



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 pyroxene¹⁶. 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 groups¹, 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 exhausted¹¹. 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 here¹².

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 die²⁷. 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 expressed²⁸. 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 poisons³². In low-density assays they cause cells to die and become stalk-like³³. 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 cells³⁴. In terms of physiology, the reason behind this is that pre-stalk cells make an enzyme, DIF dechlorinase, that breaks down DIF²⁶. 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. Loomis³⁶ and we³⁰ 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 DIF³⁵.

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

