Cladistics (1991) 7:367-394

CONCEPTS AND TESTS OF HOMOLOGY IN THE CLADISTIC PARADIGM

Mario G. G. de Pinna '

[1] *Department of Ichthyology, American Museum of Natural History,*
Central Park West at 79th Street, New York, NY 10024, U.S.A.

and

Department of Biology, City College, CUNT, New York, New York 10031, U.S.A.

Received 8 March 1991; accepted 22 August 1991

Abstract—Logical equivalence between the notions of homology and synapomorphy is reviewed **and** supported. So-called transformational homology embodies two distinct logical components, one related to comparisons among different organisms and the other restricted to comparisons within the same organism. The former is essentially hierarchical in nature, thus being in fact a less obvious form of taxic homology. The latter is logically equivalent to so-called serial homology in a broad sense (including homonomy, mass homology or iterative homology) - Of three tests of homology proposed to date (similarity, conjunction and congruence) only congruence serves as a test in the strict sense. Similarity stands at a basic level in homology propositions, being the source of the homology conjecture in the first place. Conjunction is unquestionably an indicator of non-homology, but it is not specific about the pairwise comparison where non-homology is present, and depends on a specific scheme of relationship in order to refute a hypothesis of homology. The congruence test has been previously seen as an application of compatibility analysis- However, congruence is more appropriately seen as an expression of strict parsimony analysis. A general theoretical solution is proposed to determine evolution of characters with ambiguous distributions, based on the notion of maximization of . homology propositions. According to that notion, ambiguous character-state distributions should be resolved by an optimization that maximizes reversals relative to parallelisms. Notions of homology in morphology and molecular biology are essentially the same. The present tendency to adopt different terminologies for the two sources of data should be avoided, in order not to obscure the fundamental uniformity of the concept of homology in comparative biology.

> "A similar hierarchy is found both in 'structures' and in 'functions'. In the last resort, structure (i.e. order of parts) and function (order of processes) may be the very same thing [...]."
>
> L. von Bertalanffy

> "[...] it is the fact that certain criteria enable us to match parts of things consistently which suggests that mechanisms of certain kinds must have been involved in their origin."
>
> N. Jardine **and** C. Jardine

Introduction

The notion of homology occupies a central position in comparative studies, biological or otherwise (Jardine and Jardine, 1969; Sneath, 1969). In biology in particular, homology is probably the most fundamental notion underlying not only statements within the realm of comparative biology (Bock, 1974) but in fact most generalizations about biological phenomena. Riedl (1979) suggested that homology is the only law-like hierarchic relationship in biology above the level of the individual organism.

Homology, or some logical equivalent, has been explicitly discussed in biology long before the rise of evolutionary thinking (Russell, 1916;Rieppel, 1988). In spite of its long history, the homology concept still attracts much attention. A large number of papers and even special symposia continue to be dedicated to it (e.g. Sattler, 1984; Sander, 1989).

0748-3007/91/040367 + 28S03.00/0

In its most basic form, homology means equivalence of parts. It serves, therefore, as a sorting procedure to investigate the validity of comparative information: comparisons between homologs are meaningful within a hierarchic context, comparisons between non-homologs are not. At this point consensus about homology notions ends. It is immediately clear that the term "equivalence" is not by itself precise enough (nor, for that matter, is "valid" or "meaningful"), and allows countless distinct interpretations. The plurality of potential interpretations has fueled much of the never-ending controversy that surrounds definitions of homology.

Most debate on homology centers on definitions of that term. Nevertheless, the historical background of the term homology has presently grown so diverse that attempts to constrain its various previous usages into a compromise definition appear doomed. Ghiselin (1976) made clear the difference between "lexical" and "stipulative" definitions, calling attention to the importance of the distinction for the discussion of the homology problem. A stipulative definition is a designation for the use of a term, of the kind "let *x* designate y". As such, it cannot be true or false, and simply constitutes a basis for objective discussion of an encompassing subject. A lexical definition, on the other hand, is a statement about usage, of the kind "x is used to designate y". This is the kind of definition characteristic of dictionaries, and it can be true or false. Partly as an outcome of its historical breadth, most modern redefinitions of homology have been a compromise between past usage and theory. As a result, they are neither lexical nor stipulative, but an unspecified combination of the two. Such confusion has plagued much recent literature. Controversies are frequently delimited by a homology proposition about which "most biologists would agree", as if this fact represented a valid argument *per se.* There will always be some past usages that will agree with newly formulated models or definitions; likewise, there will always be some others that disagree. This is particularly true in the case of homology, with its long history of discrepant definitions and usages. The degree of agreement with past models is not a criterion to validate or to reject an alternative model. Accordingly, definitions of terms should not have their scientific value determined by their lexical accuracy.

In this paper, I shall not be concerned with definitions of homology, because in my view this has proven to be an unfruitful way to approach the issue. Excessive concern with lexical aspects of the term homology has been detrimental to understanding of the notion it carried. Furthermore, a review of formal definitions of homology would be of limited interest, even from a historical perspective. Most definitions were proposed retrospectively, and had little if any influence upon homology recognition and testing in empirical works that followed. Symptomatically, one of the most influential papers on homology in this century (Remane, 1952) did not explicitly provide a definition of homology (cf. Schmitt, 1989). A relatively complete and updated review of the most important definitions of homology can be found in Patterson (1982). An excellent survey of the development of the notion of homology throughout the history of biology is provided by Rieppel (1988).

I agree with Schmitt (1989) that an evaluation of definitions of homology acquires sense only against a specific frame of reference, i.e. a more encompassing method or theory. Therefore, disputes about the value of particular homology definitions are pointless, unless explicitly within the context of a common method of approach to biological diversity. As a stipulative definition, and from the perspective of systematics, I adopt the view that homology and synapomorphy are equivalent notions. Justification for such a view is provided below.

One interesting aspect of the idea of homology is that individual homology propositions interact with each other, and mutually validate one another. Consequently, homology interacts with the act of homologization, and simultaneously legitimizes and is legitimized by comparisons. Homology, thus, is essentially a comparative concept. Because systematics is the formalization of the comparative method *per se* (Nelson, 1970; Funk and Brooks, 1990), the relationship between the notion of homology and systematic method is expectedly very close if not fundamental. At present, Cladistics has reached the status of standard method for systematic research, and can be considered as the current paradigm in systematics. Still, interaction between the old notion of homology and the new method of Cladistics remains fuzzy. This paper is an effort to clarify this interaction, and to provide grounds for accommodating the notion of homology within a strictly cladistic framework.

Homology as Synapomorphy: a Reappraisal

Perhaps the most relevant contribution to the homology problem in the last few decades is the one commonly attributed to Patterson (1982), who explicitly equated homology with synapomorphy. Unfortunately, this point of view has not been fully appreciated by most recent authors. For example, Roth (1988) regards Patterson's idea as an unacceptable restriction of a term that should denote a broader concept, as if his proposal was only a terminological matter ("I see no point in narrowing the definition of homology, a word of broader connotation, so drastically"; Roth, 1988:4). Along the same line, all that Wagner (1989) had to say about Patterson's suggestion was that "[e]ven if this definition is useful in Cladistics, it is counterproductive for the biological homology concept" (Wagner, 1989:1159).

In a certain way, there is no ground for disagreement with Roth's (1988) opinion that viewing homology as synapomorphy restricts the meaning of the former team. The equivalence undoubtedly implies a restriction in meaning. However, what Roth sees as a shortcoming is exactly the strength of any methodological or conceptual advance. The greater the logical specificity, the greater the empirical content of any theory or method (Magee, 1973). Accordingly, greater empirical content means increased scientific value, under almost all scientific philosophies. As an example, I, call attention to notions of monophyly, that in pre-cladistic systematic traditions were so broad as to be potentially applicable to almost any imaginable group. Hennig's (1950, 1966) redefinition of the term implied an acute restriction in meaning. Yet no systematist today would consider the restriction as a step backwards in systematics.

Another critique of the homology/synapomorphy identity comes from deQueiroz (1985). He briefly discussed the relationship between homology and synapomorphy (p. 294), and concluded a paragraph with the sentence "Homology does not equal synapomorphy." Basically, he argued that homology is a notion that applies to instantaneous morphologies, while synapomorphy (according to his definition) applies to ontogenetic transformations that characterize monophyletic groups (his view of characters). As a result, the two terms apply to different dimensions of diversity, and therefore cannot be synonymous. I disagree with his argument because propositions of homology and synapomorphy deal with the very same thing (shared attributes or organisms, i.e. characters). Whether one wants to see characters as referable to instantaneous morphologies or to ontogenetic transformations is irrelevant to the issue, because homology can be seen in both ways as well. De Queiroz's opinion seems to be the result of a restrictive conception about the term homology. Apparently for him, homology means only what Patterson (1982) called "transformational homology". The fact that "taxic homology" exists, and in fact is the most relevant aspect of the term, renders de Queiroz's argument ineffective. Apart from this general criticism, there is also some self-contradiction in deQueiroz's argument. For example, in the same paragraph mentioned above he stated that "...ontogenetic transformation of one instantaneous form into another establishes their homology" (deQueiroz, 1985: 294). This statement in itself is not beyond dispute, because in practice most propositions of homology do not rely on observed ontogenetic transformations (but rather on similarity and congruence, as discussed below), but strangely it goes against his own argument in implying that homology, after all, can also be seen as an expression of ontogenetic transformations (thus not being restricted to the realm of instantaneous morphologies). Consequently, it seems that deQueiroz's views on characters and ontogenetic transformations do not invalidate the equivalence between homology and synapomorphy.

The resistance to the homology/synapomorphy reasoning seems to stem from a view that gives priority to a definition that better fits all the previous usages of the term homology, instead of one that displays more internal consistency and objectivity, as well as empirical and heuristic value. Concern with the ideal definition will unavoidably result in great expansion of meaning, and consequently extreme vagueness. There is also a reminiscence of mechanistic thinking in such views (explicitly in some cases, cf. Wagner, 1989:1157), in the form of an expectation that homology propositions somehow represent purely factual knowledge, entirely conveyable by direct structural observation. This view has been perceived and adequately criticized by Eldredge and Cracraft (1980:38). From a mechanistic standpoint, it is natural that the equation of homology with synapomorphy appears as wrong-headed. That equation terminates whatever hope there might have been that homology is a directly observed phenomenon, somehow non-hypothetical in nature. The exposure of the intrinsically inferential and fallible aspect of each and every homology proposition is among the most relevant outcomes of the homology/synapomorphy identity.

There are some other misconceptions about the "homology equals synapomorphy" issue. One of them is that Patterson (1982) was the first and only one to propose that homology and synapomorphy are (or should be seen as) the same basic concept. As he himself repeatedly and clearly stated (cf. Patterson, 1982:29), equivalence between the two notions had been noticed on several previous occasions (e.g. Wiley, 1975, 1976; Bonde, 1977; Bock, 1977; Szalay, 1977; Platnick and Cameron, 1977; Nelson, 1978; Cracraft, 1978; Patterson, 1978; Platnick, 1979; Gaffney, 1979; all cited in Patterson, 1982). Additionally, Eldredge and Cracraft (1980:36) were as explicit as to say "... homology can be conceptualized simply as synapomorphy (including symplesiomorphy [...])". Implicitly, the idea can also be easily grasped in Rieppel (1980) when he calls attention to the deductive nature of homology propositions. Finally, some subsequent authors strongly endorsed and developed that suggestion (e.g. Stevens, 1984; Rieppel, 1988). Therefore, the view that the idea "homology as synapomorphy" is attributable to Patterson (1982) alone is in error.

The various papers cited above, especially Patterson (1982), provide clear and consistent reasons to equate homology and synapomorphy. Besides rebutting the more recent criticisms, I think there is little than can be done further to improve their explanations. However, in view of the profusion of recent misunderstandings, re-addressing the argument may not be totally out of place.

Like so many other controversies in systematics, this one seems to deal with fundamental notions and concepts. As such, it requires that the role of systematic research be made clear in the first place. Systematics is a general comparative method that permits an assessment of the generality of biological phenomena. From these generalizations, there comes a whole array of implications for studies on evolution of taxa and characters, biogeography, coevolution, ecology and other fields that can fruitfully develop upon taxonomic patterns (Funk and Brooks, 1990; Lambshead and Paterson, 1986). Consequently, systematics has the status of a metascience, providing a basis for many, perhaps potentially all, biological disciplines. Since homology is essentially a comparative notion, it is natural to expect that its inherent meaning is most adequately conveyed within the context of systematics. The cladistic method has been so far the most objective and internally consistent in disclosing hierarchical order among living organisms. It is also quickly becoming the most widely used. Therefore, if there is an area of biology in which the notion of homology should have more general applicability than in any of the others, the area is Cladistics.

The notion of synapomorphy is fundamental in the logical framework of Cladistics. By equating all derived similarities with synapomorphy, it is possible to detect a common pattern of internested attributes. Attributes that do not conform to a general pattern thus disclosed are then rejected as synapomorphies at the level where they were initially proposed. Therefore, by making all characters operationally equivalent to putative synapomorphies, the procedure of discovering a common pattern among taxa can be carried out. Within this framework, the notion of character is totally accounted for by those of shared derived condition and synapomorphy (and the derivative homoplasy). Because the idea of homology broadly refers to observable attributes of organisms (i.e. characters), it can as well be expressed as a function of the same notions of synapomorphy and derived condition.

Whether or not one judges the equivalence of homology with synapomorphy as too restrictive, the fact is that the only way presently available explicitly to test homology propositions in a systematic context is to equate them with synapomorphies and to carry out a cladistic analysis (Wiley, 1975). If the analysis supports a single position for a putative synapomorphy, then the condition shared by the various taxa with that derived state are corroborated as homologous. If a shared derived condition turns out to require independent origins in the overall scheme of relationships, then an event of non-homology has been discovered (Rieppel, 1980, 1988). Therefore, the initial working assumption "derived similarity = homology" is tested by congruence with other characters, and it is refuted if the scheme of relationships requires more than a single origin for this derived similarity. This procedure simply tests which of the cognitive perceptions of similarity agree in a general pattern and which do not. All similarities are deemed homologous initially, and non-homology is disclosed by a pattern-detecting procedure (e.g. parsimony). Against the general pattern thus obtained, non-homology is evidenced as dissonance. Each individual position of a given derived condition is a statement of homology among the conditions shared by the group at the base of which that particular origin is located in the scheme of relationships. Therefore, even characters with multiple origins enclose statements of homology at less inclusive levels of generality (see also section on the congruence test of homology).

It has been made clear that the equivalence between homology and synapomorphy requires a clear understanding of symplesiomorphy as a subset of synapomorphy (Eldredge and Cracraft, 1980; Patterson, 1982). Nonetheless, it has been argued that homology cannot equal synapomorphy because symplesiomorphic features are also homologous (Ax, 1984:183), a criticism that was rebutted by Rieppel (1988:59). Symplesiomorphic similarities are obviously homologous, but every symplesiomorphy is a synapomorphy at a higher level, and it is the knowledge of this that allows recognition of symplesiomorphies in the first place. This argument seems to revolve around semantics, whether or not homology and synapomorphy can be used interchangeably. The fundamental issue, though, is that homology and synapomorphy are logically interdependent, and that two or more structures can only be considered homologous if at some level they represent a single synapomorphy for a group including (but not necessarily restricted to) all organisms possessing them. In this sense, comparisons involving symplesiomorphies deal with homologous structures, but only insofar as such symplesiomorphies are hypothesized to represent a synapomorphy for a more inclusive group. The confusion related to symplesiomorphy and homology stems from the misplacement of synapomorphy and symplesiomorphy as terms in opposition to one another, when in fact the latter is a subset of the former.

It must be clear that the notion of homology is inseparably tied to that of a hierarchy of organisms, and loses its meaning when placed in an absolute content. Similarity or dissimilarity alone, no matter how striking, do not support or refute homology propositions. Therefore, to deny the reasoning that homology and synapomorphy are logically equivalent terms is not possible once the cladistic method is accepted as a valid system to recover the hierarchic structure of biotic diversity.

Some might argue that there is another aspect of the notion of homology that is not covered by synapomorphy. This aspect refers to the parameters used for deciding which similarities are comparable and which are not. Such parameters influence the initial recognition of homologies, by imposing *a priori* restrictions on the validity of shared similarities. For example, similarity in shape between a process on the supraoccipital bone (part of the skull) of a taxon and a process on the parhypural bone (part of the caudal skeleton) of another taxon would be considered meaningless for inferring relationship. The orthodox reasoning is that while similarity in shape undoubtedly exists, the comparison is not between homologous parts, therefore the similarity itself is not homologous. However intuitive at first sight, this orthodox view is underlain by a subtle and more general problem related to the generation of homology conjectures. It is true that the idea of synapomorphy does not include this aspect of homology propositions, which in fact lies outside strictly systematic methods. A more extended discussion of this issue is provided in the next section.

Primary and Secondary Homology

Generation of scientific hypotheses frequently lies outside the method or theory in which they eventually function. It is known that genesis of deductive scientific hypotheses is not in itself strictly subject to standard rules of scientific investigation (see Feyerabend, 1987, for a discussion of this subject). Hypotheses of homology are no exception. Every proposition of homology involves two stages, which are associated with its generation and legitimation. Such duality has long been recognized, and has been referred to by terms such as "observational and theoretical components" (Jardine, 1970), "topographical and phylogenetic homology" (Rieppel, 1980), "topographical correspondence and homology" (Rieppel, 1988), "preliminary and final testing" (Kluge and Strauss, 1985), "homology and homogeny" (Lankester, 1870), among others. Seeing the homology notion from a cladistic standpoint permits comprehending this dual nature in a uniquely clear way.

I refer to the stages of generation and legitimation of homology propositions as being "primary" and "secondary" homology, respectively. This terminology seems more appropriate than the others employed so far, because it emphasizes that the two stages are interdependent and complementary, and that any homology hypothesis is necessarily tied to both, at least potentially. Also, it indicates that one of the two stages (primary) precedes the other in any analysis.

The application of the term "homology" to both the primary and secondary levels is contrary to the idea of some other authors. In commenting on the two stages outlined above, Rieppel (1988) criticized his earlier terminology (Rieppel, 1980) for employing the terms "topographical homology" and "phylogenetic homology". In his view of 1988, calling topographical correspondence homology was inappropriate, because it implied that convergence was one form of homology. I disagree with this opinion, because it overlooks the fact that topographical correspondence is only a criterion for postulating a conjecture of homology (herein called primary homology), which in turn can be supported or rejected as phylogenetic homology (here called secondary homology) based on additional criteria. Similarity or topographical correspondence is factual, while primary homology is already a statement of putative generality, an expectation that correspondences are part of a general pattern. Thus, I deem it adequate to refer to the two stages as primary and secondary homology.

A primary homology statement is conjectural, based on similarity, and reflects the expectation that there is a correspondence of parts that can be detected by an observed match of similarities. The roots of primary homology go deep in history, and tracing their origin would be as difficult as tracing the origin of the notion of similarity itself. The means by which conjectures of primary homology come about have been the object of much attention in the pre-cladistic literature on homology (e.g. Jardine, 1967, and references therein), and are commonly referred to as the "criteria" of homology. It has been persuasively argued that in morphology there is only one basic criterion of homology, topological correspondence, of which all the others are just derivations (Riedl, 1975). Despite legitimate and insightful efforts, the proposition of primary homologies has never become satisfactorily objective (cf. Jardine, 1970: 329), and one must agree with Patterson (1982:58) that "hypotheses of homology are conjectures whose source is immaterial to their status", and with Woodger (1937:137) that "[t]here is a primary sense of 'homology' which we all use intuitively and upon which all the more sophisticated senses of the word depend."

A secondary level of homology is the outcome of a pattern-detecting analysis (cf. section below on the congruence test of homology), and its search represents a test of the expectation that any observable match of similarities is potentially part of a retrievable regularity indicative of a general pattern. Primary homologies may either fit perfectly in a general pattern or they may depart from it to various degrees. Thus, secondary homology propositions are primary homologies that have been evaluated against the framework of a general pattern, i.e. tested by congruence (see below). However, the test is partial because primary homologies, having originated from sources outside the pattern-detecting method, stand as observations on their own. Disagreement with a general pattern does not invalidate a primary homology proposition, but only prevents it from attaining the status of secondary homology *at its original level of generality.*

The distinction between primary and secondary homology is identical to that between shared derived character (or putative synapomorphy) and synapomorphy (Farris and Kluge, 1979). A character analysis may show that an observed shared derived condition is homoplastic, and consequently reject it as a synapomorphy for all taxa that share it. However, this derived condition, though rejected as a synapomorphy at its original level, is at the same time proposed as synapomorphic for less inclusive groups, i.e. for each of the groups in which it is hypothesized as independently present. So, while secondary homology analysis may refute a particular primary homology, the latter never becomes completely devoid of significance at the secondary level. Even in the extreme case of maximum homoplasy for a character (i.e. independent origins for each terminal showing the condition) each origin still encloses a statement of homology of its own, at a low level of generality. Primary homology statements may be seen as the way attributes are represented in a matrix of taxa X characters. Each derived condition in a matrix is a statement of primary homology for the condition among the taxa that share it. Secondary homologies, in turn, can be seen as characters when plotted onto a cladogram, where the general pattern of taxa and the fit of each primary homology are depicted.

It is important to observe that the interaction between primary and secondary homology is one of level. A phylogenetic analysis will unavoidably transform all statements of primary homology into statements of secondary homology, no matter how much homoplasy is present. A cladogram accommodates all available evidence under the most parsimonious configuration. The point is that each primary homology is transformed into either a single or multiple statements of secondary homology. In the first case there is perfect fit between primary and secondary homologies, i.e. the observed similarity on which primary homology is based fits into a general pattern without alteration of its observed level of generality. In the second case the primary homology needs to be subdivided into two or more statements of secondary homology, in order to fit a general pattern. In other words, the observed similarity needs to have its level of universality lowered in order to agree with the pattern dictated by other primary homologies. This case is accounted for by postulated character convergences.

Still a third alternative is that the generality of the primary homology has to be increased in order to fit the general pattern. In this case the secondary homology applies to more taxa than those in which its primary counterpart was observed. This alternative is accounted for by postulated character reversals. There is one important similarity between this last case of interaction between primary and secondary homologies and that in which the primary level of generality remains unaltered in the secondary homology. In both cases, the relation of sameness inherent in the conjecture of primary homology remains intact. Accordingly, all similarities initially observed are preserved as homologues under the postulated secondary homology. This is in sharp contrast with the case in which the primary homology is split, where the observed similarity is hypothesized as partly artifactual from the standpoint of a general pattern.

Any conclusion about non-homology stems from a mismatch between primary and secondary homologies, no matter how evident the non-homology might look at first sight. One perhaps may legitimately believe that the wings of birds and bats are valid primary homologues, representing modifications for flight of the anterior limb of tetrapods, itself homologous among all taxa sharing it. The conclusion that they are in fact non-homologous comes not as much from their structural differences as from the hypothesis that both birds and bats are more closely related to organisms without wings of any kind. The scheme of relationships derived from all known primary homologies indicates that wings in those two taxa were acquired independently, therefore are non-homologous. The primary conjecture of homology between the two kinds of wings is subdivided into two separate secondary homologies, based on a hypothesis of relationship. But notice that the non-homology in the character "wings" exists only between bats and birds. Within each group individually, i.e. at the secondary level, "wings" are still homologous, as birds' wings and bats' wings. One may speculate that if bats and birds happened to be hypothesized as sister groups, there would not be fierce opposition to considering their wings as homologous, despite all the anatomical differences.

An interesting outcome of the primary/secondary scheme explained above is that the discovery of cladistic analysis in fact is non-homology. Homology itself is assumed prior to the analysis, based on similarities that lead to the conjecture of primary homology. The mismatch between the levels of primary and secondary homology (i.e. homoplasy, i.e. non-homology) is what is newly brought to light by a cladistic analysis.

For some further considerations on primary and secondary homology and their relationship with observed similarity, see section below on the similarity "test" of homology.

Taxic and Transformational Homology

Patterson (1982:34) distinguished between two approaches to homology propositions, borrowing the terms "taxic" and "transformational" from previous usage in evolutionary biology (Eldredge, 1979). The distinction between these two approaches helps to clarify the relation between the notion of homology in Cladistics and in other approaches to comparative biology. Therefore, this distinction is relevant even though, as proposed below, most instances of transformational homology are in fact just one stage in the process of hypothesizing a taxic homology, and the dichotomy between taxic and transformational approaches in homology is artificial from a logical standpoint.

Taxic homology implies a hierarchy of groups. It is thus concerned with hypotheses of monophyly, and constitutes a statement about generality of characters, or "sameness" of attributes. The proposition that presence of hairs is a mammalian character embodies a hypothesis of taxic homology, according to which hairs in various mammals are homologous. Recognition of the character "hair" itself implies a grouping called mammals, i.e. a hypothesis of monophyly derived from the conjecture of homology among the various expressions of the attribute hair.

Transformational homology, in turn, is concerned with imagined transformation of one structure into another, i.e. with seeing attributes as modifications of one another. For example, the proposal that the incus of the mammalian ear is derived from the quadrate (a bone involved in the jaw articulation) of other tetrapods is usually regarded as an instance of transformational homology (Patterson, 1982; cf. deBeer, 1971). Transformational homology can also be proposed within the same organisms, e.g. when the mouth parts of arthropods are considered as modified locomotory appendages. In this case there is a relation of sameness, i.e. homology, between the locomotory appendages and the mouth parts within the same individual organism. Considering these two examples, it becomes clear that the term "transformational homology" is complex, in the sense that it involves more than a single basic notion. In fact, what has been called transformational homology includes two distinct ideas that can be identified with the more precise and restrictive notions of primary (discussed in the section above) and serial "homology". The essentials of this distinction were in fact noticed long ago (Serres, 1827; cf. Rieppel, 1988).

The first idea (similarity) is involved with "transformational homology" among different organisms, as in the first example mentioned above. The proposal that the incus of mammals is homologous with the quadrate of other tetrapods is based on various similarities observed in the ontogenetic dimension. Such similarities lead to the conclusion that the quadrate and incus in the organisms involved are in fact the same structure under different expressions, i.e. different states of the same character. This proposal involves a generalization about characters, and, therefore, has a taxic component relating mammals with other vertebrates with a quadrate bone. The proposal that a structure in one organism or taxon is a transformation of one in another is essentially taxic, and as a procedure it is identical to the conjecture of primary homologies (or potential, or observational, or topographic homologies; see sections above and below on the similarity "test" of homology).

"Transformational homology" that involves different parts of the same organism is a totally different notion, and is related to the idea of serial homology and its variants (homonomy, Riedl, 1979; iterative homology, Roth, 1984, 1988). In a broad sense, serial homology includes not only the classical cases of metamerism, or repetition of similar structural units along the body axis, but also instances related to symmetry and so-called mass homology (e.g. individual hairs in mammals or feathers in birds, leaves in trees, the genome in metazoans). Serial homology refers to the equivalence of parts within the individual organism. There has been some controversy about whether or not serial homology and phylogenetic homology involve the same basic notion. Some authors argue that there is no essential difference between the two ideas, and that both can legitimately be seen as expressions of homology (e.g. Roth, 1984, 1988; Ghiselin, 1976; Riedl, 1979). The opposite view, held by e.g. Remane (1952), Patterson (1982) and Boyden (1943), is well synthesized by de Beer (1971:9) when he says that "serial homology is really a misnomer, because it is not concerned with tracing organs in different organisms to their representatives in a common ancestor (.. .)".

As with so many other controversies, both viewpoints seem to have their share of reason, and preference for one opinion only makes sense from a specific standpoint. There is no doubt that recognition of serial homologues involves the same mental process as recognizing homologues in different organisms, a fact that led Riedl (1979: 38) to say that "we are dealing with the same mechanism which is of the same fundamental importance for the formation of order in living organisms—whether such identical individualities become separated from each other to occur in different individuals or whether they replicate within the same individual". However, one can also argue that any observed similarity, between any entities, is equivalent in principle to the recognition of homologues. Expanding the reasoning a little further, recognition of homologies is just an expression of the detection of any kind of order. Seeing the search for order as being essentially the same process at all levels of organization can be useful, for example from Riedl´s (1979) standpoint. Nevertheless, serial homology and taxic homology are fundamentally different from the perspective of systematics, which is concerned with interorganismic hierarchical organization. Serial homology, an intraorganismic kind of order, is therefore outside the realm of most present-day systematics (but see de Queiroz and Donoghue, 1988, and Nelson, 1989, for unorthodox views of inter-/intraorganismic approaches and their relation to taxa).

It seems that much still has to be done on the relation between serial homology and ontogenetic character polarity, but approaching this issue here would go beyond the scope of this paper. For the present discussion, suffice it to reiterate that the only form of "homology" without a taxic component is serial homology, and that the notion of homology discussed here does not include it.

Tests of Homology

The notion of homology testing has been most clearly synthesized by Patterson (1982). According to him, conjectures of homology are evaluated according to their success or failure in undergoing a series of three tests, which are: (I) similarity; (2) conjunction; and (3) congruence. My main point is that the only one of these three that conforms to the strict role of a test is the third. Below are comments on each of them.

SIMILARITY

The notion of similarity in morphology is vague (see section above on primary homology,!. Bock (1977) proposed that similarity was the "test" of homology, but by that he implied something different from the usual notion of test. Bock's view is that similarity is what allows us to recognize homology in the first place. Therefore, it is not a test, in the sense that it does not refute a homology statement (if there was no similarity, the statement would not have been proposed in the first place). Cracraft (1981) has also made the point that similarity is the factor that compels us to postulate homology, not a test of homology.

It seems that similarity is a primitive concept for systematics, which itself leads to the conjecture of homology. As Stevens (1984: 403) has put it, "without some similarity, we should not even dream of homology". It has been proposed that the principle of similarity in homology can be traced back to the "principe des connexions" of Geoffroy Saint-Hilaire (1830; cf. Rieppel, 1988). One of the interesting characteristics of the similarity criterion in organisms is that it applies to life cycles. A similarity observed during only a certain stage of development is enough to link two or more structures as primary homologues, regardless of their dissimilarity during other stages of ontogeny.

It must be observed that similarity stands at an even more basic level in systematics than usually realized, and constitutes the very phenomenon that the systematic method is supposed to account for. The apparently chaotic mosaic of similarities observed among organisms only acquires regularity by means of the order-detecting procedure of systematics. Therefore, similarity is the phenomenon that systematics addresses, and as any true phenomenon its origin lies outside the method that attempts to understand it. This is the reason why, from the standpoint of systematic method, the recognition of similarities stands as an essentially imprecise and subjective process.

Similarity cannot be considered as a test of homology, because it constitutes the very-source of primary homology propositions. It cannot possibly refute a conjecture that was derived from it in the first place, otherwise there is a logical contradiction. Consequently, conjectures of primary homology that do not conform to the criterion of similarity simply do not exist. Rieppel (1988:60) provided a scheme summarizing his and Patterson's (1982) views of the interactions between homology, similarity, characters and phylogenetic analysis. There characters can either pass or fail the test of similarity; those that fail are considered as non-homology, those that pass go on to the test of congruence. Nevertheless, characters do not exist before similarity considerations.

Observed similarities are the source of characters (i.e. primary homologies), and not a procedure that is applied subsequent to their recognition.

For some more considerations on similarity and homology, see section above on "Primary and Secondary Homology".

CONJUNCTION

This term was coined by Patterson (1982) to refer to the falsification of homology propositions in the realm of the individual organism. The conjunction test has been by far the least discussed of the "tests" of homology, even though it has been considered as a "powerful test" (Rieppel, 1988). It basically asserts that if two structures are found in the same organism they cannot be homologous. The logic behind this test is consonant with the notion of "anatomical singulars" of Riedl (1979). The unity of the individual organism stands as an assumption for the whole argument, as an indivisible empirical unit. This assumption makes sense insofar as most generalizations in systematics and evolutionary biology are concerned with diversity observed at the organismic level and do not usually question the cohesiveness of that level (cf. Riedl, 1979:41). I will not therefore try to justify it.

There are subtleties involved with the conjunction test that to my knowledge have not been investigated to date. Perhaps the best way to scrutinize the logic of this test is by means of an example. Patterson (1982, 1988a) provided the following imaginary case: "... the theory that the human arm (a mammalian forelimb) and the wings of birds are homologous would be shown to be mistaken if angels (with both arms and wings) are ever discovered." The presence of both arms and wings in angels is certainly evidence that there is non-homology involved in the comparison. However, a precise statement of where this non-homology lies depends on a more specific analysis of the phylogenetic position of angels relative to birds and mammals. The proposal that the arm of mammals is homologous with the wing of birds is a conjecture, based on similarities of various kinds. The impact of the existence of an organism with both structures is also dependent on other conjectures; namely, that the wings of angels are homologous with those of birds, *and* that angels' arms are homologous with mammals' arms. Such conjectures are no less hypothetical than that homologizing the arm of mammals with the wings of birds, being dependent on factors in addition to the similarity on which they are initially stated. A more detailed explanation will be done in coordination with Fig. 1, in which birds (or organisms with bird-like morphologies) are represented by "B", mammals (or organisms with mammal-like morphologies) by "M" and angels by "A". The multiple Bs and Ms are intended to avoid ambiguous character optimizations and render the initial argument more direct. The characters are represented by "a" (arms), "w" (wings) or "al" (anterior limb). An asterisk indicates homoplastic characters.

In Fig. 1 (A) angels are included within mammals. Therefore, all mammals are primitively characterized by arms along, and the wings of angels are a new limb exclusive to that lineage, independent from that of birds. In this case the wings of birds and arms of mammals and angels are all homologous as anterior limbs, and the non-homology is located in the wings of angels and birds.

In Fig. 1 (B) we have the opposite situation, in which all birds (in this case including angels) are primitively characterized by wings, and angels have developed an autapomorphic extra limb, homoplastic with the arm of mammals. In this case the birds' and angels' wings and the mammals' arms are homologous; the non-homology is located in the arms of angels and mammals.

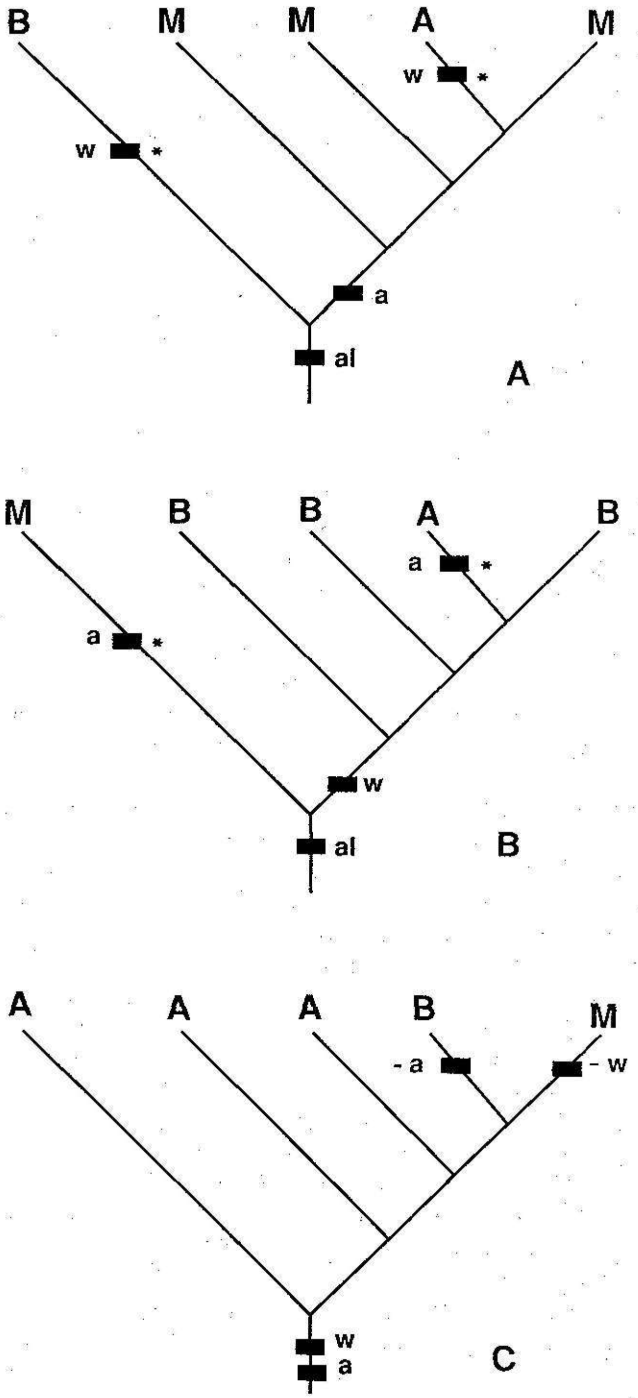

Fig. 1. Diagrams explaining the indetermination of the conjunction criterion. Terminals are birds (B), mammals (M) and angels (A); characters are anterior limb (al), arms (a) and wings (w). The asterisk indicates homoplastic characters. See text ("Conjunction") for further explanation.

Figure 1 (C) places organisms with angel-like morphologies (in this case not forming a monophyletic group) as three successive sister groups to the clade formed by mammals plus birds. Here, the primitive condition for the whole group is to have both wings and arms. Mammals are apomorphically characterized by the loss of wings, and birds by the loss of arms. At the base of the cladogram we have two characters, wings and arms. Therefore, in this case, the wings of birds and arms of mammals are non-homologous, because they cannot be traced back to a single condition. Primitively in the whole group, wings and arms are two separate characters.

Hence, the only case in which the discovery of angels would unequivocally refute homology between wings of birds and arms of mammals is that represented in Fig. 1 (C).

If angels were the sister group of mammals or birds (instead of being a subgroup of them, as in the examples of Fig. 1), the conclusions about non-homology would be less exact, because character ambiguity would permeate the analysis. However, the logic of conjunction would still be an indicator that there is homoplasy (i.e. non-homology) in the analysis, though without providing its precise location.

From the above, it is evident that the conjunction test of homology is dependent on a broader phylogenetic framework, if it is specifically to refute a homology proposition. Therefore, the conjunction test is better seen as an indicator of non-homology, rather than as a test in the strict sense. As such, it is a useful tool in detecting homoplasy in an analysis, but not sufficient by itself to determine in which pairwise comparison the non-homology lies. In order to accomplish that, it is necessary to resort to a scheme of relationships. The logic underlying the conjunction test goes back to some fundamental issues in phylogenetic analysis, related to recognition of putative independence among sources of evidence. The decision whether any two or more attributes comprise a single transformation series or two or more independent series is one of the most basic, albeit still confusing, issues in systematics (Mickevich, 1982; Colless, 1985; Mickevich and Weller, 1990). It is a decision that is made very early in any character analysis, and rarely questioned subsequently. From that perspective, the distinction between "character" and "character state", frequently (and reasonably, in the usual context) downplayed in the literature (e.g. Eldredge and Cracraft, 1980), becomes surprisingly relevant. Character states are attributes that can be proposed as transformations one of another (i.e. as a series of transformations); characters, on the other hand, are putatively independent from one another. If the distinction between character and character state is not made, then theoretically any individual attribute (i.e. any character state) could be transformed into any other, through any number of intermediate steps. Perhaps this point of view permits a more concise way of assessing the fundamental reasoning behind the conjunction argument: if any two attributes are found in the same organism, they cannot be part of a single transformation series. They must be either independent characters [Fig. 1(C)] or a result of mistaken homology assessment [Fig. 1(A,B)].

Thus, the conjunction argument serves as an indicator that there has been error in assessing the sorting between characters and character states, or a mistake in establishing primary homologies.

The functioning of the conjunction "test" seems to be logically equivalent to the impact that additional taxa with character combinations that introduce homoplasy can have on a hypothesis of relationships {Donoghue et al., 1989). There is only a distinction of level between the two procedures: one refers to individual organisms and the other to monophyletic groups.

The conclusion, then, is that the conjunction procedure is not determinate enough to be eligible as a test of homology. The conjunction argument refers to a more basic level of character analysis, and its ability to refute specific hypotheses of homology depends on a particular scheme of relationships, i.e. on other characters. Any scheme of relationships is a result of phylogenetic analysis, which leads us to the third and last test of homology: congruence.

CONGRUENCE

The notion of congruence is currently the subject of considerable attention in systematics, where it plays the role of a fundamental methodological pivot (Rosen, 1984; Mickevich, 1978). It emerged explicitly with the development of Cladistics, when Hennig (1966) discussed "reciprocal illumination" among characters. Congruence is also an implicit element in the works of pre-evolutionary taxonomists (Nelson and Platnick, 1981). The way one views congruence is a reflection of the way one chooses to express agreement and disagreement among characters. There is some consensus that strict parsimony is the most consistent method to determine character congruence (Farris, 1983). It has been convincingly demonstrated, though still not universally accepted, that the principle of parsimony stands as a methodological principle, not dependent on assumptions about evolutionary models or rates of character evolution (Gaffney, 1979; Crisci, 1982; Farris, 1983; Brady, 1983).

Another way to translate character information into hypotheses of relationship is by compatibility or clique analysis, a method that has been much less widely applied in empirical studies than parsimony analysis. The compatibility method consists basically of finding sets of mutually compatible characters (called cliques), i.e. that agree on a single scheme of relationships (Estabrook et al., 1977; Meacham, 1980; Meacham and Estabrook, 1985). Usually the hypothesis supported by the largest clique is chosen (Meacham and Estabrook, 1985:438). The relevance of compatibility analysis to the present discussion is that Patterson (1982, 1988a) proposed that this is the way the congruence test of homology is carried out (although the term "compatibility" was not employed in his paper of 1982). This view goes against his earlier opinion, which saw parsimony as playing that role (Patterson, 1978), and also against that of other authors (e.g. Rieppel, 1980, 1988).

Patterson (1982) saw the congruence test as a simplified version of Wilson's (1965) test for phylogenies (see note added in proof in Patterson, 1982: 74). Wilson's paper (1965), in turn, was considered by Estabrook et al. (1976:181) to be the first published account of compatibility analysis as an isolated concept. In fact, later Patterson (1988a: 606) explicitly stated: "… it [congruence test] is allied to compatibility methods in numerical Cladistics." In spite of the crucial importance of the congruence test, no detailed account was ever published about how, in detail, compatibility analyses can refute specific hypotheses of character homology in a cladogram.

The reliance on compatibility analysis as the means by which the congruence test should be applied is a somewhat puzzling suggestion, because of the very fundamentals of that procedure. Compatibility techniques usually dictate that the preferred scheme of relationships is indicated by the largest clique, i.e. the largest set of mutually compatible characters. Incompatible characters are thus excluded from consideration right after the largest clique is identified, or gradually when doing a secondary clique analysis. Therefore, it seems that compatibility analysis has little power in determining hypotheses of character evolution in the presence of incongruence. In fact, regarding clique analysis, Farris and Kluge (1979:405) stated that "[t]he mere deletion of a character from consideration, however, does nothing to indicate which points of similarity in a character are the result of homoplasy and which are not. Specific parallelisms or reversals are not detected by such methods." These facts by themselves already hint that compatibility analysis should not be the most efficient method to assess the number of times a given character state has arisen, and, therefore, that it should be of limited use in refuting homology propositions.

In view of the now widespread use of parsimony analysis as a means to assess hypotheses of relationship, and concomitantly of character evolution, it is necessary to investigate how this procedure can potentially relate to the congruence test of homology, and in particular how it differs from compatibility analysis in that regard. In order properly to analyse the differences in viewing the congruence test as an application of one or the other method, it is useful to resort to a hypothetical example. The most efficient example is one in which parsimony and compatibility result in different hypotheses of relationship, so that the different implications of the two methods are immediately obvious. A simple case is presented in Table 1 and Fig. 2. Twenty-seven characters are distributed among taxa A-H as shown in the matrix of Table 1. Characters 1-10 specify the group formed by taxa A-D. Characters 11-20 determine the group E-H. Character 21 determines AB and character 22 indicates EF. Finally, characters 23—27 determine the grouping BCFG.

Parsimony analysis yields the result in the diagram shown in Fig. 2(A), with 34 steps. This cladogram is one of four equally parsimonious trees (found with the program Hennig86, by J. S. Farris), and is identical to a strict consensus of the four trees. The possible resolutions of the trichotomies involving A, D, E and B are not important for the argument that follows. The five characters supporting (BCFG) become divided in two blocks, one indicating monophyly of BC and the other indicating monophyly of FG. Thus, the initial assumption that each of the five characters was homologous among the four taxa sharing them is falsified by congruence, and the conditions in BC, and FG, requiring independent steps, are hypothesized as non-homologous (but, of course, still homologous within BC and FG, separately). The single characters supporting AB and EF are also homoplastic, but their homology cannot be affirmed or denied, because of uncertainties of resolution.

If compatibility analysis is applied to the same data an alternative scheme is obtained [Fig. 2(B)], based on the largest clique formed by characters 1-22. Characters 23-27, not being part of the largest clique, are disregarded for topology considerations. A

Table 1

Matrix of distribution of 27 characters among eight taxa (A—H). This matrix yields different hypotheses of relationships when analysed according to strict parsimony and largest clique methods. See text for an explanation of the relevance of this case for the congruence test of homology.

Taxa	Characters					
A	11111	11111	00000	00000	10000	00
B	11111	11111	00000	00000	10111	11
C	11111	11111	00000	00000	00111	11
D	11111	11111	00000	00000	00000	00
E	00000	00000	11111	11111	01000	00
F	00000	00000	11111	11111	01111	11
G	00000	00000	11111	11111	00111	11
H	00000	00000	11111	11111	00000	00

secondary clique analysis (Estabrook et al., 1977) would perhaps result in a different scheme, but in view of the methodological uncertainties still surrounding secondary analysis (cf. Meacham and Estabrook, 1985: 440) it will not be considered here. If all characters are then plotted on the dendogram derived from the largest clique [Fig. 2(B)], it follows that the five characters shared by BCFG require 20 steps to be explained. Further, there is no unambiguous statement of homology above the level of terminal taxa for these five characters. The single characters for AB and EF are described by a single step each, and are therefore deemed homologous among the taxa sharing them.

Comparing the two schemes, one sees that parsimony analysis splits the homology of each of characters 21-27 once. Clique analysis, though preserving the integrity of characters 21 and 22, splits the homology of each of characters 23-27 four times. That means that parsimony analysis implies seven statements of non-homology in the data set, while clique implies 20 such statements. Therefore, parsimony analysis maximizes propositions of homology, when compared to largest-clique methods.

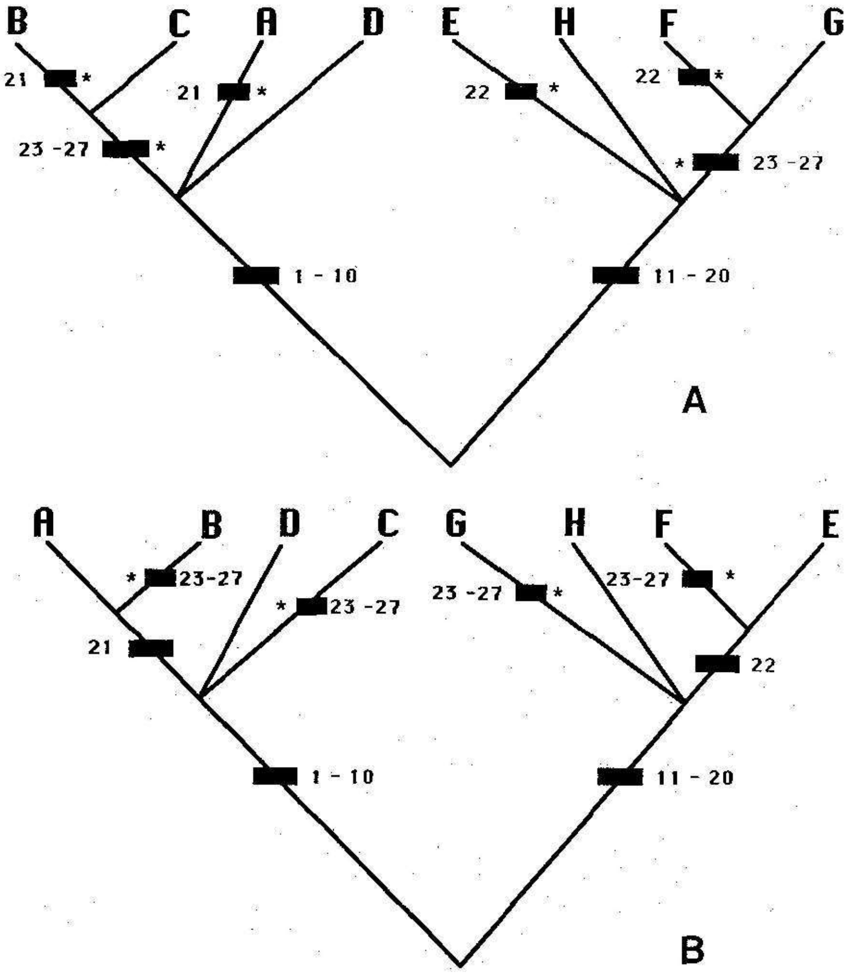

Fig. 2. Cladograms for taxa A-H derived from matrix in Table 1. (A) Arrangement based on parsimony (consensus tree); (B) arrangement based on the largest clique. Asterisks indicate homoplastic characters.

The results above can be evaluated from a number of different perspectives. Maximization of homology propositions implies more inclusive statements about character generality, and therefore represents a more concise way of conveying observed attributes. This fact in itself is a defensible quality, but its relationship to the controversy of what is the most adequate way of treating incongruent data (in this case parsimony or compatibility) is not trivial. The relationship can be understood from the standpoint of the dual nature of homology propositions outlined in previous sections. As seen, conjectures of primary homology arise as a response to observed similarities. Primary homologies, in turn, are evaluated according to their agreement with one another, and their mutual interaction results in a general pattern that takes all of them into account. Statements of secondary homology are derived from this general pattern and, in the presence of incongruence, adjust the level of universality of primary homologies so they fit into the pattern. When constructing the general pattern thus, the objective is to accommodate conjectures of primary homology with minimum alteration, so that the final scheme reflects as much as possible the observed equivalences of attributes that gave rise to the primary homology conjectures. This is accomplished by maximizing the statements of secondary homology. As seen in the example above, strict parsimony analysis results in more numerous statements of secondary homology when compared to clique analysis in an example where the two approaches give different results.

In view of the above argument, it appears that parsimony, instead of compatibility analysis, is the most comprehensible expression of the congruence test of homology. In a certain way, this reasoning is another way of seeing some of the methodological reasons why parsimony has been considered a superior method when compared to compatibility analysis (e.g. Farris and Kluge, 1979; Farris, 1983).

The logic of compatibility analysis, though, is not totally devoid of implications for homology propositions. Two characters are considered compatible if there is one or more possible hypotheses of relationship that both can support. If they are incompatible, in contrast, at least one of them is necessarily homoplastic. This means that incompatibility between two or more characters is evidence that non-homology is present in one or more of them. However, the fact of incompatibility itself is not specific about in which character(s) the non-homology is located. Compatibility considerations can serve as indicators of non-homology on a local scale, and may be useful as a preliminary assessment of the presence of non-homology. Nevertheless, in not being specific about the precise location of non-homology, they cannot be considered to be a test. In this regard, compatibility analysis stands at the same methodological level as the conjunction criterion, discussed in the above section.

Beyond Parsimony: Homology and Character Ambiguity

In the section above, the argument was made that maximizing propositions of homology is desirable from a theoretical standpoint. This topic brings us to another current issue in cladistic analysis that is closely tied to the notion of homology: character ambiguity. Homoplastic characters in Cladograms are frequently ambiguous, i.e. their distribution under a specific tree topology make it uncertain whether the derived condition had a single origin with one or more reversals, or whether the derived transition occurred two or more times independently. Parsimony considerations play no role at this level, because both alternatives require the same number of steps. The most elementary imaginable example is provided in Fig. 3. For the sake of simplicity, the topologies of the Cladograms in this illustration are regarded as constraints, i.e. assumed to be representations of the most parsimonious solution based on an imaginary complete set of characters. A derived condition, represented by the black square, occurs in taxa B and C. Because B and C are not sister groups, this derived condition is homoplastic, and requires two steps to be described in the most parsimonious arrangement. The two steps can be interpreted either as two independent derivations in B and C [Fig. 3(A)] or, alternatively, as a single origin at the base of the cladogram and a subsequent reversal to the primitive condition in A [Fig. 3(B)]. This uncertainty about the evolution of the character is what is called ambiguity, and has been occasionally referred to in the literature by other expressions (e.g. "alternative paths of minimum evolutionary change"). It has been described previously on several occasions (e.g. Lundberg, 1972; Jensen, 1981; Farris, 1982).

Although the ambiguity problem seems trivial because it has no bearing on the

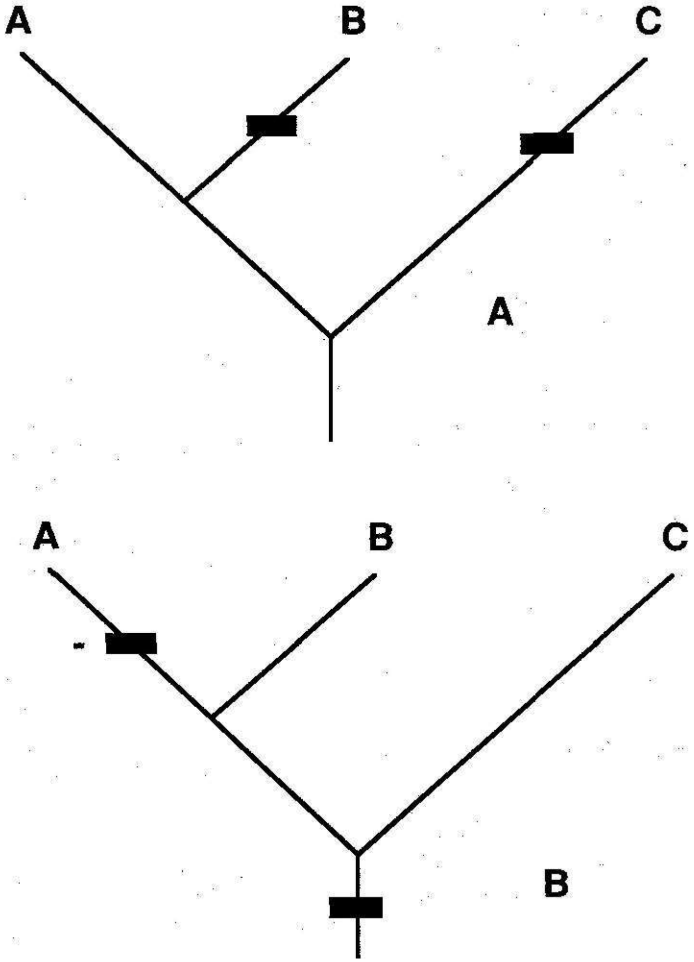

Fig. 3. Three-taxon statement showing the basics of character ambiguity. (A) Homoplastic character represented as two independent acquisitions in taxa B and C; (B) homoplastic character represented by a single origin at the base of group ABC and a subsequent reversal in taxon A. The minus sign represents the reversal.

topology of the cladogram, it can be of considerable importance for studies of character evolution that rely on cladogram information. This is because, in the presence of ambiguity, it cannot be known if the character in question can be described by single or multiple steps, and, therefore, if it is homologous among all taxa sharing it (de Pinna and Salles, 1990). Ambiguity renders uncertain the relationship between primary and secondary levels of homology of a character. Considering the relatively high levels of homoplasy commonly present in most analyses, instances of character ambiguity are expectedly common. Cases of it have been pointed out in a number of empirical studies, and Fink and Fink (1986:496), for example, were explicit about the problem: "For any such character, even if one assumes that only the minimal number of state changes allowed by the tree has occurred, more than one hypothesis of evolutionary change in that feature is possible." In fact, so far there has been no consistent theoretical reason to prefer one alternative of character evolution over the other, and ambiguous characters are simply indicated as such in Cladograms.

In order to investigate the rationale underlying ambiguous characters, we may again refer to Fig. 3 and examine the logical implications of each alternative. In Fig. 3 (A), the derived condition is independent in B and C, and the similarity observed for that character in the two taxa is artifactual. Or, in terms of the congruence test, the postulated primary homology of the derived condition in B and C is refuted. In Fig. 3 (B), alternatively, the derived condition in B and C is the result of a single event at the base of the clade ABC, inherited by those two taxa. In terms of the congruence test, the primary homology of the character in B and C is supported.

The fundamental distinction between the two alternatives in Fig. 3 is that one of them [Fig. 3(B)] agrees with the information conveyed by the conjecture of primary homology. The alternative in Fig. 3(A), contrastingly, questions this observational equivalence, and postulates that the derived conditions seen in taxa B and C are not the same, i.e. non-homologous. Therefore, the option in Fig. 3(B) is more consistent with the initial assumption, based on similarity, that the conditions in taxa B and C are the same. The independent occurrences of the derived condition required by Fig. 3 (A) unjustifiably reject the observational equivalence detected for B and C. On the basis of available information, there are no grounds for such a decision. Insofar as the number of steps is the same, the phylogenetic scheme should convey all possible information derived from observation, and observation implies that the derived conditions seen in B and C are homologous. Hence, all other factors being equal, the hypothesis of character evolution chosen should be the one that better reflects the initial assumption of character identity, i.e. a single occurrence for a putative homology.

One faulty counter-argument might be that the same reasoning, in the inverse direction, might be applied to the absence of the character in taxon A. For example, in Fig. 3 (A) the absence observed in taxon A is deemed homologous with that seen in outgroups, while in Fig. 3(B) it is regarded as independent. Accordingly, in terms of preserving observational homologies, the option in Fig. 3 (A) would be no worse than Fig. 3(B). However, absences stand at a lower ontological level as observations, when compared to presences (Nelson and Platnick, 1981:29; Patterson, 1982:30). Absences, or negative characteristics, are equivalent to the Aristotelian notion of privative term, which is an inconsistent way of assessing group membership properties (Aristotle, 1911, 642 b 21-25; 643 a 5-6; Nelson and Platnick, 1981: 71). As a consequence, preserving the unity (=conjecture of primary homology) of a presence is preferable to preserving that of an absence. It does not make sense to talk about "homology" of an absence. Evidently, absences also have to be accounted for in Cladograms, but they are totally derived from the observed presences, and do not constitute objects of primary homology propositions. What stand as primary conjectures of homologies are positive (i.e. presence) attributes, and these are the ones that should be preserved within the constraints of parsimony.

The simple case presented in Fig. 3 can be easily extended to more complex situations, even if only two-state characters are considered. For example, Fig. 4 shows a case of multiple origins [Fig. 4(A)] or losses [Fig. 4(B)] for a derived condition. According to the argument developed above, the option in Fig. 3(B) is preferable, in its implication of homology among all positive occurrences of the derived condition.

One might see the issue of character ambiguity as related to the distinctions between Wagner, Dollo and Camin-Sokal versions of parsimony used in phylogenetic reconstruction. In fact, the relation is very simple, because character ambiguity is only possible under a Wagner, or strict, parsimony analysis, the only one that imposes no *a priori* restrictions either on reversals or on convergences of character states (Farris,

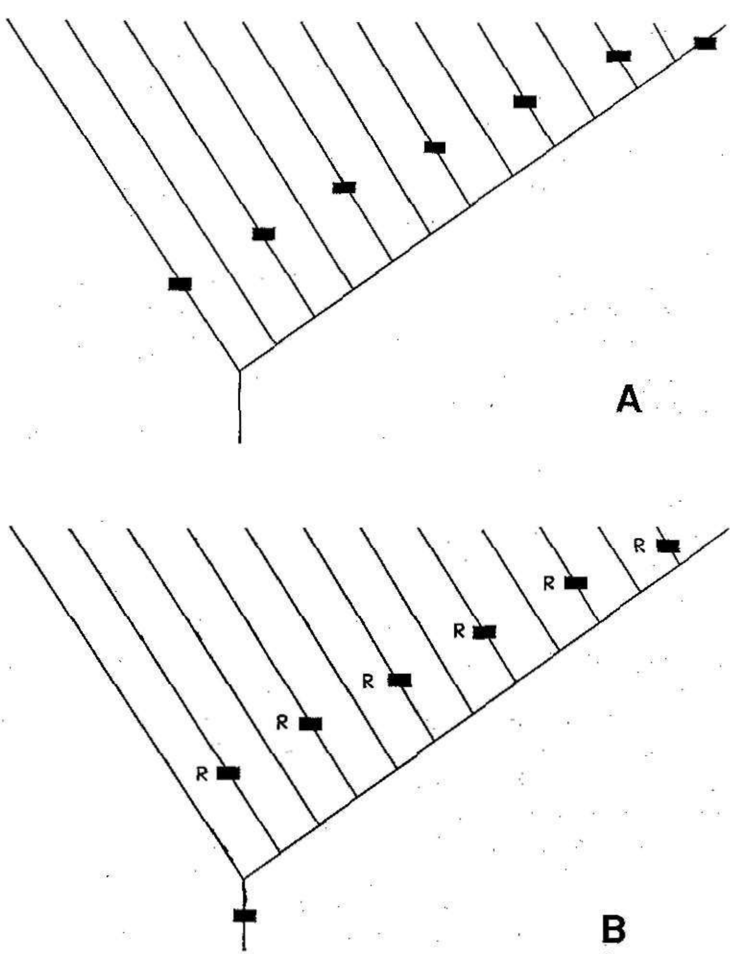

Fig. 4. Equally parsimonious interpretations of the transitions of a highly homoplastic character. (A) All occurrences represented as independently acquired; (B) a single origin of the derived condition at **the** base of the cladogram, with absences accounted for by multiple reversals. "R" represents reversals.

1970; Swofford and Maddison, 1987). Under the Camin-Sokal model, for example, the hypothesis shown in Fig. 3(B) would be excluded from consideration *a priori,* because the reversal postulated in taxon A would not be permitted as a possibility in the first place. Alternatively, under so-called Dollo parsimony, the alternative in Fig. 3 (A) would be impossible, because that model prohibits multiple gains of derived states (Farris, 1977). It must be observed that the justification provided above for favoring reversals over parallelisms in cases of character ambiguity does not imply a preference for Dollo parsimony. My suggestion of preferring reversals applies only to ambiguities that remain after a Wagner (or strict) parsimony analysis, and does not have a relationship to a *priori* restrictions on character transitions.

A more substantial relationship of the character ambiguity/homology issue is with character optimization on a tree topology. Optimization is the process of assigning character states to particular nodes in a cladogram, and therefore of tracing the evolution of characters along branches. Frequently, in the presence of homoplasy, there is more than a single possible optimization under the most parsimonious arrangement (i.e. character ambiguity). Different algorithms for character optimization may differentially favor reversals or parallelisms. The so-called "delayed transformation optimization" (DELTRAN), as presented by Swofford and Maddison (1987), maximally postpones character transitions from the root to the tip of a cladogram. Therefore, it results in an optimization that maximizes the amount of homoplasy accounted for by parallelisms. As such, it goes against the suggestion made above that primary homologies should be preserved as long as possible within the constraints of parsimony. In contrast, the so-called "accelerated transformation optimization" (ACCTRAN), which is a version of Farris' (1970) optimization algorithm (Swofford and Maddison, 1987), always assigns the maximum amount of change for each branch, as it goes from the root to the tip of the cladogram. Consequently, it maximizes homoplastic character changes that are represented as reversals, rather than as parallelisms. This being so, ACCTRAN optimization better conforms with the notion that the conjecture of primary homology should be held valid unless demonstrated false by parsimony considerations. It thus can be considered as a theoretically superior algorithm for tracing character evolution, when compared to the DELTRAN procedure.

Homology in Molecular and Morphological Data: is There a Fundamental Difference?

With the advent of application of phylogenetic inference to molecular data, a myriad of new terms and supposedly new concepts of homology came about. In part, this is an outcome of the one-dimensionality of molecular sequences, when compared to (at least) three-dimensional morphological characters (Woese, 1987).

Alignment of molecular sequences is frequently called the establishment of homologies among these sequences. However, this procedure is equivalent only to the detection of similarities in morphology, i.e. the proposal of primary homologies. While in morphology this step is mostly unquantifiable and somewhat intuitive (isolated efforts to the contrary, e.g. Jardine, 1967, notwithstanding), in molecular analyses it can involve considerable complexity (cf. Doolittle, 1981, 1986; Feng and Doolittle, 1987). It has been argued that at the genomic level similarity equals homology, and that cladistic and phenetic analyses of DNA sequences are therefore equivalent (Patterson, 1988b). The general reasoning behind such a view has been severely criticized (e.g. Nayenizgani, 1990), and it seems to be part of a trend that views similarity in sequence data as a more reliable indicator of homology (and hence history) than similarities from other biological sources (e.g. morphology). Such a stance seems unjustified, because homology among molecular sequences is as inferential as among any other source of data. As stated by Cracraft (1989:208), "[h]omology (synapomorphy) decisions, whether with morphology or molecules, will always remain a slave to parsimony." In fact, rhe very occurrence of homoplasy in molecular data is sufficient evidence that similarity does not equal homology, because character incongruence could not possibly exist in a data set where all similarity was homologous. Within molecular data themselves, it is known that sequence information is not always the most consistent way of assessing homology. Other molecular characteristics may justifiably provide equally or more valid and informative sources of homologous similarities; for example, tertiary structure of proteins (Bajaj and Blundell, 1984; Johnson et al., 1990). The equivalent ontological status of molecular and morphological data is foreshadowed by Johnson et al. (1990:44): "The construction of phyletic relationships from homologous tertiary structures is perhaps the closest molecular equivalent to classical anatomical comparisons of whole organisms." Seen from the perspective of internal consistency of particular hypotheses, recent studies also indicate that relationships derived from sequence data are not more congruent than those derived from morphological information (Wyss et al., 1987).

A common distinction between two "kinds" of molecular homology has been called orthology and paralogy (Fitch, 1970). Orthology is said to be the molecular equivalent of "classical" or "phylogenetic" homology, supposedly being informative about organismal phylogeny. Paralogy, on the other hand, corresponds to what in morphology has been called "serial homology", "homonomy", "iterative homology" or "mass homology", i.e. structures that occur in multiple copies in a single organism (e.g. metameric structures, fur, cells, genome, etc.). It has been mostly overlooked (but not totally; cf. Inglis, I966;Kaplan, 1984) that the term paralogy was first coined by Hunter (1964), to refer to a totally different concept. Hunter's paralogy, when translated to current concepts, is equivalent to the idea conveyed above by the terms "shared derived feature" or "putative synapomorphy", i.e. primary homology. His justification for creating the term was that shared similarity (his paralogy) could be either homologous or analogous, depending on conclusions derived from phylogenetic considerations. It is therefore a very pertinent term, and it would certainly have its place in current terminology if it had not been forgotten. However, the more recent and now widespread use of paralogy in Fitch's (1970) sense makes any return to Hunter's (1964) original meaning inappropriate from a practical standpoint.

Patterson (1988a) saw a problem in equating orthology with classical homology (without denying the equation, though), in that the first fails the conjunction test (in multicellular organisms there are always multiple copies of the genome) while the second passes it. To me this problem reflects the fact that the conjunction procedure does not evaluate characters in an absolute way. Perhaps more precisely, homology statements are meaningless when applied to single characters or character states. Therefore, sentences such as "these genes are paralogous or orthologous", etc., are misleading. The designation paralogous or orthologous, as well as any of their derivatives, are strictly relational, and only acquire meaning when dealing with comparisons. Such qualities (orthologous, etc.) are not factual statements about gene pairs. Accordingly, it is more precise to talk about orthologous or paralogous comparisons, thus avoiding any misunderstanding about the object of such designations. Considering the above, orthologous "genes" (just to use the common phraseology) do not fail the conjunction test, as long as the comparison is not being made with one of their copies. Accordingly, most morphological homologies would also fail the conjunction test as applied to the genome, since most organisms have structures that are repeated at least around the plane of symmetry. Therefore, there is no relevant difference between the notions of "classical or phylogenetic homology" and orthology.

Regarding paralogy, Patterson (1988a) stated that it differs from homonomy because in the latter the multiplication occurs in ontogeny, while in the former the duplication has occurred in phylogeny. I do not agree with this distinction, because duplications in homonomy evidently also occurred in phylogeny; ontogeny simply reproduces the pattern. This does not imply that homonomous duplications occurred stepwise in phylogeny, but only that any feature observed in ontogeny also at some point occurred in phylogeny, because any novelty in ontogeny is also a novelty in phylogeny. There also seems to be no grounds for the statement that paralogy and homonomy differ because duplication in the latter is observed (in ontogeny), while in the former it is inferred (Patterson, 1988a). First, because homonomous duplications are also inferred to be phylogenetic. Second, because most cases of morphological homonomy have been detected before the actual process of multiplication could be observed in the ontogeny of the organism concerned. Therefore, there seems to be no significant difference between the basic concepts of homonomy in morphology and paralogy in molecular sequences.

The term xenology has been coined to express molecular comparisons that involve cases of horizontal gene transfer (Gray and Fitch, 1983). One notorious example is the legume haemoglobin, supposed to be the result of horizontal transfer from animals by means of a viral carrier (Hyldig-Nielsen et al., 1982; but see Appleby et al., 1990). In such cases the sequence of the gene being studied is incongruent with that of the organism that carries it. Transposable elements, transfection, symbiosis and endoparasitism are some of the mechanisms by which xenologous genes may come about. According to Patterson (1988a), in failing the congruence test but passing similarity and conjunction, xenology is the molecular equivalent of parallelism. However, I see no reason why convergence should not also be included as an equivalent of xenology, since horizontal gene transfer is random, insofar as known, and does not follow any definite systematic pattern. In fact, there does not seem to be any means strictly inside the systematic method to tell xenology apart from plain homoplasy. It may be possible that many morphological homoplasies are eligible as xenology, insofar as morphological characters are in some way expressions of information at the molecular level that may itself have been the result of horizontal gene transfer. It is possible that patterns of homoplasy may in fact be good indicators of potential cases of xenology, as has been suggested, in other words, by Syvanen (1985).

In view of the above considerations, it follows that the terms "orthology", "paralogy" and "xenology" (as well as their derivatives, "paraxenology", etc.) are either logically equivalent with terms previously used in morphology (orthology, paralogy), or potentially applicable also to morphological comparisons (xenology). Consequently, their usage exclusively for molecular data should be discouraged in order not to obscure the fundamental uniformity of the notions of homology for all kinds of biological information. Those terms might either be substituted by those previously used in morphology or be adopted as well in morphological comparisons that correspond to their intrinsic concepts originally formulated for molecular data.

Acknowledgments

For conversations and/or lectures on homology, systematics and related subjects, I am grateful to S. Blum, J. Farris, B. Lieberman, J. Maisey, G. Naylor, G. Nelson, R. Page, N. Papavero, R. Prum, J. Radding, L. Salles, S. Salthe, M. Tamny, R. Voss and W. Wheeler. Several of the ideas proposed here were discussed in the Students' Systematics Discussion Group of the AMNH, and I thank all participants for their input. I am grateful to G. Nelson and N. Papavero for having called my attention to Aristotle's notion of privative property. The manuscript benefited from reviews and suggestions by M. Donnelly, G. Edgecombe, B. Lieberman, L. Marcus, G. Naylor, G. Nelson, C. Patterson, R. Prum, O. Rieppel, R. Sachsse, L. Salles, R. Schuh, R. Vari and W. Wheeler.

The author is financially supported by the Conselho Nacional de Desenvolvimento Cientifico e Tecnologico (CNPq), Brazilian Federal Government.

REFERENCES

APPLEBY, C. A., E. S. DENNIS AND W. J. PEACOCK. 1990. A primaeval origin for plant and animal haemoglobins? *In:* P. Y. Ladiges and L. W. Martinelli (eds). Plant Systematics in the Age of Molecular Biology. CSIRO, Australia.

ARISTOTLE. 1911. De Partibus Animalium. English translation by W. Ogle. Clarendon Press, Oxford.

Ax, P. 1984. Das Phylogenetische System. Gustav Fischer Verlag, Stuttgart.

BAJAJ, M. AND T. BLUNDELL. 1984. Evolution and the tertiary structure of proteins. Ann. Rev. Biophys. Bioeng. 13:453-492.

DE BEER, G. 1971. Homology, an Unsolved Problem. Oxford Biology Readers No. 11, Oxford University Press, Oxford.

BOCK, W. J. 1974. Philosophical foundations of classical evolutionary classification. Syst. Zool. 22: 375-392.

BOCK, W. J. 1977. Foundations and methods of evolutionary classification. *In:* M. K. Hecht, P. C. Goody and B. M. Hecht (eds). Major Patterns in Vertebrate Evolution. Plenum Press, New York, pp. 851-895.

BONDE, N. 1977. Cladistic classification as applied to vertebrates. *In:* M. K. Hecht, P. C. Goody and B. M. Hecht (eds). Major Patterns in Vertebrate Evolution. Plenum Press, New York, pp. 741-804.

BOYDEN, A. 1943. Homology and analogy: a century after the definitions of "homologue" and "analogue" of Richard Owen. Quart. Rev. Biol. 18:228-241.

BRADY, R. H. 1983. Parsimony, hierarchy, and biological implications. *In:* N. I. Platnick and V. A. Funk (eds). Advances in Cladistics, Vol. 2. Columbia University Press, New York; pp. 49-62.

BRADY, R. H. 1985. On the independence of systematics. Cladistics 1:113-126..

COLLESS, D. H. 1985. On "character" and related terms. Syst. Zool. 34:229-233.

CRACRAFT, J. 1978. Science, philosophy and systematics. Syst. Zool. 27: 213—216.

CRACRAFT, J. 1981. The use of functional and adaptive criteria in phylogenetic systematics. Am. Zool. 21:21-36.

CRACRAFT, J. 1989. [Review of] Molecules and Morphology in Evolution: Conflict or Compromise? (C. Patterson, ed.). Cladistics 5:202-211.

CRISCI, J. V. 1982. Parsimony in evolutionary theory: law or methodological prescription? J. Theor. Biol. 97:35-41.

DONOGHUE, M., J. DOYLE, J. GAUTHIER, A. KLUGE AND T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. Ann. Rev. Ecol. Syst. 20:431-460.

DOOLITTLE, R. F. 1981. Similar amino acid sequences: chance or common ancestry. Science 214: 349-159.

DOOLITTLE, R. F. 1986. Of urfs and orfs—a primer on how to analyze derived amino acid sequences. University Science Books, Mill Valley.

ELDREDGE, N. 1979. Alternative approaches to evolutionary theory. Bull. Carnegie Mus. Nat. Hist. 13:7-19.

ELDREDGE, N. AND J. CRACRAFT. 1980. Phylogenetic Patterns and the Evolutionary Process. Columbia University Press, New York.

ESTABROOK, G. F., C. S. JOHNSON AND F. R. McMORRIS. 1976. A mathematical foundation for the analysis of cladistic character compatibility. Math. Biosc. 29:181-187.

ESTABROOK, G. F.,s G. F. STRAUCH AND K. FIALA. 1977. An application of compatibility analysis to Blacklith's data on orthopteroid insects. Syst. Zool. 26:269-276.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83-92.

FARRIS, J. S. 1977. Phylogenetic analysis under Dollo's law. Syst. Zool. 26:77-88.

FARRIS, J. S. 1982. Simplicity and informativeness in systematics and phylogeny. Syst. Zool. 31: 413-444.

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

FARRIS, J. S. AND A. G. KLUGE. 1979. A botanical clique. Syst. Zool. 28:400-411.

FENG, D.-F. AND R. F. DOOLITTLE. 1987. Progressive sequence alignment as a prerequisite to correct phylogenetic trees. J. Mol. Evol. 25:351-360.

FEYERABEND, P. K. 1987. Farewell to Reason. Verso, London.

FINK, W. L. AND S. V. FINK. 1986. A phylogenetic analysis of the genus *Stomias*, including the synonymization of *Macrostomias*. Copeia 1986:494—503.

FITCH, W. M. 1970. Distinguishing homologous from analogous proteins. Syst. Zool. 19: 99-113.

FUNK, V. A. AND D. R. BROOKS. 1990. Phylogenetic systematics as the basis of comparative biology. Smiths. Contr. Botany 73.

GAFFNEY, E. S. 1979. An introduction to the logic of phylogenetic reconstruction. *In: J.* Cracraft and N. Eldredge (eds). Phylogenetic Analysis and Paleontology. Columbia University Press, New York, pp. 79-111.

GEOFFROY SAINT-HILAIRE, E. 1830. Principes de Philosophic Zoologique, Discutes en Mars 1830, au Sein de l'Academie Royale de Sciences. Pichon et Dider, Paris.

GHISELIN, M. 1976. The nomenclature of correspondence: a new look at "homology" and "analogy". *In:* R. B. Masterton, W. Hodos and H. Jerison (eds). Evolution, Brain and Behavior: Persistent Problems. Lawrence Erlbaum, Hillsdale, pp. 129-142.

GRAY, G. S. AND W. M. FITCH. 1983. Evolution of antibiotic resistance genes: the DNA sequence of a kanamycin resistance gene from *Staphylococcus aureus*. Mol. Biol. Evol. 1: 57-66.

HENNIG, W. 1950. Grundzuge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin.

HENNIG, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.

HYLDIG-NIELSEN, J. J., E. O.JENSEN, K. PALUDAN, O. WIBORG, R. GARRETT, P. JORGENSEN AND K. A. MARCKER. 1982. The primary structures of two leghemoglobin genes from soybean. Nucleic Acids Research 10:689-701.

HUNTER, I. J. 1964. Paralogy, a concept complementary to homology and analogy. Nature 204: 604.

INGLIS, W. G. 1966. The observational basis of homology. Syst. Zool. 15:219-228.

JARDINE, N. 1967. The concept of homology in biology. Br. J. Phil. Sci. 18:125-139.

JARDINE, N. 1970. The observational and theoretical components of homology: a study based on the morphology of the dermal skull-roofs of rhipidistian fishes. Biol. J. Linn. Soc. 1: 327-361.

JARDINE, N. AND C. J. JARDINE. 1969. Is there a concept of homology common to several sciences. Class. Soc. Bull. 2: 12-18.

JENSEN, R. J. 1981. Wagner networks and Wagner trees: a presentation of methods for estimating most parsimonious solutions. Taxon 30: 576-590.

JOHNSON, M. S., M. J. SUTCLIFFE AND T. L. BLUNDELL. 1990. Molecular anatomy: phyletic relationships derived from three-dimensional structures of proteins. J. Mol. Evol. 30: 43-59.

KAPLAN, D. R. 1984. The concept of homology and its central role in the elucidation of plant systematic relationships. *In:* T. Duncan and T. Stuessy (eds). Cladistics: Perspectives on the Reconstruction of Evolutionary History. Columbia University Press, New York, pp. 51-70.

KLUGE, A. G. AND R. E. STRAUSS. 1985. Ontogeny and systematics. Ann. Rev. Ecol. Syst. 16: 247-268.

LAMBSHEAD, P. J. D. AND G. L. J. PATERSON. 1986. Ecological Cladistics—an investigation of numerical Cladistics as a method for analysing ecological data. J. Nat. Hist. 20: 895-909.

LANKESTER, E. R. 1870. On the use of the term homology in modern zoology, and the distinction between homogenetic and homoplastic agreements. Ann. Mag. Nat. Hist., ser. 4, vol. 6: 34-43.

LUNDBERG, J. G. 1972. Wagner networks and ancestors. Syst. Zool. 21:398-413.

MAGEE, B. 1973. Popper. Fontana Modern Masters Series.

MEACHAM, C. A. 1980. Phylogeny of the Berberidaceae, with an evaluation of classifications. Syst. Bot. 5:149-172.

MEACHAM, C. A. AND G. F. ESTABROOK. 1985. Compatibility methods in systematics. Ann. Rev. Ecol. Syst. 16:431-446.

MICKEVICH, M. F. 1978. Taxonomic congruence. Syst. Zool. 27:143-158.

MICKEVICH, M. F. 1982. Transformation series analysis. Syst. Zool. 31:461-478.

MICKEVICH, M. F. AND S. J. WELLER. 1990. Evolutionary character analysis: tracing character change on a cladogram. Cladistics 6: 137-170.

NAYENIZGANI, T. N. 1990. The systematics association enters its golden years. Cladistics 6: 307-314.

NELSON, G. J. 1970. Outline of a theory of comparative biology. Syst. Zool. 19: 373-384.

NELSON, G. J. 1978. Ontogeny, phylogeny, paleontology and the biogenetic law. Syst. Zool. 27: 324-345.

NELSON, G. J. 1989. Cladistics and evolutionary models. Cladistics 5:275-289.

NELSON, G. J. AND N. I. PLATNICK. 1981. Systematics and Biogeography. Columbia University . Press, New York.

PATTERSON, C. 1978. Verifiability in systematics. Syst. Zool. 27:218-222.

PATTERSON, C. 1982. Morphological characters and homology. *In:* K. A. Joysey and A. E. Friday (eds). Problems of Phylogenetic Reconstruction. Academic Press, London, pp. 21-74.

PATTERSON, C. 1988a. Homology in classical and molecular biology. Mol. Biol. Evol. 5:603-625.

PATTERSON, C. 1988b. The impact of evolutionary theories on systematics. *In:* D. L. Hawksworth (ed.). Prospects in Systematics. Clarendon Press, Oxford.

DE PINNA, M. C. C. AND L. O. SALLES. 1990. Cladistic tests of adaptational hypotheses: a reply to Coddington. Cladistics 6: 373-377.

PLATNICK, N. I. 1979. Gaps and prediction in classification. Syst. Zool. 27:472-474.

PLATNICK, N. I. AND H. D. CAMERON. 1977. Cladistic methods in textual, linguistic and phylogenetic analysis. Syst. Zool. 26: 380-385.

DE QUEIROZ, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. Syst. Zool. 34: 280-299.

DE QUEIROZ, K. AND M. DONOGHUE. 1988. Phylogenetic systematics and the species problem. Cladistics 4:317-338.

REMANE, A. 1952. Die Grundlagen des Naturlichen Systems der Vergleichenden Anatomie und der Phylogenetik. Geest and Portig, Leipzig, Germany.

RIEDL, R. 1975. Die Ordnung des Lebendigen. Systembedingungen der Evolution. Paul Parey, Hamburg, Germany.

RIEDL, R. 1979. Order in Living Organisms. Wiley, Chichester.

RIEPPEL, O. 1980. Homology, a deductive concept? Z. Zool. Syst. Evolutionsforsch. 18:315-319.

RIEPPEL, O. 1988. Fundamentals of Comparative Biology. Birkhauser Verlag, Basel.

ROSEN, D. E. 1984. Hierarchies and history. *In:* J. W. Pollard (ed.). Evolutionary Theory: Paths into the Future. Wiley, New York, pp. 77-97.

ROTH, V. L. 1984. On homology. Biol. J. Linn. Soc. 22:13-29.

ROTH, V. L. 1988. The biological basis of homology. *In:* C.J. Humphries (ed.). Ontogeny and Systematics. Columbia University Press, New York, pp. 1-26.

RUSSELL, E. S. 1916. Form and Function: John Murray, London.

SANDER, K. 1989. Zum Geleit: Homologie und Qntogenese.Zool. Beitr. N.F. 32:323-326.

SATTLER, R. 1984. Homology—a continuing challenge. Syst. Bot. 9(4): 382-394.

SCHMITT, M. 1989. Das Homologie-Konzept in Morphologie und Phylogenetik. Zool. Beitr. N.F. 32:505-512.

SERRES, E. 1827. Recherches d'anatomie trancendante, sur les lois de l'organogenie appliquées a l'anatomie pathologique. Ann. Sci. Nat., Paris 11:47-70.

SNEATH, P. H. A. 1969. Problems of homology in geology and related fields. Class. Soc. Bull. 2:5-11.

STEVENS, P. F. 1984. Homology and phylogeny: morphology and systematics. Syst. Bot. 9: 395-409.

SWOFFORD, D. L. AND W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. Math. Biosc. 87:199-229.

SYVANEN, M. 1985. Cross-species gene transfer; implications for a new theory of evolution. J. Theor. Biol. 112:333-343.

SZALAY, F. S. 1977. Phylogenetic relationships and a classification of the eutherian mammalia. *In:* M. K. Hecht, P. C. Goody and B. M. Hecht (eds). Major Patterns in Vertebrate Evolution. Plenum Press, New York, pp. 315-374.

WAGNER, G. R 1989. The origin of morphological characters and the biological basis of homology. Evolution 43: 1157-1171.

WILEY, E. O. 1975. Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. Syst. Zool. 24: 233-243.

WILEY, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). Misc. Publs Mus. Nat. Hist. Univ. Kansas 64: 1-111.

WILSON, E. O. 1965. A consistency test for phylogenies based on contemporaneous species. Syst. Zool. 14:214-220.

WOODGER, J. H. 1937. The Axiomatic Method in Biology. Cambridge University Press, London.

WOESE, C. R. 1987. Bacterial evolution. Microbiol. Rev. 51: 221-271.

WYSS, A. R., M. J. NOVACEK AND M. G. McKENNA. 1987. Amino acid sequences versus morphological data and the interordinal relationships of mammals. Mol. Biol. Evol. 4:99-116.