CHAPTER

3

The roles of homology and convergence in studies of adaptation

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CONTENTS

Abstract

The study of adaptation traditionally has proceeded under either of two modes, here termed the homology approach and the convergence approach. In recent years, both approaches have benefited greatly by using cladistics to define homology and homoplasy (convergence is one kind of homoplasy) as alternative explanations of pattern in a comparative data set. The homology approach treats adaptation as one

potential causal explanation of synapomorphy among many. It tests the assertion that natural selection predominantly determines biological pattern (Darwin's theory) by evaluating data on the performance, utility, or function of a homologous (hence historically unique) trait under the twin strictures of an adaptive hypothesis and optimization on the cladogram. It uses data on current utility in the test, is rooted in the natural history of the case and makes falsifiable claims about particular instances. The results pertain only to the case or clade studied. Except when summed, such results are unlikely to test evolutionary 'law' or to establish overarching evolutionary pattern. The method is best used to investigate historical events perceived to be of exceptional interest or importance.

The convergence approach forgoes detailed study of particular cases to reach for statistically significant correlations between classes of non-homologous events and nearly always attributes 'significant' results to one common cause – natural selection. Neither the homology of the 'trait' under study nor monophyly of the clade circumscribe its application. It is best used to establish evolutionary laws unbounded by the particulars of history. Some subjectivity in application and the separation from the particulars of the individual cases composing the correlation poses problems for the method. Criteria governing the hypothesis (whether that under test or the null), the definition of the phenomenon and taxon sampling need clarification.

INTRODUCTION

This paper seeks to differentiate and reconcile what may appear to be two different approaches to phylogenetically based research on adaptation. They ask similar questions, have different goals, use different methods and focus on different kinds of data. One is the explanation of unique events within lineages. The other is the explanation of correlations among similar events across lineages. The former emphasizes the analysis of evolutionary novelties (apomorphies), the latter empha-sizes the analysis of coincidences (homoplasies, convergence). Both approaches are basic to the 'comparative method'. While both approaches have their own methodo-logical concerns, my intent here is to contrast and analyse their respective strengths and weaknesses, paying particular attention to the logical interrelationships.

The analysis of unique events seeks to explain single, perhaps major features of evolution (Wanntorp, 1983; Padian, 1985; Greene, 1986; Coddington, 1988, 1990; Carpenter, 1989, 1991; Donoghue, 1989; Lauder, 1990; Wanntorp et al., 1990; Baum & Larson, 1991). It studies evolutionary homologues in their phylogenetic and ecological/functional contexts, and places great emphasis on empirical assessments of the function or utility of the trait. In general, such evolutionary events are easy to delimit and richly detailed. The price is that they are unique, or nearly so. Their investigation is peculiarly open-ended, and often frustratingly inconclusive.

Correlations among non-homologues, on the other hand, are convergences, parallelisms, replicates, not unique (Ridley, 1983; Huey, 1987; Pagel & Harvey, 1988; Sillén-Tullberg, 1988; Bell, 1989; Burt, 1989; Grafen, 1989, 1992; Gittleman & Kot, 1990; Maddison, 1990; Martins & Garland, 1991; Garland Harvey & Ives, 1992; Gittleman & Luh, 1992; Pagel, 1992; Sillén-Tullberg & Moller, 1993; reviewed in Harvey & Pagel, 1991). Correlation establishes a statistical pattern, but necessarily at

great remove from the biology of any given instance. In general, this approach places greater emphasis on statistical patterns than the quality of data relevant to performance, function or the utility of traits. Correlations therefore can have a shallow quality – at worst just two series of numbers that barely achieve significance through rejection of a rather prosaic null hypothesis. Such is the price, but the payoff can be general trends verging on evolutionary law. For reasons that will become clear later, I call the study of historical uniques the 'homology' approach and the study of replicated events the 'convergence' approach.

An example may clarify the distinction. The homology approach might focus on an amazing thing, for example the origin of the orb as an architectural pattern in spider webs (Coddington, 1986a, 1986b, 1991). The convergence approach instead might focus on amazing coincidences, such as mimicry of ants by many different groups of spiders (Oliveira & Sazima, 1984; Oliveira, 1988). However different the two interests may seem, both depend on an appreciation of the amazing. The former concerns a startlingly unique event for which several alternative hypotheses are plausible, the latter concerns a improbably large set of (unique) events that possibly result from a common cause, perhaps selection to reduce attacks by predators.

Both approaches have always depended on taxonomy to structure and define the questions asked, but taxonomy has not always been equal to the task. Not until the mid 1970s did taxonomists decide to focus on one central scientific problem – reconstructing phylogeny. Since then, non-evolutionary and intuitive taxonomy has largely been replaced by cladistics, here construed as the reconstruction of the evolutionary history of lineages and traits by quantitative means. The resurgence of interest in history's role in biological pattern has more to do with the methodological innovation, that is cladistics, than it has with biologists 'remembering' or 'rediscovering' the importance of history. Prior to cladistics, taxonomic products were so often a matter of opinion, flawed and skewed by misrepresentation of lineage (paraphyly or polyphyly versus monophyly), misleading evidence (synapomorphy versus 'grades' or symplesiomorphy) and real versus imaginary categories (conflation of real taxa with artificial rank in the Linnaean hierarchy), that their reliability for structuring evolutionary research was, at best, hard to assess. Cladistics clarified these confusions, and two of the three problems mentioned above are now widely appreciated by non-systematists. The use of classically defined taxonomic ranks as objective and comparable categories to guide evolutionary comparisons remains an area of confusion, but it is as destined for the scrap pile of bad ideas as paraphyly or symplesiomorphic groupings. Part of this chapter will attempt to explain why the latter point is so. Even though all of the lessons of cladistics have not yet been learned, cladograms are now widely acknowledged as central to investigations or explanations of evolutionary history (Huey, 1987; Wanntorp *et al.*, 1990; Brooks & McLennan, 1991; Harvey & Pagel, 1991)

Both kinds of research mentioned above, the explanation of amazing things and the explanation of amazing coincidences, agree that cladograms are a prerequisite – the more detailed, complete and accurate, the better. The investigation of coincidences is necessarily statistical, and that point of view has questioned or even despaired of the 'scientific' study of uniques because they provided no replication (Lauder, 1982; Mitter, Farrell & Weigmann, 1988; Harvey & Pagel, 1991; Gittleman & Luh, 1992). In the convergence approach, phylogeny is something to be 'removed',

'extirpated' or 'controlled' because resemblance due to common ancestry is held to be non-selected.

However, statistics and 'science' are not synonymous. While commonplace statistics may be inapplicable to unique events, science is not merely the study of numerical distributions. Many valid scientific results are not testable statistically. Although many points of view on what constitutes 'science' are possible, good science uses null versus alternative hypotheses, some criterion of improbability (what it means to be amazing), unbiased observation and falsifiability or at least testability. Rejection of a null hypothesis by unbiased observation that remains testable and potentially falsifiable through additional observation (replication) seems enough like science to me. In what follows, I will compare and contrast each approach to the study of adaptation, seeking to identify its strengths and weaknesses, and how and whether these are appreciated by practioners of either the homology or the convergence approach.

DEFINING ADAPTATION

I take adaptation in the most rigorous sense to mean an apomorphic feature that evolved in response to natural (or any other kind of) selection for an apomorphic function (Fig. 1). As such adaptations are always apomorphies, though not all apomorphies are adaptations. Rigorous adaptational hypotheses include specific descriptions of the nature of the selection presumed to have operated, because the core criterion of adaptation is function (Greene, 1986; Coddington, 1988; Lauder, 1990; Baum & Larson, 1991). Williams (1966) felt strongly that the scientific study of adaptation reduced in large measure to careful analysis of function (in his terms as opposed to mere 'effect'). He thought the study of adaptation needed much improvement, constituted a distinct speciality and required a special name – teleonomy.

To this crucial link to function, cladistics has added the additional criterion of novelty or apomorphy. Apomorphy is a relative concept; all characters are apomorphic at some restricted level, and all except the latest are also plesiomorphic at a more inclusive level. Like apomorphy and homology, adaptation is a relative concept. Bird and bat wings are not homologous unless homologous as vertebrate forelimbs, thus specifying the level of apomorphy. It is as nonsensical to say that wings are an adaptation as it is to say that they are homologous. Compared to what? Because adaptation is a bridge that links evolutionary pattern and process, complete hypotheses of adaptation require comparative statements on both process (derived function) and pattern (apomorphy). Although tiresome to specify all the necessary components of an adaptive hypothesis, such details ought to be implicit in the hypothesis. With respect to the phylogeny depicted in Fig. 1, a complete adaptive hypothesis is of 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, which still persist in taxa A and B. The main intent of this definition is to distinguish adaptation clearly from current utility, as historically viewed. Like homology, adaptation is a directed, polarized concept. Current utility, on the other hand, includes both the function for which a feature was built (what Williams (1966) called 'purpose'), as well as its current use (what Williams (1966) called 'effects').
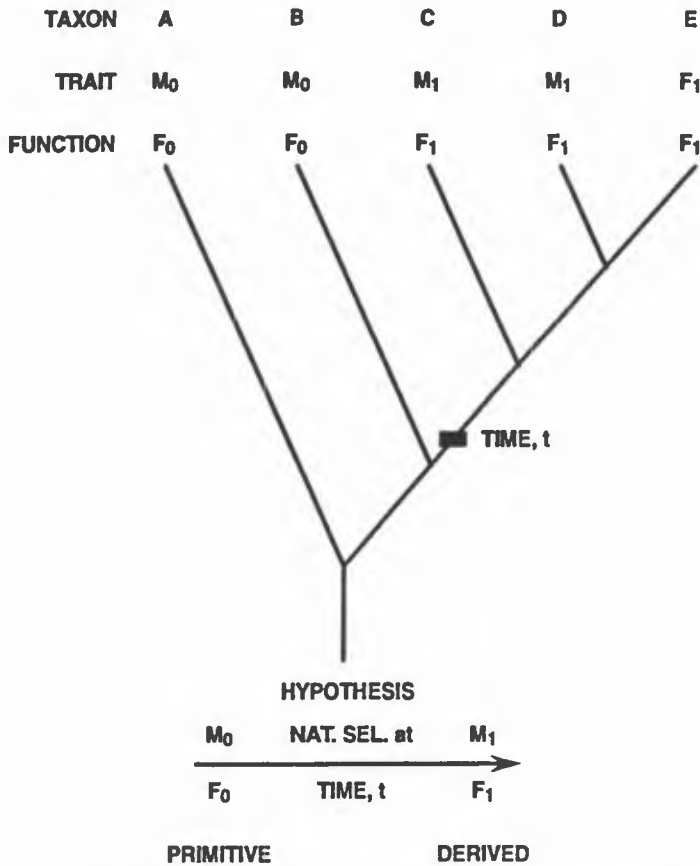
Figure 1 Cladistic model for adaptation. An apomorphic trait M_1 is built and maintained by natural selection for its function F_1 as compared to the plesimorphic trait and function (after Coddington, 1988).

An adaptational hypothesis therefore must link an observed pattern to a specific cause. The cause is particular in the case of unique events (though it may represent an instance of a common evolutionary trend) and it is common cause in the case of coincidences. If the sequence of the supposedly correlated traits is an essential part of the hypothesis (*if* A, *then* B), joint presence of A and B is insufficient to establish the relation. A must have evolved before B for the hypothesis to be supported (Greene, 1986; Donoghue, 1989; Baum & Larson, 1991). However, if A is extremely widespread in a lineage, by chance alone it will tend to pre-date the evolution of the rarer B (Maddison, 1990). An apomorphy that arose for other than the reason specified in the adaptive hypothesis may still be apomorphic and it may still be an adaptation, but the adaptive explanation was wrong. Evolutionary convergence due to several clearly distinct and logically different causes (different kinds of selection or non-selective causes such as linkage or various kinds of constraint) are not jointly evidence for adaptation, even if they all result in the 'same' startling phenotype. In most cases, distinct causes map clearly to distinct adaptational hypotheses. Pooling convergences that result from different kinds of selection is just a logical mistake. It is a mistake about evolutionary process, logically similar to the

most common mistake about evolutionary pattern – distinguishing true from false homology. Greater precision in identifying and distinguishing evolutionary processes as causes can only help to connect the explanation of pattern to process, just as great precision in identifying pattern has been recognized as essential (Farris, 1988; Nixon, 1991; Maddison & Maddison, 1992; Swofford, 1993).

For example, a classic evolutionary problem concerns the evolution of 'dwarf' males in many lineages independently. 'Dwarf' already implies that selection acted to reduce male size. If 'dwarf' is operationally interpreted as the male–female size ratio, it is ambiguous whether the size change occurred in males, females or both sexes. Derived giant females (fecundity-driven selection?) could as easily be the answer as dwarf males (mating success/mortality-driven selection?). In the spider genus *Nephila* (Tetragnathidae: Nephilinae), in which female mean body length is about 40 mm and males about 11 mm, sexual size dimorphism conventionally is interpreted as dwarf males (e.g. Vollrath & Parker, 1992). Explanations consequently tend to emphasize evolutionary change in males (Vollrath, 1980; Elgar, Ghaffar & Read, 1990). In tetragnathids most likely to be outgroups to the Nephilinae, females and males average perhaps 6 mm and 5 mm respectively. (Other nephiline genera such as *Nephilengys* and *Herennia* are also dimorphic in size, which means the generality of the hypothesis, as usually treated in the literature, is also mistaken; dimorphism probably arose in the common ancestor of these nephilines, not de *novo* in *Nephila*.) It appears that nephiline males are not 'dwarves' but larger relative to their likely ancestors, while females are much larger. Hypotheses in this case may need to explain female giantism, not male dwarfism, or perhaps selection for increased size in both sexes as the cause of size dimorphism (Cheverud, Dow & Leutenegger, 1985). In most other dimorphic spider lineages (*Gasteracantha, Mastophora, Latrodectus, Tidarren, Misumena*) the males are indeed small relative to likely outgroups, and female size has not changed dramatically. In still other lineages, such as mammals, large males are derived. Conflating distinct changes as 'dimorphism' hides rather than elucidates selective mechanisms. Other kinds of 'ratio' characters may suffer from the same confusion of mechanism and effect.

The above definition of adaptation may seem unrealistically rigorous. Admittedly it sets a high standard, but clearer and higher standards have often been called for in work on adaptation (e.g. Williams, 1966; Gould & Lewontin, 1979). Perhaps it is best seen as an upper bound, a realizable ideal that may only be attained under ideal circumstances. Debating the lower bound seems fruitless, since it is never clear whether one is merely remarking on evidence for adaptation in a noncommittal fashion, or coyly making the claim itself. The line can be drawn in many places.

This definition of adaptation can be relaxed in two main ways. An adaptational hypothesis that is consistent with the above but declared to be untestable by comparative data on current utility might still be an adaptation. This situation may frequently occur when a synapomorphy of a large clade is proposed to have originated as an adaptation (= built by natural selection for a specific function), but now is thought to be maintained by some other agent than selection, e.g. ontogeny, epistasy, linkage or lack of genetic variation. By definition, data on current utility of the derived and plesiomorphic versions of the character will not falsify or strongly test the adaptive origin. However, this lack of testability does not mean the hypothesis is false.

The criteria for a 'common' cause at work in all instances of the pattern can also

be relaxed. Relating correlation to cause is an old problem, but in my view correlation severed from its causal underpinnings breaks a necessary link. If the causes responsible for the set of distinct observations are very different, the analysis is fundamentally flawed. If mere correlation is accepted as being as close to demonstrating 'adaptation' as we can ever get, then correlation and adaptation become nearly synonymous. Defining the hypothesized cause clearly and distinctly, i.e. the nature of the selection, is one way to distinguish the claim of correlation from the more onerous claim of adaptation. Making this distinction is often trickier than it seems.

HOMOLOGY AND HOMOPLASY ARE COMPLEMENTARY

It is important to understand the provenance of the data required for either the homology or the convergence approach. For either approach, the data are conceptually a matrix or table of taxa by traits, characters, conditions or values. In what follows, I assume these traits are discrete (qualitative), but they may be continuous (quantitative) as well. Variation in this matrix is interpreted either as homology or homoplasy. Homology is similarity that is due to common ancestry. Homoplasy is similarity that is not. Homoplasy has three explanations: independent gain of the trait; independent or secondary loss; or observer error. In most real examples some variation is equivocal, meaning that although the total amount of homoplasy is known, it can be allocated to characters in various equivalent ways.

Both the homology and the convergence approach allocate variation in the matrix to either explanation based on the fit of the data to a cladogram. It is perhaps not widely enough appreciated that for any trait in the matrix, variation can be wholly attributed to homology or in large part to homoplasy, depending on the cladogram chosen. More succinctly, every character in a matrix is completely consistent with some genealogy (Farris, 1983). What then guides the choice of the cladogram that will determine the evidence for or against adaptation? In cladistics maximum parsimony thus far has been the most common criterion; homology is assumed until proven otherwise. All variation that can be explained as homology is so explained; maximizing homology (or minimizing homoplasy) specifies the cladogram of choice. *Homology is the null hypothesis of cladistics.* Variation that cannot be explained as homology is then termed homoplasy, and as many *ad hoc* hypotheses of convergence or loss as necessary are made to explain the distribution of inconsilient traits on the cladogram. Least squares regression is similar. As much variation as possible is attributed to the independent variable by the method and the remainder is termed 'error' or residual variation. Homoplasy is the 'error' term in cladistic analysis; the cladogram is the best-fit hypothesis given the data and a criterion of fit. *Parsimony is only a criterion of fit* and remains silent on whether the amount of homoplasy found is large or small, just as a least squares fit is agnostic on how much variation is explained or not.

A more important and subtler point about the use of the homology hypothesis in cladistics is that the method is also silent on whether congruence in data (no homoplasy) is due to homology, parallelism, chance, coincidence, earth history, drift or a lucky mistake. The method makes only the positive statement that given a specific cladogram, some similarities must be explained as homoplasy (Farris, 1983).

In an exactly similar fashion for least squares fits, complete prediction of variable A by variable B for any given ordered pair is silent on whether the expected causal relationship in fact underlies the results. Such an agreement between prediction and observation in any given instance might well be due to chance.

Given a cladogram that specifies how variation in a matrix is allocated between homology and homoplasy, it is significant that the data favoured by the homology and convergence approaches are complementary (Fig. 2). Each approach discards or ignores that component in the data prized by the other approach.

The homology approach looks at each evolutionary change as a unique event that requires its own explanation. Even if the trait evolves more than once on the cladogram, each instance is unique and therefore has its particular historical explanation. The method is largely silent on the significance of 'traits' that have evolved frequently (show high homoplasy), or at least it does not demand that traits be so. Even if the apomorphy is part of an impressive set of coincidences, arguing from this general trend to a specific instance of the trait may be a weaker inference than direct assessment of functional or performance data on that trait. If a coin comes up heads 49 times in a row and is tossed again, the trend predicts heads again. But if one is offered the choice of peeking at the result, is it not more secure to do so than to bet on the trend?

In contrast, the convergence approach discards homology and views homoplasy as the interesting and evidentially powerful source of information. Each convergent instance increases the coincidence, degrees of freedom and therefore statistical power – hence 'more' is always 'better'. This concern with sample size is well-founded (Ridley, 1989). The original and long-recognized problem in counting individual taxa as independent data points was precisely that it artificially inflated degrees of freedom and produced unacceptable Type I error rates (rejecting a true null). For the convergence approach homology not only is not evidence of adaptation, it is misleading and the largest source of error. Homology is 'phylogenetic inertia' or 'constraint', which should be removed or statistically 'extirpated' from a

	HOMOLOGY APPROACH	CONVERGENCE APPROACH
HOMOLOGY	**ADAPTATION?** (Alternatives exist and are likely)	Inertia, constraint, remove, extirpate!
HOMOPLASY	Error, secondary loss or gain, minimize "ignore"	**ADAPTATION** (Alternatives not commonly considered)

Figure 2 The homology and convergence approaches to studying adaptation, caricatured as extremes. They use complementary aspects of data, and in general regard the discarded portion as error or something to be minimized.

data set. How to do this properly is currently the focus of much research (Bell, 1989; Grafen 1989, 1992; Gittleman & Kot, 1990; Burt, 1989; Maddison, 1990; Pagel, 1992). Like any statistical test, the convergence approach assumes multiple independent events drawn indiscriminately or randomly from the set of all relevant comparisons. Traits that evolved once or only a few times are beyond the method.

A COMMON MODEL TO TEST HYPOTHESES OF ADAPTATION

In attempting to establish natural selection as the predominant cause of evolutionary pattern both approaches implicitly assume that selection explains change. In the literature, the hypothesis of adaptation usually seems to attribute evolutionary change to directional selection. It is peculiar that both the homology and the convergence approach focus so exclusively on change. In the limit, no change at any genetic locus is improbable (the second law of thermodynamics, if for no other reason) but very rapid change at any given locus is also unlikely. Either extreme requires explanation (Fig. 3). If 'directional' selection explains change, then 'stabilizing' selection explains stasis (Fig. 4). Extraordinary stasis is fully as interesting as extraordinary change (Levinton, 1983), and perhaps more common. For a null model like Brownian motion or Markov processes, testing for improbable stasis should make the test two- rather than one-tailed. Although the statistics to detect unusual change (reviewed in Harvey & Pagel, 1991) have attracted much attention lately, stasis has been of less interest. Adaptation has not always been so exclusively linked to change (Stebbins & Ayala, 1981). Williams (1966: 54) thought it ". . . unfortunate that the theory of natural selection was first developed as an explanation for evolutionary change. It is much more important as an explanation for the maintenance of adaptation". In contrast, the homology approach is not so dependent on finding aberrant frequencies of change, whether high or low. It relies on evidence specific to individual cases to test an adaptive hypothesis.

Figure 5 extends Fig. 4 to illustrate further the differences between the homology and convergence approach. A series of species (or taxa of any rank) occupy the tips
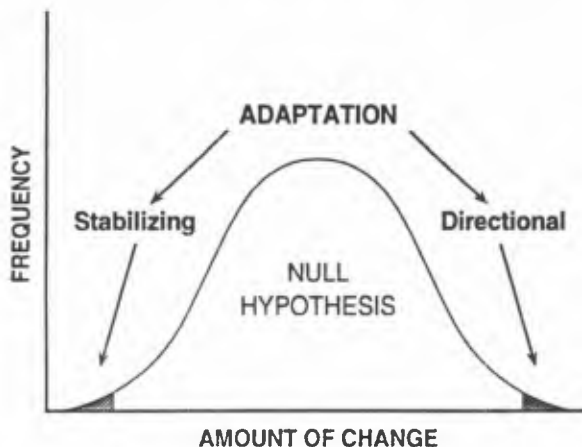

Figure 3 Both extremes in the frequency distribution of observed number of changes per traits may be rare compared to some null hypothesis. Both require explanation.
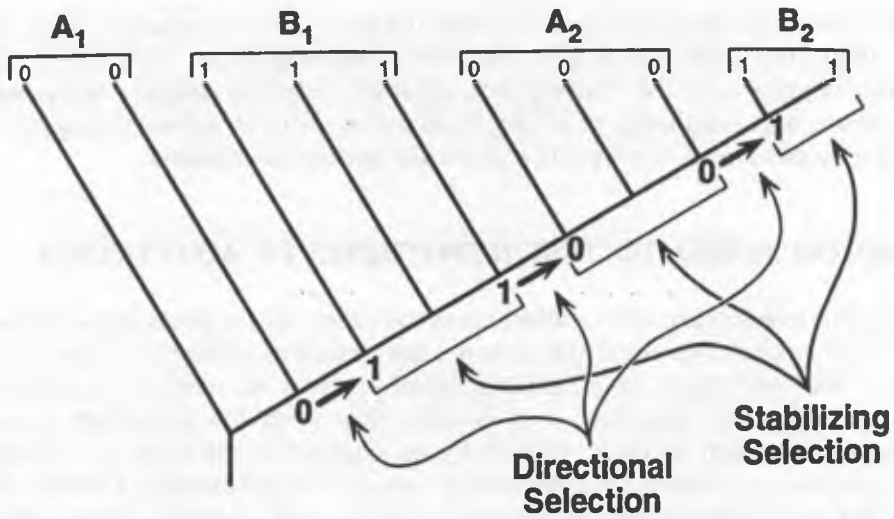
Figure 4 A cladogram for 10 taxa and one character with two states, coded as 0 and 1, each of which has evolved twice. Selection can explain both the origin and the persistence of novelties.

of the branches and display one of two conditions, A or B for 'Character 1' (initially coded as 0 and 1, respectively). A second trait, 'Character 2' also has two conditions, C and D, coded as for the first character. The traits could be continuous variates (Maddison and Maddison, 1992), but it does no violence to the logic to treat the simpler discrete case. For Character 1 on this tree three evolutionary events took place. If the tree is rooted properly, trait 'B' evolved twice (B_1 and B_2), indicated by the bold arrows, and trait 'A' has as well, once on the cladogram visible to us (A_2), and once somewhere below the displayed portion of the tree (A_1). Both conditions show homoplasy. The A at the bottom of the tree is not the same historically as the
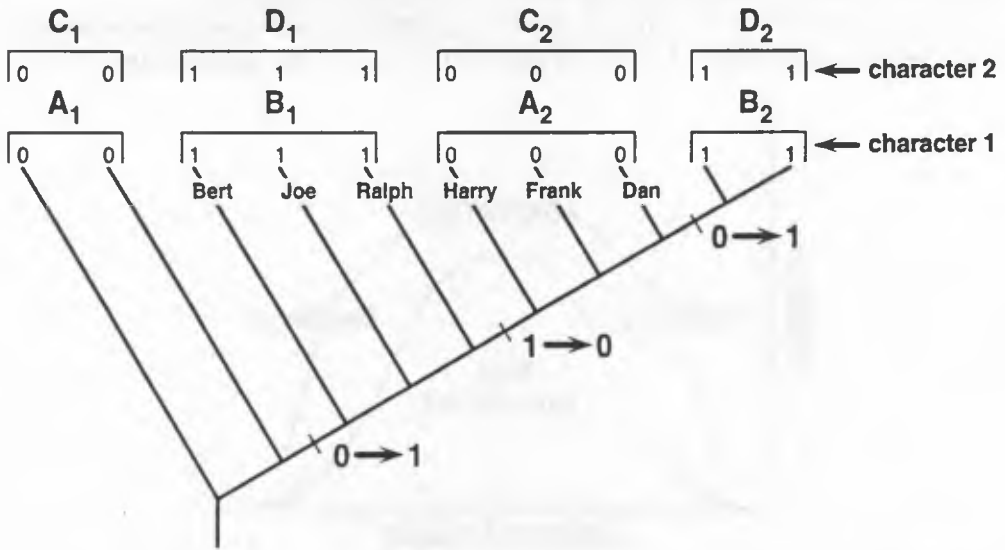

Figure 5 As in Fig. 4, but with taxa named and two perfectly correlated traits mapped on the cladogram.

A towards the top, and nor are the Bs. Even if they are phenetically and genetically identical (such as aligned, identical nucleotides), the homoplasies represent distinct historical events. To represent the convergence approach realistically Fig. 5 should be larger with A and B evolving 'n' times, but twice suffices to make the point. The varying ways to interpret the patterns of 0s and 1s for either character underlie all the differences between the homology and the convergence approaches.

With regard to the homology method as applied to character 1, Fig. 5 shows three events requiring explanation as indicated in the figure by bold arrows. The As and Bs, although similar, evolved independently and are not identical. The fact that B_2 is like B_1 or A_2 like A_1, though intriguing and worth investigating, is not *necessary* to test the hypothesis of adaptation. Perhaps B_1 and B_2 are only superficially similar (observer error). The tendency of systematists is to minimize homoplasy, and unproblematic cases of coding 'blunders' due to superficial similarity are usually re-coded as a matter of course.

With regard to the convergence method as applied to character 1, Fig. 5 shows two events, the parallel evolution of both A and B. The naive worker sees five instances of B, one for each taxon with B, whether B_1 or B_2, and improperly assumes inflated degrees of freedom. The sophisticate sees two evolutionary events with at best one degree of freedom and puts little emphasis on the pattern.

In summary, cladograms parse trait variation into either homology or homoplasy. If traits are continuous, it is still a question of dependent or independent change in two lineages. Both homology and homoplasy are interesting evolutionary patterns, both require a comparative method for analysis. The homology approach focuses on explaining individual changes. The convergence approach seeks a large ensemble of similar events because high levels of homoplasy improve the ability to detect correlated change. From a strictly phylogenetic point of view this goal is odd, as most systematic data sets are constructed to avoid homoplasy rather than to seek it out. For the convergence approach, the worse the trait fits the cladogram, the more powerful the test. If homology and homoplasy are complementary, what are the strengths and weaknesses of each?

THE HOMOLOGY APPROACH

In evolution, historical uniques are of at least two kinds, apomorphies and lineages. Together they form what O'Hara (1992) has called the evolutionary chronicle – what happened during evolution, rather than why. The chronicle is simply evolutionary 'history', as commonly construed.

Homologies are logical individuals

What is the scientific status of historical uniques? Here it becomes useful to borrow a metaphysical distinction from the philosophy of science. Philosophers define historical uniques as logical individuals as opposed to logical classes (e.g. Popper, 1965); these distinctions can also be applied within evolutionary biology (Ghiselin, 1974). Biological examples of logical individuals are the orb-weaving spider family Uloboridae (a taxon), or spider spinnerets (a set of synapomorphies). Logical individuals are considered to be 'spatio-temporally' limited, meaning that they originated in a single place and at a single time, will come to an end and will never

recur. Individuals are most easily defined ostensively, by pointing to them, by the thing itself. Classes on the other hand are atemporal logical sets sharing some defining characteristic. Examples of classes are 'red' fruit, polygyny, aposematism, mimicry, dwarfism, gynodioecy, metabolic rate, GC–AT ratio, home range, body size, etc. All past and future taxa can be scored for such categories, although sometimes a little reflection is necessary ('fruits' are progeny; polygyny and gynodioecy refer to patterns among heterogametic organisms; mimicry and aposematism may require that the communication channel be specified, etc.). The homology approach studies individuals, but the convergence approach studies classes.

Is the study of logical individuals (whether apomorphies or lineages) less falsifiable or scientific than the study of 'replicated' events? The classic models of the scientific method applied to physics, where one hydrogen atom is the same as another, and new hydrogen, identical to all other hydrogen that has ever existed, could be created at will. In contrast, many well-corroborated scientific theories concern historical uniques, e.g. continental drift, the Pleistocene ice ages or even the Big Bang. The Universe may collapse and produce another Bang in accordance with timeless physical laws, but it will be a different Bang.

Evaluating hypotheses about historical uniques is not therefore necessarily statistical in the sense that repetitive events are required. Instead we recognize that such hypotheses could be wrong (are falsifiable) but that they have been corroborated by testing multiple independent deductions against facts. Each hypothesis is richly detailed and thus offers many points where correspondence to fact can be tested. This potential multiplicity of deductive statements provides replication analogous to 'frequency' in statistics. To the extent that hypotheses survive many tests, we place more confidence in them. Other examples of logical individuals are the Yucatan bolide impact, Gondwanaland, the taxa Araneae or Vertebrata (or any other taxon), or the vicariance of ancient African and South American biotas, all relatively well-corroborated scientific theories. Historical uniques are complex (another typical difference between individuals and classes), and multiple deductions testing explanatory theories are usually feasible. In sum, if studying historical uniques is untestable science because uniques happened only once, then study of lineages (taxonomy) is as unverifiable as that of apomorphic characters, and the entire comparative method will founder for lack of a phylogenetic framework.

Given that hypotheses concerning historical uniques are 'scientific,' how does it apply to the study of unique adaptations? With respect to Fig. 5, let us say the adaptive hypothesis is that trait A_2 of Character 1 arose in the most recent common ancestor to Harry, Frank and Dan because natural selection acted on trait B_1 in the outgroup (the most recent common ancestor of Harry et al. and Ralph) for a derived function that had some average effect on fitness, given the environment. The data stipulate that Bert, Joe and Ralph have B_1, and that Harry, Frank and Dan have A_2. That B_1 arose in an ancestor basal to Bert or that descendants sharing a common ancestor with Dan evolved B_2 from A_2 is largely irrelevant to the time span in which A_2 evolved and persisted. These latter patterns concern different historical events.

Testing unique adaptations

How can this scenario be tested? There are a number of ways, most of which are straightforward, intuitive and merely pull together earlier threads of thought into a

more rigorous cladistic context (Greene, 1986; Coddington, 1988, 1990; Donoghue, 1989; Lauder, 1990; Losos, 1990; Baum & Larson, 1991). First the effect of B_1 on Ralph's fitness can be assessed, thus characterizing the plesiomorphic selective context in which the feature evolved. Likewise the performance of the novel trait in the derived context can be assessed, and the consistency of these two measures of current utility or performance with the adaptive hypothesis can be assessed. The adaptive hypothesis predicts a significant performance advantage for the derived trait. The hypothesis is testable because it could fail – if the performance advantage is equivocal or opposite to that expected, the adaptive hypothesis has failed this particular test.

If an adaptive hypothesis withstands one test under the homology approach, it can be exposed to further tests that focus on more specific aspects of the natural history or ancillary deductions from the adaptive hypothesis. As the intersection between a narrative scenario and its biological and phylogenetic context grows, the initial adaptive hypothesis is necessarily elaborated and refined, which of course implies further tests. However examples of such work are sparse, especially at low taxonomic levels where the plesiomorphic selective context is most likely to persist (Brooks, O'Grady & Glen, 1985; Basolo, 1990; Losos, 1990; McLennan, 1990; Bjorklund, 1991). The corroboration of the adaptive hypothesis is roughly a function of the number of tests it has withstood weighted by their severity. As in the case of continental drift or the monophyly of spiders, there is little profit in trying to assign a quantitative probability to the hypothesis. It seems more candid to assess corroboration directly.

Assumptions of the homology approach

The homology approach makes several major assumptions. Perhaps the largest is that the current natural history of Ralph and Harry adequately reflect the context in which Character 1 actually changed. This *ceteris paribus* assumption can itself be tested in other taxa with B_1 and A_2. These tests use the notion of falsifying taxa, the cladistic neighbours of Ralph and Harry, to offer additional, taxon-based tests that bear on the theory. These predictions state that Bert and Joe, which retain trait B_1 by descent, can also be compared to Harry as well as to Frank and Dan for the same functional contrasts applied to Ralph and Harry. In the best possible case, multiple independent tested predictions offer the same sort of scientific corroboration that replication provides in a statistical test of correlation.

If no performance-based test of the adaptive hypothesis can be developed, but the cladogram, character polarities and predicted scopes and sequences of events are sound, then at least the plausibility of the adaptive hypothesis has been established (Greene, 1986; Donoghue, 1989; Baum & Larson, 1991). Such assessments could be considered either minimum requirements (Coddington, 1988) or a set of minimal tests for an adaptive hypothesis.

Strengths and limitations of the homology approach

As explained more fully below, historical uniques are usually less ambiguous and more independent of the observer's point of view than are convergences. Problems of trait definition and taxon sampling are not as troublesome, because the

cladogram, as given in the analysis, specifies both homology and monophyly. Historical uniques are closely tied to an observable, bounded natural history context, where many different comparisons can be brought to bear, resulting in a system of high empirical content. Alternative adaptive and non-adaptive explanations are equally as rich and testable as adaptation. While adaptations are apomorphies, not all apomorphies are adaptations. Adaptive and non-adaptive hypotheses competing to explain multiple independent comparisons offers a powerful framework in which to evaluate different explanations. In contrast, if no alternative hypotheses are available or are considered, the ability to reject the adaptive hypothesis is weakened. It persists by monopoly rather than competitive merit.

Finally, only the study of historical uniques addresses the important and interesting question of evolutionary innovation, and whether or how innovations have shaped evolutionary history (Coddington, 1988; Wanntorp *et al.*, 1990). Every clade displays unique synapomorphies that are interesting evolutionary patterns and events (e.g. Coddington & Levi, 1991) and that demand explanation. If the corpus of explainable phenomena is limited to those that have happened a statistically tractable number of times, our understanding of the major features of our world will be incomplete indeed.

In the extreme in which features are truly unique, this singularity is the greatest limitation of the approach. Even assuming the adaptive hypothesis has survived test repeatedly it is necessarily a particular case – not general and not elucidating general evolutionary trends. Second, as in any empirical test, support for predictions deduced from the adaptive hypothesis can be equivocal. Third, the degree of corroboration or test is not easily quantified (although the hard 'significance' levels offered by statistics can be quite misleading if the assumptions that they require are not critically assessed (Wenzel and Carpenter, Chapter 4)). Fourth, all other things are rarely equal, which questions the basic premise that the derived and plesiomorphic functions have persisted sufficiently 'unchanged' to the present to validate investigation of past events with current data. Fifth, the notion that cladistic pattern ought to be linked to performance data or demonstrated current utility or function (Gould & Vrba, 1982; Lauder, 1990), that adaptation has something to do with selection, and that selection is demonstrable in the wild (Arnold, 1983; Endler, 1986), makes the implicit assumption that performance data available in the ecological 'here and now' can be optimized on a cladogram just as morphology can be (Baum & Larson, 1991). One must assume that selection is responsible for the origin and the maintenance of the adaptation (Coddington, 1988), and furthermore, that the nature of the selection is the same throughout. The variety of evolutionary mechanisms that explain stasis often make such a uniformitarian stance problematic. However, all branches of historical biology use the logic of character optimization (Swofford and Maddison, 1992) to elucidate past history, e.g. biogeography, morphology, physiology, behaviour, gene evolution, etc. There is no logical obstacle to using the same logic with performance data. Optimizing performance data proceeds on the same epistemological basis as optimizing anything else. A demonstrated performance advantage in all relevant modern taxa applies equally well to their most recent common ancestor.

THE CONVERGENCE APPROACH

The convergence approach uses the same data and cladistic model as the homology approach (Figs. 2, 4–5), but emphasizes correlations between multiple, independent evolutionary events. Assumptions peculiar to the convergence approach have been covered by Pagel (Chapter 2); and Wenzel and Carpenter Chapter 4). Applying commonplace statistical notions to hierarchical systems can be difficult (e.g. Maddison, 1990; Gittleman & Luh, 1992; Grafen, 1992; Pagel, 1992), but characters in Fig. 5 A and B appear to correlate with C and D. Let us assume that after a thicket of methodological and statistical problems have been solved (reasonable and appropriate null hypotheses, appropriate degrees of freedom, branch lengths, non-independence of observations, polytomies, specifying ancestral values, etc. (Pagel, Chapter 2; Wenzel and Carpenter, Chapter 4), a significant correlation has resulted. The correlation is intriguing, but can we conclude adaptation?

Homoplasies are logical classes

As mentioned above, the most fundamental difference between the homology and the convergence approaches is that homologies are logical individuals whereas homoplasies are logical classes. Philosophers of science hold that scientific laws apply to classes, but not to individuals (Popper, 1965; Hull, 1974). By 'law' I mean something of the form, 'if the following situation applies, then the following specific consequences are predicted to occur or to have occurred in a large number of cases'. Most of the classical subjects treated by the convergence approach are evolutionary laws *in statu nascendi*. Recent examples are the relation between investment in male sexual display and polygyny, sex ratio and sociality, aposematism and gregariousness, mating systems and resource monopolization, sexual size dimorphism and mating strategies/age to first maturity, home range and body size, or velocity and optimal physiological temperature. Note that many of these traits are nearly universal themselves (classes) – all organisms have had and will have metabolic rates, temperatures, sizes, home ranges, life histories, ages, resources, and most have had and will have breeding systems, population structure and sex ratios. Attempts to explain pattern in these nearly universal attributes of life are a hallmark and strength of the convergence approach. The homology approach rarely considers traits of these sorts because they are widespread, immune to ostensive definition and vary continuously. To take just the first example mentioned above, demonstrating truly widespread correlation between the evolution of males with marked secondary sex characters and polygynous mating systems would be a significant achievement (Sillén-Tullberg & Moller, 1993). To the extent that studies of these two traits across clades supports the generalization, the law (or tendency or trend) holds. Elaborating and testing such generalizations is the proper business of the convergence approach.

If the above distinction is correct, then hypotheses about homoplasies are *necessarily* about classes. In their most falsifiable form, adaptive hypotheses under the convergence approach treat the phenomena under study as true universal classes. Several interesting topics suggest themselves. If the convergence approach treats classes, then the generality of the adaptive hypothesis may not be fully unveiled in a test that is arbitrarily limited to particular historical uniques. In other

words, the true scope of the hypothesis may go unrecognized. Second, logic requires that any character fulfilling the definition of the phenomenon be included in the class. Limitations imposed on the convergence approach by characters as historical uniques concerns the definition of the phenomenon or class (class membership). Third, arbitrary inclusion and exclusion of taxa or lineages as historical uniques poses questions about sampling bias among the instances used to test the hypothesis. Fourth, if significant correlation is always, or nearly always, interpreted as adaptation, may it be falsified?

In contrast, the scope of the hypothesis, the phenomenon under study and the taxa to which it applies are straightforward in the homology approach as it is limited to historical uniques, although the assessment of the evidence is sometimes complex.

Scope of the hypothesis

As an example, consider the relation of antler size in cervids with breeding system (Clutton-Brock, Albon & Harvey, 1980). At one level this concerns only the range of one putative unique (antlers) within another (cervids). More profoundly, it concerns investment in male sexual display and its relation to male–male competition as influenced by breeding system, a hypothesis particular neither to antlers nor cervids (nor to bovids, butterflies, angel fish, jumping spiders, primates, bower birds, etc.), but perhaps to a set as large as all primitively biparental organisms. Obviously one could include a range of metazoan taxa other than cervids. Theories of sex and sexual selection are general (Maynard-Smith, 1978). If these imply trends within cervids that hold, so much the better, but the cervid case is just a particular set of instances. Game theory and evolutionarily stable strategies are other general theories in biology that explain patterns in competition reasonably well (Maynard-Smith, 1982). If given certain initial starting conditions, *Agelenopsis* spiders in desert communities corroborate the predictions of game theory (Riechert, 1986), again so much the better, but *Agelenopsis* is again just an instance. In contrast, evolutionary patterns in life histories which were once thought to be generally the result of selection are now often considered to be effects largely of descent with modification and body size (Wanntorp *et al.* 1990).

The scope of the phenomenon

Clarity about the scope of the phenomenon is important because it defines the universe under study. The intended universe dictates the sampling programme and analysis. In Fig. 5, A_1 and A_2 are linked by the defining attributes of the class, not by homology. The same holds for the characters B, C and D, of which B_1 and B_2 through D_1 and D_2 are instances of phenomena that fulfill the class definitions. Definitions of classes of homoplasies can be made precise and objective, but those definitions often are arbitrary in an evolutionary sense in a way that homology is not. Objectivity of definition is readily achieved, but non–arbitrariness is more difficult. To return to antlers as an example of investment in male sexual display in cervids, equivalent examples of such investment should not be permanently excluded from the test without justification that derives from the hypothesis itself, rather than from *ad hoc* reasons. If the sample is limited to antlers despite other traits in

the same organisms that have been affected by the same sort of selection and could equally well be studied, the sample bias should be justified or at least acknowledged.

Taxon sampling

In the same sense that a study arbitrarily limited to a single character system (historical unique) can bias the definition of the traits under study, arbitrarily limiting the taxa studied to a particular clade (another kind of historical unique) may bias the study as well (Coddington, 1992). Given the rigorously parametric statistical world-view that the convergence approach adopts (Felsenstein, 1985; Harvey and Pagel, 1991; Pagel, Chapter 2; Wenzel and Carpenter, Chapter 4), the set of taxa should represent unbiased samples of all members of the class, which, as noted above, could be something like all taxa that lek (for one trait) compared to all taxa that show sexual dimorphism (for the other). If the sample is limited to a particular lineage, the limitation should stem from a valid *a priori* reason related to the hypothesis. One good reason to limit the sample to a particular lineage (e.g. Aves, Mammalia, Araneae, Insecta, Solananceae, or some other named phylogenetic node bequeathed to us by our culture) is because the apomorphies of the lineage justify the limitation. By apomorphies here I mean not just that small subset of 'characters' used by systematists to identify the taxon, but rather the total synapomorphic biological and ecological nexus that may characterize the lineage and which may include anything from habitat preferences to metabolic rate.

For an example that such considerations are not picayune, consider the analysis of the effect of phytophagy on insect diversification rates used as a test case of adaptive zones by Mitter, Farrell & Wiegmann (1988). I choose this example because it is one of the best comparative studies published to date and because it dealt with many of the thorny issues endemic to clade-based work on convergence. Strong, Lawton & Southwood (1984: 15) had proposed that "life on higher plants presents a formidable evolutionary hurdle, that most groups of insects have conspicuously failed to overcome. Once the hurdle is cleared, however, radiation may be dramatic". Mitter *et al.* (1988) found that in 11 out of 13 cases of phytophagous:non-phytophagous pairs of sister-groups, the phytophagous lineages contained at least twice as many species as the non-phytophagous lineage (a statistically significant association). Phytophagy seems to promote diversification within insects.

How do scopes of hypothesis, phenomenon and taxa relate to such a question? The adaptive zone argument concerned shifts between fundamentally different feeding zones. Thus one might wonder why just 'to' phytophagy instead of 'from' phytophagy as well? Why not detritivory to or from predation or parasitism, or phytophagy to predation, or at a lower level sucking plant juices to sucking apocynaceous plant juices? These questions concern the scope of the hypothesis.

Second, Mitter *et al.* (1988) followed Strong *et al.* (1984) in defining higher plant feeding as "feeding on the living tissues of higher plants, which excludes algal and other non-tracheophyte feeders, wood borers, nectar feeders, and species that use dead plants and leaf litter as food. Insects feeding on developing seeds are included, but those that take only shed seeds are excluded. Pollen feeding is also excluded, even though it is often hypothesized to be transitional to phytophagy in the strict

sense ...". In addition they excluded taxa in which the adult, but not the larvae, feed on higher plants because such species depend less on the adult diet than the larval diet. Mitter *et al.* (1988) were uncomfortable with the somewhat arbitrary nature of the definition of the trait 'higher plant feeding', but accepted it as the classical formulation favoured by students of plant–insect interactions. It contains some notable inclusions and exceptions that serve to limit the scope of the phenomenon in curious ways.

Third, this general hypothesis on adaptive zones is bounded by taxa: 'higher plants' and insects. Why just these two nodes in the cladogram of life? Did the choice make a difference, was it 'conventional' in the sense that Western culture has long chosen to name these nodes as taxa, or was it to test the sense of past and present workers that if the question was limited in roughly this way that an impressive trend would be disclosed? The number of species in the lineages ranged from 1 (Joppeicidae, sister to the phytophagous Tingidae, with *c.* 1800 spp.) to 130 000 (the phytophagous Phytophaga, sister to the 'non-phytophagous' Cucujoidea with *c.* 10 000). The sister-group pairs mainly were chosen from taxa carrying traditional Linnaean names and ranks, such as subfamilies, families and super-families. However, Insecta is a large clade, and conservatively at least several hundred thousand sister-group comparisons are potentially possible, not to mention Acari, Nematoda, Mollusca, various fungal and algal taxa, Aves, Mammalia and Teleostei as examples of other lineages that have been arbitrarily chosen to receive Latin names. These questions concern the scope and possible bias in sampling.

Finally, although Mitter *et al.* (1988) did their best to consider these biases and to make conservative choices so that minor changes in definition or scope would not affect the conclusions, if just two more comparisons had been against the trend (9 out of 13 instead of 11), the sign test would have been insignificant ($P > 0.133$).

If the core prediction of the adaptive zone hypothesis concerns invasion of formerly unoccupied zones, the sample would not be limited to a set of shifts that coincidentally includes just those taxa that tradition has conventionally recognized as 'megadiverse'. All pairwise feeding zone shifts could have been the universe, and one might well have concluded that only herbivory (and probably parasitism), not shifts to new 'feeding zones' *per se*, tended to influence diversification rate. The result actually obtained (Mitter *et al.*, 1988 claimed no more) may not test the fundamental hypothesis. Perhaps it is not a new zone, however empty, however formidable the barrier, but rather just particular zones that in fact drive diversification. Perhaps there is no general trend at all between invasion of new adaptive zones and increased diversification rate. In general, if we limit tests of general adaptive hypotheses to a set that includes mainly confirming instances, we are once again committing a sort of Panglossian, observer-biased mistake (O'Hara, 1992). Monophyletic groups often share coherent biologies, and if very diverse ones are compared to miscellanies defined as 'any biology but that one' adaptation will probably emerge triumphant. A slight change in the definition of higher-plant feeding would have altered the test in yet other ways. Why 'no' to pollen, wood and shed seeds? Why 'yes' to fruits, flowers and roots?

If mammals had been included, perhaps insectivory and granivory might have yielded significant trends; in mammals, phytophagy may not be the 'thing'. Maybe diversity in mammals is different from diversity in insects, but on what basis do we

partition the general and testable hypothesis of adaptive zones into two lucky subsets, separately significant but jointly not? If it is because some of Life's disparities are obvious, suitably delimited, the sample may be biased.

As in the case of the definition of adaptation itself, these considerations seem, even to me, unrealistically high. I fully realize that data on phytophagous insects are preliminary, that other comparisons even within the definitions of the study can be made (the authors thought that phytophagy had arisen at least 50 times among extant 'orders'), and we are all just trying to add one brick more solid than the last to the wall of science. The point is not to set goals that no one can achieve, but rather to debate issues of rigor and power, and to investigate methodological issues that lurk beneath the surface. In day-to-day work on sets of replicated evolutionary events (homoplasy), it sounds odd to suggest that first the adaptive hypothesis should be clearly developed and described in detail, that the focal traits be defined without reference to homology, and that instances be sampled at random among traits and taxa to which the hypothesis applies. However, such procedures are fundamental if statistical 'significance' is to mean anything. Sampling effort could be allocated in a way that avoided the biases identified above. If nothing else, such considerations may force the real generality of the adaptive hypothesis into the open. As Williams (1966) said, "evolutionary adaptation is a special and onerous concept that should not be used unnecessarily." It is probably no accident that hypotheses such as sex-ratio theory, among the more synthetic process theories evolutionary biology has ever developed, are fully cognizant of their generality and acknowledge a much greater range of instances as potential falsifiers than typically do studies of convergent phenomena.

Falsifiability

Ignoring the above issues will have a predictable effect on adaptation as a general explanation for evolutionary pattern. Imagine a scenario in which significant correlation is found, but that on admitting either more traits (e.g. male plumage as well as antlers) or more taxa (Aves as well as Mammalia) to the analysis, the significance disappears. Two choices seem clear. We can protect the significance in the smaller data set by *ad hoc* exclusion of the contrary data, based on appeals to historical uniques (either (1) traits or (2) lineages). Examples of this dilemma already exist. Höglund (1989) studied the association between lekking and sexual size and plumage dimorphism in those 11 families of birds that lek and found no significant association between the two traits. Harvey & Pagel (1991) reported Höglund's conclusions, but singled out the data just for grouse and pheasants (Tetraonidae) where there was a 'perfect' association. Can the impressive association in Tetraonidae be protected and if so on what grounds? A hidden third variable or factor coincident with tetraonids is required. Such *post hoc* procedures are problematic in hypothesis testing. Do the apomorphies of Tetraonidae in some way differentiate their leks from others? Höglund pointed out that if males lek on the ground (as do grouse, pheasants and some other birds) as opposed to aerial or arboreal leks, size dimorphism is significantly associated. However, this observation casts great doubt on the effect on lekking *per se* on size dimorphism, and suggests consideration of all ground-lekking taxa before drawing the conclusion, not just tetraonids. Put negatively, delimiting convergence studies by vaguely justified claims about the

uniqueness of lineages or characters seems like the worse form of *ad hoc* appeal. All lineages and characters are unique.

At the other extreme, if new data are added without prejudice to the growing evidence on an adaptive hypothesis, the 'significance' of an association may wink on and off as new data are compiled. Examples of this pattern in correlations in medical and epidemiological research are commonplace (e.g. cholesterol). Larger sample sizes (more taxa) test correlations better, all other things being equal. Faced with protecting odd bits of significance here and there by *ad hoc* appeals, or adding new data to the pile, I generally favour the second. It is through bolder and more powerful tests of adaptational hypotheses that real progress towards evolutionary generalities will be made, not through a gerrymandered series of small studies. In sum, the convergence approach should strive to avoid situations in which significant correlation is inevitably interpreted as adaptation.

Taxonomic ranks

A final, unsolved problem for the convergence approach concerns the use of taxonomic ranks. De Queiroz and Gautier (1992) and O'Hara (1992) have explained in some detail the mismatch between the current Linnaean system and real phylogeny. O'Hara in particular emphasizes how rank (fundamentally an expression of the observer's biased point of view) distorts understanding of history. By judicious lumping and splitting, severely asymmetric pectinate phylogenies can be transformed into the more balanced dichotomies predicted by equable rates of stochastic change (the molecular 'clock') and visa versa. The Linnaean hierarchy is already a viciously symmetrical model because it has only seven major ranks into which thousands of cladogenetic events must be compressed. Each newly corroborated cladogram of any size identifies dozens to hundreds more new taxa that all merit a rank in the system. But orders are already bursting with families, themselves stuffed with egregious numbers of equally ranked genera. Increasing the number of ranks available will not solve the problem. Though well-intended, 'Gigapicaorders' are a bad joke. The Linnaean model is so hopelessly limited that every category must be used within every lineage, which just goads workers to count or compare families within orders, or genera within tribes, or even 'five' kingdoms within life itself. In stark contrast, cladistic analysis often results in rather asymmetric topologies, though whether more or less than that expected under some null model is debatable (Slowinski & Guyer, 1989).

The Seven Ranks of Life skew not only names but thought and analysis. The empirical excess of asymmetric cladograms may be bad news for the molecular clock, Brownian motion and Linnaean hierarchies if that excess turns out to be real rather than artifactual (Shao & Sokal, 1990; Slowinski, 1990). Simulations of evolution only with topologies balanced to mimic taxonomies (Gittleman & Luh, 1992) almost certainly mislead for the most asymmetric resolutions implied by the polytomies. Figure 6a illustrates that taxonomies, interpreted phylogenetically, usually consist of reasonably balanced polytomous nodes. Even assuming that each polytomy subtends a monophyletic group, the taxa composing the polytomy are differentially related. Given no branch length information and polytomies, several statistical approaches recommend considering the ancestor as the mean of its descendants (Burt, 1989; Gittleman & Luh, 1992; Pagel, 1992). If a continuous variate
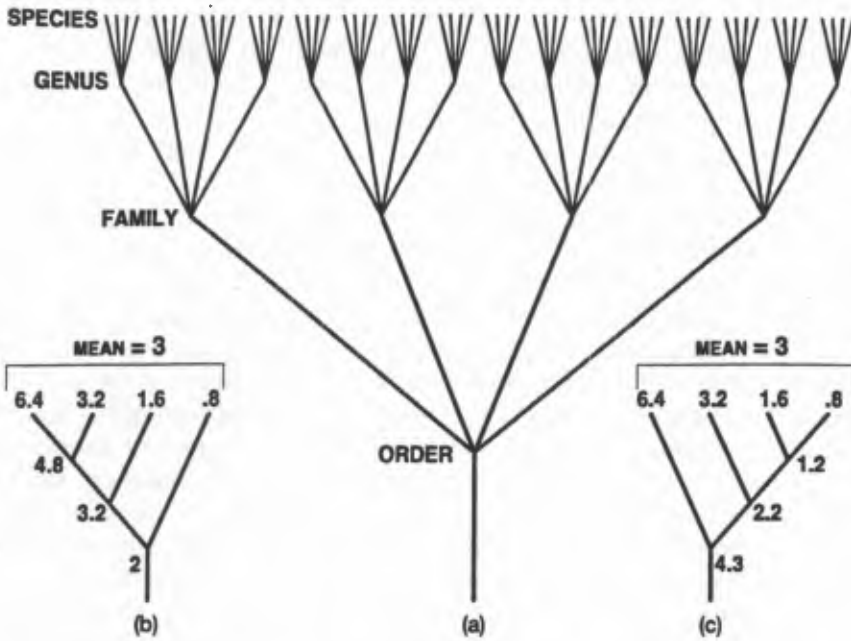
Figure 6 Linnaean taxonomies can bias comparative tests. (a) The cladogram implied by a Linnaean taxonomic classification in which all ancestral taxa contain four descendant taxa. (b) A four taxon tree with trait values known only for tips. The root value is 3 if taken as the mean of the tips, but 2 if topology is given and ancestors are the mean of their descendants. (c) As in (b), but a very different topology subtending the terminals, and therefore the root value is 4.3 rather than 2. Topology can severely affect the estimated ancestral value.

with values for four taxon topologies as in Fig. 6b and c is considered in the absence of topological information, the mean of 3 for the tips on both topologies will be the same. When the topologies are available, approximations using the mean are seen to overestimate the true values at the ancestral node by 50% in Figs. 6b or underestimate it by 30% in Fig. 6c (calculating ancestral nodes means of descendant nodes in all cases). Whether 8-fold ranges in continuous variates for unresolved polytomies are realistic, or what proportion of all possible topologies yield seriously different estimates of the ancestral mean, is currently unknown. Studies of the sensitivity of convergence approaches to topology, null models of branch length, and differential lumping and splitting are urgently needed.

SUMMARY

Neither the homology nor the convergence approach offer a royal and exclusive road to demonstration of adaptation, but perhaps proof in these cases is not obtainable. The former method requires a strong connection to trait function, because it is only the careful comparison of observed contrasts in performance or biological fact to prediction that provides the opportunity for the hypothesis to fail. Hidden third variables, ambiguous results, and events subsequent to the origin of the adaptation all conspire to cast doubt on the conclusion. Rigor in demonstrating

adaptation resides in the hope that particular scenarios must, through every test, become more detailed, and soon, like the proverbial liar, acquire enough rope to hang themselves. Textbook examples of adaptation will be those that continue to accumulate the rope but skillfully avoid the noose.

The convergence approach will usually precede the homology approach insofar as each instance contributing to a correlation awaits the study of its unique history. It seems uncontroversial to suggest that closer attention to the instances of a correlation can weaken or strengthen the relationship as a whole. In the limit, use of the homology approach on each instance could falsify enough cases to exclude adaptation as the explanation for correlation, though presumably the statistical correlation would still remain. The converse seems possible, but less likely. Detailed natural history results that strongly favour adaptation are unlikely to be controverted simply because the example conflicts with a more superficial correlation. Clearly this point is arguable (Pagel, Chapter 2). While perfect correlations that cannot adduce plausible evidence on function will always be an incomplete argument for adaptation (unless correlation and adaptation are the same thing), cases in which no evidence on function support the correlation seem unlikely, especially as it is usually anecdotal functional evidence that suggests the correlation in the first place.

Like the old children's game in which scissors cut paper, paper covers stones and stones break scissors, an obvious circularity and complementarity directs comparison of these two ways of investigating adaptation. If in a given study, the methods conflict but have available the best data according to their own lights, homology may win pitched battles with convergence by falsifying particular instances. However, the assumptions involved in such a thought experiment seems far-fetched. The homology approach, on the other hand, always loses the war to achieve general explanations of evolutionary pattern.

Both the homology and the convergence approach are alike in attempting to devise more rigorous and more powerful methodologies to the study the historical effects of natural selection. In this review, I have deliberately caricatured the two views in order to clarify their fundamental differences and the implications of those differences for the study of adaptation. As a practical matter, however, it cannot be emphasized too strongly that these methods are complementary. A large number of individuals cases, each tested by the homology approach and together making an impressively general evolutionary trend as tested by convergence approach, is obviously the best result. A blend of these approaches will mean meticulous characterization of the kind of selection thought to have resulted in the putative adaptation, because clarity of the hypothesis (or lack of it) underlies most of the sampling or bias problems the convergence approach faces. To evade those problems, limits on the scope of problems addressed by the convergence approach (traits, taxa) ought to devolve from a carefully restricted hypothesis, rather than loose or sloppy testing of a very general hypothesis. The key feature, then, is the precision of the adaptive hypothesis. With either approach one should always guard against substituting a claim of adaptation for a simpler, less mystical conclusion (current utility on the one hand, correlation on the other). The study of adaptation enters the truly evolutionary dimension when a study transcends the demonstration of these simple goals.

ACKNOWLEDGEMENTS

REFERENCES

ARNOLD, S., 1983. Morphology, performance, and fitness. *American Zoologist, 23*: 347–361.

BASOLO, A.L., 1990. Female preference predates the evolution of the sword in swordtail fish. *Science, 250*: 808–810.

BAUM, D.A. & LARSON, A., 1991. Adaptation reviewed: a phylogenetic methodology for studying character macroevolution. *Systematic Zoology, 40*: 1–18.

BELL, G., 1989. A comparative method. *American Naturalist, 133*: 553–571.

BJORKLUND, M., 1991. Evolution, phylogeny, sexual dimorphism, and mating system in the grackles (*Quiscalus* spp., Icterinae). *Evolution, 45*: 608–621.

BROOKS, D.R. & McLENNAN, D.A., 1991. *Phylogeny, Ecology and Behavior*. Chicago: Chicago University Press.

BROOKS, D.R., O'GRADY, R.T. & GLEN, D.R., 1985. Phylogenetic analysis of the *Digenea* (Platyhelminthes: Cercomeria) with comments on their adaptive radiation. *Canadian Journal of Zoology, 63*: 411–443.

BURT, A., 1989. Comparative methods using phylogenetically independent contrasts. In P.H. Harvey & L. Partridge (Eds), *Oxford Surveys in Evolutionary Biology*, (6), 33–53. Oxford: Oxford University Press.

CARPENTER, J.M., 1989. Testing scenarios: Wasp social behavior. *Cladistics, 5*: 131–144.

CARPENTER, J.M., 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. In K.G. Ross & R.W. Matthews (Eds), *The Social Biology of Wasps*, 7–32. Ithaca, NY: Cornell University Press.

CHEVERUD, J.M., DOW, M.M. & LEUTENEGGER, W., 1985. The quantitative assessment of phylogenetic constraints in comparative analysis: sexual dimorphism in body weight among primates. *Evolution, 39*: 1335–1351.

CLUTTON-BROCK, T.H., ALBON, S.D. & HARVEY, P.H., 1980. Antlers, body size, and breeing group size in the Cervidae. *Nature, 285*: 547–565.

CODDINGTON, J.A., 1986a. The monophyletic origin of the orb web. In W.A. Shear (Ed.), *Spiders: Webs, Behavior, and Evolution*, 319–363. Stanford, CA: Stanford University Press.

CODDINGTON, J.A., 1986b. Orb webs in non-orb-weaving ogre-faced spiders (Araneae: Deinopidae): a question of genealogy. *Cladistics, 2*: 53–67.

CODDINGTON, J.A., 1988. Cladistic tests of adaptational hypotheses. *Cladistics, 4*: 1–22.

CODDINGTON, J.A., 1990. Bridges between evolutionary pattern and process. *Cladistics, 6*: 379–386.

CODDINGTON, J.A., 1991. Cladistics and spider classification: Araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae; Orbiculariae). *Acta Zoologica Fennica, 190*: 75–87.

CODDINGTON, J.A., 1992. Avoiding phylogenetic bias. *Trends in Ecology and Evolution, 7*: 68–69.

CODDINGTON, J.A. & LEVI, H.W., 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics, 22*: 565–592.

DE QUEIROZ, K. & GAUTIER, J., 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics, 23*: 449–480.

DONOGHUE, M.J., 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. *Evolution, 43*: 1137–1156.

ELGAR, M.A., GHAFFAR, N. & READ, A.F., 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. *Journal of Zoology (London), 222*: 455–470.

ENDLER, J.A., 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press.

FARRIS, J.S., 1983. The logical basis of phylogenetic analysis. In N.I. Platnick & V.A. Funk (Eds), *Advances in Cladistics, 2*, 7–36. New York: Columbia University Press.

FARRIS, J.S., 1988. Hennig86, ver. 1.5. Microcomputer program. Available from author, 41 Admiral St, Port Jefferson Station, New York 11776, U.S.A.

FELSENSTEIN, J., 1985. Phylogenies and the comparative method. *American Naturalist, 125*: 1–15.

GARLAND Jr, T., HARVEY, P.H. & IVES, A.R., 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology, 41*: 18–32.

GHISELIN, M.T., 1974. A radical solution to the species problem. *Systematic Zoology, 23*: 536–544.

GITTLEMAN, J.L. & KOT, M., 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology, 39*: 227–241.

GITTLEMAN, J.L. & LUH, H.K., 1992. On comparing comparative methods. *Annual Review of Ecology and Systematics, 23*: 383–404.

GOULD, S.J. & LEWONTIN, R.C., 1979. The spandrels of San Marco and the Panglossian Paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B, 205*: 581–598.

GOULD, S.J. & VRBA, E.S., 1982. Exaptation – a missing term in the science of form. *Paleobiology, 8*: 4–15.

GRAFEN, A., 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B, 326*: 119–157.

GRAFEN, A., 1992. The uniqueness of the phylogenetic regression. *Journal of Theoretical Biology, 156*: 405–423.

GREENE, H.W., 1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana Zoologica, 31*: 1–12.

HARVEY, P.H. & PAGEL, M.D., 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

HUEY, R.B., 1987. Phylogeny, history, and the comparative method. In M.E. Feder, A.F. Bennett, W. Burggren & R.B. Huey (Eds), *New Directions in Ecological Physiology*, 76–98. Cambridge: Cambridge University Press.

HULL, D.L., 1974. *Philosophy of Bological Science*. Englewood Cliffs, NJ: Prentice Hall.

HÖGLUND, J., 1989. Size and plumage dimorphism in lek-breeding birds: a comparative analysis. *American Naturalist, 134*: 72–87.

LAUDER, G.V., 1982. Historical biology and the problem of design. *Journal of Theoretical Biology, 97*: 57–67.

LAUDER, G.V., 1990. Functional morphology and systematics: studying functional patterns in an historical context. *Annual Review of Ecology and Systematics, 21*: 317–340.

LEVINTON, J.S., 1983. Stasis in progress: the empirical basis of macroevolution. *Annual Review of Ecology and Systematics, 14*: 103–137.

LOSOS, J.B., 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs, 60*: 369–388.

MADDISON, W.P., 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on a certain branch of a phylogenetic tree? *Evolution, 44*: 539–557.

MADDISON, W.P. & MADDISON, D.R., 1992. *MacClade, ver. 3.0.* Sunderland, MA: Sinauer.

MARTINS, E.P. & GARLAND Jr, T., 1991. Phylogenetic analysis the correlated evolution of continous characters: a simulation study. *Evolution, 45*: 534–557.

MAYNARD-SMITH, J., 1978. *The Evolution of Sex.* Cambridge: Cambridge University Press.

MAYNARD-SMITH, J., 1982. *Evolution and the Theory of Games.* Cambridge: Cambridge University Press.

McLENNAN, D.A., 1990. Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): the relationships between male colour and female behaviour. *Canadian Journal of Zoology, 68*: 484–492.

MITTER, C., FARRELL, B. & WIEGMANN, B., 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *American Naturalist, 132*: 107–128.

NIXON, K.C., 1991. Clados. Program and documentation. Distributed by the author, P.O. Box 270, Trumansburg, NY 14886, U.S.A.

O'HARA, R.J., 1992. Telling the tree: narrative representation and the study of evolutionary history. *Biology and Philosophy, 7*: 135–160.

OLIVEIRA, P.S., 1988. Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). *Biological Journal of the Linnaean Society, 33*: 1–15.

OLIVEIRA, P.S. & SAZIMA, I., 1984. The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biological Journal of the Linnaean Society, 22*: 145–155.

PADIAN, K., 1985. The origins and aerodynamics of flight in extinct vertebrates. *Paleontology, 28*: 413–333.

PAGEL, M.D., 1992. A method for the analysis of comparative data. *Journal of Theoretical Biology, 156*: 431–442.

PAGEL, M.D. & HARVEY, P.H., 1988. Recent developments in the analysis of comparative data. *Quarterly Review of Biology, 63*: 413–440.

PAGEL, M.D., 1994. The adaptionist wager. In P. Eggleton & R.I. Vane-Wright (Eds), *Phylogenetics and Ecology*, 29–51. London: Academic Press.

POPPER, K.R., 1965. *Conjectures and Refutations: the Growth of Scientific Knowledge*, 2nd .edition. New York: Harper & Row.

RIDLEY, M., 1983. *The Explanation of Organic Diversity: the Comparative Method and Adaptations for Mating.* Oxford: Oxford University Press.

RIDLEY, M., 1989. Why not to use species in comparative tests. *Journal of Theoretical Biology, 136*: 361–364.

RIECHERT, S.E., 1986. Spider fights: a test of evolutionary game theory. *American Scientist, 47*: 604–610.

SHAO, K. & SOKAL, R.R., 1990. Tree balance. *Systematic Zoology, 39*: 266–276.

SILLÉN-TULLBERG, B., 1988. Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. *Evolution, 42*: 293–305.

SILLÉN-TULLBERG, B. & MOLLER, A.P., 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *American Naturalist, 141*: 1–25.

SLOWINSKI, J.B., 1990. Probabilities of n-trees under two models: a demonstration that asymmetrical interior nodes are not improbable. *Systematic Zoology, 39*: 89–94.

SLOWINSKI, J.B. & Guyer, C., 1989. Testing the stochastity of patterns of organismal diversity: an improved null model. *American Naturalist, 134*: 907–921.

STEBBINS, G.L. & AYALA, F.J., 1981. Is a new evolutionary synthesis necessary? *Science, 213*: 967–971.

STRONG, D.R., LAWTON, J.H. & SOUTHWOOD, T.R.E., 1984. *Insects on plants: community patterns and mechanisms*. Cambridge, MA: Harvard University Press.

SWOFFORD, D.L., 1993. PAUP (Phylogenetic Analysis Using Parsimony), ver. 3.1.1. Microcomputer program available from the author, Illinois State Natural History Survey, 172 Natural Resources Bldg., 607 E. Peabody, Champaign, IL 61820, U.S.A.

SWOFFORD, D.L. & MADDISON, W.P., 1992. Parsimony, character-state reconstruction and evolutionary inference. In R.L. Mayden (Ed.), *Systematics, Historical Ecology, and North American Freshwater Fishes*, 186–223. Stanford, CA: Stanford University Press.

VOLLRATH, F., 1980. Why are some spider males small? A discussion on *Nephila clavipes*. In J. Gruber (Ed.), *Verbandlungen. 8. Internationeler Arachnologen – Kongress abgehalten an der Universitat fur Bodenkultur Wien, 7–12 Juli 1980*, 165–169. Vienna: Egermann.

VOLLRATH, F. & PARKER, G.A., 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature, 360*: 156–159.

WANNTORP, H., 1983. Historical constraints in adaptation theory: traits and non-traits. *Oikos, 41*: 157–160.

WANNTORP, H.E., BROOKS, D.R., NILSSON, T., NYLIN, S., RONQUIST, F., STEARNS, S.C. & WEDELL, N., 1990. Phylogenetic approaches in ecology. *Oikos, 57*: 119–132.

WENZEL, J.W. & CARPENTER, J.M., 1994. Comparing methods: adaptive traits and tests of adaptation. In P. Eggleton & R.I. Vane-Wright (Eds), *Phylogenetics and Ecology*, 79–101. London: Academic Press.

WILLIAMS, G.C., 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.