

The role of paleontological data in testing homology by congruence

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With homology being defined as shared similarity due to common ancestry, any initial perception of similarity (or relative invariance) among organisms may be treated as a conjecture of homology to be tested by congruence. The phylogenetic information content is therefore not with the character itself, but lies in the relation of any one character to all others known. The "principle of total evidence" thus emerges as a logical corollary of the distinction of homology and homoplasy, the most severe test of homology involving all known characters in the search for the globally most congruent pattern. In a study combining fossil and extant organisms, however, the issue of missing characters raises the question of implicit *a priori* weighting, because some sources for characters (soft anatomy, molecular, physiological, behavioral) remain unknown in fossils. The issue of missing data in fossils requires further study before the potential impact of fossils on a classification based on extant organisms can be properly assessed.

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Introduction

In 1972, Martin Rudwick published a book under the title *The Meaning of Fossils*. The book is primarily a history of paleontology, but at the same time the text can be read as a critical reassessment of the contribution of fossils to the development of evolutionary theory, and the significance of fossils for phylogeny reconstruction. In 1981, Colin Patterson addressed the 'meaning of fossils' in systematic biology, and therewith the question whether fossils are, indeed, able to overturn a hierarchy of relative relationships based on extant organisms. In 1989, it was Antoni Hoffman's turn to deal with the same problem, a question which only one year before had been claimed to be answered on an empirical basis (Gauthier et al.

1988a). Gauthier, Kluge and Rowe's conclusion was: yes, fossils are able to change a classification based on extant animals only. Following their argument, the distribution of phenotypic traits as observed in the living biosphere is an incomplete record of biodiversity, and in the absence of fossils it may be misleading in the reconstruction of phylogenetic relationships!

The issue is a difficult one to deal with, and it is tightly linked to the concepts and methods of phylogeny reconstruction. I would like to use this moment of commemoration of Antoni Hoffman's contributions to paleobiology to get back to this problem under a set of premises which might not have been his: relative relationships among organisms are analyzed on cladistic principles, allowing shared derived characters only to diagnose monophyletic groups (Hennig 1966). The analysis of relative relationships must remain decoupled from evolutionary theory, in order to avoid empirical emptiness of process explanations for recovered patterns of relationship (Brady 1985). Therefore, homology is considered a conjecture of similarity to be tested by congruence and, if successful, to be explained by common descent (Patterson 1982).

Homology and congruence

Homology is a relation of similarity to be explained by common descent. However, similarity may also result from mistakes made by the investigator (mistaken conjectures of homology), from chance, or it may be due to the independent acquisition of similar traits in unrelated clades (convergence). Since homology is defined as similarity due to common ancestry, a preconceived hypothesis of common descent must not guide the search for homology, if circular reasoning is to be avoided. The threat of circular reasoning, or tautology, is the reason why Patterson (1982) proposed to treat every perception of similarity (i.e., every perception of relative invariance of structure in a continuously evolving world: de Pinna 1991) as a conjecture of homology (as a taxonomic statement *sensu* Panchen 1992) which is to be tested by congruence.

Within a given data set, a number of characters may congruently support a specific hypothesis of relationship. Other characters, or conjectures of similarity, may jointly support a conflicting classification. The test of congruence specifies that within a given data set, the largest number of characters which congruently support a specific hypothesis of relationship be considered as homologies. It is the largest set of congruent characters which will hypothetically be explained by common descent, whereas the minority data which support conflicting hypotheses of relationship (the incongruent characters) will be treated as homoplasy, i.e., as chance similarity or convergence.

The test of congruence assures that among two or more conflicting hypotheses of relative relationship derived from a given data set, the most

parsimonious solution will be selected. The principle of parsimony underlying the test of congruence aims at maximizing regularity of character distribution and as such maximizes the economy of information storage in natural classification. At the same time, and in the context of the historical (evolutionary) explanation of a cladogram, the principle of parsimony minimizes the assumptions of character transformation necessary to explain character distribution, by maximizing congruence and hence homology, and minimizing homoplasy and hence convergence or reversals.

In the last analysis the test of congruence means that the phylogenetic information content (Hecht & Edwards 1977) of any one character is not with any particular character in itself, but lies in the relation of any one character to all other characters known. Homology is not a relation emerging from the analysis of a particular character (in terms of its special form, function, ontogeny, etc.), but a hypothesis emerging from the test of congruence which relates the character under consideration to all other characters known in a process of 'character matching' (Kluge 1989; Rieppel 1992).

The 'principle of total evidence' (Kluge 1989), matching any one character to all others known, will here be explained in relation to a somewhat trivial example, using the loss of limbs in snakes as a case in point. Some primitive snakes retain rudimentary hind limbs – but how do we know that these are rudimentary limbs, rather than initial stages in the evolution of tetrapod limbs? After all, there was a time when snakes were classified with eels, i.e., with fishes often found crawling over land (Rieppel 1987)! That rudimentary limbs in snakes represent stages of limb reduction, rather than initial stages of limb evolution, cannot be gleaned from the study of limb development in snakes per se, but is a conclusion deduced from the congruence of a great many other characters (other than limbs) which diagnose snakes not as proto-tetrapods, but as a subgroup of Squamata, which is a subgroup of the Amniota, which is a subgroup of Tetrapoda.

If preconceived knowledge of phylogeny cannot be allowed to influence the assessment of homology, the latter becomes a conjecture of similarity to be tested by the congruence of other characters and, if successful, to be explained by common descent. In other words, and following cladistic principles of phylogeny reconstruction, it is not the knowledge of homology of any one character which is indicative of evolutionary relationships. Instead, every character represents a conjecture of similarity which may, potentially, be explained as a homology (due to common ancestry), or it may turn out to be a homoplasy (due to convergence). And it is not the nature of the character which indicates whether it is to be treated as a homology or homoplasy; it is the relation of any one character to all other characters known, i.e. the congruence of characters. A character congruent with the greatest number of other characters will be treated, provisionally, as a homology. Incongruent characters will, provisionally, be treated as convergences. The corollary of cladistic analysis is that the

phylogenetic information content is not with a character *per se*, but lies in the relation of any one character to all other characters known.

The meaning of fossils

In 1982, Gardiner published a highly influential paper in which he claimed, following 19th century authors (e.g. Owen 1866), that birds and mammals are sister-groups, constituting the monophyletic taxon Haemothermia. This hypothesis contradicted evidence provided by the rich fossil record of 'mammal like reptiles' (the synapsids of the classical textbooks), thought to document by an 'insensibly graded series of intermediates' (which Darwin 1859, could only dream of) the transition from reptiles to mammals. Critics of Gardiner's (1982) paper were quick to point out that endothermy in birds and mammals surely was acquired independently, i.e. convergently, without the two groups inheriting the trait from a common ancestor (see the review in Benton 1990). But how could those critics know? If homology is defined as similarity due to common ancestry, and if knowledge of common ancestry cannot be the operational criterion for the recognition of homology, the issue has to be decided by the test of congruence (Patterson 1982)! Should fossils, i.e. mammal-like reptiles, be allowed to overturn a classification based on the analysis of extant tetrapods? That is: should data obtained from fossils be combined with data obtained from extant organisms in the analysis of phylogenetic relationships based on the test of congruence?

Patterson (1982: p. 218) concluded that 'instances of fossils overturning theories of relationship based on recent organisms are very rare, and may be nonexistent'. His assessment of the state of art in vertebrate phylogeny reconstruction provoked severe criticism. Indeed, Gardiner's (1982) hypothesis of the Haemothermia was hailed as a prime example for mistaken phylogeny reconstruction following the neglect of the information provided by fossils. Gardiner's (1982) analysis of tetrapod interrelationships was based on a total of 47 characters of which 28 supported the Haemothermia. Many of the latter were dismissed, *a priori*, as instances of convergence, linked to the occurrence of endothermy in both groups. However, Gardiner's (1982) results were supported by Løvtrup (1985; but see also Løvtrup 1977), and there is a distinct molecular signal pointing in a similar direction (Bishop & Friday 1987; Hillis & Dixon 1989; Hedges *et al.* 1990)!

Gardiner's (1982) hypothesis of the Haemothermia was based on hard anatomy (osteological) data as well as on soft anatomy characters and physiological evidence. Following the doctrine that phylogenetic interrelationships should first be analyzed using extant animals only, the fossils subsequently being 'hooked' into the system obtained from extant organisms at the appropriate level of synapomorphy (Patterson & Rosen 1977), Gardiner (1982) ignored all the evidence provided by fossils which sug-

gests that mammals do not share a common recent ancestry with birds, but rather descended from mammal-like reptiles. Gardiner's (1982) hypothesis was perceived as the ideal case to test the significance of fossils which, *contra* Patterson (1981), could make a difference, i.e. overturn a classification based on extant organisms only! A problem, however, emerges with the compatibility, or rather the lack thereof, of different data sets.

To test phylogenetic interrelationships among extant amniotes, Gauthier *et al.* (1988a) re-analyzed the amniote data accumulated by Gardiner (1982), adding those of Løvtrup (1985) as well as additional characters of their own. They obtained similar results to Gardiner's (1982), the difference being that crocodiles came out as sister-group of birds, the two constituting the sister-group of mammals: (lepidosaurs (turtles (mammals (crocodiles (birds)))))) It was only after the addition of fossil data that this classification was turned over, mammals now grouping with extinct synapsids, while crocodiles and birds were nested within archosauromorph reptiles (accordingly, the Amniota comprise two major clades, the Synapsida, including the mammal-like reptiles plus their descendants, and the Reptilia, including birds: Gauthier *et al.* 1988b). Therefore, fossils had, indeed, changed the classification based on extant animals, an effect Gauthier *et al.* (1988a) attributed to a number of factors such as improved assessment of character polarity as well as the closure of major morphological gaps by the use of fossils. Extant organisms may be so different from one another that they may be difficult to be compared in detail. With the use of fossils, intermediate morphologies may become available which broaden the data base and establish transformation series for characters that would otherwise not be available.

The use of fossils in the test of classifications based on extant organisms may come at a cost, however, namely the threat of implicit character weighting! Since fossils generally do not preserve soft anatomy characters (let alone molecular or behavioral traits), Gauthier *et al.* (1988a) had to code all those characters as unknown for fossil taxa, whereas with the addition of fossils they greatly augmented the number of osteological characters which they subjected to the test of congruence. By this procedure, they may implicitly have allowed osteological features to carry a heavier weight than *all* other characters (not retrievable from fossils) in the test of congruence.

Parsimony analysis will assign a character state to empty cells, or missing entries in a data matrix which follows from the globally most parsimonious distribution of all those characters which are positively known. In other words, the most parsimonious tree will be searched for with respect to all those characters positively known. Once this tree is obtained, empty cells will be assigned character states as they follow from the given tree topology. With the addition of fossil taxa a large number of hard anatomy characters were added to the analysis of amniote interrelationships by Gauthier *et al.* (1988a), and it is these additional hard anatomy characters which overruled the classification based on extant

organisms only. What remains unanswered, however, is the question how an increase of soft anatomy, molecular and behavioral data for extant taxa would have effected the analysis, or how positive knowledge of those characters in fossils would have changed the conclusion were it at all available (D.B. Wake, quoted in Gauthier *et al.* 1988a: p.109; see also Platnick *et al.* 1991 on the effect of missing data). In essence, then, the problem does not seem to be with the distinction of extant and fossil taxa. Rather, it is the number of taxa (extant or fossil) and the pattern of known characters in relation to the number of unknown characters which determines the outcome of the analysis.

Discussion and conclusions

If homology is not an observational statement, if the phylogenetic information content is not with any character *per se*, but in the relation of any one character to all others known, then the relation of homology must be treated as a conjecture of similarity to be tested by congruence (Patterson 1982). Following this reasoning, it must be admitted that the most stringent test of any conjecture of homology involves the test of any one character against the distribution of as many other characters as are known. It is true that it will never be possible to recognize, and code, all possible characters within any one group of organisms, but this simply underscores the fact that empirical sciences can never deal with absolute truth, but only with hypothetical knowledge. Nevertheless, there is a measure of reliability of hypothetical knowledge and of the predictions it generates, and this is provided by the most severe test possible. In the case of homology, this means that any conjecture of similarity cannot be tested against all possible characters, but it can be tested as severely as possible, and the most stringent test of congruence involves all other characters known at any one time (Kluge 1989).

In the case of extant animals, there is a wide variety of sources for character analysis: hard anatomy (mineralized hard tissues like bone and teeth), soft anatomy (muscles, nerves, blood vessels, etc.), physiology and molecules, even behavior. The use of fossils severely restricts the choice of characters, hard anatomy being the only organ system generally accessible (unless some favorable conditions of fossilization preserve some soft anatomy or molecular data). The problem is aggravated by the generally incomplete preservation of the hard anatomy of fossils! In an analysis involving both extant and fossil organisms, two options therefore obtain.

One is to run the analysis including both extant and fossil animals with the inclusion of hard anatomy data only. By this procedure, osteological features are implicitly considered to carry a greater phylogenetic information content than any of the other sources of characters excluded from the analysis. In a phylogenetic analysis involving both extant and fossil organisms, characters involving soft anatomy, physiological, molecular

and behavioral traits, have all to be coded as 'unknown' for fossil taxa. This potentially allows the hard anatomy data to overrule whatever signal might be obtained from the soft anatomy, molecular and behavioral traits. Considerations and concerns such as these might advocate the separate analysis of different character sets (hard versus soft anatomy, physiological, molecular, and behavioral), and comparison of the separate results in search for the best supported tree. If all separate character sets repeatedly support a similar tree, no problem obtains, since this will be the tree to be (provisionally) accepted. The interesting question to raise is whether that same tree emerges from an analysis combining all data, and what the reason could be if such should turn out not to be the case.

If different data sets analyzed separately support conflicting trees, then the problem arises as to how to choose among those trees? In that case, combining all available data would seem to be the immediate answer, since this provides the strongest test of congruence. This is certainly true for extant organisms, where all types of characters are, potentially at least, equally accessible to analysis. The problem with this strategy originates with the inclusion of fossils in the analysis, in which case all characters other than those of hard anatomy have to be treated as unknown. The degree to which the inclusion of missing data in a parsimony analysis may result in implicit *a priori* character weighting remains a matter of debate.

In conclusion, the 'principle of total evidence' (Kluge 1989) emerges as a logical corollary of the distinction of homology and homoplasy. If homology is viewed as a hypothesis of phylogenetically relevant similarity to be tested by congruence, the most severe test of homology is logically one where all characters known are matched against each other in the search for the most congruent pattern. In a study combining fossil and extant organisms, however, the issue of missing characters raises the question of implicit *a priori* weighting, in that known data (hard anatomy) may overrule other kinds of evidence (soft anatomy, molecular, physiological, behavioral) which remain unknown in fossils. The issue of missing data requires further study before the potential impact of fossils on a classification based on extant organisms only can be properly assessed.

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Streszczenie

Jesli zdefiniuje się homologię jako podobieństwo wynikające ze wspólnego pochodzenia, każde zauważalne podobieństwo może być traktowane jako domniemanie homologii, które można poddać testowi zgodności. Przebieg filogenezy wywodzi się nie z samej cechy lecz z jej stosunku do innych znanych cech. Zasada pełności danych pojawia się jako logiczna konsekwencja rozróżnienia homologii i homoplazji. Test homologii obejmujący wszystkie znane cechy, zmierzający do odnalezienia najbardziej zgodnego ich rozkładu, jest więc testem najostrzejszym. Kiedy analizie poddaje się zbiory danych o kopalnych i dzisiejszych organizmach pojawia się problem nieznanych cech (niezachowanych w stanie kopalnym) pociągający za sobą konieczność wstępnego wartościowania cech.