

## Phylogeny and behavioural evolution in ants, with a discussion of the role of behaviour in evolutionary processes \*

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The family Formicidae is redefined on the basis of all common characters shared by its members, which allows a hypothetical sketch of its unknown presumed ancestor. The first cladistic analysis is presented of internal ant phylogeny at the subfamily level, based on the 10 extant subfamilies commonly recognized in the literature. Although some weaknesses remain, this phylogenetic reconstruction shows several concrete improvements. None of the fossil subfamilies allow comparison with the recent subfamilies by neontological criteria. Among recent subfamilies no autapomorphic characters have been found for the Aneuretinae which clearly show only primitive character states easy to identify by comparison with the Dolichoderinae. The former subfamily has been regarded as a straightforward synonym of the latter. The Ponerinae have been still characterized tentatively on the basis of two weak synapomorphies but the real monophyly of its members appears to be questionable. The subfamilial phylogeny, as a whole, appears relatively weakly documented on several branchings with exception of the Nothomyrmecinae, Dolichoderinae, and Formicinae on one side which can be easily opposed to all remainder recent subfamilies on the other side, by having a constriction after abdominal segments I and II only instead of after segments I, II, and III. Another important conclusion reached in this paper concerns the Formicinae, which can no longer be considered as the most advanced extant ants.

A variety of complex and simple behaviours, chosen as examples of general evolutionary trends within the ants, all show a mosaic picture of parallelisms and convergences.

Two reasons are offered to explain these findings. The first, particular to ants, is that eusociality represents an evolutionary constraining influence allowing further selection only for a few behaviours like nesting behaviour, communication modes, social parasitism, etc. It is not surprising, therefore, that the few rewarding options appear convergently in different stems within the ants, and among other, unrelated, social insects as well.

The second, more general, reason is the understandable tendency of taxonomists to produce phylogenies based on purely morphological characters. An analysis of the major morphological trends among ants shows that all correspond to behavioural

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evolutionary sequences. Such sequences are, of course, much more difficult to describe and to quantify than is morphology.

Only one systematically «pure» (i.e. without morphological correlates and virtually free from important selection pressures) ethological character has been found to be widely consistent with the subfamily classification proposed here and increasing its information contents. This is the manner in which ants transport other adult ants. This is probably the highest rank phylogenetically relevant character detected so far which is based on behaviour only.

**KEY WORDS:** ants, Formicidae, behaviour, evolution, phylogeny, nesting behaviour, nomadism, social parasites, monogyny, polygyny, phragmosis, communication, behavioural morphological syndroms.

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1. Introduction . . . . .	138
2. Tentative sketch of the hypothetical ant ancestor . . . . .	139
2.1. Recognizable behavioural and morphological synapomorphies of ants . . . . .	139
2.2. Inferred nature of the hypothetical ant ancestor . . . . .	141
3. The internal phylogeny of ants . . . . .	143
3.1. Pros and cons of the proposed phylogenetic tree . . . . .	145
4. Behavioural fluctuations within the ant system . . . . .	149
4.1. Some complex behaviours convergently selected among the Formicidae . . . . .	150
4.2. Some elementary behaviours convergently evolved among virtually all ant groups . . . . .	156
5. Discussion . . . . .	158
6. Acknowledgements . . . . .	162
7. References . . . . .	162

## 1. INTRODUCTION

Insect societies, from a purely behavioural point of view, are so similar to each other in virtually all major characters, that, without the support of morphological data, they could be easily regarded as monophyletic.

Important behavioural characters uniquely shared by social insects range from specialized worker caste(s), recruitment of nestmates, alarm communication and colony defence, queen control over the worker population, nest thermoregulation, monopolization of food sources, food processing by specialized individuals and food sharing (including trophallaxis) within nestmates, and, with the probable exception of termites, the evolution of specialized social parasites (see WILSON 1971 and BRIAN 1983 for a general review of most of these topics among social insects). In recent years, especially WILSON (1971) has stressed the necessity of allowing for a polyphyletic origin for eusociality among insects, although the idea is far from being new and probably represents one of the best verified predictions of kin selection theory (HAMILTON 1964). The main purpose of the present paper is to examine the occurrence of behaviour patterns among ants in relation to their concordance or discordance with the probable phylogeny. The latter is estimated by a cladistic analysis. This technique is probably the best for analyzing a small number of high rank taxa, for which only a few common and unequivocal characters are known. This should permit a close inspection of the phylogeny of ant behaviour at the subfamily level and to draw reliable conclusion about it. Ants have been nearly universally regarded as a solid monophyletic group (see, among others, BROWN 1954, BROTHERS 1975, TAYLOR

1978, and KÖNIGSMANN 1978) of fully eusocial Hymenoptera, and it is obvious that the most parsimonious hypothesis is that they all originate from a single eusocial ancestor. *A priori*, behaviours and habits which are common or at least widespread within the family Formicidae could also be regarded as monophyletic and derived from a single hypothetical ancestor.

## 2. TENTATIVE SKETCH OF THE HYPOTHETICAL ANT ANCESTOR

### 2.1. *Recognizable behavioural and morphological synapomorphies of ants*

Few morphological characters are unique to all ants and it is even more difficult to find behaviours which are probably derived uniquely within the family Formicidae. Although ants as a whole appear to be, behaviourally, the most homogeneous group of social insects, most of the frequent behavioural traits are either shared with other social insects (by convergence, of course), or are likely to have arisen independently several times within the family. This latter point will be dealt with in detail later in this paper. The most probable synapomorphies I have been able to detect among the Formicidae are the following:

2.1.1. *Queen and worker caste present* (either of these has been secondarily lost in a few specialized groups).

2.1.2. *Worker antennae with elongated scapus*. This improves cardanic movements between scapus and funiculus enabling better object inspection and recognition. This character can be very useful in splitting ants from supposed related groups like Tiphidae, Methocidae, and Vespidae.

2.1.3. *Metapleural gland present*. Its absence in males of several species and in workers of social parasites and reputed phylogenetically advanced genera like *Camponotus*, *Polyrhachis*, and *Dendromyrmex* (HÖLLDOBLER & ENGEL-SIEGEL 1984) can be easily regarded as secondary. The explanation for this absence may be given by the function of the gland itself, as explained by MASCHWITZ et al. (1970). According to these authors the gland produces antiseptic substances spread mechanically or distributed by grooming among nestmates (see also BEATTIE et al. 1985, about fungal vulnerability to metapleural gland secretions). I would suggest that the functional significance of this gland was weakened during ant evolution when additional exocrine glands started to produce compounds with antiseptic properties as now appears to be the case for most exocrine glands in ants (see e.g. HÖLLDOBLER & ENGEL-SIEGEL 1984). The same is even truer for social parasites, which, by definition, live in association with other ant species which construct the nest and keep it free from fungi and bacteria. Male ants, on the other hand, are social parasites, *de facto* in their own nest and, considering their short lives and non participation in cooperative behaviour, it appears that the energy necessary for the production of the gland might be more profitably invested e.g. in sperm production. The survival of the gland in males of some species may be due to the absence of a true negative selection pressure against production of the gland. Males still showing the metapleural gland may be interpreted as conservative.

2.1.4. *Postpharyngeal gland present.* Although evidence for this is far from being complete, this is likely to be the most widespread synapomorphic morphological character of the whole family Formicidae. I know of no ant species in which the glands have not been found. These glands are unique to the ants and have no recognizable homologue among other insects (BILLEN 1987). The information we have on their function has not advanced very much since JANET (1897) noted that food can be stored in them and slowly re-inserted in the alimentary duct. True secretory cells have never been observed with modern instruments and the purpose of the whole organ can be only guessed. It is likely that it plays a role during trophallaxis, as suggested by BARBIER & DELAGE (1967) for *Messor capitatus* and shown by MARKIN (1970) for the Argentine ant (*Iridomyrmex humilis*). At least in the latter species large quantities of the glandular product are distributed to the queens and larvae, suggesting a possible role in caste determination as well. A similar hypothesis has been formulated by BARBIER & DELAGE (1967), who underline the liposelective role of the glands and the consequent potential importance in caste determination. In this case ant trophallaxis should be regarded as a rather different phenomenon from that of other social insects. Even among social Hymenoptera, mutual regurgitation with larvae occurs only in ants and wasps (HUNT 1982). Neither wasps nor ant larvae, however, possess postpharyngeal glands. An additional important behavioural character appears to result from the combination of a predominantly liquid diet with the habit of nesting in porous material. The resultant necessity to store liquid food has been met by the development of a peculiar «replete» worker subcaste, unknown among other social insects. In at least two subfamilies (Dolichoderinae and Formicinae) this habit, which is likely to be necessary and widespread among ants, has led to the development of morphologically specialized physogastric individuals. It may be worth remembering here that these same two subfamilies are the only ones which developed a peculiar proventricular morphology adapted to liquid food ingestion (EISNER 1957).

2.1.5. *Constriction of the first metasomal segment.* The first segment after the trunk (abdominal II) is constricted anteriorly and posteriorly in all ants to form a petiole. The importance of this character, universal among ants, is weakened by its sporadic appearance among other Aculeate groups like some wasps, myzinidis, and sphecids. I am inclined to attribute a rather obvious functional significance to this structure, which would facilitate the use of the sting. Stinging prey or enemies while facing them is greatly facilitated if the mechanism allowing sting orientation possess two articulations instead of one. Moreover, two sets of intersegmental muscles now contribute to the movement instead of one, thus allowing double power without doubling the muscular mass. Some ants (subfamilies Myrmicinae, Pseudomyrmecinae, workers of Leptanillinae, some Dorylinae, and some Ecitoninae) repeated this anatomical solution, by adding a constriction to the second metasomal segment as well (postpetiole). This structure is also known outside the Formicidae among several Apterogynidae. Relatively advanced myrmicine species like some *Leptothorax* (*Macromischa*) still rely on this defence technique, which may be coupled with other morphological adaptations, e.g. increased leg musculature, to make it more efficient (BARONI URBANI 1978). However, these simple mechanical improvements were apparently not the optimal evolutionary pathway, because all ants belonging to what are currently considered as the most evolved subfamilies (Dolichoderinae and Formicinae)

— see e.g. the declared phylogenetic conspectus recently offered by WHEELER & WHEELER (1985) — have greatly reduced or entirely lost their sting in favour of other chemical defence mechanisms, and show the primitive condition of constriction at the first metasomal segment only. It is suggestive that a myrmicine genus, *Cremastogaster* which uses the double metasomal constriction to bend the gaster upwards instead of downwards and to spread the product of the poison gland, also shows a greatly reduced sting (EMERY 1916). A similar condition is approached at least by other myrmicine genera like some Cephalotini (COYLE 1966) and some species of *Monomorium* (personal observations). The smallest prerequisites allowing for this defence posture are opposite behaviour of antagonistic muscles and at least partial modification of the metasomal articulations. Other myrmicine genera, like *Messor* and the whole tribe Attini, possess very reduced stings, but no visible functional or morphological trends to invert the movement of the gaster.

2.1.6. Other structures recorded only in ants are Pavan's gland, the propharyngeal gland, the pygidial gland, and the postpygidial gland (BILLEN 1987). They all play an important role in social behaviour, but are either known from too small a number of species (Pavan's gland, for instance, appears to be confined to the subfamily Dolichoderinae, including Aneuretinae), or too inconspicuous and poorly known to be used as reliable phylogenetic characters.

2.1.7. Another character which might be regarded as synapomorphic in ants is the presence of winged females. Most remote ant ancestors previously postulated possess wingless females. Such a suggestion however implies that an originally winged hymenopteron gave rise to a female wingless ant ancestor from which evolved winged gyne ants which then, for the second time, lost their wings (as in some Ponerinae and in some myrmicine species of the genera *Chelaner*, *Lordomyrma*, *Prodidicroaspis*, and *Promeranoplus* and in the subfamilies Dorylinae, Leptanillinae, and Ecitoninae). This is a very implausible scenario; it is much more likely that all cases of female winglessness are secondary adaptations and the presence of winged gynes should, hence, be considered as plesiomorph.

## 2.2. Inferred nature of the hypothetical ant ancestor

From all that has been said so far, it appears legitimate to assume that all characters listed under Section 2.1 should be present in the hypothetical common ant ancestor. Accordingly, this should have been a fully eusocial animal, already possessing a differentiated worker caste showing a relatively elongate scapus and a petiolar constriction. This last character suggests the presence of a powerful sting — somewhat a trivial prediction among aculeate Hymenoptera — and probably, in addition, a not too reduced body size, a condition which would have favoured selection for the use of the sting and the related mechanical adaptation of the first metasomal segment. Moreover, this hypothetical creature should have had: (i) a metapleural gland to inhibit the growth of mould and fungi in its nest, and (ii) the colony members must have had a highly developed system of food exchange, different enough from that of other social insects to justify the ant antennal morphology and the unique appearance of the postpharyngeal glands. As already mentioned, these glands are likely to be

related to caste determination, an important trait shared with all eusocial insects, but extremely varied in its physiological manifestation even among ants alone (see e.g. PASSERA 1982).

If these conclusions appear trivial at a first glance, it should be remembered that they do not agree with some previously published conclusions. A diphyletic origin of ant sociality has been hypothesized by WILSON et al. (1967a and 1967b), and by WILSON (1971). The reasons for this are not clear from their text, other than the need to postulate diphyly for the character(s) «ant-like mandibles and antennae». This in turn is necessary only in order to incorporate into ant phylogeny the upper Cretaceous fossil *Sphecomyrma freyi*, in which these characters are missing, an opinion dealt with more explicitly by WILSON (1971: 31). The sole objective reason to regard *Sphecomyrma* as an ant is however the reported presence (WILSON et al. 1967a and 1967b) of the metapleural gland. This is indeed a very good character, but the gland is not visible in the original micrographs, has been not figured, and was not seen by one of the original describers (W. L. BROWN JR oral communication). The systematic position of *Sphecomyrma* is returned to below.

Another trait mentioned sometimes in the literature is the probable arboreal or terrestrial habitat of this hypothetical ancestor. The great majority of recent ants are terrestrial, and so are the majority of ant taxa commonly regarded as primitive, including *Nothomyrmecia*, considered by many as the most primitive living ant; it nests in the ground of *Eucalyptus oleosa* woodland in S Australia but forages extensively on the trees (TAYLOR 1978, HÖLLDOBLER & TAYLOR 1983). However, arboricolous and terrestrial species coexist within single genera, such as *Leptothorax*, *Campopnotus*, *Cremastogaster*, *Pheidole*, and many others, and I do not think the question can be reasonably answered. About the «primitive» characters exhibited by *Nothomyrmecia*, it is worth stressing here that it shows several plesiomorphic characters unique among ants, but no synapomorphies have been found yet characterizing all ants but *Nothomyrmecia* (see later, the cladistic analysis).

All the other characters hypothesized here for the ant ancestor fit quite well with what is known for *Nothomyrmecia macrops*. The most astonishing character of this ant, in my opinion, is the apparent complete lack of most usual kinds of pheromonal communication (excluding those involved in caste determination), which appears to be essential equipment in virtually all known ant species. No pheromonal characters have been listed in Section 2.1 because different pheromones and different organs play the same functional role in different species, to such a degree as to prevent any attempt at homology identification. *Nothomyrmecia* is also reputed to lack any kind of sophisticated chemical communication other than an alarm substance. Inhabitants of the same nest are only partly genetically related and show no aggression against intruders; trail laying and nestmate recognition have been specifically searched for and not found in this ant, although it appears to be equipped with most of the glands which normally produce pheromones (WARD & TAYLOR 1981, HÖLLDOBLER & TAYLOR 1983). As it is unlikely that an organ would be selected for before the appearance of its function, the other possibility is that the glands have a different primitive function in *Nothomyrmecia*, as is probably the case for other Hymenoptera.

Food transmission, as hypothesized for our hypothetical ancestor, has however been recorded in *Nothomyrmecia*, both between workers and between workers and larvae (TAYLOR 1978). One might wonder how such an apparently advanced behaviour can be possible in a society lacking even the most primitive communication

systems. The answer I am tempted to give, and which could be important in understanding ant phylogeny, has been already advanced by DLUSSKY (1983): trophallaxis is elicited and controlled in a largely mechanical way through antennal tactile stimuli. These stimuli are possible only for «ant-like antennae», enabling the donor and the solicitor to maintain mutual contact during food exchange. This is made possible partly by the distance between the antennal socket and the mouthparts, but more importantly, by the relative length of the scapus, which, bending backwards during the stimulation, allows contact of the last antennal joint with the oral area of the partner. Stated otherwise, a minimum length of the scapus relative to funicular length is an important social prerequisite for ants.

This conclusion brings us once again to the systematic position of *Sphecomyrma* (see above) which, besides a short scapus shows a particularly elongated funiculus. The lowest ratio (scapus length/funiculus length) I have been able to find among a selected sample of «short antennated» worker ants is  $> 0.35$  in some *Leptanilla* species. According to the published drawings, in *S. freyi*, this ratio should be about 0.28 and has been recently given as 0.3 (WILSON 1987). WILSON (1987) does not consider this character important because (i) there are ants which do not practice trophallaxis, like *Amblyopone* and *Pogonomyrmex*, and (ii) wasps, which possess antennae similar to *Sphecomyrma*, are known to practice trophallaxis. What WILSON overlooks is that *all* ants possess elongated scapi, including *Amblyopone* and *Pogonomyrmex*, which probably have lost trophallaxis as a secondary adaptation to solid food ingestion. Hence, what remains are only the wasps. This seems to me an additional important reason to consider *Sphecomyrma* as a probably non social taxon related to but not included within the family Formicidae. Moreover, *Sphecomyrma* itself is at least 10-20 million years younger than some undoubted fossil Formicidae material from different Soviet Cretaceous formations (DLUSSKY 1975 and 1983, see BARONI URBANI 1980 for discussion) which makes it unlikely to represent the ant ancestral form. However, this argument could be negated only if the older material was to be considered non-formicine or if it was to be shown identical with *Sphecomyrma*. This latter remaining option has been taken by WILSON (1987), who synonymized the older Soviet material, originally described as nine species in seven genera and three families with the genus *Sphecomyrma*, known from only two different and younger American formations. Which one is the right point of view seems to me much more a matter of faith than of science.

### 3. THE INTERNAL PHYLOGENY OF ANTS

The phylogeny of a group may represent the most useful guideline to an understanding of the probable evolutionary pathway of a behaviour. For this reason an effort has been made here to present a consistent ant phylogeny. The tree has been constructed by using presumed synapomorphic characters only, a choice which limits to 27 the number of characters I have been able to use. Additional unique autapomorphies for small groups like the Leptanillinae can easily be found, but they would have added nothing to the picture obtained (Fig. 1). For the outgroup comparison, I used the Vespidae which, together with the Scoliidae, appears the most plausible sister group of the Formicidae according to the phylogenetic analysis of BROTHERS (1975)

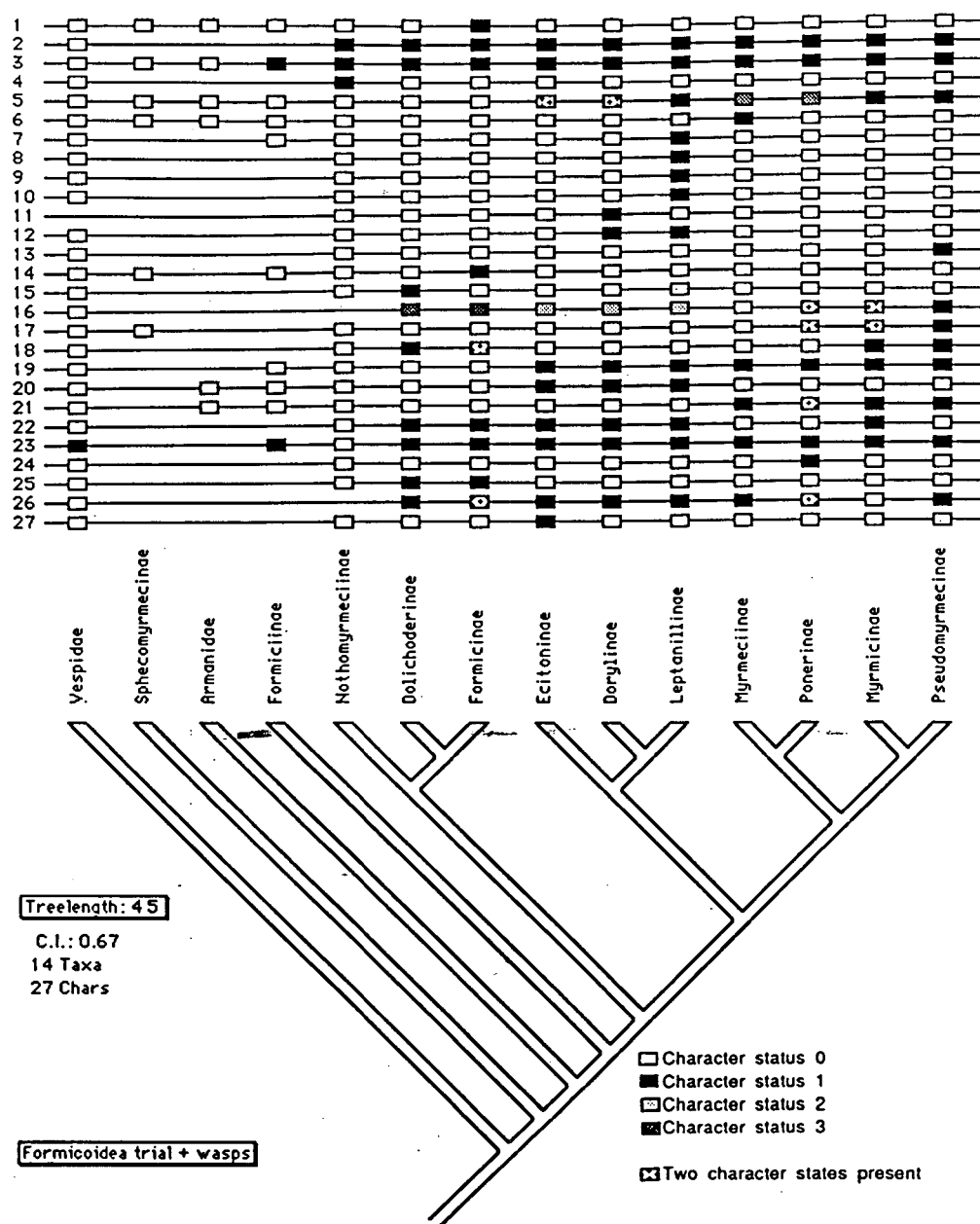


Fig. 1. — Cladogram of the internal phylogeny of ants based on the 10 extant subfamilies recognized in the present paper and on the 27 characters described in text. The character codification and description corresponds to the one used in text. Consistency index = 0.67.



which confirms a former idea of BERLAND & BERNARD (1951) and of EVANS (1958). The characters regarded as uniquely derived and on which the cladogram is based are the following:

1. Acidopore (i.e. opening of the poison spray duct separated from and ventral to the anus) present (1) or absent (0).
2. Metapleural gland present (1) or absent (0) (this character cannot be observed with confidence among fossil taxa).
3. Antennae with scapus elongated (1) or short (0).
4. Ventral stridulatory organ present (1) or absent (0).
5. Worker «postpetiole» absent (0), widely attached to the following segment (1), narrower or clearly separated from the following segment (2).
6. Mandibles long and linear, with one apical and several irregular preapical teeth on the whole internal border (1) or on the masticatory border only (0).
7. Male wing venation reduced to R only, often difficult to recognize (1) or normally developed (0).
8. Larva with a single transformed pair of spiracles on A III (1) or with more pairs of the usual morphology (0).
9. Mandibles of the larvae with outer (1) or inner (0) masticatory margin.
10. Male genitalia much larger than the rest of the gaster (1) or of normal size (0).
11. Queen with (1) or without (0) exposed bursa copulatrix.
12. Queen hypopygium prominent and extending far beyond the pygidium (1) or of normal size (0).
13. Larvae with (1) or without (0) conspicuous food pocket (trophothylax).
14. Sting present (0), absent (1).
15. Pavan's gland present (1), absent (0).
16. Adult carrying behaviour not stereotyped or missing (0), stereotyped with (a) the carried individual between the legs (1), (b) the carried individual under the head (2), and (c) the carried individual over the head (3).
17. Dorsal-stridulatory organ present (1) or absent (0).
18. Pupae naked (1) or with cocoon (0).
19. Tubulation of abdominal segment IV of workers present (1) or absent (0).
20. Queen dictyodiiform (i.e. extremely physogastric and lacking ocelli, wings, and often the eyes as well) (1) or not (0).
21. Queen always without a true postpetiole separated from gaster (0) or with a distinct postpetiole (1).
22. Worker-queen dimorphism pronounced (1) or reduced (0).
23. Male hind wings with basal hamuli (0) or without (1).
24. Worker, gaster oval if not clearly rounded, with clearly curved sides (0) or elongate, cylindrical, with parallel sides or curved downwards (1).
25. Proventriculus sclerified (1) or flaccid (0).
26. Paraglossae present (0) or absent (1).
27. Male genitalia with normally thin «lamina annularis» (0) or with very big lamina annularis, almost egg-shaped (1).

The distribution of these character states among the presently recognized ant subfamilies is given at Table 1.

### 3.1. *Pros and cons of the proposed phylogenetic tree*

Most of the characters listed above are character complexes, which could easily be decomposed into several unit characters and would automatically give an apparent but spurious increase in consistency to the cladogram presented here (Figs 1 and 2). This cladogram is the first constructed on logical rules for ants as a whole, and solves

Table 1.

Distribution of character states among the taxa considered in this paper. The character description is given in text under the corresponding numbers.

Taxa	Characters																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
Nothomyrmecinae	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	7	0
Ponerinae	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0
&																	30			1						1		
Myrmecinae	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	
Leptanillinae	0	1	1	0	2	0	1	1	1	1	0	1	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	
Dorylinae	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	1	1	0	0	1	0	
&											2																	
Ecitoninae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	
&																												
Pseudomyrmecinae	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	3	1	1	1	0	1	0	1	0	0	1	0	
Myrmicinae	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	1	1	1	0	0	0	
&																	20											
&																	0											
Dolichoderinae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	1	1	0	1	1	
Armanidae	0	7	0	7	0	0	7	7	7	7	7	7	7	7	7	7	7	7	7	0	0	7	2	2	7	7	2	
Sphecomyrmeinae	0	7	0	7	0	0	7	7	7	7	7	7	7	7	7	0	7	7	0	7	7	7	7	7	7	7	7	
Formicinae	0	7	1	7	0	0	0	7	7	7	7	7	7	7	7	0	7	7	7	0	0	0	7	1	7	7	7	
Formicinae	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	1	0	1	
&																				1						0		
Vespidae	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	

several problems which dissatisfied previous scientists. In particular the first modern graphic representation of ant phylogeny, as given by BROWN (1954) and WILSON et al. (1967a, 1967b), proved to be unsatisfactory in explaining the probable evolutionary trend of the stridulatory organ (MARKL 1973), and of ants' carrying behaviour (DUELLI 1977). These difficulties are resolved in the phylogeny presented here. TAYLOR (1978) presents a new version of that by WILSON et al. (1967a and 1967b) which obviates some of the previous difficulties; it puts the Sphecomyrminae further back in ant phylogeny and places the Pseudomyrmecinae close to the Myrmicinae, but the whole tree is still subjectively drawn, and the terminal branches and the roots are not uniquely defined. Another questionable feature of this phylogenetic reconstruction is that several extant taxa are depicted as the ancestors of other modern taxa.

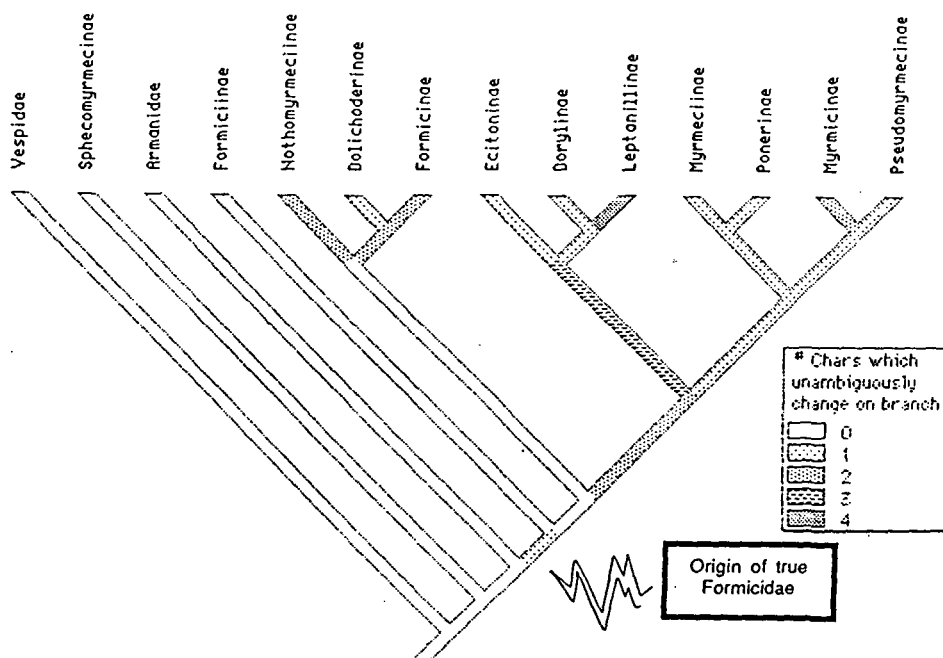


Fig. 2. — Same cladogram as in Fig. 1 showing the number of unequivocal changes in ant phylogeny assumed by the classification proposed here. Most recent subfamilies appear to be characterized by at least one unequivocal change while none of the fossil ones seems to be sufficiently defined by the characters employed in this analysis.

The tree by LUTZ (1986), while formally much better, deals with some subfamilies only, and suffers from incorrect or incomplete information.

A weak point of the phylogeny proposed here, which I have not been able to improve or to solve in a satisfactory way, is that practically all presently recognized ant subfamilies are represented as the terminal branches of the cladogram. This implies, for instance, that the Ponerinae are monophyletic (its only synapomorphic characters appear to be the broad articulation between postpetiole and gaster, a condition convergently approached by a few myrmicine species, and the gaster with parallel sides). This is a questionable point of view, but I am unable to propose a better solution. Another weakness is that the lack of a dorsal stridulatory organ among some Ponerinae and Myrmicinae is considered to be secondary, a very plausible view, but still formally subject to debate. Finally, the monotypic subfamily Aneuretinae has been sunk among the Dolichoderinae in this analysis, because no synapomorphic characters which distinguish its members are known so far. I regard the cladogram proposed here as the most reasonable that one can construct for the time being. The number of subfamilies recognized is the lowest possible if the Ponerinae are still to be separated from the Myrmicinae, and if the principle is accepted that each subfamily should be defined by at least one uniquely derived character.

The main difficulty of the cladogram presented here is within the branch in which the subfamilies Myrmicinae, Ponerinae, Myrmeciinae, and Pseudomyrmecinae are clustered together. Only the last subfamily can be regarded with certainty as well defined and clearly monophyletic. The synapomorphies used for the other three families are at least weak or debatable. Possible solutions include: (i) Synonymy of the Ponerinae with the Myrmicinae, probably much closer each other than it has been admitted until now in the literature. A particularly important and neglected piece of evidence for this lies in the common presence of paraglossae (GOTWALD 1969), although this character is probably symplesiomorphic due to its wide distribution among other Hymenoptera. Still, better synapomorphies for these two, potentially synonymous, subfamilies are not known. (ii) The other, not necessarily alternative, solution is to split the huge bunch of species included in these two enigmatic subfamilies into smaller homogeneous groups of subfamily rank. This process had already been started by CLARK (1951) by attributing subfamilial rank to the Eusphinctinae, Cerapachyinae, Amblyoponinae, Discothyridinae, Odontomachinae, and Nothomyrmecinae. At least equally good candidates to comparable rank are the members of the myrmicine tribes Metaponini, Attini, Cephalotini, Cremastogastrini, Meranoplini and Cataulacini. Clear and unambiguous synapomorphic characters are easy to find for the majority of these groups, but this solution would leave us with two additional unresolved problems i.e. the comparability in rank with other ant subfamilies, and about half of the known ant species still remaining badly defined and joining the cladogram in a no better way than the one used here.

The information necessary to overcome all these difficulties is not yet available and is not likely to become available in a near future.

An important point resulting from this analysis is that the Formicinae no longer appear to represent the most specialized ants as was thought until now. The main (and still remarkable) synapomorphic character of this subfamily remains the loss of the sting with consequent build-up of the «pillow» poison gland and acidopore. Otherwise, most formicines appear relatively unspecialized in general morphology and it is worth remembering here that similar conclusions had been already reached by REID (1941), although nobody seems to have paid too much attention to his remarks. This picture of stingless but not necessarily very advanced formicines suggests an even too easy analogy with the vestigial sting of meliponines among bees.

I feel the reader should be warned here that it is not legitimate to «ladderize» the cladogram presented at Figs 1 and 2 in the evolutionary interpretation and conclude that the pseudomyrmecines are the most highly evolved ants. The sequence of evolutionary events that the construction of the cladogram presupposes would not change if I would have published it rotated of 180° on its perpendicular axis.

It may be noticed that some «classical» characters in this analysis appear to have much less predictive value than has usually been assumed. The most remarkable one is probably the presence of cocoons, which must be regarded as plesiomorphic for all ants, which has been lost in the subfamilies Myrmicinae and Pseudomyrmecinae, and independently in the Dolichoderinae and in some genera of Ecitoninae (WHEELER & WHEELER 1976). The sclerification of the proventriculus among Dolichoderinae and Formicinae, which has been regarded as due to convergence by EISNER (1957), is tentatively considered as monophyletic here. I would not insist on this point but this character appears to represent the sole potential synapomorphy for Formicinae and

Dolichoderinae. Its suppression from the data matrix allows separation of these two families in different ways with negligible reduction of the consistency index (from 0.67 to 0.66).

#### 4. BEHAVIOURAL FLUCTUATIONS WITHIN THE ANT SYSTEM

In the remaining part of this article, both because of the evident lack of relevant information resulting from the cladogram, and also for practical reasons, I propose to ignore the fossil taxa and to see if any behavioural traits fit the ant phylogeny as depicted here, a phylogeny derived from essentially morphological characters.

The literature on ant behaviour uses the word evolution much more often and with much more nonchalance than does the taxonomic literature. Various behaviours have been proposed by previous authors to be of essential value in the evolution of ant sociality. Other traits, however, such as nesting behaviour, colony size, food preference, etc., never received much attention because they appear to have been independently selected several times within the ants by similar ecological pressures. Thus, for instance, even the peculiar habit of using the silk produced by the larvae to construct the nest has evolved at least 5 times within the formicine genera *Dendromyrmex*, *Polyrbachis*, *Camponotus*, and *Oecophylla* (HÖLLDOBLER & WILSON 1983, MASCHWITZ et al. 1985), the use of nests made out of silk of unknown provenance is recorded for the dolichoderine *Technomyrmex bicolor textor* (JACOBSON & FOREL 1909), and for the myrmicine *Leptothorax myersi* (BARONI URBANI 1978), while at least one species of the larvae-using genus *Polyrbachis* is reported to construct silk nests, but made out of silk stolen from spiders (COLLART 1932).

In this paper I already considered the presence of one or more specialized worker caste(s) as one of the major traits of ant social behaviour. Delegating the majority of reproductive tasks to one or a few individuals increases kinship, and this is allowed when sterile individuals which are morphologically better adapted to feed and defend other individuals refrain from reproducing themselves. This extraordinary adaptation has been surpassed only among a few social parasites in which only sexual individuals are present, the worker caste having been made superfluous by the capacity of using for the same purpose workers of a related (host) species. It would be difficult to imagine a more efficient strategy to maximize reproductive success with minimum energy investment, and yet, among ants, we also find traces of a clearly inverted trend. Completely queenless species are reported in the ponerine genera *Diacamma* (WHEELER & CHAPMAN 1922), *Rhytidoponera* (HASKINS & WHELDEN 1965), *Platythyrea*, *Pachycondyla*, *Leptogenys*, and *Ophthalmopone* (PEETERS & CREWE 1984 and 1985, PEETERS 1987), in at least the two myrmicine genera *Pristomyrmex* (ITOW et al. 1984), and *Megalomyrmex* (BRANDÃO 1987), although in the latter genus true queens are substituted by morphologically highly reduced queens which can be regarded as inseminated workers (gamergates). At least some of these cases are accompanied by male rarefaction and thelytoky (i.e. unfertilized workers producing parthenogenetically essentially worker brood). This phenomenon has also been sporadically reported for other ants with a normal caste system (see references in ITOW et al. 1984). However drastic this evolutionary path may appear, it seems to me that thelytokous parthenogenesis represents the only condition allowing even more genic conservation than kin selection.

#### 4.1. Some complex behaviours convergently selected among the Formicidae

The obviously convergent complex habits of constructing silk nests and of producing «replete» castes to store liquid food have been already mentioned on preceding pages. Analogous convergent evolution must in addition be invoked to explain other important behavioural traits.

##### 4.1.1. Production of «carton» nests

«Carton», made from vegetable detritus glued together by the secretion of the mandibular glands, provides an excellent insulating material for nests. Carton nests are often arboreal or suspended, but also occur in soil (e.g. *Liometopum apiculatum*) or in plant cavities (e.g. *Lasius fuliginosus*). Hence it appears difficult to argue that carton making is a typical adaptation to arboreal life. It has been recorded (see e.g. WHEELER 1910 for detailed adaptations) for some but not all the species of the formicine genera *Camponotus*, *Polyrhachis*, *Lasius*; the dolichoderine genera *Azteca*, *Liometopum*, *Dolichoderus*; and the myrmicine genera *Cremastogaster*, *Tetramorium*, and *Leptothorax*.

For this behaviour we observe a weak correlation with arboreal life (additionally, there are plenty of arboreal ants which do not construct carton nests) while the two prerequisites for the construction of carton nests, i.e. the mandibular glands and the availability of vegetable detritus, are widespread among all ants. Hence it appears that the capacity of constructing carton nests, although restricted to three subfamilies out of 10 extant considered here is obviously genetically determined and probably represents a specific ESS which has been selected for or not on several occasions within a single genus, under environmental conditions which are likely to appear perfectly equivalent to our eyes.

##### 4.1.2. Nomadic habits

All three subfamilies of legionary ants (Dorylinae, Ecitoninae, and Leptanillinae) appear clustered together in the cladogram presented here. Although the literature evidence is far from complete, it is very likely that all members of these three subfamilies share nomadic and legionary behaviour. They are also morphologically similar to each other, mostly in the presence of dictyodiiform females remarkably different from the workers, to an extent that cannot be compared to the physogastric females reported in other ants. Clearly similar behavioural traits exist in members of the subfamily Ecitoninae and in *Aenictus* (Dorylinae) (SCHNEIRLA 1971), *Anomma* (Dorylinae) (RAIGNIER & VAN BOVEN 1955), and *Leptanilla* (Leptanillinae) (MASUKO 1987).

Superficial morphological similarities may be due to functional homogeneity and sharply contrast with the important differences in the *bursa copulatrix*, male genitalia, and larval morphology already used in the cladistic analysis (see also BORGMEIER 1955 and GOTWALD 1982).

Additionally, it must be remembered that legionary habits recur sporadically among some ponerine genera (WHEELER 1936, WILSON 1958), which often show remarkable convergence with true army ants. On purely morphological grounds

WHEELER (1916) suggested that the Australian ponerine *Onychomyrmex* should have legionary habits, a prediction which appears to have been recently confirmed by observations by TAYLOR (in SCHNEIRLA 1971).

The common primary trait of all these species appears to be the frequent habit of nest migration, a phenomenon which has been often correlated with the search for the better prey supply (mostly termites) in ponerines, but described also for myrmicines of similar diet like *Myrmicaria* (ARNOLD 1914) and for other very unaggressive omnivorous ants like e.g. *Aphaenogaster* (Myrmicinae) (BARONI URBANI 1966) and *Tapinoma* (Dolichoderinae) (FOREL 1920). Recently MASCHWITZ & HÄNEL (1985) described obligatory nest migrations in the dolichoderine *Dolichoderus cuspидatus*, which apparently relies exclusively on symbiotic pseudococcids transferred to suitable feeding places as food source. This species — like true army ants — appears to be strictly monogynic and the queens are ergatoid.

It therefore seems very likely that a morphological nomadic syndrome evolved convergently in ants from apparently widespread and much less remarkable foraging habits.

#### 4.1.3. Social parasitism

Social parasites are known from all ant subfamilies except the monotypic Nothomyrmecinae, the Ponerinae, and the three subfamilies of driver ants (Ecitoninae, Dorylinae, and Leptanillinae) (KUTTER 1968). Different plausible hypotheses have been formulated to explain the circumstances and the modalities of their evolution. BARONI URBANI (1967) supposed that social parasitic species originated from interbreeding among demes of high rank females in a dominance hierarchy. This hypothesis appears even more attractive since MORITZ & HILLESHEIM (1985) demonstrated a genetic basis for dominance behaviour in honeybees. Recent researches by HILLESHEIM et al. (1989) showed, in addition, that the best colony performance was obtained by subordinate individuals, «whereas the colonies composed of only dominant bees were nearly unproductive». Presumably because this hypothetical way to social parasitism implied sympatric speciation, WILSON (1971), proposed a more orthodox model in which allopatry was required but where selection pressures to parasitize another, allopatric population were difficult to imagine. Analogous allopatry hypotheses had been already postulated by HAMILTON (1964) and by DOBRZANSKI (1965). On the other hand, the necessity for sympatric speciation of social parasites had been stressed again by BUSCHINGER (1970) and BARONI URBANI (1979). Nowadays that sympatric speciation has become a widely recognized process (WHITE 1978), it is much easier to explain the apparently unnecessary habit of killing the host queen exhibited by many parasitic species by analogy with a fully consistent  $\alpha$ -female behaviour. This route to social parasitism satisfies the conditions necessary for sympatric speciation, i.e. rapidity of adaptation and geographic restriction. Here it will be sufficient to stress that the nearly 200 species of ant social parasites described to date are far from being an exhaustive sample, yet nonetheless make up 2% of the known ant diversity. Social parasites thus represent an important trend in ant evolution. Taxonomically, they represent some 40 genera (here the views of taxonomists differ from each other) in five subfamilies. The main evolutionary character of social parasites, on which nearly everybody agrees, is the so called Emery's rule (EMERY 1909a and 1909b), which states that all true parasitic species (i.e. excluding

parabiotic and inquilines) are derived from their host species. When similar selection pressures work on similar but geographically distant host species or populations, the result is very similar, (i.e. congeneric) parasitic species or even morphologically indistinguishable parasite populations probably derived from the same host species. Under other circumstances these convergent parasites would be supposed to be polyphyletic, and nonetheless systematists usually treat them as «good» taxonomic categories because of their strong morphological uniformity (BARONI URBANI 1967).

A particularly significant example has been discovered recently in the genus *Rossomyrmex*. This genus had long been known as a slave maker of the palaearctic genus *Proformica* with one species (*R. proformicarum*) in Caucasus and Tian-Shan (ARNOL'DI 1928 and 1932, MARIKOWSKI 1974). Recently TINAUT RANERA (1981) discovered another social parasite of another *Proformica* species in the Sierra Nevada. Its similarity with *R. proformicarum* was beyond any reasonable doubt (the main difference between the two lies on the amount of hairs on the mesonotum) and it has been described as *Rossomyrmex minuchae*.

It is clear that an earlier much broader, distribution of *Rossomyrmex* is very unlikely (the species of the host genus *Proformica* are themselves rather uncommon and the social parasites have incredibly low population densities) and a common ancestor for the two *Rossomyrmex* species is at least very difficult to hypothesize. The main morphological character of the genus *Rossomyrmex* is the concavity of the occipital border. This is a well known indicator of the parasitic syndrome which occurs, among others, in parasitic species of the genus *Formica* (a formicine, as in *Rossomyrmex*) and *Strongylognathus* (a myrmicine). The easiest explanation for these observations is to postulate that the morphological social parasitic syndrome arose twice under similar selection pressures from two different *Proformica* species.

Extending this reasoning to all social parasitic genera, two-possible phylogenetic reconstructions are shown here (Figs 3 and 4) on the simplest possible data matrix for two host species and two parasitic species defined by seven characters as follows:

1. Outgroup character(s).
2. Species level character(s) of host species 1.
3. Species level character(s) of host species 2.
4. Social parasitic morphological syndrome and/or other presumed genus level character(s) of the parasites.
5. Genus level character(s) of host genus.
6. Species level character(s) of parasite 1.
7. Species level character(s) of parasite 2.

The character coding and distribution is given by the data boxes in the figures.

Something which appears to have been not yet fully understood is that strict application of the Emery's rule implies that social parasitic genera are untenable at least when they contain more than one parasitic species parasitizing at least two host species. They must automatically be considered as belonging to the same genus as the host species (Fig. 3). The only preconditions allowing at least a first formal sound separation of social parasitic genera from their respective host genera are (i) monotypic parasite genera defined on the parasitic morphological syndrome and/or additional characters, or (ii) monophyly of parasites derived from a single ancestor in contrast with Emery's rule (Fig. 4).



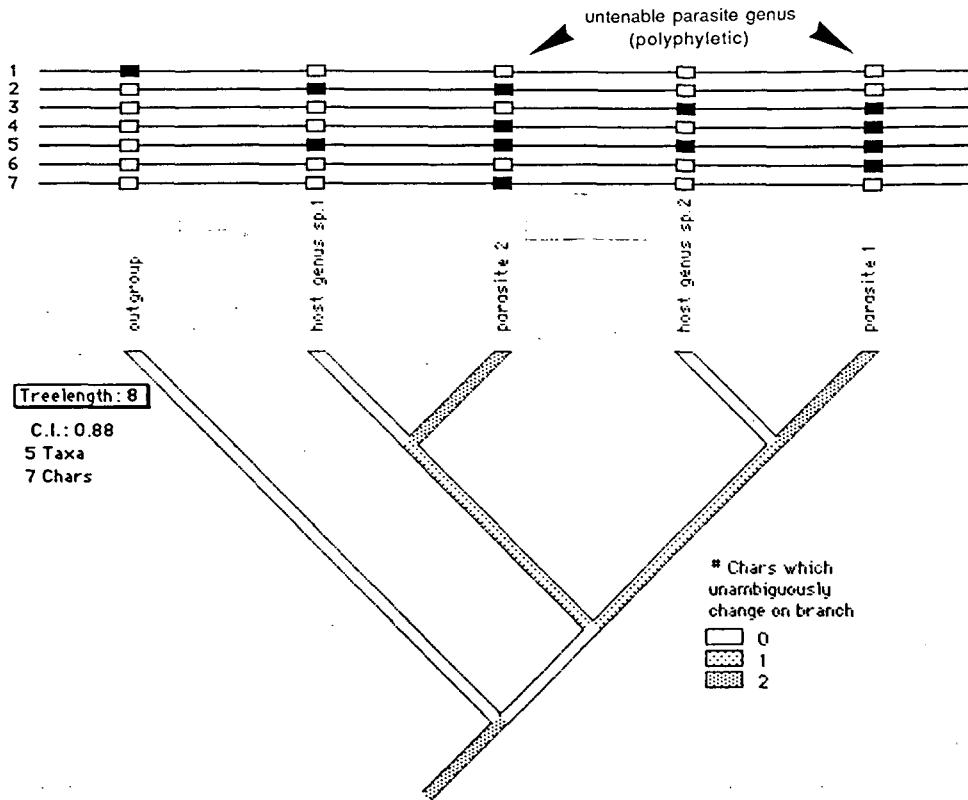


Fig. 3. — Hypothetical cladogram and relative character boxes for the simplest possible case of two social parasitic species derived from their respective host species under strict application of the Emery's rule. The character description is given in text.

The latter condition appears to be very improbable at least for some rare genera like *Rossomyrmex*.

But, even if these assumptions are accepted, another insurmountable difficulty opposes this solution: by erecting a genus for parasites uniquely derived from a single (heterogeneous) host species, one automatically dismisses the previously recognized synapomorphies of the host genus — they must unequivocally be shared with its parasites — and the host genus, in its turn, is destined to be sunk by missing uniquely derived characters... (see Fig. 4). The sole hypothesis allowing for generic separation between hosts and parasites and still accounting for their strict relatedness, is monophyletic derivation of the parasites from a monotypic host genus followed by further selection and speciation of the host. This scenario appears rather unlikely and the conclusions reached here are destined to be quite unpopular in cases where the social parasitic syndrome implied dramatic morphological changes of the parasite, like *Anergates* or *Teleutomyrmex* vs *Tetramorium*.

Nevertheless, I am unable to see another reason whatever for maintaining social

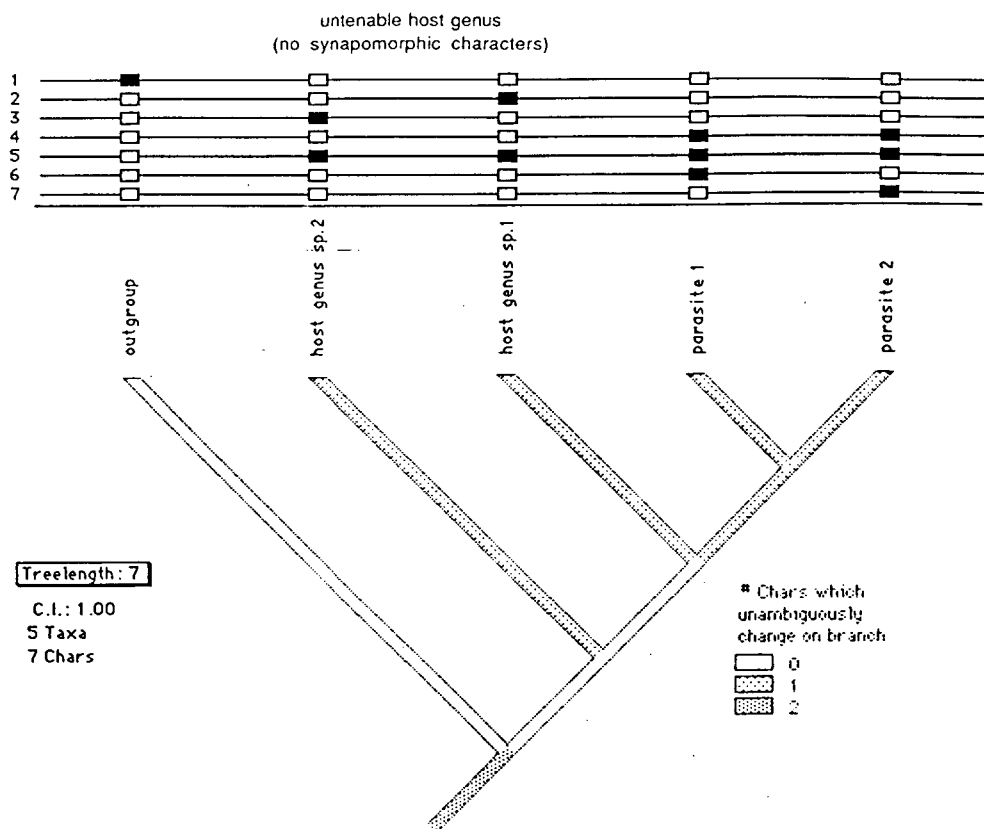


Fig. 4. — Hypothetical cladogram and relative character boxes for the simplest possible case of two social parasitic species derived from their respective host species under the monophyly hypothesis. The character description is given in text.

parasitic species in a genus different from the host one. A step in this direction has already been made by WILSON (1984), while dealing with some social parasites in *Pheidole*.

#### 4.1.4. Monogyny and polygyny

The number of queens in an ant society has been recently defined as «an important trait in ant evolution» (HÖLLDOBLER & WILSON 1977). This is doubtless true, because the presence of a single queen increases the kinship among colony members and might have drastic demographic implications as far as the fertility of a single gyne represents the upper limiting factor to colony population. Unfortunately, a straightforward correlation between the number of queens per nest and the total nest population is far from holding for all ants: there is evidence that, for instance, at least in some species, polygynous colonies contain a high number of unfertilized queens which, e.g. in *Formica polyctena*, may vary between 19 and 34% of the total (SCHMIDT 1982).

In this respect ants are somewhat exceptional among eusocial insects, where monogyny is otherwise much more widespread (see e.g. ROISIN 1987 and contained references) and polygyny is regarded as characteristic of primitive societies (WEST-EBERHARD 1981), and often coupled with dominance and functional monogyny (PARDI 1987). ROISIN (1987), however, explained how polygyny may be favoured if the gynes are genetically related each other, and this point of view, in ants, is supported by experimental work and allozyme analyses by WARD (1983) on *Rhytidoponera* and by PAMILO & ROSENGREN (1984) on *Formica*. Still, this does not completely explain why polygyny is much more frequent in ants than among other social insects and, from a phylogenetic point of view, unpredictably distributed.

Moreover, ants developed at least two independent mechanisms of queen control to maintain monogyny, i.e. by direct aggression among gynes and by control exercised by the workers (see review by BARONI URBANI 1968, and causal explanation by FLETCHER & BLUM 1983); additionally, even monogynous societies may present overt conflict situations and dominance orders between queen and workers (FRANKS & SCOVELL 1983).

A further complication is the fact that — contrary to what one would expect — the most populous individual colonies in ants are clearly monogynic, like several *Atta* and army ant species. There is even evidence that some kind of physiological compensation for monogyny may exist. In red wood ants (*Formica rufa* s.l.) the queens of monogynic forms show better developed ovaries than those of polygynic forms (GÖSSWALD 1941 and 1980); the same holds at least for some other ant species like *Myrmica* spp. (ELMES 1982), *Plagiolepis pygmaea* (MERCIER et al. 1985), and *Solenopsis invicta* (VARGO & FLETCHER 1989). At least in some species, like *Lasius flavus* there is evidence that increasing the number of coexisting queens reduces individual queen fertility (WALOFF 1957). For *S. invicta*, this has been recently explained by the mutual inhibitory effect of fertility among queens of an unknown pheromone (VARGO & FLETCHER 1989).

In conclusion, the number of queens per colony, however important it may be for ant population ecology, has been increased or reduced several times during ant evolution and, as already stressed by HÖLLDOBLER & WILSON (1977), is a widely polyphyletic behavioural trait. According to these authors, polygyny should be an adaptation to monopolize patchy habitats, a hypothesis supported, e.g., by the case of some wood ants and tramp species. Monogyny, on the other hand, should favour individuality and separation of small colonies. However one should not forget, for instance, that in S European dry habitats two species regularly coexist and are probably the numerically dominant ones in the same environment and over a very wide range: *Plagiolepis pygmaea* and *Pheidole pallidula*. The first is highly polygynic and the second strictly monogynic (argument suggested by an anonymous referee and personal observations). It is clear that the previous example cannot represent the whole story either: additional explanations are necessary and, in the case of polygyny and monogyny, the same condition must result not only several times independently from each other, and as an adaptation to entirely different ecological parameters, but even both behaviours may have arisen in the same environment as the best adaptation for different species. A probably different cause to explain polygyny among different species had been already postulated by ROSENGREN & PAMILO (1983) and by PAMILO & ROSENGREN (1984) on the basis of their experience on *Formica* ants. These authors equally favour environmental constraints in determining the number of

queens per colony and, in addition, have been able to show analytically genetic differences within the same species according to the number of queens per nest and different sex ratios.

#### 4.2. *Some elementary behaviours convergently evolved among virtually all ant groups*

It may be thought that the mosaic evolution of complex behaviours presented on the preceding pages is due essentially to the general, homogeneous constraints of eusocial behaviour; by searching for smaller behavioural units, it could be easier to trace a phylogeny parallel to the one constructed on morphological characters. The following examples show that this appears not to be the case.

##### 4.2.1. *Alarm communication*

It seems that all known ant species can transmit alarm signals to nestmates in case of danger (see HÖLLDOBLER 1978 for a review). The primitive *Nothomyrmecia* use the product of their mandibular glands (HÖLLDOBLER & TAYLOR 1983) as do some bees, the known ponerines and some myrmicines. Other myrmicines, like *Myrmica*, add to it the products of the poison gland. Some other myrmicines, like *Cremastogaster inflata*, use neither of them and exercise the same function by particularly swollen metapleural glands (other species of *Cremastogaster* «normally» use their mandibular glands). All known dolichoderines alarm nestmates through secretions of the anal gland and the formicines use the mandibular gland, the poison gland, and the Dufour's gland (references can be found in the review by HÖLLDOBLER 1978).

Leaf-cutting ants (myrmicines) add to the products of mandibular glands (BUTENANDT et al. 1959, BLUM et al. 1968, MOSER et al. 1968) a vibrational component (MARKL 1965, 1967, 1968, 1970).

From all this it should be quite evident that a strong selecting pressure for alarm communication has been exerted on all ants, but most major taxa and even different species within a genus appear to have found independently their own solution. A possible exception may be represented by the subfamily Dolichoderinae which, in spite of the small sample size, appears to alarm uniquely and consistently by means of the anal gland. Further evidence for this view is given by the fact that all known dolichoderine anal glands share the property of biosynthesizing cyclopentanoid monoterpenes, a property reported for some 20 different species in five genera and unknown in other ants (BLUM & HERMANN 1978, ATTYGALLE & MORGAN 1984). Cyclopentanoid monoterpenes, generally known as iridoids from the ant generic name *Iridomyrmex*, are likely to be synthesized from (S) - citronellal (CAVILL & CLARK 1971), a compound commonly found among Formicinae and Myrmicinae and unrecorded among Dolichoderinae.

##### 4.2.2. *Phragmosis*

Some ant species use their head as a door to close the nest entrance. The nest is excavated in wood and the shape of the entrance fits exactly the «soldier» head, which assumes a perfectly flat, shield-like, morphology on the side exposed outside the nest, while the eyes, antennae, palpi, etc. remain protected into the nest. This behaviour

and the consequent morphological adaptation have been observed mostly in some *Camponotus* (formicine) and *Zacryptocerus* (myrmicine) species. The morphological adaptations allowing a functional exploitation of this behaviour are so peculiar and extraordinary that, on the basis of head morphology alone, WHEELER (1928) supposed that the same behaviour should be exhibited by some species of other totally unrelated genera like *Cremastogaster*, *Colobostruma* and *Pheidole* (myrmicines) from different biogeographic areas. More recently, the same behaviour has been reported again in the ponerine *Proceratium melinum* which closes the nest entrance exactly as the other ants do, but using the shield-like first gastral segment (POLDI 1964). Among the species presumed by WHEELER to be phragmotictic on the basis of head morphology is the Brazilian *Pheidole colobopsis*, and a second Brazilian *Pheidole* (*Ph. embolopyx*) — with flattened gaster this time — has been supposed to use the posterior tip of the body to exploit the same function (BROWN 1967). The particular adaptation of the gaster appears to be exhibited by the female only, which makes it unlikely the situation of a nest permanently guarded by a phragmotictic queen. Further investigations (WILSON & HÖLLDOBLER 1985), however, showed that the direct «entrance blocking» function is no (? longer) displayed by females of this species which simply take advantage of a turtle-like body form in individual defence.

As there is no doubt about the strong selecting power of phragmoticity and the magnitude of its morphological consequences, it would be illogical to try to extract any phylogenetically useful information from its taxonomic distribution, except at very low taxonomic levels (e.g. species groups).

#### 4.2.3. Recruitment of nestmates

Not all ant species are able to recruit nestmates to a food source. Ants which do not recruit range from the primitive *Nothomyrmecia* (HÖLLDOBLER & TAYLOR 1983) to the supposed highly specialized *Cataglyphis* (WEHNER et al. 1983). The latter case, for *C. bicolor*, has been tentatively explained as a rewarding strategy in terms of individual muscular power and prey size, an assumption which is less defensible for the small *Cataglyphis* species which apparently also lack recruitment mechanisms (SCHMID-HEMPER 1987). Another factor which should not be overlooked and resulting from the previous phylogenetic analysis, is that the genus *Cataglyphis*, as all the Formicinae, may be not so advanced as it used to be thought until now. Some species, additionally to the usual «waggle» display in the nest at the beginning of recruitment, add a vibrational component which enables them to reach a food source within a shorter time lapse. This acoustical reinforcement mechanism is obtained through an important anatomical adaptation, i.e. the stridulatory organ situated between the abdominal segments III and IV (BARONI URBANI et al. 1988). The presence or absence of the organ itself appears to be distributed within the ant system in a way consistent with the hypothetical phylogeny, and, nevertheless, there are in a few genera species provided with the stridulatory organ and species without it (MARKL 1973).

Even the mechanics of recruitment may vary greatly from one ant to another, and the ant literature contains many mentions of «primitive» (= tandem running) and «advanced» (= mass recruitment) systems. I find the use of these two terms particularly misleading; in most contexts they can be substituted by more appropriate ones like «less efficient» and «more efficient».

HÖLLDOBLER (1978) indicates correctly that «the possession of one kind of

recruitment system as opposed to another seems to constitute adaptations by individual species to particular conditions...».

Although the hypothetical behavioural evolutionary sequence tandem running → tandem calling → group recruitment → mass recruitment → trunk trails → army ants appears plausible, the distribution of these behaviours within the ants do not fit any conceivable ant phylogeny and some of them appear or disappear in a way which seems to be completely random. Giving any phylogenetic value to the recruitment mechanism will imply, for instance, that all direct and remote ancestors of the advanced genus *Camponotus* as we know it now, recruited only by tandem running, because the recent species *C. sericeus* shows this type of «primitive» behaviour (HINGSTON 1929). By using the same logic, this conclusion should be extended to any extant genus less advanced than *Camponotus*, i.e. at least under the traditional perspective, to a good majority of the known ant species.

A much more reasonable hypothesis has been recently suggested by BECKERS et al. (1989), which suppose that the use of one or another of the above mentioned recruitment mechanisms represent specific strategies evolved independently in different species, mainly as a function of colony population. Stated otherwise, an ant species, however advanced it may be, will not need any kind of trunk trail or mass foraging if its colony population consists of a few dozens of individuals only.

## 5. DISCUSSION

In spite of the numerous statements about the necessity and the usefulness of using behavioural characters in classificatory and evolutionary studies — mostly from textbooks like TINBERGEN (1951), MAYR et al. (1953), ROE & SIMPSON (1958), SOKAL & SNEATH (1963), WILEY (1981), RIDLEY (1986), to cite just some of the best known examples — I have been able to find very few concrete examples in the literature and even less dealing with taxa of higher rank (i.e. tribes, families, etc.). Morphology and, in recent years, biochemistry appear to offer the only phylogenetic useful tools. This does not mean, of course, that (a few) phylogenetic analyses based on behavioural traits do not exist, as the pilot paper by MCLENNAN et al. (1988) on sticklebacks demonstrates, but most of these analyses deal with species or low level taxa only. The most remarkable exception I know is the monograph by BROTHERS (1975) who attempts a classification of aculeate Hymenoptera at family level by using four behavioural characters out of 92 considered complexively. This disproportion appears too big to be due entirely to the practical advantages of working on dead specimens.

While developing the ideas contained in this paper many more behavioural characters have been considered than those described in the previous examples. The ant scenario presented here appears to exhibit a concatenation of convergences and parallelisms which may make one doubt the phylogenetic relevance of behavioural studies. One explanation of the intricate ant behavioural evolutionary picture probably is that all ants arose from a single eusocial ancestor, and eusociality appears to be a very narrow evolutionary path allowing further selection in only one major direction. For this reason most behavioural characters typical of social insects, like recruitment, caste determination, other forms of social communication, nesting habits, etc. evolved in a parallel way.

Nevertheless, it is clear that behaviour and morphology are often causally

interrelated. Perhaps the major recognizable trend in ant evolution is a behavioural one: improving colony defence. This leads to two major evolutionary patterns: (i) conservation of the primitive body morphology coupled with reduction (Dolichoderinae) or loss (Formicinae) of the sting in exchange for much more sophisticated and efficient poison glands, and (ii) improving sting mobility or sting size and sting power. This can easily account for the trend in constriction behind the second metasomal segment in the sequence Myrmecinae, Ponerinae, Myrmicinae, Pseudomyrmecinae, and for the tendency for bending the gaster forward among several ponerine genera. When we are using the morphological characters sting present or absent, or abdominal pedicel 1-segmented or 2-segmented, we have the tendency to overlook that we are dealing with obvious products of behavioural selection. This point appears to have been overlooked or underestimated by most scholars. PLOTKIN (1988a), writes correctly that «biologists, by and large, have paid too little attention to the possible causal role of behaviour in the process of evolution». For this reason he edited a book «intended as a remedy to this deficiency in the literature on evolutionary theory». His point of view appears to be largely justified if one considers the relatively large number of books which should include this kind of information but from which it is generally lacking (see e.g. ROE & SIMPSON 1958, MEDIONI & BOESIGER 1977, WEINBERGER 1983). In this perspective, the older textbook by ROE & SIMPSON (1958) appears to be still richer in information. One might get the impression that evolution as discussed for behaviour is different from that understood by morphologists, geneticists, etc. In this context, it is surprising to read in PLOTKIN's (1988b) own chapter that «the first question is: ...can tree climbing be distinguished from... digit... length?». I find it difficult to imagine any natural selective system working in an efficient way on the metacarpus and on the phalanges of a non-climbing animal. It is seldom recognized that even the standard morphological characters commonly used in phylogenetic analyses, e.g. presence or absence of legs, lungs, or wings among vertebrates, represent merely the (easier to describe) morphological manifestation of what was originally a shift in behaviour.

In the same way, in this paper, I defined as «true» ants all those sharing a ratio scapus length/funiculus length  $> 0.35$  in at least one female form. What I really mean are those species able to exercise a sophisticated means of tactile and chemoreceptive control via the antennae during trophallaxis.

It appears, therefore, that many evolutionarily important behaviours exist but that they tend to be neglected in phylogenetic analyses because of the more practical approach offered by their morphological manifestation.

Additionally, there are behaviours which exerted a strong selecting pressure on morphology in a phylogenetically random way, like phragmosis, or, more generally, passive defence, which modified the anterior end of the body in one Brazilian *Pheidole* and the posterior end in another, or the anterior end of the body in some species of different genera.

I suppose that the behavioural characters which the textbooks suggest should be searched for were thought to be essentially simple ethological properties implying no or very little morphological or physiological adaptation. One should not forget that simple behavioural shifts like transition from diurnal to nocturnal habits or minor changes in the nesting behaviour are likely to be selected many times according to the changing environmental conditions, just as are e.g. pigmentation or body size, on which nobody would attempt deep phylogenetic analyses. The behaviours described

in this paper are of complex nature and this may be a reason for the displayed mosaic evolution. Subdividing these behaviours into simpler components might provide good characters useful for a phylogenetic analysis at a lower hierarchical level.

Behaviour, in this sense, appears as the principal factor in «form making» during evolution, an assumption recently defended by GRAY (1988) who insists that «behaviour is not just the product of evolution but also an agent for further change». However, its usefulness for practical classificatory purposes is greatly overshadowed by the important morphological correlates of behaviour which so frequently occur. Thus, it seems difficult to use purely behavioural traits to characterize major evolutionary trends: it seems much more advisable to use the behavioural information in trying to understand them. Similar approaches, however, already exist in the literature and reference to the textbook by MANTON (1977) would be sufficient to show the high standard of results obtained in this way.

In addition, morphology shows at least one other important property, apart from its practicality: it seems to be much more conservative than behaviour. There are several examples of structures surviving for millions of years after their function has been lost. Among ants, for instance, it could be very useful to split them as «ants with sting» and «ants without sting», but it would make no sense to distinguish between stinging and not stinging ants. Several species normally equipped with a sting invested their evolutionary potential in improving the toxicity of the products of the poison glands annexed to the sting rather than in magnifying the sting's ability of piercing the skin of enemies. In such cases, the sting, although regularly present, lost its original function and, during defence, is pointed upwards to spread a kind of repellent aerosol, as in some species of *Monomorium* (BARONI URBANI & KANOWSKI 1974, ADAMS & TRANIELLO 1981).

A large number of behaviours (like e.g. social parasitism, phragmosis, nomadism, etc.) imply a characteristic morphological syndrome among ants. I doubt that this correspondence and its meaning had already been entirely recognized and it seems hence legitimate here to expand upon a statement by GOULD (1980: 192) giving as an «ancient truth that similarity of form need not designate common cause». In ants, morphological similarity often designates common cause, but this seldom implies a common origin. The word «behaviour» can easily be interchanged with «form» in the previous sentence. The main problem with behavioural characters is the lack of pertinent embryological information which prevents homology identification by the ontogenetic criteria. Behavioural homology can be only inferred by using external additional information (i.e. the outgroup comparison) which needs to be reinforced by characters of morphological or biochemical nature. This difficulty in homology recognition among behavioural characters has been already recognized as early as 1957 by SCHNEIRLA and has been discussed in details, among others, by BAERENDS (1958), WICKLER (1961), and reviewed by ATZ (1970). According to ATZ (1970), behavioural homologies cannot be identified with certainty, but this author does not consider the possibility of outgroup comparison. The use of outgroup comparisons, however, may be subject to debate for high rank taxonomic categories and it is probably for this reason that MANNING (1979) limits her discussion to the «micro-evolution of behaviour» among closely related species.

In this perspective phylogenetic analyses of behaviour and rules for such analyses were already presented in several papers by K. LORENZ. In his comparative study of the movements of the Anatidae (LORENZ 1941), one can already find a cladogram for



the anatids based on purely behavioural characters. This cladogram is quite similar to those proposed later by HENNIG. While discussing the rules with which the cladogram was constructed, LORENZ correctly identified the problem of different levels of universality of character states but his attempt to define more consistent synapomorphies through a correct «Beurteilung der relativen Dignität» remains vague. LORENZ wrote again on the same subject at the same time as and after publication of the first methodological book by HENNIG (1950) (LORENZ 1950 and 1954). In these papers the need to differentiate between homology and convergence in behaviour is correctly discussed and credit for a proper definition of the problem is given to former behaviour students like Heinroth and even Whitman in the last century. In the work of these authors LORENZ recognizes the principle that similar functions exercised by homologous organs must also be regarded as homologous. I consider this point of view an early recognition of the need for external (i.e. outgroup) comparison in order to detect behavioural synapomorphies. It is unfortunate that LORENZ relaxed this criterion (LORENZ 1950) stating that «Gleichheit oder auch nur Ähnlichkeit gleichbedeutender Ausdrucksbewegungen bedeutet immer phyletische Homologie» without requiring that these behaviours be performed by homologous organs. This statement can be interpreted as a very generous allowance for the inductive method of homology detection as stated by BOCK (1974). Between the two extremes mentioned here, i.e. behavioural homology cannot be detected (ATZ 1970) which means, among other things, that behavioural studies are useless in any evolutionary context, and the other extreme represented by LORENZ (1950) for whom behavioural similarity always means homology, a compromise solution exists: the hypothetico-deductive method used during out-group comparisons. This difficulty is not exclusive to ethology. There are other disciplines (e.g. paleontology) which cannot employ embryological information to settle homology problems as it can be done in morphology (though this is seldom the case in practice). In this context each presumed homology can be treated just as a hypothesis to be tested by other, associated, homology hypotheses (WILEY 1975 and 1976). It may be worth recalling that this kind of solution is purely statistical, i.e. numerical, which seems perfectly homologous to a phenetic approach...

Previous attempts to use behavioural characters in ant classification appear to be essentially concentrated on different dates and times of the day for the nuptial flight (McCLUSKEY 1973, McCLUSKEY & SOONG 1979, MACKAY & MACKAY 1984). Besides the inevitable incompleteness of the available evidence (geographical variation, among other possible sources of variability, has never been considered), these studies tended to underline an agreement between behaviour and morphologically established classification. This approach made the behavioural information subordinate to the morphological one and redundant. These papers, moreover, dealt with species level or genus level categories only.

From all this follows that the «ideal» behavioural character, in order not to be trivial, nor subject to parallel selection, nor redundant because it is correlated with morphological traits, should be some kind of «useless» character which must (i) not imply striking morphological adaptations, and (ii) be so free from selection pressure as to be kept unchanged during long geological times.

I know of no similar definitions from the literature, but the sole purely ethological character I have been able to use in the cladistic analysis of the Formicidae, the stereotyped adult carrying behaviour, satisfies both prerequisites. In spite of the relatively low number of species in which it has been observed (MÖGLICH & HÖLL-

DOBLER 1974), I am quite confident in its different consistency e.g. among the Formicinae, the Pseudomyrmecinae and all three subfamilies of army ants. The purely behavioural plesiomorphism I have been able to use in the cladistic analysis performed in this paper is contained in one single character out of 27 considered, but given the scanty information available and the high rank categories studied, I am inclined to regard it as a major contribution of behaviour to phylogenetic analysis of the ants.

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