

Similarity

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Recent debates concerning conflicting hypotheses of higher-level phylogeny such as the sister-group relationships of tetrapods, turtles, birds and snakes, serve as examples in the analysis of the nature of morphological evidence as it is currently used in phylogeny reconstruction. We note a recent shift of emphasis towards ever-larger data matrices, which may come at the cost of detailed character analysis and argumentation. Because the assessment of morphological characters necessarily entails a conceptual element of abstraction, there is also a threat that pre-conceived notions of phylogeny influence character analysis. Because the test of congruence does not address character analysis in itself, we argue that character hypotheses, i.e. primary conjectures of homology, need to be testable, and potentially refutable, in their own right. We demonstrate the use of classical criteria of homology (topological relations and/or connectivity, in conjunction with the subsidiary criteria of special similarity and intermediate forms) in the test, and refutation, of morphological characters. Rejection of the classical criteria of homology in the test of morphological character hypotheses requires the formulation of alternative methods of test and potential falsification of morphological characters that have so far not been proposed. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 75, 59–82.

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INTRODUCTION

Progress in science is generally believed to result from discourse or debate, the *critical attitude* characterized by Popper (1972a). In the field of vertebrate systematics, a number of issues have been and/or still are at the centre of debates, such as the origin of tetrapods (Schultze & Trueb, 1991), the sister-group relationships of birds with mammals (Haematotherma: Gardiner, 1982, 1993), or theropod dinosaurs, respectively (Gauthier, 1986; Gauthier *et al.*, 1988) and, more recently, the origin of turtles (Rieppel & Reisz, 1999) and snakes (Coates & Ruta, 2000). Of these, only the origin of tetrapods has been dealt with between the covers of an edited volume that brings together all the controversy and contradictory viewpoints on the subject (Schultze & Trueb, 1991). Since all contributors to this controversial subscribed, in essence, to the same method (i.e. cladistic analysis based on parsimony), the debate focused on the thorny issue of

contradictory character delimitations. However, in the entire text 'there is virtually no discussion of what constitutes a character' (Clark, 1992: 535). 'Not surprisingly, the book again and again demonstrates that similarity lies in the eye of the beholder, and that the particular hypothesis being advocated strongly colours perceptions of morphological resemblance' (Clark, 1992: 533).

As stated most recently by Poe & Wiens (2000), morphologists are generally not explicit, or not explicit enough, about their choice of characters. The apparent elusiveness of the concept of *character* in morphological studies may also lie at the root of criticisms of morphology-based phylogenetic analyses such as: '... morphological studies typically include too few characters ...' (Hillis & Wiens, 2000: 4) and '... to train and label systematists as either morphological or molecular is to produce too many over-specialized graduates with a limited appreciation for the breadth and diversity of the field.' As a consequence, 'There may always be room for some specialists, but we expect that the future will favour broader training ...' (Hillis

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& Wiens, 2000: 15). We are concerned that this outlook may encourage quantity over quality of data and that it may discourage in-depth comparative anatomical studies as the basis for morphology based phylogenetic analysis. There is no question that scientific knowledge in general increases as investigation broadens and deepens in context, and as more critical evidence is incorporated into analyses. But broadening the basis of investigation must not come at the cost of a critical attitude and of a concern for the quality of data as potential falsifiers of competing hypotheses. At this time, the balance between the two fundamental aspects of morphological systematics—character analysis and phylogenetic analysis—has become highly skewed, with a tendency to emphasize the latter and subjugate the former. As evidenced by an examination of recent publications in journals dealing with systematics topics, more and more emphasis is being placed upon methods and programs for analysing data, and less and less on the critical evaluation of the data themselves. A superficial approach to comparative anatomy and morphological characters results in superficial phylogenetic hypotheses that cannot be improved solely by making data matrices larger, because every hypothesis will be corroborated only to the degree that its weakest evidentiary link permits. A superficial approach can also lead to potentially irresolvable debates about characters, such as are seen in the controversies over bird, tetrapod and snake origins, to name a few.

We believe that the step where the systematist makes his or her initial conjecture of homology, i.e. the step where he or she conceptualizes a ‘character’, has become increasingly trivialized. Here we attempt to address this one specific aspect of morphological systematics—the generation of character hypotheses stemming from comparative anatomical study—using as examples characters that have been controversial in analyses of the relationships of tetrapods, reptiles, birds and other groups. We suggest that, in contrast to the opinions mentioned above, much greater profundity is required in the study of anatomy and in the translation of those studies into characters for morphological phylogenetic analysis, if testability of character hypotheses is to be realized. The examples we use illustrate the fundamental relationship between the depth of complexity considered in formulating character hypotheses and our ability to test or refute those hypotheses.

It has been widely argued that character delimitation for phylogenetic analysis entails an element of subjectivity, the ‘*bête noire*’ of systematics (Pogue & Mickevich, 1990). It is perhaps because of this element of subjectivity that morphological similarity appears to lie in the eye of the beholder (Clark, 1992). As an example, ‘Depending on the phylogenetic view in

favour, similarities and differences between paired appendages of particular sarcopterygian groups and tetrapods often have been either exaggerated or discounted’ (Chang, 1991: 20). Similarly, in his discussion of the notion of *character* as a key word in evolutionary biology, Frisrup (1992: 51) noted that ‘Some use character to refer to unprocessed observations; others introduce additional restrictions or analyses to produce characters that more closely resemble the information they would like to have.’ We maintain that there is no such thing as an ‘unprocessed observation’ (Hanson, 1958; Popper, 1972a; Brady, 1994). Instead, it is precisely because of the impossibility of theory-free observation that falsification plays such an important role in natural sciences. For morphology-based phylogenetic analysis, this means that character hypotheses must be testable in their own right, and we attempt to show here that such testability can only be achieved by due consideration of structural complexity in character analysis.

THE WHOLE AND ITS PARTS

Living organisms are developmentally and functionally integrated wholes (Robert, 2001), but systematics requires the decomposition, or atomization, of the organismic whole in order to generate characters useful for phylogenetic analysis (Rieppel, 1988a). This ‘atomization’ of the organismic whole was characterized by Wagner (2001: 3) as the ‘individuation’ of ‘meaningful characters within the context of the . . . integrity of the organism.’ The ‘individuation’ of a character entails an element of conceptual abstraction, which will be discussed in greater detail below. Here, the question will be pursued as to what a ‘*meaningful character*’ is, or should be.

Definitions of ‘character’ abound in the literature, and range from the most complex as that proposed by Wagner (2001), to the most simple: a character is ‘Any feature that is an observable part or attribute of an organism’ (Liem *et al.*, 2001: G-6). Sneath & Sokal (1973: 74) defined a ‘unit character’ as ‘a taxonomic character of two or more states, which within the study at hand cannot be subdivided logically, except for subdivision brought about by the method of coding.’ This is an eminently operational definition, which views character delimitation as a function of coding procedures. By contrast, Pimentel & Riggins (1987: 201) attempted to define characters relative to mutual exclusivity: ‘a character is a feature of organisms that can be evaluated as a variable with two or more mutually exclusive and ordered states.’ Hennig (1966: 7) stressed the nature of characters as intrinsic properties of semaphoronts. The total form (holomorphy) of the semaphoront comprises the ‘totality of its physiological, morphological, and psychological (ethological)

characters . . . We will call those peculiarities that distinguish a semaphoront (or a group of semaphoronts) from other semaphoronts "characters," keeping in mind that this designation . . . always means the multidimensional totality.' The important point that Hennig (1966) captured is the notion that a character is a relational concept, a peculiarity that has discriminating, or distinguishing, properties.

We agree with Hennig (1966) that a character is not just 'any observable feature' of an organism, but rather an observation that captures distinguishing peculiarities amongst organisms. Those distinguishing peculiarities must be intrinsic properties of the organisms under analysis, not extrinsic properties attributed to those organisms by the observer. However, observation *per se* (the unprocessed observation *sensu* Fristrup, 1992) is impossible, because all observation is theory-laden. It is impossible to observe 'white' as an attribute of an object without the notion of blackness and, furthermore, both observations require a theory of colours. Hence, a character is a logical relation established between intrinsic attributes of two or more organisms that is rooted in observation (Rieppel, 1988a) and that, if corroborated by congruence, is hypothetically explained as an historical relation.

Given the broad conceptualization of the notion of 'character' in contemporary systematics, however, it will be expected that different authors delineate characters in different ways in morphology-based phylogenetic analyses. Poe & Wiens (2000: 25) investigated the decision-making criteria used by systematists to include or exclude characters and found that: ' . . . there is evidence of greatly differing opinions among morphologists as to where the dividing line is between a marginally acceptable and unacceptable character. The results of our survey suggest that people select characters differently.' Poe & Wiens (2000) concluded that most morphologists are not explicit about how or why they choose their characters and that explicit criteria should instead be followed by systematists for choosing or rejecting characters. However, no such criteria for rejection were formulated. Instead, Poe & Wiens (2000: 33) suggested that many of the character rejection criteria they discovered in past studies lacked justification and that therefore 'much more variation could be included in phylogenetic analyses than is used presently.' Perhaps this criterion applies well to studies at low taxonomic levels (intrageneric or intraspecific). In contrast, our analysis of phylogeny reconstruction at higher taxonomic levels suggests the opposite conclusion: that explicit criteria must be formulated and followed to test character hypotheses before admitting them into data matrices in order to render primary conjectures of homology testable.

A *meaningful* character is thus based upon a character description that can in itself be critically evalu-

ated, tested and potentially rejected. As stated by Wiley (1975: 237), a primary conjecture of homology can be argued to carry a prediction, for example, 'that the structure will continue to be similar at finer and finer levels of morphological comparisons, or perhaps two rather dissimilar structures can be traced back to the same embryological structure . . . I think it is important to precision of methodology that some form of testing be done at this lower level . . .', i.e. prior to the search for congruence among the primary conjectures of homology. According to Wiley (1975), the critical evaluation of primary conjectures of homology is based on topology, as revealed by the investigation of structural complexity and connectivity.

Meaningful characters for use in phylogenetic analysis must also be (assumed to be) independent from one another because, within a falsificationist framework, cladistic analysis based on parsimony assumes the independence of characters that are subjected to the test of congruence (Farris, 1983).

QUANTITY AND QUALITY OF DATA (CHARACTERS)

Phylogenetic analysis using cladistic methodology has originally been cast in falsificationist (Popper, 1992) terms (e.g. Gaffney, 1979; Farris, 1983), and more recently in terms of sophisticated falsificationism (Kluge, 1997a,b, 2001). Sophisticated falsificationism *sensu* Lakatos (1974) views science as a dynamic process engaged in the evaluation of relative corroboration of competing scientific theories (Chalmers, 1986). Insofar as this philosophy is applied to the conceptual framework of cladistic analysis, the finite number of cladograms possible for a given number of terminal taxa is claimed to constitute the competing hypotheses and the characters (character states or synapomorphies of some authors) are considered the evidence, i.e. the potential falsifiers (Kluge, 1997a,b, 2001).

Since Popper (1992) related the degree of corroboration of competing theories to the severity of test (itself dependent on the degree of falsifiability of the theory under critical consideration), one could argue that it is either the *kind* of characters that provide different degrees of severity of test, or it is the *number* of characters that determine the severity of test. Since no empirical methods are currently available for differential weighting of characters in an objective manner, it would appear that the severity of test increases with the number of taxa and characters that are involved in phylogenetic analysis (Kluge, 2001). Hence the goal of maximizing the number of informative characters over a maximum number of terminals.

Quantity of data seems to have gained more focus over quality of data in modern systematics, as re-

flected in this recent criticism by Hillis & Wiens (2000: 4, emphasis added): 'In morphological systematics, the characters must be discovered and delimited by the systematist, usually without any explicit criteria for character selection and coding. Morphological data sets have the potential to be quite arbitrary... *and morphological studies typically include too few characters anyway.*' The current trend is therefore to build ever larger data matrices, (i) in the hope that errors cancel out as noise in the face of an overwhelming signal of phylogenetically informative characters, (ii) to achieve a better balance of morphological vs. molecular data in phylogenetic analysis, and (iii) to increase the degree of corroboration of a given phylogenetic hypothesis (see Kluge, 1997a,b; for a discussion of some of these issues). However, degree of corroboration is not based solely on a 'numbers game'. Popper (1972b), for example, in his discussions of corroboration of scientific hypotheses, emphasized such attributes as independence, nonambiguity and nonarbitrariness of evidence, beyond the simple *quantity* of evidence, as critical for the severity of test.

Thus, severity of test must also critically address the *quality* of the data as potential falsifiers, not just their number. Poorly delimited characters provide no severity of test, no matter how many of those are involved in the analysis or, in other words, a theory will only resist falsification as strongly as is its weakest link. Hanson (1958; see also Popper, 1972a; Brady, 1994) showed that all observation is theory-laden; theory, therefore, always precedes observation. From this follows that if a theory appears to be falsified by an observational statement, it might be the observational statement itself, rather than the theory, that is wrong. This is the reason why a falsified theory is not necessarily false (Popper, 1992; Farris, 1995). In the absence of absolute certainty about the correctness of an observational statement, there can never be an absolute empirical falsification of a theory.

At this junction, Popper (1992) made the difference between the individual (personal) experience of observation and what Chalmer (1986) called a public observational statement. A public observational statement is one that can be scrutinized by the scientific community, in the context of the current standards of the science within which it is proposed. In Popper's (1992: 99) own words:

'Any empirical scientific statement can be presented (by describing experimental arrangements, etc.) in such a way that anyone who has learned the relevant technique can test it. If, as a result, he rejects the statement, then it will not satisfy us if he tells us all about his feelings of doubt or about his feelings of conviction as to his perceptions. What he must do is to formulate an assertion that contradicts our own, and give us his instructions for testing it. If he fails to do this we can ask

him only to take another and perhaps a more careful look at our experiment, and think again.'

If cladistics is cast in a falsificationist paradigm, then character descriptions become the observational statements that test competing hypotheses of relationships. In that sense, character descriptions become 'basic statements' *sensu* Popper (1992). Because the occurrence of falsification may result from erroneous basic statements, the latter must be formulated in a way that allows them to be tested, and potentially refuted, in their own right (they must be formulated as theories of lower universality). At one level, tree topology is the hypothesis to be tested (h) with characters constituting the evidence (e), and at another level, the characters themselves constitute hypotheses (h) and the evidence (e) to test them lies in comparative anatomical work/experiments. Relative to character descriptions, we use the notion of 'test' in its broad sense, that is, as 'the critical discussion of competing theories which is characteristic of good science' (Popper, 1972a: 80). The 'critical discussion' entails 'attempted refutations, including empirical tests' (Popper, 1972a: 20). In order to render the critical discussion of basic statements possible, we must, according to Popper (1992), provide the 'relevant technique' by which those statements can be evaluated, i.e. tested, it being understood that such basic statements 'are accepted as a result of a decision or agreement... the decisions are reached in accordance with a procedure governed by rules' (Popper, 1992: 106).

What this means for character descriptions is that these are acceptable as potential falsifiers of phylogenetic hypotheses only if they can be critically evaluated relative to some agreed upon technique. Acceptance or rejection of characters cannot be based merely on personal doubt or conviction, but must proceed hand in hand with the acceptance or rejection of the agreed upon technique used to critically evaluate character delineations. If rejection of the latter is preferred, the formulation of new techniques for character delimitation will be required. This is necessary, because if it becomes impossible to reach intersubjective agreement on basic statements, the language of science breaks down (Popper, 1992).

The 'technique' that traditionally forms the basis of 'morphological testing' (Wiley, 1975: 237), first rigorously introduced by Etienne Geoffroy Saint-Hilaire and still in use today (Rieppel, 1988a; Brady, 1994; Rieppel, 2001), is his '*principe des connexion*', today referred to as topological relations or connectivity between constituent elements of an organic structure. One might argue that it is not the principle of connectivity that potentially refutes character descriptions, but rather phylogenetic analysis itself, in that

demonstrated homoplasy rejects a character as a hypothesis of synapomorphy (homology). This perspective leads to the notion of research cycles (Kluge, 1989, 1997b), which calls for continuous critical re-examination of the character descriptions. Even in the context of research cycles, critical discussion (i.e. testing) of character descriptions must proceed on the basis of some standard or technique, if character descriptions are to qualify for basic statements *sensu* Popper (1992). It is the consequences of neglect of the principle of connectivity in comparative anatomy, and the possibility of its use in critically evaluating, or testing, character hypotheses, that we propose to investigate in this paper.

THE TESTS OF SIMILARITY AND CONGRUENCE

Similarity has become a vague concept in systematics because it sometimes refers to positional similarity (topographical correspondence), and sometimes to resemblance in form, shape or size. Patterson (1982), and others before him, suggested similarity as the initial test of homology. Patterson (1982: 38) initially linked the 'test of similarity' to the classical criteria of homology, beyond which he found ontogeny to be the most important arbiter of morphological similarity. The broad concept of 'morphological similarity' requires qualification in order to be useful in any 'test of similarity.' Morphological similarity in a broad sense bears no exact relationship to conjectural historical 'sameness' (homology, defined as similarity due to common ancestry), the former referring to a perceived degree of resemblance between two structures within a certain conceptual framework (topology, connectivity; see below), the latter referring to conjectural historical identity. Morphological similarities in terms of size, shape (or function) may be non-homologues and morphological dissimilarities in terms of size, shape (or function) may be homologues. Instead, if there is a 'test of similarity', it must transcend mere similarity in terms of size, shape, and function, and refer specifically to topological similarity, connectivity or structural correspondence.

A primary conjecture of homology, or character hypothesis, corresponds to the delimitation of morphological characters for phylogenetic analysis. In cladistic analysis, the inference of homology has been previously suggested to be at least a two-step procedure (Rieppel, 1988a; dePinna, 1991; a three-step procedure according to Brower & Schawaroch, 1996—see the distinction of character identity and manifestation discussed below). The first step is the hypothesis of structural correspondence of constituent elements, or parts, in two or more organisms, i.e. the delimitation of characters by comparison. The second

step subjects these character hypotheses to the test of congruence. Congruence corroborates characters as synapomorphies, i.e. as correspondences of structure that are hypothetically explained as homology. Incongruence indicates homoplasy, i.e. a correspondence of structures that cannot be hypothetically explained in terms of descent with modification.

Our main concern with character hypotheses is whether they can be tested and potentially refuted in their own right. Testability should play a role at all levels of analysis in phylogenetics—both in character analysis and in the analysis of relationships based on those characters. Commenting on the debate on the origin of tetrapods, Schultze (1991: 60) remarked that: 'The entire question of relationships turns on an evaluation of similarities and dissimilarities of features in order to assess their homology accurately. The most frequently used criterion for homology is topography.' We suggest that a test of character hypotheses (conjectures of homologies) does exist within the classical criteria for postulating homology (Remane, 1952), but that those criteria are not necessarily followed by systematists, or else they are followed in a superficial sense only, which results in decreased severity of test.

STRUCTURES, CHARACTERS AND ANATOMICAL TERMS

A dictionary of anatomy, for example the *Nomina Anatomica*, as approved by the International Congress for Anatomical Nomenclature for human anatomy, will define anatomical structures and refer to those with a technical term. To refer to structures observed in two or more organisms by the same anatomical term bestows a putative identity on these structures, i.e. it renders these structures a character for which similarities and dissimilarities can be assessed by a comparison of its various manifestations. Topographical relations, and/or connectivity, allow the identification of the structural correspondence of the part that is referred to as the 'heart' in vertebrates. The anatomical term 'heart' bestows an identity on the heart that transcends its various manifestations, such as its two-, three- or four-chambered structure in various subgroups of vertebrates. To propose a conjecture of homology is to 'individuate meaningful characters within the context of the functional [and developmental] integrity of the organism', an approach that is 'radically more ambitious' than the conceptualization of a character as 'any observable difference between two groups of organisms' (Wagner, 2001: 3). Reference to the paired elements in the skull roof of two or more organisms as 'parietals', irrespective of variation in shape or form, constitutes the use of an anatomical term ('parietal') that individuates

(logically, not historically) these bones among all skull roof elements and confers identity upon them, in other words, postulates 'sameness', despite some degree of difference (different manifestations of the same structure).

As was recognized by Richard Owen (1843; for an analysis of the writings of Étienne Geoffroy Saint-Hilaire and Étienne Serres on the same subject see Rieppel, 1988a, 2001; Brady, 1994; Panchen, 2001), recognition of 'the same but different' (Hawkins *et al.*, 1997) in a primary conjecture of homology will necessarily be based on an observation that entails a conceptual element sometimes referred to as 'abstraction' or as a 'subjective element in character delimitation.' The primary conjecture of homology (i.e. the establishment of the putative identity of constituent elements of the organismic whole) rests first upon the establishment of structural correspondence that may entail an abstraction from particular form and function. As stated by Woodger (cited by Hennig, 1966: 94): 'In 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.'

The establishment of a one-to-one relationship among constituent elements is not based primarily on shape or function, but on topological relationships or, in the dynamic context of ontogeny, on connectivity (Shubin & Alberch, 1986). Topology, or connectivity, establishes a logical relation among constituent elements of an organic structure, and represents the conceptual element entailed in the observation of characters (Brady, 1994). 'Sameness' stems from invariant relative topological relations, 'difference' from differing 'executions of invariant topology', the differences explained as evolutionary transformations by Darwin (Brady, 1994). The earliest documented application of the principle of connectivity is that of Belon (1555) in his comparison of the skeleton of a bird and man, and the empirical application of this principle in comparative anatomy proves its general success, not without the occasional failure, however (see below for further discussion).

Designating corresponding parts with the same anatomical term bestows upon them a structural (or logical) identity that, if congruent, is hypothetically explained as historical identity. As the putative identity of shared structures becomes increasingly corroborated over time, the anatomical terms designating such structures become part of the background knowledge rooted in the tradition of comparative anatomy.

Primary conjectures of homology find themselves subject to the same dependence on background knowledge as do conjectures of outgroups. Just as any choice

of outgroups depends on a hypothesis of higher-level relationships that can be tested in its own right, the establishment of topological relations for a given structure requires a frame of reference which, again, can be tested in its own right (Rieppel, 1988a; for an example of such a test see the discussion below of the topological relations of the epipterygoid relative to the trigeminal nerve branches in the amphisbaenian *Trogonophis*). Not referring to individualized anatomical structures by their proper name may signal the perceived need to test and potentially refute the background knowledge, i.e. the established frame of reference on which the putative identity of that structure is based. In its most radical form, the avoidance to refer to a structure by its anatomical term may stem from the desire to reject the principle of connectivity as a technique by which to test character hypotheses, in which case another such technique will have to be supplied, however (Popper, 1992; see discussion above).

An example is provided by Scanlon & Lee (2000; supplementary information, character 69), in their analysis of snake interrelationships. In that analysis, the stylohyal of snakes (Rieppel, 1980a) is referred to as a 'small ossification' which may or may not be present on the quadrate. Rieppel (1980a), however, contended that the stylohyal is present in all alethinophidian snakes (the ontogeny of scolecophidian snakes remains unknown). According to him, the principle of connectivity indicates that the stylohyal corresponds to the tip of the dorsal process of the reptilian stapes, which in 'lizards' forms the intercalary cartilage with no function in sound transmission. In snakes, the stylohyal forms a synovial joint with the stapedial shaft proximally, and fuses with the quadrate distally. In most advanced (macrostomatan) snakes that have lost the suprastapedial process of the quadrate, the stylohyal fuses to the quadrate shaft, but in anilioids and some basal macrostomatans, it fuses to the posteroventral margin of the suprastapedial process. Its degree of ossification is variable among snakes, and the stylohyal generally fails to ossify (but may calcify to a variable degree) in anilioids.

We assume that the vocabulary used by Scanlon & Lee (2000) is motivated by the desire to test the identity of the 'small ossification' and that the recognition by Rieppel (1980a) of the stylohyal as the tip of the dorsal process of the stapes, and its correspondence to the intercalary cartilage of 'lizards', might be viewed as a theory-laden conceptualization of a character, and for that reason rejected. As mentioned above, Frisrup (1992: 51) argued that the introduction of additional restrictions or analyses in character delimitation (of which the principle of connectivity could be construed as one) may 'produce characters that more closely

resemble the information they would like to have.' Accordingly, the putative historical identity of the stylohyal suggested by identifying it as the tip of the dorsal process of the stapes that becomes detached from the latter and attached to the quadrate during ontogeny, might be viewed as just such an 'additional analysis' that could threaten the objectivity of phylogenetic analysis.

Conversely, if one recognizes the stylohyal as a structure that individualizes from the dorsal tip of the stapes through ontogenetic differentiation, the following insights relevant to the analysis of snake relationships obtain: the stylohyal is present in all alethinophidian snakes (perhaps in all snakes; the ontogeny of the scolecophidian stapes remains unknown), and is hence uninformative for the analysis of alethinophidian (or snake) interrelationships; the degree of ossification of the stylohyal is variable, and the absence of a 'small ossification' (Scanlon & Lee, 2000) on the quadrate is therefore no indication for the absence of a stylohyal; the character 'small ossification absent/present' does not refer to the presence or absence of a stylohyal, but rather to the degree of its ossification, which is subject to ontogenetic, individual and taxonomic variation; and finally, this character is at least partially correlated with character 126 of Scanlon & Lee (2000; type of association of the distal end of the stapes to the quadrate).

We conclude that avoiding the designation of conjectural homologies by their proper anatomical term (if available) in order to avoid pre-judgements of putative historical identity is fallacious in principle because this approach cannot be consistently applied. For instance, the stylohyal may be an example of how complex the interpretation of structural correspondence can be (Rieppel, 1980a), but the complexity of structures is in principle a matter of degree, certainly not objectifiable (Wicken, 1984), and so cannot be used as justification for the use of 'unprocessed observation' (Fristrup, 1992). Naming the stylohyal as such may indeed relate to complex background knowledge. But naming the parietal as such in a nontetrapod osteichthyan and a tetrapod, for example, is no less complex, and in this case, even controversial (e.g. Schultze, 1985, 1993; Bjerring, 1995). Naming the parietal as such throughout tetrapods or squamates again bestows putative historical identity upon these elements, yet is an identification never questioned in any tetrapod or squamate analysis.

Reference to structurally correspondent parts by the same anatomical term is a necessary element in the inference of homology, and one that unavoidably relies on the background knowledge of comparative anatomy. In principle, there is no limit of complexity beyond which designating constituent elements of organisms by the same anatomical term (if available)

should be avoided. Similarly, there is, in principle, no limit to what degree the background knowledge of comparative anatomy should or should not be rejected, and/or put to test in any specific analysis. There has been one school of thought, however, which recommended calling into question, even transcending, the background knowledge of comparative anatomy for the sake of *repeatability* and *objectivity* of systematic analysis (Sneath & Sokal, 1973: 11), and that is numerical taxonomy: 'One way to deal with problems of homology is to ignore details of structure' (Sneath & Sokal, 1973: 87). The question is whether a strategy that ignores structural detail still allows the test, and potential refutation, of character hypotheses. We attempt to show below that the answer to that question is negative.

SEARCHING FOR 'THE SAME BUT DIFFERENT' IN COMPARATIVE ANATOMY

Poe & Wiens (2000) stress the lack of explicitness by morphologists as to how they identify or select the characters used in their analyses. This lack of explicitness is viewed as the major cause of debates relating to morphology-based analyses yielding conflicting results with respect to the same set of taxa. 'If the selection of characters remains a "black box" . . . morphological phylogenetics will continue to be vulnerable to attack from those who accuse researchers of manipulating data to reach a preconceived phylogeny' (Poe & Wiens, 2000: 26). True—but none of the authors who have addressed this problem (e.g. Pogue & Mickevich, 1990; Patterson & Johnson, 1997; Poe & Wiens, 2000) have suggested what the explicit criteria for the selection of characters, and for their testability, should be.

Performing cladistic analysis within its traditional falsificationist context, the primary conjecture of homology precedes the 'test of congruence', and has itself been claimed to be subject to the 'test of similarity' (Patterson, 1982). In comparison to congruence, the 'test of similarity' is perhaps somewhat elusive. How exactly do we reject characters? The 'test of similarity' was historically linked to the operational criteria of homology (Patterson, 1982), most cogently argued by Remane (1952). Remane (1952) recognized three 'principal criteria' used in the primary conjecture of homology, i.e. the criterion of topological equivalence (criterion of 'sameness of position'), the criterion of special quality of structures, and the criterion of linkage by intermediate forms. As was argued by Hennig (1966), the recognition of special quality of structures, as well as the recognition of intermediate forms, requires primacy of the criterion of topological correspondence (see also Riedl, 1975; Rieppel, 1988a). Among the different kinds of linkage by intermediate

forms (ontogeny, morphoclines among extant organisms, fossil intermediates), Remane (1952) recognized ontogeny as the most important one. As ontogeny adds a dynamic component to topology, the latter becomes connectivity (Shubin & Alberch, 1986).

As articulated by Remane (1952; see also Riedl, 1975), the operational criteria of homology are all inductive. These criteria only provide guidelines to the search for similarity that results in a primary conjecture of homology. By contrast, a 'test of similarity' requires the possibility to critically evaluate, test and potentially refute, a character hypothesis. The seeming inability to test character hypotheses often results in the stagnation of systematics debates, as evidenced in the current debates about snake origins and tetrapod origins, for example. However, we hope to show below that the operational criteria of homology can be used just as well in the critical discussion, test, and potential refutation, of conflicting character conceptualizations, if they are used deductively.

The first requirement for making character hypotheses testable is the repeatability of the observation that underlies a conjecture of homology according to some technique or standard. As such, morphology-based phylogenetic analyses should use intrinsic, not extrinsic, properties of the organisms under comparison. Because extrinsic properties are attributed to the organism by the observer, they elude another observer following objectifiable techniques or standards (as those provided by topology and connectivity). As Popper (1992: 99) stated: 'it will not satisfy us if he [the observer] tells us all about his feelings of doubt or about his feelings of conviction as to his perceptions' when attempting to falsify a character that constitutes an extrinsic property of the organisms under study. A feature extrinsic to the organism under study entails a much higher degree of subjectivity and is difficult, if not impossible, for another observer to test. For example, in his analysis of squamate relationships, Lee (1998; character 220; modified from Estes *et al.*, 1988) used 'Separable cranial osteoderms tightly connected to skull roof (0), loosely connected to skull roof (1)' as a character. Lee & Caldwell (2000) later modified this observation slightly in their character 248: 'Separable cranial osteoderms. Tightly connected to skull roof, tough separable (0); very loosely connected to skull roof (1).' A character that describes an action taken by the observer relative to the observed is not open to test, as observers will presumably vary in their abilities to remove, and in their approaches to removing, osteoderms from skull roofs. In Lee & Caldwell's (2000) data matrix, the osteoderms are scored as 'very loosely connected to skull roof' in *Lanthanotus* and Varanidae, but 'tough separable' in *Heloderma*, *Shinisaurus*, *Xenosaurus*, Anguillidae, Scincidae, Cordylidae and Lacertidae.

Analysing this character in morphological terms, rather than as an action exerted by the observer on the organisms under comparison, shows that the osteoderms in the head region of *Lanthanotus* and *Varanus* are embedded in, and confined to, the skin, i.e. they are not directly 'connected to' the underlying skull bones (McDowell & Bogert, 1954). The osteoderms in the head region of *Lanthanotus* are very few and much reduced (McDowell & Bogert, 1954: plate 4, fig. 2), while those of *Varanus* (where present) are also reduced yet much more numerous and of a very distinctive morphology (McDowell & Bogert, 1954: plate 12). These morphologies contrast with *Heloderma*, where osteoderms covering the skull are partially or fully fused to the underlying skull bones. In our experience, the osteoderms on the posterior part of the skull roof of *Heloderma* separate more easily than anterior osteoderms, which, in adult specimens, are fully fused to the underlying bones (Rieppel, 1980b). The degree of difficulty of removing osteoderms from the skull roof may be experienced differently by different workers and therefore does not, in itself, constitute an objectively testable character hypothesis. Indeed, in many taxa for which cranial osteoderms have been coded 'tough separable' they are not separable at all, at least in the adult. For some taxa, such as Lacertidae, the ontogenetic fusion of initially free osteoderms to the underlying skull roof remains to be demonstrated. Alternative conceptualizations of the character would appear to be more readily testable by other observers if rooted in reference to topology, such as: osteoderms confined to skin, or partially or fully fused to underlying skull bones.

Apart from representing intrinsic properties of organisms, characters may also be tested and potentially refuted by a greater consideration of anatomical complexity (see Wiley, 1975). For example, Gardiner (1982) homologized hair in mammals with feathers in birds, and this character was refuted by Gauthier *et al.* (1988; see also Oster & Alberch, 1982) for ignoring complexity in both morphology (hairs are interscale features, feathers are not; hairs grow continuously, feathers do not) and ontogeny (hairs arise from dermal invaginations, feathers arise from dermal evaginations). Greater consideration of structural complexity is the path to the test that might be found in topological non-correspondence; in the example here, a test was realized by more detailed study of hair and feather development.

A test may also be realized in comparative ontogenetic studies. For example, a character used in the analysis of snake interrelationships by Rieppel (1988b) was the presence or absence of a free-ending posterior process of the supratemporal (Fig. 1E). As constructed, this character describes the free-ending posterior process of the supratemporal as an autapo-

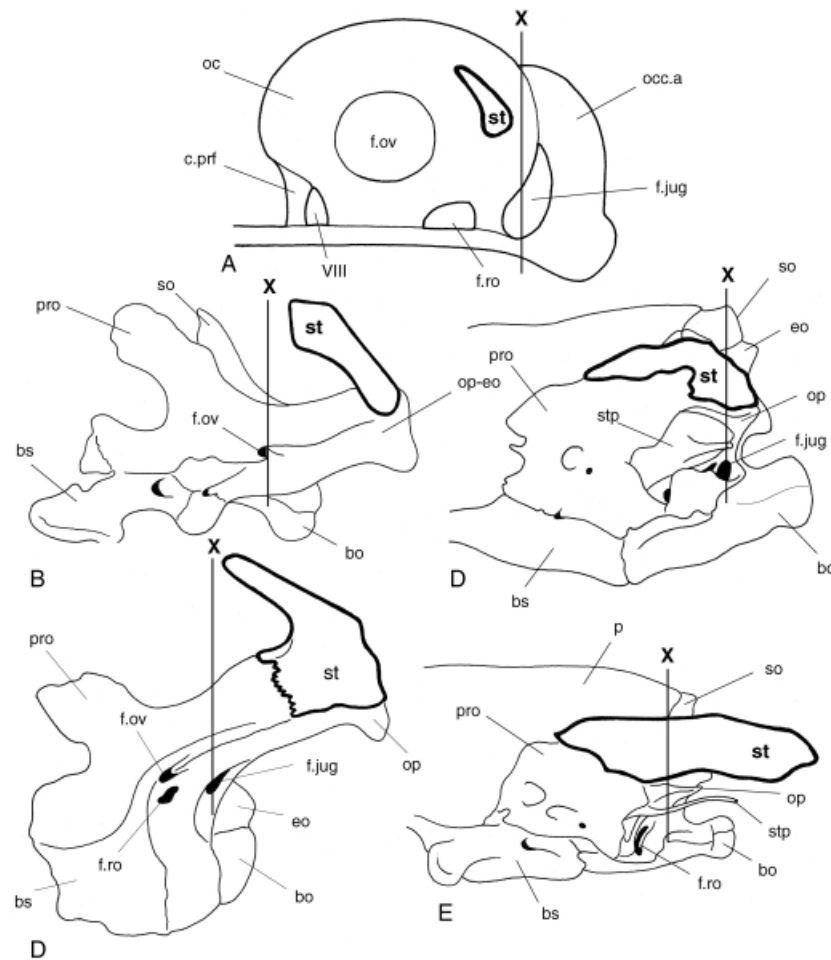


Figure 1. The relationship of the supratemporal to the otic capsule in squamates. (A) Schematic representation of an embryonic squamate; (B) the monitor lizard *Varanus*; (C) the basal (anilioid) snake *Cyindrophis*; (D) the mosasaur *Platecarpus*; (E) the macrostomatan snake *Python*. Not to scale. Abbreviations: bo, basioccipital; bs, basisphenoid; c.prf, commissura praefacialis; eo, exoccipital; f.jug, jugular foramen; f.ov, oval window; f.ro, round window; oc, otic capsule; occ.a, occipital arch; op, opisthotic; op-eo, opisthotic-exoccipital; pro, prootic; so, supraoccipital; st, supratemporal; stp, stapes; VII, passage of the facial nerve; X, passage of the vagus nerve.

morphy of macrostomatan snakes, and has no equivalent in non-macrostomatan snakes or 'lizards.' It cannot therefore be considered an attribute of all the organisms under study and must be scored as absent in some taxa, a procedure that violates a rule for taxonomic characters proposed by Jardine (1967: 137), 'a character must be such that its states are either attributes of whole organisms in all the organisms studied, or attributes of parts homologous in all the organisms studied.' The character was redefined in character 67 of Scanlon & Lee (2000; supplementary information) in their analysis of snake interrelationships: supratemporal projecting greatly beyond otic capsule (0); projecting slightly beyond otic capsule (1); not projecting posteriorly beyond otic capsule (2). In

contrast to Rieppel's character description, the character as defined by Scanlon & Lee (2000) can be coded for all the organisms under study, but this approach to the character could also be seen as testable to a lesser degree for several reasons. First, there is the problem of discriminating objectively between a supratemporal that projects greatly, or only slightly, beyond the otic capsule. This problem is correlated with the difficulty in identifying the posterior end of the otic capsule in the ossified 'lizard' skull with well-developed, laterally or posterolaterally extending paroccipital processes. In the embryonic skull (Fig. 1A), the posterior limit of the otic capsule is easily established as the posterior wall of the cavum cochleare within which ossifies the opisthotic. In the

adult skull, the opisthotic forms a complex with the exoccipital which itself ossifies in the occipital arch behind the otic capsule. Both opisthotic and exoccipital contribute to the formation of the paroccipital process as is present in most 'lizards.' If the posterior extent of the paroccipital process is equated with the posterior limit of the otic capsule, then the supratemporal of varanoids and mosasaurs does not project posteriorly beyond it (Russell, 1967). If, by contrast, the level of the vagus foramen (located in the fissura metotica which separates the posterior wall of the otic capsule from the occipital arch) is chosen as reference for the posterior limit of the otic capsule, the supratemporal lies behind it in varanids and mosasaurs (Figs 1B,D; Russell, 1967; see also Rieppel & Zaher, 2000a).

There exists, however, an even more fundamental difference between the supratemporal of 'lizards' and that of macrostomatan snakes. In 'lizards', the supratemporal starts to ossify in its posterior part, the ossification then extending anteriorly (e.g. Rieppel, 1994a). In 'lizards' with a reduced supratemporal, the latter is correspondingly seen to regress from front to back (Rieppel, 1981). In macrostomatan snakes, the supratemporal is peramorphic (relative to the phylogeny of extant snakes as currently understood: Scanlon & Lee, 2000; Tchernov *et al.*, 2000), and grows out posteriorly during ontogeny (Fig. 1E). This particular assessment of similarity recognizes the free-ending posterior process of the supratemporal as a macrostomatan autapomorphy, but uses ontogeny as an arbiter in the primary conjecture of homology. On the other hand, Jardine (1967: 134) rejects ontogeny as a valid criterion because 'there are many cases where obviously homologous adult structures differ in embryological origin' and 'The Recapitulation Theory is now discredited, and with it the embryological criterion of homology' (Jardine, 1967: 127). Two questions arise from this perspective: how do we know that structures with different embryonic origins are 'obviously' homologous in the adult, and how does Recapitulation Theory relate to ontogeny as a criterion for primary homology?

ONTOGENY AND HOMOLOGY REVISITED

As was noted by Darwin (1859: 449), '... community in embryonic structure reveals community of descent. It will reveal this community of descent, however much the structure of the adult may have been modified and obscured.' In the fourth edition of the *Origin* (1866: 312; see Peckham, 1959), Darwin added: '... community in embryonic structure reveals community of descent; but dissimilarity in embryonic development does not prove discontinuity of descent.' In modern terms, this means that similarity of the onto-

genetic trajectory corroborates a conjecture of homology, whereas dissimilarity of the ontogenetic trajectory does not necessarily refute a conjecture of homology. This observation, i.e. that homologous structures may differ in their ontogenetic pathways, has been much debated in the recent literature (see Hall, 1995; references therein), and has been used to dismiss the role of ontogeny in the primary conjecture of homology. However, as indicated by the quote of Jardine (1967: 127) given above, the relationship of ontogeny to homology has mostly been investigated from a recapitulationist, i.e. from a transformationist or process point of view, when in fact homology is inferred from hierarchical pattern. It remains to be seen whether the role of ontogeny might be reframed in testing primary conjectures of homology.

Hall (1995) presented the most recent review of the role of ontogeny as a criterion of homology, concluding that 'homology can no longer retain its historical links to shared embryonic development' (Hall, 1995: 8). The reason is that 'there are so many examples of homologous structures arising from non-homologous developmental processes.' This conclusion is at odds with the idea that homology of different structures is inferred from the pattern of shared embryonic rudiments, not from shared ontogenetic processes of transformation, as was recognized by von Baer (Rieppel, 1993a; Hall, 1995).

The relationship of ontogeny to phylogeny reconstruction has traditionally been cast in a recapitulationist context (see Rieppel, 1993a; for a review and further references). This approach is rooted in the transformationist tradition, whereby characters are conceptualized as transformation series. The hyomandibula is not only homologous with the stapes, the hyomandibula is also the character that is 'ancestral' to the character 'stapes.' The application of the ontogenetic method to character polarization was motivated by the hope to be able to establish the nature of character transformation empirically, i.e. by observation, instead of having to infer the nature of character transformation on the basis of out-group comparison which implies a *priori* hypotheses of higher level relationships. It is evident that that hope is fulfilled in cases of terminal addition only, and since this is not the universal mode of transformation in ontogeny (Mabee, 1989), the ontogenetic method was rejected, or at least relegated to a method that must be evaluated on a case-by-case basis. It certainly is not a method by which to universally test primary conjectures of homology. But can we use ontogeny from another than this transformational perspective?

It has long been recognized that cladistic analysis cannot recover actual ancestors, but can only recover a hierarchy of *relative* relationships. Based on this insight, Nelson (1994: 137) suggested that 'Cladistics

may possibly be improved if parts of organisms were treated in the same fashion in character (state) trees, with the implication that ancestral characters, too, are artifacts.' The 'hyomandibula' as a character ancestral to 'stapes' is indeed problematic, just as is the notion that 'fishes' are the ancestors of some tetrapod group. If cladistics does not recover direct ancestor–descendant relationships among taxa, then it also does not recover direct ancestor–descendant relationships among characters. If characters are no longer conceptualized as directly ancestral or descendant relative to one another, there is no longer any need to refer to 'homologous' transformational processes of ontogeny in support of primary conjectures of homology. In this way, the ontogenetic method becomes what it had been in the hands of von Baer (Patterson, 1983; Rieppel, 1993a; Larsson, 1998), i.e. a tool which shows the less general condition of form (synapomorphy at a subordinated level of inclusiveness) to differentiate (or individuate) from the more general condition of form (synapomorphy at a higher level of inclusiveness), no matter how that process of differentiation proceeds. Such a conceptualization, divorced from the requirement for direct transformational sequences in ontogeny, may allow for ontogeny to provide one test of primary conjectures of homology.

Hall (1995) compiled a number of examples of homologous structures originating by different developmental processes. The gastrula, he notes, is readily identifiable, always preceded by a blastula stage and always followed by a neurula stage, but processes of gastrulation may differ widely among metazoans. However, the insight that the gastrula originates by different processes in different metazoans requires a previous identification of the gastrula as a homology of Metazoa, and this identification is based upon topological relationships of cell layers (an observation of pattern) derived from a multicellular blastula, no matter by what process this derivation occurs. The alimentary canal is not considered homologous because it differentiates by a process common to all vertebrates, but because it is formed, no matter how, from an ontogenetic rudiment common to all vertebrates, i.e. the endoderm. The central nervous system is considered homologous not because it forms the same way in all vertebrates, but because it forms, no matter how, from an embryonic rudiment common to all vertebrates, i.e. the neural plate. Meckel's cartilage derives from an ontogenetic rudiment common to all gnathostomes, i.e. from mesencephalic-level neural crest (or, at a different level of complexity, from the ventral half of the first visceral arch), and for this reason is considered homologous throughout gnathostomes, no matter how its formation is variously induced. The lens of the vertebrate eye always differentiates from an ectodermal lense placode, no matter

whether through self-differentiation or by induction. A good example provided by Hall (1995) is the development of internal and external cheek pouches in mammals. Again, both types of cheek pouches develop from the same ontogenetic rudiment, i.e. outpocketings of the epithelium lining the inside of the mouth in the embryo, thus demonstrating 'constancy of location and connection, a constancy obscured in adults through differential growth and response to a different inductive environment' (Hall, 1995: 19). But just as potential homologues (recognized on the basis of relative topological relations) can develop along different ontogenetic trajectories, so can a similar developmental background generate very distinct morphologies: 'The transcription factors "distal-less", "engrailed", and "orthodenticle" each have orthologs involved in patterning very different structural features in different metazoan taxa' (Mindell & Meyer, 2001: 435). It is clear, as was stated by Hall (1995: 20), that '*homology is not at the level of developmental processes*', but again, 'Homology is all about *pattern recognition* in the face of change and *not about processes*' (Hall, 1995: 21).

A primary conjecture of homology entails a conceptual element of topological correspondence, as 'sameness' for 'the different' is claimed at some chosen level of structural complexity. A classic example is provided by the homology of the hyomandibula and stapes in gnathostomes (Reichert, 1837; see Rieppel, 1993a; for a review). Given the vastly different appearance of the hyomandibula in sharks and the stapes in mammals, a conjecture of 'sameness' is certainly not trivial, nor is an identity of developmental processes to be expected. However, both structures originate from a shared embryonic rudiment, i.e. the dorsal half of the second visceral arch, and it is at this level of complexity that the 'sameness' of these structures becomes evident. It is on the basis of topology that the hyomandibula and stapes are identified as 'the same' (i.e. as the dorsal half of the second visceral arch, which is a gnathostome homology), and it is the 'differing execution of invariant topology' (Brady, 1994: 16) which creates the difference among the 'same' parts that are hyomandibula and stapes. Referring back to Nelson's (1994) point of view, which is that characters should not be treated as directly ancestral and descendant to each other, the following obtains: The hyomandibula is not ancestral to the stapes, just as 'fishes' are not ancestral to tetrapods. But because tetrapods are nested amongst gnathostomes, and may therefore be assumed to have originated from *some* kind of 'fish' (from some kind of nontetrapod gnathostome), it may seem that the tetrapod stapes must be historically derived from the hyomandibula of some kind of 'fish.' It is this hypothetical ancestor–descendant relationship of some kind of 'fish' to

tetrapods on which the claim is based that the hyomandibula is ancestral to the stapes. In fact, no hyomandibula has ever been transformed into a stapes. Instead, all gnathostomes inherit the information to develop a second visceral arch with a major dorsal (hyomandibula) and ventral (ceratohyal) component (the more general condition of form), while some, but not all, gnathostomes inherit the additional information to form a stapes from the dorsal half of the second visceral arch (the less general condition of form). The shape and pattern of ossification in the dorsal half of the second visceral arch (different 'kinds' of 'hyomandibulae') of non-tetrapod gnathostomes may carry systematic information at less inclusive hierarchical levels among the latter group.

An example of a test of a conjecture of homology on the basis of ontogeny is provided by examining the claims by Zaher & Rieppel (1999) and Lee & Caldwell (2000) that squamates share the occurrence of interdental plates. Historically, interdental plates have been identified only in thecodont dentitions. In crocodiles, the roots of the marginal teeth are set in longitudinal grooves of the tooth-bearing elements (on the maxilla and dentary). Interdental plates develop ontogenetically from front to back within those grooves, separating the roots of the teeth, as well as the dental lamina, into discrete sockets. These interdental plates are formed from alveolar bone, which is defined as bone laid down by 'osteoblasts whose product fills a gutter between buccal and lingual plates of jaw bone' (Osborn, 1984: 570–571). Alveolar bone is thus not part of, but added to, the jaw bone. Furthermore, alveolar bone, and hence the interdental plates, are not resorbed during tooth replacement. The definition and recognition of alveolar bone, and of the interdental plates it forms, is thus tied to ontogeny, and no comparable tissues or structures have so far been identified in, or described for, squamates.

Correspondence of shared embryonic rudiments allows the test of a conjecture of identity and individuality of structures that may differentiate in very different ways in the adult. At the same time, however, the identification of embryonic rudiments as shared characters requires operational criteria of homology itself, and these are again topology, connectivity, and the establishment of a one-to-one relationship of the parts being compared.

TESTING CONJECTURES OF HOMOLOGY WITH THE TOPOLOGY CRITERION

Shared embryonic rudiments indicate the putative historical identity of structures that may appear vastly different in their adult condition. Yet the recognition of those embryonic rudiments as 'the same' is again based on criteria of topology, connectivity, and

in the establishment of a one-to-one relationship of the parts being compared. If there exists a 'test of similarity', it would seem to have to be based on these criteria. Recognition of the importance of these criteria for hypotheses of homology is manifest in Belon's (1555) famous illustration (Fig. 2), which established correspondences based on topological relations (connectivity) and a one-to-one relationship of the elements in the skeleton of a bird and of a human. In order to do so, Belon had to abstract from the specific shape and function of the constituent elements of the skeletons. He did this by illustrating both skeletons as hanging down from a ceiling, which showed the bird skeleton in an abstract (i.e. unnatural) pose, but one that rendered it readily comparable to the human skeleton (Rieppel, 1994b). Here, we will discuss an example, which indicates that topological relations can be used, along with ontogenetic information, to test conjectures of homology.

In his analysis of squamate interrelationships, Lee (1998) found the derived state of the following character to be synapomorphic for mosasaurs and snakes (Pythonomorpha): character 73, Stapedial footplate not surrounded (0), tightly surrounded (1) by bony ridges projecting from lateral surface of braincase. The character 'bony ridges' surrounding the footplate of the stapes proposes only morphological similarity in shape, and does not account for the relative topological relations of the flanges in question. In a later paper, Lee & Caldwell (2000: 934) rejected this character because 'the flanges in mosasaurs tightly encircle only a tiny area around the stapes, while those of snakes encircle a much greater area and might be argued to fail the test of similarity.' Accordingly, it was the relative size of the area surrounded by bony flanges that was considered a potential falsifier of this conjecture of homology, which is at odds with the insight that conjectures of homology may transcend specific form and function, rendering those weak falsifiers of character hypotheses; size is only a function of the specific form and does not relate to topological criteria at all.

Instead, we believe that the character fails the test of similarity for a different reason, namely because of the lack of topological correspondence of the bony flanges in mosasaurs and snakes (Fig. 3). In 'lizards' (Fig. 3B) in general (not just in mosasaurs), the footplate of the stapes is located between the anterior crista prootica and the posterior crista interfenestralis, the latter separating the oval from the round window (Oelrich, 1956). Behind the round window, the 'lizard' braincase carries another crest, the crista tuberalis, which separates the round window from the jugular (vagus) foramen. In the squamate embryo, the crista tuberalis is represented by the cartilaginous subdivision of the fissura metotica. In basal snakes

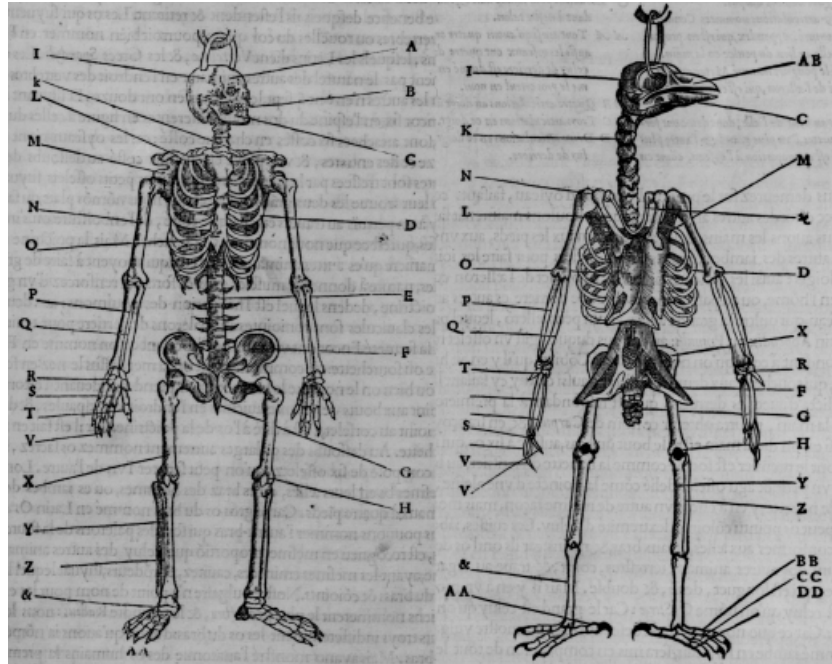


Figure 2. Comparison of the skeleton of man and a bird by Belon 1555; courtesy of the Field Museum Library, Mary W. Runnells Rare Book Room).

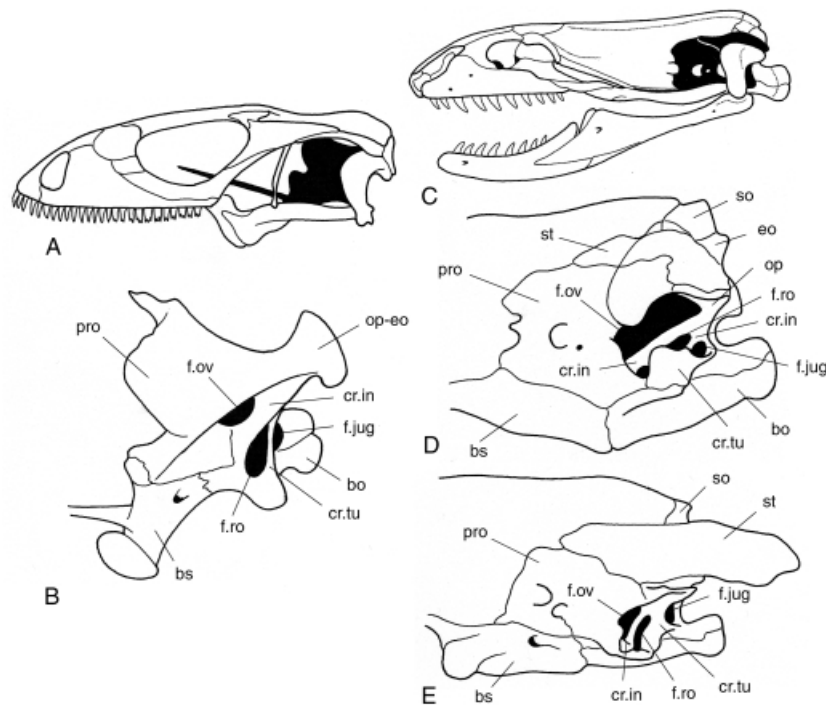


Figure 3. Brainscase structure in squamates. (A) The skull of *Ctenosaura* in left lateral view (redrawn after Oelrich, 1956; Fig. 5); (B) the brainscase of *Ctenosaura* in left lateral view (redrawn after Oelrich, 1956; Fig. 8); (C) the skull of *Cyllindrophis* in left lateral view; (D) the brainscase of *Cyllindrophis* in left lateral view; (E) the brainscase of *Python* in left lateral view. Not to scale. Abbreviations: bo, basioccipital; bs, basisphenoid; cr.in, crista interfenestralis; cr.tu, crista tuberalis; eo, exoccipital; f.jug, jugular foramen; f.ov, oval window; f.ro, round window; op, opisthotic; op-eo, opisthotic-exoccipital; pro, prootic; so, supraoccipital; st, supratemporal.

(Fig. 3D), the footplate of the stapes is surrounded by bony flanges that involve the crista prootica and the crista tuberalis, which together form a crista circumfenestralis. Defined by the crista circumfenestralis is the juxtastapedial recess, within which are located both the oval and the round window. In derived, i.e. macrostomatan snakes, the basal part of the crista interfenestralis is exposed in the ventral rim of the crista circumfenestralis (Fig. 3E). The differentiation of the juxtastapedial recess is related to an elaborate re-entrant fluid circuit of the middle ear in which a pericapsular sinus of the perilymphatic system forms an integral part (Wever, 1978).

The test of similarity for the homology of the bony flanges surrounding the footplate of the stapes should involve the establishment of a one-to-one relationship of the structures involved. These structures are: the crista prootica (first bony flange, located in front of the oval window), the crista interfenestralis (second bony flange, located between the oval and the round window), and the crista tuberalis (third flange, located behind the round window, i.e. between it and the jugular foramen). In 'lizards', it is the first and second flanges, which surround the footplate of the stapes; in basal snakes, it is the first and third flanges; in derived snakes, it is the first and third flanges with some contribution of the second flange.

The example of the crista circumfenestralis is particularly informative of conflicting methods of character delimitation in the debate about snake origins and relationships. Conceptualized as 'bony flanges surrounding stapedial footplate present or absent', the character can be scored as present or absent for *all* taxa subjected to the analysis. Coded as such, the character was found to support the monophyly of Pythonomorpha on the basis of congruence. However, describing the character in that fashion does create a conflict of topological correspondence. Conversely, a description of the character as the absence or presence of a crista circumfenestralis satisfies the test of similarity based on topological correspondence, but renders it an autapomorphy of snakes and hence uninformative for the analysis of the relationships of snakes relative to 'lizards.'

The example of the conceptualization of the crista circumfenestralis as a character in the analysis of squamate relationships also shows that Jardine's (1967: 137) rule (conceptualizing characters such that they can be coded for *all* taxa subjected to the analysis) is really dependent upon taxon sampling, i.e. on the choice of terminal taxa. If, in the analysis of snake relationships among squamates, *Serpentes* is coded as a single terminal taxon (except for fossils in which the crista circumfenestralis remains unknown: Lee, 1998; Lee & Caldwell, 2000), the crista circumfenestralis is arguably an autapomorphy of snakes, and thus unin-

formative for the analysis of snake relationships among squamates. However, if *Serpentes* is split up into several terminal taxa, the detailed morphology of the crista circumfenestralis (posterior closure of the juxtastapedial recess: Tchernov *et al.*, 2000; participation of the crista interfenestralis: Rieppel *et al.* 2002) becomes informative for the analysis of phylogenetic relationships among snakes.

The type of testing described above for conjecturing homology is rigorous and requires in-depth and time-consuming study of structural complexity, which is at odds with recent trends that diminish the role of careful character analysis in morphological systematics. We think the payoff is worth the effort because a higher degree of testability is realized for phylogenetic hypotheses.

IS THE TOPOLOGY CRITERION INFALLIBLE?

The current debate about snake relationships (Coates & Ruta, 2000) is not the first one to suffer from disparity of opinion regarding the 'correct' approach to character conceptualization. Another well-known example was the debate referred to as the 'Haematotherma Affair' by Kirsch & Mayer (1998). One of the characters used in support of the monophyly of *Haematotherma* was the hypothesis of homology of the alisphenoid of mammals with the pleurosphenoid of birds (Gardiner, 1982), while it was well-established that the pleurosphenoid of birds is of neurocranial origin (e.g. Goodrich, 1930), whereas the alisphenoid is, at least in part, of splanchnocranial origin (Presley & Steel, 1976). The different topological relationships of the mammalian alisphenoid and the avian pleurosphenoid are again unequivocally revealed by the ontogenetic rudiments from which these ossifications derive, as well as by their different topological relations to the branches of the trigeminal nerve in the adult.

Not all cases are so straightforward, however. As already mentioned, the establishment of topological relationships among constituent parts of a structure requires a frame of reference which must be held constant (as part of the background knowledge) while a particular character hypothesis is under test. The case of the reptilian epipterygoid (absent in birds) does perhaps provide an example of confounding topological change affecting a landmark structure. In the amphisbaenian *Trogonophis*, the maxillary branch of the trigeminal nerve passes medial to the epipterygoid, whereas in all other reptiles it passes lateral to the epipterygoid (Bellairs & Kamal, 1981). Topological relations of skeletal elements to nerves or blood vessels are traditionally used in the primary conjecture of homologies, but obviously appear to fail in this

example. Examples like this one might be used to reject the principle of connectivity and its role as a potential falsifier of character hypotheses. But again: just as outgroup comparison requires a higher-level hypothesis of relationship that can be tested in its own right, so does the establishment of topological relationships require a frame of reference that can be tested in its own right. For the question again has to be asked how it is that we know that we are dealing with the epipterygoid and with the maxillary branch of the trigeminal nerve that have changed their topological relationships in *Trogonophis*? The answer is that it is possible to identify this change of topological relations between the epipterygoid and the maxillary branch of the trigeminal nerve because the identifications of these structures are independently testable. The epipterygoid is well characterized by its topological relationships and connectivity to the pterygoid and palatobasal articulation due to the fact that it ossifies in the ascending process of the palatoquadrate (small but present in *Trogonophis*: Bellairs, 1949), and the maxillary branch of the trigeminal nerve is identifiable by its relation to the Gasserian ganglion and its projections to brain centres on the one hand, and its peripheral targets of innervation on the other (Song & Boord, 1993). In general, however, innervation patterns are widely and successfully used in conjectures of homology, and emphasize the need to recognize topological relationships in terms of connectivity (Shubin & Alberch, 1986) between parts that stand in a one-to-one relationship to each other.

Nevertheless, there are cases where topological relations change more radically than is the case with the epipterygoid and trigeminal nerve branches in *Trogonophis*. Two long-standing problems of homology assessment are that the occipital condyle is formed from different segments in different vertebrates (Goodrich, 1913; deBeer, 1971), and that tetrapod limbs develop from different body segments in different taxa as do the nerve plexus innervating them (deBeer, 1971; Goodrich, 1913).

Even worse is the case of the teleost pelvic fin (Dollo, 1909), which has been described as 'migrat[ing] through segments' (Winterbottom, 1974: 226). There is important variability among teleosts with respect to the location of the pelvic fins relative to the vertebral segments, relative to the segments from which their innervation derives, and relative to the pectoral fin (Parenti & Song, 1996). Conjecture of the pelvic fins as homologues throughout teleosts cannot therefore be based on a strict correlation of their position and innervation relative to serially homologous body segments (the same appears to be true for the occipital condyle). Yet the paired appendages of gnathostomes have not been recognized as homologues with refer-

ence to their position relative to serially homologous body segments. The paired appendages of gnathostomes were recognized as outgrowths of the ventrolateral body ridge (Jarvik, 1980; Wolffian ridge in tetrapods) extending along the trunk (i.e. the part of the vertebrate body located between the head and the tail), and establishing a one-to-one relationship between them allows us to identify the pectoral appendages, connected to the dermal skeleton at the back end or behind the skull, as different from the pelvic appendages. Additional information, as provided by the connectivity expressed in the pattern of innervation, is required to analyse such complex modifications as the transformation of the pelvic fin into a ventral sucking disk in gobiesoid fishes (Parenti & Song, 1996). Indeed, the relationship of the pelvic appendages relative to body segments is a problem of serial homology (of body segments), not of taxic homology (of paired appendages as a gnathostome [vertebrate?] synapomorphy). Conversely, a different relationship to body segments provides no basis to test, and potentially refute, the homology of paired appendages.

The pelvic fin of teleosts is perhaps one of the most extreme examples of a structure changing its position relative to the body axis and relative to the pectoral fin. What is made clear by the examples discussed above, however, is that the topology criterion still holds in the test of primary conjecture of homologies even if structures change *relative* position. Their homology can still be conjectured and tested with reference to topological correspondence of early ontogenetic rudiments and connectivity.

ONTOGENETIC REPATTERNING: LOSS OF A ONE-TO-ONE RELATIONSHIP

It is possible to encounter instances in comparative anatomy where a one-to-one relationship of structures cannot be established, even among organisms that are thought to be closely related on other grounds. Such instances are hypothetically explained as the result of 'ontogenetic repatterning' (Wake & Roth, 1989). Ontogenetic repatterning refers to presumed processes where changes of ontogeny result in fundamental changes of morphology that disrupt the one-to-one relationship of constituent parts. A simple example is the amniote astragalus. Believed to have originated by fusion of the amphibian tibiale, intermedium and proximal centrale (Peabody, 1951), the astragalus originates from a single ossification centre within a single cartilaginous precursor in extant reptiles. Although the cartilaginous precursor of the astragalus forms through the fusion of multiple procartilaginous precursors, it is impossible to establish a one-to-one relationship between these early centres

of cartilage condensation and the single ossification that represents the astragalus. In turtles and lepidosaurs, a single proximal tarsal cartilage provides the matrix within which both proximal tarsal ossifications (astragalus, calcaneum) originate from a single ossification centre each (Rieppel, 1993b). In chameleons, a single proximal tarsal cartilage again originates by the fusion of separate procartilagenous rudiments, but within that proximal tarsal cartilage ossifies a single bone that cannot unequivocally be interpreted as either astragalus or calcaneum, because a one-to-one relationship cannot be established with the tarsal ossifications in other 'lizards' (Rieppel, 1993c).

Ontogenetic repatterning may result in a novel bauplan, which renders a comparison across a broad array of terminal taxa problematical, if not impossible. One of the best-known and much discussed examples is provided by turtles (Rieppel & Reisz, 1999). Our understanding of the phylogenetic relationships of turtles remains very incomplete due to their highly derived body plan that results from ontogenetic repatterning. Lee (1993) presented a scenario intended to explain the origin of turtles from pareiasaurs. In the context of this scenario, the turtle carapace evolved from the fusion of ancestral osteoderms, while the scapula is believed to have assumed its position inside the rib cage by a posterior shift of the pectoral girdle. In fact, the complex morphology of the turtle carapace cannot be explained by fusion of osteoderms (Rieppel & Reisz, 1996) because it comprises endoskeletal components, and the position of the scapula inside the rib-cage has been shown to result not from a posterior shift of the pectoral girdle but instead from early ontogenetic deviation (Burke, 1989, 1991), which also involved repatterning of the paraxial mesoderm (Rieppel & Reisz, 1999). In the case of turtles, ontogenetic repatterning resulted in a radically novel bauplan which causes problems of comparison with the adult morphology of other amniotes, and which may also be the reason why a well-corroborated hypothesis of turtle relationships has so far remained elusive (Rieppel & Reisz, 1999).

Another example of early ontogenetic repatterning is the snake body, which is largely a consequence of the cephalad extension of Hox gene expression domains, resulting in a thoracalization of the snake body from the skull back to a sharp boundary of Hox gene expression in the area of the last precloacal vertebra (Cohn & Tickle, 1999). In later developmental stages, a series of vertebrae behind that posterior boundary of Hox gene expression carry distally bifurcating lymphapophyses. Although the occurrence of pelvic rudiments in scolecophidians, anilioids and basal macrostomatans shows the cloacal region of snakes to broadly correspond to the sacral region of

'lizards', a one-to-one relationship cannot be established between the two sacral ribs typical of 'lizards' (other than amphisbaenians and dibamids) with the more numerous (five to six are generally well-developed) lymphapophyses of snakes. The sacral ribs are fused with the respective vertebrae in 'lizards', whereas in snakes the first or the first two lymphapophyses articulate with the respective vertebrae, while the more posterior ones are fused (Hoffstetter & Gasc, 1969). The attempt to code this character across all squamates is likely to create confusion, as ontogenetic repatterning has obscured topological equivalence.

In their re-description of the fossil snake *Pachyrhachis*, Lee & Caldwell (1998: 1542) described a distally expanded sacral rib which 'appears forked; however, this may be the result of breakage.' In a different paper (Lee, 1998; char. 189), the same structure was coded as a shared derived character of *Pachyrhachis* and Serpentes with a character definition that reads: 'distally forked cloacal ribs ("lymphapophyses")' absent (0)/present (1) (see also Lee & Caldwell, 2000; char. 209). To that character definition and coding was added the caveat: '*Pachyrhachis* has been coded with a forked sacral rib, but this is only tentative due to poor preservation' (Lee, 1998: 404; deleted in Lee & Caldwell, 2000). By contrast, Scanlon & Lee (2000; supplementary information) later coded *Pachyrhachis* for the character state 'no forked free ribs or lymphapophyses', when in fact a first (articulated) lymphapophysis is present, as is typical for snakes in general (Hoffstetter & Gasc, 1969: 287). By contrast, other snakes were characterized by the presence of 'three or more free-ending cloacal vertebrae with lymphapophyses' (Scanlon & Lee, 2000; character 183). The history of this character shows several permutations of its definition which revolve around two main problems: the putative historical identity of 'lizard' sacral ribs with the lymphapophyses of snakes in general, and the topological equivalence in terms of numbers in particular. Both of these issues cannot be resolved, which may be the reason for another character definition offered by Caldwell (2000: 190): 'Pelvis: when present, external to ribcage with sacral contact (0); when present, lies within ribcage, sacral contact absent.' In *Pachyrhachis*, the pelvic rudiments lie essentially below and behind the much-shortened posterior-most thoracic (cloacal) ribs, and the conjecture of a presence or absence of a sacral contact will critically depend on the interpretation of the incompletely and poorly preserved 'sacral' (cloacal) region of *Pachyrhachis*. Assuming the presence of a broken sacral rib will indicate the presence of a sacral contact; observing the presence of an anterior, free and distally bifurcated lymphapophysis will indicate the absence of a sacral contact.

The ontogenetic repatterning of the snake body which resulted in its thoracalization (Cohn & Tickle, 1999) obviously creates confusion, not only with respect to the analysis and comparison of the sacral and cloacal regions, respectively, in 'lizards' and snakes, but also in the comparison of the neck, or cervical region (Caldwell, 2001). As discussed by Cohn & Tickle (1999), the same Hox gene expression domain which determines the trunk region of tetrapods, and hence the location of forelimb and pectoral girdle development, extends to the level of the pectoral fins in fishes. This reflects the fact that, compared to 'fishes', the differentiation of a neck in tetrapods resulted from the topological dissociation and posterior dislocation of the pectoral girdle (and its associated fore-limb) from the back end of the skull. In snakes, these Hox gene expression domains extend anteriorly to the back end of the skull (Cohn & Tickle, 1999), as does the peritoneal cavity (Cundall & Greene, 2000). This ontogenetic repatterning obliterates the possibility of distinguishing a cervical from a trunk region in snakes. In the absence of a pectoral girdle and forelimbs, Caldwell (2001) proposed instead to identify cervical vertebrae in snakes on the basis of the presence of hypapophyses. But, by that standard, snakes with hypapophyses that extend along the entire precloacal vertebral column (Hoffstetter & Gasc, 1969: 290) would have lost the trunk and consist of a neck and tail only. Furthermore, in some 'lizards' (particularly skinks), elongation of the body and regression of limbs and girdles renders the distinction of the cervical and dorsal regions problematic (Hoffstetter & Gasc, 1969: 281). Given ontogenetic repatterning, it is difficult to claim that some ancestral (by comparison to 'lizards') cervical vertebrae are inherited by snakes. There is no possibility of establishing a one-to-one relationship between cervical and dorsal vertebrae across 'lizards' and snakes. Snakes have a precloacal vertebral column and a tail, as suggested by Hoffstetter & Gasc (1969), and in that respect are autapomorphic relative to other tetrapods.

In cases such as those discussed above, where the establishment of topological equivalence is impossible, and in the case of fossil taxa where the assessment of topological relations in ontogeny are impossible, the testing of homology conjectures may have to lie in subsidiary criteria, such as special quality and intermediate forms—criteria that go beyond topology.

BEYOND TOPOLOGY

As discussed above, Remane (1952) recognized three 'principal criteria' used in the primary conjecture of homology, i.e. the criterion of topological equivalence, the criterion of special quality of structures, and the

criterion of linkage by intermediate forms. As was argued by Hennig (1966), the recognition of special quality of structures, as well as the recognition of intermediate forms, requires a primacy of the criterion of topological correspondence (see also Riedl, 1975; Rieppel, 1988a), because to establish a special quality or intermediacy of a structure requires the previous recognition of the potential equivalence of the structures based on topology. However, topology can still fail as a test of character hypotheses, or it may be unattainable, as in fossil taxa, in which case either the alternative primary conjectures of homology must remain equivocal, or criteria other than topological equivalence must be invoked in an attempt to test character hypotheses.

For example, it has to the present day not been possible to identify the putative historical identity (as expressed by primary conjectures of homology) of the supra- and postorbital ossifications in snakes. The discussion of superior and posterior circumorbital bones in snakes has invoked the postfrontal, the postorbital, and the neomorph (by comparison to 'lizards') supraorbital. The lack of stringent topological criteria caused by the potential for ontogenetic fusion of postorbital and postfrontal in 'lizards' (varanids: Fejervary, 1935), by the ossification of a single postorbital element from two separate ossification centres in some snakes (*Acrochordus*: Rieppel & Zaher, 2001), and the lack of intermediate forms (Haas, 1964, 1968), as well as the potential for the differentiation of neomorph elements (supraorbital), have rendered the identification of postorbital bones in snakes controversial. Presumably because of this problem, Scanlon & Lee (2000; supplementary information), in their analysis of snake interrelationships, simply code for 'postorbital ossification(s)'. It should be noted, however, that the postfrontal portion of the postorbitofrontal described for *Pachyrhachis* by Lee & Caldwell (1998) is a separate (broken?) element, i.e. not continuous with the postorbital (Rieppel & Zaher, 2000b; Fig. 15, claims to the contrary by Lee & Caldwell, 2000; notwithstanding). Identified as the broken descending flange of the parietal by Rieppel & Zaher (2000b), it might still be seen as worthwhile to investigate the putative identity of this bone with the supraorbital seen in some basal macrostomatans such as pythons. Such a primary conjecture of homology could have a major impact on tree topology, placing *Pachyrhachis* close to pythons, which indicates the necessity for an attempt to work out the topological relationships of the elements under consideration in future analyses, or to subject alternative interpretations to the test of congruence.

In other cases, the primary test of homology may remain equivocal, but the situation can perhaps be further analysed, and character argumentation

further specified, by recourse to 'special quality,' Remane's (1952) second criterion. A case in point would be the putative presence or absence of a jugal in the fossil snake *Pachyrhachis* (Fig. 4). The presence of a jugal in any snake is highly conjectural. In fact, the only snake it had been described for previously is the fossil *Dinilyisia* (Estes *et al.*, 1970), but a re-examination of the specimen indicated that the putative jugal is, in fact, part of the ectopterygoid (Caldwell & Albino, cited in Lee, 1998; Caldwell, 2000). This finding is important because *Dinilyisia* would have been the only squamate with a broad suborbital portion of the jugal, which has a flat dorsal surface approached by the vertically descending postorbital. The fossil snake *Pachyrhachis* shows a postorbital that closely approaches that of macrostomatan snakes such as *Python* or *Boa* in its morphology as well as in its articulation to the parietal (Rieppel & Zaher, 2000b; fig. 15). In the intact skull, the vertically descending postorbital appears to have provided an almost complete posterior border to the orbit, terminating in a blunt tip. This tip approaches the smooth dorsal surface of an elongated element, which, as preserved, lies in the floor of the orbit (best seen on the right side of the skull: Rieppel & Zaher, 2000b; fig. 15), overlapping the posterior end of the maxilla (Fig. 4B). The bone, as preserved, is dislocated to some degree with its anterior end turned medially or its posterior end turned laterally, but due to its topological position

in front of the postorbital and in the floor of the orbit, it was identified by Lee & Caldwell (1998, 2000) as a jugal. An alternative interpretation would be to consider the element in question an ectopterygoid, broken across the posterior end of the maxilla. If *Pachyrhachis* has a jugal, all other snakes share the synapomorphic loss of a jugal; this is one character that influences the finding of a basal position for *Pachyrhachis* to all other snakes (Lee & Caldwell, 1998). However, if the element is conjectured to represent the ectopterygoid, its topological relations suggest the presence of a macrostomatan-type ectopterygoid in *Pachyrhachis*, because only in macrostomatans does the ectopterygoid overlap the posterior end of the maxilla broadly enough to extend anteriorly to a level below the ventral tip of the postorbital, and beyond into the floor of the orbit (Tchernov *et al.*, 2000).

Because topology and connectivity do not unequivocally resolve the putative identity of the bone in question, the criterion of special quality may perhaps be brought to bear on this issue. In all squamates that have a jugal, the suborbital process of the latter is a relatively slender, three-dimensional structure, with an anterior end that tapers off along the dorsomedial surface of the maxilla, unless it is received in a well-defined contact between maxilla, lacrimal and prefrontal. This contrasts with the 'suborbital' element in *Pachyrhachis*, which is a flat sheet of bone that widens anteriorly, thus resembling the anterior part of a macrostomatan ectopterygoid. In all squamates that have a jugal, the latter turns dorsally behind the orbit, meeting the postorbital in an obliquely overlapping contact (in those 'lizards' that have a complete postorbital arch). This contrasts with the 'suborbital' element in *Pachyrhachis*, which represents a flat sheet of bone that is still relatively broad posteriorly. It could be argued therefore that the relationship between this 'suborbital' element and the postorbital in *Pachyrhachis* more closely resembles, in its detailed morphology, the relationship between the ectopterygoid and the postorbital in macrostomatan snakes such as *Boa* or *Python* (Fig. 4C), than the relationship between postorbital and jugal in those squamates that have an unequivocally identifiable jugal (Fig. 4A).

The criterion of special quality can play a subordinate role in the test, and potential refutation, of character hypotheses, if used in conjunction with the criterion of topological equivalence. Recently, interesting evidence has emerged suggesting that 'special quality' can be based on a sequence of gene expression that is separate from the sequence of gene expression that determines topology. The most famous example for this is certainly the debate surrounding the origin of birds. Cladistic analysis shows birds to be nested within theropod dinosaurs, but whereas the latter

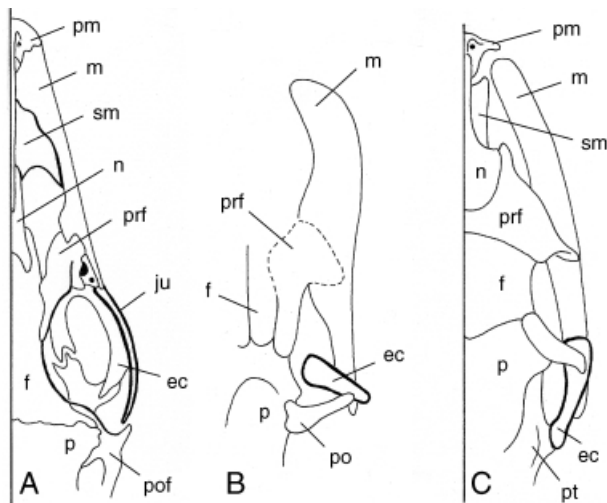


Figure 4. The circumorbital bones in squamates. (A) *Varanus*; (B) the fossil snake *Pachyrhachis*; (C) the macrostomatan snake *Epicrates* (redrawn after Frazzetta, 1959; Fig. 8). Not to scale. Abbreviations: ec, ectopterygoid; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; pof, postfrontal; prf, prefrontal; pt, pterygoid; sm, septomaxilla.

retain digits I, II and III in their hand, birds lose the digits I and V, retaining the digits II, III and IV (Burke & Feduccia, 1997). To solve this conundrum, Wagner & Gauthier (1999) proposed the so-called frame shift hypothesis, which calls for a dissociation of pattern formation from the individualization of the elements of that pattern. Although this hypothesis remains untested, it has generated research that demonstrated the independence of pattern formation (digit number) from the individualization (differentiation) of digit identity (Drossopoulou *et al.*, 2000). The experiment involved the production of the same number of supernumerary digits, with a subsequent induction of different digit identities among these by a manipulation of successive phases of gene expression(s). It should be noted, however, that the recognition of the existence of supernumerary digits, and of different digit identities (II, III or IV) of those supernumerary digits, is possible only with reference to the pentadactyl hand with the standard phalangeal formula 2-3-4-5-3. That is, the special quality, i.e. identity, of different digits is established for digits that have already been individualized on the basis of topology.

In certain cases, the impossibility of establishing the 'special quality' of a structure may render a primary conjecture of homology impossible, even though the structures in question conform to the criterion of topological equivalence. A well known example is the debate about the putative identity of a choana in lungfish, rhipidistians and tetrapods (Rosen *et al.*, 1981). The example is based on the premise that structures observed in fossils are necessarily interpreted in the light of an extant model, and that such interpretations hence run the risk of being biased by preconceived notions of relationships (Patterson, 1981). Empirical research led to the recognition that there is a topologically equivalent opening in the floor of the nasal capsule, and a gap in the underlying dermal palate, in the fossil rhipidistian *Eusthenopteron*, as well as in the extant cladistian *Polypterus* (Rosen *et al.*, 1981). The opening in the floor of the nasal capsule transmits the choana in tetrapods, but a choana is absent in *Polypterus*. Using tetrapods as a model for the interpretation of *Eusthenopteron*, the latter will be conjectured to share a potential synapomorphy with tetrapods, viz. the choana. This assumption could be criticized as being based on the preconception that rhipidistians are the putative sister-group of tetrapods. As an alternative, *Polypterus* might be chosen as a model for the interpretation of *Eusthenopteron*, in which case there would no longer be any reason to assume the presence of a choana in this fossil.

Remane's (1952) third criterion, the criterion of intermediate forms, may also play a secondary role in testing character hypotheses. This criterion is implemented via dense taxon sampling and the inclusion of

fossil taxa that may break up long branches and shed light on ambiguous homology propositions. At the bottom line, special quality and intermediate forms can add to the test of primary conjectures of homology that are equivocal with respect to the topology criterion, but the latter has prevalence. If the interpretation of structures remains equivocal with respect to topology, 'special quality' and intermediate forms, the obvious solution to the problem would be to subject alternative interpretations to analysis in order to test their respective significance for phylogeny reconstruction.

SYNTHESIS VERSUS ANALYSIS

Arguments about characters, their similarity, and their significance for 'affinities' (i.e. relationships in pre-evolutionary terms) go back to the very beginnings of comparative anatomy. The most famous example is no doubt the debate between Étienne Geoffroy Saint-Hilaire and Georges Cuvier (see Rieppel, 1988a, 2001; Brady, 1994; Panchen, 2001; for analysis and comments). The debate originated with Geoffroy Saint-Hilaire entertaining the idea of 'analogies' ('homologies' in modern usage) shared by organisms that Cuvier had classified in different groups ('embranchements') that he believed to be radically different and hence completely separated from one another. On the basis of topological relations (connectivity), Geoffroy found 'analogies' (homologues) among Cuvier's Vertebrata and Articulata, although the putative 'analogue' of the nerve cord in the two groups required a rotation of the organisms around 180°, since the nerve cords of articulates are ventral, and those of chordates are dorsal (Panchen, 2001). Although there is commonality of the underlying dorsoventral signalling system in 'articulates' (invertebrates) and vertebrates (Panchen, 2001; references therein), there is little doubt that the dorsal side of vertebrates and the ventral side of invertebrates are non-homologous in phylogenetic terms.

The search for the 'hidden bond of connexion' between organisms (Darwin, 1859: 433) sparked the debate between Geoffroy and Cuvier. This debate was interpreted by Panchen (2001) as one between a functionalist–adaptationist programme as advocated by Cuvier (more accurately, a teleological programme: Brady, 1994), and a programme searching for 'relationships' as advocated by Geoffroy. While this is certainly a legitimate interpretation, there are other possible interpretations. J.W. Goethe characterized Cuvier as the analytical mind, tirelessly seeking distinctions and differences, whereas Geoffroy to him represented the synthetic mind, seeking underlying similarities of form in order to raise the study of organismic diversity to a new and higher level of understanding (Rieppel, 2001).

As is shown by the example of Geoffroy finding a similarity of the dorsal side in a vertebrate with the ventral side of an articulate, rejection of topology as a potential falsifier of character hypotheses removes all methodological limits to the search for morphological similarity that may render anything comparable to anything else. In Panchen's (2001: 45; but see Rieppel, 1946) rendition, Geoffroy's support for the thesis proposed by Meyranx and Laurencet (which actually sparked the historic debate in 1830) implied that the vertebrate body becomes comparable to—and hence linked to—that of a mollusc if it is visualized as being 'bent backwards at the umbilicus, so that the nape of the neck was attached to the buttock . . . Cuvier, however, was easily able to refute the proposal.'

The problem with the search for morphological similarity revealing the 'hidden bond of community of descent' (Darwin, 1859: 426) is that mental abstraction in character delimitation can be carried to levels that transcend correspondence of topological relations (or other subordinate criteria for the test of character hypotheses), thus proclaiming morphological similarity beyond the realm of testability. Worse, the discussion of tetrapod origins (Schultze & Trueb, 1991) shows how easy it is for preconceived notions of relationships to influence character delimitation. Because there is no theory-free observation (contra Fristrup, 1992; see the discussion above), the search for potential homologies pursued in the light of a preferred theory of relationships may likely provide confirming primary conjectures of homology and these may also be found to be congruent. A critical attitude towards character delimitation cannot be found in the deliberate, theory-free and methodologically unconstrained search for the same in the different, but instead must respect due consideration of structural complexity and stress distinctions between the (potential) nonequivalence of topological relations as they are exposed by the analysis of structural complexity. This allows primary conjectures of homology to be tested and (potentially) refuted.

DISCUSSION AND CONCLUSIONS

The ideas presented in this paper stemmed mainly from our desire to understand the limits of current debates in systematics and whether those limits can be transcended. It has become apparent that at least some debates in systematics devolve into what appear to be irresolvable arguments over character interpretations. If character descriptions are conceptualized as basic statements within a falsificationist framework, irresolvable arguments over character interpretations illustrate the breakdown of the scientific language. For example, the analysis of the relationships of fossil

snakes with well-developed hind limbs has sparked an intense debate about the origin and evolution of snakes (see the review by Coates & Ruta, 2000). Given that this debate involves the same taxa and the same (cladistic) method of analysis, the reason for the widely disparate results must lie in different character interpretations (Rieppel & Kearney, 2001). We believe that this is amply documented by the discussion of a selected number of disparate character descriptions presented above.

We believe that the test of congruence provides a necessary, but not a sufficient, basis for cladistics to be an empirical science. By contrast, we hope to have shown in the discussion above that it is possible to have greater explicitness in the delimitation of morphological characters, and that explicitness itself provides the basis for a test and a potential refutation of character hypotheses. Explicitness is achieved by an in-depth consideration of structural complexity, and by reference to the classical (operational) criteria of (primary) homology: equivalence of topological relations as the primary criterion, used in conjunction with special quality, and intermediate conditions of form (ontogenetic, fossil).

It must be acknowledged that there may be cases in which topological transpositions occur or in which ontogenetic connectivity is disrupted, such that a test of character hypotheses based on topology (connectivity) may no longer be possible. A test of character hypotheses may also fail to yield unequivocal results. Individual workers may choose to include or exclude such characters from their analysis, or to run the analysis both ways. Although such cases may be encountered, and some have been discussed above (see also Remane, 1952; for further examples), the test of character hypotheses is ultimately based on the assumption that topological relations and ontogenetic connectivity are preserved in the absence of contrary evidence. If this assumption is rejected, comparative anatomy falls back on overall similarity, and does not allow for a critical evaluation, test and potential refutation of primary conjectures of homology. The same caveat that applies to the test of primary conjectures of homology also applies to the test of congruence (M. Coates, personal communication), which is tied to Hennig's auxiliary principle that states that homology must be assumed in the absence of evidence to the contrary.

We must also acknowledge that there is not one way, and one way only, to define morphological characters for phylogenetic analysis and that others may disagree with our approach to character analysis and/or the characters themselves. Indeed, if progress is to be made in science, there must be potential for changing rules and methods and, in some ways, the approach suggested here may be viewed as too traditional, or

even outdated. It is, however, unrealistic to expect agreement of morphology-based phylogenetic analyses if these analyses are based on vastly different approaches to morphological character analysis. One may argue for other approaches to character analysis, but if the classical operational criteria of homology are abandoned, there must be explicitness as to which alternative approach to character conceptualization is pursued so that character hypotheses satisfy the criteria for Popper's 'basic statements'. Such alternative methods of character delimitation must be explicit not only about the operational criteria underlying conjectures of homology, but also about what would constitute a potential test, and refutation, of those conjectures of homology.

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REFERENCES

- deBeer GR. 1971.** Homology: An unsolved problem. *Oxford Biology Readers*, No. 11. London: Oxford University Press.
- Bellairs Ad'A. 1949.** The anterior brain-case and interorbital septum of Sauropsida, with a consideration of the origin of snakes. *Journal of the Linnean Society (Zoology)* **41**: 482–512.
- Bellairs Ad'A, Kamal AM. 1981.** The chondrocranium and the development of the skull in recent reptiles. In: Gans, C, Parsons, TS, eds. *Biology of the Reptilia*, Vol. 11. London: Academic Press, 1–263.
- Belon P. 1555.** *L'Histoire de la Nature Des Oyseaux*. Paris: Guillaume Cavellat.
- Bjerring HC. 1995.** The parietal problem: how to cut this Gordian knot? *Acta Zoologica, Stockholm* **76**: 193–302.
- Brady RH. 1994.** Pattern description, process explanation, and the history of morphological sciences. In: Grande, L, Rieppel, O, eds. *Interpreting the Hierarchy of Nature. From Systematic Patterns to Evolutionary Process Theories*. San Diego: Academic Press, 7–31.
- Brower AVZ, Schawaroch V. 1996.** Three steps of homology assessment. *Cladistics* **12**: 265–272.
- Burke AC. 1989.** Development of the turtle carapace: implications for the evolution of a novel bauplan. *Journal of Morphology* **199**: 363–378.
- Burke AC. 1991.** The development and evolution of the turtle body plan: inferring intrinsic aspects of the evolutionary process from experimental embryology. *American Zoologist* **31**: 616–627.
- Burke AC, Feduccia A. 1997.** Developmental patterns and the identification of homologies in the avian hand. *Science* **278**: 666–668.
- Caldwell MW. 2000.** On the phylogenetic relationships of *Pachyrhachis* within snakes: a response to Zaher (1998). *Journal of Vertebrate Paleontology* **20**: 187–190.
- Caldwell MW. 2001.** On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in squamates. *Journal of Vertebrate Paleontology* **20**: 720–735.
- Chalmers AF. 1986.** *Wege der Wissenschaft*. Berlin: Springer Verlag.
- Chang MM. 1991.** 'Rhipidistians', Dipnoans, and Tetrapods. In: Schultze, HP, Trueb, L, eds. *Origins of the Higher Groups of Tetrapods. Controversy and Consensus*. Ithaca: Comstock Publishing Associates, 3–28.
- Clark JM. 1992.** What good are fossils? *Journal of Vertebrate Paleontology* **12**: 532–536.
- Coates M, Ruta M. 2000.** Nice snake, shame about the legs. *TREE* **15**: 503–507.
- Cohn MJ, Tickle C. 1999.** Developmental basis of limblessness and axial patterning in snakes. *Nature* **399**: 474–479.
- Cundall D, Greene HW. 2000.** Feeding in snakes. In: Schwenk, K, ed. *Feeding, Form, Function, and Evolution in Tetrapod Vertebrates*. San Diego, CA: Academic Press, 293–333.
- Darwin C. 1859.** *On the Origin of Species*. London: John Murray.
- Dollo L. 1909.** Les Téléostéens à Ventrales abdominales secondaires. *Verhandlungen der K.K. Zoologisch-Botanischen Gesellschaft in Wien* **59**: 135–140.
- Drossopoulou G, Lewis KE, Sanz-Ezquerro JJ, Nikbakht N, McMahon AP, Hofmann C, Rickle C. 2000.** A model for anteroposterior patterning of the vertebrate limb based on sequential long- and short-range Shh signaling and Bmp signaling. *Development* **127**: 1337–1348.
- Estes R, deQuieroz K, Gauthier J. 1988.** Phylogenetic relationships within Squamata. In: Estes, R, Pregill, G, eds. *Phylogenetic Relationships of the Lizard Families*. Stanford, CA: Stanford University Press, 119–281.
- Estes R, Frazzetta TH, Williams EE. 1970.** Studies on the fossil snake *Dinilysia patagonica* Woodward. Part I. Cranial morphology. *Bulletin of the Museum of Comparative Zoology* **140**: 25–74.
- Farris SJ. 1983.** The logical basis of phylogenetic analysis. In: Platnick, NI, Funk, VA, eds. *Advances in Cladistics*, Vol. 2. New York: Columbia University Press, 7–36.
- Farris SJ. 1995.** Conjectures and refutations. *Cladistics* **11**: 105–118.
- Fejervary GJ. 1935.** Further contributions to a monograph on the Megalanidae and fossil Varanidae—with notes on recent varanians. *Annales Historico-Naturales Musei Nationalis Hungarici* **29 (Pars. Zoologica)** **1935**: 1–130.
- Frazzetta TH. 1959.** Studies on the morphology and function of the skull in the Boidae (Serpentes). Part 1. Cranial

- differences between *Python sebae* and *Epicrates cenchris*. *Bulletin of the Museum of Comparative Zoology* **119**: 453–472.
- Fristrup K. 1992.** Character: current usages. In: Keller, EF, Lloyd, EA, eds. *Keywords in Evolutionary Biology*. Cambridge, MA: Harvard University Press, 45–51.
- Gaffney ES. 1979.** An introduction to the logic of phylogeny reconstruction. In: Cracraft, J, Eldredge, N, eds. *Phylogenetic Analysis and Paleontology*. New York: Columbia University Press, 79–111.
- Gardiner BG. 1982.** Tetrapod classification. *Zoological Journal of the Linnean Society* **74**: 207–232.
- Gardiner BG. 1993.** Haematothermia: warm-blooded amniotes. *Cladistics* **9**: 369–395.
- Gauthier JA. 1986.** Saurischian monophyly and the origin of birds. In: Padian, K, ed. *The Origin of Birds and the Evolution of Flight*. San Francisco: California Academy of Sciences, 1–55.
- Gauthier JA, Kluge AG, Rowe T. 1988.** Amniote phylogeny and the importance of fossils. *Cladistics* **4**: 104–209.
- Goodrich ES. 1913.** Metameric segmentation and homology. *Quarterly Journal of Microscopical Science* **59**: 227–248.
- Goodrich ES. 1930.** *The Structure and Development of Vertebrates*. London: McMillan.
- Haas G. 1964.** Anatomical observations on the head of *Liotyphlops albirostris* (Typhlopidae, Ophidia). *Acta Zoologica, Stockholm* **45**: 1–62.
- Haas G. 1968.** Anatomical observations on the head of *Anomalepis aspinosus* (Typhlopidae, Ophidia). *Acta Zoologica, Stockholm* **49**: 63–139.
- Hall BK. 1995.** Homology and development. *Evolutionary Biology* **28**: 1–37.
- Hanson NR. 1958.** *Patterns of Discovery*. Cambridge, UK: Cambridge University Press.
- Hawkins JA, Hughes CE, Scotland RW. 1997.** Primary homology assessment, characters and character states. *Cladistics* **13**: 275–283.
- Hennig W. 1966.** *Phylogenetic Systematics*. Urbana, IL: University of Illinois Press.
- Hillis DM, Wiens JJ. 2000.** Molecules versus morphology in systematics. Conflicts, artifacts, and misconceptions. In: Wiens, JJ, ed. *Phylogenetic Analysis of Morphological Data*. Washington, DC: Smithsonian Institution, 1–19.
- Hoffstetter R, Gasc JP. 1969.** Vertebrae and ribs of modern reptiles. In: Gans, C, Parsons, TS, Bellairs Ad A, eds. *Biology of the Reptilia*, Vol. 1. London: Academic Press, 201–310.
- Jardine N. 1967.** The concept of homology in biology. *British Journal for the Philosophy of Science* **18**: 125–139.
- Jarvik E. 1980.** *Basic Structure and Evolution of Vertebrates*. London: Academic Press.
- Kirsch JAW, Mayer GC. 1998.** The platypus is not a rodent: DNA hybridization, amniote phylogeny and the palimpsest theory. *Philosophical Transactions of the Royal Society of London B353*: 1221–1237.
- Kluge AG. 1989.** A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology* **38**: 7–25.
- Kluge AG. 1997a.** Testability and the refutation and corroboration of cladistic hypotheses. *Cladistics* **13**: 81–96.
- Kluge AG. 1997b.** Sophisticated falsification and research cycles: consequences for differential character weighting in phylogenetic systematics. *Zoologica Scripta* **26**: 349–360.
- Kluge AG. 2001.** Philosophical conjectures and their refutation. *Systematic Biology* **50**: 322–330.
- Lakatos I. 1974.** Falsifikation und die Methodologie wissenschaftlicher Forschung. In: Lakatos, I, Musgrave, A, eds. *Kritik und Erkenntnisfortschritt*. Braunschweig: Vieweg, 89–189.
- Larsson HCE. 1998.** A new method for comparing ontogenetic and phylogenetic data and its application to the evolution of the crocodylian secondary palate. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **210**: 345–367.
- Lee MSY. 1996.** Correlated progression and the origin of turtles. *Nature* **379**: 811–815.
- Lee MSY. 1998.** Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Zoological Journal of the Linnean Society* **65**: 369–453.
- Lee MSY, Caldwell MW. 1998.** Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. *Philosophical transactions of the Royal Society of London B352*: 1521–1552.
- Lee MSY, Caldwell MW. 2000.** *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. *Journal of Paleontology* **74**: 915–937.
- Liem KF, Bemis WE, Walker WF, Grande L. 2001.** *Functional Anatomy of the Vertebrates*. Fort Worth, TX: Harcourt College Publishers.
- Mabee P. 1989.** An empirical rejection of the ontogenetic polarity criterion. *Cladistics* **5**: 409–416.
- McDowell SB, Bogert CM. 1954.** The systematic position of *Lanthanotus* and the affinities of anguinomorph lizards. *Bulletin of the American Museum of Natural History* **105**: 1–142.
- Mindell DP, Meyer A. 2001.** Homology evolving. *TREE* **16**: 434–440.
- Nelson G. 1994.** Homology and Systematics. In: Hall, BK, ed. *Homology: the Hierarchical Basis of Comparative Biology*. London: Academic Press, 101–149.
- Oelrich TM. 1956.** *The Anatomy of the Head of Ctenosaura pectinata* (Iguanidae). Miscellaneous Publications, Museum of Zoology, University of Michigan, 94, 1–122.
- Osborn JW. 1984.** From reptile to mammal: evolutionary considerations of the dentition with emphasis on tooth attachment. In: Ferguson, MWJ, ed. *The Structure, Development and Evolution of Reptiles*. London: Academic Press, 549–574.
- Oster G, Alberch P. 1982.** Evolution and bifurcation of developmental programs. *Evolution* **36**: 444–459.
- Owen R. 1843.** *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals. Delivered at the Royal College of Surgeons, in 1843*. London: Longman, Brown, Green and Longmans.
- Panchen AL. 2001.** Étienne Geoffroy St.-Hilaire: father of ‘evo-devo’? *Evolution and Development* **3**: 41–46.
- Parenti LR, Song J. 1996.** Phylogenetic significance of

- the pectoral–pelvic fin association in acanthomorph fishes: a reassessment using comparative neuroanatomy. In: Stiassny, MLJ, Parenti, LR, Johnson, GD, eds. *Interrelationships of Fishes*. New York: Academic Press, 427–444.
- Patterson C. 1981.** Significance of fossils in determining evolutionary relationships. *Annual Reviews of Ecology and Systematics* **12**: 195–223.
- Patterson C. 1982.** Morphological characters and homology. In: Joysey, KA, Friday, AE, eds. *Problems of Phylogenetic Reconstruction*. London: Academic Press, 21–74.
- Patterson C. 1983.** How does phylogeny differ from ontogeny. In: Goodwin, BC, Holder, N, Wylie, CC, eds. *Development and Evolution*. Cambridge: Cambridge University Press, 1–31.
- Patterson C, Johnson GD. 1997.** The data, the matrix, and the message: comments on Begle's 'Relationships of the Osmeroid Fishes'. *Systematic Biology* **46**: 358–365.
- Peabody FE. 1951.** The origin of the astragalus of reptiles. *Evolution* **5**: 339–344.
- Peckham M. 1959.** *The Origin of Species by Charles Darwin. A Variorum Text*. Philadelphia: University of Pennsylvania Press.
- Pimentel RA, Riggins R. 1987.** The nature of cladistic data. *Cladistics* **3**: 201–209.
- dePinna MCC. 1991.** Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**: 367–394.
- Poe S, Wiens JJ. 2000.** Character selection and the methodology of morphological phylogenetic. In: Wiens, JJ, ed. *Phylogenetic Analysis of Morphological Data*. Washington, DC: Smithsonian Institution. 20–36.
- Pogue MG, Mickevich MF. 1990.** Character definitions and character state delineation: the *bête noire* of phylogenetic inference. *Cladistics* **6**: 319–361.
- Popper KR. 1972a.** *Objective Knowledge: an Evolutionary Approach*. Oxford: Oxford University Press.
- Popper KR. 1972b.** *Conjectures and Refutations: the Growth of Scientific Knowledge*. London: Routledge and Kegan Paul.
- Popper KR. 1992.** *The Logic of Scientific Discovery*. London: Routledge.
- Presley R, Steel FLD. 1976.** On the homology of the alisphenoid. *Journal of Anatomy* **121**: 441–459.
- Reichert C. 1837.** Über die Visceralbogen der Wirbelthiere im allgemeinen und deren Metamorphosen bei den Vögeln und Säugethieren. *Archiv für Anatomie, Physiologie, und Wissenschaftliche Medizin* **1837**: 120–222.
- Remane A. 1952.** *Die Grundlagen Des Natürlichen Systems, der Vergleichenden Anatomie und der Phylogenetik*. Leipzig: Akademische Verlagsgesellschaft.
- Riedl R. 1975.** *Die Ordnung Des Lebendigen*. München: Paul Parey.
- Rieppel O. 1980a.** The sound transmitting apparatus of primitive snakes and its phylogenetic significance. *Zoomorphology* **96**: 45–62.
- Rieppel O. 1980b.** The phylogeny of anguimorph lizards. *Denkschriften der Schweizerischen Naturforschenden Gesellschaft* **94**: 1–86.
- Rieppel O. 1981.** The skull and jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus* and *Feylinia*. *Journal of Zoology, London* **195**: 493–528.
- Rieppel O. 1988a.** *Fundamentals of Comparative Biology*. Basel: Birkhäuser-Verlag.
- Rieppel O. 1988b.** A review of the origin of snakes. *Evolutionary Biology* **22**: 37–130.
- Rieppel O. 1993a.** The conceptual relationship of ontogeny and phylogeny: The taxic approach. *Evolutionary Biology* **27**: 1–32.
- Rieppel O. 1993b.** Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *Journal of Vertebrate Paleontology* **13**: 31–47.
- Rieppel O. 1993c.** Studies on skeleton formation in reptiles. II. The postembryonic development of the skeleton in *Chamaeleo hoehnelii* (Reptilia: Chamaeleoninae). *Herpetologica* **49**: 66–78.
- Rieppel O. 1994a.** Studies on skeleton formation in reptiles. VI. Patterns of ossification in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia: Squamata). *Journal of Herpetology* **28**: 145–153.
- Rieppel O. 1994b.** Homology, topology, and typology: the history of modern debates. In: Hall, BK, ed. *Homology: the Hierarchical Basis of Comparative Biology*. London: Academic Press, 63–100.
- Rieppel O. 2001.** *Etienne Geoffroy Saint-Hilaire (1772–1844)*. In: Jahn, J, Schmitt, M, eds. *Darwin & Co*. München: C.H. Beck, 157–175.
- Rieppel O, Kearney M. 2001.** The origin of snakes: limits of a scientific debate. *Biologist* **48**: 110–114.
- Rieppel O, Kluge AG, Zaher H. 2002.** Testing the phylogenetic relationships of the Pleistocene snake *Wonambi naracoortensis* Smith. *Journal of Vertebrate Paleontology*, in press.
- Rieppel O, Reisz RR. 1999.** The origin and early evolution of turtles. *Annual Review of Ecology and Systematics* **30**: 1–22.
- Rieppel O, Zaher H. 2000a.** The braincases of mosasaurs and *Varanus*, and the relationships of snakes. *Zoological Journal of the Linnean Society* **129**: 489–514.
- Rieppel O, Zaher H. 2000b.** The intramandibular joint in squamates, and the phylogenetic relationships of the fossil snake *Pachyrhachis problematicus* Haas. *Fieldiana (Geology) n.s.* **43**: 1–69.
- Rieppel O, Zaher H. 2001.** The development of the skull in *Acrochordus granulatus* (Schneider) (Reptilia: Serpentes), with special consideration of the otico-occipital complex. *Journal of Morphology* **249**: 252–266.
- Rieppel. 1984.** Atomism, transformism and the fossil record. *Zoological Journal of the Linnean Society* **82**: 17–32.
- Robert JS. 2001.** Interpreting the homeobox: metaphors of gene action and activation in development and evolution. *Evolution and Development* **3**: 287–295.
- Rosen DE, Forey PL, Gardiner B, Patterson C. 1981.** Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bulletin of the American Museum of Natural History* **167**: 159–276.
- Russell DA. 1967.** Systematics and morphology of American mosasaurs. *Peabody Museum of Natural History, Yale University, Bulletin* **23**: 1–240.

- Scanlon JD, Lee MSY. 2000.** The Pleistocene serpent *Wonambi* and the early evolution of snakes. *Nature* **403**: 416–420.
- Schultze HP. 1985.** The panderichthyid fish *Elpistostege*: a close relative of tetrapods? *Palaeontology* **28**: 293–309.
- Schultze HP. 1991.** A comparison of controversial hypotheses on the origin of tetrapods. In: Schultze, HP, Trueb, L, eds. *Origins of the Higher Groups of Tetrapods. Controversy and Consensus*. Ithaca: Comstock Publishing Associates, 29–109.
- Schultze HP. 1993.** Patterns of diversity in the skulls of jawed fishes. In: Hanken, H, Hall, BK, eds. *The Skull*, Vol. 2. Chicago: The University of Chicago Press, 189–254.
- Schultze HP, Trueb L, eds. 1991.** Origins of the higher groups of tetrapods. *Controversy and Consensus*. Ithaca: Comstock Publishing Associates.
- Shubin NH, Alberch P. 1986.** A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* **20**: 319–387.
- Sneath PHA, Sokal RR. 1973.** *Numerical Taxonomy. The Principles and Practice of Numerical Classification*. San Francisco: W.H. Freeman.
- Song J, Boord RL. 1993.** Motor components of the trigeminal nerve and organization of the mandibular arch muscles in vertebrates. *Acta Anatomica* **148**: 139–149.
- Tchernov E, Rieppel O, Zaher H, Polcyn MJ, Jacobs LJ. 2000.** A new fossil snake with limbs. *Science* **287**: 2010–2012.
- Wagner GP. 2001.** Characters, units, and natural kinds: an introduction. In: Wagner, GP, ed. *The Character Concept in Evolutionary Biology*. San Diego: Academic Press, 1–10.
- Wagner GP, Gauthier JA. 1999.** 1,2,3 = 2,3,4: a solution to the problem of the homology of the digits in the avian hand. *Proceedings of the National Academy of Sciences* **96**: 5111–5116.
- Wake DB, Roth G. 1989.** The linkage between ontogeny and phylogeny in the evolution of complex systems. In: Wake, DB, Roth, G, eds. *Complex Organismal Functions: Integration and Evolution in Vertebrates*. New York: John Wiley & Sons, 361–377.
- Wever EG. 1978.** *The Reptile Ear*. Princeton: Princeton University Press.
- Wicken JS. 1984.** On the increase in complexity in evolution. In: Ho, MW, Saunders, P, eds. *Beyond Neo-Darwinism*. London: Academic Press, 89–112.
- Wiley EO. 1975.** Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. *Systematic Zoology* **24**: 233–243.
- Winterbottom R. 1974.** A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy of Natural Sciences of Philadelphia* **125**: 225–317.
- Zaher H, Rieppel O. 1999.** Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. *American Museum Novitates* **3271**: 1–19.