Chapter 17

Homology in Morphometrics and Phylogenetics

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Abstract

Homology is neither an empirical nor a conceptual problem, but a relation enabling a two-part method for classifying the descent and modification of characters. The two parts are operational and taxic.

Location of homologous characters in terms of landmark topology is a necessary operation prior to comparative anatomical and phylogenetic analyses. Operational homology is a similarity relation defined by positional correspondences among internal and external landmarks. In evolutionary biology, the relation assumes the existence of unknown transformation series of character states which descended with modification and branching from an unknown common ancestor. The analytical construct is a phylogenetic hierarchy of taxa in which the observed character states are derived expressions of ancestral characters. Operational homology cannot remain independent of the evolutionary concept of homology (similarity due to common ancestry) because at some point observed similarities must be put into historical context with a phylogenetic test that discriminates homology from homoplasy (similarity due to reversal, parallelism, or convergence). Speculation about evolutionary transformations of a character may be logically circular until corroborated by congruence with the state distributions of other characters in a cladistic hypothesis (Hennig, 1966).

Taxic homologies are corroborated synapomorphies, i.e., shared, derived character-state identities that diagnose monophyletic groups. Such homologies are correctly named by reference to the character (and usually its state), and the monophyletic group it diagnoses (e.g., the cap-like tarsals of the Dinosauria). The homologous states of a character have a polarized general-to-particular hierarchical relation, which corresponds, except for homoplasy, to the cladistic tree hierarchy for the taxa.

Morphometrics serves to define the relations among landmarks that identify operationally homologous characters and to quantify shape differences across ontogenetic and taxic transformation series. Morphometrics plays an important post-cladistic role in the analysis of trends and responses to evolutionary causes and constraints.

Introduction

This review of the relationship between morphometrics, cladistics, and homology is motivated by claims to exclusivity by advocates of operational homology and taxic homology. I will argue that neither of these approaches, nor a developmental approach, can stand alone. Operational homology is traditionally associated with morphometrics and phenetics; taxic homology is the core of cladistics. Morphometrics is the quantitative, comparative description of shapes of organisms as measured among sets of landmarks on homologous, and therefore comparable, anatomical units. Cladistics is a method that infers the sequence of branching
lineages from hierarchical arrangements of derived character-state identities—taxic homologies. Phylogenetics is the analysis of amount and trend in evolutionary changes through time, as measured along transformations among homologous character states.

Phylogenetic information, based on homologous characters from comparative anatomy, molecular genetics, behavior, etc., provides a context for framing or testing hypotheses about evolution of species or clades. Morphometrics may contribute to evolutionary biology by quantifying comparative information about the states in transformation series of homologous structures and by ordinating trajectories of ontogenetic or taxic transformations in morphospace. These steps may provide characters for cladistic analyses or describe evolutionary trends in phylogenetic analyses.

A "character" is a variable used in cladistic estimation or other systematic studies. Morphometric characters are defined by several (not fewer than two) anatomical landmarks. Selection of landmarks, characters, and variables depends on the concept of homology to justify comparability among attributes of different species. Homology, defined as similarity due to descent from a common ancestor, is the methodological basis for studies of character-state transformations and diagnosis of monophyletic groups. The definition of homology in terms of descent from a common ancestor means that comparable structures in related organisms are taken to be complementary evolutionary representations of the "identical" ancestral structure (Simpson, 1961). Two current concepts of homology have developed around the two seemingly separate issues involved: (1) recognition by anatomical similarity and (2) definition in terms of descent with modification.

1) Homologous anatomical structures are operationally identified by similar material and shapes, as indicated by internal landmarks, and similar position, as indicated by spatial relations to external landmarks, at appropriate stages of development (Remane, 1956, 1971; Sneath and Sokal, 1973). The topological relations are of the anatomical sort, "anterior to," "dorsal to," and "distal to" (Jardine, 1967). For example, a homologous pair of bones, nerves, amino acid sequences, or DNA segments is recognized by correspondence of compositional, spatial, and ontogenetic relations among the landmarks in and around each complementary member of the pair. Two sets of structures that maximally satisfy these internal and external landmark relations in appropriate ontogenetic stages of different individuals are operationally said to be homologous (Boyden, 1947; Remane, 1956, 1971; Sneath and Sokal, 1963; Withers, 1964; Inglis, 1966; Fitch, 1966; Key, 1967; Jardine, 1967, 1969; Jardine and Jardine, 1967, 1969; Sokal and Sneath, 1973:78-82; Bookstein et al., 1985). Features of different organisms hypothesized to be homologous in this sense are acknowledged as such by application of the same anatomical name (Owen, 1848), e.g., the fifth gill arch of Elasmobranchii; the protocochonch of Gastropoda, the alpha hemoglobin sequence of hominoids. Quantitative aspects of these homologies usually vary continuously, for example when the transformations are tracked vertically through the hierarchy.

2) The evolutionary concept defines homology in terms of the descent of complementary structural identities from their hypothetical complement in a common ancestor (Simpson, 1961). In its recently refined form (Patterson, 1982), this concept creates a special role for the relationship between a character identity and the group of species in which it is found: A homolog is a synapomorphy that helps diagnose a monophyletic group, i.e., a group that is restricted to all of the descendants of a common ancestor. In this concept, the monophyly of the group implies the homology of the synapomorphic character state (Bock, 1969). Analytically, this synapomorphic character state is evidence for the monophyly of the group (Wiley, 1975). Such a "taxic" homology is named with a qualifier indicating the monophyletic taxon it diagnoses, e.g., the feathers of Aves, the spinnerets of Arachnida. A taxic homology bears
an all-or-none relation to other character states within a cladistic hypothesis.

Conflict between advocates of the operational and cladistic schools is not new. In 1961, Simpson observed that usage seemed to demand two different terms, but that if "the argument were only about which concept is to bear the name 'homology', it would be quite useless." He favored using "homology" for the evolutionary concept, suggesting "morphological correspondence" (Woodger, 1945; see also Ghiselin, 1969) to indicate the identity relation that is methodologically independent of evolution. The vocabulary has changed because of the growth of morphometrics and cladistics, but "homology" retains the dualism it has had since Darwin provided a causal mechanism for Owen's idea and substituted the common ancestor for Owen's archetype. The dualism consists of (1) concern to find a conceptual basis and method for identifying comparable characters independent of the evolutionary conclusions sought, and (2) analysis of character identities in the framework of descent with modification. In the spirit of Inglis (1966), I will advocate the necessity of iterative interaction between operational and taxic homology. [Operational homology is necessary because cladistic methods cannot begin with characters chosen because they are known to be descended from a common ancestor (it is not possible and if it were, it would be circular). Taxic homology is necessary because only a phylogenetic test can distinguish homologies from homoplasies—"similarities due not to common ancestry but to independent acquisition of similar characters" (Haas and Simpson, 1946).

**Operational Homology**

The operational concept of homology—correspondence of landmark positions from form to form (Sneath and Sokal, 1973)—refers to designation and definition of characters whose states are being compared in a systematic study. This use of the homology relation is near that which Owen (1848) called general homology—correspondence of parts in relation to an archetypical body plan. Several problems will be discussed to clarify operational homology: some practical procedures by which homology can by identified (e.g., Nieuwenhuys and Bodenheimer; 1966, Jardine; 1969; Bookstein et al., 1985), difficulties of definition (Bookstein et al., 1985), and the nature of the circularity in the operational concept of homology (Inglis, 1966; Rieppel, 1980).

**Historical background.** Simpson (1961) discussed a broad range of practical homology criteria, emphasizing "minuteness of resemblance and multiplicity of similarities" of anatomical structure, as well as criteria for recognizing non-homologous parallelisms and convergences. Simpson's discussion of contemporary statistical methods for evaluating similarity was unenthusiastic, but he suggested that, conclusions on affinities (which means largely on homologies) are stronger the more the characters involved." Simpson's criterion for improved inference applies to the number of landmarks in operational homology (and the number of characters in taxic homology, see below).

D'Arcy Thompson (1942) elaborated the geometrical foundation of the operational concept of homology, based on his "naturalist's" concept: "invariant relation of position." Woodger (1945) is credited with developing the modern logical framework for the concept. N. Jardine made it more operational. [In Jardine's (1967, 1969) system, like D'Arcy Thompson's, homology is a function specifying the geometrical transformation of one form to another: it is an optimized level of correspondence of position among landmarks.] A sufficient matching correspondence relative to external landmarks is a necessary condition for the recognition of homology. [Internal landmark correspondence may be adequate for structures that are sufficiently unique due to the complexity of landmarks, e.g. fossil mammalian teeth. But internal similarity is not a necessary condition (Bock, 1963) if structural changes are being studied across higher taxa (Sattler, 1984), e.g., the transitions between fish jaw bones and mammalian ear bones.]
Difficulties of definition and the role of development. Difficulties arise when homologous structures have different ontogenies (Kluge, 1985, 1988; de Queroz, 1985; Roth, 1988), or when different structures have evolved to occupy the same position relative to external landmarks (Van Valen, 1982), or when iterative homologs confuse character ancestry (Roth, 1984; Wagner, 1989). For example, as a character, the mammalian upper premolar 4 of a taxon must have a number of recognizable correspondences of internal and external landmark locations to justify its comparison to other fourth premolars in a systematic study. We wish not to mistakenly compare a premolar of one taxon to a molar of a related group. This problem is complicated by similarity of internal landmarks of some premolars and molars due to their serial homology. At some point in the evolutionary history of mammals, premolars and molars had a common ancestry; at a later point, premolars and molars differentiated into daughter lineages.

Van Valen (1982) defined homology as continuity of information. In a detailed history of a specific case of the above example, he demonstrated that landmark similarity is not always an unambiguous criterion for homology. Ontogenetic changes, such as growth, movement, regression, repetition, addition, deletion, and changes in genetic and embryonic origin of parts can create missing or iterative homologies that confound comparison (Van Der Klaauw, 1966; Ghiselin, 1976; Roth, 1984, 1988; Kluge, 1985). Wagner (1989) described possible relationships between iterative homologs in radial symmetry. But tracking the continuity of information still requires identification of potentially homologous characters by landmark correspondence (quantitative or not).

Bookstein et al. (1985, Figure 5.1.1a) illustrated several kinds of homology relations that require additional information for resolution of morphological correspondence. Structures with accretionary growth may exhibit material as well as anatomical landmark relations resulting from growth along "point paths" (Skalak et al., 1982; Bookstein et al., 1985, Figure 5.1.1a). The paths are a source of homologous position information. Material landmarks enable visualization of the process of growth and its meaning for homologous landmarks and homologous development. Landmark fusion and division (Bookstein et al., 1985, Figure 5.1.1b,c) in ontogeny and evolution create ambiguity regarding new or lost space in the structure. Shape change through truncation of development (Bookstein et al., 1985, Figure 5.1.1d) also renders landmarks ambiguous and requires that we look to developmental processes for homologous pathways (Alberch et al., 1979; Roth, 1984, 1988).

Missing landmarks create problems for the operational comparison of potentially related forms (Jardine, 1969), but there are operational methods for facilitating comparisons. Changed or missing internal landmarks can be imputed from external landmarks, using a displacement vector model or an elastic mapping model, as illustrated by Bookstein et al. (1985, Figure 5.1.2). Accuracy of the inferred landmark position depends upon the extent to which the morphometric model mimics growth of tissues. (Missing terminal additions, due either to plesiomorphy or truncation, are a different problem, see below.)

van der Klaauw (1966) provided a classification of different kinds of modifications of homology in development (see also Alberch et al., 1979). Fitch (1970) and Patterson (1987) reviewed the comparable sources of variation in data from molecular biology. Wagner (1989) suggested three criteria—conservatism, individuality, and uniqueness—as three biological properties expected of homology on the basis of developmental considerations. The theoretical importance of developmental information to recognition of homology has been emphasized by Owen (1848), Gould (1977), Nelson (1978), and Roth (1984, 1988).

Even if developmental information is included in the definition of homologous characters (e.g., Wagner, 1989), the discernment of its alter-
nate states in different lineages ultimately depends on correspondence of landmark sets, which must be determined empirically as matching similarities across topographic comparisons (Jardine, 1969). Jardine (1969) explored alternative definitions of homology in terms of topology, structure, and ontogenetic status, and concluded that topographic position was more basic because of changes in the migration and orientation of parts during development.

It is clear that homology must be located by landmarks in ontogenetic time as well as anatomical space if we are to gain information about the role of development in evolutionary processes. This can be seen most clearly when ontogenetic changes involve serial replacement of homologous characters or states, e.g., when teeth or exoskeletons go through replacement cycles. The most subtle and informative examples of ontogenetic homologs will involve discovery of the role of heterochrony in evolution (Alberch et al., 1979; Bookstein et al., 1985).

In an insightful review of the developmental basis for character conservatism, individuality, and uniqueness, Wagner (1989) suggested that there are problems with the concept of homology. But the difficulties cited pertain to the attempt to derive process information from a concept with no content extrinsic to the theory of evolution. The historical existence of descent with modification is assumed by evolutionary homology, therefore its role can be no more than the classification of character-state identities. It is a part of a method for describing the character-by-character chronicle, given a hierarchy. Using homology as part of cladistic methodology (see below) has conceptual utility, but no theoretical or predictive content. The difficulty is breaking out of the circularity of operational homology. Wagner's (1989) excellent discussion of development contributes to understanding the processes of transformation of homologous characters, but less to the methodological problem of homology.

**Operational tests.** Attempts to test homology operationally involve landmark consistency among the groups constituting the larger taxonomic unit. Riedl (1978) and Patterson (1981) discuss probabilistic contexts for considering homolog identity, based on consistency of included homologous structures among given groups. Riedl considers the consistency of a homologous structure to be a function of the number of homologous parts it comprises. He also considers the uniformity of its occurrence in the groups that possess it, as well as its absence in the groups that lack it. Knowledge of groups is an evident requirement.

Patterson's function calculates the probability $P$ that $h$ homologs will specify the same taxon by chance as:

$$P = \frac{(S! \cdot (N-S)!)}{N!} \cdot \frac{1}{h!}$$

where $N$ is the total number of groups available for sampling (i.e., the number of groups involved in the disagreement) and $S$ is the sample of groups displaying the homology. The calculated probabilities that $h$ homologies represent $S$ out of $N$ groups by chance ranges from $1/3$ to astronomical values for more or less unconvincing homologs, leading Patterson to abandon the method (if not the principle) and evaluate the homologies on the basis of subjective considerations of taxic distribution and anatomy (Patterson, 1982:42; see also Ax, 1987:168).

Patterson (1982, 1987) suggested additional tests for rejection or acceptance of homology, independent of evolutionary theory. These include similarity, congruence, conjunction (two different homologous structures must not both be present in the same individual, within constraints imposed by symmetry relations and iteration), endoparasitism, etc. Of these, only similarity and congruence can play a major role—in hypothesized operational homology and cladistic tests, respectively.

**Circularity in operational homology.** Potential circularity arises from lack of satisfactory internal tests of two assumptions underlying decisions about operational homology: (1) that the study set of OTUs consists of a related group of organisms, and (2) that the characters are not parallel, reversed, or
convergent homoplasies. Operational methods by themselves are insufficient for unambiguous resolution of homology because of the inadequacy of non-cladistic tests. This is most easily seen in the following kinds of difficulties: reversed or lost characters, parts that changed through amplification of serial homologies (Patterson, 1987), or structures that became spatially reoriented during ontogeny and phylogeny (Jardine, 1969). Bookstein et al. (1985) admitted, "The resolution of conflicts in homology, if resolution exists, lies mostly outside the arena of morphometrics." Roth (1984), after discussing the possibility that independently evolved developmental pathways might result in serial and (or) parallel homologs, stated, "For good biological as well as methodological reasons, it may be impossible to distinguish homology from parallelism within a population, or even between species." These authors are speaking of the difficulty of resolving homology from homoplasy, using only information from landmark matching and developmental similarity. At this (precladistic) stage of analysis, resolution requires external testing to relate homologous states to the historical taxonomic hierarchy upon which they are conditional (Bock, 1973, 1977; Ghiselin, 1969).

**Taxic Homology**

Referring to homology as "synapomorphy" defines it as a derived character state shared by the members of a monophyletic group (Patterson, 1982). Discovery and validation of a shared, derived character state as a homology is the objective of a cladistic procedure that establishes monophyletic groups and identifies the derived character states that diagnose them. Not all synapomorphies diagnose monophyletic groups. Confidence in the homology of a synapomorphy is established by its congruence with the distribution of the states of other characters over a cladogram. The homologies of special interest are those that uniquely diagnose well-supported monophyletic groups.

This sense of homology, called taxic homology by Eldredge (1979b), corresponds to the special similarity function that characterizes cladistic but not phenetic classifications. A derived character state is homologous with respect to a specific branch of a cladistic tree; the homologous state diagnoses the monophyletic group that descended from the stem on which it originated. The common ancestor replaces the hypothetical archetype (Rosen, 1973:500; Patterson, 1987:4). In this special sense, a character state is not homologous with less-derived states of the same character below it on the tree or with more-derived states of the same character higher in the tree.

But all states of the character must be generally homologous in their hierarchic relations throughout the tree to justify the comparisons: Hennig (1966:93) regarded homologous characters as "transformation stages of the same original character." This transformational homology, as it is called by Eldredge (1979a), is established by evidence that the observed representations of the character descended from one source through a hierarchic path indicated by the cladistic tree. Unlike taxic homology, it is a vertical, not an instantaneous, relation in the tree.

The homology of each synapomorphy is ultimately tested by its congruence with other characters (Hennig, 1966:112). Character states whose similarities are not concordant with the tree are homoplasies (Haas and Simpson, 1948) or "convergent homologies" and "parallel homologies" (Ghiselin, 1976). I would add a third category, "homoplasies that are introgressively transferred homologies."

**Circularity in taxic homology.** Can taxic homology stand alone, without an operational concept for identification of comparable characters? The possibilities might be illustrated by examples of taxic homologs that would not ordinarily be recognized by operational methods. For example, characters that are not operationally recognizable as homologs because they are dissimilar in composition and development may be indicated by a cladistic tree to be homologous. The horns of the Bovidae and the bone antlers of the Cervidae may
be homologous as frontal ornaments at the level of the Pecora of the Artiodactyla, although operationally one finds different composition and different development, with little more than frontal position to suggest homology. But homology is suggested by congruence with other characters.

Non-operationally "similar" synapomorphic attributes in different anatomical positions provide a more extreme example, and we can begin to see the potential for circularity. Operational criteria would not ordinarily suggest that the black-and-white color patterns of spotted and striped skunks are homologous, but the congruence with morphology (and scent) leads to such a hypothesis. These synapomorphies are congruent; they encourage one to search for additional synapomorphies satisfying the congruence criterion.

The emergence of congruence as a prime criterion does not suggest a sufficient, non-circular methodology for the discovery of homology. The red color on the sides of the rainbow trout is homologous at some level with the orange color on the lower jaw of the plesiomorphically similar cutthroat trout. "The search for synapomorphies" could well begin with a plesiomorphic similarity, corroborated with such a "homology," and supplemented by other characters "tested" by congruence, bypassing landmark correspondence and operational homology. Given the available morphological and biochemical variability, additional congruent homoplasies could be found and listed, ad hoc, if not ad infinitum.

A test independent of congruence is clearly necessary as a check on the possibility of beginning with a plesiomorphic similarity and selectively adding homoplasies that agree with it. Since an initial step in cladistics is the assembly of a collection of comparable characters, this is an optimal time for application of morphometrics of landmark data to operationally posit homology. Initial selection of characters with a method independent of phylogenetic considerations avoids the possibility of adding evidence sorted by prior expectations. (But the taxa chosen for comparison are not so independent.) The other necessary defense against circularity is the use of numerical phylogenetic methods based on a suitable criterion for tree selection, such as the parsimony methods of Farris (1983; Kluge and Farris, 1969) or the maximum likelihood methods of Felsenstein (1982). These also provide safeguards against biased chains of evidence.

**Homology, synapomorphy, and paraphyly.** Are homology and synapomorphy redundant terms (Patterson, 1982)? This suggestion has been made by Patterson, but it is weakened to the extent that some synapomorphies do not diagnose monophyletic groups and some unambiguous homologies may characterize paraphyletic assemblages. An occasion arises when an apomorphy is shared by all but a derivative part of a group—for example, where parallel, reversed, lost, or replaced states contribute to the designation of a monophyletic subgroup, leaving the homologous state incompletely represented in the larger group. The lepidotrichia of bony fishes, a paraphyletic group, stand as an example because of the loss or replacement of lepidotrichia in tetrapods, a derived group, as pointed out by Patterson (1982) in presenting the opposite point of view. Other cases exist wherever character states are introgressively transferred between species that are not sister groups. Although the logical and methodological relationship between homology and synapomorphy is fundamental to the homology concept and to cladistic methods, not all synapomorphies are taxic homologs, and the distinction justifies retention of the concepts of transformational as well as taxic homologies in hierarchical relation to each other (Ax, 1987).

In a comprehensive summary of the view that homologies are synapomorphies, Patterson (1982:33) argued that symplesiomorphy and synapomorphy are terms for homologs that stand in hierarchic relation to one another. This is a fundamental point, but, contrary to Patterson, I take this to imply that hierarchic relations of characters validate transformational as well as taxic homologies (see above). Patterson (1982) has
criticized attempts to document character transformations, especially those utilizing fossils, on the grounds that they are founded upon paraphyletic groups, which are unnatural (unreal) inventions. If the groups are unnatural, much of what we think we know about evolution is invention of questionable reality (Patterson, 1982). Further, if paraphyletic groups are by definition without homologies, homology has nothing to do with evolution: "If phylogenies have to say something about evolution, then it is evident that homologies can have no role in them" (Patterson, 1982:58).

There are several important points in Patterson's exploration. First is the observation that paraphyletic groups have dominated classifications since their beginnings, and when we restructure systematics to monophyletic form, reflecting the historical chronicle of evolutionary divergence, our inferences about processes can only be improved (O'Hara, 1988). In addition, there is the problem that historical processes of transformation are unknowable because of our dependence on inferences based on extinct and paraphyletic (i.e., unnatural) groups. I think this problem is misspecified, however. Inference based on an assemblage made paraphyletic by misclassification of a monophyletic group is no more misleading than one made false by our ignorance of extinct group members. Conclusions confidently based on groups erroneously thought to be monophyletic will be most damaging of all. Documentation of anagenic transformations through (technically paraphyletic) lineages within monophyletic groups can generate and test important historical hypotheses (Roth, 1988). Ironicaly, tests of evolutionary hypotheses are most informative, as well as safest, when based on groups at the species level, where the processes occur, where morphometric methods are least in need of corroboration, and where evolutionary units are most likely to be paraphyletic. The natural order in a cladistic hierarchy is necessarily consistent with most evolutionary processes, as understood, as well as the historical narrative implicit in phylogenetic trees (Riedl, 1979; O'Hara, 1988). The results of past cross-testing of these bodies of theory and data justify some optimism for continuing. The correction of the paraphyly problem is desirable but trivial; we should strive toward a monophyletic classification for groups above the species level. Granted that, for many or even most groups, the true cladistic chronicle may be unknown and unknowable, nevertheless, molecular data and the fossil record provide independent consistency tests by which cladistic estimates can be improved.

Patterson (1982:58) seemed to be reaching still deeper: his rejection of the use of transformational homology—the transitions in states from ancestors to descendants over a cladogram—was accompanied by denial of evolutionary content in homology, presumably to avoid circularity in the study of evolutionary events and processes. His argument persuades me that we cannot regard homology as a concept with predictive content about the process of evolution. Homology cannot provide independent confirmation or challenge to any evolutionary hypothesis because the concept is merely a restatement of descent with modification applied to characters rather than taxa. But the definition "similarity due to common ancestry" is essential as a relational statement that facilitates the operational and taxic methods for inferring character-by-character chronicles of evolution. Assuming that the concept of homology is burdened with the circularities discussed above, we can also turn to empirical and conceptual aspects of geology and molecular biology for the theoretical tensions (Laudan, 1977) necessary to develop tests of hypotheses. Transformational homologies and homoplasies will play decisive roles in investigation of predictions from genetic, ontogenetic, ecological, stratigraphic, paleontological, and paleoecological studies of evolution in the context of cladistic hypotheses (Eldredge, 1979b).

The Relationship between Morphometrics and Cladistics

Morphometrics can contribute identification of characters and quantification of character states for
cladistics, but cannot contribute directly to cladistic inference. Morphometric character analysis is either precladistic or postcladistic. Precladistic character analysis contributes to the definition of homologous characters and the quantitative description of character states for cladistic analysis. Character states can be quantified by morphometric methods and, when necessary, coded for treatment by a tree-forming algorithm (see Wagner, 1980; Kluge and Farris, 1969). We can define the cladistic character and character state in relation to the concepts of homology and landmarks as follows:

A "character" may be strictly defined as an among-taxon set of putatively homologous structures whose correspondence is recognized by (1) similarity of internal and external landmark positions on the organisms at appropriate stages of their developmental histories, and (2) identity due to inheritance from a common ancestor (as initially indicated by a previous, more inclusive phylogenetic analysis). However loosely the investigator satisfies these two criteria, they are necessary to establish general homology prior to carrying out a comparative and phylogenetic study. For example, an investigator studying Gardiner's (1982) group, "Homiothermia," may assume that numerous parallel aspects of bird and mammal homiothermy are homologous and therefore comparable characters. The investigator compiles characters from more amniote taxa, based on previous broader studies, and cladistically tests the monophyly of the Homiothermia as well as the taxic homology of all of the characters (see Gauthier et al., 1988). (The problem of redundant information content in genetically or functionally covarying characters is treated by Felsenstein, 1988.)

A "character state" is the quantified or coded condition of a varying character (see Colless, 1967; and Hull, 1968). Character states at one level of analysis often become characters at a finer analysis, as the character hierarchy parallels the taxic hierarchy. In morphometrics, the quantitative value or state of a character might be, for example:

1) a distance between landmarks;

2) ratio shape-ratios of distances measured over a structure defined by landmarks;

3) a measure of size, e.g., centroid size: the sum of squares of all of the interlandmark distances (Bookstein, 1991).

Shape characters are rarely independent of size, i.e., are usually allometric, and therefore should be analyzed as ontogenetic trajectories (Creighton and Strauss, 1985; Kluge and Strauss, 1985). An ontogenetic character state might be the allometric trajectory describing shape difference between juvenile and adult structure (Strauss and Fuiman, 1985). Diverse morphometric methods, such as principal component and factor analysis, biorthogonal analysis, medial axis data (Bookstein et al., 1985) or Fourier analysis, (e.g., Ferson et al., 1985), can be used to define ontogenetic trajectories that can be given character-state values. In general, these are less rigorously specified than Bookstein's (1991) shape variables based on transformations of triangles. Analytical triangles, digitized over the form or its parts (e.g., bones or sclerites), can yield at least one character per triangle; these may prove to be the most subtle and information-rich morphometric products for cladistic use. Each triangle can provide a within-group allometric trajectory, the values of which form a hyperbolic metric (Bookstein, 1991).

The states of morphometric characters usually vary continuously and may require some interpretive coding for use in most algorithms used in phylogenetic reconstruction. Homogeneous subset coding and generalized gap coding are solutions to this problem provided by Archie (1985) and Goldman (1988). In principle, states of continuously varying characters need not be treated as coded homology-identities. Most current parsimony algorithms do not take continuously varying characters as input, but this constraint is not inherent in the parsimony method. In principle, multi-state characters may be subjected to Transformation Series Analysis (Mickevich, 1982) to optimize the distribution and order of their state transformations over the tree, although an algorithm is not
yet available. The most unconventional aspect of the use of continuous characters in estimating synapomorphies would be the use of continuously varying states as putative estimators of homology, with certain states becoming homology identities only after becoming cladistic characters in the sense of Mickevich (1982). Here, morphometric characters would be similar to molecular sequence characters in displaying relative homology. Morphological characters are less likely to provide satisfactory taxonomic distances, presumably because their tempo and mode of evolution is less clock-like (Fitch and Atchley, 1987; Patterson, 1987).

In cladistics, the character-state value must be accompanied by information about direction of evolution as well as similarity of character states. Morphometric methods currently do not distinguish plesiomorphic and synapomorphic information. Inclusion of outgroup taxa in the analysis, and designation of the direction of the character states to be away from outgroup values, may place the morphometric data in the directional context necessary for cladistic analysis. Optimization of the distribution of character states is accomplished by a function based, for example, on a parsimony criterion (Farris, 1983). Quantified ontogenetic information may also be used to indicate polarity and sequence among multiple character states (Creighton and Strauss, 1985; Strauss and Fuiman, 1985).

When a terminal ontogenetic character state is missing, morphometric and ontogenetic data are incapable of discriminating between loss due to truncation of development and absence due to plesiomorphy, except in the context of a cladistic hypothesis (Fink, 1982). The first step in solving this dilemma is assignment of a character-state code value by reference to outgroups (the larger hierarchy), when possible, or entering an agnostic code value into the data matrix when necessary. The next step is a cladistic analysis, which will provide a homology decision based on congruence with other characters (Hennig, 1966). In numerical phylogenetic analysis, all of the characters are used; they are not sorted by the systematist's prior evaluation of "good" and "bad" characters from other contexts. Good taxic homologies arise from numerical parsimony analysis, although these analyses almost always show reversed and potentially parallel characters among the taxic homologies—i.e., non-unique homologies little different from homoplasies play a role in diagnosis of monophyletic groups. However, prior selection of taxic homologies by their fit to "known" groups, with the discard of characters known to show some homoplasy, is not different from other methods of subjective prejudging. It is potentially circular.

**Phylogenetics.** Postcladistic character analysis is the use of morphometric methods to describe character variation and the direction and amount of evolution. This is usually approached by measuring the changes in size and shape differences among related lineages. Cladistic methods ignore random-walk fluctuations and amounts of evolution and are unable to control for secondary factors and effects of uncontrolled variables that affect processes driving groups of characters. One may use morphometrics and cladistics together to estimate the sequence of lineage branching and the patterns of responses among characters. Character correlations may be summarized and analyzed as consequences of genetic, developmental, functional, and ecological factors (Bookstein et al., 1985). Together, the cladistic tree and the morphometrically derived factors provide information about the relative timing, amounts, and directions of evolution. When the morphometric factors are examined in the context of ontogenetic or ecological hypotheses, we have a framework for investigating possible forces and constraints influencing evolutionary change.

Not only is a cladistic framework necessary for such an analysis (Fink, 1982), but the study must utilize a different data set to avoid methodological circularity (Ghiselin, 1966; Hull, 1967). For example, in a test of a hypothesis about the evolution of shape change through heterochrony, the shape/size trajectories would not be appropriate cladistic
characters. Biochemical data are sometimes available for estimating branching sequences, or at least branch distances. Distances may be useful indicators of taxonomic distance wherever biochemical divergence is consistent and monotonic (Sibley and Ahlquist, 1987). Morphological evolution is still an objective of such studies, however, and morphological data will continue to be necessary for cladistic tests. Once a cladistic frame of reference is established, morphometrically quantified data may be analyzed by regression, ANOVA, or factor analysis, etc., to provide information about how the morphological differences relate to ecological processes (Bookstein et al., 1985).

**Summary**

Homology is not a concept with theoretical predictive content about processes, but part of a method for classifying character-state identities in terms of their transformations in a hierarchy of monophyletic groups. (Homology of characters is not a conceptual problem unless the paradigm is something other than descent with modification, in which case homology is the central mystery to be divined.) The ultimate goal in evolutionary biology is to understand the history of change and the ecological, genetic, and ontogenetic processes by which change occurs. Progress toward this goal may not change the concept of homology, but it should be aided by effective application of methods based on it.

Operational homology is a character correspondence, among taxa, based on the optimal matching of internal and external landmarks on exemplars, samples, or developmental series of OTUs. It is usually a quantified construct within which landmarks, variables, and characters are oriented for comparison in systematic biology. In this context, morphometrics can provide quantitative values for character states.

Taxic homology is an identity relation that diagnoses a monophyletic group. By diagnosing monophyletic groups, taxic homologs provide evidence for hypothetical ancestral states and a historical context for tests of evolutionary hypotheses. The validity of a taxic homology is tested against homoplasy by congruence with other characters over a hierarchical tree.

Operational and taxic homology are often discussed as concepts that exclude each other's validity. But each definition refers to a necessary step in the process by which homologous characters are chosen, tested, and analyzed in studies of evolution. The circularity in each half of the dual concept is avoided by appropriate use of the other.

A transformational homology is the sequence of modified states of a character over the inferred course of descent from a common ancestor through a cladistic tree hypothesis. It is the basis for study of genetic, ontogenetic, and ecological processes in the context of phylogenetics.

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**References**


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