The Rotifer

Bdelloid rotifers are frequently cited as a kind of litmus test for theories of sex. Because, whatever one may say about the tendency of asexual lineages to fizzle out on an evolutionary timescale, bdelloid rotifers (and other groups such as oribatid mites and darwinulid ostracods) buck this trend by having survived quite happily for tens of millions of years without, so far as can be determined, any meiosis at all.

On the view presented here, it's not entirely clear why such arcane groups should trouble us much, but given the status of these organisms in the debate, we cannot just brush them aside. There must be a reason why asexual groups tend not to last long, and why these do not follow that trend.

Nonetheless, it is important to note that none of these groups is primitively asexual. All have sexual ancestors and relatives. As a reason to ponder the very existence of sex, organisms that cannot even come to exist without it seem a somewhat paradoxical choice. We seem to be being invited to consider only the two horns of a dichotomy: either sex is universally beneficial, in which case there should be only sexual organisms, or (absent a twofold benefit) it should be universally detrimental, in which case there should only be asexual descendants of anisogamous sexual organisms plus sexual isogametes. That clearly can't be right. What precludes those intermediate situations in which other proportions of species exist? Such as the one we have, in which a tiny handful of species represents a counterexample.

The general problems for secondarily asexual lines comprise
- Gene conversion
    - increase in deleterious homozygosity
    - loss of complementation
- Slower rate of evolution
- Interference of loci
- Muller's Ratchet
- Selfish genetic elements
- The resident sexual
- Coevolution in the wider, frequently sexual, ecology.
- Heterogenous niches

These are, I think, perfectly adequate to explain the general trend towards elimination of asexual lines on an evolutionary timescale. Even asexual offshoots of a dioecious species suffer these penalties. It is not at all certain that producing twice as many grandchildren is sufficient to cause the extinction of the parent, from a standing start, in every single case, nor even in most of them. To the extent that this happened, we would not see it. If the tendency is for asexual lines to go extinct, this may happen before or after extinction of the parent population, if they compete. In both cases, the modern eukaryote clade would be dominated by species to which this had not happened.

But what about the rotifers?

A near-universal issue for asexual lineages is gene conversion. This is a consequence of homologous recombination during repair. It causes loci to become increasingly homozygous, which can expose deleterious recessives and decrease the complementation of heterozygous alleles. If chromosomes are too closely related, this results in reduction of ‘vigour’, or inbreeding depression when there actually is breeding. Gene conversion causes a kind of inbreeding depression in a non-breeding setting. Rotifers, however, appear to lack recombination between homologues. The haploid chromosome sets have become highly divergent. It is difficult for us to identify their homologous chromosomes; it would be equally difficult for the repair system to locate homology for repair. Presumably repair uses sister chromosomes outside of the G1 phase, in much the same way as prokaryotes, but only end joining within G1.

It’s not clear whether the lack of HR is a consequence of the divergence of chromosomes, or whether its suppression was a preliminary to it, but either way, rotifers have a greater than expected amount of sequence divergence (Welch & Meselson, 2000).

Many of the other challenges in the rotifers are dealt with by their indulging a form of ‘parasex’ through gene transfer. Evidence for extensive gene transfer has been found (Deborteli, et al., 2016). The mechanism is currently unknown, but is likely to be a significant cause of the sequence divergence noted above. If sequences diverge too far, homologous repair may become positively mutagenic, and not merely a source of increasing homozygosity.

And finally, we can consider their ecology. Rotifers tend to blow around the world in dust, colonising freshwater puddles until these evaporate in their turn. They do not find a population of resident, ecologically indistinguishable sexual organisms, over whose continued existence we might wish to puzzle. It is not clear whether the rotifers’ sexual immediate ancestors have diverged or have gone extinct, but in either case, the rotifer’s life cycle and ecology would suggest that they would not be expected to be in close competition with sexual forms globally.

A related group, the monogonont rotifers, may represent the situation in the immediate ancestors of the bdelloids. They have a series of parthenogenetic generations, but intermittently return haploids. Occasionally, a pathenogenetic lineage becomes permanent, but this has not reached the widely divergent state we see in the bdelloids. If we wish to ponder the bdelloids, it seems more appropriate to consider the monogononts than to export their peculiarities to the whole of the sexual world.

Taking these considerations in sum, rotifers do not seem particularly troubling for the views expressed here.