

BRIDGES BETWEEN EVOLUTIONARY PATTERN AND PROCESS

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"Most of the distinctive characteristics of higher taxa are surely adaptations that evolved by natural selection..." Futuyma (1979: 434).

"All of biology compels us to recognize that organisms are not optimally designed, that many features are not adaptive, and that species may differ for reasons other than natural selection." Futuyma (1986: 254).

De Pinna and Salles ask for clarification on how cladistic analysis tests adaptational hypotheses (de Pinna and Salles, 1990; Coddington, 1988). They also point out that an alternative optimization exists for character 3 in my (1988) fig. 2. Yup, OK, I'll admit it. All readers of the previous paper are hereby instructed to believe that a new taxon has been discovered, identical to taxon D except for some convincing autapomorphies which need not concern us. Based on this new information, the previously reported optimization wins by one (and only one) step. Hey, close don't count in cladistics!

Passing on to a more profound issue, I have to confess a long-standing difficulty with the allegedly important distinction between "states of becoming" and "states of being". If something already is, I would guess it probably became in order to be, and if it is only becoming, it had to become from somewhere, and probably to somewhere as well, not to mention be while it is becoming. I am not sure whether I view adaptation as becoming rather than being or whether the distinction makes a difference.

Most of de Pinna and Salles's remaining arguments tend to the same point: however desirable, no amount of mapping characters on cladograms has yet provided an "empirical bridge", "bridge concept", "empirical link", or even "true and empirical relations" to processes such as natural selection or process theories such as adaptation. Although I think the jargon peculiar to theories about theories often obfuscates simple issues (anyone care to define "individual" in 50 pages or less?), I hope I understand more or less what they mean by "empirical bridge". In fact, I think the argument reduces to the question, "What is a bridge?" When bushwhacking through chasm-filled forests (real or theoretical), people do differ on what they accept as trustworthy bridges (e.g. rock hoppers, waders, fallen tree walkers, vine swingers). It is a fair question. I will first summarize what I said, and then use the rhinocerotid example, or at least a fictive extrapolation of it, to demonstrate the tests.

To review the backbone of the 1988 argument:

1. Adaptation is generally agreed to be the modification of existing features by natural selection so as to increase fitness of the organism.
2. In cladistic terms, the novel modification is an apomorphy. Hence adaptations are a special class of apomorphy, and the study or analysis of their historical dimension requires recognition as such.

3. Adaptation makes at least two special claims about apomorphies.
 - (a) Natural selection is responsible for their origin (the initial role of mutation aside).
 - (b) The novel modification (apomorphy) is better than the pre-existing feature (plesiomorphy). Better means that increased fitness is conferred by the apomorphy relative to the plesiomorphy.
4. Selection operates on the performance (broadly construed) of the apomorphy in its environment (broadly construed).
5. Taken together, points 2–4 imply a variety of ways in which predictions deduced from adaptational hypotheses can be compared to real, yes, *empirical*, data on performance (effect on fitness or its corollaries, reproductive success, efficiency of design or function, etc.) and character distributions.
6. Other things being equal, it helps if the adaptational hypothesis claims that selection is responsible for both the origin and maintenance of the feature. Otherwise the hypothesis eschews a uniformitarian assumption about history. That makes any test of an historical hypothesis with current data ambiguous. Requirements of the claim of origin and maintenance can be relaxed, but doing so sacrifices some measure of testability (Coddington 1988: 17–19, fig. 8).

In my view surviving such a series of tests does not “prove” adaptation, it just fails to disprove it. I, at least, am comfortable with identifying such a procedure as a test, and calling it science. These comparisons are without doubt tests, and rigorous ones at that. I demonstrated that several classical adaptationist stories fail to survive these trials.

Given 1–4, what, precisely, is adaptation? It seems that the theory of adaptation contributes two unique components to the explanation of the origin and persistence of apomorphies. These are the stipulation that natural selection is involved at least in the origin of the feature, and a prediction about the performance, or function, of the apomorphy relative to the plesiomorphy. Hence the most restrictive cladistic definition of adaptation would be apomorphic function due to natural selection. It is worth reiterating here that competent adaptationist hypotheses will generally have the form: “the derived trait M_1 arose at time (t) in the stem lineage of taxa C, D and E via selection for the derived function, F_1 , with respect to the primitive trait M_0 with primitive function F_0 in taxa A and B (Coddington 1988: 4 and fig. 1; see below as well).

However, adaptationist theory rarely has, and need not, couch its hypotheses in cladistic terms (point 2, above), although my whole discussion tried to emphasize the scientific efficiency that would result if it did. Personally, I think adaptationist hypotheses concerning events at or above the species level that ignore cladistic context do not deserve the name; others may feel that this is too restrictive. At a minimum, however, even adaptationists wholly ignorant of cladistic methods would require a precise description of the putative adaptation, a measure of its performance, and predicted outcomes of comparisons between organisms or populations bearing the adaptation and control groups.

As de Pinna and Salles point out, some of the tests I outlined address whether any given adaptational hypothesis makes sense in a cladistic context. Whether these stipulations are regarded as tests, or merely as necessary prerequisites for admission to the company of competent scientific hypotheses, is a quibble. Because they can cause hypotheses to be rejected outright or seriously modified, they do function as tests.

Also with regard to point 2, I pointed out early on that “adaptation is one possible

general explanation of empirically observed synapomorphy among many". Thereafter I focussed on alleged adaptationist explanations of synapomorphies as a subset of all possible explanations of synapomorphies. To say that I operationally "equated" adaptation and synapomorphy is therefore an error. Because all hypotheses about the origin of adaptations must concern apomorphies, I discussed adaptations from that perspective.

With regard to point 4 above, I am puzzled that de Pinna and Salles are puzzled that I placed "emphasis on natural selection as a necessary component in the definition of adaptation". Adaptation *sans* natural selection at some level or at some point disembowels the Darwinian explanation for descent with modification. I agree that natural selection as a theory has nothing to do with cladistic methods. Their mutual independence gives strength to the test. I hope no more needs to be said on that point.

In contrast to the methodological nature of cladistics, "process theories" are causal explanations of evolutionary change. They make predictions about how and why particular features change through evolutionary time. Cladistics outlines the structure of the test to assess the truth of that statement, and the process theory explains how and why "before" changed into "after". I restricted the argument to change involving speciation, in which case the "before" and "after" versions of the feature are, in systematic terms, homologous characters or alternate "states" of a homolog. I did this mainly because explaining the existence or persistence of synapomorphies is a central question in macroevolution, and because cladistics presumes hierarchy which, with few exceptions, is hard to document within demes. I very much doubt if adaptation is the sole answer to the big question. Significantly, cladistics has nothing to say on the subject, nor should it, given that cladistics is merely a method. That is both its strength and ultimately a source of sterility (Coddington, 1985).

In my view, therefore, the most testable theories about adaptations at the species level or above offer detailed explanations for the origin and maintenance of apomorphies. It is the responsibility of the adaptationist hypothesis (not the cladistics) to specify as exactly as possible the nature of the adaptation, an appropriate measure of function, and to predict the outcome of pair-wise comparisons between taxa bearing the derived and the primitive trait. Many extant hypotheses of adaptation are of this form, even if the outgroup, the primitive trait, and the function of the primitive trait are implicit.

Given the above, the bridge requested by de Pinna and Salles seems obvious to me. If natural selection, or any process theory, predicts its own particular polarity or ordination of evolutionary change, and if cladistics provides an independent polarity, then fruitful science can be done by investigating the whys and wherefores of agreement or disagreement between predictions of process theories and observed phylogenetic pattern.

The possibility of conflicting polarities is a test. If the polarities agree in all respects, the predictions of the process theory have survived the test. The theory may be elaborated and applied to other test cases in order to assess its generality. Further, perhaps ingenious, deductions can be made about the relation between the posited cause of the directed change - morphological, physiological, behavioral, genetic, biochemical, etc. - and these new deductions can be tested in the same taxa. If the predictions do not survive the test, the prediction as stated is falsified. In my experience, failed predictions are rarely accepted as inflicting mortal wounds on their parent theories. The authors regroup, study the new evidence, and issue a modified version of the theory or modified deduction from it that accounts for the previously falsifying evidence. The modified prediction is necessarily more detailed, but that just affords further chances for new tests.

For de Pinna and Salles to condemn this sort of scientific progress as "*ad hoc*" is not very realistic and perhaps extreme.

In order to use the rhinocerotid example cited by de Pinna and Salles, one has to rework it, because the hypothesis presented by Lewontin (1978) fails even the rudimentary test of homology, as I pointed out. It seems pointless to argue about what Lewontin meant; I (and presumably most other readers) interpreted his example (1978: 228 and figure on p. 225) to mean that the ancestral rhino had neither the one-horned nor the two-horned condition (frequency of alleles A and B is zero at the origin, p. 225), and that two species "evolve" (= change in gene frequency) along "alternative evolutionary paths" (Lewontin, 1978: 225) to fixation of these alleles as mutually exclusive apomorphies of distinct species.

Lewontin said predator defense. De Pinna and Salles ask how you test it. Although two adaptive hypotheses are involved (due to the mistake in homology determination), let us focus on the less general of the two and presume that the hypothesis of predator defense still stands for the origin and maintenance of one horn in the Indian rhino. The cladogram is ((*Diceros*, *Ceratotherium*), (*Dicerorhinus*, (*Punjabitherium*, *Gaindatherium*, *Rhinoceros*))) (Groves, 1983). The sister taxon of *Rhinoceros* is either the extinct two-horned *Punjabitherium* or *Gaindatherium*. I assume we have no little or no reliable evidence on their predators or defensive behavior, although paleobiologists can deduce some amazing things. The next outgroup is the two-horned *Dicerorhinus*, the Asian rhino (not the African rhino, as Lewontin implied), and the next is the two-horned *Diceros-Ceratotherium* clade. Because frontal horns are homologous as dermal outgrowths above the frontal bone and nasal horns likewise above the nasal bone, and because *Rhinoceros* lacks the frontal horn present in the outgroups, the hypothesis concerns secondary loss of the frontal horn, not gain of a nasal horn, as Lewontin implied. The complete adaptive hypothesis (cf. general form above) therefore is: *Rhinoceros* lost the frontal horn present in the outgroup taxa due to natural selection acting to reduce the incidence or severity of predatory attacks through increased efficiency of a single horn as a predatory defense, as compared to the plesiomorphic two-horned condition in the outgroups.

First, gather information on predators of *Rhinoceros* and *Dicerorhinus* especially, but do not ignore *Diceros* or *Ceratotherium*, as it makes a stronger case to establish the retained primitive function and context of the two-horned condition though parsimony and the doublet on the cladogram. Hope that predators of all genera are ecological or behavioral equivalents, so that from the rhino's point of view, it does not much matter whether they are being attacked in Africa, India, or Asia.

The tests are at least the following, not counting the tests derived directly from the implied cladistic context (which, by the way, falsified the original formulation):

1. If no rhinocerotid uses its horn at any ontogenetic stage to deter predators, stop. The adaptational hypothesis is falsified because the statement of horn function was awry.
2. If for all predators, *Rhinoceros* suffers more predation (implying net fitness decrease) than its outgroups, stop. The adaptive hypothesis as stated is falsified, because selection cannot have acted on the two-horned condition to yield the one-horned condition via a decrease in fitness.
3. If for some predators, *Rhinoceros* does suffer less predation or less serious predation (say by tigers, since tigers are sympatric with rhinos), focus on detailed analysis of the defensive behaviors of rhinos and of offensive behaviors of tigers (and their

outgroups) to specify exactly how tigers and rhinos interact during a predatory encounter. If it turns out that Indian tigers are apomorphic in their predatory behavior such that *Rhinoceros* is at less risk, stop. The adaptive hypothesis is falsified because *Rhinoceros* apparently lost its frontal horn through the reduction of stabilizing selection to maintain two horns, not directional selection for a superior adaptive state.

4. If tigers have not changed their attack behavior in any significant way, find out exactly how the absence of the frontal horn enables *Rhinoceros* to evade predation or reduce its severity. Perhaps the frontal horn interferes with infliction of maximum damage by the nasal horn. Perhaps the frontal horn, or its proximity to the nasal, affords the tiger a better grip on the rhino during the attack sequence. Perhaps the frontal horn area is more frequently damaged than the nasal area, and thus two-horned rhinos suffer greater mortality as a result of secondary infection. The last conjecture is intriguing because it raises the possibility that the loss of the horn may be an adaptation to prevent secondary infection, and not solely against predation. This might be especially relevant if frontal areas are injured through other agents than tiger attacks. These questions can be addressed with data, and are the stuff of good research.
5. Make all six pair-wise comparisons among taxa (neglecting the fossil taxa because we assumed that comparable data were lacking). The adaptive hypothesis as stated predicts no significant differences among any two-horned rhinos, and always a significant difference between *Rhinoceros* and any two-horned rhino. Deviations from these predictions may lead merely to further research on the transformation series among horns in rhinocerotids and its ecological implications, or they could weaken the adaptive hypothesis or make it equivocal. The worst case of the latter might be that if either *Ceratotherium* or *Diceros* horn function is used as the null hypothesis against which *Rhinoceros* horn function is judged, the adaptational hypothesis cannot be rejected, but the opposite happens if *Dicerorhinus* is used.

Assuming that some creditable explanation emerges from the above, the adaptive hypothesis has survived the test. One now has a lot of data on the outgroup condition, its plesiomorphic function in a plesiomorphic context (deterrence of predation by tigers), and its apomorphic function in the same context. Based on competent analysis of adequate samples of predatory interactions between all species of rhino and the tiger, as well as detailed study of the use of the horn and the attack behavior of tigers and other cats, the adaptive hypothesis cannot be rejected. (This is getting increasingly unrealistic because you could not possibly get the permits to do this kind of work with endangered species, to say nothing of problems of sample size . . .)

Note that none of the above 10 or so tests emerges solely from the cladistic side of the "bridge", although cladistics is central to each. They all derive chiefly from the adaptational hypothesis.

Relative to the general statement of a competent adaptational hypothesis (above), de Pinna and Salles comment (1990:), "although he allows that M_1 may be an inferior solution for the design problem posed by F_0 , no reason is given why one should consider this situation as less likely than its inverse". I take this to mean that they do not understand why the theory of adaptation predicts that M_0 should be an inferior design solution to the design problem posed by F_1 . The reason is simply that selection is a

directional, polarized process. Adaptive innovations arise because they are in some sense better. Also, "he proposes that the outgroups (A and B in his example) are the null hypothesis to test derived state M_1 as an adaptation in the ingroup. Evidently this is not the case: the outgroups are the null hypothesis when proposing simply that state M_1 is derived relative to state M_0 ". Perhaps de Pinna and Salles missed the point that the theory of adaptation makes predictions about comparisons of performance and efficiency of plesiomorphies and apomorphies. It is the posited relationship of apomorphy to apomorphic function that makes these cladistic tests more than an exercise in outgroup comparison or character state optimization. Cladistics, by itself, makes no predictions as to the outcome of these comparisons; adaptation does.

I think I have shown how cladistics, and, most particularly the synergy of adaptation viewed in cladistic context, can be used to test adaptation. It is fairly clear what the theory of adaptation contributes to cladistics: predictions about comparisons on which cladistics, if by cladistics we mean merely hierarchical pattern mappings, is silent. Adaptation contributes a causal explanation of apomorphy. As I said (Coddington, 1985, 1988) cladistics without process theory verges on sterility. Cladistics contributes the essential independent estimate of character change, organizes the program of research on function and performance, and, crucially, identifies which taxa provide the best controls, or null hypotheses, against which data on apomorphic function should be judged.

Using present data, whether on character distributions, functions, or ecological interactions, to reach back in time to reconstruct history will never achieve the rigor of, say, experiments in which all evidence suggests that past, present, and future apples always have, do, and will fall down. History is a series of unique events and it is harder to explain unique events than replicable ones. Given that difficulty, I do not know whether de Pinna and Salles would trust themselves to the bridge outlined above or not, especially given their inclination to view anything mapped on cladograms as only pattern, and never relevant to process. The introductory quotes from the major text on evolutionary biology (Futuyma, 1979, 1986) makes it clear why we should try. Anyway, the history of life is a whole lot more interesting than the direction favored by apples.

Other authors (Donoghue, 1989; Greene, 1986; Maddison, 1990), have argued that convergences, parallelisms, and other such instances of homoplasy can shed light on features as adaptations. In a particular way, I agree, and certainly would not dismiss studies of exceptional or surprising instances of convergent evolution if carried out carefully and logically. Indeed, the homology approach and the convergence approach relate as part to whole. Studies of homoplasy can build to a generality that studies of unique events never will. There are, however, several difficulties with exclusive reliance on an approach that not only requires homoplasy, but whose strength is actually proportional to homoplasy. The above authors did not advocate exclusive reliance on studies of homoplasy, but it seems worthwhile to point out some of the pitfalls.

One supposed strong point of the convergence approach is that each instance of homoplasy on the cladogram is regarded as independent, and therefore statistical procedures can be applied to test for significance (Maddison, 1990). Leaving aside the issue of whether the assumption of independence is well-conceived, the strength of the convergence approach is proportional to the number of independent gains, transformations, or losses on the cladogram. This result is at least ironic: the worse the fit of the character is to the cladogram, the better chance it has to be accepted as an adaptation. Since statistics on small sample sizes is difficult, the method may impel one to broaden the definition of the feature, a slippery slope at best.

Second, even supposing a cogent definition and an adequate sample size, a method that ignores the homology approach (i.e., ingroup-outgroup comparisons of function, as described above) can show only superficial correlation as the result of the analysis. Nothing thus far has provided evidence that adaptation explains the homoplasy better than other possible explanations of evolutionary change. Adaptation remains untested. In order to link the theory of adaptation to apomorphy, it seems to me that one must have evidence on function. Strictly speaking, to have two or more instances of adaptation, one needs evidence on function in each.

Third, even supposing a statistically significant association between characters or whatever, the homology approach can falsify any single instance counted as confirmation by the convergence approach. A conclusion based solely on the observation of convergence will always be vulnerable to test by the homology approach, whereas the opposite is less likely. Even though nine out of 10 instances of convergence fail the homology-based tests, the tenth cannot have less status as an adaptation only because it is unique. If one insists on replication of adaptation in order to invoke it as an explanation of evolutionary history, one places the study of unique synapomorphies (by far the largest class of interesting and significant evolutionary events) beyond the reach of science.

Luckily the homology approach and the convergence approach are compatible. Compilations of careful research on apomorphies similar enough to justify the term "convergent" may substantiate general evolutionary trends. At the other extreme, no amount of hastily compiled and superficially considered "convergences" can sum to a convincing demonstration of adaptive value if each instance fails the sort of tests outlined above. After a history of work on adaptation marked by sloppy thinking and armchair speculation (Gould and Lewontin, 1979), the theory of adaptation as a general explanation of descent with modification perhaps has more need of meticulous attention to detail than broad but shallow demonstrations of correlation. However, the approaches complement each other; both need precise and independently corroborated cladistic context to function.

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