

Social evolution – has nature ever rewound the tape?

Raghavendra Gadagkar

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India and Animal Behaviour Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur, Bangalore 560 064, India

Social insects such as ants, bees, wasps and termites exhibit extreme forms of altruism where some individuals remain sterile and assist other individuals in reproduction. Hamilton's inclusive fitness theory provides a powerful framework for investigating the evolution of such altruism. Using the paper wasp *Ropalidia marginata*, we have quantified and delineated the role of ecological, physiological, genetic and demographic factors in social evolution. An interesting feature of the models we have developed is their symmetry so that either altruism or selfishness can evolve, depending on the numerical values of various parameters. This suggests that selfish/solitary behaviour must occasionally re-emerge even from the eusocial state. It is useful to contemplate expected intermediate states during such potential reversals. We can perhaps envisage three successive steps in such a hypothetical process: i) workers revolt against the hegemony of the queen and challenge her status as the sole reproductive, ii) workers stop producing queens and one or more of them function as egg layers (functional queen/s) capable of producing both haploid as well as diploid offspring and iii) social evolution reverses completely so that a eusocial species becomes solitary, at least facultatively. It appears that the third step, namely transition from eusociality to the solitary state, is rare and has been restricted to transitions from the primitively eusocial state only. The absence of transitions from the highly eusocial state to the solitary state may be attributed to a number of 'preventing mechanisms' such as (a) queen control of workers (b) loss of spermathecae and ability to mate (c) morphological specialization (d) caste polyethism and (e) homeostasis, which must each make the transition difficult and, taken together, perhaps very difficult. However, the discovery of a transition from the highly eusocial to the solitary state can hardly be ruled out, given that little or no effort has gone into its detection. In this paper I discuss social evolution and its possible reversal and cite potential examples of stages in the transition from the social to the solitary.

Altruism and eusociality

Competitive selfishness is the corner-stone of natural selection. Nevertheless, we see many instances of the evolution of cooperation and even altruism in the animal

kingdom. In studies of animal behaviour, altruism is defined as any act which increases the fitness of the recipient of the altruistic act and decreases the fitness of the actor. While there are some examples of altruism in birds and mammals, especially in cooperative breeding species, the most extreme forms of altruism are to be found among eusocial insects such as ants, bees, wasps and termites¹. Eusociality, considered as the most developed form of social life, is characterized by (1) cooperative brood care, (2) differentiation of colony members into fertile reproductive castes and sterile worker castes and (3) the coexistence within a nest of individuals belonging to more than one generation^{2,3}. Among the eusocial insects, some are considered even more advanced than the rest. In these so-called highly eusocial species, queens and workers are morphologically differentiated and caste determination, which takes place before the adult stage, is essentially irreversible. The less advanced, so-called primitively eusocial species, have the opposite set of characters – little or no morphological caste differentiation coupled with flexibility and reversibility of caste roles³. Although there may not be a very sharp dividing line between the primitively and the highly eusocial groups, termites, ants, honeybees, vespine wasps and most polybiine wasps are considered to be highly eusocial³. Conversely stenogastrine wasps, independent founding polistine wasps, halictine bees and meliponine bees, as well as the recently discovered eusocial aphids⁴⁻⁶, thrips⁷, ambrosia beetles⁸, shrimps⁹ and the naked mole rat^{10,11} are all considered to be primitively eusocial.

The evolution of altruism and of eusociality have been the subject of extensive theoretical and empirical investigations during the last three decades^{1,12-18}. In contrast, the possibility of reversal of social evolution, namely, the transition from the eusocial to the solitary has received surprisingly little attention. During a brief discussion, Wilson³ concludes that although the solitary habit may have sometimes evolved from primitively eusocial ancestors, highly eusocial species have probably reached a point of no return. In halictine bees, however, which have a great diversity of social organizations, frequent alternations occur between solitary and eusocial states, both between different habitats and between different species within a genus. Halictine bee research-

ers have therefore been long concerned about transition from the primitively eusocial to the solitary state¹⁹⁻²⁴. My own interest in such reverse social evolution, which I metaphorically call 'rewinding the tape' arises from our investigations of traditional 'forward' social evolution. To set the stage, therefore, I will first briefly describe our attempts and some modest success in understanding the evolutionary forces that promote the evolution of eusociality.

Hamilton's inclusive fitness theory

As is now well known, Hamilton^{25,26} showed that altruism will not necessarily be eliminated by natural selection if it is directed towards close genetic relatives. If fitness is defined not simply as the number of offspring, but as the number of copies of one's genes that are transmitted to the next generation, aiding genetic relatives who also carry copies of one's genes, is an alternative, equally legitimate way of enhancing one's fitness. Hamilton therefore proposed that we should be concerned with inclusive fitness which combines propagation of genes through production of one's own offspring and through aiding genetic relatives. More formally, Hamilton showed that an altruist allele would be favoured by natural selection if:

$$b/c > 1/r, \quad (1)$$

where b is the benefit to the recipient of the altruistic act, c is the cost to the altruist and r is the coefficient of genetic relatedness between the altruist and the recipient. This so-called Hamilton's rule has proved to be a powerful theoretical framework for investigating the evolution of altruism.

Ropalidia marginata

Ropalidia marginata is a polistine wasp abundantly distributed in peninsular India. New colonies may be initiated throughout the year by one or a group of female wasps. In single foundress colonies, the lone female builds a nest, lays eggs, cares for her larvae by foraging for them and guarding the nest and thus brings at least the first batch of her offspring to adulthood, unaided by conspecifics, much like a solitary wasp. In multiple foundress colonies, however, there is a dominance hierarchy, leading to division of labour such that only one individual functions as the queen and lays all eggs while the rest function as workers and perform all the tasks involved in colony maintenance and brood care. Daughters eclosing from single and multiple foundress nests may either leave to start their own new colonies or may stay back and function as workers in their natal nests. This means that wasps have the option of repro-

ducing (by becoming solitary nest foundresses) or of becoming workers (by staying back in their natal nest or by joining newly founded nests as subordinates). *Ropalidia marginata* is therefore ideally suited for empirical measurements of the costs and benefits of solitary and social life and to the use of Hamilton's inclusive fitness theory to gain some insight into the evolution of altruism²⁷. The task before us, therefore, has been to measure and contrast the inclusive fitness of a solitary nest founding wasp on the one hand and a wasp choosing to function as a worker in her mother's or sister's nest, on the other hand¹⁸.

Factors promoting the evolution of altruism

For our purpose, Hamilton's rule can be rewritten as:

$$\beta \rho \sigma > b r s, \quad (2)$$

where β is the intrinsic productivity of a worker, defined as the number of individuals she can rear to adulthood provided she survives for their entire developmental period, ρ is the coefficient of genetic relatedness of a worker to the brood she rears and σ is the demographic correction factor for a worker, defined as that factor by which a worker's intrinsic productivity should be devalued because of the probability of her dying before the brood under her care completes development. The corresponding parameters for a solitary foundress are b , r and s (refs 28-30). Clearly at least 3 classes of factors, exemplified by β , ρ and σ or b , r and s can contribute to inequality (2): ecological or physiological factors ($\beta > b$); genetic factors ($\rho > r$) and demographic factors ($\sigma > s$)^{18,30}.

During the last ten years or so, we have been engaged in attempts to assess the relative roles of ecological, physiological, genetic and demographic factors in the evolution of worker behaviour in *Ropalidia marginata*. This work is continuing and has been reviewed from time to time^{15,16,18,27,31,32}. In summary, we have concluded that worker behaviour in *R. marginata* is favoured because the ecological, physiological and demographic factors tend to tilt the balance in favour of worker behaviour although the genetic relatedness terms, if anything, favour solitary nesting behaviour.

We are currently in the process of considering all of these factors simultaneously and of developing a unified model for the evolution of the observed mix of worker behaviour and solitary founding in *R. marginata*. As seen from inequality (2), our model has six parameters, namely β , ρ , σ , b , r , and s . To put it very briefly, we have estimated the values of these parameters as, $\beta = 12.3$, $\rho = 0.11$ to 0.23 , $\sigma = 0.43$, $b = 4.2$ to 12.3 , $r = 0.5$ (this is assumed) and $s = 0.01$ to 0.12 (refs 18, 29, 30, 33-35). Exploring the entire parameter space over the range of these numerical values, we find that the

observed parameter space includes regions where the net balance is in favour of worker behaviour and also where the net balance is in favour of solitary nesting behaviour. This is satisfying because both strategies are known to coexist in populations of *R. marginata*³⁶. An overwhelming proportion of the parameter space favours the worker strategy and this is even more satisfying because solitary nests are notoriously hard to find. To be more precise, worker behaviour is favoured in 96.2% of the parameter space while the solitary nesting behaviour is only favoured in 3.8% of the parameter space³⁷. In an extensive empirical investigation of colony founding in *R. marginata* we recently estimated that 92.5 to 94% of the wasps in *R. marginata* populations naturally choose to nest in groups while only 4.6 to 5.7% choose the solitary nesting strategy³⁶. This extremely close fit between the observed and expected proportions for the solitary and worker strategies is most impressive. However, that our model has certainly not considered several other factors which must also play a role, is a very sobering thought!

Reverse social evolution or, the evolution of selfishness

What can the foregoing analysis of the evolutionary forces favouring worker behaviour tell us about the possibility of reversal of social evolution? As mentioned in the beginning, there has seldom been an attempt to examine if selfishness can re-emerge in a group of altruists. In our context this is equivalent to asking whether social insect species can retrace their evolutionary pathway and eventually become solitary. It is obvious that Hamilton's rule itself provides a theoretical framework to explore the emergence of selfishness. It follows, therefore, that inequality (2) can again become a useful tool if we reverse the inequality sign. In other words, we could say that selfishness would be favoured over altruism if:

$$\beta \rho \sigma < b r s. \quad (3)$$

Indeed, this is exactly why solitary nesting is favoured over worker behaviour in *R. marginata* in a small portion of the parameter space that we have explored above. Thus the inclusive fitness model developed here for understanding the evolution of altruism is symmetrical with reference to direction and may favour the evolution of altruism or selfishness depending merely on the numerical values of the parameters. It is this symmetry in the model that has created in me an interest in the possibility of reverse social evolution. That solitary nesting strategy is favoured in some portion of the parameter space, in the case of *R. marginata*, is itself, however, not sufficient evidence of reverse social evolution. To demonstrate this, we must find the solitary

nesting strategy in the descendants of an obligatorily eusocial ancestor or the loss of eusociality in the descendants of an ancestor that was at least facultatively eusocial.

Can solitary behaviour re-emerge in highly eusocial species?

In spite of admitting that 'social evolution can be reversed and a eusocial species can revert to a solitary condition', Wilson³ concludes that 'there are reasons for believing that a point of no return (in social evolution) does indeed exist'. The reason for this dichotomy is that all suspected examples of possible reversion from eusociality to the solitary state concern primitively eusocial species and as Wilson³ says, 'the highest insect societies have lost elements of behaviour that would be very difficult to reattain in evolution'. Is it pointless then to persist with the question of the possibility of reversal of the highly eusocial state? I believe that there is still some merit in persisting with the question and suggest a three-pronged attack: (i) intensify investigations of suspected reversals from the primitively eusocial state, (ii) identify and investigate possible intermediate states in potential reversals from the highly eusocial state and (iii) identify and investigate 'preventing mechanisms' or factors responsible for the rarity of reverse social evolution both at the primitively eusocial as well as the highly eusocial level. Let us proceed in the reverse order!

Preventing mechanisms

While discussing the evolution of eusociality, it is customary to talk about additional enabling mechanisms over and above the parameters in inequality (2). In the context of eusociality in the Hymenoptera, the sting, the nest and advanced parental care are the three most commonly discussed enabling mechanisms^{13,14}. In other words, the presence of the sting which greatly facilitates defence of large aggregations of adults and helpless larvae, the habit of building elaborate nests that protect and provide environmental control and the possession of well-developed abilities of extended parental care are all expected to make it easier for sociality to evolve if inequality (2) is satisfied. It is reasonable, therefore, that we must consider corresponding 'preventing mechanisms' that might make it difficult for solitary behaviour to re-emerge even if inequality (3) is satisfied. Based on the discussion of this question in Wilson³ and what we know about social insects today, there appear to be at least five major preventing mechanisms that make it difficult or impossible for solitary behaviour to re-emerge from the highly eusocial state. Of course, all five factors are not likely to be equally powerful—

morphology would be hardest to reverse and behaviour would be the easiest with chemistry somewhere in between.

Queen control of workers

A fundamental property of all social insects colonies is the control of worker behaviour and especially worker reproduction by the queens^{3,17,38}. This is accomplished by queen pheromones in the advanced social insects whereas in the primitively eusocial species it may be accomplished entirely by direct physical interactions. In the case of the honey bee, for example, the queen produces a host of chemical substances that influence the behaviour and physiology of the workers in her colony. Owing to the fact that each colony consists of a single queen and many thousand workers, communication between the queen and her workers is, as expected, primarily mediated by chemicals. The well-known effects of queen pheromones on workers include rapid detection of the presence or absence of the queen. A retinue of some 8 to 10 workers, the composition of which changes every few minutes, feeds and licks the queen and thereby acquires the queen pheromones and passes them on to other workers. The pheromones also inhibit the development of worker ovaries and stimulate building and foraging activities. Workers of a queen-right colony almost never lay eggs. Instead, they engage in building combs, feeding the larvae, grooming and feeding the queen, protecting the hive from intruders, foraging, and storing honey and pollen³⁹. Similar chemical control of workers by the queens probably occurs in all highly eusocial species although the nature of the chemicals and the extent of their effects remain to be studied in most cases. The alternative point of view that queen pheromones in highly eusocial insects are not agents of control but are signals that workers use to forgo reproduction which is best left to the queens^{40,41} does not alter our argument that queen pheromones can act as a preventing mechanism for reverse social evolution. Situations where it is to the advantage of the workers to remain sterile and let the queens lay eggs are hardly expected to be conducive for workers to revolt against the hegemony of the queen/s.

In the primitively eusocial wasp *Polistes fuscatus* on the other hand, the queen is behaviourally extremely active and thus regulates the behaviour of workers. The fact that worker activity is stimulated by queen activity was most strikingly demonstrated in an experiment whereby introduction of a cooled inactive queen into a colony, depressed worker activity even more than the mere absence of the queen⁴². Queen control of workers must surely serve to prevent reversal of social evolution and the strength of such prevention must depend on the strength of queen control. It is reasonable to think that

workers in primitively eusocial species can relatively more easily escape from the nudging and biting of the queen compared to a honey bee worker whose behaviour and physiology are strongly influenced by the presence of queen pheromones.

Loss of spermatheca and ability to mate

In most highly eusocial species workers cannot mate and store sperm. In the queens, the spermatheca, a small sac-like diverticulum which opens into the vagina dorsally, acts as a reservoir for sperm and has associated glands to secrete nutrients and keep the sperm viable. In most highly eusocial species, workers have reduced and non-functional spermathecae. Barring one or two exceptions (see below) this completely prevents workers from producing female offspring. In many species workers retain rudimentary ovaries and can lay a few haploid eggs upon the death of the queen⁴³. However this does not give them complete freedom from the queen and this has probably been a major preventing factor for the reversal of social evolution.

Morphological specialization

With very few exceptions, highly eusocial insects, especially ants and termites, are unparalleled in the extent of intra-species and intra-sexual variations in size and allometry. The most widespread differentiation is between fertile reproductives (queens) and sterile workers³. In the ants and termites, sub-groups among workers may also be morphologically differentiated into major (soldier), minor and media workers⁴⁴⁻⁴⁶. Such morphological caste differentiation can be so extreme that different castes, if encountered separately, may get classified as different species⁴⁷. The greatest size variation has been recorded in the Asian marauder ant *Pheidologeton diversus*⁴⁸ where major workers weigh 500 times as much as minor workers and have a head width 10 times as large. Such morphological specialization of workers for non-reproductive and non-colony founding roles has also probably been a significant factor in making reverse social evolution difficult.

Caste polyethism

Division of labour is a striking feature of colony organization in most social insects. While the most fundamental division of labour is between the reproductive and the worker caste, further division of labour within the workers is accomplished either by physical or by temporal means or by combination of both^{3,45}. When castes are physically differentiated, behaviour is correlated with size and when castes are temporally differentiated, be-

behaviour is correlated with age. Physical castes are most strongly developed in termites⁴⁹ and ants⁴⁶, although temporal castes are also seen. Temporal castes are most strongly developed in stingless bees⁵⁰ and honey bees⁵¹. In halictine bees⁵², bumblebees⁵³ and wasps⁵⁴, the correlation of behaviour is less pronounced both with size and with age. There is now evidence that age polyethism can precede the evolution of morphological differentiation between queens and workers⁵⁵. Although such caste polyethism is relatively flexible and allows readjustment of behaviour in response to unusual age or size distribution of workers and unusual levels of demand for work, behavioural specialization based on size and/or age is expected to put some restrictions on the ability of workers to revert to a solitary mode of existence.

Homeostasis

The ability of social insects to regulate the environment of their nest, sometimes called social homeostasis, is most impressive, especially in the highly eusocial species³. While such homeostasis has permitted social insects to gain a considerable measure of independence from the environment, it has also made them dependent on the nearly constant conditions prevailing in their nests. It is a common observation that individual bees and ants that lose their way to the nest die very quickly. This dependence on the homeostatic conditions provided by the nest is also likely to have been a preventing factor in the reversal of social evolution.

Intermediate steps in reverse social evolution

As a consequence of the unlikelihood of complete reversal from the highly eusocial state to the solitary state, it is useful to contemplate possible intermediate states during potential reversals. We can perhaps envisage three successive steps in such a hypothetical process. 1) Workers revolt against the hegemony of the queen (whether morphologically differentiated queens or merely functional queens) and challenge her status as the only reproductive individual, 2) workers stop producing queens and one or more of them function as egg layers capable of producing both haploid as well as diploid offspring (functional queens) and 3) social evolution reverses completely so that the species becomes solitary.

Thelytoky

There are at least two good examples of workers having successfully revolted against the hegemony of the queen and having challenged her status as the only reproductive individual. This appears to have been accomplished

by a phenomenon termed thelytokous parthenogenesis which permits unmated workers to lay diploid, viable eggs which will develop into fertile adult females and, given the right conditions, will develop into morphologically differentiated queens. This has happened in the Cape honey bee, *Apis mellifera capensis*, a unique race of honey bees found at the tip of South Africa. Unlike in any other race of honey bees, virgin workers in the Cape honey bee lay diploid eggs by thelytokous parthenogenesis and the laying workers have many queen-like characteristics including well-developed ovaries with many ovarioles per ovary, well-developed spermathecae, production of queen-like pheromones, possession of queen-like retinue of workers, high reproductive dominance and ability to inhibit production of queen cells⁵⁶⁻⁶⁰. Another example is the ant *Cataglyphis cursor*⁶¹⁻⁶⁴ where, like in the Cape honey bee, thelytoky is facultative and has not led to the elimination of the queen.

Queenless ants

There are several examples among ants where, on an evolutionary time scale, workers have stopped producing morphologically differentiated queens so that present-day colonies consist of one or more egg-laying workers who can produce both haploid and diploid offspring (functional queens). In many ponerine ants, workers routinely mate and reproduce and there has sometimes been a permanent loss of true queens. In some species a single, mated, laying worker, called the gamergate, suppresses ovarian development of all nest-mates and functionally behaves like a queen⁶⁵⁻⁶⁸. The ponerine workers appear to have accomplished this unusual evolutionary feat on account of their morphological primitiveness which includes retention of a functional spermatheca. Nevertheless, queenlessness (and perhaps also the presence of mated workers) appears, from phylogenetic studies⁶⁹ to be a derived condition (Figure 1), justifying this as an example of an intermediate stage in reverse social evolution. Despite the loss of spermatheca, in the Japanese myrmicine ant *Pristomyrmex pungens*, the same result appears to have been accomplished by the evolution of thelytoky as in the Cape honey bee and the ant *Cataglyphis cursor*. However because thelytokous parthenogenesis is obligatory in *Pristomyrmex pungens*, I place this species in the second step of reverse social evolution, ahead of the Cape honey bee and of *Cataglyphis cursor*. Queens are entirely absent in *P. pungens* and workers are unusual in that each one of them performs egg laying as well as other non-reproductive tasks through a curious mode of division of labour – young workers remain inside the nests and reproduce while older workers come out of the nest and forage⁷⁰⁻⁷².

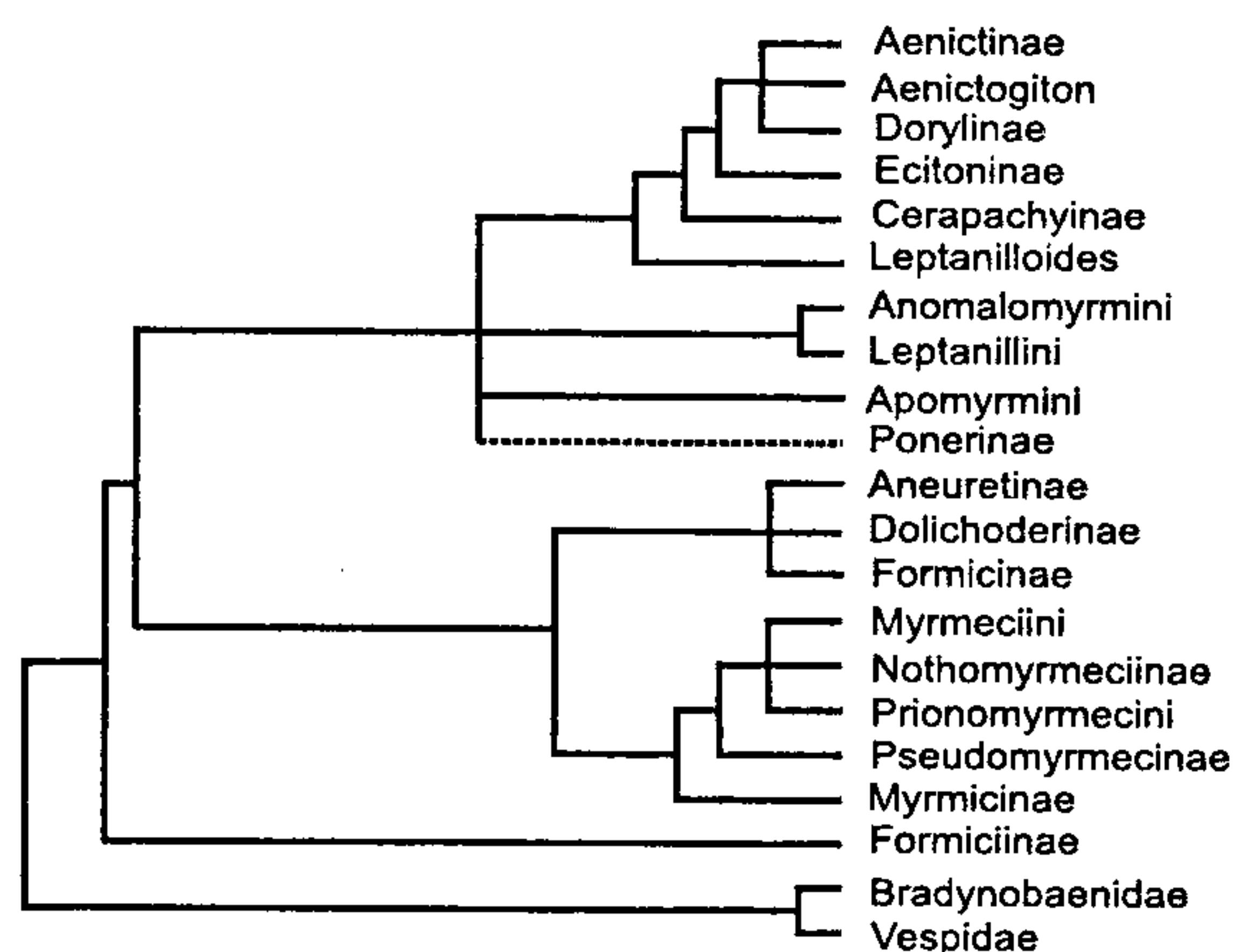


Figure 1. The internal phylogeny of ants as revealed by the strict consensus tree calculated from 72 equally most parsimonious trees resulting from a cladistic analysis of 17 ant taxa and 2 vespoid outgroups. Notice that the position of the morphologically primitive, queenless subfamily Ponerinae indicates that queenlessness in this subfamily appears to be a derived character. (Reproduced with permission from Baroni Urbani and *Systematic Entomology*.)

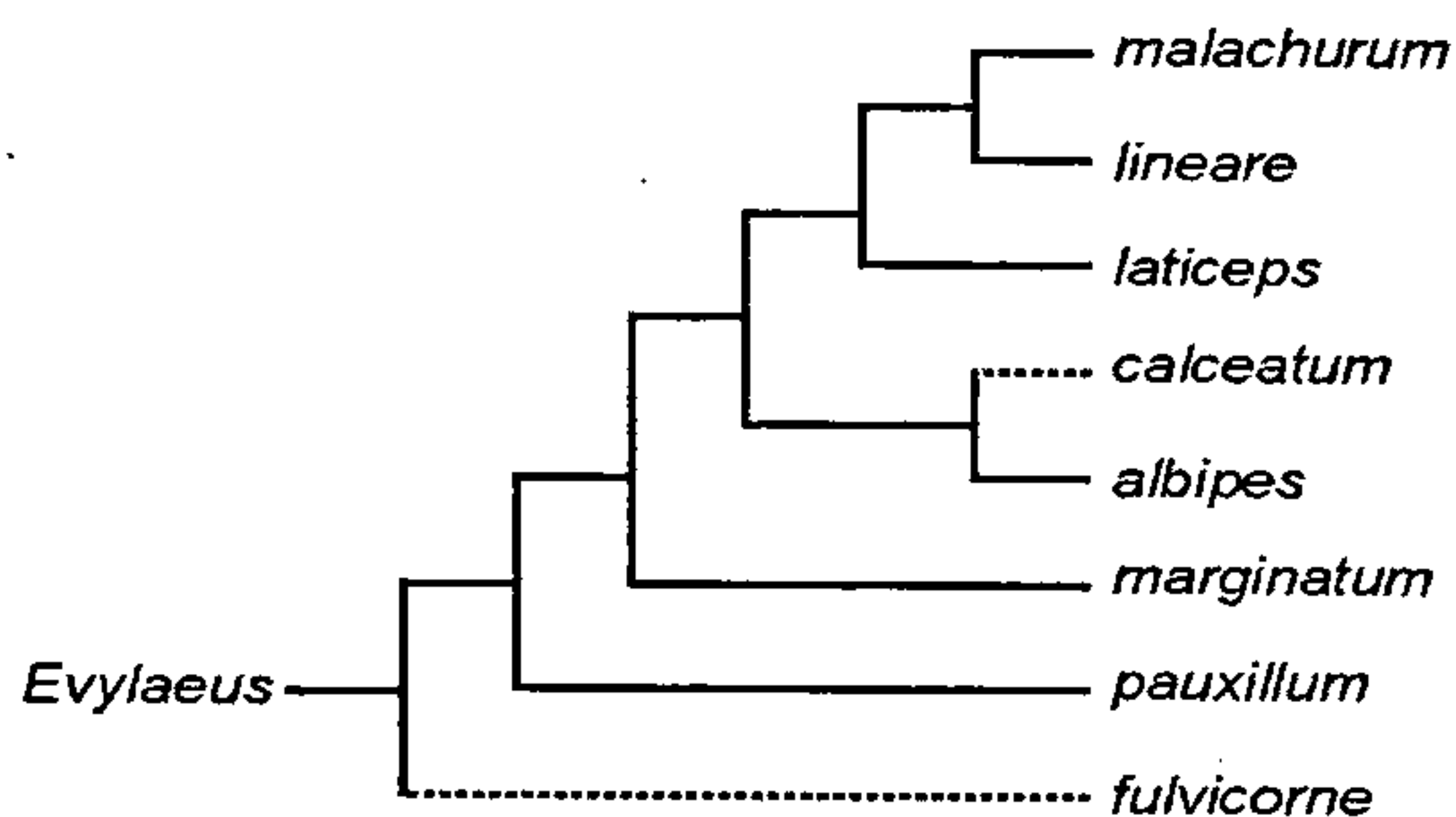


Figure 2. Behavioural evolutionary changes in the halictine subgenus *Evylaeus* mapped upon the phylogeny derived from allozymes. Notice that solitary behaviour observed in the species *calceatum* is a derived condition. The solitary state in the species *fulvicorne* may also be a derived condition because the sub-genus *Evylaeus* may itself be descended from a eusocial ancestor. (Reproduced with permission from Lawrence Packer and *Behavioural Ecology and Sociobiology*.)

From eusocial to solitary?

As mentioned earlier, the final step of going from a morphologically well-differentiated highly eusocial state, all the way to the solitary state, does not appear to have been taken by any social insect. However, transitions from the primitively eusocial to the solitary are not uncommon in the halictine bees⁷³. In the context of the evolution of the Halictinae, Michener²¹ suspects that 'eusocial behaviour has arisen repeatedly, dozens or hundreds of times, and that reversion to solitary behaviour is easy'. A particularly clear example emerges from a phylogenetic study of social behaviour and nest architecture in the sweat bee sub-genus *Evylaeus*⁷⁴. When

behavioural changes are mapped on to the phylogeny derived from allozymes, it becomes obvious that the solitary state of the species *calceatum* is a condition that is derived from the ancestral eusocial state (Figure 2).

It must be mentioned that in all this discussion, I have not considered a different kind of reversion from the eusocial state namely, reversion to a socially parasitic state, rather than the solitary state. This phenomenon has received considerable attention⁷⁵⁻⁷⁷ although its integration with the phenomenon of reversion to the solitary state remains to be achieved.

Concluding remarks

Although highly eusocial species may not have reverted entirely to the solitary state, investigation of suspected intermediate states in the process of reversion may lead to an understanding of why reverse social evolution is not so common and might perhaps even lead to the discovery of true reverse social evolution. At the very least, it will lead to a better understanding of why reversal from the highly eusocial state is difficult or impossible.

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