Social insects and social amoebae

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Abstract. The evolution of social groupings in insects, especially wasps, is compared to that of social amoebae (cellular slime moulds). They both show a gamut of colony sizes, from solitary forms to complex colonies with a division of labour. The various ideas as to how there might have been an evolution of complexity within insect societies, such as the role of genetic relatedness, the role of mutualism, the origin of sterility, the manipulation and exploitation of some individuals by others within a colony, are discussed, and then applied to social amoebae. The result is both interesting and instructive: despite some differences, there are many striking parallels, which suggests that there are some common denominators in the formation and evolution of a social existence among organisms.

1. Introduction

It is often useful to compare two different organisms of similar habits for, the information from one may lead to insights into the other. Or to put the matter more specifically, social insects make a good model system for social amoebae (or the cellular slime moulds) and social amoebae make a good model system for social insects. It is a particular aspect of these social organisms that will be considered here, namely their evolutionary origin. One wants to know for both what are the relative advantages for being social, and how did their communal existence arise in the first place?

These questions are old ones, and ones that have received much recent attention for the social insects. There is a large and fascinating literature and at the moment further important progress is being made. This is not so for social amoebae where relatively little thought has gone into these questions, and for that reason slime moulds may have more to learn from insects; the exchange may be far from even in the two directions.

Unfortunately, we cannot satisfactorily describe the actual sequence from solitary forms to those of increasing complexity for most groups, although with modern molecular methods of exploring phylogenetic sequences, this ought to be possible in the future. At the moment we must resort to making the uncertain assumption that a series of existing forms of increasing complexity represent different evolutionary stages of increasing social integration and complexity.

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Despite the hypothetical nature of such a proceeding, it does have some merit By such studies we can see how social groups of varying size and complexity function, and we can come to some conclusion as to what their selective advantage might be We can be confident that there must be such an advantage for, after all they do exist and show a continuous stability in their organisation—were this not so they would be rapidly eliminated by natural selection. In a recent discussion of social insects, Wilson (1990) points out that the fossil evidence favours the idea that solitary and social insects have existed side by side for many millions of years.

It is fortunate that both slime moulds and social insects show a clear, living series of increasing social complexity from solitary forms, to ones involving large numbers of cells (in the slime moulds) and individuals (in the social insects). Based largely on studies of a tropical primitively eusocial wasp *Ropalidia marginata,* one of us has previously proposed a hypothetical route to social evolution in insects (Gadagkar 1990b, 1991a). Here we will first describe this sequence, but more than that the emphasis will be on understanding the reason for the proposed evolutionary sequence; what is the selective advantage of the association of individuals and the progressive increase in the size and complexity of their societies? The same approach will be followed for social amoebae, applying the causal hypotheses of social evolution developed for insects to the less well understood evolution of slime mould societies As we shall see, many of the arguments apply equally well to both groups, in this way reinforcing the plausibility of some of the basic arguments (which will be reviewed here) for the evolution of a social existence.

2. Social insects

In social insects such as ants, bees, wasps, and termites there are many levels of complexity of the colonies, but social wasps are especially helpful for they show a splendid sequence of the degrees of sociality from solitary forms to large, structured colonies. Let us begin, therefore, with a description of a relatively simple social wasp.

A new colony of the tropical social wasp *R. marginata* may be initiated either by a single female or by a group of females. In the single- foundress nest, the lone female acts like any solitary female wasp. She collects building material (in this case cellulose fibres scraped from twigs of nearby bushes), builds the nest, lays eggs in the cells of the nest, coats the pedicel of the nest with an ant repellent chemical, guards the nests from parasites of various sorts and leaves the nest periodically to hunt for caterpillars, bugs and spiders which she brings back to the nest and feeds to her growing larvae. In a multiple-foundress nest on the other hand there is a clear division of labour. One of the females becomes the queen and enjoys exclusive egg-laying rights and does little other than that except occasionally to build new cells for laying more eggs. The rest of the females in the group become workers and perform all the other duties required for the growth and well being of the nest and its brood. The queen's daughters who gradually begin to enclose are usually recruited into the worker force. However, workers among the cofoundresses as well as among the newly eclosed daughters are not doomed to life-long sterility. Remaining on their natal nest and working for its

welfare is only one of the many options open to them. Alternatively they can go off and (i) found a new solitary foundress nest by themselves and start reproducing (ii) go off in a group or join a group of females who have already started a nest and become either a worker or a queen there, and (iii) stay back as a worker for a while and eventually take over the present colony as the next queen (figure1) (Gadagkar 1991a). Why do many females accept a subordinate non-reproducing sterile worker role when they are capable of reproducing as solitary foundresses? What evolutionary forces might have been responsible for the origin of this social habit from the ancestral state that consisted entirely of solitary wasps?
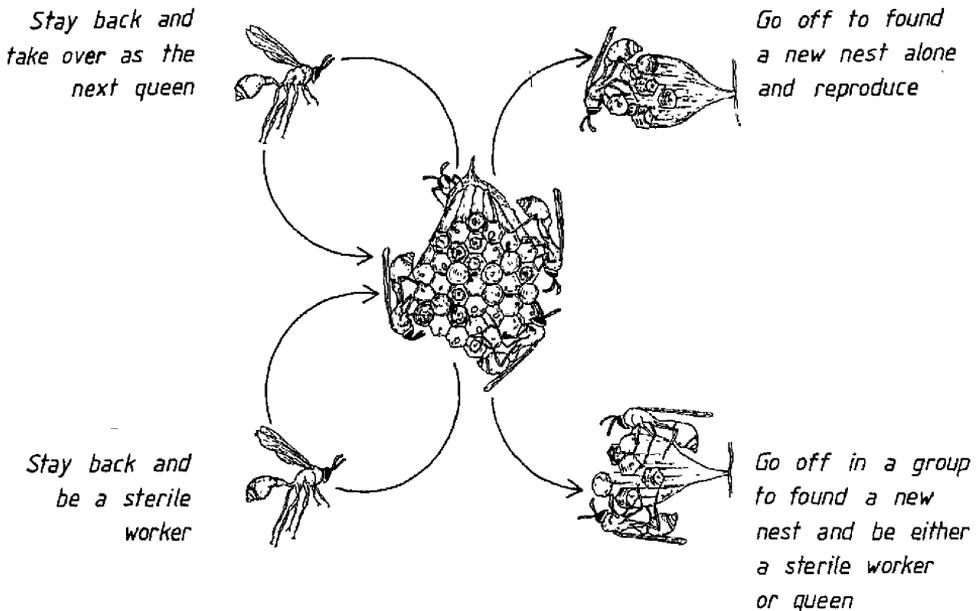
Figure 1. Behavioural options available to females of the primitively eusocial wasp *R. marginata.* (Drawing by Harry William).

Before grappling with these interesting questions we should remind the reader that the highest degree of social existence is *eusociality* where the colony consists of more than one generation, where there is cooperation in brood care, and where reproduction is relegated to one, or a small number of individuals (Wilson 1971). This degree of social organisation is common among the Hymenoptera and the termites (Isoptera). Recently it has been discovered among some species of aphids (Aoki 1977; Itô 1989), in two species of thrips (Crespi 1992), an ambrosia beetle (Kent and Simpson 1992) and in a mammal, the remarkable naked mole rat, whose social organization was revealed by Jarvis (Shermann *et al* 1991).

One distinction between primitively and highly eusocial insect societies is useful. In highly eusocial species such as termites, most ants and honeybees, the reproductive and worker castes are morphologically differentiated. In primitively eusocial species such as many species of wasps and bees, morphological differences between queens

and workers are lacking and there is considerable flexibility in the social roles that a freshly eclosing adult individual can adopt. More importantly, in many primitively eusocial species, unlike in the highly eusocial species, new colonies or nests are founded either by a group of individuals or by a single individual. In the latter case, the solitary foundress can successfully raise her offspring to adulthood, unaided by other members of her species. For these reasons, primitively eusocial species are often considered ideal model systems for understanding the evolutionary forces that may have been responsible for the development of eusociality. Thus the problem of the evolution of eusociality, for practical purposes, can be usefully rephrased as the problem of how some individuals in primitively eusocial species are favoured by natural selection to accept sterile worker roles in spite of being potentially capable of starting their own solitary foundress nests. But the fact that such a selection has taken place suggests that social life, even if it means partial or total sterility, must sometimes be more "advantageous" than solitary life.

How can social life be genetically more advantageous than solitary life if it means sterility? This question seemed impossible to answer until the advent of the concept of inclusive fitness (Hamilton 1964). Today, in any calculation of fitness, it is common practice to include both direct transmission of genes to future generations *via* offspring production and indirect transmission *via* helping the survival of relatives. The inclusive fitness of an individual is thus computed as the summed product of the number of individuals so helped (be they offspring or genetic relatives) and the coefficient of genetic relatedness between each individual and those he or she helps. Given this definition, there is no reason why the inclusive fitness of a worker in a social insect colony should not be greater than that of a solitary foundress. In other words natural selection can, in principle, promote the adoption of the worker strategy. Indeed there can be a variety of reasons why the inclusive fitness of a worker can be greater than that of a solitary foundress. The problem then is not so much to show that this can be so but to show for what reasons it is so. And that is what various theories proposed for the evolution of eusociality attempt to do.

2.1 *The role of haplodiploidy*

One way in which the inclusive fitness of a worker may be greater than that of a solitary foundress is for genetic relatedness between the worker and the brood under her care to be greater than the genetic relatedness between a solitary foundress and her offspring (which of course will be 0·5 under outbreeding). This may be achieved with a haplodiploid genetic system, where genetic relatedness between a female and her full-sister is 0·75, which is greater than the value between a female and her daughters ($r = 0·5$). Since many origins of eusociality have occurred in the insect order Hymenoptera, in which haplodiploidy is nearly universal, much attention has been paid to the possibility that haplodiploidy predisposes Hymenopterans to the development of eusociality. In order to be validated, however, this so-called Haplodiploidy Hypothesis requires several conditions. Colonies should consist of a single egg-layer mated to a single male, so that workers do not rear half-sisters or more distantly related individuals. Workers must either succeed in skewing investment in favour of their sisters or must be able to rear their own sons instead

of brothers. The latter condition is necessary because workers are related to their brothers by only 0·25 while they are related to their sons by 0·5.

Many features of the biology of *R. marginata* suggest that these conditions may not always be met, Foundress associations may not consist exclusively of former nestmates; there is considerable drifting of individuals during colony foundation so that cofoundresses probably are not often closely related (M Shakarad and R Gadagkar, in preparation). Even when they are, subordinate cofoundresses are at best sisters of the egg-layer and are thus helping raise nieces and nephews ($r = 0·375$). Queens mate multiply and simultaneously use sperm from two or more males so that the average genetic relatedness among their daughters is reduced to about 0·5 (Muralidharan *et al* 1986; Gadagkar 1990d). Even more important, frequent queen supersedures lead to serial polygyny, further reducing intra-colony genetic relatedness to values that may be as low as 02 (Gadagkar *et al* 1991c, 1993).

Polygyny or multiple mating by the queen should pose no great difficulty for the haplodiploidy hypothesis if workers discriminate between full-sisters and less related individuals and preferentially aid the former (Gadagkar 1985). However, studies of nestmate discrimination in *R. marginata* suggest that the labels and templates used in discrimination are not produced individually, but rather are acquired from a common external source, namely the natal nest or nestmates, making it unlikely that different levels of genetic relatedness can be effectively recognised among members of the same colony (Gadagkar 1985; Venkataraman *et al* 1988). Thus *R, marginata* workers often rear complex mixtures of full-sisters, half-sisters, nieces, daughters, brothers, nephews, sons, and cousins, and even more distantly related individuals, and probably do so without the ability to discriminate among them on the basis of genetic relatedness. It seems reasonable to conclude therefore that the genetic asymmetry created by haplodiploidy is broken down to the extent that there is no longer any predisposition for worker behaviour on account of it.

2.2 *The roles of parental manipulation and subfertility*

There is another way by which the inclusive fitness of workers can be higher than that of solitary foundresses. Ecological conditions may exist in which a parent who manipulates a fraction of her offspring into being sterile and helps rear her remaining (fertile) offspring leaves behind more grandchildren than a parent that does not manipulate offspring (Alexander 1974). A significant problem with this *parental manipulation* hypothesis is whether counter-selection on the offspring would not be successful in making them overcome parental manipulation. A related idea which gets around this problem is the subfertility hypothesis of West-Eberhard (1975), which simply reminds us that subfertility females produced by whatever cause (even by accidental variation in the quantity of food obtained as larvae) will find it 'easier' to give up reproduction and accept a worker role. The general ideas embodied in the parental manipulation and subfertility hypotheses have found support in theoretical modelling (Craig 1979, 1983; Stubblefield and Charnov 1986), and in empirical studies (Michener and Brothers 1974), and there seems to be little doubt that subfertility caused by parental manipulation or other factors plays a major role in maintaining eusociality in highly social insects.

As far as primitively eusocial species are concerned, the role of parental manipulation or subfertility has not been adequately tested. Instead, it has been common to assume that caste is determined entirely in the adult stage (*e.g.,* Brian 1980; Röseler *et al* 1980; Wheeler 1986; Queller and Strassmann 1989; Reeve 1991). There is however evidence for pre-imaginal caste bias in *R. marginata.* Only about 50% of freshly eclosing female wasps are capable of initiating nests and laying eggs even when they are isolated from conspecifics. Even among the egg layers there is considerable variation in the time required to initiate egg laying (Gadagkar *et al* 1988, 1990, 1991a), Both of these forms of pre-imaginal caste bias namely, differentiation into egg layers and non egg layers and into early and late reproducers is mediated through larval nutrition. Relatively better nourished larvae develop into egg layers and early reproducers while relatively poorly nourished larvae develop into non egg layers or late reproducers (Gadagkar *et al* 199 1b).
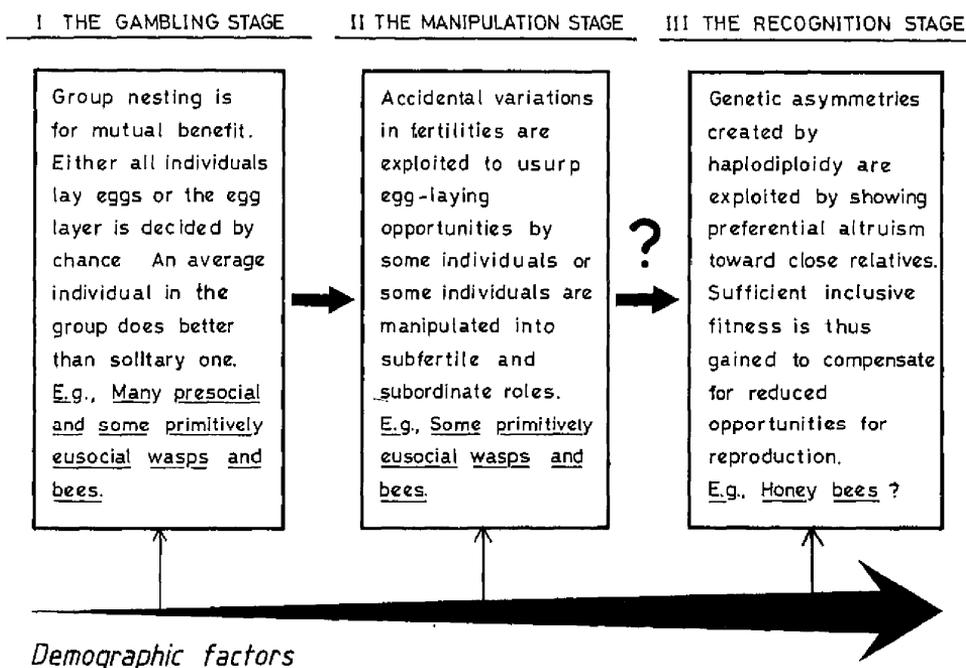
2.3   *The role of mutualism*

Cautioning against an excessive concentration on the role of genetic relatedness in driving social evolution, Lin and Michener (1972) drew attention to a large number of social insect species where sterility is absent or incomplete and suggested the possibility that individuals in such groups may be selected to come together for mutual benefit. This theory of mutualism has often been dismissed as incapable, by definition, of explaining the evolution of a sterile worker caste because the term mutualism suggests that both or all participants benefit. In contrast the sterile worker caste and the fertile queen are not usually thought of as benefiting equally from the associations (*e.g.,* Crazier 1977; Ito 1989). However this argument deserves a second examination. Consider a situation where two individuals nesting together can rear more brood than the sum of their individual capabilities and further that the roles of fertile queen and sterile worker among these two individuals is decided by the toss of a coin, so to speak. In such a situation an average individual that nests in the group may obtain more fitness than a solitary individual. If we replace the concept of alleles programming individuals into workers with alleles programming individuals to take the risk of being part of the group, then it is possible to show that under certain ecological conditions the 'gamblers' will be fitter than the risk-averse solitary individuals (Gadagkar 1991a). The losers in the 'gamble' will leave behind no offspring and we will see them as sterile workers. Nevertheless, it is a form of mutualism that has given rise to this situation. One advantage of such a model is that it requires no assumption of increased genetic relatedness or parental manipulation. The fact that foundress associations in primitively eusocial species may consist of distant relatives and that workers can become queens before they die suggests that the possibility of direct reproduction at some future point of time may itself drive the evolution of group living.

An important assumption of this so called 'gambling hypothesis' is that the *per capita* productivity in the group mode is higher (or more reliable; see Wenzel and Pickering 1990) than in the solitary mode. In *R. marginata* a solitary foundress produces on the average no more than one or two offspring (M Shakarad and R Gadagkar, in preparation) whereas a queen of a multi female colony produces on the average, 76 offspring (Gadagkar 1990d).

2.4 *A possible route to eusociality*

Assuming that existing species of increasing social complexity correspond to sequential stages in social evolution, the evidence reviewed above suggests a possible route to eusociality. First, it seems reasonable to assume that the initial incentive for group living comes from mutualism and the benefits of "gambling". This may be called The Gambling stage (figure 2). This stage requires no pre-adaptation for intra-group manipulation or for recognition of genetic relatedness, although group living among kin (who might come together merely by virtue of being neighbours) will evolve more easily (West-Eberhard 1978; Schwarz 1988). The only *pre-requisite* for the evolution of incipient societies by mutualism is a sufficiently complex behavioural repertoire to permit the necessary interactions; solitary wasps seem to possess an appropriately diverse array of behaviours (Tinbergen 1932, 1935; Tinbergen and Kruyt 1938; Brockmann and Dawkins 1979; Brockmann *et al* 1979). It is easy to imagine that many presocial wasps such as those listed in West-Eberhard (1978) and described by West-Eberhard (1987) and Wcislo *et al* (1988) are either already at this stage or are forerunners of this stage.

THE ROUTE TO EUSOCIALITY

I THE GAMBLING STAGE	II THE MANIPULATION STAGE	III THE RECOGNITION STAGE
Group nesting is for mutual benefit. Either all individuals lay eggs or the egg layer is decided by chance. An average individual in the group does better than solitary one. E.g., Many presocial and some primitively eusocial wasps and bees.	Accidental variations in fertilities are exploited to usurp egg-laying opportunities by some individuals or some individuals are manipulated into subfertile and subordinate roles. E.g., Some primitively eusocial wasps and bees.	Genetic asymmetries created by haplodiploidy are exploited by showing preferential altruism toward close relatives. Sufficient inclusive fitness is thus gained to compensate for reduced opportunities for reproduction. E.g., Honey bees ?

?

Demographic factors

Figure 2. The route to eusociality, a hypothesis concerning the evolution of the highly eusocial state from the solitary state through the Gambling, manipulation, and recognition stages. The examples given for each stage are tentative as our knowledge of the causes and consequences of group living in most social insect groups is still sketchy. The arrow below indicates the increasing importance of demographic factors through the course of the evolution of eusociality (modified from Gadagkar 1990c).

Once group living is established, the stage is set for the second step which may be called the Manipulation stage, Accidental variations in food supply leading to sub-fertility can now be exploited and the ability to manipulate offspring or other nestmates can be selected for. As manipulation becomes increasingly effective, the benefits of group living become increasingly unavailable to some individuals who begin to lose reproductive options and get trapped into worker roles. Workers in many highly eusocial species for example have become morphologically differentiated and have lost the ability to mate and become queens. It is precisely at this stage that the ability to recognize and give preferential aid to closer relatives will begin to have selective value. This final stage may therefore be called the Recognition stage. In other words, the benefits of haplodiploidy for social evolution become available at this final stage. This appears to leave open the question of why eusociality has evolved repeatedly in the Hymenoptera compared to other groups of animals. We have no definite answer to this question but can offer two kinds of speculations. The first is that the paradox of the taxonomic distribution of eusociality cannot really be understood until we begin to ask why is eusociality restricted for example, to the aculeata within the Hymenoptera? A second speculation is that there may be features other than haplodiploidy that are also peculiar to or exaggerated in the Hymenoptera which make the evolution of eusociality more likely (Alexander *et al* 1991). Extended parental care, elaborate nests, the ability to sting and perhaps unusual demography are examples of factors that deserve attention in this regard.

There is a growing impression that primitively eusocial species may not have the ability to discriminate between different levels of genetic relatedness among individuals belonging to the same colony (Gadagkar 1985; Gamboa *et al* 1986; Venkataraman *et al* 1988; Queller *et al* 1990). On the other hand, there is some evidence that the highly eusocial honey bees have the ability to distinguish between levels of relatedness within a colony (Gadagkar 1985; Page *et al* 1989), although whether bees use this ability to show differential altruism remains controversial (see, Carlin and Frumhoff 1990; Page *et al* 1990; Oldroyd and Rinderer 1990; Page and Robinson 1990). If haplodiploidy was important for the origins of insect sociality one would expect workers in primitively eusocial species to exploit the genetic asymmetries thus created, by discriminating between close and distant relatives. But if the origin of eusociality is due to mutualistic benefits, and its subsequent maintenance in highly eusocial forms is due partly to haplodiploidy, the observed, distribution of kinship discrimination abilities is not surprising. Indeed, it is difficult to imagine how the ability to manipulate conspecifics or to discriminate between different levels of genetic relatedness among conspecifics (of the same sex) would have had selective value prior to the advent of group living.

2.5 *Demographic predisposition to the evolution of eusociality*

In addition to the factors mentioned above, demographic factors can also promote the evolution of a worker caste. For example, if there is any delay in the attainment of reproductive maturity, solitary foundresses will have to wait until they become reproductively mature before they start rearing offspring. Workers however can begin to work immediately because they are supplied with brood by the queen.

Even if solitary foundresses or workers have identical age dependent mortality rates, workers will be at an advantage whenever there is a delay in the attainment of reproductive maturity. If there is substantial variation in the population in the time required to attain reproductive maturity, one can expect a coexistence of the solitary founding and workers strategy because the early reproducers would prefer the solitary founding strategy while the late reproducers would prefer the worker strategy (Gadagkar 1991b). Even when there is no delay in the attainment of reproductive maturity, there is a curious asymmetry between solitary foundresses and workers. A solitary foundress necessarily has to survive for the entire duration of the development of her brood. If she dies before her brood reach the age of independence, then she loses all her investment in them and gets no fitness at all. A worker is relatively better off because even if she dies before the brood under her care reach the age of independence, there is a chance that another worker in the group will continue to care for the brood and bring them to independence (Queller 1989; Gadagkar 1990a, 1991b). A worker can therefore hope to get at least some fitness in proportion to her contribution in rearing the brood. In other words, a worker has relatively assured fitness returns for her labour relative to a solitary foundress. Empirical data on mortality rates and time taken to attain reproductive maturity in the primitively eusocial wasp *R. marginata* show that such demographic factors can be powerful in selecting for a worker strategy (Gadagkar 1990a, 1991b).

There still remains the problem of integrating the demographic factors discussed in this section with the route to eusociality discussed in the previous section. Demographic predisposition may best be thought of as having an influence on the evolution of eusociality throughout the proposed route. The reason for this is that demographic factors such as delayed reproduction and variation in age at reproductive maturity can themselves coevolve with eusociality. For instance, the disadvantage of delayed reproduction is relatively large in a solitary species but not so in a eusocial species where individuals with delayed reproduction can compensate by adopting worker roles. Selection against delayed reproduction is therefore expected to become weaker as opportunities for taking up worker roles increase. Prior to the evolution of eusociality, any accidentally occurring delay in attaining reproductive maturity could facilitate the evolution of eusociality. However, the extent of delay and variation seen in today's eusocial species may reflect a combination of initial values plus selection for higher values since achieving eusociality. One might therefore argue that demographic factors have become increasingly important as eusociality evolved.

3. Social amoebae

In the cellular slime moulds *Dictyostelium discoideum,* dispersal from one habitat to another is by means of spores. Finding themselves on a suitable habitat, the spores yield a single celled free-living amoeba each. The amoebae move about freely, feeding on bacteria in the soil until the local food supply is exhausted. At that time dispersal to a new food rich habitat is the best strategy but the amoebae are not up to this task themselves. They therefore go through a social phase to achieve this objective. The hitherto free living amoebae come together by using

an elaborate means of chemical communication and form a multicellular slug or pseudoplasmodium which migrates to a suitable location and eventually transforms into a fruiting body. In this process some of the cells in the slug differentiate into spores and disperse to new habitats. This is only made possible by what must be a supreme sacrifice or altruism on the part of the remaining cells that die and form a stalk that hold the spore bearing sphere high in the air to facilitate dispersal to reasonable distances (figure 3) (Bonner 1967). Why do some cells accept the role of "subordinate" sterile "worker" status to help the rest find a new life in a new habitat? What might have been the evolutionary forces responsible for the origin of this social habit from the ancestral condition that lacked it?
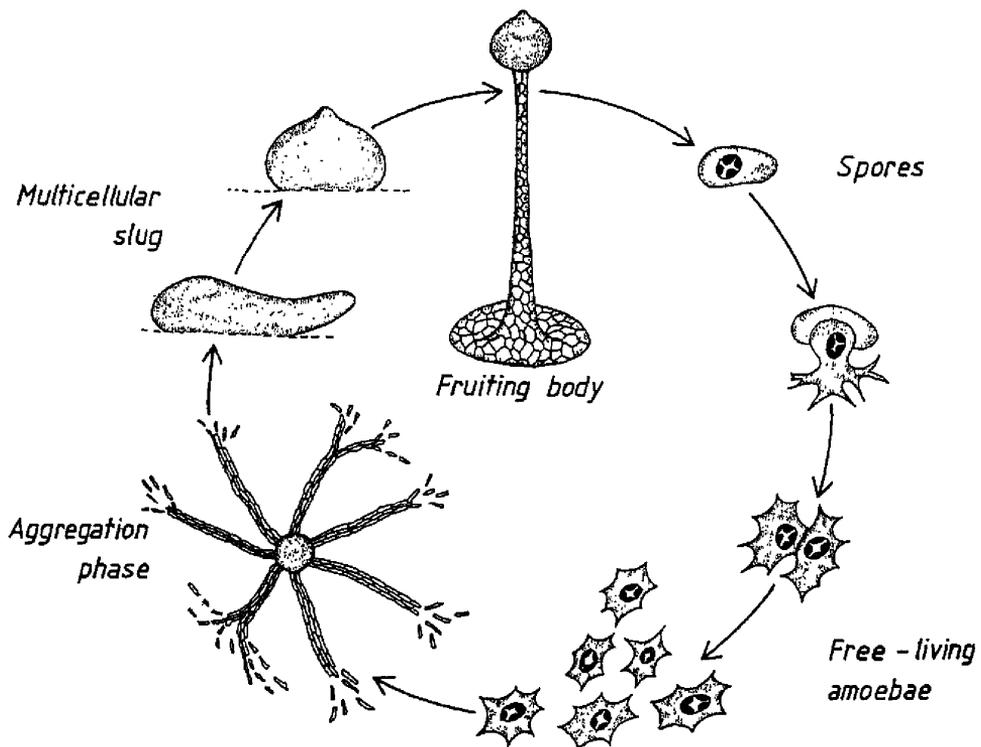
Figure 3. Diagram of life cycle of *D. discoideum.* From Olive (1970). (Drawing by Harry William).

Can those cells that ended up as stalk cells be said to have behaved altruistically (Nanjundiah 1985)? On the face of it they appear to have performed no act of altruism since in all laboratory experiments (and most experiments with slime moulds are in the laboratory anyway!) the amoebae that aggregate are clones of each other with a coefficient of genetic relatedness of 1·0. The question of interest therefore is whether amoebae, related to each other by less than 1·0, aggregate in nature so that some cells become stalk cells to help others, not related to them by 1·0, to disperse to favourable habitats? This question is not easy to answer because of the great paucity of field studies on slime moulds. There are three lines

of evidence however to suggest that aggregating amoebae in nature may not be related to each other by 1·0 after all. Francis and Eisenberg (1993) examined restriction fragment length polymorphism (RFLP) patterns in 44 strains of *D. discoideum* isolated from a small area in North Carolina, USA and found that 29 strains had a unique RFLP pattern each and three additional patterns were shown by 10, 3 and 2 strains respectively, suggesting that different strains must have opportunities to coaggregate. More convincing is the discovery of a stalkless form of *D. mucoroides* and the demonstration that such a stalkless "selfish" form can coaggregate with the normal stalked form and increase in frequency when rare and stabilise at some equilibrium level (Filosa 1962; Buss 1982). Perhaps the most definite case of selfishness and altruism in slime moulds comes from experiments of DeAngelo *et al* (1990) who showed that when a mixture of 2 strains of *D. discoideum* are forced to coaggregate in the laboratory, they produce larger spore masses and thus display a higher spore to stalk ratio.

It is obvious from the above that we really know little about the genetic make-up of individual cells in an individual slime mould aggregate and can only make inferences from the indirect observations just described. What those observations show is that there is a good chance that genetically mixed pseudoplasmodia, or cell masses, do exist in nature; but there is an equally good chance that some of the pseudoplasmodia are clones and all the cells are genetically identical. It is so easy to raise an entire population of fruiting bodies from one spore in the laboratory, that it is hard to imagine it does not happen frequently in the wild. We would like to argue that multicellular cellular slime moulds normally exist in two forms: some are genetically mixed like social wasps, while others are clones comparable to the social, polymorphic aphids. If these assumptions are correct, then it allows us to make two different kinds of arguments for grouping and division of labour among slime moulds. In the case of clones if the cells are identical genetically, the advantage of producing a sturdy stalk made up of dead cells, must be more than compensated for by the advantage gained in more effective dispersal. On the other hand when a multicellular individual is made up of cells of more than one genotype then there will be competition between those cells and the arguments that we used to explain the evolution of social wasps could apply to the social amoebae. The slime moulds are unique in that they can have it both ways.

The cellular slime moulds fall into two major groups: the acrasids, and the dictyostelids (Olive, 1975; Raper 1984). Between them they show a complete series of different degrees of complexity and division of labour, although it must be cautioned right from the outset that there is every reason to believe that the two groups arose independently, and their amoebae are only distantly related.

Besides these groups there are a number of species of solitary amoebae which never come together in groups. They may either encyst as separate cells during unfavourable or starvation conditions (*e.g., Hartmainella)* or they may rise on a minute acellular stalk; each individual cell has its own pedestal (protostelids) (Olive 1975). All these organisms, including the acrasids and the dictyostelids live primarily in the soil or humus, although some are found on bark and other plant surfaces. Because in all cases their feeding stage involves separate, single amoebae, they require a moist environment during the vegetative part of their life cycle and they can only withstand desiccation in the form of spores or cysts with resistant cell walls.
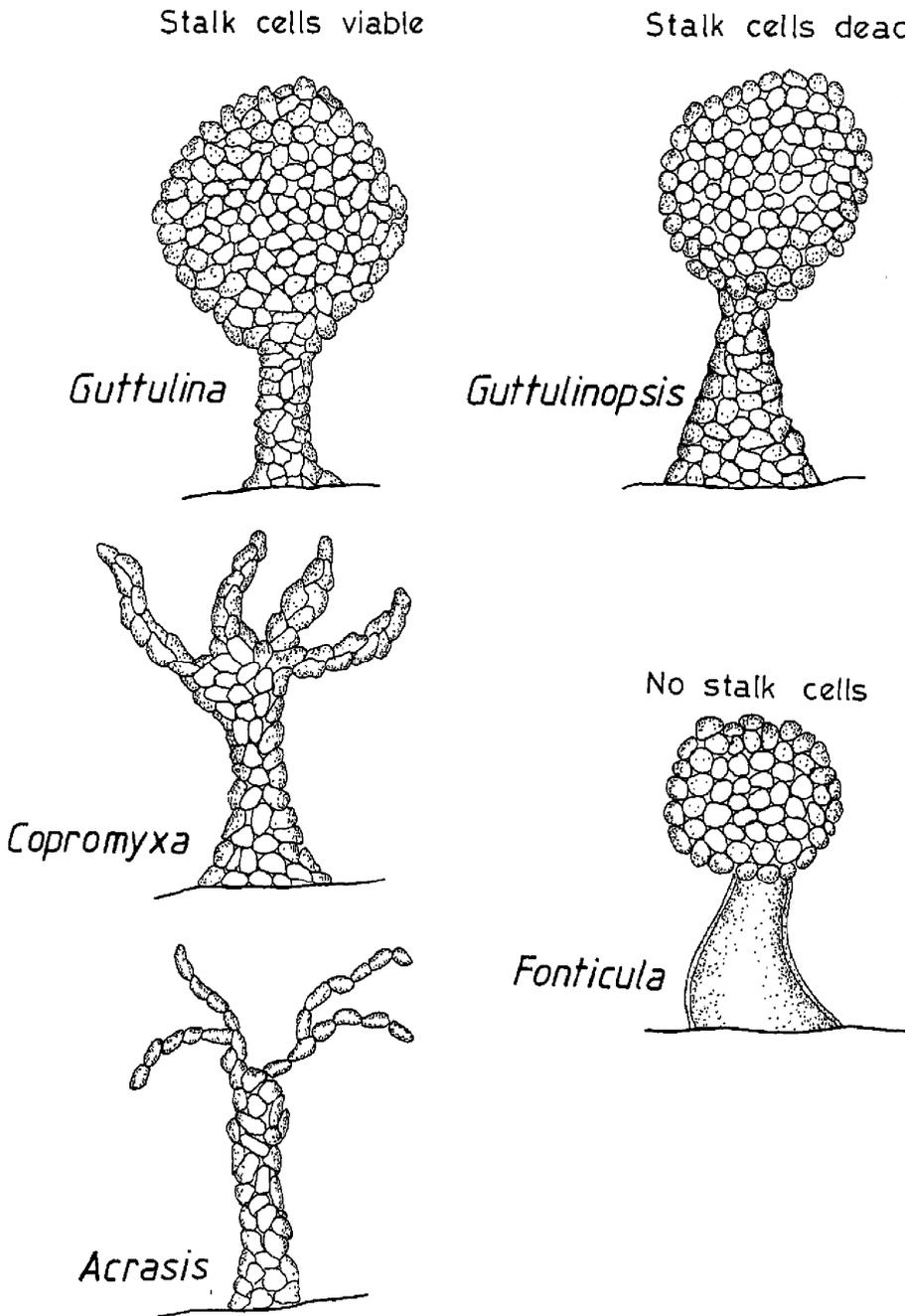
3.1   *The Acrasids*

The acrasids are characterized by a very loose, and almost casual aggregation of amoebae which become progressively clumped into a knob-like structure (review: Olive 1975). This will rise into the air, in some species putting out branched columns of spores at its upper end *(Acrasis, Copromyxa,* while others, with a similar stalk-like base, will have a globular mass of spores *(Guttulina, Guttulinopsis, Fonticula)* (figure 4). These fruiting bodies are small, involving thousands of cells, and standing about 1 mm high. Their method of construction is varied: in some the cells simply keep climbing on top of one another *(Copromyxa);* in yet others the cells at the apex of the mound squirm around to form branching chains of cells *(Acrasis)*; in others the whole mound seems to rise being presumably pushed upwards by the cells as they crowd inward at the bottom *(Guttulina, Guttulinopsis);* and finally there is one extraordinary case where the mound secretes a conical tube and the amoebae within the tube propel themselves to the upper neck and form a spherical cluster at the tip *(Fonticula)*.
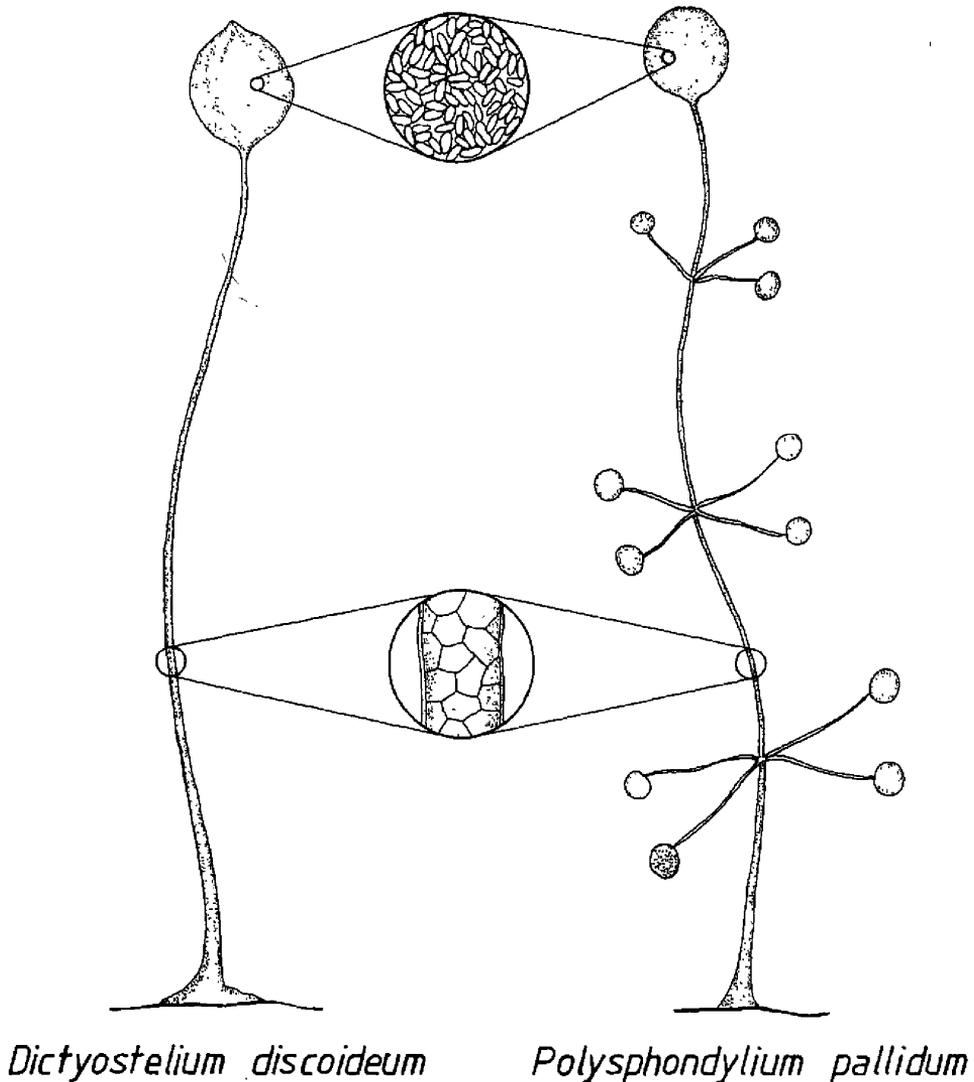
3.2   *The Dictyostelids*

The dictyostelids, which are presumed to have a separate origin because their internal cell structure is so different from the acrasids, produce fruiting bodies that are far more perfectly formed, and there is a sharp distinction between the structure of stalk cells and spores, something that is totally lacking in the acrasids (review: Olive 1975; Raper 1984) (figure 5). In general they have a slender, tapering stalk which is covered by a sturdy cellulose sheath, and the stalk cells inside become large and vacuolate; they are dead as well as permanently trapped in the sheath as they reach maturity. In some cases the stalk bears a single sorus or spore mass at its tip (most species of *Dictyostelium*) while in others there are, besides the terminal sorus, branches which form whorls at regular intervals along the stalk, each one of which has a small sorus at its tip (*Polysphondylium*). There is one curious group which lacks the two cell types; $_{all}$ the cells secrete an acellular cellulose stalk as they rise into the air, and then they all turn into spores (*Acytostelium*) (figure 6). As one might expect, *Acytostelium* is small and more delicate than other dictyostelids. They vary in height from 0˙1 to 1˙2 mm, and while a few other species of dictyostlids are this small, the majority are in a size range of 1–5 mm, some attain a height of 10 mm (and even higher if grown under unidirectional light).

3.3   *The advantages of group living*

The key question, and the very one we asked for social insects, is what might be the advantage of coming together in groups. The most obvious answer is that of dispersal, but Reginald Deering has pointed out to us that another advantage might be to avoid noxious substances. This would be especially effective when the spores are lifted up into the air on a stalk. (Note that the stalked nests of wasps also serve to protect the young in the nest.)

Stalk cells viable

Stalk cells dead

Guttulina

Guttulinopsis

Copromyxa

No stalk cells

Fonticula

Acrasis

Figure 4. Acrasids. A diagrammatic representation (in which the cells are drawn disproportionately large) of five genera of acrasids. In *Guttulina, Copromyxa* and *Acrasis* all the cells in the fruiting body are viable. In *Guttulinopsis* the stalk cells are dead, and the spores appear somewhat differentiated. In *Fonticula* all the cells contribute to the formation of the secreted stalk cylinder and then appear as a mass of well formed spores at the top of the crater they have formed. (Drawing by Harry William).

Dictyostelium discoideum   *Polysphondylium pallidum*

Figure 5. Dictyostelids. The fruiting bodies of *Dictyostelium* and *Polysphondylium* are compared. Note that the stalk cells and spores are similar in both. (Drawing by Harry William).

It is easy to imagine that well developed, stalked fruiting bodies with terminal spores might be especially effective in facilitating spore dispersal. These organisms are dispersed in the humus and soil by having the spores adhere to passing invertebrates: mites, insects, worms of various sorts—all the animals that move about near the surface of the soil. The reason for favouring such a view is that the spores are in an open mass (sorus) and that if any object touches it, the spores will immediately stick to that object, be it an inoculation needle of an experimenter or a passing insect. The question is how did the complex and beautifully constructed dictyostelids evolve from solitary amoebae?
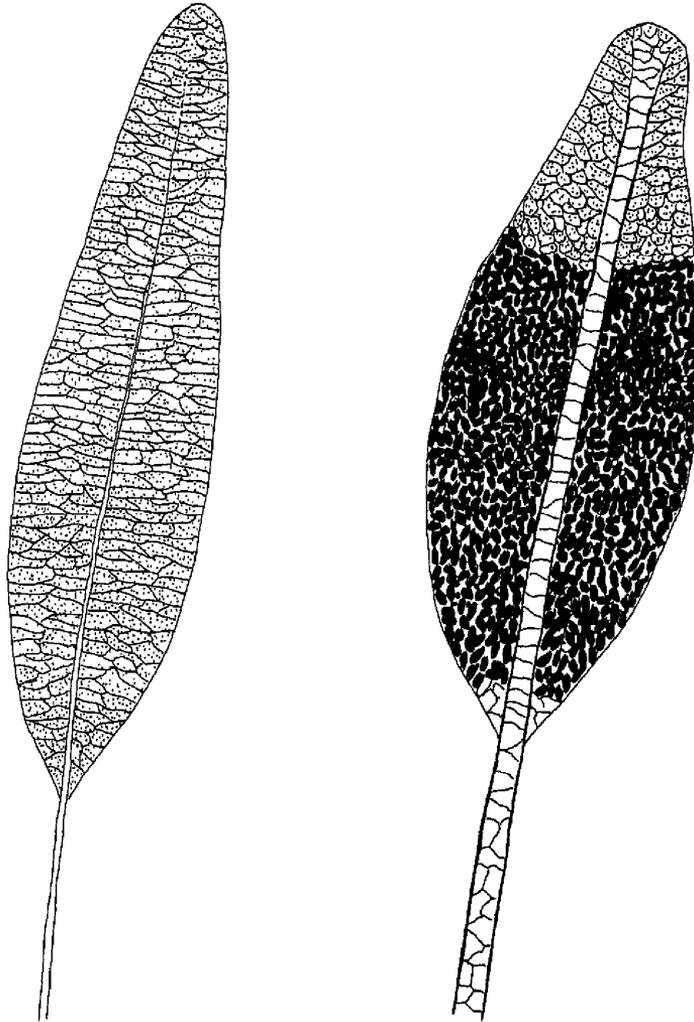
Figure 6. *Dictyostelium* and *Acytostelium* compared. Semidiagramatic drawings of saggital sections through the rising cell masses. In *Acytostelium* (left) all the cells secrete the non-cellular stalk and then each one turns into a spore. In *Dictyostelium* (right) the anterior cells form the stalk by first secreting the sheath and then entering at the tip by a "reverse fountain" movement. Once inside, the cells swell and die. The remaining posterior cells form spores. *(Dictyostelium* species are larger than those of *Acytostelium*. In order to compare them, a small *Dictyostelium* is placed alongside a large *Acytostelium*.)* From Bonner (1988).

It is conceivable that the most significant factor that has driven solitary amoebae to become social is dispersal (Bonner 1982, 1988). There is good reason to believe that this has a potent selective force in soil microorganisms. Amoebae feed on bacteria, and their distribution in the soil is bound to be patchy because the distribution of decaying vegetables or animal matter will be patchy, depending on where a beetle died, or where animal droppings fell. If a patch of bacterial food is discovered by an amoeba, then soon, amongst the rich food, it will proliferate

and produce a region of high density of amoebae. Once the food is consumed the amoebae must wait to be transported to a fresh bacterial patch. Waiting may be perilous should environmental conditions change for the worse, and therefore it is not surprising that $_{\text{all}}$ soil amoebae, solitary and social, have some form of resistant stage—a spore or a cyst. These cysts will be clumped since they will form in the region of the exhausted food patch of bacteria. To disperse effectively they must be able to latch onto a mobile animal. This could be by being eaten and passing through the gut, which clearly happens, for spores of amoebae are found in earthworm casts. But the probability of dispersal would be greatly enhanced if the spores could stick to the side of a passing invertebrate.

To do this, two properties would be desirable and would thus be favoured by selection. One is making the spores adhesive, and the other is bunching them up in a mound so that should they be brushed by an animal, they will adhere in large numbers. The reason for the latter might be that the greater the spore load on the carrier animal, the greater the chance that it will still have a spore to drop when it passes through a distant fresh food patch. Furthermore, it may not just be passing through, but the animal might be attracted to the very bit of decay which is bound to be loaded with bacteria. The spores will inevitably keep being scraped off the animal as it wanders and the greater the number of spores it carries, the greater the chance the animal might drop off a spore on a fresh patch of food.

3.4   *The Gambling stage in amoebae*

Therefore we argue that in the case of soil amoebae, the more bunched the propagules, the better the chance of their producing a next generation. Just as there are advantages for the grouping together of fertile female wasps in communal nests, for other reasons it is advantageous for amoebae to become social. Yet despite the difference in the reasons, grouping ensure greater reproductive success in both cases. This clumping of amoebae is equivalent to the gambling stage in social wasps. The only real difference is that there is no risk involved for the odds are so much in favour of the grouped versus the solitary cells. As in the wasps the association is of mutual benefit to all the cells, even if they have some genetic differences from one another. It is reasonable to call this mutualism in the case of simple wasp aggregations, but perhaps the term is less apt for amoebae. In wasps they come together by behavioural means and genes which govern such behaviour will be favoured in selection. In slime moulds the first clumping is assumed to be fortuitous because that is where the original food patch was located. If genes then appear that reinforce togetherness and perhaps even encourage aggregation by cell Chemotaxis to central collection points, then such a signal-response system will find, new patches for further reproduction. It is at this point, when one has an active communication system between cells, either by Chemotaxis, or perhaps initially by cell adhesion, one might come closer to think of the individual amoebae behaving in a mutualistic fashion.

3.5   *The manipulation stage in amoebae*

In the next stage, the manipulation stage, one first must look for evidence that some of the cells which are helper cells (the functional equivalent of social insect

workers) become sterile, perhaps initially by chance, exactly as is postulated for insects. There is an excellent example of this if one compares *Guttulina* with *Guttulinopsis* (Olive 1975). Their general appearance is much the same (figure 4); they have rough stalks topped with a globular mass of cells. In *Guttulina* all the cells appear the same, both those in the stalk and in the apical bulb. They have thin, resistant cell walls and if placed in a suitably moist environment each one will germinate to produce a single amoeba. As far as the cells are concerned, they all are essentially the same; there is no division of labour. *Guttulinopsis,* on the other hand has a number of cells in its stalk which are swollen. They appear to be dead (and therefore sterile) and one presumes that their swelling might in some way increase the strength of the stalk. The cells in the stalk of the branched species, *Copromyxa* and *Acrasis* also are capable of propagation, as in *Guttulina* (Olive 1975).

Let us shift the discussion to dictyostelids because we know so much more about how they form their social groups. One of the important features of the second, or manipulative stage in insects is some kind of dominance. Dominance exerts itself in two ways in the slime moulds. First of all it is well known that in dictyostelids the cells aggregate by Chemotaxis. The chemoattractant, or acrasin, is a small diffusible molecule (*e.g.* cyclic AMP, folic acid, a dipeptide called glorin—Reviews: Bonner 1982, 1983) which is given off by one cell or a small group of cells that literally commands the surrounding cells to stream towards them. In many ways it is analogous to a queen bee being, through the scent or pheromone she gives off, the center of attraction for the other bees in the hive.

Perhaps even more to the point, there is a manipulation of the aggregated cells so that the fertile spores become the reproductives and they literally suppress, by producing an inhibitor, some of the cells from following suit; they force those cells to become sterile stalk cells (Inouye 1989). Presently the nature of this chemical inhibition will be compared to the inhibitory control of sterile workers by reproductive in social insects. However, first we wish to point out an important similarity on how these two very different kinds of organisms divide the labour. In both cases the difference between castes in insects, including the difference between reproductive and sterile workers, and the difference between spores and sterile stalk cells in slime moulds, is not a genetic difference, but a phenotypic one. In insects the fate of an individual in terms of what caste it becomes as an adult depends upon environmental factors, of which diet during development and inhibition of the development of one caste by another are the most significant.

If one considers food intake, there is a close parallel between slime moulds and insects. In slime moulds one can, by experiment, be certain that all the cells in an aggregate are genetically identical, because one can start a colony from one cell and produce many amoebae which will aggregate into clumps and differentiate into spores and stalk cells. In this case their relatedness equals 1·0; they are a clone. But it has been known from early work (Bonner 1959; Takeuchi 1969) that although the cells may be genetically identical, they certainly are not phenotypically identical. Some cells show early signs of leaning towards the spore direction, and others towards stalk cells and these differences first show *before* aggregation (Nakahara *et al* 1985). There is clearly a sorting out of these different cells so that the cells with stalk tendencies go to the anterior of the migrating slug, and cells with spore tendencies settle in the posterior two thirds of the slug. In other

words they are different and there is evidence that this difference may be connected to nutrition. This was clearly demonstrated in some experiments of Leach *et al* (1973) (see also Inouye and Takeuchi 1982) in which they fed amoebae two different ways: one with an excess of carbohydrate, and the other with a minimum of food. When they mixed the two types of cells together they found that the well fed cells became spores, and the lean cells became stalk cells. Note that in both slime moulds and insects the reproductives receive the richest diet. Therefore in both organisms there is a phenotypic variation (or range variation: Bonner 1965) and it is exploited for the dividing of the labour.

Slime moulds also have a temporal element in their division of labour. It is well known that worker bees and ants of some species change jobs as they age, Initially a worker's role will be one near the centre of the nest cleaning cells and feeding and caring for the brood, but it will slowly move to more peripheral activities such as receiving nectar, or guarding the nest. Ultimately it will take on the most perilous task of leaving the nest and foraging for food (Seeley 1985). A temporal phenomenon is also known to occur in slime moulds (McDonald and Durston 1984; Weijer *et al* 1984). Cells that start their period of starvation just prior to mitosis and cell division are those with stalk tendencies, and those that begin their starvation period just after cell division have a high probability of becoming spores. This is, of course, related to their nutritional state, while in the example we gave for insects the tasks performed are related to the internal physiological state of the worker which changes with age. It is not quite the same thing, but a time element in their division of labour plays a role in both cases.

A closer parallel with the "cell-time of starvation" situation in slime moulds may be found in the variation in the age of reproductive maturity in wasps (Gadagkar 1991b). The age at which a queen becomes sexually mature varies and this variation appears to be the result of differences in the nutrition of larvae of the future queens. This variation has important consequences for colony size because queens that mature early are more likely to exist a solitary queens and successfully raise a brood. The less well fed queens that develop slowly and have a delayed maturity are more likely to exist in a colony for they need helpers to ensure the survival of their offspring. Therefore, as in slime moulds, the nutritional state of the individuals has a profound effect on some aspect of the social state. In slime moulds it affects the probability of a cell becoming either a spore or a stalk cell; in wasps it affects the probability of the individuals being a solitary reproductive, or a worker or queen in a colony.

Let us return to the basic point of manipulation of one caste by another, generally by inhibition. A queen insect can produce a substance that either directly inhibits other females from becoming reproductives, as is found in termites, or it may inhibit the workers from forming large queen cells, as in honey bees. There are also examples among worker castes; termite soldiers produce an inhibitor that prevents other nymphs from molting into soldiers. If the soldiers are all removed from a colony, so is the inhibitor, and soon the worker-soldier ratio will be restored and maintained because the new soldiers will, in turn, produce an inhibitor. The mechanism was conclusively demonstrated by Light (1942, 1943) who removed the soldiers, ground them into a paste and fed them to the workers in the colony with the result that no new soldiers appeared at the next molt; the paste contained the inhibitor.

In slime moulds there is also evidence of chemical messengers that ultimately control the ratio of spore cells to stalk cells. The ratios of early cells with stalk tendencies and those with spore tendencies are very rough and there is ample evidence that a prestalk cell can be converted to a prespore cell and vice versa (Raper 1940; Sakai 1973). Even though the initial differences between stalk and spore may be influenced by nutrition and the time at which starvation sets in after feeding, the final ratio is established with considerable precision by chemical signal-response systems. Unfortunately we do not know the exact details of how this signaling system works—it is currently a subject of intensive research in a number of laboratories. Inouye (1989) has shown that prespore cells give off a substance, or substances that inhibit prestalk cells from changing into prespore cells. It is known that there is a substance called DIF [and there is some evidence that it is produced primarily by prespore cells that stimulates the initiation of stalk cell formation, or in other words, inhibits the anterior prestalk cells from becoming fertile spores (review: Bloom and Kay 1988; Nanjundiah and Saran 1992)]. Such inhibitors would seem to be an obvious analogue for a queen substance which inhibits other reproductives from appearing in social insect colonies.

Unfortunately, the problem in slime moulds is not so simple. There are a number of substances which act as morphogens and seem to play a role in determining the final proportions between stalk cells and spores. It is the relationship of these morphogens and how they interact which is drawing so much attention by workers in the field (review: Williams 1991). It would seem paradoxical that social insects, which are so complex and so advanced on an evolutionary scale, should have such a simple control system for inhibiting fertility, while the lowly slime moulds have a complex chorus of signals that together manage to control sterility in just the right proportion of cells. Why there should be such a difference is a puzzling question. Perhaps when all is known about slime mould morphogens, the final story will not be so complex as it appears at the moment, but that is no doubt wishful thinking.

One further point should be made on the matter of proportions. Wilson (1968) and Oster and Wilson (1978) have made the interesting argument that the proportions of different worker castes appear to be optimal to accomplish the task necessary to keep the colony in a prime competitive position. They call the analysis of energy efficiency by a division of labour, ergonomics. Some species of slime mould, of which *D. discoideum* is an excellent example, illustrate the point that in slime moulds the proportions of cell types might also be determined by efficiency or optimality. For the best possible dispersal of spores to new food patches it is presumed necessary to hold the spore mass as high up in the air as possible and to have as many spores as possible in the terminal sorus. One assumes that the existing proportions of stalk cells and spores achieve just such a balance: not too many sterile stalk cells to reduce the number of fertile spores, and not too few stalk cells so that the spore mass is in the most effective position to be touched by passing invertebrates.

In social insects there is evidence that genes have crept in which produce a bias both in sex determination and in some worker castes in bees (Kerr 1962; Kerr and Neilson 1966; Robinson and Page 1988). The idea is that the ancestral methods of sex and caste determination were totally non-genetic, but that if certain races or species of bees continuously favoured a bias towards a particular behaviour in

a caste, genes might arise that would reinforce the development of such behaviour, and there would be no selection to eliminate them.

If we look at slime moulds, there is no real evidence for a parallel phenomenon, but it is tempting to make a wild suggestion as to how the accumulation of new genes might play a role in slime moulds as well. We have emphasized how the variation in spore versus stalk cell tendencies is a phenotypic variation and is not only reversible, but the final fate of the cells appears to be determined by the spacing of various morphogens. This is the case for many species of the genus *Dictyostelium,* including *D. discoideum.* In the genus *Polysphondylium* the situation is quite different (figure 5). There is no evidence for any preliminary prestalk and prespore zones—all the cells in the rising cell mass have a prespore character, and conversion to prestalk and stalk cell occurs only at the very tip of the rising cell mass (review: Schaap *et al* 1985). In this case it seems hard to imagine any phenotypic variation being directly responsible for the difference in the proportions of the two cell types for it is only the cells at the tip that turn into stalk cells, and this last minute conversion occurs at a specified time (or when a specific ratio of mature stalk and prespore cells) has been reached. The constants are two-fold: one is the stopping of the formation of the stalk at a particular time (or geometry) and the other is the budding off of masses of prespore cells at regular intervals that can subsequently break up into whorls of branches, each one of which is a miniature fruiting body formed in the same way the apical stalk and sorus is formed. From the work of Cox and his collaborators (Cox *et al* 1988; Cox 1992; Vocke and Cox 1992) we know that many aspects of the symmetry of the budding and branching of the whorls can be explained in terms of turing type models involving activators and inhibitors, but as far as the differentiation is concerned it seems to be far more rigid and fixed than is found in those species of *Dictyostelium* that have been studied. The suggestion then, is that in *Polysphondylium* there has been a progressive accumulation of pattern genes which appear to depend much less on phenotypic variation than is the case for *Dictyostelium.*

It should be added parenthetically that there is the unanswered problem of *Actyostelium,* the small and delicate species that has only one cell type that performs all functions (Raper 1984). First all the cells secrete an acellular stalk tube, and then all the cells turn into spores (figure 6). Is this a descendent of *Polysphondylium,* for it seems to be even more rigidly, genetically programmed, or is it an ancestor so primitive that it lacks any division of labour? This is a question that perhaps how it will be possible to answer when the phylogeny of the various species of slime moulds are analysed using molecular methods. The only thing that is clear is that there are niches which exist today for small, simple forms and large complex forms. In the case of both social insects and social amoebae there must be a selection for both ends of the size-complexity spectrum, as well as for the intermediate forms.

3.6 *Recognition stage in amoebae*

Once social grouping was established in the evolution of social insects there entered a "recognition stage" in which the genetic advantages of kin selection began to play a part. As we saw this is especially important in the haplodiploid Hymenoptera

in order to insure that sterile individuals benefited from helping their nest mates even though they themselves could only have offspring and perpetuate their genes directly. They could only do this by caring for those individuals with whom they shared many genes. The closer the relatedness, the greater the possibility of the genes of sterile individuals being passed on. One way to ensure that one helps kin and not total strangers is to have some kind of recognition system. In social insects this is largely by nest odors; a particular colony will have its characteristic odor and any individual from an foreign nest will not be allowed to enter.

In slime moulds relatedness usually not a problem. As already pointed out, it is possible to have a fruiting body made of genetically identical cells and this must occur quite often in nature in the soil. It is equally likely that in nature cells of different strains might co-aggregate in which case there will be a mixture of genotypes. But the extent of that mixture has strict limits, and even in any one species there may be strains that will not form mixed or chimaeric fruiting bodies; there is some form of reconginition in the slime moulds.

This was illustrated dramatically in some old experiments of Raper and Thom (1941) who mixed two closely related species together (and the same phenomenon can be shown between strains of a single species). They used a species with purple spores and one with white spores which co-aggregated to form central collection points, for they had the same chemoattractant (in this case cyclic AMP) but after a period of time the centre divided into two, producing two fruiting bodies side-by-side. One had a purple sorus and the other one was white; the amoebae in the centre sorted out, and because of selective adhesion, combined with their own kind, as they milled about in the cell mass. This is a clear case of recognition in the slime moulds. In species that are distantly related they even have different chemicals for their aggregation chemoattractants (or acrasins) and so they avoid mingling by being unable to aggregate to a common centre. Therefore there are two ways of maintaining isolation between species and strains, which is the opposite way of saying that they recognize kin.

3.7 *Demographic factors in social amoebae*

There is no exact equivalent among social amoebae to assured fitness returns in social insects where the success of reproduction of a solitary queen wasp depends on whether she survives the period of brood care or not (Gadagkar 1990a). For this reason the continuous presence of workers assures that the brood reaches maturity even in the event of the queen's premature death. In slime moulds there is no brood care, but on the other hand there is an analogy to the assured fitness returns of insects. Consider the probability of a one-spore fruiting body dispersing to a distant food patch to be equivalent to the probability of a solitary queen wasp living as long as it takes to raise its young. Then the probability of any one spore encountering a food patch would be greatly increased if there were many spores together, just as in the wasp when there are many workers to see that the young come to maturity. For both there is a safety in numbers, and for both this is a strong reason for selection favouring a group effort. Furthermore, as with demographic factors for social insects, this advantage in numbers plays a role from the simplest amoeba colonies to the most complex dictyostelids (figure 3).

3.8   *Another similarity and some differences between social insects and social amoebae*

It is important to mention an obvious difference between insects and slime mould societies. The former are sexual and the progeny within the colony are the offspring of a female, while in slime moulds we have been describing an asexual cycle, which is the reason they can be clonal. Dictyostelids also have a sexual cycle, but it is infrequent and is not associated with a social phase. This difference in the sexuality of the two societies is a secondary issue, but important to keep in mind.

There is, however one way in which they can both reproduce in an asexual fashion, for they are both capable of fission. In insects, especially in bees and wasps, there may at one point be more than one queen. These will ensure a great popularity contest between two queens, and one will fly away with a large entourage of workers, leaving the other queen with its followers in the old hive or nest. This is the normal mode of founding new colonies in honey bees and may be adopted occasionally by primitively eusocial species to reduce aggression from reaching levels that become detrimental to efficient brood rearing *(e.g.* Gadagkar and Joshi 1985). In slime moulds it is a common observation to see a migrating slug "twin", The dominant tip will suddenly split into two, and the amoebae that follow will slowly separate into two halves each following one of the leading tips to make two, smaller migrating slugs. The only difference is that in the insect fission, both colonies will continue to produce offspring and enlarge. In the slime moulds, where growth occurs first before aggregation, the fruiting bodies that result from the fission will merely have half the number of spores; there is no further cell proliferation. But nevertheless both societies are capable of asexual reproduction by fission.

There is one big difference between social insects, and slime moulds. Because growth occurs first in solitary amoebae and this is followed by the social phase, the cells cannot help one another in any way other than by forming fruiting bodies. In insects the workers can continuously help in all the tasks of the colony, from feeding the larvae to foraging and all the other jobs that need doing for the growth of the colony. So their contribution is a non-stop process in which there can be a series of workers successively taking over the functions of one another. This leads not only to reproductive success as discussed above, but also to a long life of the colony. In cellular slime moulds the life history is episodic; a fixed period of growth followed by a fixed period in which the labour is divided, with the fruiting body representing a terminal, static, resting stage,

Yet another important difference between them is the difference in the external forces that are selecting for a social existence. In wasps no doubt a combination of protection of the young and an added reliability in providing food for them were the ultimate reasons why they became social. In the case of slime moulds the prime reasons for coming together to form a fruiting body is most likely to help in the dispersal of the spores (although it is also possible that some protection may be involved, by isolating the spores from toxic substance in the substratum), The main reason that selection acts in such different ways on these two groups of organisms has to do with the radically different life cycles. However, the fact that selection for a social existence is so different between the two does not affect the fact that there are some striking and interesting similarities in how they became social.

A final point should be emphasized, which again stresses a difference rather than a similarity between the two societies. It is the question of what are the units of selection, In the case of social insects it has been recognized since the ideas expressed by Darwin (1859), that the colony is the unit of selection. The fertilized queen is the sole source of zygotes and offspring for the succeeding generations, and all the sterile workers are essentially non-reproductive members of her family. It is this point that stimulated W M Wheeler to write his famous essay, *The Ant Colony as an Organism* (1911) in which he compared the queen to the germ plasm and the sterile workers to the soma. Even though this is true, it is clear from the ideas of Hamilton (1964) that the individual insect is also a unit of selection, for each worker, as well as the male and the queen, is promoting its genes. This means, as Dawkins (1976) expressed so eloquently, that the genes are the ultimate units of selection; it is their survival in the last analysis, that is the crux.

In the slime moulds, there are only two levels of selection: the genes and the individual amoebae, Even though stags and fruiting bodies behave like multicellular organisms, they do not pass through a stage with a single zygote—the infrequent sexual cycle involves the simple fusion of separate, isolated amoebae. However, it could be argued, as Nanjundiah (1985) suggests, that whole fruiting bodies, which are populations of amoebae might be capable of group selection, providing a possible third level of selection,

4. Conclusion

As said in the beginning, the similarities, and even the differences, between insect and amoeba societies, give insights both ways, as is so often the profit gained from comparative biology. There are many points of interest, but perhaps the most valuable lesson is that the ideas of bow insect societies arose in the first place during the course of evolution might also apply for social amoebae. There first must be a stage in which grouping increases reproductive success, and this is followed by clever devices to improve that success so that the reproduction in the group can be increasingly efficient. Yet in both societies it must always be remembered that the niches for groups of intermediate sizes and intermediate complexity—even niches for solitary individuals—do not disappear. Rather than successively supplanting niches, increases in the elaborateness of the societies has meant an increase in the number of niches.

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