

Supporting Information

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SI Text

Possible Advantages of Indigestion

Because the crucial argument against early phagocytosis is questionable, we are free to return to the idea of early phagocytosis. In this context, it must be stressed that, in the recent scenario, no full-blown archezoan-type cell is imagined. The critical transitional form is the very origin of rudimentary phagocytosis (figure 2b in ref. 1), still without many of the known cell organelles, such as the nucleus. This transitional form could well have been sustained by a genome in the higher prokaryotic range, while already providing the ecological benefits of internal digestion. The question we still have to discuss is the initial advantage. The final advantage is of course ATP production, but the ADP/ATP antiporter is a eukaryotic invention, the emergence of which must have taken some time. So unless some benefit from the promitochondrion to the urkaryote (mutualist transitional forms) could have been provided, the initial symbiosis was endoparasitic, which would have meant another burden for the fragile transitional prokaryote. In other words, cells without the protomitochondrial indigestion would have been better off, especially because, in this picture, the protomitochondrion would have been obligatorily endosymbiotic, so evolution could not have been driven by parasitic selfishness with frequent horizontal transfer between hosts. There are two possible ways out. Because mitochondria seem to descend from α -proteobacteria, protomitochondria could have still been photosynthetic. Some of these bacteria are known to eject photosynthate into their environment, which could have benefited the prokaryote (2). Another (not exclusive) way out is farming/prudent predation of protomitochondria (3). Interestingly, there exists today a similar phenomenon in the social amoeba *Dictyostelium* (4) although there the bacteria are carried extracellularly by the multicellular slug and fruiting body. In the case of the protoeukaryote, the symbiont would have been intracellular private property, and it would have been inherited through division.

Replicators Versus Reproducers

Griesemer (5) insightfully analyzes the problem of transitions in the light of the problem of reproduction. Compare replication by photocopying of a sheet of paper with, say, bacterial reproduction. As we have seen, a cell is a collectively autocatalytic system. DNA is an autocatalyst in need of obligatory heterocatalytic aid by proteins. The photocopier is not part of such a collectively autocatalytic system. This observation relates to the problem of whether viruses are alive or not. My resolution is that there are units of evolution and units of life, and, between these sets, the overlap is large but not complete (6). Viruses are, in this

light, only units of evolution. Or, as others would say, autonomous living systems (7) can propagate only through reproduction: replication is necessary but not sufficient. In Gánti's minimal life model (8), there are three autocatalytic subsystems: (i) a metabolic network, (ii) template replication, and (iii) a growing boundary. This chemoton model shows perhaps what Griesemer's reproducer is. "Special or developmental progeneration is multiplication with material overlap of mechanisms conferring the capacity to develop. Development is acquisition of the capacity to reproduce. Reproduction therefore, is progeneration of entities that develop. Because development is analyzed in terms of the capacity to reproduce and progeneration transfers the capacity to develop, reproduction can be understood as the recursive realization of the capacity to reproduce. The capacity to reproduce is the capacity to progenerate entities with the capacity to acquire the capacity to reproduce. Reproduction requires both progeneration and development" (ref. 9, p. S361). It is in this sense that Szathmáry and Maynard Smith (10) adopted the view that evolutionary transitions can create new levels of reproduction.

The Confrontational Scavenging Scenario

Although animal communication systems do exist (11), they mostly include self-regarding signals about things here and now (12). Natural language is very different: There is a lot of displacement (referring to items that are not present now or are purely imaginary), and it is full of symbolic (arbitrarily conventional rather than indexical or iconic) reference, aided by complex syntax. No other species comes nearly close to such a synergistic package, the origin of which we need to explain. This transition happened in early *Homo erectus*, who faced the problem of starvation due to the disappearance of fruits in that period. There was, however, plenty of meat around, including carcasses of the megafauna. Whereas weapons of the time were not good for hunting elephants or rhinos, they were sufficient to butcher carcasses that rival predators were unable to access before the carcasses exploded. To use this resource, three crucial actions are needed: First, members of the group who cannot know about the carcass must be informed about its nature, location, and distance; second, they need to be recruited; and, third, execution of the task requires intense cooperation with limited opportunity to cheat. The work consists of fighting off the predators around, butchering, and transporting home the carcass. It was this niche that allowed a wedge to penetrate the previous animal communication system by signals for displaced items. Given the fact that by then *erectus* had already had a large brain and was very likely equipped with Machiavellian social intelligence (13, 14), the process did not stop there, and protolanguage with increasing richness of symbolic reference started to evolve, to be followed by syntax that presumably emerged with the speciation of *Homo sapiens* (12).

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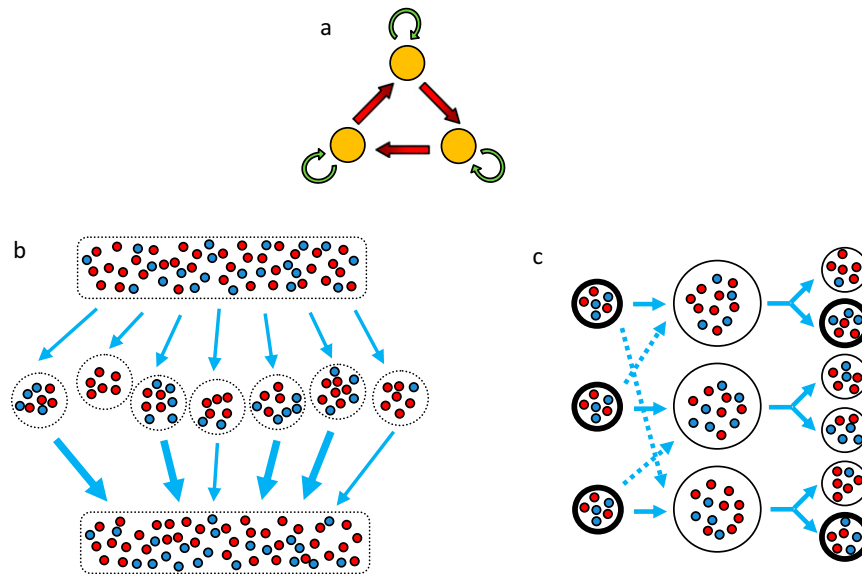


Fig. S1. Replicator topologies and forms of multilevel selection (MLS). (A) There are three different information carriers. Green arrows stand for autocatalysis, and red arrows depict heterocatalytic aid. Without the green arrows, we have a collectively autocatalytic system whose members are not replicators (1–5). With all of the arrows, we see a hypercycle of replicators (6). Both systems are ecologically stable, but, without some multilevel selection, the hypercycle is evolutionarily unstable. (B) Multilevel selection of the first type (MLS1), where the focal units are the different (red and blue) replicators, and transient groups provide the context of selection (7–11). Suppose that red replicators are faster than blue ones, but groups with more blue replicators produce more particles. There is an equilibrium frequency in the global population of altruists and selfish replicators, even with random group formation, if the altruists pay a relative cost (they help the reds more than themselves). [A difference between many of the cited models and the original trait group model of Wilson (10) is that, in the former, more than one round of reproduction within a group is possible.] (C) In multilevel selection of type 2 (MLS2), the groups are bona fide evolutionary units that multiply and show hereditary variation with fitness effects at the collective level. In the stochastic corrector model (12, 13), the two different types of replicator complement each other synergistically, but there is also intragenomic conflict: Reds replicate faster than blues. Nevertheless, group selection among protocells can maintain a stable population. An Eigen equation at the compartment level can thus be derived, where the mutation terms correspond to the change in gene composition between parent and offspring, due to internal competition and stochasticity. The construction is, unlike many others, fully analytic. Variation is generated by demographic stochasticity in protocells and the chance assortment of replicators into offspring cells. This model is a prototype of how MLS2 can treat egalitarian transitions, including the origin of simple and, later, eukaryotic cells. Note that there was some inconsistency in treating such transitions in the original publications about major transitions. Whereas generally a kin selectionist view was endorsed (12, 14), in some cases, it was complemented by true multilevel selection (*Bottom*, MLS2). Replication of genes and reproduction of protocells are not synchronized, time is continuous, and generations overlap. The model is set up in such a way that protocells reproduce when the total number of genes reaches a threshold. Thus, upon division, each protocell contributes the same number of particles (genes) to the population. However, because of the effect of genes on metabolism, collectives (protocells) with more balanced gene content reproduce faster. Such cells contribute more particles, as well as protocells, per unit time to the population.

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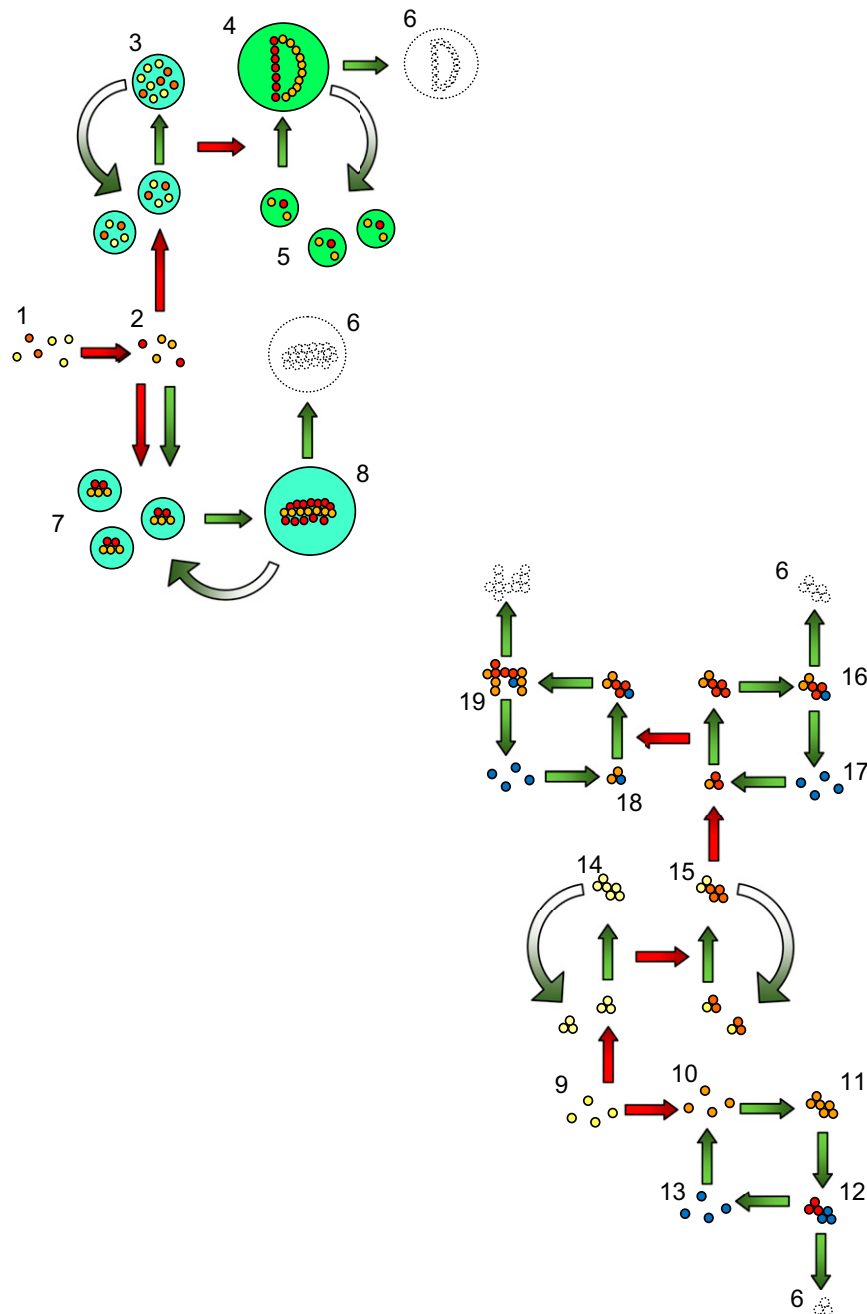


Fig. S2. (Egalitarian and fraternal) \times (cohesive and aggregative) origins of higher-level evolutionary units, exemplified by the origin of multicellularity. Green arrows stand for lifecycle transitions, and red arrows indicate evolution. (*Top*) Egalitarian transitions. The cohesive route: different replicators interact (transition 1) in an MLS1 manner, which results in a coevolved set (transition 2), which then can be encapsulated in a common reproducing unit (transition 3) that may evolve into a morphophysiologicaly complex organism (transition 4), possibly producing propagules of different size (transition 5) and possibly dead bodies (transition 6). The aggregative route: different units may optionally reestablish the higher-level unit repeatedly (transition 8) that may produce propagules of different size (transition 7). (*Bottom*) Fraternal transitions. Units of the same type (transition 9) may follow different evolutionary routes. The aggregative route: units can evolve into populations of interacting (transition 10) and aggregating (transition 11) cells that can differentiate to establish reproductive division of labor (transition 12) and produce unicellular propagules (transition 13). The cohesive route: a blob of cells may stay together (transition 14) and reproduce by fragmentation. This form may evolve some cell differentiation, maybe based on location in the clump (transition 15). Further evolution can produce larger, differentiated bodies (transition 16), with late sequestration of germ cells that produce unicellular propagules (transition 17). However, further evolution yields early sequestration of germ cells (transition 18), which allows the evolution of even more complex organisms (transition 19).