	4	4	4	6	0	0	0	6	4	0	4	4	4	0	0
7 <i>Ecton hamatum</i>	10	10	8	4	0	8	8	8	4	8	2	6	4	0	8	6	6	2	0	4	6	6
8 <i>Formica fusca</i>	6	4	2	0	8	8	12		4	0	4	6	4	0	0	6	4	4	2	6	6	6
9 <i>Linepithema humile</i>	0	4	2	0	6	8	8	4		4	4	4	6	0	8	6	4	4	2	4	6	4
10 <i>Lasius fuliginosus</i>	6	4	2	0	8	8	12	0	4		4	6	4	0	0	6	4	4	2	6	6	6
11 <i>Leptogenys chinensis</i>	6	6	4	2	4	8	2	6	6	6		10	8	2	6	2	10	2	2	2	10	10
12 <i>Monomorium pharaonis</i>	8	6	4	2	10	0	8	8	6	8	10		0	2	8	6	0	4	4	6	0	0
13 <i>Myrmica rubra</i>	10	8	6	4	8	2	8	8	10	8	10	4		0	8	6	0	4	4	4	2	2
14 <i>Nothomyrmecia macrops</i>	0	0	0	0	0	0	0	0	0	0	0	0	0		2	0	0	0	0	0	2	2
15 <i>Oecophylla longinoda</i>	8	2	0	0	8	8	10	0	6	0	6	8	10	0		10	6	6	4	8	10	8
16 <i>Onychomyrmex hedleyi</i>	10	6	4	2	4	6	6	8	8	8	2	8	8	0	10		6	2	0	0	8	6
17 <i>Orectognathus versicolor</i>	8	8	6	4	10	2	10	8	8	8	12	2	4	0	8	8		6	6	6	0	0
18 <i>Pachycondyla laevigata</i>	6	6	4	2	2	6	2	6	6	6	2	6	6	0	6	2	8		0	2	4	4
19 <i>Pachycondyla obscuripes</i>	6	6	4	2	4	0	8	2	6	6	2	8	6	0	6	0	10	0		0	4	4
20 <i>Paltothyreus tarsatus</i>	8	6	4	2	4	6	4	8	6	8	2	8	6	0	8	0	8	2	0		6	6
21 <i>Pogonomyrmex badius</i>	10	6	4	2	10	0	8	8	8	8	10	6	6	0	10	10	2	6	6	8		0
22 <i>Solenopsis invicta</i>	8	6	4	2	10	0	8	8	6	8	10	6	4	0	8	8	2	6	6	8	6	

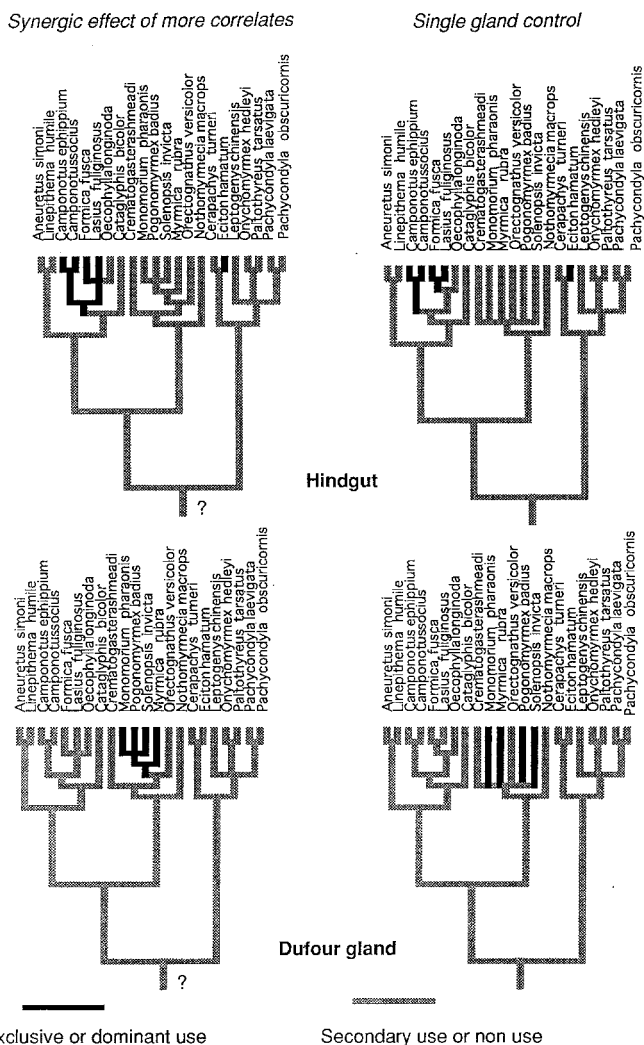


Figure 5. Different evolutionary pathway for the use or non use of the hindgut and of the Dufour gland during recruitment in the two hypotheses of a synergic effect of more glands or of a single gland behavioural control. Optimisation by delayed character transformation

in *Aneuretus* (Aneuretinae), and in the Formicinae genera *Formica*, *Lasius*, and *Oecophylla*.

Hypothesis 2, hence, with the evolutionary pathway described here, is retained as the most probable one not because of its relative tree length and consistency, but simply in terms of biological plausibility.

This hypothesis, i.e. the stepwise evolution of recruitment efficiency within different clades, appears to represent the best hypothesis, among those available in the literature, at least according to our data and to the assumptions formulated in this

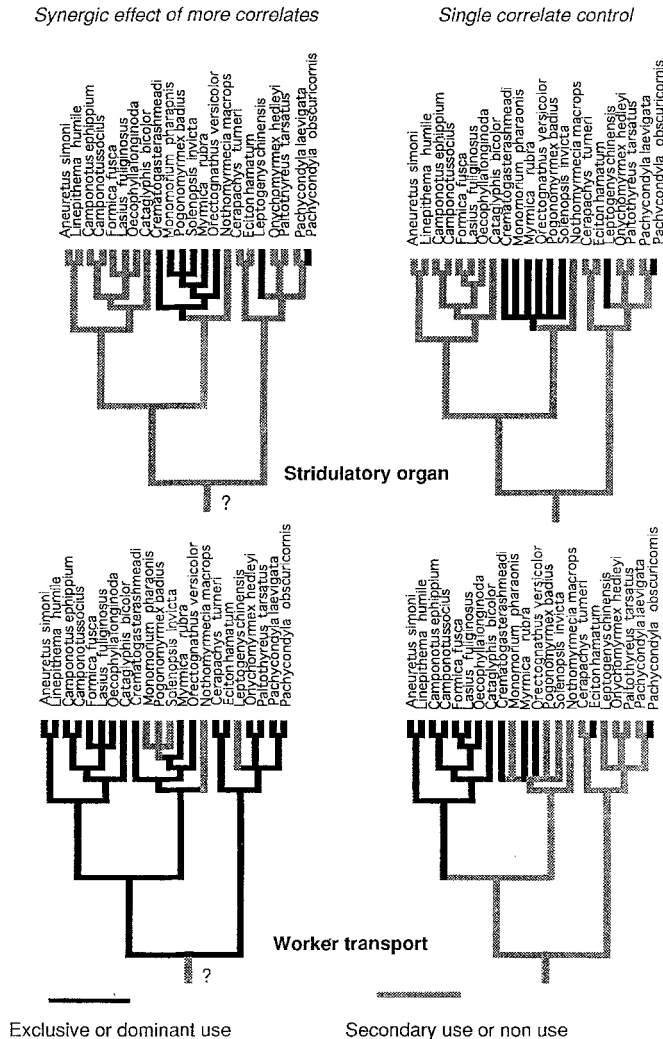


Figure 6. Different evolutionary pathway for the use or non use of the stridulatory organ and of the worker transport during recruitment in the two hypotheses of a synergetic effect of more correlates or of a single correlate behavioural control. Optimisation by delayed character transformation

paper. Considering the sample of species included in this analysis as representative, of course, will imply that, with a larger data set, the difference in tree length between Hypothesis 2 and the other two hypotheses is likely to increase. If one finds all these assumptions and the necessary number of hypothetical ancestors they imply as cumbersome, one should not forget that all the other hypotheses considered here imply lower degrees of homoplasy (i. e. are more parsimonious) at the expenses of very improbable evolutionary pathways. Mass recruitment, just to take an example, according to Hypothesis 2 arose 5 times independently each other among the 9 species exhibiting it and included in the data matrix.

On the other hand, assuming that current views on ant phylogeny represent a reasonable picture of the true evolutionary history, we already have abundant proof of considerable amount of homoplasy among characters playing an important role in ant communication, like the presence/absence of the stridulatory organ within species of the same genus (Markl, 1973). Since we are forced to admit that this relatively important morphological trait (and hence its function) appeared and disappeared in the course of ant evolution in a rather unpredictable way, it should be easier to assume that just the quality of a behaviour like recruitment, once it has been selected, may have changed in a non-parsimonious way. The idea that homoplasy is very widespread is not new in evolution (see e. g. Cain, 1982), and a convincing set of important probable polyphyletic paths in invertebrates has been recently produced by Willmer (1990).

Additionally, it may be worth recalling some implications of the ancestral sequences assumed here. Figure 2.1 shows, for instance, a nicely polarized evolution of recruitment behaviour. Army ants raiding evolved, according to this cladogram, in *Onychomyrmex* from a hypothetical ancestor which showed mass recruitment, a character maintained in the other terminal taxon present on the clade: *Paltothyreus tarsatus*. This is, however, a conventional cladistic oversimplification. Mass recruitment is just the most parsimonious behaviour which can be attributed to that hypothetical ancestor in order to construct the cladogram. In truth, if such an ancestor ever existed, it must have been represented by populations exercising mass recruitment and populations showing army ant behaviour at the same time, in order to have the latter selected from the first. The same reasoning, i. e. the existence of coeval behaviourally polymorphic populations, must apply to all branchings of the cladograms of this paper where a character state change occurred. This, a priori, may not appear more plausible than the convergence already described.

B. Polythetic analysis including the correlates of recruitment

Specific increase of recruitment efficiency within each phyletic line should, hence, be retained as the most reasonable hypothesis consistent with our present knowledge of ant phylogeny and character conservation. In addition, a synergic effect of several glands is more likely than a single gland to represent the real behavioural releaser, at least within the limits of the cladistic test performed in this paper.

Having reached this conclusion, I feel compelled to comment on what is probably one of the most stimulating and least understood papers on this subject, Jaffe (1984). Jaffe constructed an ant phylogeny based on recruitment behaviour which resulted rather different from inductive phylogenies known at that time and much closer to more recent ones obtained by means of cladistic analyses. In order to verify this interesting result which sharply contrasts with the conclusions just reached in this paper, I performed a cladistic analysis of Jaffe's original data, coding his characters as irreversible which – I believe – reflects the spirit of his paper. The phylogeny presented by Jaffe has a tree length of 8 and there are 96 389 other, different trees of equal length, 33 390 of length 7, 5040 of length 6, and one of length 5. Stated otherwise, at least in terms of parsimony alone, there are 134 820 equivalent or

“better” reconstructions of the evolution of ant recruitment behaviour based on the same data set. The explanation for this result is that Jaffe inferred a process analogous to the one performed analytically in this paper, i.e. he sacrificed parsimony to his inductive picture of ant phylogeny and recruitment evolution.

The conclusions reached in the present paper, of course, preclude further retention of the strictly phylogenetic hypothesis (Hypothesis 1), but they are not mutually exclusive with the convergence one (Hypothesis 3). Although this is not formally demonstrable, one may still profit from the convergence assumptions in trying to explain the big behavioural differences encountered among the species included in this analysis. Beckers et al. (1989), by correlating recruitment ability with colony population gave the sole presumptive evidence available to date about the factors which may have shaped the terminal branches of the cladograms of Figures 3.1 and 3.2 in different ways. Comparative studies of the recruitment behaviour of congeneric species with very different colony population numbers, like some *Camponotus* or *Formica* are expected to give the most promising results in this direction.

Fig. 7 summarizes the present understanding of the evolution of ant recruitment behaviour and of its correlates. The reconstructed character-states for the nodes recognized within ant phylogeny are given in it. The hypothetical ant ancestor, according to this phylogenetic reconstruction and character optimization, was a non-recruiting animal but it should already have been capable of worker transport and motor display in the nest. Among contemporary ants, at least members of the genus *Cataglyphis* appear to match perfectly this description.

The Australian *Nothomyrmecia* lacks both these presumably ancestral behavioural traits, but – contrarily to *Cataglyphis* – lack of worker transport should be a plesiomorphic character and not a secondary loss for it.

Figures 4–6 give the most probable evolution of the use of the significant correlates of recruitment behaviour and should be self-explanatory. Nonetheless I would like to stress at least one additional example of their basically different meaning. Lack of use or reduced use of the hindgut during recruitment by *Oecophylla* (Fig. 5) should be a secondary loss according to hypothesis 2A and a symplesiomorphically shared character according to hypothesis 2B. I would rather favour the first interpretation and a confirmation of it should be available when the generic phylogeny of the subfamily Formicinae will be known and the presumed plesiomorphic status of *Oecophylla* vs. *Camponotus*, *Formica* and *Lasius* – as implied by hypothesis 2B – will be confirmed or not.

C. Discussion of the parsimony criteria used for the analyses

Hypothesis 1 is by far the most parsimonious one and this quality is intrinsic to the formulation of the hypothesis itself. It is primary intuition that a cladogram with less constraints about the evolution of characters and/or the clustering of taxa must be more parsimonious than all the others described here. A similar philosophy – applied to character evolution – has been already codified in the literature by Fitch (1971), while comparing nucleotide sequences. Fitch (l.c.) regarded it as “the most

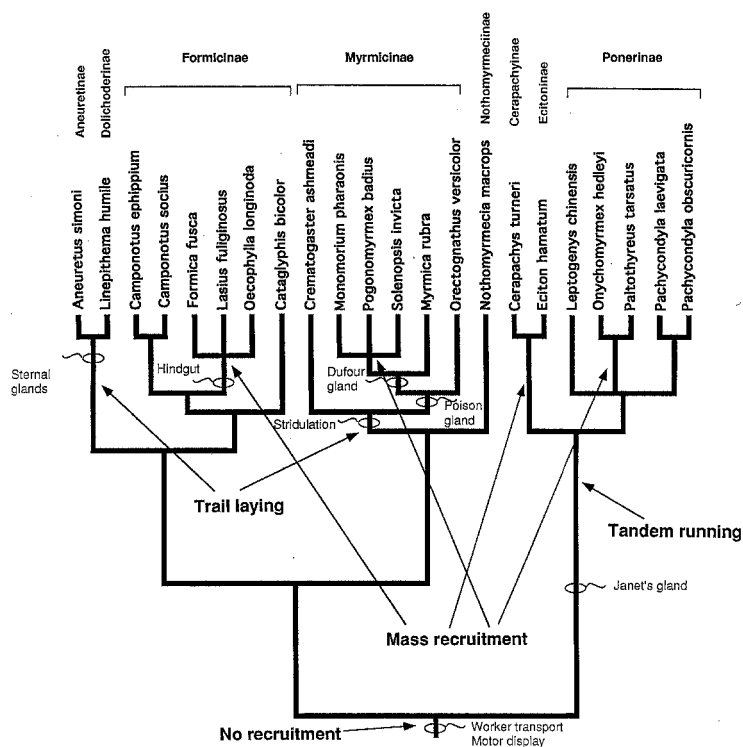


Figure 7. Reconstruction of the most parsimonious evolutionary path of recruitment behaviour and of its correlates in the hypothesis of synergetic effect of multiple glands and independent increase of efficiency within different clades. Optimization of characters by delayed transformation. Secondary losses are not indicated. Only the reconstructed states for internal nodes are given. The states of the terminal branches can be deduced from Table 1. Use of the tibial, rectal, and cloacal glands and presence of motor display are not given in the figure since they are uninformative in this context

reasonable hypothesis". This view became later established in the cladistic literature under the name of "Fitch parsimony" (e.g. in Maddison and Maddison, 1987). Applying "Fitch parsimony" to recruitment behaviour gives a cladogram of length 4, i.e. by far more parsimonious than the others constructed in this paper, as predicted. Actually – as I already said while describing Hypothesis 1 – a very high number of such trees exist, but, for reasons which should be clear by now, I am convinced that describing the potential evolutionary meanings of any one of these cladograms will be too long and unimportant in this context. I must acknowledge that assuming Fitch parsimony of character evolution can be the best working hypothesis while dealing with nucleotide sequences, but it may imply undesirable assumptions when the characters have clear functional/adaptive meanings. What made the recruitment case different, is that some students, believing to understand recruitment evolution, started adding constraints fitting their understandings, and inevitably destined to reduce parsimony. When, later, different ways of "understanding" started to appear, they have been compared again in terms of parsimony. Such an approach, actually, is

very likely to be the correct one. If, in the available literature, sometimes it failed to offer a convincing explanatory hypothesis (as shown by the references given in the introduction), it is essentially because the modern analytical tools were not yet available.

Parsimony was, in fact, the undeclared but dominant idea behind all previous papers debating the evolution of ants' recruitment behaviour. However, parsimony is not a good working hypothesis for trying to reconstruct evolution of a single character like recruitment *per se* and making abstraction from what is already known on ants' evolution in general. The principle of parsimony, first fully formulated by Pearson (1892) (cited by Allee et al., 1949) represents one of the leading and most frequently used ideas of the last century of biological thought. Parsimony is, of course, the sole support for the book of Ridley (1983) which represents the first fully justified and most detailed set of analyses of the kind conducted in this paper. Biologists themselves do not universally agree on the validity of parsimony. According to Ghiselin (1966), parsimony is "an assumption without which science would not be possible"; Pielou (1979) states that "the principle of parsimony seems often to be invoked as an excuse for what are in fact unjustifiably grandiose claims to generality". Its use and misuse have been subject to discussion by several philosophers like Popper, Sober, and many others, who, by simply calling it "simplicity", did not succeed in simplifying its biological meaning (see e.g. the review by Beatty and Fink (1979) for the evolutionary implications of the philosophical approach). Parsimony is a non-evidential criterion. Some philosophers, though admitting that simple hypotheses are not necessarily more probable than complex hypotheses, supported nevertheless the use of the simplest alternative because of the "quality of nature" (Wrinch and Jeffries, 1921). More recent methodological discussions, of course, are much more careful and are ready to admit that "parsimony arguments can be strong in some contexts and weak in others", or that "one must be careful not to sacrifice *plausibility* for the sake of parsimony" (*italics mine*) (Sober, 1984). However vague this statement may appear, I must recognize that it represents the best description of the attitude I have been forced to adopt in this paper. In his last book Sober (1988) offers an extremely competent and detailed discussion of the phenomenon, from which I am unable to extract any additional operational directions. Adherence to the principle of parsimony by a given discipline or school of thought has been often used as the main or the sole proof of scientific orthodoxy (see e.g. Williams 1966, Dawkins 1976, Kluge 1988, Wiley 1988, Presch 1989, and Nelson 1989, among others). If the parsimony criterion has been often used throughout this paper, it was not in order to respect traditional or established biological thinking, but merely because I have been unable to formulate a better or equivalent alternative. Felsenstein (1978 b, 1983) already formulated serious criticisms about the indiscriminate use of parsimony criteria on the basis of statistical arguments. His arguments are refuted nonetheless by Farris (1979). More recent cautionary statements about the decisional power of parsimony include Bryant (1989) manifesting some skepticism about their practicability, Hendy and Penny (1989) using purely mathematical reasonings, and Sluys (1989) on logical ones.

In this perspective, one should not forget that Hypothesis 3 (the second parsimonious one, among those resulting from the literature) is the only one favoured

by some external evidence (Beckers et al., 1989). These authors have been able to show graphically a correlation between the logarithm of colony population and six ascending recruitment categories in a sample of 98 ant species. Although, of course, correlation need not imply causal interrelationship, this is still the sole available external evidence in favour of any one of the three hypotheses discussed here.

The present paper provides the first description of the logical pathways inherent to the different available hypotheses about the evolution of recruitment behaviour in ants and of a few implications easy to formulate. Apparently, the crux of the problem is deciding how much convergence is *plausible*, and this, however, is again a subjective decision.

Acknowledgements

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