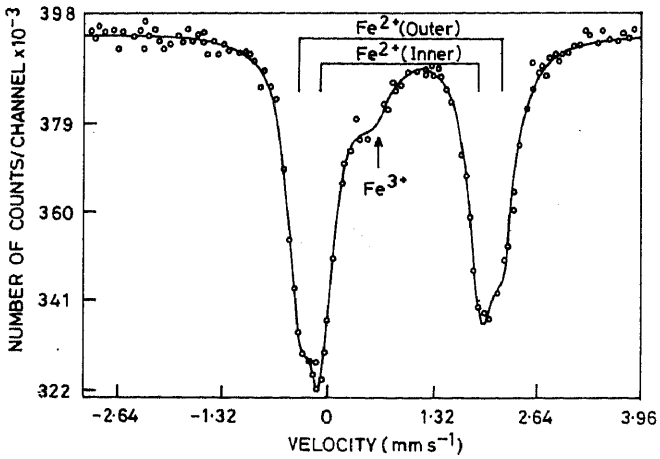


**Figure 5.** Mössbauer spectrum of terrestrial augite sample at 300 K (ref. 4).

assuming that the '*f*-fraction' (recoil free fraction) for pyroxenes in both the types is the same (which is generally the case).

The ratio of $Fe^{2+}$ inner/$Fe^{2+}$ outer is dependent on the geothermal history of the pyroxene[16]. Table 1 shows that the $Fe^{2+}$ inner/$Fe^{2+}$ outer ratio for rock type A is 3.28 and for rock type B is 2.47. It shows that rock type B has more equilibrium distribution and must have undergone slow cooling in comparison with the fast cooling of the rock type A. The conclusion is in accordance with the interpretation in the text.

The fine-grained texture of rock type A is evidence of fast cooling in comparison with the medium-to coarse-grained texture of rock type B showing slow cooling.

A $Fe^{3+}$ doublet of weak intensity has been fitted in the Mössbauer spectra. This peak could have been due to the change in the oxidation state of $Fe^{2+}$ in the meteorite itself because of shock phenomenon. However, this assignment should be considered with caution because the intensity of the doublet is quite weak.


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# Altruistic behaviour in *Dictyostelium discoideum* explained on the basis of individual selection

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**It is often argued that natural selection acting at the level of the individual may not be sufficient to explain the evolution of altruism. We suggest that before accepting such a point of view in any specific instance, the parsimonious course would be to examine all possible ways in which individual-level selection might act and rule out its sufficiency only when the postulated means for its action are either inherently improbable or experimentally disproven. As an illustration we propose an evolutionary model, based on the individual cell as the unit of selection, for the maintenance of 'altruistic' behaviour by pre-stalk cells in the social amoeba *Dictyostelium discoideum*.**

EVOLUTION by natural selection proceeds via the accumulation of successive adaptations that serve to increase the reproductive fitness of an individual measured over its lifetime. Obviously, traits that appear to be detrimental to the fitness of an individual but advantageous to another individual – or to a group – are difficult to reconcile with this view of natural selection. It has been proposed that in order to explain the existence of such traits, one may need to invoke the action of selection at the group, meaning supra-individual, level. Group selection can work in two ways. It may operate directly, between groups[1], or indirectly, within groups – thereby superficially resembling individual selection –, when the groups contain individuals with a significant degree of

tion in *D. discoideum*[21], but aspects of its methodology make interpretation somewhat difficult: the authors take the ratio of sorus diameter to stalk height as a measure of the ratio of spore to stalk numbers, and this may not be a good approximation when the stalk is more than one cell thick. In contrast to these earlier models, we now proceed to argue in favour of the proposal that the seemingly suicidal behaviour of pre-stalk amoebae may have a conventional, Darwinian (meaning, individual selection-based) explanation. Under laboratory conditions, *Dictyostelium* aggregations are commonly clonal; but the average degree of relatedness within aggregations in the wild is unknown. Therefore, quite apart from the fact that a high degree of genetic relatedness *per se* would not argue against individual-level selection, the relevance of kin selection in the wild remains a moot question. However, as will be made evident, the reasoning that we use remains valid irrespective of the degree of kinship.

*Dictyostelium* amoebae emerge from spores, go through a phase of feeding and cell division via mitosis, and proceed to aggregate once the local food supply is exhausted[11]. Our central assumption is that at the time of aggregation there are cell-to-cell variations in phenotypic quality. By quality we mean a parameter that is related to individual fitness; for example, quality may be measurable in terms of the level of metabolizable sugars accumulated by a cell during feeding[22,23]. Quality is, firstly, a relative measure. Secondly, it varies from one cell to another in a quasi-continuous manner. However, for the sake of simplicity we assume that cellular quality can have just two (relative) values. Thus there are high quality (HQ) and low quality (LQ) cells. Our basic contention is that phenotypic selection will ensure that HQ cells stand a high chance of sporulating whereas LQ cells have a low chance of doing likewise. It is evident that such an outcome is intrinsically stable. Genetic differences need not come into the picture at all: obviously, quality may have a genetic component, but as far as the theory goes the cells could be genetically identical. We point out that there is experimental support for a functional non-equivalence between pre-aggregation amoebae as assumed here[12].

A second assumption is that amoebae can assess each other's quality by means of intercellular signals. Signalling may either precede aggregation (for example, via Conditioned Medium Factor, CMF; ref. 24) or follow aggregation (for example, via cyclic AMP; ref. 25 or via Differentiation Inducing Factor, DIF; ref. 26). HQ cells proceed to differentiate along the pre-spore pathway and also attempt to coerce LQ cells to adopting the pre-stalk pathway. The metabolite DIF may be an agent of coercion (see below). The options open to LQ cells are severely restricted. They can choose to stay out of the aggregate and remain solitary, but if they do so they are certain to die[27]. Alternatively, they can join the aggregate and cooperate with pre-spore cells to begin with, all the while exploring opportunities to escape what appears to be their fate and survive, perhaps eventually sporulate. The probability of succeeding in the enterprise is small but not zero: there is evidence that spores can arise from amoebae in which pre-stalk-specific genes were previously expressed[28]. Also, undifferentiated amoebae have been reported in the spore mass and may be a second kind of 'escaper' pre-stalk cells[29,30]. In any event, LQ cells will favour the pre-stalk option even when by doing so their chances of survival are infinitesimal, because the other option – not to aggregate – results in certain death.

DIF (a doubly chlorinated hexanone; ref. 31) and closely related compounds with similar effects are produced by amoebae after aggregation and act as cellular poisons[32]. In low-density assays they cause cells to die and become stalk-like[33]. Curiously, while it is the pre-stalk cells that die and pre-spore cells that give rise to the next generation, the level of DIF is higher in pre-spore cells than in pre-stalk cells[34]. In terms of physiology, the reason behind this is that pre-stalk cells make an enzyme, DIF dechlorinase, that breaks down DIF[26]. But in terms of group (or kin) selection, this does not make sense. Why should pre-stalk cells actively lower the level of a metabolite that is pushing them further, as it were, along the pathway of altruism? On the other hand, individual level selection would suggest that pre-stalk cells (being of relatively lower quality) are inherently more susceptible to DIF than pre-spore cells. Therefore, whereas pre-spore cells are able to continue on the pre-spore pathway in the face of a high local concentration of DIF, pre-stalk cells need to take active steps to break it down in order to prevent early death. Loomis[36] and we[30] have discussed models for pattern formation involving intercellular interaction based on assumptions similar to the ones made here (in particular, Loomis suggests that pre-spore cells may be more resistant to DIF than pre-stalk cells). Recent evidence indicates that there is a heterogeneity even within the pre-spore class; only some pre-spore amoebae exhibit a transient shift to the pre-stalk class (in the sense that their level of intracellular calcium increases) upon stimulation by DIF[35].

A number of testable inferences follow from our model. The existence of a cell-to-cell variation in quality can be tested by sorting presumptive stalk and spore cells at the pre-aggregative stage and probing individuals from each class in respect of fitness-related variables. If the (internal) nutritional reserve available when (external) food supply runs out is a measure of cellular quality, and if DIF plays the role that we suggest it does, one would expect that there is both a higher level of DIF, as well as a greater resistance to DIF, in amoebae grown on a rich medium when compared to amoebae grown on a poor medium. Finally, if DIF acts like an intercellular poison, as it appears to, the operation of individual-level selection would imply that its use as a poison must be a side effect. The primary reason why DIF is made by individual cells would be for their own direct benefit. For, suppose the sole use of DIF was as

genetic relatedness. In the latter situation, known as kin selection, kinship makes it possible for the fitness of either of two interacting individuals to be greater than that of the same individual in the absence of interaction[2]. This is because kinship leads to an increase in the probability that both of them carry copies of one or more genes for promoting altruism that are identical by descent. Thus, although an individual may choose to reduce the number of offspring that it has, it may nevertheless benefit genetically if it thereby enhances the reproductive fitness of the second individual to a sufficient extent. Here 'sufficient' means that after devaluing for the coefficient of genetic relatedness, the first individual leaves behind more copies of its genes (albeit indirectly) than it would otherwise. Then, the frequency of an 'altruistic' gene can increase in time and the gene can spread through the population. Indeed, it is often held that such a gene's eye-view is the correct way to think of all evolutionary adaptations, whether in solitary organisms or in social groups[3]. In an extreme situation the first individual may forego reproducing entirely and yet the trait may persist successfully through generations.

Although sound in principle, the concepts of group selection and kin selection have problems in practice[4,5]. Group selection involving non-kin demands special population structures that may not always exist, and explanations based on kin selection can flounder if genetic relatedness is not as high as is demanded by theory[6]. Besides, both models, as well as those based on 'reciprocal altruism'[7], are potentially unstable[8]: they are susceptible to exploitation by 'cheaters', individuals whose contribution to the group is in some sense lower than the benefits they derive from the group. Therefore groups also need to possess the ability to detect cheaters and nullify their effect. The inherent instability of group selection (in which term we also include kin selection) makes it a matter of paramount importance to push arguments based on individual-level selection to their logical conclusion. Except when it can be shown to be inherently improbable or experimentally disproven, such an undertaking has two merits. One, it forces us to think of all possible routes whereby the expected lifetime reproductive success of an individual might be enhanced. And two, it opens up a far richer picture of the evolutionary process for subsequent analysis and testing than a group-selection explanation does; see ref. 9 for an example. We now develop this thesis for the case of division of labour in *D. discoideum*.

But before doing so, it might help to reiterate the essential operational differences between the various models for the evolution of sociality listed above. These differences pertain to the calculation of fitness. For illustrative purposes, let us imagine that we are dealing with a pair of interacting individuals at a time and are comparing expected values of lifetime fitnesses between two situations, one in which cooperation (apparent altruism) is exhibited and the other in which it is not. In a group selection model the average fitness of the pair increases by virtue of altruism. Reciprocal altruism guarantees that each individual gains by cooperation, but only if reciprocity is assured. With kin selection each member of the pair benefits by cooperation because it shares genes with the other (the relevant measure of fitness being inclusive fitness). And under all three schemes a prospective cheater gains most of all unless appropriate counter-measures are implemented. On the other hand, in an individual selection model the only relevant parameter is the intrinsic phenotype of the individual. Given differences in phenotype, reproductive fitnesses will also differ. There is no question of a cheater exploiting the situation because a prospective cheater will also have to take its place, so to speak, in the phenotypic hierarchy – which is equivalent to a fitness hierarchy.

The Dictyostelid slime molds, of which *Dictyostelium discoideum* is the best-studied species, are among the most primitive examples of social organization[10]. Unicellular amoebae aggregate to form a colony within which division of labour takes an extreme form: one subset of amoebae dies and forms a rigid, upright stalk and the other subset forms a ball of spores above the stalk[11]. By making use of a variety of criteria based on staining with vital dyes[11], fluorescence-activated cell sorting[12] and patterns of gene expression[13] it is possible to distinguish between pre-stalk and pre-spore amoebae. Also, the two presumptive cell types are spatially segregated: in the migratory, slug-shaped stage of development that the aggregation goes through, pre-stalk cells occupy approximately the anterior fifth and pre-spore amoebae the posterior four-fifths[14].

After differentiating into spores, pre-spore amoebae come to lie on top of the stalk, meaning at a height above the level of the substratum. It seems reasonable to assume that spore fitness is enhanced thereby, because elevation should improve the chances of successful spore dispersal. On all grounds the pre-spore strategy makes obvious reproductive sense. On the contrary pre-stalk amoebae appear to exhibit altruistic behaviour because in the course of improving the chances of spore dispersal and so increasing the fitness of pre-spore amoebae, their own direct reproductive fitness is reduced to zero. It has been questioned whether such altruistic traits can be accounted for on the basis of individual-level selection (see, for example, ref. 15).

Previous attempts to explain the evolution of sociality in the cellular slime molds have made use, either implicitly or explicitly, of group selection or kin selection arguments[16–19] or have used Evolutionarily Stable Strategy-based reasoning[20] that gives rise to a situation that is also unstable with respect to exploitation by cheaters. There is one experiment that seems to favour kin selec-

an agent of coercion against other cells. In that case it would be a metabolic saving, and so of selective advantage, to a pre-spore cell to derive the benefit of the DIF made by other pre-spore cells but to make none itself. Thus a putative 'cheater' pre-spore cell that derived the benefits of the DIF made by many other pre-spore cells, but made none itself, would be selectively favoured over the rest. Of what direct benefit might DIF be? One possibility is that DIF protects individual amoeboe or spore cells from microbial attack. It would be worthwhile to look for the presence of DIF in spores. These experiments are currently underway.

In conclusion, we point out that *D. discoideum* by no means exhausts the enormous range of developmental strategies that are seen in the Dictyostelids and their relatives[10,16]. There are species in which a single amoeba can sporulate, species in which the stalk is an extracellular product and species in which cells die and produce a stalk continuously during the course of migration. A careful and detailed study of each case will be needed before we can similarly attempt to explain its evolutionary origins on the basis of individual-level selection.


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# Possible evidences of animal life in Neoproterozoic Deoban microfossil assemblage, Garhwal Lesser Himalaya, Uttar Pradesh

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**An exceptionally well-preserved microfossil assemblage comprising bacteria, cyanobacteria, algae, fungi, acritarchs and forms exhibiting rather complex/unusual morphology from the black-bedded chert of the Deoban Formation (Garhwal Lesser Himalaya) points to a complex ecosystem of the Neoproterozoic times. The Deoban assemblage is interpreted to have been preserved in the algal-mat facies. Of special interest in this context is the discovery of three problematic forms of questionable affinity. These are comparable to the members of Nematoda and Annelida phyla of the animal kingdom. This suggests that the advent of heterotrophy among animals in its incipient form started in Neoproterozoic which ultimately facilitated the evolution of more complex and advanced communities of multicellular organization in later geological times.**

THE late Proterozoic life is represented by Ediacaran soft-bodied animals, acritarchs, prokaryotes, eukaryo-