



development is to restrict (rather than provide opportunities for) evolutionary change (but see 111, 200). The previous generation of evolutionists interested in development (see 133, 136, 183, 215) likewise frequently emphasized conservative aspects—canalization and stabilizing selection—the suppression of deviant variation during development and evolution to produce a functional phenotype near a single adaptive norm. Indeed, there can be no doubt that environmental variance introduced by phenotypic plasticity sometimes dilutes the effects of selection and retards evolutionary change [13, 64, 75, 82, 198 (but see 199), 203]; and that nonmorphological plasticity sometimes contributes to morphological stasis by compensating environmental and genetic perturbations (216).

This review emphasizes the additional importance of plasticity as a diversifying factor in evolution—a factor contributing to the origin of novel traits and to altered directions of change. It consists of four main parts. The first outlines the nature of plasticity and its special relationship to natural selection. The remaining sections show how phenotypic plasticity may act to facilitate and accelerate three major processes in evolution: the origin of novelty, speciation, and macroevolution. The discussion emphasizes how plasticity influences the course of evolution, not how plasticity itself evolves. Thus it does not extensively review models for the maintenance and evolution of plasticity (110, 130, 131, 213, 214), or information on environmental assessment and the regulation of adaptive plastic traits. Nor does it attempt an exhaustive review and classification of examples, although many are cited in order to substantiate particular points. The main object is to introduce a new framework for analyzing plasticity as a potential cause of diversity in particular groups of plants and animals.

### *Terminology*

The “phenotype” includes all aspects of an organism other than the genotype, from the enzyme products of the genes to learned behaviors and the effects of disease. If one considers the “environment” to include both the external surroundings of an organism and the internal conditions affecting gene expression, “phenotypic plasticity” is seen to encompass an enormous diversity of kinds of variability. Not surprisingly, the literature on this subject contains a bewildering and inconsistent profusion of terms for classifying kinds of plasticity, with different authors and schools of thought preferring different sets (see 67a, 130, 183, 235). I use only a few terms needing special definition:

*Alternative phenotypes*—Two or more forms of behavior, physiological response, or structure maintained in the same life stage in a single population and not simultaneously expressed in the same individual.

*Conditional (or condition-sensitive)*—The alternative adopted by a particular individual or at a particular time depends on environmental conditions.

*Allelic-switch*—The alternative adopted by a particular individual depends on the allele(s) present at one or more genetic switch loci.

*Combined-switch*—The alternative adopted depends on a combination of allelic and environmental factors.

*Polyphenism*—The existence of environmentally cued alternative phenotypes in a population (133).

*Polymorphism*—The existence of morphologically distinct alternatives in a population (usually: “allelic-switch alternatives”—67a, 133, 185; however, I use the broader definition, modified by “allelic-switch” where appropriate).

## THE SCOPE OF *PLASTICITY* AND ITS RELATION TO NATURAL SELECTION

For whole-organism biologists, especially those interested in behavior, ecology, and systematics, phenotypic plasticity offers a familiar set of phenomena with which to begin thinking about the evolutionary significance of environmentally influenced processes (including development). It includes both nonadaptive environmentally produced variation and adaptive conditional responses such as seasonal polyphenisms, alternative behavioral tactics of resource acquisition, and facultative polymorphisms. Plasticity usually refers to environmentally influenced variability in a particular life-stage, or (in plants and colonial invertebrates) to variation in the behavior, form, physiology, or sequence of modules produced at a particular stage of growth. A single genotype can also produce highly differentiated life-stage variants, such as distinctive juvenile and adult forms, or organs, such as roots and flowers. But obligate, developmental forms produced in fixed sequence are not usually considered aspects of plasticity. Plasticity is of interest to evolutionists because it represents production by a single genome of a diversity of potentially adaptive responses, whose timing, structural relations, and environmental sensitivity are subject to natural selection.

Since evolution is generally defined as a change in gene frequencies, the variants associated with environmental conditions and plasticity are frequently classified as “nongenetic” in nature, and therefore unimportant for evolution. It is important, however, to realize that plasticity itself is a trait subject to natural selection and evolutionary change (230): The direction and degree of response to environmental factors (the “norm of reaction”) is genetically variable (38, 88, 147) and known to respond to selection (19, 38, 182, 199, 203, 215). So it is a mistake to consider phenotypic plasticity a “nongenetic” phenomenon.

At the same time, it is important to appreciate the deterministic role of the

environment, alongside the genes, in the production and evolution of the phenotype. The environment is not only the agent of selection, in the sense of being the arena where different phenotypes achieve different degrees of survival and reproductive success. It is also an agent of development, which importantly influences the range of phenotypes that will be produced by a given genotype (see 88; 143). As phrased by Gupta & Lewontin (88), plasticity renders selection “myopic” in that it sees not the entire potential of a genotype’s plastic response, but only the phenotypes that happen to be produced in a particular environment. The same could be said for the role of development in affecting selection. In affecting the range of phenotypes actually expressed, the environment influences which phenotypes are exposed to selection and modified during evolution. Thus, through its role in development, the environment can affect the direction of evolution. Only expressed phenotypes can be genetically modified under selection.

Given the ubiquity of gene-environment interaction in development, phenotypic plasticity can be considered a universal quality of life. It means that per generation there will usually be a greater variety of phenotypes available to selection than there are genotypes. To the degree that a particular phenotype among those possible is repeatedly produced (e.g. due to repeated environmental conditions) selection can modify its form. This is true even if there is a large nongenetic component (e.g. larval starvation or shaded conditions) determining its expression—even if the *difference* between individuals showing the phenotype in question and those having an alternative phenotype is entirely nongenetic. Environmentally induced nongenetic effects on phenotypes, while not transmitted genetically to the next generation, thus have considerable evolutionary importance (see also Ref. 200, on “latent selection potential”). They can alter the strength and direction of selection affecting transmitted gene frequencies by markedly shifting the range of phenotypes *expressed* and thereby subjected to selection and evolutionary (genetic) modification. This rule, that selection acts on expressed phenotypes (and can lead to their genetic modification), is basic to the following discussion of specific ways in which plasticity can affect evolution.

## PLASTICITY IN THE INITIATION AND AMPLIFICATION OF CHANGE

### *The Special Role of Behavior*

Behavior (movement), as an especially plastic aspect of phenotypes, illustrates well how plasticity can initiate new directions of evolutionary change.

Although morphology can undoubtedly direct or constrain the evolution of behavior (see 35, 81), many authors have noted that the form of behavior is often the first aspect of the phenotype to evolve in a new direction or to bring

a population into a new habitat or niche [40, 62, 75, 133, 134, 156, 159, 165, 218, 233—see Wcislo (218) this volume]. The impression that behavior takes the lead in evolution is commonplace, but it is not immediately obvious why this should be so: What quality of a more plastic trait (like behavior) would make it *evolve* more rapidly than a less plastic trait (like morphology)? There are several reasons why plastic traits are likely to be important initiators of new directions in evolution:

1. Both morphology and behavior are plastic. But behavior (including the growth movements of plants) is more “labile” than morphology (191): For every fixed morphology there may be several optional behaviors, whereas the reverse is probably seldom true. Therefore the probability of producing a favorable variant (in a new or challenging situation at a particular time) is greater for behavior (and other relatively plastic traits) than for morphology.

The key to the evolutionary role of behavior, however, is not lability alone, but a combination of lability and the consistency with which given behaviors occur in given conditions: A genetic (evolutionary) response to selection depends on a repeated association, under selection, of a particular phenotype (e.g. hiding in a hole) and a particular fitness-affecting condition (e.g. the approach of a predator) (233). If the consistent response happens to enhance fitness, then the genetic underpinnings that enable it to be consistent will be favored by selection, as will modifiers improving its performance. Thus behavior patterns must often be established first, followed by morphological improvements. For example, in studies of courtship in *Drosophila*, Carson (29) observed that males of 14 related species performed a vibration of the upwardly curved abdomen near the female’s head. In 13 of the species there is no associated morphological modification of the male abdomen, but in one (*D. clavistae*) it bears a brush of long clavate hairs which sweep the female’s head during the display, an apparently secondary embellishment of a repeated behavioral trait.

2. *Adaptive* behavioral plasticity is expected to evolve more readily than does adaptive morphological plasticity, because of the greater abundance of potential cues for regulating the expression of an *immediate* (behavioral) adaptive response. Adaptive plasticity requires some mechanism (cue) for matching the expressed phenotype to the environmental situation in which it functions. The number of contingency-associated cues that can evoke a potentially adaptive response is likely greatest for contemporaneous responses like behavior (see 156).

Overlap of contingency and response also characterizes the modular development of plants and colonial invertebrates. In modular development each successively produced segment (module) functions in the place where it developed, and as growth produces movement through different conditions (of light, shade, obstacles and support), structure and physiology change

accordingly, often, like behavior, in response to environmental cues and in adaptively appropriate ways (26, 100, 101, 116). The evolution of an adaptive plastic *morphological* response in animals, by contrast, requires a cue operating early enough in ontogeny to trigger the development of the appropriate morphology. It must be predictive enough of future circumstances removed in both time and (due to locomotion) space to allow appropriate choices (see 42). This more stringent requirement for an adequate cue must severely limit the commonness of adaptive morphological plasticity in animals, but it is clearly not an impossible condition. Many facultatively expressed adult morphologies are size-dependent such that a structure is developed prior to adulthood but appropriate to a certain size-class of adults, e.g. a thoracic horn in large (fighting) males (57, 58). Facultative seasonal polymorphisms involving morphology (rather than just physiology and behavior) (185) are evidently more common in insects than in vertebrates (see 128). This is at least partly explained by the fact that the development and lifespan of most insects is short relative to the duration of particular seasonal conditions, so that seasonal cues (such as photoperiod) can signal the impending onset of a climatic or resource-abundance phase that will characterize the environment of a given life stage (82a). Longer lived organisms with fixed morphology cannot “track” seasonal fluctuations in this way (see 110).

3. Behavior during development can extensively influence morphology (14, 138, 192), but much of behavior is ephemeral in that its expression can take a particular, novel form (e.g. of movement or intensity) and then be turned off, independent of other phenotypic or behavioral traits (without permanently altering their form). Depending on the phase of ontogeny affected (195) morphological innovation—especially very early in ontogeny—may seriously disrupt the relations of developing systems (195).

An extensive literature treats the evolutionary importance of learning and culture—aspects of behavioral plasticity that can speed phenotypic change (e.g. via invention and imitation) and enable plastic individuals to make adaptive decisions among alternative behavioral phenotypes (4, 10, 18, 155, 157, 181; see 218, this volume).

### *The Accommodation of Novelty*

Much has been written about the difficulties of evolutionary change in highly coadapted and canalized organisms, an idea reinforced by the fact that most genes are pleiotropic, and most if not all characters are polygenically influenced (30, 72, 133). Focussing on the phenotype gives a more optimistic view of the ability of organisms to undergo change. Two aspects of plasticity facilitate phenotypic change: the capacity for immediate correlated shifts in related traits, and the occurrence of condition-sensitive expression of phenotypes.

ACCOMMODATION AND AMPLIFICATION VIA CORRELATED SHIFTS A classic illustration of the accommodation and amplification of a mutant novelty via a plastic shift of related traits is the congenitally two-legged goat described by Slijper (192; from 162). An otherwise normal goat which was born with greatly reduced front legs adopted an upright posture and walked on its hind legs (initially, a behavioral change). It then developed enlarged hind legs, a curved spine, modified muscle insertions, an unusually large neck, and an oval (rather than V-shaped) thoracic cross-sectional shape. All of these novel phenotypic traits except the abnormal front legs were products of plasticity of the structures and behaviors involved, which were pressed to extremes to accommodate and amplify a basically simple but extreme phenotypic mutation. The result amounts to a complex co-expressed character set, produced by an apparently small genetic change.

There is evidence that plasticity has this effect during the normal course of evolution of both morphology and behavior. Hanken (90; see also 113) describes several examples in the evolution of vertebrate morphology, where "a relatively minor, but genetically based, alteration in the development of a given nonskeletal head component (e.g. the intrinsic growth rate of the eye) may initiate a series of compensatory responses in the surrounding skull, thereby effecting a major change in overall head morphology" (90, p. 266). Meyer (138) experimentally demonstrated a similar phenomenon without genetic change: Persistent behavioral differences associated with different diets during ontogeny caused marked differences in trophic morphology of the cichlid fish *Cichlasoma managuense*; Bernays (14) demonstrated a similar effect of diet in a caterpillar. As shown by Strauss (202) environmentally induced (non-evolutionary) size change alone (e.g. in haplochromine cichlids) can lead to allometric shape changes. These may prove adaptive in some context and/or lead to new directions of evolution. A cascade of effects may likewise explain the origin of corn from a teosinate, where a simple and easily induced change (the shortening of branch internodes), by bringing the (male) tassel into the zone of feminizing hormones, automatically could have produced several distinctive morphological features of *Zea mays* (98). And a possible example of behavioral trait amplification due to plasticity is represented by the origin of the nonreproductive "worker" phenotype in social insects (140, 178–180, 225, 226): A single small behavioral change (reuse of the parental nest by some offspring females) can account for a chain of effects not requiring further genetic change, including formation of groups, reproductive dominance of aggressive nestmates, and care of larvae by subordinate non-ovipositing females—all conceivably derived from the plastic traits of species that do not nest socially. Thus complex, coordinated, and adaptive phenotypes can originate rapidly and with little genetic change, via correlated shifts in the expression of plastic traits. "Pleiotropy" accurately embraces

these effects; but it does not capture their dynamics, which result from the sphere of plasticity ("norm of reaction") that surrounds virtually every genetically transmitted trait.

A remarkable feature of these composite characters produced by correlated phenotypic shifts is that once in place they give the impression of a co-evolved character set. In effect, the initial change acts as a developmental "switch" canalizing the associated traits in a particular direction (1). In the case of the social insects (225, 227) the switch regulating caste is immediately "conditional" on dominance rank (relative aggressiveness) and associated differences in ovary size and hormone titer (172). Thus, the "worker" caste of social insects likely originated as a condition- (rank-) and hormone-sensitive alternative, subject to the evolution of thresholds for escape (221) and manipulation (3).

**THE IMPORTANCE OF FACULTATIVE EXPRESSION** Condition-sensitive expression of alternative phenotypes means that in a variable environment a novel phenotype (such as worker behavior, or a new trophic specialization) can evolve alongside an established specialization without being expressed (competing) in the same situations. Even when an established phenotype is more efficient in most situations or in most individuals, an alternative that happens to be profitably associated with particular conditions or individual traits can be positively selected (47, 58, 82a, 121, 222). Such a phenotype can persist and be elaborated alongside a usually superior established trait, because the former is expressed in conditions where it is likely to be more advantageous (187). Crucial to this process is the ability of organisms to assess environmental conditions accurately and respond to them appropriately. The evolution of conditional responses and the evidence that organisms do in fact perform amazingly complex adaptive "decisions" comprises an extensive literature beyond the scope of this review. Interested readers should especially consult studies of mating behavior (5, 28, 42, 210), sex change in fish (217), foraging behavior (201), kin recognition (65), and decision or game theory (131, 132).

The importance of facultative expression for the intraspecific evolution of divergent traits cannot be overemphasized. Condition sensitivity not only reduces negative selection by assuring that traits are expressed in appropriate conditions. It also contributes to divergence by increasing the consistency with which particular phenotypes are matched to the particular contrasting conditions which mold their divergent forms. For these reasons facultative expression should prove both more common and more often associated with complex alternatives than is allelic-switch control. Facultative expression is associated with "difficult to evolve" complex traits such as "altruism" (self-sacrificing beneficence) (225-227) and the ecological transitions often



characterizing speciation and macroevolution (128 and below). Most of the nonplastic “genetic polymorphisms” (allelic switch alternatives) reviewed by Mayr (133) involve relatively simple color and structural variants.

The multidimensional plasticity of a living organism means that the functional phenotype is complexly malleable, like a clay figure that can be variously reshaped without falling apart. Plasticity is one reason why, to borrow the apt metaphor of Frazetta (69), an evolving organism can be extensively remodeled while it is running.

### *The Evolutionary Significance of a Switch*

The consequences of plasticity discussed so far apply whether the variation due to plasticity is unimodal or polymodal. When plasticity gives rise to a bi- or poly-modal distribution of forms (polymorphism or polyphenism, including discrete behavioral alternatives), the consequences for selection are particularly marked: Selection is focussed at more than one mode and, to the degree that the alternative phenotypes are functionally and developmentally independent (see 32), can produce divergent phenotypic evolution without reproductive isolation of forms (212, 224). Once a switch is established there is an opportunity to accumulate modifiers sensitive to it, or additions to the sets of developmental or behavioral events initiated by the switch (212). As Thoday long ago pointed out (209; see also 125), this is true whether the switch mechanism is allelic (the different forms produced differ by an allele or linked set of alleles), or condition-sensitive, or a combination of the two. The same principle underlies the divergent development and evolution of sexual dimorphisms, and of differentiated cells and tissues.

Familiar examples of the divergent evolution of complex morphological alternatives (polymorphisms) controlled by condition-sensitive switches are provided by the workers and queens of social insects (231), the alternative leaf forms of heterophyllic plants (38), and the major and minor males of horned beetles (57). Far more common than morphological alternatives are complex behavioral alternative tactics of resource procurement (9), e.g. in mating (5, 97, 210), foraging (50a, 201), and hunting (44); and in seasonal polyphenisms (51, 185, 207, 208).

Genetic and endocrinological studies of alternatives in both plants (164) and animals (22, 148, 170, 189, 212, 232) indicate that all have a similar regulatory architecture: Each alternative has a distinctive (or distinctively expressed) set of specific modifier genes, whose expression is ultimately regulated (often via hormonal or neuronal mediation) by a relatively simple cue (environmental, or allelic, or both). Not surprisingly, this is the structure hypothesized to characterize the development of co-expressed traits in general (see 103). This well-supported model of development helps explain why complex traits can be lost and shifted as units (94, 98, 103, and below); and it

enables one to visualize how alternative phenotypes can evolve semi-independently: The increase in genetic correlation of traits that occurs as alternatives become increasingly divergent and specialized (108) can amount to bringing an increasing number of morph-specific modifiers under the control of a switch (neural or hormonal system). [The idea that co-expressed, co-functional sets of genes must be neighbors on the same chromosome or controlled by a “supergene” has been disproven (103, 212).]

As in the case of plasticity producing continuous variation, degree of plasticity (environmental sensitivity) in the expression of discrete alternatives is subject to selection (110). Thus, sensitivity to particular environmental cues can be selected for or against; and the threshold at which a response occurs (and/or is exceeded by a given individual) is known to be genetically variable and therefore subject to selection (see 27, 70). Environmentally influenced alternative phenotypes, therefore, represent a range of degrees of plasticity. Some, such as certain alternative behavioral tactics of mating (5, 54, 210), dispersal (11), predation (44) and foraging (150, 201) have highly condition-sensitive control. Others, such as certain behaviors of worker honeybees (27, 70, 167), some trophic alternatives in salamanders (37), and some wing polymorphisms in insects (21, 52, 92, 169, 170) have “combined” switches, with both an allelic and an environmental component (see also 126) (a wing-polymorphic cricket showed 0.65 heritability of wingedness—170). At the extreme nonplastic end of this continuum are “allelic-switch” alternatives, in which genetic differences between individuals irreversibly determine the alternative adopted (as in the Batesian mimicry morphs of butterflies—212). Still others (e.g. the statary and migratory forms of locusts) have a “ganged switch,” in which different functionally correlated alternative traits are differently cued (104, 125). For a discussion of combined genetic and environmental influences on the expression of behavioral alternatives, see Dominey (54). That selection can alter the degree of plasticity of the switch is demonstrated by evidence of secondarily derived allelic morph determination in ants (95).

The comparative rarity of nonplastic (allelic-switch) alternatives (54, 128, 210) (the frequency-dependent “mixed ESS” of game theorists—130) probably reflects in part the stringent conditions for their stable maintenance (110, 130). As shown by Cavalli-Sforza (31, p. 50), in a variable environment “potentially there is a multitude of plastic genotypes that have a substantially higher fitness than the best nonplastic genotype.” Accordingly, extensive surveys indicate that complex *conditional* alternatives are exceedingly common in plants (85, 115, 116) and animals (5, 50a, 54, 128, 210). They probably characterize all forms of life; one of the best-studied examples occurs in a virus (161).

Conditional alternatives appear to fall into two broad categories, in terms of the selective contexts that give rise to them and (in some cases) induce their

expression: alternatives fundamentally due to environmental heterogeneity, and alternatives enabling escape from strong intraspecific competition for resources (e.g. nutrients, space, or mates). Heterogeneity-dependent examples include seasonal polyphenisms in color, dispersal propensity, and reproductive behavior (51, 82a, 207, 208); responses to flooding and dessication (38, 79, 229); different morphology and/or behavior in the presence or absence of predators (50a, 114); and some dispersal polymorphisms (11, 92, 104), although these may have a competition-dependent component (e.g. under high population densities).

An early review of competition-dependent alternatives was given by Wynne-Edwards (234). Some are associated with individual differences in competitive ability (especially, size) (see 121, 141, 152, 210). Others respond to resource scarcity and/or crowding, which can give rise to dispersal (11, 53a, 104), alternative trophic behavior and morphology (50a, 113), accelerated metamorphosis (36, 229), and cannibalism (36, 37, 68, 158). Competition-dependent alternatives may take advantage of environmental heterogeneity to “escape” strong competition with conspecifics; however, competition-dependence should be suspected if the two alternatives are of unequal profitability, with the less profitable one adopted in conditions of stress or resource scarcity by a facultative specialist. For example, Liem & Kaufmann (113) showed that the molariform morph of a cichlid fish switched to eating snails if food was scarce; and Grant (81) observed facultative consumption of difficult-to-crack large seeds by large-billed finches during times of food scarcity. However, alternative phenotypes also could evolve as a result of opportunistic use of different resources (e.g. different prey species) that are similar in value and cost, and which yet repay plasticity or optional specialization in mode of exploitation (201). All of these conditional alternatives represent intraspecific occupation of different “adaptive zones” or niches.

The evolutionary significance of a switch is twofold: It permits this persistence and modification of divergent intragenomic forms; and it means that the divergent forms can become dissociated (shifted, or lost) with little or no genetic change (78) (see sections on speciation and macroevolution, below). Divergence and dissociability characterize all kinds of switch-regulated traits. Tissues and organs represent developmentally switched “compartments” that can be experimentally and spontaneously displaced (74, 163), as can juvenile traits (via environmentally induced heterochrony—17, 77, 116, 128, 138). Similarly, sexually dimorphic traits can be shifted to the opposite sex (43) or remodelled in new contexts controlled by the sex-determination switch, as in the diverse caste systems of termites (149) and as hypothesized for the evolution of corn (above, after 98). Again, it matters little whether the switch involved is allelic or conditional; in either case the covariant sets of traits

controlled by the switch can be temporally shifted, changed in frequency, modified, or lost via selection affecting regulatory (especially, hormonal) thresholds.

Same-stage alternative phenotypes are of special interest for the evolution of diversity because they are “independent” of each other in the sense of being readily dissociable into separate lineages. “Dependent” or complementary forms (different organs of the same individual, queens and workers of social insects, male and female, and juvenile and adult) are relatively nondissociable in that they cannot readily reproduce on their own without the presence of complementary forms. Complementary divergent forms characterize “cooperative” entities, like colonial and multicellular organisms (222); “independent” alternatives can more easily lead to speciation, a point discussed in the next section.

## PLASTICITY AND SPECIATION

Several authors (33, 34, 67a, 124, 129) have presented theories of sympatric speciation suggesting that the evolution of a stable “genetic” (allelic-switch), multiple-niche polymorphism could lead to the evolution of assortative mating of like morphs, reproductive isolation between morphs, and the formation of two species, each resembling one of the original morphs. Mather (124) suggested that allelic-switch polymorphisms could, via local fixation of one form (or a subset of forms), determine the distinctive characteristics of new species, whether derived in sympatry or in allopatry. Other authors, having observed a resemblance between a particular species and one morph of another, closely related (polymorphic) species, have suggested that polymorphism could lead to speciation in particular groups (12, 38, 56, 113, 139, 145, 193). Rosenzweig (173) and Gibbons (76) have proposed that competition-driven disruptive selection can lead to sympatric speciation by simultaneously favoring extreme phenotypes and homogamy. This hypothesis is easily confused or lumped with the above theories involving the prior evolution of a stable polymorphism, especially because polyphenism is so often competition dependent (above).

All of these (except 124) are models of sympatric speciation. They presume that sympatric divergence must be “genetic” (governed by allelic differences between individuals of different forms) to play a role in speciation. And (with the exception of 124) they link phenotype divergence to assortative mating (e.g. the formation of seasonal or host “races” or separate lineages). Condition-dependent phenotypes have long been considered “of no significance for the student of speciation” (203a, p. 498). How could environmentally cued optional traits play a role in speciation?

The hypothesis to be outlined below differs from these previous models in

proposing that: (a) extensive divergence via intraspecific alternative phenotypes may occur *prior to* the assortative mating or reproductive isolation of distinctive forms; (b) this divergence can involve condition-sensitive or environmentally cued (not only allelic-switch) alternatives; and (c) polyphenism facilitates speciation, whether sympatric or allopatric (it is not a theory restricted to sympatric speciation).

### *Alternative Phenotypes and Speciation: A Hypothesis*

The special role of a switch (allelic or conditional) in promoting character divergence without breeding isolation has already been discussed. Once alternative adaptations have evolved, rapid speciation could occur by the following steps (224);

**PHENOTYPE FIXATION** The expression of only one of a set of alternative phenotypes in a population, phenotype fixation, can occur with little or (in the case of conditional alternatives) no genetic change, if the environment of the population uniformly induces or selects for a single alternative. By this means an entire complex set of traits can become suddenly characteristic of an isolate.

**INCREASED DIVERGENCE DUE TO PHENOTYPE FIXATION** Although phenotype fixation can be entirely nongenetic in nature (if the alternatives are environmentally controlled), this process is likely to be accompanied by an increase in the evolutionary (genetic) modification of the form approaching and attaining fixation (34, 145). This is expected because (a) selection should be increasingly effective (evolution more rapid) as one phenotype is increasingly common in a population (expression of alternatives represents a dilution of selection on particular forms). In addition, (b) divergent specialization of alternative phenotypes in polyphenic populations must sometimes be constrained by the ability of the rest of the genome (nonspecific modifiers—212) to be simultaneously compatible with two forms or behaviors, which in a sense “compete” for support from the rest of the genome. [Levins (110, p. 111) noted a possible macroevolutionary significance of this effect of “releasing alternatives” for rapid specialization or evolution in new directions.] This episode of adjustments of the newly monomorphic lineage might diminish as the features previously held in check become concordant with the newly fixed form. Evolution would then proceed at a relatively slow rate (potentially leading to a “punctuated” pattern of evolutionary change).

**ACCELERATION OF REPRODUCTIVE ISOLATION DUE TO DIVERGENT SPECIALIZATION** Divergence produces speciation if it is sufficient to cause reproductive isolation—pre- or post-mating incompatibility (8, 112, 133).

Although there is controversy over how much genetic divergence is involved in reproductive isolation (93), in general, it seems reasonable to argue that if divergence contributes to speciation, the greater the phenotypic and genetic divergence the greater the likelihood of speciation. From this it follows that the increase in divergence occasioned by phenotype fixation (above) contributes to the likelihood that reproductive isolation (speciation) will occur.

**RAPID ATTAINMENT OF COMPATIBILITY IN SYMPATRY** Ability to persist in sympatry following (secondary) overlap of a parental and a derived population is sometimes considered the final step in completion of speciation (133). Alternative phenotypes fixed in different populations are preadapted for sympatry by the fact that they originated in sympatry, often as a device for alleviating or escaping competition (above). This could facilitate coexistence of sibling species derived via phenotype fixation, with each population adopting a contrasting former alternative, or niche. A specialist derived from a polyphenic ancestor would be a superior competitor for the corresponding phenotype of closely related polyphenic populations. This might drive the latter toward fixation of a contrasting alternative, further increasing divergence and compatibility in zones of overlap. Thus, species derived via phenotype fixation are expected to achieve sympatry more readily than do those derived via allopatric speciation from monophenic populations (see discussion of “species swarms,” below). Species derived in allopatry from monophenic ancestors may be reproductively isolated (e.g. due to sexual selection—223), yet show little ecological divergence (Indeed, parapatric distributions—failure to overlap—are a notable though poorly investigated feature of some species pairs with divergent socially selected traits—223).

### *Evidence that Polyphenism Contributes to Speciation*

Demonstrating that phenotype fixation has contributed to a particular instance of speciation requires four kinds of evidence:

1. Evidence that a monophenic population (or one with a reduced number of alternative phenotypes) was derived from an ancestral polyphenic population characterized by that form and one or more alternatives. [This requires a group with both polyphenic and monophenic populations (or a polyphenic one in transition) and some evidence of direction of evolution, e.g. from cladistic analysis of phylogeny];
2. Evidence (e.g. from analysis of single broods and/or genetic study—177, 212) that the polyphenic population of origin (or considered to show incipient speciation or represent the ancestral condition) contains alternative phenotypes regulated by a switch and not some other phenomenon (such as sibling species, transient polyphenism due to evolutionary change, overlap-

ping forms of geographic origin, "balanced" polymorphism due to heterozygote advantage, or racial divergence entirely due to assortative mating);

3. Evidence that phenotype fixation occurred prior to, or along with, reproductive isolation (otherwise it could not be held to contribute to the speciation process);

4. Evidence of accentuated divergence due to phenotype fixation.

Many taxa contain both polyphenic species and monophenic populations or species that may have originated via phenotype fixation (reviewed in 224). In at least some of these cases there is increased specialization of the fixed phenotype in the monomorphic species. For example, intraspecific social parasites in wasps are behaviorally but not morphologically specialized. However, all socially parasitic species (believed derived from them by phenotype fixation—224) have independently evolved parallel morphological traits associated with aggressive parasitism, namely enlarged mandibles, a thick cuticle, and a recurved sting (224). Matsuda (127) noted that an accumulation of new specialization commonly accompanies phenotype fixation involving neotenous morphs. Although he regarded this as a kind of reaction to neotenous simplification ("material compensation"), the pattern may represent that predicted here as a result of phenotype fixation.

Morphological specialization following behavioral phenotype fixation can be rapid, as illustrated by the change in bill structure in the Laysan finch after only 20 years of isolation and restriction to a specialized diet (founder effects were apparently not responsible for the divergence) (154). Once speciation is complete (as in the case of the social parasites), however, it is impossible to ascertain whether the observed divergence has accompanied speciation, or occurred later, entirely as a result of reproductive isolation. For this reason it is of interest to examine populations showing some genetic divergence but not yet considered full species (e.g. known to hybridize readily in the laboratory or occasionally in the field, or occupying the extremes of an interbreeding cline). The following examples describe subspecific divergence that appears to satisfy all of the requirements (above) of the phenotype-fixation hypothesis.

Experiments by Cook & Johnson (38) demonstrated divergence accompanying phenotype fixation in the heterophyllic buttercup *Ranunculus flammula*. The conditionally dimorphic leaves are broad and lanceolate when they develop in the air, and linear (facilitating gas exchange, and persistence in turbulent water) if they develop under water. Populations from wet meadows consist entirely of individuals with lanceolate leaves; populations under constant immersion in lakes consist of individuals with only linear leaves; and individuals in lakes with seasonally fluctuating water levels regularly produce both leaf forms as a facultative response to conditions during the development of a particular leaf. When plants from a population with a

long history of constant immersion were transplanted to the land, they still developed the terrestrial leaf form but were weak and usually did not survive. Those from a constant terrestrial population produced aquatic leaves when transplanted to water, but failed to survive long-term submergence. Plants from dimorphic populations, on the other hand, survived both constant immersion and terrestrial conditions. Furthermore, the aquatic and terrestrial populations showed some morphological specialization, toward narrower and broader leaves, respectively; hybrids produced intermediate forms. These results show that while the particular phenotype adopted is under environmental control, the alternatives are modified independently under different selective regimes; and divergence is particularly marked when a single alternative is expressed over a period of generations (phenotype fixation). Cook & Johnson discuss the consequences of plasticity and phenotype fixation for the invasion of new ecological zones, and accelerated speciation in plants (especially, near borders between mesic and xeric regions in California): "There appears to be a set of habitats which, by being unpredictable, subject organisms to disruptive selection and consequently act as generators of evolutionary novelty" (38, p. 512).

In Pitcher-plant mosquitos (*Wyeomyia smithii* Coq.) the ratio of two alternative reproductive patterns varies along a South-North cline, ending in fixation of a single physiological and behavioral phenotype in the Northern United States. In the south adult females emerge with undeveloped ovaries and show both alternatives: some are entirely blood-feeding; and others mature their first batch of eggs "autogenously"—without a blood meal (using resources derived from larval feeding). However, if southern (30° N. latitude) larvae are given an artificially superior diet, nearly all (99%) resulting females produce a clutch of eggs without a blood meal, showing that autogeny is facultative. A South-to-North cline of increasing frequency of autogeny corresponds to a cline of decreasing larval densities within pitcher plants (20), with bloodfeeding completely absent North of 40 N. latitude even if females are reared on an inferior larval diet (117). There has thus been an evolutionary change permanently fixing the autogenous phenotype in Northern populations. Furthermore, obligatorily autogenous Northern females emerge with precocious ovarian development and mate earlier than Southern (Florida) females (151). The Northern populations (designated a "geographic race" by Bradshaw & Loubinos; 20) thus appear to show increased specialization to autogeny associated with fixation of the autogenous phenotype. In species and genera of mosquitos with obligate autogeny, females often have even more extreme autogenous specializations, such as modified mouthparts unable to pierce vertebrate skin and copulation in the female pupal stage (151, 196).

An additional example that satisfies nearly all of the above conditions is described by Shapiro (184). *Pteris virginiensis* (Pieridae) is a monophenic, univoltine butterfly closely related to polyphenic, multivoltine species of the



*P. napi* group. Experiments using this group showed that “univoltinism and monophenism were normally secondarily derivative from multivoltine-polyphenic ancestry” (188, p. 337). Furthermore, when reared in continuous light at high temperature, *P. virginiensis* could be induced to breed without diapause (like a multivoltine species), and to produce an alternative estival phenotype indistinguishable from that of its multivoltine relative *P. napi oleracea* (184). Biogeographic study showed that “univoltinism accompanies invasion of seasonally limiting environments” (188, p. 337); and recent work has shown the adaptive nature of these environmentally cued phenotypes in the situations where they occur (107). Thus, if *P. virginiensis* achieved species status as an isolate in the geographic region to which it is now adapted, phenotype fixation could have contributed to its divergence and speciation. This hypothesis would be further supported if recently derived, secondarily monophenic populations of these butterflies (or populations with a long-term strongly skewed phenotype ratio) show evidence of increased behavioral, morphological, or physiological specialization when compared to the homologous phenotype of related polyphenic populations. The finding of relatively dark wings in a species (*Reliquia santamarta*) showing obligate monophenism (cf species maintaining a latent polyphenism) (186, Figure 1) is consistent with the additional expectation of increased specialization in populations with a long history of monophenism.

Moran & Whitham (142) demonstrated geographic variation in the ratio of two alternative life-cycles in an aphid, one with host alternation and the other without. They state (p. 717) that “sudden life-cycle evolution through deletion of a phase has occurred in most major taxa showing complex life cycles.” Geographic variation in complex alternative phenotypes will likely prove as usual as geographic variation in morph ratios of allelic-switch polymorphisms, described in an extensive review by Mayr (133) as being as common as polymorphism itself. Martin & Simon (123) provide evidence that 13-year periodical cicadas may be descended via phenotype fixation from a life-cycle polyphenic ancestor capable of density-dependent switching between a 13- and a 17-year cycle.

As illustrated by the study of pierid butterflies (above), evidence that phenotype fixation has occurred is sometimes provided by the finding, in nature and in the laboratory experiments, of “lost” alternative phenotypes in individuals from monophenic populations believed (on the basis of phylogenetic study) to be descended from polyphenic ones. Such atavistic reversion has been described in salamanders (discussed in 127, 224) (see 185, 126–128 for additional examples). In some groups (e.g. stickleback fish—12) the same alternative phenotypes seem to have disappeared and reappeared repeatedly, since they occur in different combinations and with slight modifications in different species of the group (12, 83, 187).

If speciation occurred strictly according to this scheme, with the prime

mover of divergence and reproductive isolation the alternative phenotypes of an ancestor, it might deserve a special name—like “polyphenic speciation” (or speciation via phenotype fixation). More often, however, intraspecific alternative phenotypes may *contribute* importantly to speciation and accelerate it, along with other sources of divergence such as sexual selection and ordinary natural selection in allopatry. A synergism of polyphenism and sexual selection may contribute to extraordinarily rapid speciation, as suggested by Dominey (55) for African Cichlids and amphipods, and Hawaiian *Drosophila*. Sexual selection (competition for mates) produces two kinds of divergence: rapid allopatric divergence of traits involved in courtship and male-male interaction (223); and intraspecific divergence in the form of alternative mating tactics (5, 210). The first could combine with phenotype fixation to cause rapid speciation in allopatric isolates; and the second could combine with parallel (e.g. size, seasonal- or host-dependent) polyphenisms to segregate a population into spatially and/or assortatively mating cohorts of like phenotype, where any genetic differences affecting phenotype determination would be exaggerated, enhancing the likelihood of speciation. Such a process may be occurring in salmon, where partial assortative mating of combined-switch anadromous and nonanadromous phenotypes differing in size and habitat (but spawning together) is associated with genetic divergence of forms (66, 67). This may prove an important phenomenon, since homogamy by size is widespread in animals (166), as are size-associated alternative phenotypes in mating (21, 54, 57, 58, 176, 210), and ecological behavior (62, 91, 121, 138, 175).

Several hypothesized examples of sympatric speciation need to be reexamined in light of the ideas presented here, at least to the extent of considering (and specifically rejecting) the hypothesis that the original sympatric character divergence may have been polyphenic. They include (a) the *Rhagoletis* host-race example of Bush (24, 25), where, as previous authors have suggested (73, 82a, 133), the ability to occupy a new host and associated characters potentially contributing to reproductive isolation (size, host selection, ovipositor length and emergence time (23, 25) could originate as facultative responses to photoperiod and/or host plant; (b) the lacewing (*Chrysopa*) of Tauber & Tauber (204, 205), where, although *species* differences in diverged traits (timing of diapause and reproduction) are known to involve genetic divergence as expected, in a California population “polymorphic” for these traits they are environmentally cued (“directly dependent on the availability of prey”) (206); and then (c) the “competitive speciation” example of Gibbons (76), in which three *Megarhyssa* wasp “species,” differing primarily in ovipositor length, may be morphs [they are now known to interbreed in the field (41); progeny of single females were not examined (necessary in order to distinguish morphs from species); and ovipositor polymorphisms are

known in several species of parasitoid Hymenoptera (7, 144, 146, 175), some of them formerly named as separate species, and differing in body size, color, and host—(175; see 86)]. This is not to say that sympatric speciation has not occurred, but much of the observed divergence may be polyphenic in origin rather than a result of assortative mating or race formation, as proposed by these authors.

Although sympatric divergence (polyphenism) could facilitate sympatric speciation, it could also create the mistaken impression that sympatric speciation has occurred. It may sometimes “prime” populations for rapid speciation, given even a short episode of allopatric isolation, and then “preadapt” them for coexistence in sympatry, a point I have already discussed. Thus, when circumstances are particularly favorable to speciation (e.g. isolated islands of habitat are repeatedly formed and fragmented, or colonized at intervals sufficient to permit genetic divergence), polyphenism may contribute to spectacular local radiations. There is increasing evidence of polyphenism paralleling species differences in the taxonomic families involved in such radiations, e.g. in the Cichlidae (see 84, 113, 137, 138, 211, 224 for evidence and references), which have formed “species swarms” in African Lakes; and in the trophic morphology and behavior of finches (81, 154, 194, 219), which have trophically radiated in the Galapagos islands. In crowded communities of closely related species and morphs, interspecific competition could help drive alternative phenotypes to fixation. However, the tempting conclusion that sympatric speciation is involved (113, 137, 139) is not yet justified. It would require finding two sympatric, reproductively isolated forms likely derived from a known, assortatively mating, polyphenic (sibling) population, with no evidence of secondary overlap following morph fixation (monophenism) in a geographic isolate (a difficult condition, since even if monophenic isolates are not found they could be claimed by cynics to have existed in the past).

## PLASTICITY AND MACROEVOLUTION

Macroevolution, or transspecific evolution, is evolutionary change greater than that usually characterizing species in a particular group of organisms (133). Such “higher level” change is sometimes associated with major adaptive innovation, followed by the radiation of a lineage in a new adaptive zone, although these two phenomena do not necessarily go together (89, 174, 200).

Naturalists have long used plastic traits as a source of ideas about macroevolutionary transitions, without focussing on plasticity itself as an agent facilitating change (but see 62, 134). For example, Romer (171) recognized that the facultative alternative phenotypes of lung-bearing fish (airbreathing, and terrestrial locomotion) occur in response to conditions (periodic or sea-

sonal drought) thought to have accompanied the vertebrate transition from water to land in the Devonian; but he did not pay special attention to the fact that this implied that a major transition was represented within the confines of a single genome. The facultatively airbreathing fish (79, 80) could serve as a prototypical example of how plasticity may be involved in macroevolutionary change.

### *Properties of Alternatives Promoting Extreme Divergence*

Two factors may render intraspecific alternatives disproportionately important (compared to allopatric divergence) in macroevolution (224): First, selection for contrasting alternatives. The conditions producing selection for alternative modes of resource procurement—e.g. strong intraspecific competition, individual phenotypic handicaps (such as small size), and seasonal fluctuations in resource availability or population density—place a premium on novel alternative phenotypes that contrast with established ones. They may move individuals of low fitness into a contrasting “niche” where their former handicaps become advantages, and the advantages of their competitors become handicaps (222); or where a different, more abundant resource is exploited. Degree of allopatric change, on the other hand, depends on degree of difference in allopatric environmental conditions, or drift, processes not involving selection for divergence per se. And second, the buffering effect of alternatives, discussed above: facultatively expressed novel traits can be elaborated as alternatives alongside established characters, allowing a species to develop a new specialization without abandoning an old one. By means of facultative expression, new niches can be entered without passing through the “maladaptive” transitions (“valleys between peaks”) sometimes visualized as accompanying major adaptive change (15, 133, 197, 212).

### *Evidence of Macroevolutionary Change via Alternatives*

Alternative phenotypes that show a macroevolutionary degree of divergence by the above definition have been discovered in a variety of taxa, in spite of the fact that they are difficult for taxonomists to recognize as being of the same species without special study, e.g. laboratory rearing or genetics (electrophoresis). Some have already been discussed in the section on speciation, for example, upright and crustose forms of marine algae (118), phoretic and normal forms of mites (145), trophic morphs of fish (87, 113), and parasitoid wasps differing in size, ovipositor length, and host (175). Examples involving behavior are undoubtedly more common and important in phylogenesis and adaptive radiation (134). A spectacular example is provided by the Cocos Island finch, in which different individuals show lifetime, learned specializations in feeding (on diverse arthropods, floral and extrafloral nectar, 17 species of fruit, seeds, molluscs, and small lizards) that would span those of

several families of mainland birds (219). Liem & Kaufmann (113) suggest that such "intraspecific macroevolution" may be an important mode of transpecific change in fish and other organisms.

Most convincing are examples of polyphenisms that represent within a single species both the ancestral and derived states of changes considered to have been major transitions in the history of life, with the polyphenic species in a group considered (in phylogenetic analysis) close to the common ancestor. The facultative alternative trophic specialization (to saprotrophy, necrotrophy, and biotrophy) of certain fungi represents within species the dietary specializations of different trophic radiations (39); and the facultative carnivory (cannibalism) of some primarily phytophagous wasps resembles the central *Phytophaga*—*Terebrantia* transition in the evolution of the Hymenoptera (122). Facultative group life is widespread in species of primarily solitary wasps and bees, in the families closely related to those that gave rise to highly social families showing obligatory life in groups (140, 231).

Moran (141a) discusses how occupation of secondary hosts by aphids having complex life cycles has permitted exploitation of diverse plant resources not available to the older, hyperspecialized morphs inhabiting primary hosts (woody plants). A common pattern of evolution in the aphids is invasion of a new niche via seasonal polyphenism involving a new (secondary) host (e.g. a herbaceous plant), followed by evolution of a reduced cycle specialized to the secondary host. When life cycle reduction has been accompanied by transfer of both sexual and dispersing forms to the secondary host (in effect rendering occupation of the secondary host a fully independent "dissociable" alternative) it has led repeatedly to "extensive radiation on the more recently acquired plant groups" (142). Moran (141a) estimates that although only about 10% of aphid species have seasonal alternative host plants, most modern aphids probably had heteroecious (host-plant-alternating) ancestors. Thus, host plant alternation, although not the most common life-cycle pattern, may have been disproportionately important for aphid radiations in the adaptive zone represented by herbaceous plants.

Heterochrony (phyletic change in the timing of development of a particular trait—77) can contribute to macroevolutionary change in both plants (116) and animals (77). The sudden change represented by heterochrony may often be accomplished via a polyphenic stage characterized by multiple alternative pathways of development. T. S. Ray (submitted) has shown how the advent of switches in the evolution of aroid plants (*Araceae*) has led to the multiplication of dissociable shoot-development pathways, and the evolution of different numbers and arrangements of pathways in different species. In three subfamilies (*Pothoideae*, *Calloideae*, and *Colocasioideae*) heterochronic shifts and multiplication of pathways have produced climbing vines allowing the invasion of a new "adaptive zone" (trunks and branches of trees) not

available to terrestrial taxa. Matsuda (128) provides extensive evidence that heterochrony very often originates as a developmental defect ("abnormal metamorphosis") creating a condition-sensitive polymorphism. And Gould (77) used intraspecific alternative morphs to illustrate the niche specializations of heterochronic forms. Recently Meyer (138) showed that heterochrony is involved in diet-induced morphological differences between individual cichlid fish. All of these findings are of great significance in the present context, because they mean that complexly distinctive heterochronic morphs, being facultatively expressed, would not have to be superior to established forms, or immediately finely adapted to their circumstances, in order to persist. If (like any other successful mutation) they happen to be relatively advantageous in the environmental conditions inducing them (or associated with their production), they can persist as alternatives and be gradually modified by selection. Then (via phenotype fixation) they could come to characterize a distinctive lineage.

Phenotypic fixation need not involve speciation. A long history of gradual (Micro-evolutionary) elaboration of a novel alternative, followed by its fixation, could occur entirely as an aspect of phyletic evolution (anagenesis). Thus, a single, unbranched lineage can both move into a new adaptive zone and abandon an old one without speciation (140, 224). Macroevolution via polyphenism thus differs from the classical Darwinian idea of gradual divergence via a series of speciations eventually adding up to a large change (see Darwin's figure in 45, p. 87). Nor does it fit the "punctuated equilibrium" pattern of macroevolution (61), which is like Darwin's except that speciation-associated divergence occurs in sudden (but small) bursts followed by stasis (and differential extinction of species), giving rise to a pattern that might be called "punctuated gradualism"; neither does it fit Simpson's (190) idea of "quantum evolution," in which a lineage undergoes rapid and drastic change involving a poorly adapted intermediate stage. In all of these previous descriptions, divergence requires lineage separation (speciation) (see also 135), whereas in the cases described here macroevolutionary change has occurred without lineage bifurcation.

## CONCLUSION

Most of the points discussed here have been made many times before, as is indicated in the references. Taken together, they indicate that phenotypic plasticity deserves increased attention as a factor influencing rates and directions of evolution. This requires a change in how many biologists currently view the evolution of phenotypes. Especially, it requires understanding the sense in which characters do not have to be "genetic" (immune to envi-

ronmental effects) to be evolutionarily important; and the manner in which phenotype expression, especially when there is a switch or bimodal distribution of forms, can focus natural selection to produce extensive divergent specialization without reproductive isolation. These ideas do not contradict the tenets of conventional evolutionary theory. They simply put to use the sometimes forgotten dicta that the phenotype is a product of both genotype and environment, and is also the focus of selection. When exploited more thoroughly and more expertly than is possible for one person in one review, attention to the nature of the phenotype will clarify many issues (e.g. regarding modes of speciation, social traits, and the origin of major novelties) sometimes considered "difficulties" for theories of evolution that neglect plasticity.

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