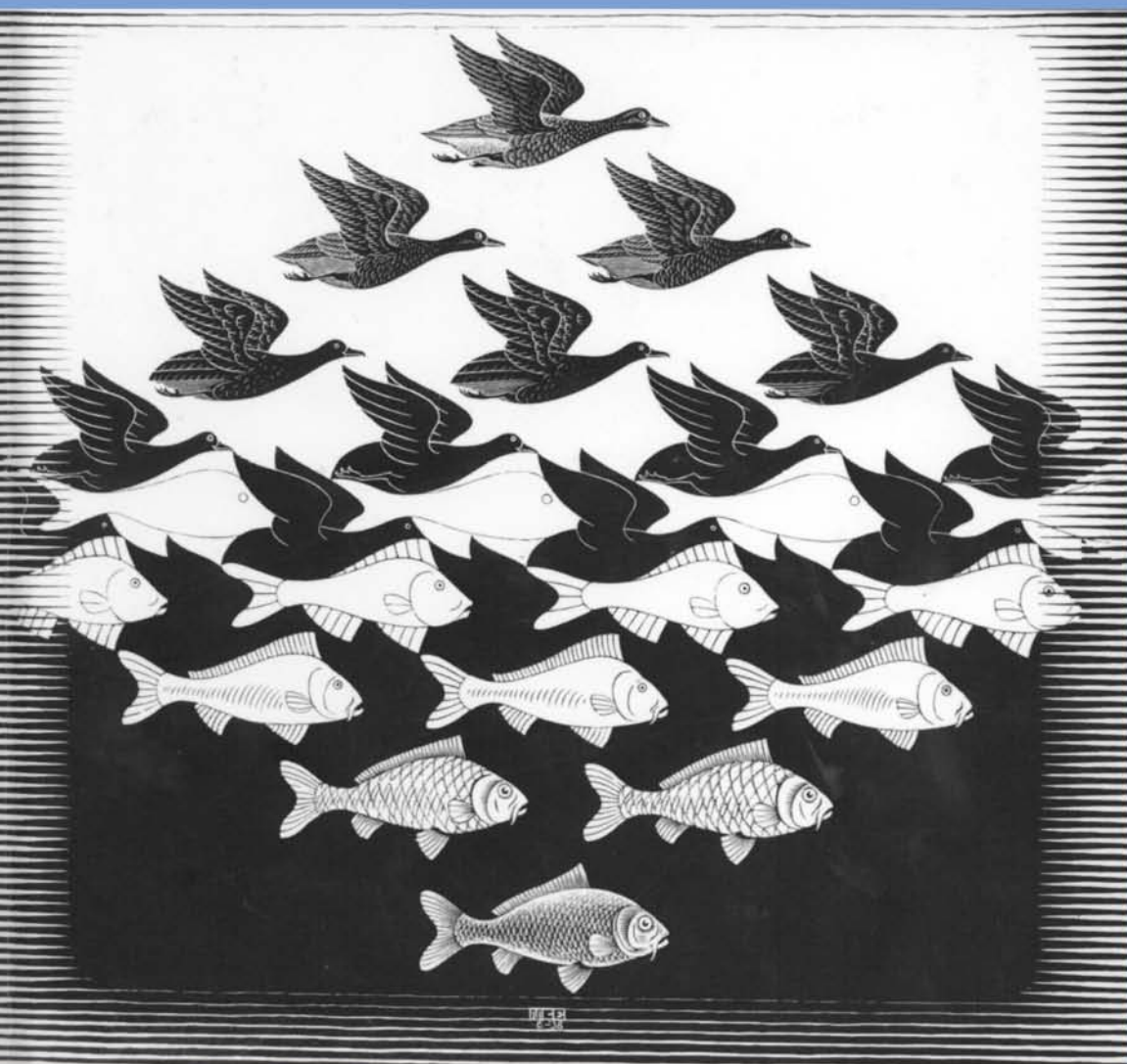


# Morphology, Shape and Phylogeny

Edited by Norman MacLeod and Peter L. Forey



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# Morphology, Shape and Phylogeny

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*Department of Zoology, The Natural History Museum,  
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Systematics Association Special Volume Series 64

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Edited by  
Norman MacLeod  
Peter L. Forey  
Department of Palaeontology  
The Natural History Museum  
London  
UK



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# Contributors

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**Fred L. Bookstein**, Center for Human Growth and Development, University of Michigan, Ann Arbor, Michigan 48109, USA.

**Theodore M. Cole III**, Department of Basic Medical Science, School of Medicine, University of Missouri, Kansas City, MO 64108, USA.

**Joseph Felsenstein**, Department of Genetics, University of Washington, Box 357360, Seattle, WA 98195-7360, USA.

**William L. Fink**, Department of Biology and Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, USA.

**Peter L. Forey**, Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK.

**Christopher John Humphries**, Department of Botany, The Natural History Museum, London SW7 5BD, UK.

**Subhash Lele**, Department of Mathematical Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada.

**Norman MacLeod**, Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK.

**Mark Pagel**, School of Animal and Microbial Sciences, University of Reading, Whiteknights, Reading, RG6 6AH, UK.

**P. David Polly**, Molecular and Cellular Biology Section, Division of Biomedical Sciences, Queen Mary and Westfield College, London E1 4NS, UK and The Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK.

**Andy Purvis**, Department of Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, UK.

**Todd C. Rae**, Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, 43 Old Elvet, Durham, DH1 3HN, UK, and Department of Mammalogy, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA.



**Geraldine Reid**, Department of Botany, The Natural History Museum, London SW7 5BD, UK.

**Joan T. Richtsmeier**, Department of Cell Biology and Anatomy, School of Medicine, The Johns Hopkins University, Baltimore, MD 21205, USA and Department of Anthropology, The Pennsylvania State University, University Park, PA 16802, USA.

**F. James Rohlf**, Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA.

**Karen Sidwell**, Department of Botany, The Natural History Museum, London SW7 5BD, UK.

**Donald L. Swiderski**, the Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, USA.

**Andrea J. Webster**, School of Animal and Microbial Sciences, The University of Reading, Whiteknights, P.O. Box 228, Reading RG6 6AJ, UK.

**Miriam L. Zelditch**, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109, USA.

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# Preface

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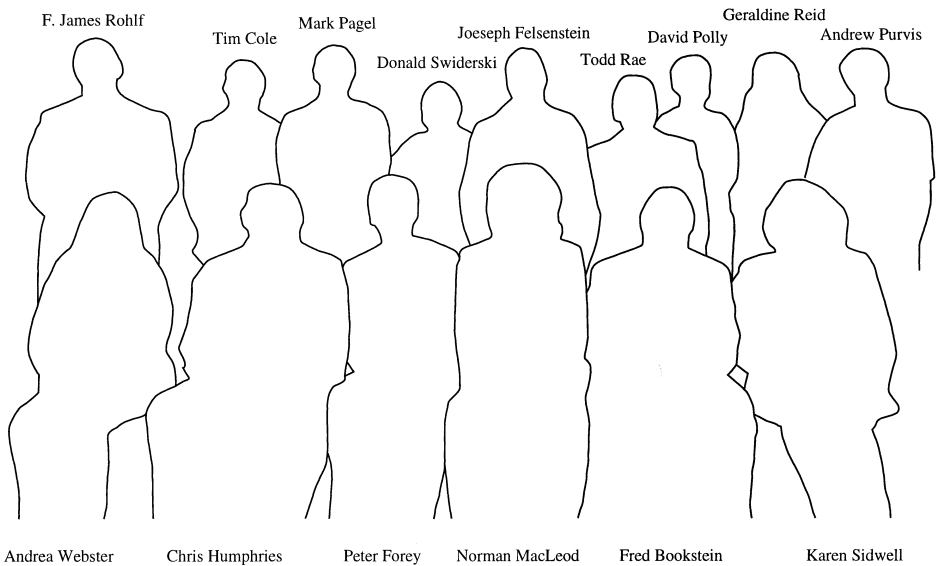
This book arises from a symposium 'Morphology, shape and phylogenetics' which formed part of the Second Biennial International Conference of the Systematics Association held at the University of Glasgow in August 1999. The aim of the Biennial conferences is to encourage discussion between many systematists who, although they specialise in specific taxonomic groups, confront common methodological and theoretical problems. The aim is to encourage younger scientists both to present their own work but also to become involved in broader systematic issues. As a catalyst these symposia bring together scientists with contrasting views.

This particular symposium, dedicated to the relationship between morphometrics and systematics, was stimulated by recent publications which have suggested ways in which morphometric data may be used in phylogenetic systematics as well as a synthesis of morphometric methods. The time seemed right for a compilation of ideas.

We would like to thank the Systematics Association, Dr Gordon Curry, University of Glasgow and his team of organisers who made the symposium possible.

Norman MacLeod and Peter L. Forey

The Natural History Museum, London, 2001



Speakers participating in the symposium 'Morphology, shape and phylogenetics' at the Second Biennial International Conference of the Systematics Association held the University of Glasgow in August 1999.

# Introduction: morphology, shape, and phylogenetics

*Norman MacLeod and Peter L. Forey*

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This book is about the ways in which the study of morphology can be used in phylogenetic analysis and how the results of phylogenetic analysis can provide meaning for the study of morphological variation. Through the text phylogeny is understood to be the organizing principle for all biological data. Even though variations in organismal form can be studied from non-phylogenetic points-of-view, it is generally acknowledged that such variations are not different in principle, from any other type of biological data and cannot be fully understood in the absence of the historical perspective provided by phylogeny. Similarly, phylogenetic analysis is impossible in the absence of some way of describing the morphological variation between individuals, populations, species, and higher taxa. Even molecular phylogenetic studies are dependent on morphological data in that the molecular samples are typically collected from specimens that have been identified as belonging to morphologically defined species on the basis of shared morphological attributes. Additionally, the molecules themselves have form manifested as secondary and tertiary molecular structure.

Morphological correspondences form the basis of phylogenetic reconstruction. However, modern methods of phylogenetic analysis treat morphological data in an inconsistent manner. For example, the coding conventions demanded by most parsimony-analysis algorithms require that morphological data be described as discrete characters and/or character states (e.g., spine: present, absent). While this descriptive convention works well for some discrete morphological attributes (e.g., tail red or tail blue), many of the morphological descriptors used routinely by phylogeneticists represent variables that, at least in principle, can adopt a range of values (e.g., height of tooth cusps, location of eyes, see Thiele 1993). Despite the fact that character and character state descriptions such as 'spine: short, long' imply precise metrical definitions of 'short' and 'long', such terms are often used in an ambiguous manner. Even more subtle are the descriptors of shape such as 'leaf shape: oval, round'. Just where in the context of any particular systematic comparison does 'round' stop and 'oval' begin? Most scientific papers using coding of morphological variation for phylogenetic analysis are vague or completely silent on this issue. Additionally, many meristic observations (e.g., counts of vertebrae or numbers of leaves per whorl) are variable within taxonomic groups. All of these data raise the question of coding observations in discrete ways for what are inherently variable observations. Some authors (e.g., Pimentel and Riggins 1987; Felsenstein 1988) have rejected outright the use of continuous variation in phylogenetic analysis. Other authors have suggested that state delimitation must necessarily be arbitrary and therefore such data are inappropriate for

phylogenetic analysis. However, a number of delimitation methods have been devised (Mickevich and Johnson 1976; Colless 1980; Almedia and Bisby 1984; Thorpe 1984; Archie 1985; Chappill 1989; Thiele 1993), and although each may have advantages and disadvantages, a simple rejection of such data, at the very least, deserves more discussion.

In another direction the techniques of geometric morphometrics are able to describe shapes accurately by using the language of mathematical geometry and can potentially have a significant input to the theory, as well as to the practice or morphological characterization. If we are able to describe shape more accurately there may be more potential sources of morphological variation available for analysis. However, there is a general issue of the suitability of using such variables which takes us to the heart of evolutionary and phylogenetic theories – the concept of homology.

Phylogenetic homology is the most important unifying principle in biology (Bock 1973) and is probably the subject most written about within the biological literature. In phylogenetic systematics homology is equated with synapomorphy (Patterson 1982). This means that propositions of homology are theories to be tested rather than self-evident truths to be acknowledged or assumed. In order to propose a theory of homology an initial postulate of identity is followed by testing (the tests applied are conjunction – meaning that no two presumed homologues can occur simultaneously in the same organism – and congruence with other postulated homologies). The initial postulate of morphological identity is sometimes called primary homology (de Pinna 1991) and consists of two activities: identifying that structures are similar in composition and topological relationships and coding the similarity for phylogenetic analysis (see Hawkins 2000 for discussion). As an example consider the wing of a bird and a bat. These structures share a similar composition (bone) and topological relationships with, for instance, the shoulder girdle. The presence of a wing would be congruent with other characters such as warm-bloodedness and the presence of amniotic membranes. However, the wing of a bird and a wing of a bat would be non-homologous in a phylogenetic sense because, despite being compositionally and topographically the same, the wing of a bat is not congruent with the many other character-state distributions (e.g., fur, mammary glands, three-ear ossicles) suggesting that bats are more closely related to animals without wings (e.g., tree shrews and primates). The important aspect of this concept of homology relevant to the subject of this book is that there is an initial proposition of structural identity.

The concept of homology in geometry (and by extension, in morphometrics) is somewhat different since, there is no initial estimation of primary homology and no tests of conjunction and congruence are applied. Standard morphometrics would recognize potential homology between the dorsal fin of a salmon, an ichthyosaur, and a killer whale as homology of shape (triangular) and position (centrally located along the dorsal surface) while ignoring the fact that these structures had arisen quite independently in the phylogenetic history of these lineages as evidenced by the state distributions of other characters. Therefore, the extension of structure-level concept of homology in phylogenetic analysis to the geometrical point-to-point correspondences typical of many morphometric data sets raises several difficult – and therefore interesting – problems. In many morphometric shape studies it is descriptions of curvature, angularity, ratios, etc. that are being assessed and compared such that it is difficult to see how a particular angle formed by or ratio of parts (e.g., 1.543) can be regarded as being

homologous. As pointed out by Zelditch *et al.* (2000: 80) “morphometric variables are not, in and of themselves, equivalent to characters”. There would seem to be a preliminary hypothesis of analysis necessary so that shapes of homologous structures are being compared. In some morphometric analysis form is described with reference to landmarks without any justification that the landmarks are homologous in the sense used above. However, if those landmarks are chosen respecting the concept of homology used in phylogenetic systematics there may be much more that we can learn from the morphometric study of form.

Many of the problems systematists have encountered in the efforts to use morphological data in phylogenetic contexts derive from the nature and descriptive complexity of those data. Organisms exhibit a bewildering array of structures that are often very difficult to abstract meaningfully into the scalar values (e.g., lengths, widths, breadths, and depths) of traditional systematic measurement systems. In addition, geometric concepts such as size and shape (not to mention shape translations) have proven to be more complex – and to require more complex descriptive-analysis tools – than had been widely appreciated. But, recent advances in morphometrics have, at least partially, addressed this descriptive problem. To some extent these advances have been possible because of recent dialogues within the morphometrics community (e.g., Marcus *et al.* 1993, 1996).

Geometric morphometrics represents a quantitative synthesis of two themes that have dominated the study of form for well over a century (Bookstein 1993). The older of these can be traced from the Renaissance studies of form by Leonardo da Vinci, Albrecht Dürer, Michelangelo, and others through its introduction into the modern scientific literature by D’Arcy Thompson (1917). This theme visualizes morphological change as a smooth mapping transformation between the starting and ending forms of implicit form classes. Thompson was intrigued particularly by the manner in which geometrically simple deformation patterns could combine with existing organic geometries to produce seemingly complex results. In order to give graphical expression to the underlying simplicity of the deformation pattern Thompson employed a Cartesian grid system in which the intersections of the grid lines were taken to represent corresponding or ‘landmark’ points on both the starting and final forms. Although Thompson’s ‘transformation-grid’ approach to shape characterization intrigued generations of morphologists and geometers, his invention proved stubbornly resistant to precise quantitative formulation. Biological acceptance of such transformationist notions were also not helped by Thompson’s own goal of using transformation grids to demonstrate that interspecific variation obeyed law-like rules reflecting the predominance of physical forces in the creation of morphological novelty.

The second theme united by the morphometric synthesis grew out of Francis Galton’s biometric ‘regression analysis’ by way of the distinction between the truly linear aspect of patterning between a pair of morphometric variables (quantified in terms of their covariance or correlation) and the non-linear aspect of their patterning (quantified in terms of the residual scatter about a linear regression line). Galton’s original insight was expanded into what has now come to be known as the generalized linear model which includes bivariate/multiple regression analysis, component/factor analysis, discriminant/canonical variates analysis, canonical correlation analysis and path analysis). From this beginning, attention came to focus on the abstraction of synthetic linear components from covariance or correlation matrices that can be thought of as vectors

existing within a multidimensional space defined by the original variables. In the more extreme forms of this research program these synthetic vectors – and not the original variables – came to be regarded by some as being closer to ‘true’ observations. In terms of morphological analyses though, the problem with this approach was that these methods in their original formulation failed to preserve the inherently geometric nature of the data and failed to support techniques, whereby the analytic results could be expressed in terms of the original geometries.

The geometric morphometric synthesis combines these two established themes in quantitative morphological analysis by, (1) focusing on the representation of landmark configurations (= geometries) as variables, (2) registering geometric data collected from actual specimens to remove size and orientation differences. This operation effectively projects these data onto the surface of a  $k-3$  dimensional hypersphere (where  $k$  = number of landmarks) with the inter-specimen distance representing the great circle distances between all pairs of taxa, and (3) formalizing Thompson’s transformationist approach through the use of an algorithmic-graphical device known as the ‘thin-plate spline’. Discussions detailing various methods included within the geometric synthesis and examples of applications can be found in various publications (e.g., Rohlf and Bookstein 1990; Bookstein 1991; Reyment 1991; Marcus *et al.* 1993; Marcus *et al.* 1996) as well as herein. At present, these methods represent a very large and somewhat abstract body of largely theoretical work whose practical application to the understanding of morphological variation, the creation of morphological novelty, and covariances between form and a variety of non-geometric covariates has yet to be explored in detail. What is clear, however, is that these tools can detect, represent, and describe morphologies in ways that are analytically superior to all previous methods. Their existence, at the very least, provides systematists with an opportunity to revisit a number of long-standing issues regarding the employment and interpretation of morphological data in systematic contexts and the relation of these to phylogenetic studies.

During the past 15 years the morphometrics community has been as slow to embrace, explore, and exploit the phylogenetic aspects of their data (e.g., through various ‘comparative method’ strategies, see Harvey and Pagel 1991), as mainstream phylogeneticists have been slow to embrace, explore, and exploit the new geometric approaches to morphological analysis. Fortunately, however, there are signs of a rapprochement between phylogenetic systematics and morphometrics. Some systematists have begun to re-evaluate their traditional phylogenetic-systematic taboos regarding the use of continuously-distributed variables (e.g., Zelditch *et al.* 1995; Rae 1998) while others have begun to explore methods whereby phylogenetic information can be included in morphometric studies (MacLeod 2001). This book represents an attempt to further this dialogue by undertaking a comprehensive exploration of the relationship between continuously-distributed morphological (morphometric) variables and phylogenetic. In particular the essays contained herein focus on four fundamental questions.

1. Can continuously-distributed variables (of any type) be used in phylogenetic inference?
2. Can morphometric variables be used to constrain and/or test phylogenetic hypotheses?

3. What strategies are available for taking advantage of morphometric information within the context of a phylogenetic analysis?
4. What strategies are available for taking advantage of phylogenetic information within the context of a morphometric analysis?

The authors represent a cross-section of phylogenetic systematists, morphometricians, and comparative-method specialists with a collective expertise that encompasses a wide spread of biological subdisciplines. Above all, these are biologists who have thought deeply and creatively about the relation between morphology and phylogeny. While they would not be expected to agree entirely with one another's positions on a variety of controversial practical and methodological issues, they are united in their belief that the phylogenetic treatment of morphological data represents a frontier of systematic research whose time has come and that promises to yield important new insights into the questions of the origin, patterning, and maintenance of organic morphological diversity that have always stood at the heart of biological systematics.

Christopher J. Humphries leads off with a re-evaluation of the homology problem in the context of morphological and especially morphometric characters. The concept of a character in phylogenetic analysis is intimately tied to a concept of homology, which in turn is a theory based on constant and repeatable observation. How this relates to the data used in morphometric analysis is discussed to set the scene for later essays.

Joseph Felsenstein continues the discussion of quantitative characters and their use in phylogenetic systematics by considering the question of whether it is necessary – or even desirable – to transform such characters into discrete states. Felsenstein asks difficult questions about the current state of our knowledge of the genetic, developmental, and functional aspects of morphology and suggests possible ways for future collaborations between morphometrics and these disciplines.

Todd Rae points out that complete harmony between morphometric analysis and phylogenetic analysis may not be possible since the aims are different. However, he suggests that there may be areas of overlap in measurement data and that metric data can be used in phylogenetic analysis as characters as long as due caution is exercised.

Karen Sidwell and Geraldine Reid deal specifically with the different ways in which continuously variable characters have been coded as discrete integers prior to phylogenetic analysis. They point out that different ways of coding lead to different descriptions and different sensitivity to reflecting the variation in the original observations. But more importantly, they demonstrate that some of the methods used to assign codes to continuous variables may be forcing us to recognize differences, and hence different codes for phylogenetic analysis, than are truly there.

Donald Swiderski, Miriam Zelditch, William Fink open the discussion of how morphometric data can be used to recognize phylogenetically meaningful characters by reviewing a variety of morphometric methods and asking the question of whether the variables produced by these methods conform to the concepts of correspondence and homology. In the context of this review these authors offer an alternative strategy for characterizing inter-landmark boundary curves in a manner consistent with the needs of phylogenetic systematics.

Norman MacLeod focuses on the use of landmark-based morphometric summaries and their specific relationship to the concepts of spatial localization, biological



homology, and the character coding problem. In a series of examples MacLeod demonstrates a variety of ways landmark-based morphometric strategies can successfully contribute the analysis of morphology in phylogenetic contexts, culminating in a reconsideration of Naylor's (1996) simulated fish morphology dataset.

Fred L. Bookstein closes this subsection with the first presentation of a new method for the analysis of spatially localized shape deformations that may be of use in discovering and describing new phylogenetic characters and character states. Since the discovery of new morphological characters has long been recognized as a principle advantage of the metrical description of morphology, this new class of morphometrically defined features – called creases – holds great potential for helping to fulfil the potential of morphometrics in systematic and phylogenetic analyses.

F. James Rohlf's contribution initiates a subsection of essays dealing with the mechanics of combining phylogenies with morphometric descriptions of shapes to model the morphological aspects of evolutionary processes (e.g., ancestral character state estimation). Rohlf's method employs the squared-change parsimony estimation criterion and results in a series of deformation-based shape change models that can be used to illustrate shape change as a continuously variable parameter along any phylogenetic tree.

David Polly continues this discussion by considering the question of how best to assess the divergence times among taxa that are crucial to ancestral character state estimation. Using an example dataset drawn from fossil carnivorans Polly employs a combination of phylogenetic and stratigraphical data to determine an expected per generation rate of shape divergence to which actual shape divergence estimates can be compared. Results of these types of comparisons will allow systematists to use phylogenetically-referenced morphological data to quantitatively test a variety of functional and developmental hypotheses.

Andrea Webster and Andrew Purvis continue this theme of using given phylogenies to estimate ancestral character states for continuous characters and from these deducing rates of evolution. Their chapter emphasizes that the results of different methods which have been used to infer ancestral states for continuous characters are inherently dependent upon the assumptions of the model of evolution and do not always correspond to states observable in fossils. These discussions have implications for the way in which we infer ancestral states in general.

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# Homology, characters and continuous variables

*Christopher John Humphries*

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### ABSTRACT

Owen (1849) coined ‘homology’ to describe relationships between organisms, using corresponding morphological parts (homologues) of vertebrate skeletons. Since that time it has been recognised that homology is the central relation in comparative biology. Relationships of taxa are recognised through homologues that are discovered through analysis of characters. Characters have been described for myriad purposes – operationally as entities diagnostic of taxa, as identifying attributes of organisms, as transformation series in evolution and as taxic homologues. Characters come from many sources and the debate on what constitutes a ‘good’ character lies on a scale of preferences from clear-cut qualitative morphology to continuous variables (measurements, ratios, counts) that need to be manipulated with a range of special coding procedures to extract cladistic signal. It will be shown that, for measurement data, characters are described in terms of positional correspondence of parts between internal or external points. In evolution and phylogenetic systematics, homologues are described as transforming relations from unknown common ancestors. In cladistics, characters are seen as hypotheses of taxic homology subject to the tests of similarity, conjunction and congruence. It will be proposed that the recognition of primary homologues is possible for discrete variables and operationally defined states derived by gap-coding methods applied to continuous or overlapping variables. However, because continuous or overlapping variables are transformation series equivalent to manipulated range data, the lack of theory for the coding methods and the need for prior assumptions makes it difficult to find cladistic structure in measurement characters.

### Introduction

The term ‘homology’ was first used to describe relationships between organisms, with particular reference to corresponding morphological parts (homologues) of vertebrate skeletons (Owen 1843, 1849). After 150 years of debate it is recognised today that homology is neither an empirical problem, nor a theoretical one, but the central relation in comparative biology. Acres of print have been written on the subject of homology. In the last 10 years there has been considerable discussion of how to deal with characters and particularly how one determines homologies through character analysis. A recent re-consideration of morphometric data, and the purpose of this book, explores what characters, character states, continuous variables, transformation

and homology mean in systematics and morphometrics. On top of all this are the different points of view as to which phylogenetic and cladistic methods are actually appropriate in systematics. These distinctions are critical as the debate revolves around what is meant by character transformation and how this is seen in our understanding of homology.

The problems of characters and character analysis are not new but stretch back at least two centuries (Rieppel 1988). However, the use of continuous variables and morphometrics has its origins amongst the ideal morphologists at the turn of the twentieth century. Irrespective of this history, the use of morphometrics in systematic contexts has undergone a clear revival over the last 10 years or so. Indeed, it has come full circle from being considered of little or no use in cladistics (Pimentel and Riggins 1987; Cranston and Humphries 1988; Farris 1990), to being apposite for the discovery of natural groups (e.g., Fink and Zelditch 1995; Zelditch *et al.* 1995, 2000; Swiderski *et al.* 1998; MacLeod 1999, 2002, in press). My purpose is to review these differences of opinions in the light of recent studies from the perspective of an unreconstructed cladist interested in morphological characters.

## Homology

Homology refers to the property of topological relations between different organisms. Owen (1849) distinguished homology from analogy, the latter interpreted as meaning something different in terms of relations, comparability of function, for example. As pointed out by David Williams (person. comm.) it is not only possible for comparable organs to be homologous and analogous, but also to be homologous and not analogous, or even analogous and not homologous. Wings in birds and forelimbs in hoofed mammals are clearly homologous in form but not analogous in function. Owen was quite clear on the subject of this distinction. This impinges on the great 1830 debate between Cuvier and Geoffroy St. Hilaire, that concluded animals were all based on the same fundamental 'ground' plan. Owen used St. Hilaire's 'principle of connections' to describe the similarities and subtle differences of form and the 'principle of composition' to describe the topographical relations of organs, the two combining as the basic properties of homology (Brady 1985; Rieppel 1988; Schuh 2000).

As Brady (1994) pointed out, Geoffroy St. Hilaire had already emphasised the importance of homology in the mid-nineteenth century when he drew connections between similar organs of animals; for example, when comparing the paddle of a porpoise, the hand of man and the foot of a horse. As Brady discusses, Darwin, when commenting on Geoffroy's insight, noted it was possible to shift from figurative into a historical explanation by connecting together those forms more closely related to each other by comparison to other organisms. Different organs have changed into many forms of varying shape and size. Yet the main body organs, although showing some differences, always remained in the same order, such as the relative positions of forelimbs in tetrapods, whether frogs, birds, bats or shrews. Such was the realisation of constancy of topological position. The concept of sameness and difference has been the centrepiece of homology debates ever since (Patterson 1982).

Explanation, according to most accounts, is the real task of science and description is just one procedure to achieve this end. Darwin (1859) gave great emphasis to

explanation, and argued in the *Origin of Species* that patterns of morphology and classification await explanation, implying that both are descriptive activities. Darwin never gives account of the science that produces these patterns, but his assumption that taxonomic relations are discovered prior to the inception of explanation remains an interesting one (Brady 1994). Darwin used natural selection by successive gradual changes to explain that the different forms changed or transformed from an ancestral archetype into the visible structures that we see in modern organisms. Consequently, Darwin changed Geoffroy's philosophical relations of corresponding parts into historically literal or actual transformations. For example, limbs of crabs turned into jaws and stamens and pistils were derived from leaves. All transformations were gradual transitions from one form into another. When there were no intermediate forms between real ones, he imagined them (Brady 1994). From this it follows, as Brower (2000) points out, that modern concepts of homology are all manifestations of our conviction that there is a single natural system that explains all of biodiversity. It follows, too, that homology is considered as similar due to common ancestry because the natural system can be explained by evolution by common descent.

Consequently, the correspondence of parts between one organism and another is the establishment of a hypothesis to suggest that particular characters belong to a phylogenetic transformation series from one taxon to another or between modern organisms and their common ancestors (Hennig 1966). However, Nelson (1994) has shown that modern cladists never treat species, Recent or fossil, as ancestors and descendants of one another, but rather as taxa, characters, or character states at the terminals of a cladogram. In systematic research one determines correspondences between organisms through correspondence of their characters. Woodger (in Cain and Harrison 1958) noted that; '[i]n comparing two things we set up a one-to-one relation or correspondence between the parts of the one and those of the other and proceed to state how corresponding parts resemble or differ from one another with respect to certain sets of properties'. Remane (1952) elaborated the procedure and stated that homology is recognised only through the relative position or organs and tissues, similarity of special structures and connections by intermediate taxa (see Schuh 2000). Remane suggested, therefore, that the relationships of taxa are recognised through homologues that are discovered through analysis of characters.

According to Brady (1985) Remane's viewpoint was empirical because it distinguished between the condition to be explained, similarity of structure, from the explanation, the theory of evolution. This was a critical observation because it demonstrated that empirical work on characters and taxa must precede interpretation, and reference to unknown ancestors is interpretation of that pattern. However, Hennig (1966) had already criticised Remane's approach. Hennig (1966: 94) stated of Remane that 'the criterion of linkage of intermediate forms' and the 'criterion of special quality of the structures' are accessory criteria to the 'criterion of sameness of position in comparable fabric systems', an observation that turns out to be more or less identical to Woodger's set theory approach.

In developing his principles of phylogenetic systematics, Hennig (1966: 93) noted that 'different characters that are regarded as transformation stages of the same original character are generally called homologous'. He made it clear that that transformation 'refers to real historical processes of evolution' and not from deriving one character from another in the sense of ideal morphology. Rather cladograms were hypothesised to be artificial constructs, with hypothetical ancestors at the internal nodes, which

Patterson (1982) likened to archetypes in transformational homology and morphotypes if viewed taxically (see below). Hennig thus fleshed out the Darwinian notion of historical transformation, but was absolutely clear that, as one is never in a position to observe phylogenetic transformation, the question arises as to what criteria could convince one that transformation series are comprised of homologues. Hennig (1966: 93–94) stated that ‘[a]pparently it is often forgotten that the impossibility of determining directly the essential criterion of homologous characters – their phylogenetic derivation from one and the same previous condition – is meaningless for defining the concept of “homology”’. Thus, he went on to describe a range of auxiliary criteria, of geological character precedence, chronological progression and ontogenetic character precedence as independent means to establish potential synapomorphies.

Hennig’s auxiliary criteria have since all been rejected (see Wiley 1981). But critically, Hennig changed the concept of homology to allow for losses as well as gains to be used in phylogenetic systematics. He realised that genealogy implied similarity, but the reciprocal was not necessarily true. Similarity could be misleading owing to parallel and convergent changes. He thus coupled particular kinds of similarity with particular kinds of groups.

As any student of systematics will know, Hennig used synapomorphy to diagnose monophyletic groups, parallel and convergent changes gave rise to polyphyletic groups and grouping on symplesiomorphies rendered paraphyly. Allowing for losses as well as originations in characters meant that transformation series could equally be the reduction of organs as to their gain. The rejection of Hennig’s auxiliary criteria, and the realisation that theories of characters (synapomorphies) gave theories about groups (monophyly), Patterson (1982, 1988) equated synapomorphy with homology, a viewpoint that has been held by many since (Janvier 1984; Stevens 1984; de Pinna 1991; Panchen 1994; Nelson 1994; Brower 2000). The implication of such a viewpoint is that homology is discovered through analysis of characters and does not impinge *a priori*. If then, character analysis – the discovery of homologues – is an empirical procedure discovered by comparing similar organs, but synapomorphies are evidence of homology as a relation and thus monophyletic groups, it follows that homology is both part of character analysis and cladistic analysis.

Rieppel (1988) started to resolve the issue of primary homology by suggesting that one could apply tests of similarity to discover whether homologues could be erected as hypotheses with similar topological correspondence before cladistic analysis and a ‘test’ of congruence.<sup>1</sup> De Pinna (1991) further resolved Rieppel’s ‘relation of homologous similarity (synapomorphy)’ by distinguishing between primary and

1 However, it must be borne in mind that it could be possible for a morphological transformation between two non-homologous characteristics (e.g., character states that were incorrectly ascribed to the same character [= transformation series]) to be consistent with a cladogram. We are not so bound by Patterson’s (1982) logic to consider that any transformation between any set of morphological descriptors must be accepted as homologous so long as it is congruent with the majority of other characteristics. It is especially true that Type 1 and Type 2 statistical errors can occur and this is worrying. For example, Zelditch *et al.* (1995) consider that partial warps are homologous characters, it seems, based on the proposition that, so long as partial-warp ordinations are consistent with an established cladogram they must be homologues. However, independent work since then has shown that, when evaluated on their own, partial warps do not behave like the morphological characters traditional systematists use. Partial warps are prone to homoplasy, and different studies have shown that morphometric characters were not able to reconstruct a credible phylogeny if used in the absence of traditional, qualitative characters (MacLeod person. comm.).

secondary homology. Primary homology is the discovery of characters and character formulation, literally the generation of new characters through thorough sampling of taxa. Secondary homology equates with the discovery of synapomorphy, through collective cladistic analysis of primary homologues, the so-called legitimisation phase of homologous similarity. Brower and Shawaroch (1996) after comparing morphological and molecular data suggested that primary homology assessment in itself is a two-step process, the determination of topographic identity followed by character state identity. Operationally, this comprises first the recognition of characters and then scoring of the characters into a matrix for further analysis (e.g., Hawkins 2000). The final outcome is that synapomorphies are distinguished from homoplasy and symplesiomorphy as interpretations on rooted trees after one or more rounds of cladistic analysis (Brower 2000). Cladograms are chosen in terms of best fit through optimisation of characters and thus the primary homology statements (similarity and topographic alignment) are 'tested' by showing the greatest congruence with other characters (Patterson 1982). Congruent characters are generally considered as homologues associated with monophyletic groups and incongruent characters, or homoplasies, are associated with paraphyletic and polyphyletic groups.

The shared presence of homologues is the basis for recognising monophyletic groups (Patterson 1982). Shared presence of a homologue between two or more taxa is thus the only evidence we have of relationship, that the taxa form a group, taxic homology. The shared presence of homologues is indicated by a qualifying phrase, such that all vertebrates share vertebrae as distinct from those organisms that lack vertebrae. For a character to become an established homology the feature in question must also occur in the same topographical position within the organisms being compared. Rieppel (1988) states that the relative positions of organs or structures in topographical correspondence are essential conceptually, to initially generate primary homology propositions. This is true for all organisms it seems. In addition to the tetrapod example given above, in flowering plants bisexual flowers invariably display the same sequence of whorls from the outside to the centre of the flower, sepals, petals, stamens and ovules, whatever myriad modifications might occur amongst them.

Homologising the features of topographical correspondence then becomes the basis for hypotheses of groups. Patterson (1982) called this taxic homology which he contrasted sharply from transformational homology. The crucial point about the transformational approach is perhaps indicated using a binary character. Given two states, 0 and 1, only one, but not both, but either at any one time can be a synapomorphy in a rooted tree (Farris *et al.* 1970). Brower (2000: 13) summarised succinctly the potency of such an approach: 'While evolutionary systematists (and Hennig) had no method to realise their phylogenetic theories, and pheneticists had no theory to discriminate among the many possible methods of grouping based on similarity, cladists, particularly pattern cladists who saw fit to separate and discard the metaphysical husk of common ancestry, were able to compare the advantages of both, using the method of grouping by parsimonious patterns of shared character state change.'

As Scotland (2000) noted, in cladistics the taxic approach is concerned with the monophyly of groups. The transformational approach is concerned with change. Patterson (1982) first described taxic homology to imply hierarchy of groups, when he recognised that transformational homology does not necessarily. Using the same two-state example, 0 means absence and the 1s become the only candidates for

synapomorphy on a rooted tree. Transformational homology (for example as in an ordered multistate character) seems to be a complex interplay between topological correspondence and literal transformation through metamorphosis, a concept that need not imply hierarchy at all. It is this aspect that raises problems for the use of continuous variables in systematics. As described by Patterson (1982) in Owen's conception, general homologies between organisms are the result of transformations from an archetype. Patterson went on to show that such an interpretation does not lead to new insights in grouping, but goes more to provide an empty hypothesis of difference between a modern form and an ancestor. Taxic homologies on the other hand are considered to be those characters that diagnose groups relative to other organisms. Transformation from one character to another might be implied, but the important distinction is that the grouping characters form the morphotype or list of homologues of a group. Morphotypes imply definite hierarchies of relationships and can be interpreted to equate with the internal nodes of cladograms.

## Characters

To be of use in systematics, characters have to be extracted from a mass of observational data and turned into matrices of consistent scores for further analysis. There are various procedures for the determination of primary homologues and the range of methods for coding has many choices (e.g., Forey and Kitching 2000; Wiens 2000). There is considerable debate about how characters and character states might be defined. As Brower (2000) noted, the process of sampling organisms for characters is still largely an intuitive process done in the same way now as hundreds of years ago. Attempts at quantifying the approach is still fraught with difficulties largely because two or more systematists rarely look at organisms and score characters in the same way (Gift and Stevens 1997). Nevertheless, it is generally agreed amongst biologists that a character is any feature or attribute that is shared among organisms that has the potential for becoming synapomorphies after cladistic analysis (e.g., Colless 1985; Fristrup 1992; Scotland and Pennington 2000). For characters or character states to be cladistic and hence be features of taxa, they ideally would be invariant in some taxa and completely absent in others. However, this is rarely the case. Characters and character states must be extracted from observations on the sampled organisms and summarised into a data matrix that (hopefully) contains some pattern reflecting relationships among the taxa that can be discovered via appropriate analysis. For most computerised cladistic analyses characters are arranged into binary and multistate columns with each integer representing a different state. For multistate characters each column represents a transformation series of dependent variables that can be ordered (in the sense of Mickevich 1982) or unordered during cladistic analysis.

There has always been a tension between the notion of defining characters in order to identify and distinguish organisms and the discovery of homologies in comparative biology to systematise the relations among organisms. Smith (1994: 37), for example, stated that '[c]haracters are observed variations which provide diagnostic features for differentiation amongst taxa'. He showed that characters must occur in two or more



states (one of which may be absence<sup>2</sup>) and they should be defined as objectively as possible (see also Mayr *et al.* 1953; Cain and Harrison 1958; Stuessy 1990). Features that are relatively indistinguishable from one another are generally coded as the same character state so as to reflect the underlying notion of primary homology.

Wiley (1981: 116) stated that: 'A character is a feature of an organism which is the product of an ontogenetic or cytogenetic sequence of previously existing features, or a feature of a previously existing parental organism(s). Such features arise in evolution by the modification of previously existing ontogenetic or cytogenetic or molecular sequence.' Such a definition recognised that features of organisms are the products of evolution and hence have arisen as changes in ontogeny and transformation through time. Pimentel and Riggins (1987) stated that a character can only be a feature of an organism when it can be recognised as a distinct variable. For cladistic analysis, Farris *et al.* (1970) made it clear that, in order to be able to determine characters for phylogenetic reconstruction, it was necessary to recognise that they were mutually exclusive states that could be considered transformations with a fixed order of evolution. Hennig's interpretations of characters and transformation series was refined by Farris *et al.* (1970) so that characters have a 'fixed order of evolution', 'each state is derived from another state' and 'there is a unique state from which the every other is ultimately derived'.

Jardine (1969) considered diagnosing taxa and describing individual organisms using the same character to be a confusing process. He said that the presence of a backbone is not a property of Vertebrata, but all of the organisms within the group Vertebrata possess backbones. Jardine made the distinction between taxa and organisms on the basis of characters and character states. Taxa have characters and organisms have individual attributes or character states.

For phylogenetic systematists, characters to convey cladistic information must transform from one state into another through time. However, this does not mean that a brown eye changes into a blue eye or that ovate leaves change into obovate leaves. Similarly, invertebrate animals lacking backbones do not change into those possessing them. What actually changes is the frequency of a particular character state for a given character and the frequencies of different character states change through time. Thiele (1993) stated that cladistic character states are frequency distributions and conversely, all cladistic character states have particular frequencies of distribution. Thus, desirable cladistic characters are those with large, clear-cut changes rather than small, gradual ones and a 'good cladistic character' is, in effect, a value judgement on data.

As Stevens (2000: 82) noted: 'a character is the sum of features showing particular similarities (e.g., Patterson 1982; Stevens, 1984), topographical homologies (Jardine 1969), topographical identities (Brower and Schawaroch 1996), or relationships of primary homology (e.g., de Pinna 1991)'. Stevens (2000) elaborated on the scheme proposed by Brower and Schawaroch (1996) and suggested that the stages between the beginning of a study on a particular group through to the cladistic analysis comprised a sequence of at least three operations between choosing characters and delimiting states.

2 The arguments against using absence are compelling (e.g., Nixon and Carpenter 1993). Using absence as a state confuses the obvious differences between genuinely absent, not yet developed and secondary loss. Therefore, absence as a state is logically flawed, except in the case of 'not present'.

The first stage was the lining up of characters thought to be the same (similarity or topographic identity). The second stage involved the actual measurement of individuals (which he called data 1) and grouping the measurements in some way for the taxa to be analysed (data 2). Finally the third stage compared all the measurements between taxa to create the data matrix (data 3). All three stages offer opportunities for making errors largely because there are so many different ways of undertaking them. Gift and Stevens (1997) had noted that even the first stage of delimiting similarities gave as many different solutions as recorders collecting the data. Patterson and Johnson (1977) also brought attention to this problem. In a pungent criticism Patterson and Johnson (1977: 361) noted that 'the emphasis has shifted from observation, the source of the matrix, to whatever message can be extracted from the matrix ...'. In a reanalysis of the characters of osmeroid fish an 11 per cent error rate in the original observations and subsequent coding of the errors had immense consequences for the topologies obtained by cladistic analysis. The third stage is highly significant. As indicated already the ideal character states for cladistics are those that have distinct gaps. However, when it comes to coding measurement data it appears that the methods are frequently operationally less clear-cut than those for qualitative variables (see Farris 1990 for example).

## Continuous variables

Considering that there are a number of ways for determining and coding qualitative characters the question arises of whether continuous and non-continuous characters and overlapping and non-overlapping distributions of observations along the variable axes can actually yield cladistic characters given the requirements of synapomorphy and secondary homology. Variables are observed variations of some attribute or characteristic feature, ergo characters = variables. The three-step procedure of Stevens becomes complicated when applied to overlapping distributions on variable axes. The first stage of determining the similarities or topographical identities involves the fixing of points for determining geometric locations on the organisms concerned. The second stage involves the actual collection of observations (= measurements) of the variables to obtain distributions on which to apply a comparative method. Comparisons between the organisms use methods for distinguishing geometric transformations. There are a variety of methods, but they all make a general scheme of size, shape or meristic values. The third stage is the different morphs (recognised on the basis of observed discontinuities in the distribution of observations along the variable axis) are then coded into a taxon  $\times$  character matrix for cladistic analysis. If reproducible ways can be found to recognise discontinuities in the distribution of the observations along the variable/character axes those discontinuities can be used to delimit different states. Provided discontinuities in the distribution of observations are present, quantitative character analysis proceeds in a manner identical to qualitative character analysis. However, if no discontinuities in the distribution of observations along a quantitative variable axis are found, the third stage of this process cannot be completed and the quantitative variable must be regarded as unsuitable for inclusion in a cladistic investigation. Under these circumstances the variable/character cannot be used for diagnosing a group.

## Primary homology and topographical identity

Determination of topographic identity of continuous variables in things such as the shape of jaws or length/width ratios of leaves is complicated by a number of factors: complexities of shape, allometric change during ontogeny and sheer variation that superficially appears to render unique values for every specimen under consideration. This is not saying that qualitative variables are any less problematic, just that detailed variation such as measurements become inherently less easy to divide into gaps. The problem of ontogeny is fundamental to all methods and Hennig (1966) was careful to point out that because individuals change throughout the life cycle the same stages or semaphoronts had to be compared. For different stages of an insect's life cycle semaphoronts are possibly easily identified but for subtle changes in measurement data defining semaphoronts becomes a more difficult problem. Løvtrup (1988) was at pains to point out that allometric trajectories (especially after birth in vertebrates) differ from one organism to another and show great variation within taxa. Kluge (1988) even suggested that maybe the whole allometric phase might be the level of comparison for morphometric data.

For complex shape data, Zelditch *et al.* (1995) and Swiderski *et al.* (1998) suggest two strategies, either examine the shape as a whole or subdivide the shape into individual dimensions, including aspect ratios and distances between landmarks as a measure. Both approaches have advantages and disadvantages. Viewing complex morphology as single items of comparison can lead to problems of coding as sampling increases. Determining the information content of characters with many different states shuffle in other problems of direction, order and polarity during cladistic analysis. Although one is naturally using quantitative analysis to search for discontinuities, there are instances where artificial gaps are created (Chappill 1989). Thus comparing suites of unique shapes can lead to creating columns of variables that are effectively autapomorphs in the final matrix. Atomising the components of any character as a reductionist pursuit can lead to separate columns of independent variables that are both logically and biologically correlated. Stevens (2000) notes that problems also emerge when characters are wrongly linked biologically and logically. In all characters finding the logical and biological divisions becomes increasingly difficult when overlap increases. Several characters might only be one, but theory is lacking on the precise course of action to follow for coding them (see also Fink and Zelditch 1995; Pleijel 1995; Hawkins *et al.* 1997; Hawkins 2000).

One of the complicating issues in quantitative and morphometric literature is the language surrounding units of comparison and the use of the term homology. Homology tends to bridge the formalisms of geometric shape analysis and the evidential use as character hypotheses supporting monophyletic groups in systematics. Following a tradition set by D'Arcy Wentworth Thompson (1942), shape analysts frequently apply homology to mean comparisons between discrete geometric structures, such as comparable points or curves, and, by a further extension, to the multivariate descriptors that arise as part of the subsequent multivariate analyses. Smith (1988: 335) distinguished this aspect as operational homology: '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 very precise quantitative values for character states.'

In Smith's context, the term 'homologous' means something other than the primary and secondary homology in systematics. Rather, it is used for corresponding parts in different samples of taxa or developmental stages during life cycles. In morphometrics, then, to declare something 'homologous' is an assertion about comparison of structures in a consistent manner rather than anything to do with historical transformations gradual or otherwise. However, Zelditch *et al.* (1995: 180) note that 'when systematists choose particular landmarks, the choice is often defended on the grounds that they sample parts of the organism judged to be homologous at the most inclusive level being studied'. MacLeod (1999) challenges the Zelditch *et al.* assertion on this issue and provides several examples where biologically non-homologous features have been used as landmarks. Moreover, a homologue is a structure, part of an organism, not an infinitesimal location point. MacLeod (1999) also challenges the notion that landmarks can be homologous with one another in the absence of evidence for point-to-point correspondence. Similarly, to declare an interpolation (such as a thin-plate spline) a 'homology map' means that one intends to refer to its features as if they had something to do with valid biological explanations pertaining to the regions between the landmarks, about which there is frequently no data (MacLeod 1999, 2002, in press). This is an important point as systematists use outlines to make comparisons between taxa and it is a key source of relevant information that could be used in cladistic analysis. For detailed discussions of the landmark-outline debate see Bookstein *et al.* (1982, 1985), Ehrlich *et al.* (1983), and Bookstein (1990, 1991, 1996a,b, 1997).

Thus, homology in morphometrics is a complicated interplay between precise topological correspondence and differences amongst taxa as literal transformations through ontogenetic and phylogenetic metamorphosis. This might explain the sharp criticisms of Pimentel and Riggins (1987), Cranston and Humphries (1988) and Bookstein (1994) who felt that it was impossible to apply taxic homology to overlapping variables, but these are all comments that did not take full cognizance of primary homology assessment. To put it into the context of this paper however, determining similarity and topographic identity can easily be undertaken with both measurements and morphometric data as with any other procedure used for determining primary homologies, and which like any source of data, has potential for cladistic analysis. Stevens (2000) has already noted that there is so much confusing baggage around the word homology that the word should be replaced with pertinent and relevant replacements. Bookstein *et al.* (1985), and Bookstein (1991), attempt to simplify and marry two concepts of homology by arguing that the 'traditional' concept of homology should be extended to cover morphometric homology. However, they are quite clear that there is a distinction. MacLeod (1999) disagrees with the idea of extending the concept because biological homology refers to structures, not infinitesimal points on structures. Thus, landmarks simply abstract the spatial position of putatively homologous structures relative to other such structures. These points are not themselves homologous because alternative, but nearby, locations can serve equally well for morphometrics. Indeed outlines and outline segments have a firmer claim on correspondence to the biological concept of homology than landmarks (MacLeod, person. comm.). Unsurprising then that Fink and Zelditch (1995), Zelditch *et al.* (1995) and Swiderski *et al.* (1998)

have suggested that the term 'homologous' should be replaced with 'corresponding' or 'comparable' when dealing with landmarks at the character definition phase in morphometrics. Various authors are at pains to point out that morphometric and quantitative data are somehow different from qualitative data. But, all character sources can be assessed along a scale of good to bad or best to worse in terms of the chances for yielding cladistic classifications (Chappill 1989; Thiele 1993).

## Character state identity

Character coding for both continuous or overlapping variables and qualitative variables has been the subject of intense scrutiny over the last few years. The question is simple: how are measurements of raw data coded into the 0s, 1s and 2s of a data matrix (see Scotland and Pennington 2000; Wiens 2000)? Stevens (2000) commenting on Brower and Schawaroch's (1996) division for primary homology assessment noted that topographic identity for morphological characters was somewhat factual and uncontroversial. The real problems for morphological characters emerge at the character state identity stage and the problem becomes even more acute for overlapping variables. Here, the problem is what to call a character, or a character state. A useful rule of thumb is to consider that characters are equivalent to variables, and discontinuities are equivalent to the character state boundaries. If there are no discontinuities the character is invariant having only one state. Pimental and Riggins (1987) recognise conventional nominal variable coding for obvious characters and states as the normal way to proceed, but given the range of character variation from obvious discontinuities to gaps made by gap-coding methods, suggest that only qualitative gaps be coded. Hawkins (2000) presents several challenges to conventional coding variously known as composite coding (Wilkinson 1995), unspecified homologue coding, ratio coding, logically related coding, unifying coding, inapplicable data coding, positional coding and mixed coding. In addition to these there are coding schemes for multistate characters, contingent coding methods and a variety of different ways for coding presence and absence (Pleijel 1995; Forey and Kitching 2000).

Given all the vagaries associated with relatively clear-cut situations the situation becomes more complicated with continuous distributions of observations or measurements. Usually opaque to assessment in raw form, one can only begin to discover grouping homologies through specific methods for converting raw data into discrete codes for subsequent cladistic analysis. Thus undertaking the second and third stages of primary homology assessment, delimiting and coding the features of organisms as characters and character states, is part of the process of recognising their systematic value. Despite these difficulties, Thiele (1993) believes that continuous variables should only be excluded if the cladistic analysis cannot handle such data or if it can be shown empirically that those characters convey no information or phylogenetic signal relative to other characters in the data matrix. It is also obvious that there are many manipulations to continuous variables that can be undertaken, principally coding features in a matrix and the question of whether manipulations such as scaling and weighting (e.g., Goldman 1988; Thiele and Ladiges 1988) are justifiable with respect to the results obtained.

In theory, continuous variables have an infinite number of potential values. However that does not mean that observations/measurements must be continuously distributed along such variable axes, and the continuity of the variable scale has nothing necessarily to do with the nature of the distribution of observations that might be made along that scale. Although there are several methods (e.g., in MacClade) that can be used to examine continuous variables without recoding and have some limited use for looking at character evolution over trees (e.g., Swofford and Berlocher 1987; Huey and Bennett 1987), there are few computer algorithms available for cladistic analysis of raw data (but see Felsenstein 1988). Most methods manipulate the raw scores. The values can be bounded within a certain range but the potential list of values can still be large. Some argue that there are few variables that can actually be considered as continuous because our ability to measure values to the  $n$ th degree are so imprecise that the potential values are in fact finite. Of the few studies available in order to compare continuous variables with qualitative variables on cladograms, all raw data are invariably filtered during coding as discrete integers (e.g., Cranston and Humphries 1988; Thiele and Ladiges 1988; Chappill 1989; Thiele 1993).

Methods include simple gap coding (Mickevich and Johnson 1976), segment coding (Colless 1980), divergence coding (Thorpe 1984; Almeida and Bisby 1984), homogeneous subsets coding (Simon 1983), generalized gap coding (Archie 1985; Goldman 1988; see also Thiele and Ladiges 1988), range coding (Baum 1988) and gap weighting (Thiele 1993). Samples of taxa are ranked along a scaled attribute axis, and then simple rules are applied to create gaps, segments or subsets in an effort to produce discrete codes for the continuous values. The attribute axis is rescaled into states for cladistic analysis.

Simple gap coding divides the axis at those points where no values occur or between the means of the frequency distributions at the point where the 'gap' exceeds a particular preconceived value, such as one standard deviation about the mean. Usually, the attribute axis will be divided into fewer states than there are taxa and for most computer programs there is an upper bound to the number of states per character that can be analysed. Chappill (1989: 220) indicated that desirable attributes for any method should be that it should 'reflect the proportional differences between taxa', ... have '[T]he ability to discriminate between divergent taxa', ... 'using a particular character should be equal for all comparisons between pairs of such taxa', ... 'the number of states produced should be proportional to the variability of the character', ... 'it should not recognize insignificantly small differences between taxa', ... 'and the addition of new taxa, or improved sampling, should not reduce the discrimination possible between the original taxa.'

It turns out there are problems with all of the methods. Farris (1990) provided a characteristically robust critique indicating that each method had its drawbacks and most damning of which that these were techniques more commonly used by pheneticists (e.g., Sneath and Sokal 1973), as incorporated into the studies of Cranston and Humphries (1988), Goldman (1988), Thiele and Ladiges (1988), and Chappill (1989). More specifically, it is the assumptions for scaling multistate characters to unit range (so as to reduce their effect in comparison to binary characters and confounding weighting with scaling) that causes most problems. That there is no real justification for scaling or weighting multistate characters a priori confounds the outcomes in cladistic analysis.

Coding methods invariably consist of four stages: the terminal taxa are identified, a sample of each is measured and scored with sample means and variance, and then the means and ranges are converted to integers using a gap, segment or range-coding method. It seems that the problem with all coding methods (quantitative and qualitative) is that the rules for converting the measurement data into codes lack any justifiable theory. What is needed in a systematic morphometric analysis is agreement about the discontinuities in the distribution of observations (MacLeod, person. comm.; Zelditch *et al.* 1995). The existence of discontinuities represents the practical justification, congruence provides the operational test and an agreed definition of discontinuity. Farris (1990) showed explicitly that for generalised gap coding (Archie 1985) as used by Thiele and Ladiges (1988), for example, varying the sample size, using different standard deviations between the means, and thus varying the critical gap size had profound effects on the outcomes. This method like all others attempts to formulate ‘*ad hoc*’ rules for subdividing a continuum. Gradual continua simply cannot be used as a basis for unambiguous grouping. Farris (1990) further demonstrated that homogenous subset coding and gap coding gave very different results on the same data set and that generalised gap coding could yield nonsensical codes. He elaborated further saying that it was of no use to rescale codes as these invariably produced meaningless character states. Farris concluded by saying that if a character can be broken up into several meaningful distinct conditions there are no rational grounds for reducing weights of the distinctions but to code the states in an appropriate manner. This would surely justify morphometric methods at least in some cases. On the other hand, if the coded states obtained by one of continuous variable techniques reflect no meaningful distinction, the remedy is to eliminate the arbitrary differences. Of the many examples I have examined I would say that many of the states are meaningless except by justification on statistical differences.

Furthermore there are those who have used morphometrics to justify using their collected data (e.g., Chappill 1989) regardless of whether those data uniquely characterise taxonomic groups or not. The problem is that those who have used morphometrics have wanted to find ways of using the data they collected, regardless of whether those data characterised groups of taxa or not. That was wrong, but some cladists have overreacted in regarding all morphometric data as being unacceptable (e.g., Pimentel and Riggins 1987). They considered (1) continuous variables imply possibility of a continuous distribution of observations (irrespective of whether this possibility is realised in nature), and (2) no theoretical justification for *ad hoc* methods of subdividing a continuum could be found. On the contrary, morphometrics is important for systematics because it (1) can yield additional variables that can be used to define groups (provided it is realised that the subject of morphometric analysis is to uncover the discontinuities that separate taxa from one another), (2) can test hypotheses of the correctness/objectivity of state definition for qualitative characters, and (3) can render the assignment of states to taxa/individuals more precisely. Sadly it seems that some cladists and traditional systematists avoid morphometrics because they are innumerate and apprehensive at the idea of having to learn new skills, (2) they question the cost-benefit of morphometric analyses, and (3) they understand that if they subject many of their personal/traditional character state definitions (which are rarely defined in precise terms) to the rigour of morphometric analysis, those definitions might be found wanting. All of those reasons are understandable at some level, but none of them have

anything to do with the theory or logic of cladistic analysis. The mistakes of the past will need to be explained and acknowledged by systematists and morphometricians before progress in this area will be able to be made.

## Cladistic analysis

Given the difficulties encountered by coding methods it might be considered perverse to enquire whether the performance of such characters can be applied. Nevertheless, Thiele (1993) asked the question whether morphometric data were of any use for inferring phylogenies. Of the few studies available, he noted that Cranston and Humphries (1988), Thiele and Ladiges (1988) and Chappill (1989) all used consistency indices as performance indicators to determine the differences between explicit quantitative and qualitative characters. Thiele (1993) tested the efficacy of continuous variables by suggesting that if a set of morphometric characters induces one phylogeny, the matrix should contain cladistic co-variation. Also cladograms derived from quantitative characters should be similar to those derived from other data sets. In all three analyses, morphometric data gave lower consistency indices on the cladograms in comparison to the qualitative data. He noted, however, that in his own study of *Angophora*, the morphometric variables performed well and mapped well onto cladograms produced from the qualitative data. Later Thiele (1993) applied a more elaborate test on morphometric data in studies of *Banksia*. Again, he found that morphometric characters produced lower consistency indices than qualitative data, but did perform better than results obtained from random data. In studies of partitioned data sets, representing difference sections of *Banksia*, in all but one out of four studies, the morphometric and qualitative characters were significantly similar, and both produced similar cladograms. It was significant to notice that both qualitative and quantitative data sets produced similar trees.

## Conclusions

It would seem that any source of data is suitable for cladistic analysis. It is obvious that the more clear-cut observations can be, the more obvious divisions can be made in coding characters. However, unlike Pimentel and Riggins (1987) and Chappill (1989) I agree with Thiele (1993) and Stevens (2000) that all data should be scrutinised for potential analysis. It is obvious that the more quantitative observations become, the more difficult it becomes to partition that information into characters and character states. The methods for doing so become elaborate and lack obvious underlying theory to justify the methods. In at least some cases (e.g., Thiele 1993, Fink and Zelditch 1995 and subsequent papers) cladistic analysis appears to have succeeded in inferring hypotheses of relationship. Rather than considering that some data are better than others, not all data sets can be considered as one homogenous class. What might be true for one class of characters might not be true for others. As Thiele noted the best data are not necessarily different in kind from the worst.

Nevertheless, at the end of the day the most robust classifications are those with the highest information content. There is no doubt that manipulating measurement data into long transformation series reduces the information content and creates gaps



where none can actually be agreed upon except by convention. For measurement data, of the kinds that compare different leaf lengths or widths, for example, transcribing the results into clear-cut integers becomes vacuous, especially when individual scores or codes are given for each taxon in the analysis. There is little doubt too that recommendations for analysing continuous variables to include such things as aligning the variation into series from the smallest to largest or *vice versa*, and insisting on ordered transformation series is a perverse use of transformation series analysis in the sense of Mickevich (1982). Homology is about relations and at the minimum refers to the fact that at least one homologue must be present in two taxa and absent from a third to be useful. In this context it appears that overlapping variables have less in the way of relational information. The use of gap-coding methods to determine discrete states appears not to have any particular theory, and like many phenetic studies, are methods devised on statistical or algorithmic ground without clear reasons for doing so (Farris 1990). In this context the gap-coding procedures have little in the way of theory as compared with some morphometric methods (see MacLeod, this volume) and it is clear that the different procedures have their drawbacks, but especially in attempting to create gaps when none are really present. Stevens (2000) noted that there are two kinds of data: 'one in which the states are taken from visual inspection of overlapping variation and one in which states are taken from largely non-overlapping variation'. The latter invariably contained stronger cladistic signal.

I believe that Patterson (1982) was right to draw attention to the distinction between transformational and taxic homology. It seems to me that much of the ambiguity that exists in cladistics today is a direct result of worrying about transformation. Taxa and characters are really the same thing. Characters are variables and thus portions or fragments of organisms. To overcome the ambiguities what is needed is to bring the activities of morphometrics and cladistics closer together to find nested hierarchies of characters and taxa. It still worries me that the arguments about transformation and character evolution have got muddled up with the business of sorting out homology and classification, and if these were teased fully apart I am sure the activities of both groups could come closer together.

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