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Daniel G. Blackburn

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From Whale Toes to Snake Eyes: Comments on the Reversibility of Evolution

DANIEL G. BLACKBURN

Department of Anatomy, New York State College of Veterinary Medicine,
Cornell University, Ithaca, New York 14853

In his recent discussion of evolutionary reversibility, Macbeth (1980) argued that the views of Lande (1978) conflict with classical evolutionary theory as put forth by Simpson (1953). Macbeth discussed two types of evolutionary phenomena that represent extremes of a continuum: large-scale reversal, which is widely assumed to be highly improbable or impossible; and small-scale reversal, which is believed to have produced a variety of reversions or atavisms observed in single specimens or entire populations. The former can be termed "macroevolutionary reversal" and the latter "microevolutionary reversal." Lande's (1978) analysis cited cases of horses, guinea pigs, canids, and cetaceans in which digits or other limb elements have apparently been re-expressed 10^6 to 10^7 generations after their loss. Macbeth (1980) regarded Lande's interpretation of these structures to be incompatible with Simpson's (1953) statements on the impossibility of large-scale evolutionary reversal. In a brief rebuttal, Laurent (1983) pointed out that—because Lande's (1978) model invoked the suppression and the subsequent re-expression of regulatory genes—it actually represented a case of small-scale reversal. Here, I respond to the implication that an interpretation of the structures in question as evolutionary atavisms is somehow in conflict with Simpson's ideas, and comment upon some implications of issues raised in the exchange of viewpoints.

SIMPSON'S VIEWS

Macbeth (1980:402) quoted Simpson (1953:311) on the improbability of large-scale reversal, and then stated:

On my first reading of Lande's paper, I was startled by his temerity in setting out his (and Wright's) rather frail speculations in the face of Simpson's crushing pronouncement. Further reflection, however, has led me to believe that he was not utterly rash, reckless, or irreverent. Lande does not mention it (and may not have noticed it), but Simpson's position, when closely examined, has certain frailties of its own First, Simpson's prohibition of reversals is so strong that it conflicts with the Second Phenomenon, the observed throwbacks Thus Simpson's argument is an overkill; he is so vigorous in prohibiting reversibility that he leaves no room for the known reversals.

Simpson, of course, was quite familiar with atavisms and the time frame of their expression. To illustrate a point, Simpson (1953:311) even cited the same case of the polydactylous guinea pigs (*Cavia cobaya*) analyzed by Lande (1978). A typical quote will illustrate his views:

There is nothing in the analyzably separate factors of evolution that prohibits reversion. Back mutations occur. Lost combinations can be reconstructed by recombination. Variation is practically always present on *both* sides of the mode. Selection can reverse its direction. As regards particular characters and trends, therefore, if genetic variation and selection really are essential features of evolution, it should be reversible—and it is [Simpson, 1953:311].

The magnitude of evolutionary reversal generally regarded by Simpson to be so highly improbable was that which would be required to recreate an ancestral form from a derived taxon:

Nothing quite like an earlier form of life ever evolves again, for the simple reason that time does not double back on itself. If there is a sequence of ancestral and descendant organisms $a \rightarrow b \rightarrow c$, then b evolved from a and would have been different if a had been different in any respect. Evolution cannot be reversed: b cannot evolve from c ,

because c is different from a and cannot possibly give rise to quite the sort of organisms that arose from a [Simpson et al., 1957:469].

Macbeth (1980) claimed that the views of Simpson (1953) and Lande (1978) were in substantial disagreement. However, I can find no conflict between their views beyond minor differences in interpretation directly attributable to the historical context of their works. In a sense, each author was fighting a different battle with different weapons. Lande's (1978) analysis interpreted evolutionary reversals in the light of modern genetics. In contrast, Simpson's efforts were often directed against those of his contemporaries who sought to apply Dollo's Law inappropriately (e.g., see Simpson 1945:11). As Laurent (1983) pointed out, Lande's (1978) interpretations are fully consistent with the theoretical framework constructed by Simpson. It is true that Simpson seldom engaged in elaborate speculation on the genetic basis of reversibility. However, most of his work preceded by decades various crucial experimental and conceptual advances whose influence has only begun to be felt in the field of evolutionary morphology (e.g., see Frazzetta [1975], King and Wilson [1975], Bush et al. [1977], Gould [1977]). Thus, his reticence on the subject seems eminently judicious:

This principle is not theoretically demonstrable: complete reversion and complete convergence are not wholly excluded by present genetical or general evolutionary theories, but they are highly improbable in the light of those theories [Simpson, 1945:11].

Unfortunately, this does not seem to be the first time Simpson's views have been misconstrued. Regarding the hypothesis that a very low selection coefficient (s) may be effective in evolutionary change, Macbeth (1971:43) stated:

Simpson candidly concedes "it might be argued that the theory is quite unsubstantiated and has status only as a speculation." From the evidence, I would have thought this had already been demonstrated rather than merely being arguable, but Simpson pursues this line of thought no further.

In actuality, as the full quotation demon-

strates, Simpson not only made no such concession, but thoroughly rebutted the argument in question:

Since theoretically effective very low values of s cannot be directly observed and determined, it might be argued that the theory is quite unsubstantiated and has status only as a speculation. In fact there is excellent indirect evidence on this point, from both neontology and, particularly, paleontology, the bearing of which has often been completely misunderstood [Simpson, 1953:118].

As a matter of fact, the best and I think quite conclusive proof that very small values of s are often effective in nature is precisely the evidence so often cited against the effectiveness of selection. This evidence shows that adaptation may begin and proceed on the basis of very small variations and may reach a very intricate and high degree of perfection, so that its continued trend, and the point reached must have involved very small selective values if selection was involved [Simpson, 1953:144].

Such misrepresentations may make for effective polemics, but they are of little value in the resolution of biological issues and ill-serve the reputation of a great biologist. Simpson's extensive work (see Hecht et al. [1972] for a partial bibliography) is permeated by intellectual honesty and the acceptance of new approaches (e.g., see Simpson, 1975). Under the circumstances, perhaps it should be left to Simpson to state whether he found Lande's (1978) paper to be "rash, reckless, or irreverent" (Macbeth, 1980:403).

FILM ANALOGY

Laurent (1964) suggested that macro-evolutionary reversal would require a highly improbable orderly sequence of individual genetic changes, which he compared to the unreeling of a movie film. The analogy is quite appropriate both for its visual impact and for its explanatory value. A major reason that one instantly recognizes when a movie is being run in reverse is that the apparent causal connections observed are so highly implausible, not to mention the fact that the physical laws are seemingly violated indiscriminately. An ancestral condition is, in a broad sense, a major cause of those that are derived from it; for this reason, one can speak

TABLE 1. Comparison of the eyes of lizards and snakes. For the characters listed, snakes exhibit the derived condition and lizards the primitive condition based on outgroup comparison with other reptiles. Data are from Walls (1942) and Bellairs and Underwood (1951).

| Characters | States | |
|--------------------------|------------------|-------------------|
| | Lizards | Advanced snakes |
| 1 Nictans | present | absent |
| 2 Transversalis muscle | present | absent |
| 3 Retractor bulbi muscle | present | absent |
| 4 Scleral cartilage | present | absent |
| 5 Lacrimal canaliculi | two | one |
| 6 Retinal fovea | present | absent |
| 7 Conus papillaris | ectodermal | mesodermal |
| 8 Iris muscle | ectodermal | mesodermal |
| 9 Accommodation | lens deformation | lens displacement |
| 10 Lens shape | flat | subspherical |
| 11 Intraocular filter | retinal | lens |

of preadaptations and constraints. Reversal of a complex evolutionary transformation would require improbable reversals of causal sequences at both phenotypic and genotypic levels. Thus, the analogy is applicable to the sequence of events as well as to their presumed causal relationships.

THE OPHIDIAN EYE

In his reply to Macbeth (1980), Laurent (1983) cited the snake eye as an example of a structure that was lost evolutionarily and subsequently reappeared, although with some modification. In so doing, Laurent drew upon Walls' (1942) theory on snake origins. According to this theory, snakes are derived from fossorial ancestors with atrophied eyes; upon reinvasion of the surface by early ophidians, the eye was essentially rebuilt from existing materials, which accounts for its many peculiarities. Laurent indicated that this apparent evolutionary reversal probably involved the inhibition of a suppressor regulatory gene affecting eye development.

Underwood (1957) suggested that, rather than having undergone atrophy during the fossorial ancestry of snakes, the eye merely became simplified and never lost the capability for simple visual performance. His modification of Walls' (1942) theory was based largely upon evidence

that burrowing snakes presumed to be close to ophidian ancestry possess eyes that are simplified but not degenerate. An outgroup comparison of snakes with other reptiles supports Underwood's (1957) scenario more strongly than Laurent's (1983) genetic hypothesis. The derived features of the ophidian eye comprise two categories (see Table 1): those reflecting simplification due to loss (characters 1 through 6); and those representing innovations (characters 7 through 11). In some ways the eyes of advanced snakes have become simplified, but they have apparently also evolved new structures for such functions as retinal nutrition, iris control, and filtration of incident radiation.

The scenario most consistent with these data is one that involves simplification followed by convergent modification, rather than atrophy or loss followed by re-expression or de novo re-evolution. There seems to be little reason to invoke explanations involving the suppression of hypothetical regulatory genes, nor is it clear for what features these genes would code.

TESTABILITY AND REVERSIBILITY

The fact that the case cited may not be an ideal example of regulatory gene suppression does not affect Laurent's (1983) argument; plausible cases can be found elsewhere in Laurent's work as well as in the massive teratological and evolutionary

literature. However, the example does relate to a final issue raised by Macbeth (1980)—the question as to what criteria can be used for the detection and characterization of evolutionary reversals.

Two major bodies of evidence support Underwood's (1957) scenario. The simplification hypothesis is based upon morphological and phylogenetic evidence coupled with theoretical considerations. The modification hypothesis rests upon detailed embryological and physiological data of a sort unavailable for most organ systems of most vertebrates. If the latter body of information were lacking, the ocular features of lizards and advanced snakes could be assumed to be homologous, and a scenario involving regulatory gene suppression and reactivation would seem quite plausible. The case illustrates the need for careful analysis of suspected reversals by means of all biological tools possible; anatomy alone may be insufficient to distinguish gene re-expression from latent convergence.

As the ophidian example suggests, evolutionary reversals are seldom recognized on the basis of detailed knowledge of the genetic mechanisms involved. Rather, reversals are detected through reference to particular phylogenetic hypotheses. Reversal is typically invoked only when alternative explanations such as convergence and ancestral retention seem especially unlikely (e.g., see Raikow et al., 1979). The systematist routinely accepts a certain number of microevolutionary reversals as the most economical explanation for a given character state distribution and, in fact, often constructs his phylogenies so as to minimize such reversals.

Unfortunately, we risk miscalculating the frequency of an evolutionary reversal to the same extent that we miscalculate its probability of occurrence. The problem does not arise for reversals at the extremes of the spectrum; we have excellent reason to accept the likelihood of microevolutionary reversal and to reject the possibility of macroevolutionary reversal. It is hypothetical reversals of uncertain prob-

ability, such as the transition from oviparity to viviparity, that seem to present something of a tautological dilemma (Blackburn, 1984). In constructing a phylogeny, if we reject the possibility of reversals exceeding a certain magnitude, our phylogeny will be of little value in the detection of such reversals. The reversed features will simply be interpreted as plesiomorphic, with the concomitant phylogenetic and evolutionary implications.

How, then, are we to detect and characterize such reversals? The systematist is in much the same situation in attempting to judge the probability that a given character state complex has arisen convergently. Intuition no longer seems adequate to the problem, for as we now know, minor genotypic changes can have unexpectedly large phenotypic consequences. The implications of recent genetic advances do not seem to have been fully recognized in systematics; I am frequently struck by the casualness with which developmental biologists dismiss the same phenotypic changes to which systematists attach great importance.

In questioning the testability of our genetic hypotheses, Macbeth (1980) voiced what should be very real concerns. As long as the genotypic basis for specific phenotypes remains mysterious, one risks sacrificing accuracy in the name of parsimony. Whether evolution is always as conservative as we tend to assume still seems to be something of an open question.

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Cladograms Should Be Called Trees

M. D. HENDY¹ AND DAVID PENNY²

¹Department of Mathematics and Statistics and ²Department of Botany and Zoology, Massey University, Palmerston North, New Zealand

"But 'glory' doesn't mean 'a nice knock-down argument,'" Alice objected.

"When I use a word," Humpty Dumpty said, in a rather scornful tone, "it means just what I choose it to mean—neither more nor less."

"The question is," said Alice, "whether you can make words mean so many different things" [*Through the Looking Glass*, by Lewis Carroll].

Graph theory is usually regarded as a branch of mathematics. However, it has been independently discovered many times with origins in physics (Kirchoff, Uhlenbeck, Feynmann), chemistry (Cayley), psychology (Lewin), and probability theory (Markov), as well as in mathematics (Euler, Hamilton). Because of its multiple origins, some graph theoretic terms have many synonyms. Harary's (1969) is a good expository text which refers to these

early applications and it lists the diverse nomenclature. In contrast, his fourth chapter entitled "Trees" begins, "There is one simple and important kind of graph which has been given the same name by all authors, namely a tree."

This widely accepted definition is: A tree is an acyclic connected graph. The generic term tree has been specialized to a number of types such as directed trees, labelled trees, binary trees, etc. (see Fig. 1). Thus, the taxonomic diagrams such as cladograms and evolutionary trees are specialized types of trees. This terminology is not universally accepted in biology, and it is disturbing to read (as one example) in Nelson and Platnick's (1981:171) text that, "A cladogram, therefore, is not a tree." This