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Alternative adaptations, speciation, and phylogeny (A Review)

(polymorphism/epigenetic plasticity/macroevolution/punctuated equilibria/regulatory evolution)

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ABSTRACT Alternative adaptations—different adaptive phenotypes maintained in the same life stage and the same population but not necessarily simultaneously expressed in the same individual—represent contrasting character sets produced by the same genome, in effect allowing a single species to occupy more than one sympatric niche. Such alternatives are particularly likely to give rise to novel adaptations because of selection for extreme dissimilarity between them and because established traits buffer populations against extinction while independently expressed alternatives evolve in new directions. Particular alternatives can be suddenly fixed in populations with little or no genetic change, leading to a period of rapid evolution (especially, of morphology) exaggerating the characteristics of the newly fixed form. This burst of change would facilitate rapid speciation and could produce “punctuated” patterns of evolution. Evidence from a wide variety of organisms shows that alternative phenotypes are exceedingly common in nature and that they are probably important in speciation and macroevolution. Although many of these ideas and observations have been noted piecemeal by previous authors, bringing them together demonstrates the probable importance of alternative adaptations in the origin of major evolutionary novelties and calls for a revision of current and traditional ideas about the role of behavior and ontogeny in the genesis of organic diversity.

The Alternative-Adaptation Hypothesis

The purpose of this paper is to suggest a change in the way biologists think about the origins of organic diversity: character divergence, speciation, and macroevolution or the invasion of major new adaptive zones.

The usual way to visualize phylogenetically important divergence begins with reproductive isolation, or speciation: a branching point of a phylogenetic tree marks both the beginning of a new lineage and the beginning of character divergence. New characters may conceivably arise without reproductive isolation via gradual evolution over time, with the eventual formation of a new “chronospecies”. But increased diversity and major innovation begin with speciation, and macroevolution leading to the origin of a new higher taxon requires a series of such events. On this evolutionists have generally agreed, even when holding otherwise disparate opinions (e.g., see p. 524 of ref. 1, p. 171 of ref. 2, and p. 174 of ref. 3 and, for an exception, ref. 4).

I propose a very different view of divergence and phylogeny. In this “alternative adaptation” hypothesis, novel traits originate and become elaborated as stable alternative phenotypes or morphs within species, prior to reproductive isolation and speciation, when they come to characterize distinctive new lineages. That is, drastic innovation can begin not with the branching of a phylogenetic tree but with the bifurcation of a developmental or behavioral program (“epigenetic divergence”) giving rise to intraspecific alternative adaptations.

Alternative adaptations are different, often complex, evolved phenotypes occurring in the same lifestage and the same population but not necessarily simultaneously expressed in the same individual. [When “adaptation” *sensu* Williams (5) is not applicable or intended I will use the more general words “phenotype” or “form.”] Examples are familiar to everyone. They include the “workers” and “queens” of social insects (6); males and females of sexually reproducing species; and the contrasting morphs of batesian mimics in butterflies (7). The particular phenotype expressed in a given individual or at a given time depends on the state of a regulatory (“switch”) mechanism, which can be either condition-sensitive or genetic (allelic, chromosomal, or a supergene), producing “facultative” and “genetic-switch” alternatives, respectively (7–10). For purposes of the present argument it matters little which type of switch mechanism is involved; in both cases the phenotypes themselves are “genetic” in that they involve the coordinated expression of different suites of genes (different coadaptive gene sets); and, with the exception of the relatively small number of genes involved in a genetic-switch mechanism, the genes required for the production of both or all alternative phenotypes are borne by all individuals in the population.

In brief outline, evolution in accord with the “alternative adaptation” hypothesis proceeds as follows: A set of alternative phenotypes becomes established as a stable feature of a population, and is gradually improved by selection, possibly leading to a “macroevolutionary” degree of distinctiveness between alternatives. Then conditions (e.g., in a geographically isolated population) may favor only one of the alternatives, leading to its exclusive expression with little or no genetic change. This may be accompanied by rapid evolution as the genome is released from the constraints of having to accommodate multiple alternatives. This could facilitate speciation by accentuating divergence from the parent population, producing a new lineage characterized by the newly fixed and now modified form.

These occurrences are further discussed below, along with examples from a variety of organisms.

Evolutionary Properties of Alternative Adaptations

Alternative phenotypes are a kind of “covariant character set” (8). Others include hormonally regulated sets of male and female traits, functionally and morphologically differentiated larval and adult characters, and even the contrasting tissue and organ systems of a multicellular individual.

In all of these cases the coordinated expression of an underlying set of genes is governed by switch mechanisms. The developmental significance of a switch mechanism is that it determines that one set of genes shall be expressed instead of another, alternative, set. The *evolutionary* significance of a switch is that it determines which of an array of potential phenotypes will be expressed and, therefore, exposed to

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selection in a particular timespan and context. Insofar as one set of characters is independently expressed relative to another, it is independently molded by selection. Therefore, different covariant character sets evolve semiindependently, taking on different forms in accord with their different functions. Like juvenile and adult forms, different alternative phenotypes of the same species may show dramatic differences in morphology, behavior, and ecological niche. This is possible because once a switch mechanism is established, contrasting phenotypes can evolve simultaneously within the same genome—without reproductive isolation between forms.

It has been noted previously that sets of covariant characters can be rapidly shifted and lost “in blocks” via regulatory evolution, but the result would usually be a maladapted freak, or “hopeful monster” (8). The special significance of alternative adaptations is that, except for mutually dependent forms (like male and female, hymenopteran worker and queen, or specialized organs of a multicellular individual), a single alternative (e.g., a single mimic morph of a polymorphic butterfly) can conceivably persist without the others being expressed in the population. It could therefore come to characterize an independently evolving lineage. This means that of all the kinds of covariant sets of characters that might be subject to sudden macroevolutionary change via regulatory mutation, the most likely important for speciation and phylogeny are noninterdependent alternative adaptations.

The Buffering Effect of Alternative Adaptations. One requirement for the gradual evolution of a novel complex specialization is the ability of a single lineage to persist while undergoing extensive change. The likelihood of extinction while crossing deep “valleys” between adaptive peaks is an important argument against gradualist explanations for the origin of major new forms (11–13) and has posed a dilemma for evolutionary biology for more than a century (8). In species with alternative phenotypes, however, new forms evolve as additional options in lineages maintained by established adaptations.

Numerous theoretical models describe stable maintenance of genetic-switch alternatives without heterozygote advantage (see, e.g., refs. 13 and 14) and the evolution of facultative switch mechanisms (14–16). Facultative alternatives are particularly well buffered from the effects of negative selection. Shapiro (17) describes how they can be environmentally cued so as to be expressed only when likely to be advantageous, in effect screening the action of selection so that it is usually positive. Genetic-switch alternatives may achieve some condition-responsiveness via the evolution of specific modifiers (*sensu* Turner, ref. 13), e.g., for habitat selection. But they must be equally advantageous to be maintained (14, 18–20). Facultative alternatives, on the other hand, can remain as options even when not expressed for many generations (17). The superior buffering effect of flexible expression may explain why facultative-switch alternatives are proving more common in nature (10, 21–23) and in discussions of macroevolution (8, 10, 24, 25) than are genetic-switch alternatives.

The role of behavioral and physiological flexibility (e.g., in diet or mode of locomotion) in the origin of major innovations has long been recognized (1, 26). But previous neodarwinian discussions of “behavioral shifts” (26) have focused mainly on the fact that gradual behavioral change precedes gradual anatomical change in monomorphic populations. The possibility should be considered that these crucial shifts originated as alternative adaptations within species, rather than via a series of intermediate stages in which the original pattern was lost as it was modified.

Selection for Contrasting Alternatives. Widely accepted theory holds that divergence begins with breeding isolation,

as already mentioned. Since sympatric divergence via assortative mating (e.g., of different ecological types) has not proven common (27) despite repeated assertions of its feasibility (e.g., 19, 28, 29), it is now generally believed that most divergence begins with geographic separation (allopatry) between populations of the same species (12). Some allopatric divergence is virtually inevitable due to differing mutation, selection, and drift (4, 12). However, the direction of change in a given allopatric isolate is independent of the characteristics of other isolates. Thus allopatric change can involve a large number of loci yet be only slightly divergent or even parallel. Alternative adaptations, on the other hand, are often selected for divergence with respect to the others present: disruptive selection against intermediates may move different extremes into different adaptive zones, and selection for escape (in time or place) from competition with sympatric conspecifics may favor traits that contrast sharply with those already in existence. In other words, there can be a premium on a capacity for “saltation” into a very distinctive competitive mode, especially if it takes advantage of recurrent individual traits (e.g., small size) or environmental conditions (e.g., seasonal crowding or drought) that are suboptimal for performance of an established pattern (30). Escape to a different milieu (via facultative change, or genetic “bet hedging”), even with imperfect adaptation, can be more advantageous than improved adaptation to a grossly hopeless or deteriorating situation. It is therefore not surprising that “macromutations”—drastic changes in form or life history characteristics brought about by sudden regulatory change such as heterochrony—are apparently common sources of new alternative adaptations (8, 10). Phylogenetically important heterochrony may usually occur via a polymorphic evolutionary stage.

Consequences of Phenotype Fixation. If conditions consistently favor or induce one alternative it may become the only one expressed. “Phenotype fixation” (exclusive expression of a single alternative) can occur with little genetic change, via fixation of a single allele (or set of alleles) at a switch locus, or without any genetic change at all, via the consistent environmental induction of only one facultative form.

Phenotype fixation may be accompanied by accelerated evolution (or “character release”) in a population having the newly fixed form, tending to make it diverge genetically and phenotypically from the ancestral group. This is expected because a genome freed from the constraints of producing multiple specializations can accumulate modifiers that might previously have been selected against because of their incompatibility with other alternatives. Character release in a population approaching fixation of one alternative can accelerate the process of fixation itself, tending to drive it to completion (31). This would speed divergence between isolates having different ratios of alternative phenotypes and contribute to the likelihood of speciation. Completion of speciation should additionally be facilitated in groups having alternative adaptations because [as pointed out by Clarke (32) and Vane-Wright (33)] ancestral alternatives preadapt sibling species for coexistence in sympatry by having originated in sympatry, often under selection for alleviation of competition.

These conclusions apply regardless of the mode of speciation visualized—i.e., whether the isolates in question are allopatric, sympatric (assortatively mating or allochronic), or parthenogenetic in origin [for a review of different modes of speciation, see Mayr (12), Bush (34), and White (35)].

Several authors (32, 36, 37) have suggested that the differently adapted morphs of polymorphic species could form the basis for new species. Others propose models of speciation depicting sympatric character divergence under disruptive or competition-dependent selection (18, 19, 28, 36,

65) or due to allochryony (38, 39). However, only three of these (18, 19, 38) involve stable intrademic alternative adaptations of the kind being discussed here.

In addition to facilitating speciation, character release associated with phenotype fixation could produce "punctuated" (3) accelerations of (especially) morphological change. Species having multiple behavioral or physiological adaptations (e.g., different diets) may require a versatile or "compromise" morphology; then, if a single specialization is rapidly fixed, rapid structural modification could occur (e.g., producing specialized teeth and jaws). This might be especially important in groups such as the higher vertebrates, in which morphology is conservative (not often showing polymorphic variation) but behavior is flexible (40).

The Evolutionary Importance of Alternatives: Evidence

The conventional view of the species as an interbreeding population occupying a single niche implies that bi- or polymodal adaptation is rare. Stable genetic polymorphisms are expected to be rare because of the "severe conditions" for their evolution (7, 41), and facultative alternatives are often assumed to be rare, perhaps by analogy with genetic (allelic-switch) alternatives. However, alternative phenotypes are far more common than is usually realized. In groups for which only morphology is known, there are numerous examples of polymorphism. And in more broadly investigated groups, complex polymorphisms, polyphenisms, and behavioral "alternative tactics" are proving so common as to be considered virtually universal concomitants of strong competition. Alternative adaptations seem to characterize all forms of life, from viruses (in which phage λ is a famous example, ref. 42) to higher plants and animals. Common kinds include the batesian mimicry polymorphisms of insects (7); complex trophic polymorphisms and polyethisms in protozoa (43), rotifers (44), fungi (45), and birds (46); dispersal polymorphisms in plants (47), mites (36), insects (24, 48), birds (49), and mammals (50, 51); seasonal polyphenisms in insects (52, 53) and amphibians (54); and the leaf, flower, and branching heteromorphisms of plants (55–57) (which even though often present on the same individual may qualify as "alternative adaptations" by virtue of their capacity for independent expression in monophenic individuals).

There are numerous examples of intraspecific alternatives showing a "transspecific" degree of divergence—morphological divergence so extreme that it would qualify them to be classified as different genera or higher taxa were they not known (through laboratory rearing) to be members of the same species (e.g., see refs. 36, 57, 58). But the most convincing evidence for the macroevolutionary role of alternatives is the occurrence of facultative traits that repeat within a single extant species both the "primitive" and the "derived" states of changes considered major innovations in the history of life. For example, facultative airbreathing and terrestrial locomotion occur in lung-bearing fish in response to conditions (periodic or seasonal drought) (59) like those thought to have accompanied the vertebrate transition from water to land in the Devonian period (60). The facultative alternative trophic specializations (saprotrophy, necrotrophy, biotrophy) of certain fungi represent within species the dietary specializations of different trophic radiations (45). And the facultative carnivory (cannibalism) of some primarily phytophagous wasps resembles the "central" (Phytophaga–Terebrantia) transition in the evolution of the Hymenoptera (61). Facultative group-living and worker behavior occur in species of primarily solitary wasps and bees, accompanied by the kinds of complex behavioral capacities that distinguish (and probably gave rise to) highly social families (25, 62). Many of the examples of neoteny and paedomorphosis in extant species listed by Gould (8) and

Matsuda (10) are expressed as morphs in polymorphic species. Thus, while focusing on the macroevolutionary role of heterochryony they incidentally document the likely importance of alternative phenotypes in the origin of major adaptive novelties.

What is the evidence that such alternatives can form the basis of a new lineage as hypothesized here, via phenotype fixation, character release, and associated speciation?

Geographic variation in ratios of alternatives, including phenotype fixation, commonly occurs as predicted—in accord with geographic variation in the suitability of alternatives. For example, the ratio of two alternative nutritional patterns of pitcher-plant mosquitoes (*Wyeomyia smithii* Coq.)—blood-feeding, and oogenesis using resources derived from larval feeding—varies along a cline of increasingly favorable larval trophic conditions, created by a cline of decreasing larval densities within pitcher plants (63). In northern populations, where larvae are least dense, the non-blood-feeding (autogenous) alternative is fixed: adult females cannot be induced to feed even if undernourished as larvae (64). Similarly, the geographic ranges of batesian mimic morphs in papilionid butterflies usually correspond closely to those of their models, disappearing or degenerating in form where the model is absent (13). And the dimorphic (aerial and aquatic) leaves of buttercups (*Ranunculus flammula* L.) are monomorphic where plants are either constantly immersed or constantly terrestrial (55).

In populations in which phenotype fixation is permanent or approaches completion, character release seems to be the rule: northern autogenous pitcher-plant mosquitoes are more specialized to autogeny than are their southern autogenous counterparts, showing precocious ovarian development and earlier mating (64), and completely autogenous mosquito species often have modified mouthparts unable to pierce vertebrate skin and copulation in the female pupal stage (64). Similarly, buttercups from monomorphic populations show increased specialization of leaf morphology (to the terrestrial and aquatic forms, respectively) as well as reduced ability, compared to individuals of heteromorphic populations, to survive in extreme (aquatic or terrestrial) environment unlike their own. Hybrids have intermediate characteristics, demonstrating that these changes are evolved (55).

The genetic basis of "character release" accompanying phenotype fixation is further illuminated by studies of the butterfly *Papilio dardanus*. In populations in which a nonmimetic, tailed form is common (80% of the population), the "tailless" allele is absent. However, in populations in which a mimetic morph improved by the "tailless" allele predominates, that allele evolves to fixation, being no longer frequently selected against as a deleterious "nonspecific modifier" of the tailed alternative form (13).

Many taxa contain both polymorphic species and monomorphic populations or full species believed likely to have originated via phenotype fixation (refs. 36, 56, 57, and 66–68 and J. P. Collins, personal communication, on salamanders). One kind of evidence that this has occurred is provided by experimentally and naturally evoked "missing" alternatives, or atavisms. Shapiro (17, 53) describes seasonally polyphenic butterflies whose alternative color patterns and associated behaviors function in temperature regulation. Certain related populations are monophenic, producing only the dark-winged "vernal" form in nature, but the light-winged alternative "estival" form can be induced in the laboratory, showing not only that the monophenic populations are likely derived from polyphenic ones but also that the genes responsible for the lost alternative form are still present. Similarly, some salamanders have two facultatively induced adult forms ("normal" and "neotenus"), whose occurrence varies in accord with variation in ecological conditions (69). In other species only the (derived) neotenus form is produced in

nature, but a normal form can be induced by hormonal treatment, suggesting a polyphenic origin as in butterflies. Still other salamanders are permanently neotenus and the normal form cannot be hormonally induced (ref. 10, see also ref. 70). This suggests that a long history of phenotype fixation has led to sufficient evolutionary (genetic) change to make atavistic recall of the suppressed alternative impossible.

A related phenomenon is the recurrence of parallel sets of alternative adaptations in polyphenic groups. Adaptive light/dark polyphenisms similar to those studied by Shapiro recur in scattered species of three different families of butterflies (53). Parallel sets of alternative phenotypes also recur in cladocerans, rotifers, aphids, gerrid bugs, and salamanders (10, 53) and in stickleback fish (71). Once epigenetic flexibility has evolved in a certain context it may come and go in the history of a subsequently labile lineage. As Bell (p. 509 of ref. 71) points out, such "parallelisms" may be products of homologous genes carried by related forms and "likely to be exposed to selection regimes that will assemble the same phenotypes repeatedly." In view of these findings the discovery of recurrent feeding specializations in Lake Victoria *Haplochromis* species (72) and of remarkable "multiple detailed convergence" between the feeding morphology of nine African snail-feeding cichlids and the molariform morph of a polymorphic species (*Cichlosoma minckleyi*) (73) invites a search for polymorphism in African lake cichlids. Alternative adaptations may have contributed to their spectacular "explosive" trophic diversification and speciation (74), as well as to the sympatric coexistence of many closely related forms.

Hundreds of examples of speciation likely involving fixation of alternative adaptations are provided by the obligately socially parasitic Hymenoptera (wasps, ants, and bees) (6). In these species females usurp the positions of host queens and use the conquered nest and workers to rear their own young. They employ specialized behavior and morphology to find and dominate or kill host queens and are unable to reproduce independently (they do not rear workers on their own). All of the major types of social parasitism believed to lead to obligate workerless social parasitism in the Hymenoptera—nest usurpation, trophic parasitism, and slave-making—occur (and are thought to originate) as within-species alternative tactics in related groups (6, 75–79). Populations of facultatively parasitic species are largely maintained (buffered from extinction) by the reproduction of nonparasitic queens.

With only a few exceptions (see, e.g., ref. 80), socially parasitic species are more closely related to their host species than to any other extant species—a generalization called "Emery's Rule" (6). Given the commonness of intraspecific social parasitism in the groups concerned, it appears likely that this originally alternative specialization has repeatedly become fixed in association with the reproductive isolation of a particular lineage. [The origin of reproductive isolation in social parasites has been discussed by Richards (81) and by Wilson (6).]

Intraspecific social parasitism is a strictly behavioral alternative adaptation without external morphological correlates. However, obligatory social parasites often show evidence of character release in the form of specialized morphological traits associated with their parasitic role, such as (in vespids) large mandibles, a thickened cuticle, and a recurved sting (75), presumably used in combat with host queens.

The evolution of social parasitism in the Hymenoptera thus illustrates virtually all of the special features of speciation and macroevolution via alternative adaptations: intraspecific origin of a complex specialization as an alternative adaptation; the buffering effect of alternatives in facilitating the evolution

of a complex novel trait; character release following fixation of a single alternative; and recurrent speciation associated with a recurrent intraspecific alternative.

Conclusions

These facts call for a fundamental revision of ideas about the origins of organic diversity. In particular, the vision of adaptive evolution as being unidirectional in nature, and of populations as unimodal entities, must be reexamined, along with its correlate—that divergent innovation, whether gradual or sudden, requires speciation. The "typological thinking" of early darwinian taxonomists, criticized by Mayr (12) as neglecting geographic variation within species, has given way to a new typology—that of the unimodally adapted species. Polymodal selection and alternative phenotypes, especially, facultative and behavioral alternatives, must be incorporated into the body of evolutionary theory as important sources of novel traits.

In the unimodal-population models conventional in dealing with speciation and phylogeny, the conditions cited as favoring marked divergence in allopatric isolates—strong ecological competition, very different or changing environments, small founder populations, and/or long periods of time (2)—also favor population extinction. In such models "pure gradualism with conventional control by selection cannot extend across the gaps in basic design" (8). Yet the survival of lineages undergoing brusque (e.g., heterochronic) change has remained a dilemma. Gould (8) deals with this problem by invoking "the immensity of geological time," in which even the rare prospering of a hopeful monster might be sufficient to explain the likewise rare origin of a new phylum. The alternative adaptation hypothesis shows how the capacity for sudden drastic epigenetic change can actually be favored by natural selection as a response to strong competition or fluctuating conditions and how an epigenetically flexible lineage is protected from extinction while undergoing a "saltatory" reorganization. One important consequence of thinking in terms of alternative adaptations is understanding how genetically small but phenotypically great regulatory alteration or "macromutation" is possible and perhaps even common without lineage extinction, and why it is capable of producing the kinds of novelties (especially neotenus and paedomorphic forms) long associated with the origin of major taxa.

Although sometimes interpreted as contradicting the gradualist theory of evolution (8, 82), punctuated patterns of evolutionary change, especially in morphology, are expected under the (gradualist) alternative-adaptation hypothesis. This represents a further step in reconciling these two perhaps only superficially contradictory points of view. Kirkpatrick (83), reasoning via a genetic model, proposes a similar reconciliation and notes the "protective" effect of a bimodal fitness distribution.

The alternative adaptation hypothesis also supplies a missing link for relating development to evolution and phylogeny. It shows how epigenetic bifurcation can lead to phylogenetic (lineage) bifurcation, and it calls for recognition of the fact that (disruptive) selection against intermediates in nature very often leads neither to sympatric speciation (28) nor to genetic polymorphism, but to *developmental* elimination of intermediates and the subsequent intraspecific elaboration of alternative forms.

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