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Evolution: The End of an Ancient Asexual Scandal

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Bdelloid rotifers were believed to have persisted and diversified in the absence of sex. Two papers now show they exchange genes with each other, via horizontal gene transfers as known in bacteria and/or via other forms of non-canonical sex.

Asexual organisms are believed to be evolutionarily short-lived. Most asexual lineages occur on the tips of the tree of life and few have succeeded like their sexual counterparts. Only a handful of asexual lineages have diversified into different types considered as ‘species’ — sets of morphologically and ecologically distinct forms classified into different genera, or even families, of exclusively asexual organisms. The most prominent examples of lineages that have persisted and diversified over millions of years in the absence of sex include oribatid mites [1], darwinulid ostracods [2] (a group of freshwater Crustaceans) and, up to now, bdelloid rotifers [3] (Figure 1). These lineages have been referred to as ‘ancient asexual scandals’ as they appear to challenge the view that sex is a prerequisite for the long-term evolutionary success of a lineage [2,4]. They have also been considered a ‘holy grail’ for developing insights into one of the most notorious unresolved questions in evolutionary biology: why is sexual reproduction so universally favored in natural populations?

The idea is that if we can understand how ancient asexual scandals persisted and diversified in the absence of sex, we might develop insights into what the most fundamental benefits of sex are [5].

A new study in this issue of *Current Biology* by Debortoli *et al.* [6] shows that the answer to how bdelloid rotifers have persisted and diversified in the absence of sex might be that bdelloids engage in an unusual form of ‘parasex’ that allows for horizontal genetic exchange between individuals in the absence of regular meiosis and the production of gametes. The mechanisms mediating these horizontal gene transfers between individuals remain unknown. But the phenotype, horizontal gene transfer, brings an outstanding example of convergent evolution between bacteria and eukaryotes. Furthermore, elucidating the molecular details of horizontal gene transfer in bdelloids may open novel avenues to large-scale genome editing.

Bdelloid rotifers are abundant micro-invertebrates that occur in aqueous habitats throughout the world [7]. There

are 461 described species, distinguished from each other mainly on the basis of morphology [8,9]. Many species are able to survive dry, harsh conditions by entering a desiccation-induced state of dormancy from which they can emerge upon re-hydration [7]. The first hint for horizontal gene transfers in bdelloid rotifers was published in 2008 when Gladyshev and colleagues showed that bdelloid genomes harbor unusually many genes of bacterial, fungal, and plant origin [10]. Later work in the species *Adineta ricciae* then demonstrated that many of these foreign genes are expressed, and that as many as 8–10 % of all transcripts are of foreign origin [11]. The publication of the genome of a related species, *Adineta vaga* [12], revealed a similar level of foreign gene content, with 8 % of predicted genes of non-metazoan origin. Finally, foreign gene uptake is ongoing in bdelloids and has contributed to functional differences among species [13] and therefore to adaptive evolution in bdelloids.

Given the evidence that bdelloid rotifers acquire and use genes from

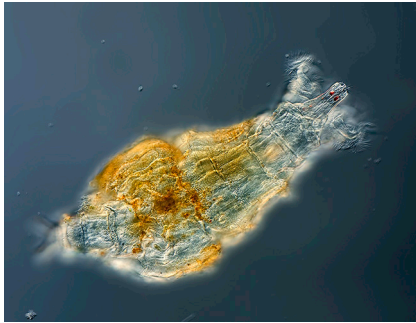


Figure 1. Bdelloid rotifers.

Bdelloid rotifers are abundant, ubiquitous microinvertebrates that inhabit aqueous habitats [7]. Depicted is an individual of the species *Rotaria tardigrada*. Picture courtesy of Michael Plewka (<http://www.plingfactory.de>).

non-metazoans, it seemed more than likely that horizontal gene transfers would also occur between bdelloid individuals and perhaps provide an alternative form of sex. The first evidence that bdelloids do indeed exchange genes with each other was provided by Signorovitch *et al.* [14], who identified a pattern of allele sharing between individuals of the species *Macrotrachela quadricornifera* that was incompatible with strict asexual reproduction. In this issue of *Current Biology*, Debortoli *et al.* [6] now provide additional evidence for genetic exchange between individuals without canonical sex in the species *Adineta vaga*. In combination, these two studies show beyond doubt that genetic exchange between individuals occurs in different bdelloid species and in different regions of the genome.

Both papers thus provide direct evidence for some form of genetic exchange between bdelloid rotifer individuals. They disagree, however, as to how such genetic exchange occurs. Signorovitch *et al.* [14] suggest that the patterns of allele sharing are best explained by extremely rare sexual reproduction involving an unusual form of chromosomal rearrangements found in some evening primroses of the genus *Oenothera*. These rearrangements, referred to as permanent translocation heterozygosity (PTH), result in chromosomes organized into a ring during meiosis and restrict recombination to the chromosome tips [15–17]. While there is currently no evidence for PTH in bdelloid rotifers, the proposed mechanism would be compatible with the highly rearranged genome structure

characterizing bdelloids, which is incompatible with canonical forms of meiosis and sexual reproduction [12]. By contrast, Debortoli *et al.* [6] suggest that allele sharing patterns in bdelloids are best explained by the same mechanism of horizontal gene transfers that led to the high proportion of foreign genes in the rotifer genomes. How these horizontal gene transfers generate allelic replacements, rather than genome expansions via the addition of horizontally acquired genes to the core genome, remains unclear and opens extraordinary avenues for future research directions. Another interesting open question is linked to the finding by Debortoli and colleagues [6] that there is more extensive allele sharing between individuals within cryptic species than between individuals of different cryptic species of *A. vaga*. This finding indicates that horizontal gene transfer does not occur at random between individuals, but the mechanisms mediating these non-random gene exchanges remain unknown.

The two proposed mechanisms underlying allelic exchange between bdelloids, although not mutually exclusive, should generate different genome-wide patterns of divergence between rotifer individuals and species. For example, PTH would predict decreased divergence levels at chromosome tips relative to the genome-level average while horizontally acquired genes might *a priori* be scattered randomly across the genome. However, the currently available data do not allow to formally confirm or exclude the hypothesis of PTH in bdelloid rotifers, or to ascertain that the documented allele exchanges among bdelloid individuals solely stem from horizontal gene transfers.

Given the evidence for genetic exchange between bdelloid individuals — through whichever mechanism — the question arises whether the amount of exchange is sufficient to provide the benefits of ‘canonical sex’ observed in the majority of metazoans. This may be quite likely since even small amounts of recombination and genetic exchange between individuals appear to be enough to provide all the benefits of sex [18,19]. As such, bdelloids should no longer be considered as asexuals and the starring role of the most notorious asexual scandals should be transferred to a different group, perhaps oribatid mites

or darwinulid ostracods, unless these groups have also found alternative ways for parasexual reproduction in the absence of meiosis and males.

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Locomotion: Electrical Coupling of Motor and Premotor Neurons

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A new study has found that zebrafish motor neurons can contribute to the generation of locomotor rhythms by feedback modulation of their premotor interneurons via gap junctions.

Motor neurons, while essential for the activation of muscle groups that participate in locomotion, are not classically thought of as active participants in the oscillatory spinal cord activity that leads to their rhythmic activation. Rather, locomotor rhythms are believed to emanate from an upstream network of premotor interneurons that is collectively referred to as spinal central pattern generators, with motor neurons acting solely as output neurons. However, a new study [1] now suggests that, in the zebrafish (*Danio rerio*), motor neurons could contribute to rhythm generation and pattern formation by directly modulating the premotor interneuron pool.

In the spinal cord, *Chx10*⁺ V2a neurons (also referred to as dIN neurons in *Xenopus* and CiD neurons in fish) are glutamatergic premotor interneurons that exhibit an oscillatory firing pattern during locomotion in phase with and preceding motor neuron spiking. These neurons constitute a major drive to motor neuron activation during locomotion [2–4] and contribute to the maintenance of left–right locomotor alternation [5,6]. V2a neurons show a wide range of intrinsic properties, connectivity, and recruitment frequency, indicating that they include multiple subtypes that could account for different locomotor speeds and distinct patterns of motor neuron recruitment [7–9].

V2a premotor interneurons have been assumed to lead motor neuron activity in order to generate locomotion.

Some V2as and Motor Neurons Are Electrically Coupled beyond Early Development

Other groups [4,10] had previously reported electrical coupling between V2as and motor neurons in zebrafish, but at early stages of development. Generally, widespread electrical coupling was thought to be a general feature of developing networks that is lost in adulthood. Paired recordings of motor neurons in mammals suggested that electrical coupling in the spinal cord was eliminated gradually over developmental time [11,12], but paired recordings between motor neurons and premotor V2a interneurons have not been performed in mammals.

In their new study, Song *et al.* [1] combine dye-coupling experiments with immunohistochemistry and paired whole-cell recordings in juvenile/adult zebrafish to show that the mature spinal cord remains networked to an extraordinary degree by gap junctions. In addition to observing V2a–V2a and motor neuron–motor neuron coupling, the authors observe that approximately 30% of V2a–motor neuron pairs are dye-coupled, suggesting the two populations are also

electrically coupled. In paired recordings, applying a current step to either partner correspondingly alters the membrane voltage of the other cell (Figure 1).

How Might This Electrical Coupling Influence the Locomotor Central Pattern Generator?

Pharmacological blockade of gap junctions in the spinal cord indicates that electrical coupling is necessary to synchronize functional elements in order to generate rhythmic activity, even postnatally [13]. The recent study [1] in juvenile/adult zebrafish now suggests that gap junctions might additionally act as a feedback mechanism from motor neurons onto premotor pools. Within pairs of neurons connected with mixed synapses, depolarizing currents applied to motor neurons reliably increased V2a spiking whereas hyperpolarizing currents decreased V2a spiking. Crucially, this direct feedback mechanism appears to be effective during induced bouts of locomotion as well. When the authors induced fictive locomotor bouts by stimulating descending brainstem projections, the hyperpolarization of motor neurons was sufficient to inhibit, and in some cases completely abrogate, V2a spiking.

Previous studies have shown in mouse and in zebrafish that motor neurons and their cognate V2as are