

How do major evolutionary changes occur?¹

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Received 1 August 1987

Mechanisms of Morphological Evolution, by Wallace Arthur. 1984. Chichester and
New York: Wiley. 275 pp. \$53.95.

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It may be necessary to remind geneticists that morphologists have thought about form and its evolution for a long time and that some of their conclusions may be worthy of attention (to crib from Maynard Smith in a different context.)

I hadn't planned to review this book, but the negative tone of some previous reviews changed that. Arthur has interesting ideas on a basic but commonly ignored subject, and he is familiar with (and largely sympathetic to) most relevant existing theory. His book is important, if overpriced, and the subject won't go away by ignoring it or simply asserting by the undulomaniac method (hand-waving) that there is no problem. My presentation here is partly based on Arthur's book but modifies aspects I find dubious and adds others.

The subject is the origin of the major structural types (or Baupläne, or whatever other term you can think of if "type" raises hackles of fixist or anti-population views, which it shouldn't any more), say at the level of phyla or classes. Arthur restricts himself to animals, but that isn't necessary. The problem exists not merely because intermediate phenotypes often seem at least unlikely, and because gradual and diverging transitions from a common ancestor aren't much better; these difficulties may possibly be due to our lack of imagination, although whether this escape suffices in general is arguable.

More basically, the problem exists because development is integrated. Normal evolution operates in the framework of normal development; modifications are mostly relatively superficial and must not interfere with basic morphogenetic processes. Just as adaptations to life in a desert may be cumulative and interrelated, making invasion of a swamp or even a prairie awkward at best, so the existing mode of development becomes less subject to basic modification as its superstructure evolves in its presence and subject to its veto. Also, mechanisms often exist to correct deviations which do occur before late stages. There is an internal environment as well as an external one, and it demands more than lip service. Such entrenchment occurs because development ramifies out; later developmental decisions depend on earlier ones which are much fewer and have consequences which interact. Development is not a linear sequence and not even merely a tree, but an expanding network even in animals with mosaic development (Priess and Thompson, 1987; Van Valen, 1962: 136-137.)

Major morphological mutations are normally deleterious and perhaps usually lethal, and there are good reasons to expect this. It is nevertheless appropriate to ask to what extent this low fitness is conditional on the existing pattern of developmental integration. In other developmental (genetic) environments their fitness may differ. We may see this in some of the alleles which are lethal in some backgrounds but normal in others (Thompson, 1986); major mutations also tend to have their expressivity reduced and fitness increased as natural selection provides a more congenial developmental context, so that occasional outcrossing is often necessary to maintain their expression.

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¹Contribution 68, Lothorien Laboratory of Evolutionary Biology.

Evolutionary Theory 8: 173-176 (May, 1988)

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The above examples differ from the reshuffling of genetic background which commonly reduces fitness in artificial-selection experiments, because the major mutation occurs in an initially normally integrated background. That the integration is appropriately seen as developmental rather than merely genetical results from the emergent properties of development. Also relevant are the commonly equivalent potential effects of genotype, tangible environment, and intangible environment. (Goldschmidt [1955] gave what is still the best review of phenocopies I know, and the equivalence in kind of effect is apparent throughout quantitative genetics, canalization, and morphological correlations.) Developmental integration is a powerful stabilizing force. (Its relevance to species-level punctuation is a different question, as Arthur notes.)

A geneticist might want to explain developmental entrenchment by a negative genetic correlation between fitness and amount of deviation from the optimal phenotype, appropriately scaled for nonlinearities. This would be a canalizing response to stabilizing selection, but it isn't enough. With only a negative correlation, the phenotype-fitness curve can be changed merely by a shift in position of the optimum, although it may take a few generations for linkage disequilibria and such to get sorted out. With entrenchment, on the other hand, diverse developmental paths are affected and may need modification when their center changes. At the genic level this involves substitutions and the like rather than primarily recombination. The natural selection which usually opposes artificial selection can have both components. The rapid reversal of response when selection is relaxed contrasts with, e.g., the diverse and often severe malformations produced as byproducts of artificial selection for different breeds of dogs (Stockard, 1941). Strong selection of the hard type (independent of population composition) presumably often leads to extinction rather than a successful response. It would be useful to measure aspects of fitness during and after relaxation of some reasonably prolonged artificial selection.

Although allometry is often considered a major developmental constraint, it is a character like others and is commonly modifiable by selection (Kurtén, 1954). Genetic variation for it is well known (Cock, 1966), but the clearest evidence for its modifiability probably comes from the usual difference between intraspecific and interspecific slopes (Gould, 1966). The former reflect, mostly, development, but the same development would then give the same slope in interspecific comparisons. The latter therefore are evolved by many changes, one or more for each derived species whose intraspecific slope differs from the overall slope. It must therefore be an adaptive response, and it provides one of several general reasons for believing in the preponderance of adaptation in phenotypic evolution.

Evolution of allometry has another important evolutionary consequence. A common assumption in evolutionary quantitative genetics is that the within-species covariance matrix for additive genetic effects remains constant. Schluter (1984) has even calculated evolutionary distances among species of Galapagos finches using this assumption as central. Like any covariance, these change as size changes, but correlations, which are insensitive to this difficulty, are equally sensitive in another way. A negative genetic covariance provides the greatest difficulty in selecting in the same direction on two characters (and vice versa), but if there is variation in the allometric relationship between them the same selection will select for a more nearly positive relationship. This selection is as strong as that on the characters themselves. If there is a response, it may or may not be reversed later (internal developmental adjustments again), but it provides an expectation of common and predictable shifts in genetic covariances and correlations. Such shifts do empirically occur (Lofsvold, 1986), although their rates and frequency are not yet clear, and other, if more diffuse, mechanisms exist.

"The idea of some sort of 'generalized' ancestor not highly [integrated]

and adapted to a particular ecological niche seem nonsensical; and in any ancestral form whose modifiers have been progressively refined so that they modify a major gene's effect in a particular way for a particular ecological purpose, a major mutation will result in an imbalance between the gene concerned and its modifiers . . ." (p. 236), although it is possible that less entrenched (and even less complex) development characterizes early stages of adaptive radiations (Simpson, 1953), when many of the major changes occur.

How then to escape from a local developmental adaptive peak? At least four ways suggest themselves. One is gradual (but not necessarily slow in geological time) modification as the adaptive landscape changes. This is of course the usual view, and both adaptive and developmental thresholds may be relevant to it. A second way, perhaps a variant of the first, is by a change (or gain) of function: protoadaptation, in the felicitous term of Gans (1979), who emphasized initial unnecessarily high or low amounts of a structure or behavior. A third way is Simpson's quantum evolution, a geologically rapid shift across an adaptive threshold in a perhaps constant landscape. Each stage may be more fit than the preceding, or there may be an inadaptive phase (most likely caused by change in the physical or biotic environment rather than by drift, as Simpson had it). Wright's shifting-balance theory is related to all these alternative escapes. However the transition occurs, the occupants of the new adaptive zone should tend to diverge from those of the old, by both selective extinction of intermediates and consolidation of the new adaptations and associated development.

A fourth possibility is a non-Goldschmidtian macromutation or other very rapid shift to a new but relatively unintegrated developmental pattern. To be successful, this shift must land in an effectively unoccupied adaptive zone; competition would presumably be fatal. But if it can survive without competition, the new form can evolve its own integrated development and undergo adaptive radiation. The change is of a keystone or a large threshold jump, not the establishment of a new pattern mit einem Schlag. Wilson and Turelli (1986) have recently discussed one mechanism in this general approach from a genetical viewpoint.

The usual arguments against this third general approach don't destroy it. A large modification of early development may not always be lethal; at least we can't say that it is. There need not be any sort of isolation, spatial or reproductive, between the forms, as shown empirically by the coexistence of conspecific morphs of the fish Ilyodon which are different enough to have originally been placed in different genera (Grudzien and Turner 1984a, b). Reliance on spatial isolation means either a coincidence of the developmental shift with arrival on an island or the like, or the likely swamping of the new form by further dispersal. Reproductive isolation, which Arther does want, can be plausibly obtained in several ways (which he discusses) even for sexual organisms. But none is necessary: developmentally integrated but ecologically distinct morphs occur together in various species of plants and animals; why not, more rarely, larger differences? The change can initially be induced even by a continuing environmental stress (see Van Valen, 1974, for theory and an example.) An improbable concatenation of events, but that is a reasonable expectation for very rare phenomena. Neoteny is a variant of this general approach, but it has its own difficulties (Cohen and Massey, 1983) in addition to sharing the others except, probably, for as large a reduction in integration.

The apparent difficulty in escaping from entrenched early development is the main reason to suspect that the third, saltational, mechanism has occurred. I don't know how either of these subjects can be investigated seriously rather than undulomaniacally, with what we know now, although miniaturization may have promise (Hanken, 1984, 1985; Trueb and Alberch, 1985). The recognition of an important and unstudied subject, though, is a first and perhaps threshold step.

I thank W. Arthur for discussion.

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