

obligatory mutualists¹. Dedeine *et al.* report that, in the hymenopteran parasitoid *Asobara tabida*, eliminating *Wolbachia* inhibits oogenesis, resulting in sterility. We see two possible evolutionary scenarios to explain this phenotype.

A first possibility, considered by Dedeine *et al.*, is that *Wolbachia* became involved in oogenesis and a loss of host function followed, rendering *Wolbachia* indispensable to reproduction. *Wolbachia* would have crossed the border that separates reproductive parasites from true mutualistic symbionts, which actively contribute to host physiology.

Another interpretation is the following. Consider a *Wolbachia wA* that induces CI (allowing it to invade a host population), but which has an imperfect maternal transmission (i.e. infected females fail to transmit bacteria to some of their offspring). Consider now a mutant *wB*, which occurs within a host population infected with *wA*, and which expresses both a poison that inhibits oogenesis, and its antidote. Infected females

are protected from the poison. However, uninfected daughters from infected mothers are sterile. Biochemically, this would imply: (1) that the antidote has a more rapid turnover than does the poison (the poison is still active when the antidote is absent); and (2) that the poison induces epigenetic modifications of gene expression (e.g. alteration of chromatin structure) so that its effect can be maintained after the active molecule has been lost. Such a trait can be selected for if the host population is structured sufficiently so that larval competition between the offspring of closely related females is more likely than that between unrelated females. In such a situation, having sterile sisters would be advantageous. The trait will approach neutrality as the population structure decreases. Consequently, *wB* becomes fixed either by selection (strong population structure) or by drift (weak population structure). If this happens, the host population can no longer eliminate *Wolbachia*, even if CI is lost: uninfected females, occurring through imperfect transmission, are all sterile. Under

such a scenario, Dedeine *et al.*'s results illustrate a fifth *Wolbachia* reproductive manipulation, imposing a no return situation, which could be termed 'sterilization of aposymbiotic sisters' (SAS).

The mutualism and SAS hypothesis can be tested experimentally using *Wolbachia* injections into a novel host species. Under the mutualistic hypothesis, the response to *Wolbachia* elimination is presumably host specific: *Wolbachia* in a novel host should not be necessary to oogenesis. Conversely, under the SAS hypothesis, the poison-antidote system could be expressed in a new host, and uninfected daughters from infected mothers would be sterile.

1 Dedeine, F. *et al.* (2001) Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in a parasitic wasp. *Proc. Natl. Acad. Sci. U. S. A.* 98, 6247–6252

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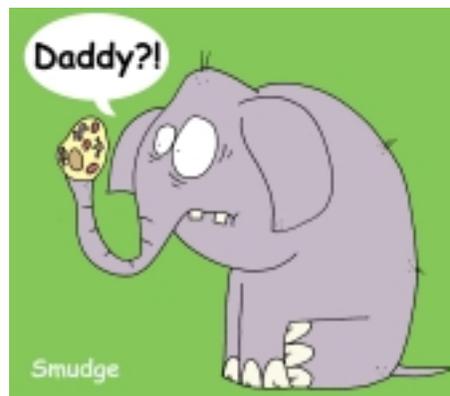
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The evolution of individuality and conflict mediation

Understanding how multicellular organisms evolved from unicellular forms is fundamental to our comprehension of evolution. But, apart from the enthusiastic reception given by evolutionary biologists to the books by Buss (1987) and Maynard Smith and Szathmáry (1995), the formative role of this transition has received little attention. However, new models, recently developed by Michod and Rose¹, which highlight the important role in evolution of the transition from selection at the cellular level to selection at the level of the multicellular individual, will hopefully attract the attention of 'evo-devo' scientists to this fundamental area of research.

The models support the hypothesis that increasing cooperation between cells, together with the emergence of conflict mediation between cells, was crucial for the evolutionary transition from cells to multicellular individuals. Furthermore, these models predict an even larger role for conflict mediation during the evolution of organisms with macroscopic body plans and of organisms with maximal indirect development [the development of the adult body plan from undifferentiated set-aside cells (sacs) that are separate from the cells that form the larva]. To control potential conflict between cell lineages (based upon the



proliferative ability of sacs) that might lower the fitness of the individual, Michod and Rose's models predict the evolution of novel or stronger mechanisms of conflict mediation concomitant with the origin of sacs.

Michod and Rose, following Blackstone and Ellison², suggest that germ-line sequestration might be the requisite novel conflict mediator that limits the accumulation of heritable mutations in multicellular organisms as sacs continue to divide in the formation of the adult body plan. Both studies cite research by Ransick and co-workers³ that supports the predicted correlated occurrence of sacs and germ line sequestration in extant animals. Perhaps unsurprisingly,

co-occurrence does occur. Germ-line sequestration is widespread among bilateral organisms and is only absent in animals that are capable of vegetative propagation. In most directly developing bilateral organisms, germ-line sequestration occurs even earlier than in maximally indirect developing organisms. Nevertheless, the co-occurrence is in agreement with the models of Michod and Rose.

As with all hypotheses about the evolutionary past, designing suitable tests is difficult. We hope that Michod and Rose's article will stimulate the design of more powerful tests that will aid our understanding of the evolution of multicellular organisms.

1 Michod, R.E. and Rose, D. (2001) Cooperation and conflict in the evolution of multicellularity. *Heredity* 81, 1–7

2 Blackstone, N.W. and Ellison, A.M. (2000) Maximal indirect development, set-aside cells, and levels of selection. *J. Exp. Zool.* 288, 99–104

3 Ransick, A. *et al.* (1996) Postembryonic segregation of the germ line in sea urchins in relation to indirect development. *Proc. Natl. Acad. Sci. U. S. A.* 93, 6759–6763

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