Clades versus Clones in Evolution: Why We Have Sex

Abstract. *Sexual reproduction predominates among organisms mainly because most evolutionary change is concentrated in speciation events and asexual species cannot speciate in the normal sense. Asexual clones seldom diversify rapidly enough to overcome normal rates of extinction. In contrast, phylogenetic groups of sexual species (clades) commonly develop broad, heterogeneous adaptive zones rapidly enough to ensure survival.*

Sexual reproduction has conventionally been viewed as serving the basic function of accelerating evolution within lineages by providing either for efficient genetic recombination or rapid spread of useful mutations. There nevertheless remains much debate as to how and even whether it may actually produce rapid evolution (*1, 2*). One unresolved problem is why rapid evolution should be at such a premium as to account for the near-ubiquity of sexuality among higher organisms. Are we really to believe that the normal plight of slowly evolving species is rapid extinction? Judging from the fact that many living invertebrate genera have fossil records extending back more than 100 million years, it seems evident that rapid evolution is by no means a universal requirement.

Williams (*2*) developed two hypotheses for the prevalence of sexuality that do not relate to rates of evolution. The first is based on the idea that genetic variability is at a premium even when evolution is extremely slow. It is assumed that selection pressure is very intense in nature, that fitness tends to be lognormally distributed within species, and that only individuals of extraordinary fitness tend to survive. Sexuality is then alleged to be of short-term benefit: it provides a greater range of genotypes and fitnesses than does asexual reproduction and is therefore present in a larger proportion of the extraordinary individuals that survive. A major drawback of this hypothesis is that it applies only to species having high fertility. It can account for the predominance of sexuality in low-fertility groups (birds, mammals, and many insects) only on the assumption that it arose ancestrally and cannot be eliminated (*2*). Williams' second hypothesis is that high genetic diversity may be of long-term benefit merely for survival, without evolutionary response, against the agents of extinction.

I develop here the alternative idea that the dominance of sexuality is due to its long-term value to groups of species (clades), not because of differential rates of extinction for sexual and asexual taxa but because of differential rates of diversification. My argument is incompatible with all hypotheses suggesting that the primary function of sexuality is to accelerate phyletic evolution, but compatible with Williams' extinction hypothesis. The latter

is vulnerable to skepticism, however, because, as Williams (*2*) has noted, neither reduced genetic variability nor reduced evolutionary longevity has been shown to characterize asexual "species." Stebbins (*3*) first explicitly considered the value of sexuality not just to individual lineages, but to clades. He offered evidence that apomictic (secondarily asexual) groups of higher plants tend to go extinct rapidly and concluded that this fate befalls them not only because of an inability to evolve rapidly in the face of environmental change, but also because of a poor ability to diversify (he suggested that they could not easily give rise to new genera or subgenera). Van Valen (*4*) further suggested that an equilibrium frequency of apomicts might result from a characteristic rate of production of these forms, combined with characteristic disadvantages relative to sexual forms, both in evolving to avoid extinction and in speciating. Adopting the approach of Stebbins and Van Valen, I propose to show that the typical shape of phylogenetic trees of sexual taxa implies that speciation, not evolution to avoid extinction, is the critical factor.

The traditional idea that sexual reproduction functions to accelerate evolution arose in the context of phyletic gradualism (*5*). This is the view that most evolutionary change occurs within established species (*6*). The alternative, that most change is concentrated in speciation events, has been advanced by Mayr (*7*) and favored by various paleontologists (*5, 8, 9*). According to this second view, homeostatic mechanisms
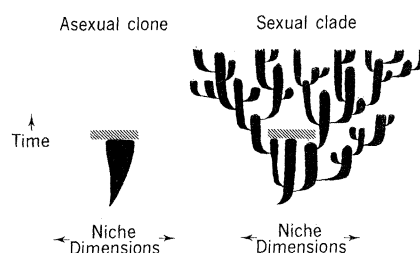

Fig. 1. Hypothetical early extinction of an asexual clone compared to survival of the clade of a similar group of sexual organisms. The clade is composed of numerous species, each of which diverges rapidly from its parent species and evolves slowly thereafter. An extinction event (hatched bar) eliminates all individuals falling within a small range of niche dimensions. The entire clone goes extinct, as compared to only two species of the clade.

tend to prevent change from occurring within a species after the species becomes established. This view implies a typical pattern for phylogeny that resembles not a tree with diagonal branches, but one with nearly vertical branches that arise, one from another, by nearly horizontal connections of varying length (*9*). I have termed this the rectangular model of phylogeny and have tested it against phyletic gradualism using various types of fossil data (*10*). The results clearly uphold the rectangular model. They show that gradual change may occur within established species, but is much too slow to account for rates of large-scale change observed in the fossil record. Not every speciation event produces significant change, but a "genetic revolution" (*11*) sometimes takes place, and we must attribute most evolutionary change in the history of life to the restructuring of genotypes in such events. Large-scale evolution, then, is not generally a race of phyletic change, as Darwin and most subsequent workers have believed, and we must de-emphasize the view that sexual reproduction is a group-selected feature required for species to succeed in such a race. Futhermore, abandonment of phyletic gradualism, in eliminating the idea that phyletic change is at a premium for survival, raises the possibility that asexual clones, once established, may actually tend to survive longer than similar sexual species. The reason is that clones may diversify more rapidly in a genetic and ecological sense, being unconstrained by interbreeding.

Acceptance of the rectangular model requires that we analyze the importance of genetic recombination in a framework that emphasizes speciation. Because change is concentrated in speciation events, large-scale evolutionary trends cannot reflect long-term phyletic evolution guided by persistent selection pressures (*5*). Furthermore, we cannot generally predict for any interval of time the set of new species that will arise within a higher taxon. The times and locations of speciation events and the directions the events take will be heavily affected by geographic and other environmental factors that are to a large degree randomly distributed with respect to the biology of the taxon (*7, 12*). I have therefore argued that large-scale evolutionary change is decoupled from microevolution within established species, and we must view trends as being determined by the process of species selection (*10*). Species selection is analogous to natural selection but operates upon species within higher taxa, rather than upon individuals within species. It favors species that tend to survive for long periods or speciate at high rates. Extinction of a higher taxon repre-

sents failure to respond to environmental change by species selection. Because most lineages are short-lived, exhibiting little phyletic change and containing few successional species, speciation is essential for long-term survival of higher taxa. An asexual clone may diversify, but will not speciate in the normal sense and will be much more susceptible to extinction than the entire clade formed from a successfully speciating sexual species. The clade typically will include a variety of species occupying an adaptive zone much broader and more heterogeneous than the niche of the clone. Species selection, which determines the course of large-scale evolution, must rapidly eliminate most asexual taxa (see Fig. 1).

The foregoing arguments provide an explanation for the success of the prokaryotes without extensive genetic recombination. It is not simply that prokaryotes have short generation times and, hence, can evolve phyletically to adjust to changing conditions. Even without phyletic change it is hard to envision the extinction of a typical bacterium or blue-green alga having enormous population size, worldwide distribution, and a broad niche. Extinction rates are so low, with or without sexuality, that rapid diversification is not needed to offset them. It is also evident why asexual taxa of higher plants (3, 13) and animals (7) tend to occur only sporadically, having close sexual relatives. Such taxa tend not to persist on an evolutionary time scale (3, 7).

The major exception (7) is readily explained. This is the rotifer class Bdelloida. The fact that all 300 or so recognized "species" of the Bdelloida are parthenogenetic suggests a monophyletic origin for this condition (14, 15). Bdelloids typically inhabit minute bodies of water, such as those found at the base of the leaflets of damp mosses, and individual types have extraordinarily broad niches. In general, they are capable of extreme anabiosis (15). Many can remain frozen or in states of extreme dessication for months or even years, and most types are cosmopolitan (16). Thus, it is easy to see how, even in the absence of normal quantum speciation, the bdelloids, which are very simple creatures and may well have originated in Paleozoic times, have been able to survive by virtue of low rates of extinction. Freshwater members of the Chaetonotoidea (Gastrotricha) are also exclusively parthenogenetic (15), and similar arguments would seem to apply to this group of minute, abundant, and commonly cosmopolitan forms. Existing "species" in such groups are discrete simply because they represent scattered adaptive peaks surviving from a continuum of forms (14, 15).

In summary, recombination permitted by sexual modes of reproduction may have some value among eukaryotes for survival of lineages in the face of environmental change, but phyletic evolution is much more sluggish and less significant than has generally been recognized and there is no evidence that asexual species are appreciably shorter-lived than sexual species. The overwhelming dominance of sexual reproduction among eukaryotes must result from the fact that for most taxa, normal extinction rates can only be balanced by high rates of diversification provided by the frequent formation of divergent new species.

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Direct Observation of Domains in Wet Lipid Bilayers

Abstract. *Domain structure and phase separation in hydrated lipid bilayers have been imaged directly by selected reflection dark-field electron microscopy. Domains in multicomponent bilayers are much smaller than those in single component bilayers, in agreement with results obtained by selected area electron diffraction.*

The hexagonal packing of acyl chains in phospholipid bilayers has been known for some time (1), yet the extent of the coherently packed areas (domains) in a bilayer is still uncertain. Little information has been obtained from x-ray diffraction because of the large diameter of the x-ray beam. If the areas of continuously striated surface seen in freeze-fracture electron micrographs are regarded as domains, the domains would measure from a fraction of a micrometer to several micrometers across, depending on the material, the cooling rate, and the quenching temperature of the membranes (2, 3). Separation of multicomponent bilayers into small, single phase domains has also been indirectly indicated by calorimetric (4) and spin-label electron paramagnetic resonance studies (2). By using an environmental stage in an electron microscope and applying techniques of electron diffraction and dark-field electron microscopy, we have been able to directly observe the sizes and shapes of domains of different compositions, as well as different orientations in molecular packing in bilayer membranes under physiological conditions.

Bilayers of pure dipalmitoylphosphati-

dylcholine (DPPC), of mixed DPPC and dilauroylphosphatidylcholine (DLPC), and of mixed DPPC and cholesterol were formed without support on an electron microscope grid by a previously described method (5). By using an environmental stage for a Siemens Elmiskop IA electron microscope (6), the specimen may be viewed in a fully hydrated state in the temperature range between –10° and 50°C. Results were recorded on sensitive Kodak No-Screen x-ray films, although the patterns were normally invisible on the phosphor screen of the electron microscope because of the extremely low beam current in the experiment (10^{-6} amp/cm^2 at the specimen level).

Selected area electron diffraction was done by restricting the illumination area to a few micrometers in diameter, using a pointed filament and a 10 μm second condenser aperture. Below the transition temperature of DPPC bilayers, three orders of a hexagonal pattern were recorded, whereas diffuse rings only were seen above the transition temperature (5, 7). Differently oriented diffraction patterns were distinguishable between adjacent membrane areas (domains) 5 μm apart. Occasionally,