EVOLUTION

Stable Heterozygosity?

Matthew Meselson and David Mark Welch

Evolutionary change in organisms that reproduce asexually may be driven in part by the divergent function of genes that were formerly alleles.

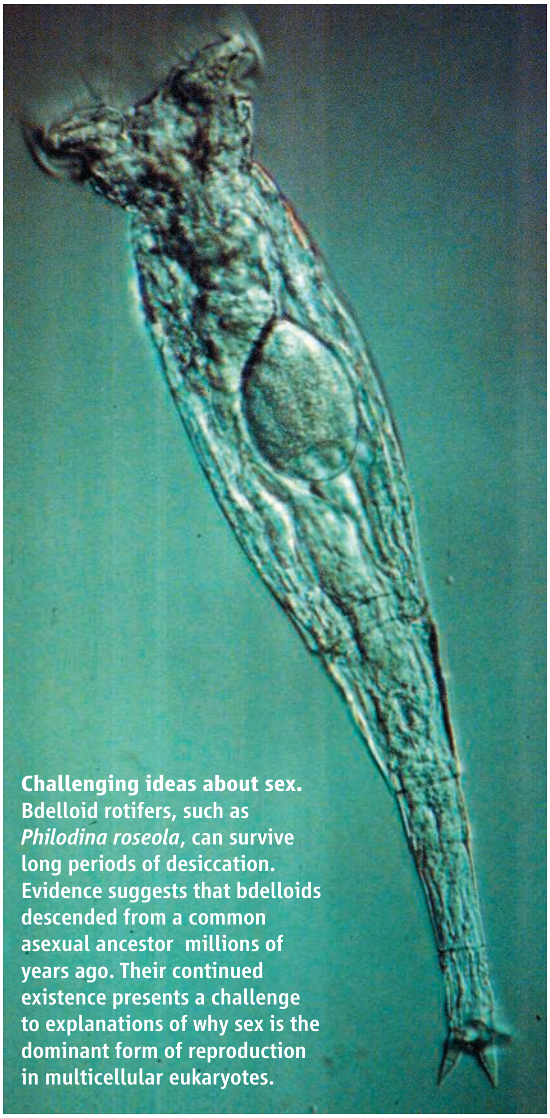
Bdelloid rotifers (see the figure), comprising some 380 described species, are common aquatic invertebrates with highly unusual properties, most famously their putatively ancient asexuality and ability to survive desiccation at any life stage. If truly asexual, their evolutionary success may hold the answer to why nearly all higher eukaryotes reproduce sexually and why asexual eukaryotes, arising occasionally from sexual ones, are almost always evolutionarily short-lived. On page 268 of this issue, Pouchkina-Stantcheva *et al*. (*1*) present evidence of functional divergence between two copies of a gene expressed in bdelloids during desiccation. Such genes encode proteins involved in desiccation resistance in plants, invertebrates, and microorganisms. The authors argue that such divergence could provide bdelloid rotifers with greater phenotypic variation and a potential advantage from asexual reproduction.

The most sturdy evidence for bdelloid asexuality is that despite much observation and study in the field and in laboratory culture since bdelloids were described by van Leeuwenhoek more than 300 years ago, males, hermaphrodites, vestigial male structures, and meiosis (the reductional cell division process that gives rise to gametes in sexually reproducing organisms) have never been documented. Instead, bdelloid eggs are produced from primary oocytes by mitosis (the cell division process by which most cells divide).

Another sort of evidence for asexuality has been sought in the form of high divergence between gene copies that were alleles—that is, alternative forms of a gene that occupy the same position on a chromosome—before sex was abandoned (*2*). In sexual species, meiosis separates alleles, and not all alleles in the parental gene pool are transmitted to the next generation, thus limiting the divergence that can accumulate within a species. But if sex, and therefore meiotic segregation of alleles, is abandoned (so the argument goes), former alleles should diverge, with only occasional homogenization by molecular recombination processes such as gene conversion or mitotic crossing-over. Under such conditions, in which former alleles are allowed to evolve more or less independently for sufficiently long intervals, alleles at some loci might be imagined to diverge in function. This is how Pouchkina-Stantcheva *et al*. interpret their findings.

In a screen for genes involved in desiccation resistance, Pouchkina-Stantcheva *et al*. identified two copies of a late embryogenesis abundant (*lea*) gene from a complementary DNA (cDNA) library of the bdelloid rotifer *Adineta ricciae*. Although differing at only 12 of 376 aligned amino acid positions, the two proteins encoded by the genes are found, when tested in vitro, to have putative desiccation-protective activities that are distinct. Analyses of bdelloid nuclei with a *lea* probe indicate that the two *lea* genes are likely located on two different chromosomes. The authors interpret this to mean that the two *lea* genes descended from former alleles that had not segregated for a very long time—long enough to accumulate 13.5% divergence at those sites that do not change the amino acid sequence of the LEA protein. By contrast, a broad survey of invertebrate species found an average of only 2.7% divergence between alleles at sites that do not change the amino acid sequence (*3*). Arguably, the ~5-kb region of homology that the authors identify as containing the *lea* copies could represent a duplication of the *lea* gene rather than allelic segments. Nevertheless, their results are consistent with indications of divergent function between gene copies on characterized allelic segments of the bdelloid *Philodina roseola* (*4*, *5*).

Assuming that the two *lea* genes are located in allelic segments of different chromosomes, as Pouchkina-Stantcheva *et al*. conclude, could they represent an extremely polymorphic locus in a sexual population? Or, if bdelloids really are ancient asexual organisms, are the *lea* genes descendants of former alleles that have escaped homogenization? It would be evidence for the latter if the divergent *lea* copies were found on separate chromosomes in bdelloid species other than *A. ricciae*. Although it could be argued that selection against homozygotes (identical alleles at a particular locus) could have maintained heterozygosity even in a sexual population, it is striking that, other than the textbook case of excess heterozygosity at the human β-hemoglobin locus (in populations in malarial regions), compelling evidence for other



Challenging ideas about sex. Bdelloid rotifers, such as *Philodina roseola*, can survive long periods of desiccation. Evidence suggests that bdelloids descended from a common asexual ancestor millions of years ago. Their continued existence presents a challenge to explanations of why sex is the dominant form of reproduction in multicellular eukaryotes.

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examples is almost entirely lacking (*6*).

If bdelloids are asexual, such divergence might be quite stable if the lethality of homozygosis from occasional homogenizing events is offset by the benefit of having two gene copies with divergent function. In that case, heterozygosity might persist even across species and higher taxonomic groups. In addition to firming up the evidence that the two *lea* genes are indeed on allelic segments of separate chromosomes, it could therefore be most informative to study their population genetics. The persistence of both gene copies on separate chromosomes would constitute independent evidence for bdelloid asexuality and, as Pouchkina-Stantcheva *et al*. suggest, such stable heterozygosity may have contributed to the fitness of bdelloid rotifers.

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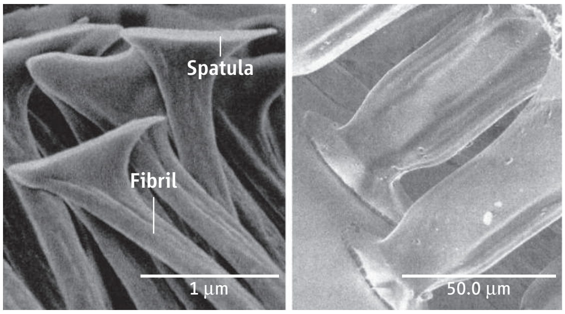
MATERIALS SCIENCE

Biomimetic Solutions to Sticky Problems

In a smart adhesive inspired by biological adhesive structures, subsurface structures dramatically increase adhesive strength.

W. Jon. P. Barnes

Many biological surfaces have remarkable properties, some of which have inspired materials science. For example, Velcro was developed from the interlocking mechanism of the seeds of burdock that readily attach to one's clothes as one walks through the countryside. Similarly, self-cleaning materials have been developed based on the "Lotus effect" (the way in which water drops roll off the superhydrophobic leaves of lotus plants, taking dirt particles away with them).



Of lizards and robots. The spatula-tipped adhesive setae in an anoline lizard (*Anolis*)] (**left**) inspired the structured adhesive used by Daltorio *et al.* (*7*) in the development of climbing robots (**right**).

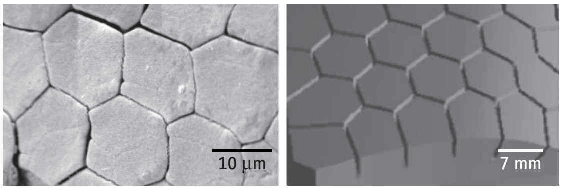
The adhesive mechanisms of climbing animals have also guided materials scientists. An excellent example is provided by Majumder *et al.* (*1*) on page 258 of this issue. Inspired by the complex subsurface structure of the smooth adhesive pads of tree frogs and insects such as grasshoppers and ants, they show that adhesive force can be increased by up to a factor of 30 by subsurface structures such as air- or fluid-filled pockets.

Climbing animals have many abilities that are the envy of materials scientists. First, they have remarkable powers of adhesion. Even a large gecko can run across a ceiling; a tree frog jumping from branch to branch does not fall so long as a single toe pad makes good contact with the tree; ants can carry more than 100 times their own weight while walking upside-down. Second, the adhesive mechanisms are reversible (geckos can walk at more than 10 steps a second), and detachment is effortless. Third, animal adhesive pads can have self-cleaning properties and thus do not get fouled. Finally, the adhesive pads of geckos only stick when required.

How different these abilities are from the properties of parcel tape! Following contact and mild pressure, parcel tape will adhere quite well, but it does not detach easily and is seldom reusable, because its tacky nature means that it is quickly fouled by adhering material. It also has an uncanny knack of sticking to anything it comes into contact with, making the wrapping of presents a lot less pleasurable than it ought to be.

So how do climbing animals stick? In addition to claws, present in many species but not tree frogs, two rather different adhesive structures have evolved: hairy and smooth adhesive pads. The toe pads of geckos and other lizards are covered with millions of tiny branching hairs, which can get so close to the substrate that intermolecular forces provide excellent adhesion (*2*). In contrast, the smooth adhesive pads of tree frogs, arboreal salamanders, and insects such as ants secrete a fluid so that they adhere by wet adhesion (*3*, *4*). In tree frogs at least, the main force appears to be capillarity, but viscosity and direct molecular contact may also play a role because of the thinness (0 to 35 nm) of the intervening fluid layer (*5*). (The hairy pads of insects also carry tiny amounts of fluid; adhesion is thus also likely to be mainly by capillarity.)

Such mechanisms have inspired materials scientists in a number of ways (*6*). For example, both Daltorio *et al.* (*7*) and Santos and colleagues (*8*) have used microstructured polymer adhesive feet based on the hairy pads of geckos (see the first figure) in the development of robots that can successfully climb a vertical glass sheet. Another particularly successful biomimetic structure—reusable tape that adheres equally well in wet and dry conditions—combines the microstructure of gecko pads with a thin layer of synthetic polymer that mimics the protein glue of mussels (*9*). Also, car tires are in production with a honeycomb tread pattern that closely resembles the surface structure of tree frog toe pads (see the second figure).



From toe pads to tires. Hexagonal toe pad epithelial cells surrounded by mucus-filled channels in the tree frog, *Litoria* (**left**). A similar hexagonal tread pattern is used in a Continental winter tire (**right**).

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