

Asexual Evolution: Can Species Exist without Sex?

Most explanations for the existence of species involve a role for sex. A new study of a group of asexual rotifers supports the idea that selection for a common ecological niche can produce a pattern that mimics sexual species, even in the absence of sex.

David M. Hillis

Biological diversity is not organized in a continuum. When we think of the Tree of Life, we envision the discrete, individual branches of the tree (the species), as well as the larger groups of related branches (the clades). The fact that individual organisms are organized in lineages of similar organisms that we call species is evident to specialists and laypersons alike [1]. Individuals within species evolve along the same trajectory, and remain morphologically similar to one another through time, whereas organisms in different species continuously diverge. Theoretically, this need not be the case. What maintains these discrete species, and holds them together?

Most discussions of this question immediately focus on the role of sex (for example [2–4]). From a geneticist's perspective, sex is simply another word for genetic recombination between individuals. Sex allows sharing of genes within a reproductive community (a sexual species), which helps keep the organisms in that sexual community similar to one another. The entire species changes through time as new mutations become shared and fixed throughout the species, so that variation among individuals within the species remains similar through time. If barriers to sex arise between subgroups of individuals within the species, then those subgroups evolve on their own trajectories and we say that a speciation event has occurred. One branch on the Tree of Life has now split into two. The individuals between these two species will now diverge, whereas individuals within a species will remain similar to one another through time, even as the species evolves.

Sexual reproduction and sexual isolation are clearly sufficient explanations to account for the existence of species, and for the generation of new species, respectively. But even though they are sufficient explanations, are they necessary? Some organisms reproduce asexually, at least most of the time, and appear to have too few opportunities to exchange genetic material with one another for us to expect a role for sex in maintaining a cohesive lineage. Therefore, if sex is the only answer to the discontinuous nature of species, we would expect asexual organisms to exhibit much more continuous variation than do sexual species, rather than displaying the distinct breaks that we typically see between species.

A new study by Fontaneto *et al.* [5] suggests that biological diversity among asexual bdelloid rotifers is distributed very much like the diversity seen in sexual organisms. Bdelloid rotifers show high similarity among individuals within clusters that can be called species, and exhibit distinct discontinuities (genetically and morphologically, for example) between these species. A casual observer might well suspect that bdelloid rotifers were reproducing sexually, as the patterns of discrete species appear to be similar to those seen in many sexual species.

Before discussing the possible explanations for species-like variation in asexual organisms, we should consider the evidence for asexuality in bdelloid rotifers. Many groups of supposed 'asexual' organisms have been found to have some sort of sexual recombination, at least on occasion [6–8]. In fact, a complete lack of sex over long evolutionary timescales is problematic, because deleterious mutations accumulate with every genomic replication.

Sexual recombination (followed by selection for the individuals with fewer deleterious mutations) is the usual means of reducing the number of these disfavored alleles in the genome. Lack of recombination, as in asexual organisms, leads to a phenomenon known as Muller's Ratchet: every generation, more deleterious mutations occur in the genome, with no way to remove them [9]. Selection can still favor the individuals with the fewest deleterious alleles, but eventually, all the individuals will incorporate too many errors to function normally [10]. Thus, some kind of genetic recombination is usually viewed as essential for the long-term existence of a species.

Bdelloid rotifers are viewed, however, as a potential exception to this rule of the necessity of sex for long-term persistence. Fontaneto *et al.* [5] cite the facts that no males have ever been observed in bdelloid rotifers, and there is no evidence of any kind of meiosis in the group. In many cases, their genomes contain highly divergent alleles of genes, indicating that any sexual recombination must be rare [11]. Fossil bdelloid rotifers are known from 35-million-year-old amber, and these fossil bdelloids are female [12]. Molecular phylogenetic analyses of bdelloid alleles were originally thought to provide support for the asexual reproduction of bdelloids across their evolutionary history [11], although re-analysis of these data show inconsistencies in this interpretation [13]. For instance, some virtually identical alleles are shared between otherwise divergent species, suggesting that bdelloids may have some unusual means of occasionally sharing genetic material. That may help explain how they avoid the effects of Muller's Ratchet, but bdelloids clearly reproduce asexually over long periods of time. Therefore, sex is not a reasonable explanation for the species-like distribution of morphological and genetic variation within this group.

One possible explanation for the species-like variation of the

asexuals is simply that differential diversification and extinction rates lead to self-similar clusters of organisms with discontinuous variation among the clusters. In this scenario, neutral drift produces variation, extinction produces gaps between related clusters of individuals, and periods of high reproductive success produce clusters of similar individuals. In contrast to this idea, Templeton [14] has argued that species-like clusters may be maintained by common selection pressures within different ecological niches [15], with each niche filled by a different cluster of asexual individuals. Thus, the 'cohesion mechanisms' of asexual species may be ecological, rather than sexual.

If the constraints of ecological niches function as a cohesion mechanism for asexual species, then we would expect low rates of divergence between individuals for traits under selection within species, compared to the rate of divergence between species. Low divergence rates within species are consistent with stabilizing selection operating to maintain a relatively uniform 'species', while higher rates between species would be expected under selection for different niches. Fontaneto *et al.* [5] scaled the divergence of bdelloid mouth parts along a phylogenetic tree of the rotifers, with the branch lengths of the tree estimated from silent nucleotide

substitutions in a mitochondrial gene. They found support for greater rates of evolution in the mouth parts of the rotifers between traditional taxonomic species than within species, in both size and shape of the rotifer mouths. This provides support for the ecological cohesion hypothesis as an explanation for the existence of species-like entities in the absence of sex.

Sex still rules as the primary explanation for the existence of species, and sexual isolation is still considered the primary mechanism of speciation [16]. However, the typically asexual bdelloid rotifers demonstrate that very similar patterns of variation can and do exist among asexual organisms. In their case, they have largely given up sex, but are still held together in cohesive lineages of related organisms by virtue of common selection for distinct ecological niches.

References

1. Sites, J.W., and Marshall, J.C. (2003). Delimiting species: A renaissance issue in systematic biology. *Trends Ecol. Evol.* **18**, 462–470.
2. Mayr, E. (1963). *Animal Species and Evolution* (Cambridge: Harvard Univ. Press).
3. Maynard Smith, J., and Szathmary, E. (1995). *The Major Transitions in Evolution* (New York: W.H. Freeman).
4. Coyne, J.A., and Orr, H.A. (2004). *Speciation* (Sunderland: Sinauer Associates).
5. Fontaneto, D., Herniou, E.A., Boschetti, C., Caprioli, M., Melone, G., Ricci, C., and Barraclough, T.G. (2007). Independently evolving species in asexual bdelloid rotifers. *PLoS Biol.* **5**, 914–921.

6. Belshaw, R., Quicke, D.L.J., Volkl, W., and Godfray, C.J. (1999). Molecular markers indicate rare sex in a predominantly asexual parasitoid wasp. *Evolution* **53**, 1189–1199.
7. Normark, B.B. (1999). Evolution in a putatively ancient asexual aphid lineage: Recombination and rapid karyotype change. *Evolution* **53**, 1458–1469.
8. Normark, B.B., Judson, O.P., and Moran, N.A. (2003). Genomic signatures of ancient asexual lineages. *Biol. J. Linn. Soc.* **79**, 69–84.
9. Felsenstein, J. (1974). The evolutionary advantage of recombination. *Genetics* **78**, 737–756.
10. Gabriel, W., Lynch, M., and Bürger, R. (1993). Muller's Ratchet and mutational meltdowns. *Evolution* **47**, 1744–1757.
11. Mark Welch, D., and Meselson, M. (2000). Evidence for the evolution of bdelloid rotifers without sexual reproduction or genetic exchange. *Science* **288**, 1211–1215.
12. Waggonar, B.M., and Poinar, G.O. (1993). Fossil habrotrichid rotifers in Dominican amber. *Cell. Mol. Life Sci.* **49**, 354–357.
13. Mark Welch, D.B., Cummings, M.P., Hillis, D.M., and Meselson, M. (2004). Divergent gene copies in the asexual class Bdelloidea (Rotifera) separated before the bdelloid radiation or within bdelloid families. *Proc. Natl. Acad. Sci. USA* **101**, 1622–1625.
14. Templeton, A. (1989). The meaning of species and speciation: A population genetics approach. In *Speciation and its Consequences*, D. Otte and J. Endler, eds. (Sunderland: Sinauer Associates), pp. 3–27.
15. Gavrilets, S. (2004). *Fitness Landscapes and the Origin of Species* (Princeton: Princeton University Press).
16. de Queiroz, K. (2005). Ernst Mayr and the modern concept of species. *Proc. Natl. Acad. Sci. USA* **102**, 6600–6607.

Section of Integrative Biology and Center for Computational Biology and Bioinformatics, University of Texas, Austin, Texas 78712, USA.
E-mail: dhillis@mail.utexas.edu

DOI: 10.1016/j.cub.2007.05.015

Mitotic Motors: Kinesin-5 Takes a Brake

A kinesin-5-dependent 'sliding filament' mechanism is commonly used to actively push apart the poles during mitotic spindle assembly and elongation, but a recent study now shows that, in *C. elegans*, kinesin-5 is deployed as a brake to slow down spindle-pole separation.

Gul Civelekoglu-Scholey
and Jonathan M. Scholey

Faithful chromosome segregation depends upon the formation and function of a bipolar, microtubule (MT)-based mitotic spindle, which uses multiple mitotic motors to

assemble itself and to separate sister chromatids [1]. Among these motors, members of the kinesin-5 family [2] are thought to have critical and often essential mitotic functions, by pushing apart the spindle poles, for example during anaphase B spindle elongation [3].

Curiously, however, the single kinesin-5 present in *Caenorhabditis elegans*, BMK-1, is dispensable for mitosis. Now, new work from the Saxton and Strome laboratories, published recently in *Current Biology*, shows that, in this system, BMK-1 has novel mitotic functions, serving as a brake that restrains the rate of anaphase spindle-pole separation driven by other cortical force generators [4].

Saunders *et al.* [4] studied the role of kinesin-5 in early *C. elegans* embryos, where anaphase B spindle elongation represents the major mechanism for chromosome segregation and where anaphase