

## [On interspecific hybridization]

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There is a good reason why closely related species in general can so often hybridize in the laboratory, yet do not in the natural situation. This reason can be used to explain why orchids hybridize easily, even between species so strikingly different that they are often classified in different genera.

Charles Darwin noted that natural selection cannot favor the evolution of sterility between species. This simple statement holds the key. Selection also cannot favor the evolution of mere reductions in reproductive success. Indeed, by definition it always favors increases in reproduction, whether in matings between individuals of different species or between individuals within species. To understand why different species are so often able to produce hybrids thus requires understanding how sexual selection evolves within species. Selection does not operate to serve the species as a whole. It changes entire species incidentally by differentially retaining the genetic materials of the more reproductively successful individuals within species.

In matings both within and between species, selection favors attributes that reduce the likelihood of time, effort, and risk-taking in efforts to reproduce with mates that will yield inferior offspring – meaning whenever such matings, or hybridizations, are less reproductive than matings with other, genetically different, superior mates. This means that within species there will be rapid evolution of traits yielding superior matings, and disappearance of inferior mating-sequence traits. For matings between species it means something different: that all of the events in the reproductive sequence, especially those earliest in it, will strongly diverge between the species (more specifically, between any two populations for which interbreeding leads to reproduction inferior to that occurring within each of them). Whenever an event that occurs earlier in mating sequences involving different species becomes so effective as to prevent events later in the sequence from even occurring, selection can no longer promote divergence per se between the later events. Early events, such as pair-forming signals, minimize time, effort, and risk-taking in futile or inferior mating efforts, thereby canceling selection on later events. Sterility or fertility, the last pair of alternatives in the mating sequence, can come about only incidentally, not as a result of selection per se – not as a species-level adaptation.

Considering the way orchids are pollinated, one sees that, just as the long-range pair-forming signals of animals are their most obvious species-distinctive attributes, so are phenotypic differences between orchid populations that remain interfertile when those differences actually involve the “mating” (fertilization) sequence. That orchids vary vastly in size, shape, color, form of the plants and flowers and reproductive parts is almost exactly what is predicted. Moreover, actual divergences between populations, as opposed to mere independent evolutionary changes in the different forms, will not be accidental or incidental because they will be evolving to serve the function of avoiding wasted time, effort, and risk-taking in the mating sequence. Orchids have evolved ways to discourage pollinators that would cause their gametes to be united with members of other species with which they may or may not remain inter-fertile, but with which they are not as reproductive as in within-species matings.

If one were to assign taxonomic status by appearance alone, as systematists have done generally, many non-interbreeding but interfertile populations of orchids would be seen

as different enough to be classified in different genera, not merely as different species within genera. In other words, taxonomists who used degrees of difference in morphological features to set up the artificial groupings that we call genera would be impressed by the degree of differences in the orchids. They would not necessarily have realized that traits in the reproductive sequences of the different species should evolve divergently at very rapid rates.

It is also predictable that rapid and dramatic divergence in traits making up the reproductive sequence (here, involving pollinators) will be accompanied by pleiotropic genetic effects, or incidentally evolved traits, that will also be divergent but may involve vegetative (or any other) aspects of the plants. In other words, such divergences may occur non-adaptively in other traits that can be changed without having much effect on reproduction -- specifically, not enough effect to prevent the evolutionary divergence of the genetically related reproductive traits. They are, however, likely, in subsequent evolution, to revert slowly toward trait expressions that are more reproductive, causing the slightly deleterious pleiotropies of highly adaptive changes in reproductive traits to be slowly weeded out.

Orchid traits that astonish the observer in their extraordinary profusion, and as species differences, are the equivalents of long-range pair-forming signals in animals. A useful example is the tens of thousands of species of singing insects (crickets, katydids, cicadas, and some grasshoppers). The vast majority of systematists have to distinguish species and classify them mostly on morphological traits that nearly all the time have no reason whatever to reflect accurately species limits, makeups, and differences. But during the past 50 years, owing to the advent of sophisticated field sound recording and analyzing devices, students of the singing insects have been able to identify species accurately by their loud (long-range) songs, only subsequently looking for distinguishing morphological and other (ecological, geographic, life history) differences. They can do this because the songs of interspecific hybrids produced in the laboratory are quite obvious, so that it is easy to know that field hybridization is not occurring between microsympatric species that nevertheless hybridize readily under laboratory conditions. In orchids, floral and other morphological differences are "long range" signals roughly equivalent to the songs of insects.

Consider what may at first seem to be a counterexample. In many groups of grasshoppers, copulation is not a matter of males signaling at long range and receptive females then seeking them out. Instead, males stalk females, and copulation is pretty much a leap-on, seize-and-hold, near-rape. Just as careful thought suggests, the most divergent attribute among grasshopper species thought to be closely related is genital morphology. This is the main feature systematists use to distinguish the species. Thus the first event of the mating sequence is still crucial, but it isn't dramatically "long-range" because it becomes operative only after the male has seized the female. Here, though, another factor must also be included. In species that mate as these grasshoppers do, females will surely evolve to resist copulation sometimes, or else be doomed to spend much more of their lives in risky, protracted copulations than benefits them: the interests of conspecific males and females in such species differ dramatically, partly because in insects the last sperm into the female's storage pouch is more likely to be successful than the first sperm in. Resistance to copulation in these species ("selection" of superior males) sometimes involves females kicking males off their backs or otherwise eluding them. It also involves rapid changes in the female genitalia that give the female more control over whether genitalic engagement is successful. Males will evolve to thwart the females' thwarting. The result will be an endless race in the evolution of genitalia between males and females, even within the same species. Such rapid evolution can lead to great complexity in the genitalia because each sex can only respond to whatever

change occurs in the other sex. Such rapid evolution, though not strictly divergent in nature between species that sometimes initiate cross-copulation, leads to incidental divergence of genitalia between species. It is not surprising that in such grasshoppers even small, presumably fairly recently isolated populations have distinct genitalia.

For orchids the race is between evolution of changes in the reproductive parts of the orchids receiving pollen to prevent just any old pollen (or inferior pollen, including when it is from the “wrong” species) from successfully fertilizing the ovum; this race necessarily involves the evolution of signals to the carrier of the pollen. It is these signals that give orchids their great floral and other morphological diversities, and the evolution of these signals takes care of all problems of reduced reproduction in the field including that which results from result interspecific fertilization. Intersterility is frequently absent, and sometimes surprisingly so, because it is always incidental – therefore not consistent. It is not an adaptation, and it cannot be achieved directly by evolutionary selection.

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