

EVOLUTION

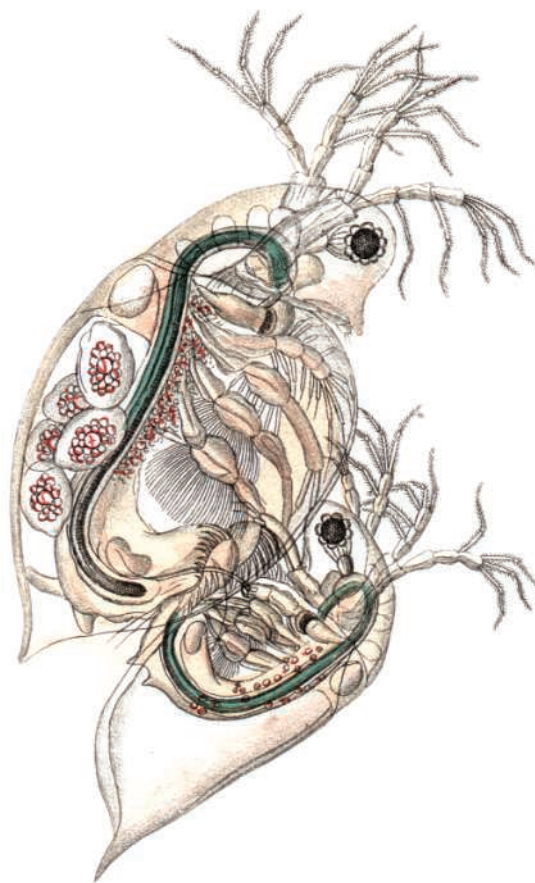
Why Sex?

Rasmus Nielsen

Why sex? This has been one of the most fundamental questions in evolutionary biology. In many species, males do not provide parental care to the offspring. Clearly, the rate of reproduction could be increased if all individuals were born as females and reproduced asexually without the need to mate with a male (parthenogenetic reproduction). Parthenogenetically reproducing females arising in a sexual population should have a twofold fitness advantage because they, on average, leave twice as many gene copies in the next generation. Nonetheless, sexual reproduction is ubiquitous in higher organisms. Why do all these species bother to have males, if males are associated with a reduction in fitness? The main solution that population geneticists have proposed to this conundrum is that sexual reproduction allows genetic recombination, and that genetic recombination is advantageous because it allows natural Darwinian selection to work more efficiently. New empirical evidence supporting this theory now comes from a study by Paland and Lynch on page 990 in this issue (1).

One reason why selection works more efficiently in the presence of recombination—that is, the exchange of genetic material between chromosomes—is that selected mutations tend to interfere with each other in the absence of recombination (2, 3). Imagine, for example, a beneficial mutation (A) arising in one individual and another beneficial mutation (B) arising in another gene in an individual that does not carry mutation A. In the absence of recombination, mutation B would be eliminated when mutation A reaches a frequency of 100% in the population, and vice versa. No individual carrying both beneficial mutations could be created, and only one of the mutations could eventually reach a frequency of one in the population. Recombination speeds up the rate of adaptive evolution because it allows several beneficial mutations to be combined in the same individual. Likewise, when multiple deleterious mutations are present in the population, recombination has the potential for creating new offspring chromosomes with fewer deleterious mutations than either of the parental chromosomes. The famous population geneticist John Maynard-Smith compared this situation to having two cars: one with a broken engine and one with a broken transmission. Neither of them can run,

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Lessons from the flea. The water flea, *Daphnia pulex*, may shift from being sexual to being asexual and is, therefore, an excellent research tool for testing theories regarding the evolution of sexual reproduction. The drawing [from (9)] is by J. J. Paschoud in the late 1700s.

but if you can replace the broken part in one car with a part from the other car you can produce a new functional car. Recombination allows broken parts to be shuffled among chromosomes, allowing new combinations to arise for selection to act on. Under suitable assumptions regarding the way deleterious mutations affect organismal fitness, the advantage of recombination in eliminating deleterious mutations can outweigh the twofold cost of sex (3).

However, the selection theories are not free of contradictions and problems. Some of them rely on so-called group-selection arguments, where adaptive properties are properties of a whole population and not of individuals. If sexually reproducing individuals and their offspring do not have an immediate selective advantage in otherwise asexual populations, it is hard to see how populations can ever evolve from asexual to

sexual reproduction. Additionally, the best explanations regarding deleterious mutations rely on strong assumptions regarding the distribution of selective effects (3), and there may be other factors favoring sex, such as increased resistance to pathogens (4). An observed genomic correlation between the rate of recombination and variability within species (5) suggests that there is an interaction between selection and recombination, but a direct difference between sexual and asexual populations has been hard to establish.

However, the new study by Paland and Lynch (1) provides direct empirical support for an excess accumulation of mutations in asexually reproducing populations compared to sexual populations. They examined different populations of the small crustacean *Daphnia pulex*, a type of water flea. *Daphnia* are excellent organisms to study in this regard because parthenogenetic *Daphnia* populations have arisen multiple times from sexual populations. Comparing asexual and sexual populations of *Daphnia* is, therefore, the perfect tool for examining the population genetic consequences of sexual reproduction (see the figure).

Paland and Lynch (1) compared the number of mutations with possible functional effects (nonsynonymous mutations) to the number of mutations with no functional effects (synonymous mutations) in 14 asexual and 14 sexual *Daphnia* populations. They observed a clear excess of nonsynonymous mutations in the asexual populations. They also estimated that close to 90% of the nonsynonymous mutations were subject to selection. These results suggest that the asexually reproducing species carry a higher load of deleterious mutations and that selection is not as efficient in the asexual as in the sexual populations. It does not directly demonstrate that selection against deleterious mutations is what maintains sexual reproduction, but the results do confirm the most important component of the selection theory: Asexual reproduction leads to an accumulation of deleterious mutations. It seems that males are allowed to exist after all, because they help females get rid of deleterious mutations.

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point of view. The estimate of the proportion of new mutations in *Daphnia* that are under selection is fairly high (>90%). Over the past 30 years, the paradigmatic theory in molecular evolution has been the Neutral Theory (6), which assumes that the vast majority of genetic polymorphisms have little or no selection acting upon them. However, the study by Paland and Lynch (1), and other recent studies (7, 8), suggest instead that many or most polymorphisms may be under selection. Slowly, our weltan-

schauung in evolutionary biology is changing from a static view of a largely optimized genome to a dynamic view of organisms constantly challenged by selection and struggling with the large genetic load imposed by deleterious and new advantageous mutations segregating in the population.

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PLANETARY SCIENCE

Ringing the Changes

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It all seemed so simple for a while. As far as we knew, Jupiter, Saturn, Uranus, and Neptune each had a ring system, a suite of small moons orbiting just beyond or close to the rings, followed by an impressive set of large moons and finally an irregular collection of outer moons in eccentric, inclined orbits. But now Uranus has yielded a few more secrets in the form of new moons and new rings. The moons may be tiny and the rings faint, but the research reported by Showalter and Lissauer (1) on page 973 of this issue reveals a complicated, evolving system that provides a fascinating insight into how rings and small moons are inextricably linked.

Of all the ringed planets, Uranus's ring system has seemed the most straightforward. It was made up of a series of dark, narrow, sharp-edged rings, the most unusual of which was the outermost ϵ ring complete with its two "shepherding satellites," Cordelia and Ophelia. Beyond the rings but still well within the orbit of Miranda (see the figure) lay an additional eight small moons discovered by the Voyager 2 spacecraft during its flyby in 1986. The largest and most distant of these was Puck, with an estimated diameter of 162 km. Karkoschka (2) later found an additional small moon, Perdita, lurking in the Voyager archive. Perdita orbits between the moons Belinda and Puck and is the outermost member of the "Portia group" of moons. In a series of numerical simulations, Duncan and Lissauer (3) had already shown that these moons were likely to be unstable, leading to a possible tragic climax of Shakespearean proportions with Desdemona colliding with Cressida or Juliet within the next 4 million to 100 million years.

In their new work, Showalter and Lissauer have used sequences of images from the Hubble Space Telescope to show that the pic-

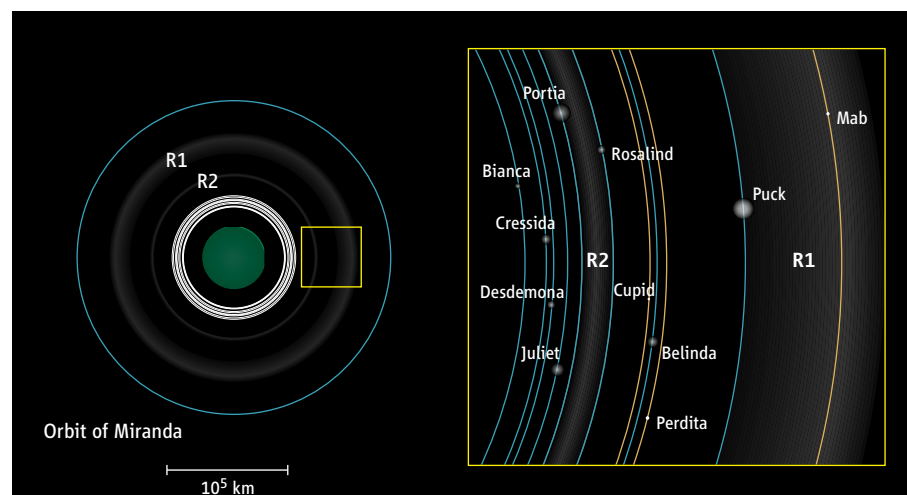
ture is not yet complete. Observations of small moons this close to a planet are notoriously difficult; long exposures are required, and the brightness of the planet tends to result in pictures with extensive "bloom" where saturated detector pixels engulf the image. However, by making use of the fact that the bloom on Hubble's High Resolution Camera is always in the vertical direction, the authors were able to align and time their images such that all the inner moons would show up in sufficiently long exposures. This led to the discovery of two new moons, Cupid and Mab, and two faint, diffuse rings that they refer to as R1 and R2.

The outer ring, R1, peaks in intensity at the orbit of Mab. This suggests that Mab is the source of the ring material, probably as a result of impacts from meteoroids or continuing collisions with the ring material already produced. Although the ejected particles can escape from

The Hubble Space Telescope has revealed two new moons and two new rings orbiting Uranus. The images indicate a dynamic, evolving, and possibly unstable ring system.

the surface of the moon, they still have orbital energies comparable to their parent body and so remain in a broadly similar orbit. Jupiter, Saturn, and Neptune all have examples of small moons embedded in faint rings. There are still some anomalies in Mab's orbit that need to be understood, but the association with R1 seems clear. The Hubble observations have also shown that Puck, which orbits at the inner edge of R1, appears to have one side that is 10% brighter than the other. Puck, like our own and many other moons, is tidally locked to its planet and therefore has well-defined leading and trailing hemispheres. Given that it is Puck's trailing side that is brighter, the clear implication is that Puck's leading hemisphere has been darkened by impacts of material from R1.

The second new ring, R2, is neatly bounded by the orbits of two of the known moons, Portia and Rosalind.



Inner region of Uranus system. (Left) The newly discovered rings R1 and R2 lie between the orbit of Miranda (the innermost of the large, regular satellites of Uranus) and the narrow rings detected by stellar occultation in 1977. (Right) A schematic close-up of the region near the new rings, showing the locations of the orbits of all satellites, including the recently discovered Cupid, Perdita, and Mab. The satellites are shown to their correct relative sizes (based on their mean radii), but these have been exaggerated by a factor of ~16 compared with the radial scale of the satellites' orbits.

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