

## **Similarity, parsimony and conjectures of homology: The chelonian shoulder girdle revisited**

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### **Abstract**

Much has been written about the definition and recognition of biological homology. Homology is usually defined as similarity inherited from a common ancestor (e.g., papers in Hall, 1994). It is recognised through cladistic analysis: Patterson (1982) and de Pinna (1991) have cogently argued that homology can be equated with synapomorphy (a shared evolutionary novelty uniting a monophyletic group). Such identification involves two stages: first, a possible homology is proposed on the basis of morphological similarity. This similarity might be structural, topological, developmental, or any combination thereof. Next, a cladistic analysis is performed, involving the trait in question and all other informative traits identified. If the trait is congruent with the resultant phylogeny, it is accepted as homologous in all taxa which possess it. If the trait is incongruent with the phylogeny, it is interpreted as homoplasious in certain taxa. This has been termed the test of congruence (Patterson, 1982; de Pinna, 1991).

Rieppel (1996) has recently suggested that the test of congruence might be circular, and that as a result certain inferences about the evolution of the chelonian shoulder girdle (Lee, 1996) are poorly substantiated. Here I argue that the test of congruence is not circular, and that the disputed conclusions about the evolution of chelonian shoulder girdle can be defended on the basis of parsimony. More generally, I suggest how considerations of parsimony can and should be used to arbitrate between conflicting conjectures of homology that are *both* congruent with an accepted phylogeny.

### Is the congruence test circular?

Rieppel (1996) has made the important point that the test of congruence only evaluates a particular hypothesis of homology (e.g., structure A in taxon A is homologous with structure B in taxon B). If this hypothesis passes the congruence test, it is provisionally accepted. But it has not been evaluated against *alternative* hypotheses of homology (e.g., structure A in taxon A is homologous with structure X in taxon B). Thus, even if a particular hypothesis of homology is corroborated by the congruence test, there might still exist an alternative, conflicting hypothesis of homology which also passes the test and which explains the observed morphological pattern just as successfully. For this reason, Rieppel (p. 1395) suggested that the congruence test "may entail a serious element of circularity".

According to dictionary definitions, a circular argument is an invalid form of reasoning in which "a proposition is used to establish a conclusion, and afterward the proposition is justified by means of the very conclusion that it was previously used to establish" (de Queiroz, 1996, p. 702). Thus, in order for the test of congruence to be circular, the following must occur. The conjecture of homology must result in a phylogeny where all taxa with that putative homologue form a clade, and that phylogeny in turn must be used to support the initial conjecture of homology.

It will be clear that this is almost never the case. Unless the phylogenetic signal in the data is very weak, the initial conjecture of homology will not have the above effect on tree topology. Thus, the proposition (homology) does not affect the "conclusion" (phylogeny). Since the phylogeny is (except in rare instances) independent of the initial conjecture of homology, it can be legitimately used to test this conjecture. If the conjecture passes this test, it is provisionally accepted. Of course, the fact remains that other (conflicting) conjectures of homology might pass the same test, and explain the morphological observations just as elegantly. However, this problem is a universal feature of the scientific method. A hypothesis consistent with observed data is provisionally retained, but there will always be the possibility that there exists another hypothesis consistent with the data (Popper, 1959).

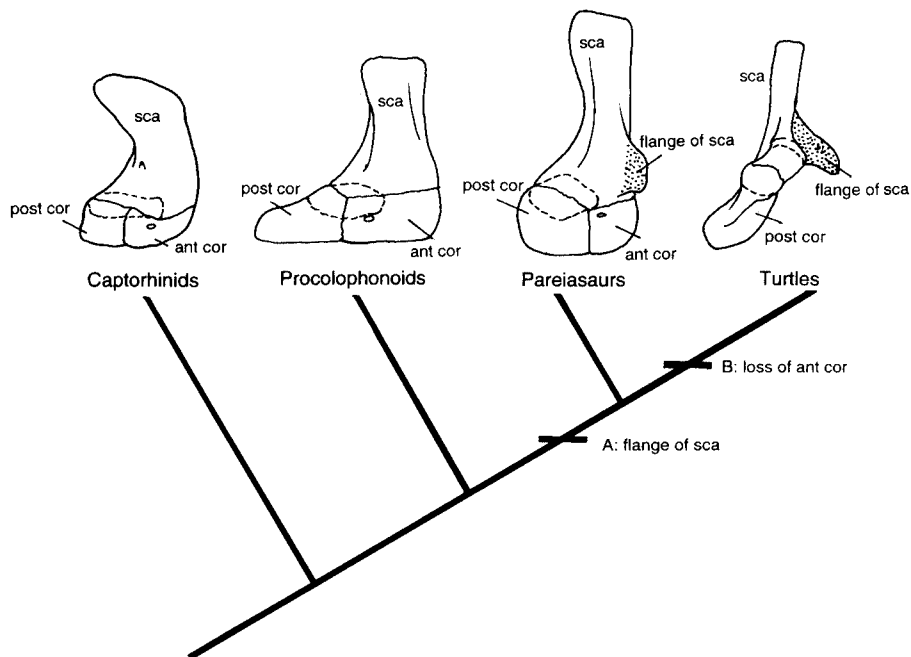
The test of congruence will be circular only in certain instances where the phylogenetic signal in the data is very weak. In such circumstances, it is conceivable a particular conjecture of homology, when included in a cladistic analysis, changes tree topology in such a way as to make all the taxa with the putative homology form a clade, whereas previously they were not united. Such instances, however, are undoubtedly rare: I know of no example of a worker justifying an assumption of homology on the basis of a phylogeny that rests on that particular morphological hypothesis.

### Parsimony and conjectures of homology

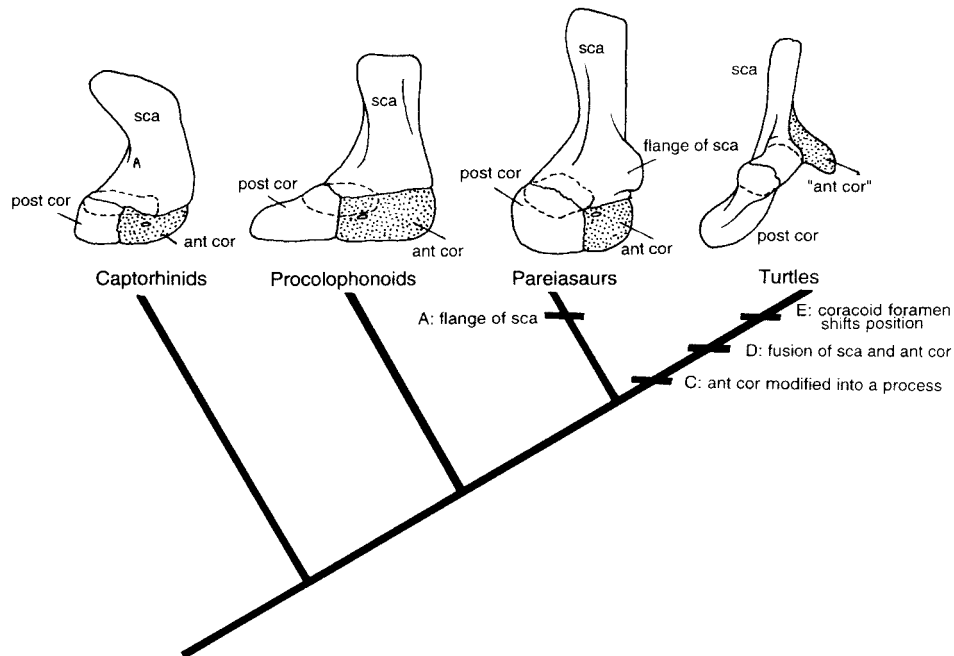
Thus, as demonstrated above, even if we accept that the test of congruence does not always arbitrate between conflicting conjectures of homology, the test is not

circular except in very rare instances. It should also be mentioned that usually the test of congruence *does* arbitrate between conflicting conjectures of homology – when one hypothesis is congruent and the other is not. Nevertheless, the problem identified by Rieppel (1996) remains. When alternative (and conflicting) hypotheses of homology are both congruent with the accepted phylogeny, how does one choose between them?

Rieppel (1996) discussed an example of this dilemma involving the homologies of the shoulder girdle in turtles (Lee, 1996). A more complete description of the relevant anatomical structures can be found in Lee (1996) and references therein. Briefly, as shown in Figures 1 and 2, the endochondral shoulder girdle (scapulocoracoid) in primitive reptiles, such as captorhinids and procolophonoids, consists of a scapula (lacking any anterior process) and two discrete coracoids. The coracoid foramen is positioned entirely within the anterior coracoid. In pareiasaurs, the



**Fig. 1.** The scapulocoracoid in turtles and related reptiles in right lateral view. The phylogeny is the one used in Lee (1996) and Rieppel (1996). Changes required to explain the morphology of the entire scapulocoracoid in all taxa are indicated. These are the changes implied if one assumes that the acromion process in turtles and acromion-like process in pareiasaurs (shaded) are homologous. The data matrix for the relevant scapulocoracoid characters is shown in Table 1. Abbreviations: ant cor – anterior coracoid; post cor – posterior coracoid; sca – scapula.



**Fig. 2.** The scapulocoracoid in turtles and related reptiles in right lateral view. The phylogeny is the one used in Lee (1996) and Rieppel (1996). Changes required to explain the morphology of the entire scapulocoracoid in all taxa are indicated. These are the changes implied if one assumes that the acromion process in turtles and anterior coracoid in other reptiles (shaded) are homologous. The data matrix for the relevant scapulocoracoid characters is shown in Table 2. Abbreviations as in Figure 1.

scapulocoracoid consists of a scapula with an anterior, acromion-like<sup>1</sup> process, and two discrete coracoids. As in other primitive amniotes, the coracoid foramen is positioned entirely within the anterior coracoid. Because the anterior coracoid and acromion-like process co-occur in pareiasaurs, the acromion-like process cannot be a modified anterior coracoid, and must be an extension of the scapula. In turtles the scapulocoracoid consists of a scapula with an anterior acromion process, and a single discrete coracoid. The coracoid foramen remains small in primitive turtles such as *Proganochelys*, where it is positioned between the acromion process and the coracoid (Gaffney, 1990). It is greatly enlarged in derived turtles.

The phylogenetic framework for this discussion is the cladogram in Lee (1995; Figs. 1 and 2). At this point, the caveat must be made that this phylogeny is not universally accepted: in particular, alternative views exist that turtles are related to procolophonoids (Laurin and Reisz, 1995) or, more controversially, advanced

<sup>1</sup> Because the homology of the process in pareiasaurs and turtles is under dispute, and much of the discussion in this paper concerns only one structure or the other, I will use different terms for them to avoid confusion. The structure in pareiasaurs will be termed the "acromion-like process", while the structure in turtles will be termed the "acromion process".

diapsids (Rieppel and de Braga, 1996; but see Lee, 1997 and Wilkinson et al., 1997). However, as emphasised by Rieppel (1996), this does not affect the methodological argument investigated here, which is: if two conflicting hypotheses of homology are consistent with a particular phylogeny, is there any way to arbitrate between them? I will therefore accept the phylogeny in Lee (1995) for the purposes of example only – as did Rieppel (1996) even though he disagreed with it (Rieppel, 1995; Rieppel and de Braga, 1996).

Lee (1996) suggested that the acromion process in turtles is homologous to the acromion-like process in pareiasaurs (Hypothesis 1), and noted that this was consistent with his phylogeny (Lee, 1995) in which pareiasaurs and turtles are nearest relatives. Rieppel (1996) preferred an alternative hypothesis proposed earlier by Gaffney (1990): that the acromion process in turtles is a modified anterior coracoid (Hypothesis 2), and thus could not be homologous with the acromion-like process in pareiasaurs, which is an extension of the scapula (see above). Rieppel (1996) made the important observation that this hypothesis is *also* consistent with the phylogeny in Lee (1995): the loss of the anterior coracoid, and origin the acromion process, both occur at the base of turtles (assuming, of course, non-homology with the acromion-like process in pareiasaurs). The two changes diagnose the same clade (turtles) on the phylogeny: this is exactly the pattern expected if the anterior coracoid evolved directly into the acromion, leading to simultaneous “loss” of the anterior coracoid and “origin” of the acromion.

My feeling is that Hypothesis 2 does not really pass the initial test of similarity, from which conjectures of homology are derived, and thus should not have been proposed for evaluation by congruence at all. The acromion of turtles is very different from the anterior coracoid of primitive reptiles (including pareiasaurs), and this conjecture of homology seems strained. Furthermore, anterior processes on the scapula have evolved in therapsids (e.g. Kemp, 1982; King, 1990) and diapsids (e.g., Benton, 1990; Sereno, 1993) – always from extensions of the scapula, and never from modification of a coracoid. My impression is that Hypothesis 1 passes the initial test of similarity quite comfortably: the acromion-like process of pareiasaurs and the acromion process of all basal turtles (Gaffney, 1990; Rougier et al., 1995) are both anteriorly-directed flanges located on the anteroventral edge of the scapula. However, this argument is obviously subjective and thus not compelling – Rieppel (1996) and Gaffney (1990) clearly think that the acromion of turtles is similar enough to the anterior coracoid of primitive amniotes to warrant an initial conjecture of homology.

However, there is a more objective method to arbitrate between these conflicting conjectures of similarity, and it involves parsimony. Each hypothesis about the homology of the acromion process of turtles entails particular consequences for the homology and evolution of the other structures of the shoulder girdle. For instance, the assumption that the turtle acromion is a modified anterior coracoid (Hypothesis 2) implies that the anterior coracoid in turtles has fused with the scapula and changed its shape from a plate-like structure to a process. It also implies that the acromion-like process on the scapula of pareiasaurs evolved independently. Conversely, the assumption that the acromion in turtles is homologous to the acromion-

like structure on the pareiasaur scapula (Hypothesis 1) implies a very different set of changes. It is therefore possible to compare hypotheses 1 and 2 in terms of global parsimony: which hypothesis results in the more parsimonious explanation of the evolution of the entire shoulder girdle in the taxa concerned<sup>2</sup>.

Thus, conflicting “conjectures of homology” are not subjective similarity assessments that cannot be tested *against each other* if they are both congruent with an accepted phylogeny. Rather, their relative merits can be determined on the basis of global parsimony. The “better” hypothesis should result in the more globally parsimonious interpretation of the evolution of all relevant traits. A good conjecture of homology (and its correlates), if consistent with a phylogeny, will explain many similarities as homologies, and result in a highly parsimonious overall tree. Very few evolutionary changes will be required in order to explain all the morphological differences of the relevant organisms. A poor conjecture of homology (and its correlates), on the other hand, even if consistent with a phylogeny, will not explain very much similarity as homology, and result in a less parsimonious overall tree. Many more evolutionary changes will need to be assumed in order to explain all the morphological differences of the relevant organisms. Simply put, the conjecture of homology based on the greater similarity will give the more parsimonious the overall tree.

Given that the phylogeny in Lee (1995) is strongly corroborated based on that particular data set (but see caveat above), it is clear that alternative codings of the acromion process (and related changes) will not change tree topology. Hypotheses 1 and 2 can therefore be evaluated against this phylogeny, tentatively accepted as correct (Lee, 1995; Rieppel, 1996), in order to determine which is more globally parsimonious.

### *Hypothesis 1*

The hypothesis that the acromion of turtles is homologous to the acromion-like structure of pareiasaurs (Lee, 1996) implies:

- (A) The anterior process of the scapula evolved once, in the common ancestor of turtles and pareiasaurs.
- (B) The anterior coracoid is lost in turtles.
- (C) The shape of the anterior coracoid in turtles cannot be determined.

<sup>2</sup> Pattern cladists (e.g. Gardiner, 1993) might object by arguing that detailed interpretations about evolutionary transformations should follow, rather than precede, phylogenetic reconstruction. However, such an approach is impossible: during character analysis, every time different structures are coded as alternative states of the same character, one is assuming homology and thus, implying transformation. In any case, it is possible (but awkward) to couch the above arguments in non-transformational terms. For instance, “the assumption that the turtle acromion is a modified anterior coracoid . . . implies that the acromion-like process on the scapula of pareiasaurs evolved independently” can be rephrased as “if one codes the acromion in turtles as an anterior coracoid, then the acromion-like process in pareiasaurs must be coded as a separate character, since the acromion-like process and an anterior coracoid *both* occur in pareiasaurs and only the latter can be equivalent to the acromion in turtles”.

- (D) The anterior coracoid is not fused to the scapula in turtles.  
 (E) The coracoid foramen in turtles retains its original position. In captorhinids, procolophonoids, and pareiasaurs it is positioned within anterior coracoid, i.e., between the scapula and posterior coracoid. Turtles have lost the anterior coracoid, but the foramen still retains the same topological relationships with the remaining structures, i.e. it is positioned between the scapula and posterior coracoid.

The data matrix that results from this hypothesis is shown in Table 1, and the implied changes necessary to explain the form of the shoulder girdle in all the relevant taxa are shown in Fig. 1. Only two changes are implied: origin of the anterior process of the scapula in the common ancestor of pareiasaurs and turtles, and loss of the anterior coracoid in turtles.

### *Hypothesis 2*

The hypothesis that the acromion of turtles is a modified anterior coracoid (Gaffney, 1990; Rieppel, 1996) implies:

- (A) The anterior process of the scapula in pareiasaurs evolved independently from the acromion (= anterior coracoid) in turtles.  
 (B) The anterior coracoid is retained in turtles.  
 (C) The anterior coracoid changes shape, from the plate-like structure characteristic of captorhinids, procolophonoids and pareiasaurs into the process-like structure of turtles.  
 (D) The anterior coracoid is completely fused to the scapula in turtles, so that it resembles an anterior process of the scapula.  
 (E) The position of the coracoid foramen has changed in turtles. In captorhinids, procolophonoids, and pareiasaurs it is positioned within anterior coracoid, i.e. between the scapula and posterior coracoid. In turtles, it is now between the anterior coracoid ("acromion") and the posterior coracoid.

The data matrix that results from this hypothesis is shown in Table 2, and the implied changes necessary to explain the form of the shoulder girdle in all the

**Table 1.** The data matrix for implied homologies of the shoulder girdle in turtles and related reptiles, based on the assumption that the acromion process of turtles and the acromion-like process of pareiasaurs are homologous. The traits are as follows. **A.** Anterior flange formed by scapula. Absent, 0; Present, 1. **B.** Anterior coracoid. Present, 0; Absent, 1. **C.** Shape of anterior coracoid. Plate-like, 0; Flange-like, 1. **D.** Anterior coracoid. Discrete, 0; Fused with scapula, 1. **E.** Position of coracoid foramen. Within anterior coracoid (when present) and between scapula and posterior coracoid, 0; Between anterior and posterior coracoids, 1.

	A	B	C	D	E
Captorhinids	0	0	0	0	0
Procolophonoids	0	0	0	0	0
Pareiasaurs	1	0	0	0	0
Turtles	1	1	NA	NA	0

**Table 2.** The data matrix for implied homologies of the shoulder girdle in turtles and related reptiles, based on the assumption that the acromion process of turtles and the anterior coracoid of basal reptiles are homologous. The traits are the same as in Table 1, however, note that the distribution of the states in the taxa differs (e.g. turtles are now coded as lacking an anterior extension of the scapula but retaining an anterior coracoid). **A.** Anterior flange formed by scapula. Absent, 0; Present, 1. **B.** Anterior coracoid. Present, 0; Absent, 1. **C.** Shape of anterior coracoid. Plate-like, 0; Flange-like, 1. **D.** Anterior coracoid. Discrete, 0; Fused with scapula, 1. **E.** Position of coracoid foramen. Within anterior coracoid (when present) and between scapula and posterior coracoid, 0; Between anterior coracoid (= "acromion" in turtles) and posterior coracoid, 1.

	A	B	C	D	E
Captorhinids	0	0	0	0	0
Procolophonoids	0	0	0	0	0
Pareiasaurs	1	0	0	0	0
Turtles	0	0	1	1	1

relevant taxa are shown in Figure 2. Four changes are implied: origin of an anterior process of the scapula in pareiasaurs, modification of the anterior coracoid from a plate-like structure into a process in turtles, fusion of the anterior coracoid with the scapula in turtles, and movement of the coracoid foramen in turtles to between the anterior and posterior coracoids.

Thus, if characters are delineated as above, hypothesis 1 is clearly superior to hypothesis 2, as it requires fewer evolutionary events to explain the variation in morphology of the entire shoulder girdle in turtles and other reptiles. Of course, an element of subjectivity remains in this assessment: if a different set of shoulder girdle characters is compiled, the relative merits of these hypotheses (in terms of number of implied evolutionary changes) might be different. However, such subjectivity pervades any argument based on parsimony. The relative support for conflicting phylogenetic hypotheses will change, just as the relative merits of conflicting homology hypotheses will change, as different suites of characters are identified and employed in a cladistic analysis. Continual reevaluation and additions to the character set should result in increasingly accurate and powerful tests of both phylogenetic and morphological hypotheses.

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