

AN EVALUATION OF THE PHYLOGENETIC RELATIONSHIPS OF THE PTEROSAURS AMONG ARCHOSAUMORPH REPTILES

David W. E. Hone*

Department of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK

Michael J. Benton

Department of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK

SYNOPSIS The phylogenetic position of pterosaurs among the diapsids has long been a contentious issue. Some recent phylogenetic analyses have deepened the controversy by drawing the pterosaurs down the diapsid tree from their generally recognised position as the sister group of the dinosauromorphs, to lie close to the base of Archosauria or to be the sister group of the protorosaurs. Critical evaluation of the analyses that produced these results suggests that the orthodox position retains far greater support and no close link can be established between pterosaurs and protorosaurs.

KEY WORDS Pterosauria, Prolacertiformes, Archosauria, Archosauromorpha, Ornithodira

Contents

Introduction	465
Methods and Results	466
Discussion	467
Re-analysis of Bennett (1996)	467
Re-analysis of Peters (2000)	467
Conclusions	469
Acknowledgements	469
References	469

INTRODUCTION

The basal archosaurs and their phylogenetic positions relative to one another within the larger clade Archosauromorpha have been a source of controversy among palaeontologists for decades. Extensive cladistic revision has led to general agreement on the composition, position and ancestry of most archosauromorph clades. However, some recent publications (Evans 1988; Unwin 1995; Bennett 1996; Benton & Allen 1997; Jalil 1997; Dilkes 1998; Peters 2000) have shown that prolacertiforms and pterosaurs are the groups that have the most variable positions in phylogenetic analyses of Diapsida.

The prolacertiforms are the sister group of Archosauria (*sensu* Benton 1985) and there was a consensus that they form a clade (Evans 1988; Bennett 1996; Benton & Allen 1997; Jalil 1997; Peters 2000). Some recent analyses, however, indicate that prolacertiforms are paraphyletic. Both Dilkes (1998) and Modesto & Sues (2004, using a modified version of Dilkes' dataset) showed that *Prolacerta* did not belong to the prolacertiforms (although the rest of the clade was re-

tained). Müller (2003, 2004) also suggested that the prolacertiforms were not a valid clade, with *Trilophosaurus* splitting his two prolacertiform taxa (*Prolacerta* and *Tanystropheus*). The analysis performed by Senter (2004) also found the prolacertiforms to be paraphyletic, although here he removed the drepanosaurs to form a new clade with *Longisquama*. Most importantly, Peters (2000) has presented a heterodox view, in which the prolacertiforms are allied with the pterosaurs (see below for details). It is true that prolacertiforms have widely divergent body plans (Fig. 1), but they do appear to share a number of apomorphies. We use the term 'prolacertiforms' here to indicate the wider clade that includes *Protorosaurus*, *Macrocnemus*, *Tanystropheus* and their relatives (as in Evans 1988) and the term 'protorosaurs' to refer to the clade consisting of *Protorosaurus*, *Macrocnemus*, *Tanystropheus* and relatives, but excluding *Prolacerta*, as recovered by Dilkes (1998).

The Pterosauria has been a notoriously difficult clade to place in the diapsid tree: pterosaurs appear suddenly in the fossil record and in full possession of all their highly derived characters. Pterosaurs have been allied to virtually every basal and crown-group archosaur clade as well as to the dinosaurs, but few characters can be found that unite them

*Current address: Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, D-80333 München, Germany, E-mail address: d.hone@lrz.uni-muenchen.de

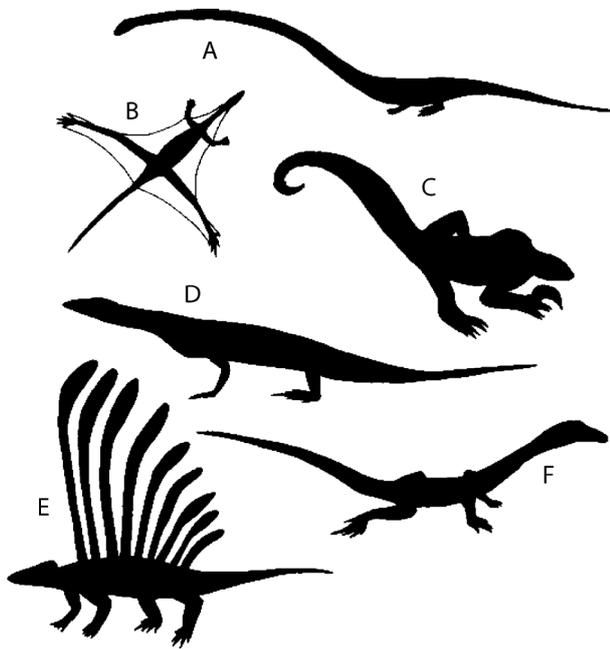


Figure 1 The 'prolacertiform' body plan. Prolacertiforms show highly variable bauplans as highlighted by these taxa (not to scale, with approximate head–tail lengths). **A**, the aquatic *Tanystropheus* (2 m); **B**, the glider *Sharovipteryx* (0.3 m); **C**, the arboreal *Drepanosaurus* (0.5 m); **D**, the terrestrial *Prolacerta* (1 m); **E**, the enigmatic, possible prolacertiform *Longisquama* (0.15 m); **F**, the terrestrial *Macrocnemus* (0.8 m).

with any other clade among the archosaurs (Bennett 1996). The appearance of pterosaurs in the Late Triassic without obvious antecedents, their complex flight-adapted anatomy and the fact that the basal pterosaurs have already acquired all those adaptations, gives few opportunities to compare structures to those of other archosaurs or diapsids.

The majority of studies (e.g. Padian 1984; Gauthier 1986; Benton 1990, 1999; Sereno 1991; Benton & Allen 1997) place pterosaurs close to the apex of the tree among the ornithodirans, often as a sister clade of the dinosauromorphs. Recently, both Bennett (1996) and Peters (2000) have argued that the pterosaurs may not even be archosaurs, but are more basal diapsids and that they belong among (Peters), or are closely allied to (Bennett), the protorosaurs (see Fig. 2).

Bennett (1996) provided two cladistic analyses, the first of which indicated the 'standard' result with the pterosaurs allied to the dinosauromorphs. His second was based on the assumption that pterosaurs and dinosauromorphs showed convergence in their bipedal, digitigrade hindlimbs, so he removed all characters of the leg, ankle and foot. On re-running the analysis, the pterosaurs appeared among the more basal archosaurian taxa.

Peters (2000) presented four separate analyses. Each was a reworking of an existing dataset, one from Bennett (1996), two from Evans (1988) and one from Jalil (1997), with characters and taxa both added and deleted. Peters modified some characters and added some newly coded taxa (*Cosesaurus*, *Langobardisaurus*, *Longisquama*, *Sharovipteryx*) and he recovered the Pterosauria nested within

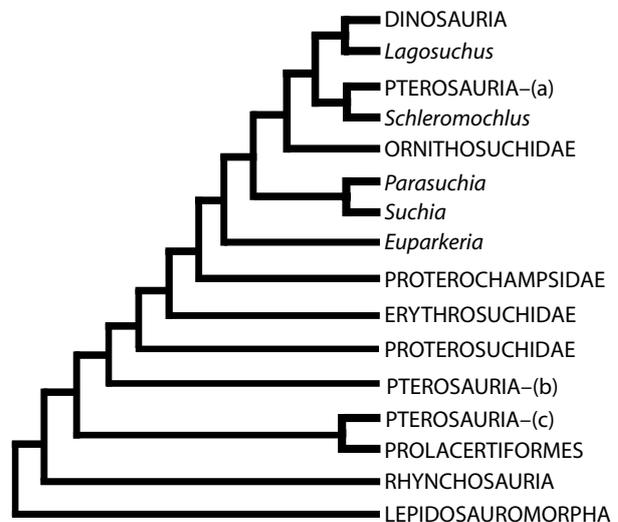


Figure 2 Possible positions of the pterosaurs based on Bennett (1996). The Pterosauria are shown in three possible positions: (a) as ornithodirans, close to the dinosaurs (e.g. Evans, 1988) (b) as basal archosauromorphs, e.g. Bennett's (1996) second analysis, or (c) as sister taxa to, or within, the prolacertiforms, e.g. Peters, (2000). See the text for further details.

the Prolacertiformes. However, the trees produced by Peters after he had made his additions and recodings were more poorly resolved than the trees produced by the original authors. These re-analyses by Bennett (1996), Dilkes (1998) and Peters (2000) have shown that the otherwise emerging consensus on the phylogenetic positions of pterosaurs and prolacertiforms is not uniformly supported. The aim of this study is to evaluate the evidence of Bennett (1996) and Peters (2000) critically and to consider the likelihood or not of a close relationship between the pterosaurs and basal archosauromorph reptiles.

METHODS AND RESULTS

For this paper the datasets of both Bennett (1996) and Peters (2000) were re-analysed to confirm the results they produced. Figures are not included, as although each analysis performed here produced a different result to those published, differences in topologies were subtle. The original figures of the respective authors should be consulted for details.

Bennett's (1996) main analysis was one of 13 ingroup taxa and a total of 126 characters. He recovered three Most Parsimonious Trees (MPTs) with 209 steps. This analysis was repeated here using PAUP* 4.0 (Swofford, 1998) with the settings given by Bennett (1996) and recovered three MPTs with 212 steps. The shapes of the trees were only subtly different, with *Scleromochlus* and the Pterosauria appearing successively below *Lagosuchus*, rather than as sister taxa in this position (Bennett 1996: fig. 2). The Consistency Index (CI) was almost identical to that published and presumably reflects the subtly different nature of the trees and the number of steps recovered here. A further bootstrap analysis was carried out (1000 replicates without replacement, 100 maximum trees) with the majority of the branches being well supported.

Peters (2000) presented four datasets that had been previously published and then modified by him. The three analyses from which Peters constructed edited data matrices (Evans 1988; Bennett 1996; Jalil 1997) were briefly re-analysed. However, Peters (2000) did not state which outgroup taxa were used and he did not state what settings were used in PAUP* or how the trees were compiled (where consensus trees were shown). He did not perform bootstrap analyses.

Peters (2000) completed two analyses of Evans' (1988) work although he only published a matrix and resultant tree for one of them. This had a total of 66 characters and 21 in-group taxa. The outgroup taxon was not specifically identified by Peters (2000) so the most basal taxon from the figured tree (*Petrolacosaurus*) was selected (this was also necessary for the other analyses below). Peters (2000) recovered six trees of 186 steps using a heuristic search. However, our re-analysis produced eight trees of 191 steps, both using heuristic and branch-and-bound techniques. Although the topologies were broadly similar, consensus trees of these eight (including a strict consensus) were more resolved than the tree published (Peters, 2000: fig. 14, which was probably a strict consensus tree). A bootstrap analysis (performed as above) collapsed seven branches of the cladogram and six of the surviving branches had support of just 67% or lower.

Peters' (2000) recoded analysis of Bennett's (1996) data yielded one tree of 268 steps, but here we recovered one tree of 263 steps (using both heuristic and branch-and-bound searches) with a subtly different topology. *Cosesaurus* becomes the sister taxon to *Longisquama*, as opposed to being basal to it in the original tree (Peters, 2000: fig. 16) and *Suchia* also becomes the sister taxon to *Parasuchia*, having previously held a more basal position. Bootstrap results were high.

Finally, in his re-analysis of Jalil's (1997) data, Peters (2000) recovered 120 trees with 151 steps, but here we find 140 trees at 153 with an heuristic search. Using a branch-and-bound approach, however, yielded 240 trees. The topologies were again different compared to Peters' published tree (which is assumed to be a strict consensus as it nearly matches that of our analysis), with the pairing of *Sphenodontia* and *Iguana* nesting with the main polytomy of the other taxa and not basal to them as recovered by Peters (2000: fig. 15). Bootstrap values were low (half were less than 65% for the 6 branches retained). In all three analyses, the recovered CI and Retention Index (RI) values were comparable to those published by Peters (2000).

DISCUSSION

Re-analysis of Bennett (1996)

Bennett (1996) has asserted that certain hindlimb characters of pterosaurs are non-homologous, but convergent with those of the higher archosaurs. In his second analysis, he removed these characters (removing first 11, then a further 36 out of 126) and the pterosaurs took a new position in the tree, lying among more basal taxa (although not among the prolacertiforms and no other taxa were markedly moved), namely the Erythrosuchidae, Proterochampsidae and *Euparkeria*.

Bennett's (1996) argument is logically sound since, if these characters are non-homologous, their elimination

should reproduce the true phylogeny. However, his assumptions do not appear to be valid: cladistics does not allow us to pick and choose which characters we can and cannot use based on an assumption of convergence. A more precise demonstration of non-homology has to come from detailed anatomical analysis of each of the disputed characters. Such fine-scale differences between the supposedly non-homologous features of the pelvis, hindlimb, ankle and foot of pterosaurs and dinosauromorphs have not been identified by Bennett (Benton 2004).

Moreover, Bennett's assertion of non-homology violates Hennig's 'Auxiliary Principle', that is: 'never presume convergent or parallel evolution; always presume homology in the absence of contrary evidence' (Brooks & McLennan 2002: 36). In other words, non-homologous characters should be determined *a posteriori* and, thus, Bennett (1996) was incorrect in deleting what he asserted were *a priori* homoplastic characters.

Re-analysis of Peters (2000)

The unexpected results produced by Peters (2000) and the re-analysis here, suggest that his codings should be examined more closely, particularly with reference to the pterosaurs. There are numerous methodological errors throughout the paper as well as errors in the interpretations of some specimens and the resulting codings. In summary, Peters (2000) includes and excludes characters without explanation, he biases his character codings by unwarranted functional assumptions about some taxa, he includes character codings for bones that do not exist in certain specimens and there are methodological problems in the cladistic analysis. These problems are outlined below.

Peters (2000) deleted over two-thirds of the characters from Evans (1988), but retained many identical characters in the other analyses (e.g. his characters 6, 52, 60, 136, 142, 182, 184, 245, 287): if a character holds for one analysis, then it should be maintained for the others. Peters (2000) gave no justification for the extensive pruning of the work of Evans (1988), despite having deleted more than 150 characters out of 226 in all. Although there are numerous characters and taxa that are irrelevant to the subject matter (and therefore can be justifiably excluded), many more that were removed could have aided the resolution of the cladograms.

A number of Peters' character recodings are based on unjustified assumptions and reconstructions. Characters for *Eudimorphodon* are coded as if it were a digitigrade biped capable of both walking and running (330–336). This reconstruction of pterosaurs is discounted by many and contradicts trackway evidence (Mazin *et al.* 2003), the distribution of mass and the issues of balance (Pennycuik 1988) and the structure of the metatarsal/tarsal joints (Clark *et al.* 1998). The reconstruction includes a 'hypothetical' centre of balance, but no justification is given for its location and this was significantly anterior to the pelvis, which would cause the animal to fall forwards. If Peters had examined the specimens and had made no biomechanical assumptions, those seven characters (330–336) would be coded differently. Furthermore, in his four analyses, Peters (2000) codes certain identical data cells differently in each of his analyses (e.g. characters: 'shape of maxillary ramus of premaxilla', 'nasals taper anteromedially', 'nasals longer than the frontals', 'subtemporal process of jugal', 'transverse processes of trunk

vertebrae well developed', and 'relative lengths of metacarpals 3 and 4'). These different codings of the same characters are not explained.

Cosesaurus is treated as a biped by Peters (2000) with characters coded based on this assumption. Peters (2000) argues that the Australian frilled lizard (*Chlamydosaurus kingii*) shares remarkably similar hind limbs and is capable of bipedalism. *Chlamydosaurus* is indeed capable of bipedalism at high speeds, but its primary mode of locomotion is as a sprawling quadruped. To consider *Cosesaurus* a true biped is misleading, as while it *might* have been capable of bipedalism, it is not a biped in the strict sense and should be considered quadrupedal. *Cosesaurus* is also given a 'centre of balance' again without justification and well forward of the pelvis and these biomechanical assumptions colour the coding of hindlimb characters.

Peters (2000) also suggests that the elongation of the metatarsals in both prolacertiforms and pterosaurs is an indication of digitigrade bipedality. Comparative diapsid analogues suggest that this is not the case. Lizards are mostly obligate quadrupeds and yet have elongated metatarsals and those that are capable of facultative bipedalism may have reduced metatarsals and elongate tarsals and phalanges compared to other species (e.g. *Cnemidophorus tigris*, *Dipsosaurus dorsalis*). Other digitigrade bipeds such as ornithischian and theropod dinosaurs do not always show lengthened metatarsals.

A significant number of characters also appear to have been coded by Peters (2000) in the absence of physical evidence. *Sharovipteryx* has been coded for characters that are missing in the single specimen or are buried in the matrix and so cannot have been observed. Some examples of these are: the 'lacrima fails to meet nasal' although this part of the skull is disarticulated, 'twelve cervical vertebrae' are coded although this section is obscured by matrix and the character 'last few dorsals with fused ribs' when some of the bones are disarticulated and the rest obscured. Furthermore, there are codings for three humerus characters, 'loss of intermedium in carpus', 'ulna lacks olecranon and sigmoid notch' and 'manual asymmetry' even though the arms are not preserved in the specimen.

Peters (2000) reconstructed *Sharovipteryx* with highly reduced arms and he identified the three main bones (humerus, radius and ulna). He did not identify the carpus or hand and yet he was able to code some carpal characters. The bones identified by Peters as a forelimb, however, lie along a series of disarticulated and broken ribs and it is likely they are part of that series. Were this an arm, it would have had to have become detached from the pectoral girdle and moved down towards the sacrum as a single articulated piece, which is highly unlikely with such delicate bones. In any case, the true arms of *Sharovipteryx* have now been found buried in the matrix (R. Reisz, pers. comm., 2003) and this confirms that Peters' (2000) supposed arm was incorrectly identified.

Peters' (2000) cladistic analyses do not follow normal practice. Outgroups are not defined, whether selected from the data, taken as all '0's, or left unrooted. Peters discusses his outgroups, stating that a number of prolacertiforms were used as pterosaurian outgroups within the study. One outgroup was apparently a species of *Langobardisaurus*, but since another species of that genus is included in the ingroup, it is hard to see how this can be considered an appropriate outgroup. Bennett's work (1996) would suggest that at the

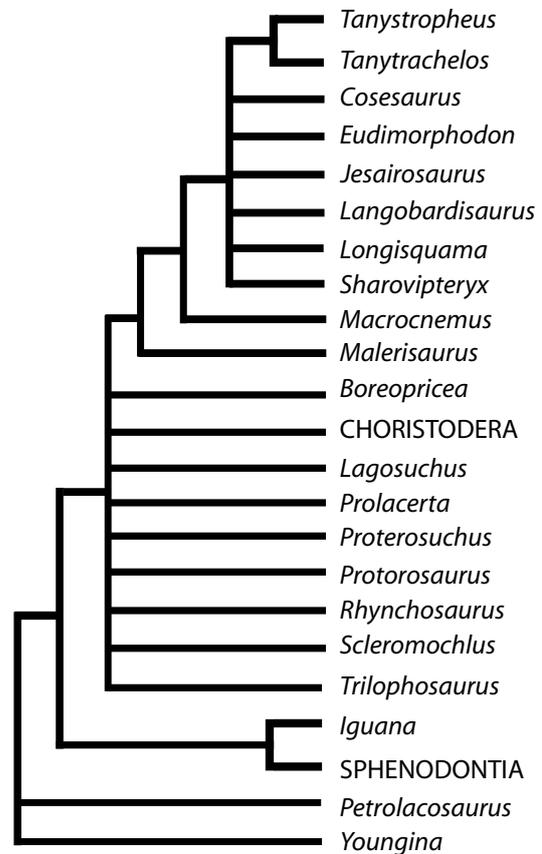


Figure 3 Strict consensus tree produced by Peters (2000) based on a dataset by Jalil (1997) with 23 taxa and 71 characters. Redrawn from Peters (2000: fig. 15). No branch support figures were given.

very least taxa from outside the prolacertiforms should be used. However, in the final trees, more basal taxa appear at the base of the trees, so it is unclear how these prolacertiforms were used as outgroups, if at all. For his re-analysis of Evans' work, Peters (2000) used only a heuristic algorithm (and may have done so on other analyses), which is not guaranteed to find the shortest trees available.

This ambiguity in coding and in cladistic method is reflected in the trees produced by Peters (2000), for example, the re-analysis of Jalil's (1997) work produces two large polytomies with scattered taxa between them, including all the key taxa, hardly a resolution (Fig. 3).

The choice of representative taxa is also problematic: *Eudimorphodon* is a poor choice as a basal pterosaur. Cladistic analysis shows it to be placed among the relatively advanced rhamphorhynchoids (Unwin 1995, 2003) and it is, therefore, not especially close to the base of the pterosaurian phylogeny. Its relative *Dimorphodon* is a better candidate, being more basal (Unwin 1995, 2003) and significantly more complete. Similarly, although *Longisquama* had been used as a putative outgroup for previous analyses (Sharov 1970) its revision as a neodiapsid (Unwin *et al.* 2000) was ignored by Peters and would at least suggest that it is not suitable for inclusion in analyses focused on pterosaurs and prolacertiforms. In fact, its inclusion may result in the generation of spurious trees since the outgroups used in the analysis would be more derived than *Longisquama* as an ingroup taxon.

CONCLUSIONS

The results of the re-analyses of the supermatrix suggest that the Prolacertiformes should be considered the sister group to the Archosauria. The Pterosauria are not closely related to the Prolacertiformes and should instead remain among the Archosauria and probably among the derived archosaurs. However, the large amount of missing data for many taxa makes it difficult to confirm their true position. Removal of hindlimb characters has no significant effect on their position and so cannot be used as an argument for convergence and non-homology between the dinosauromorphs and pterosaurs. Finally, there are such serious questions about Peters' (2000) cladistic methods and about his original reconstructions and character codings in certain fossil material, especially for *Longisquama* and *Sharovipteryx*, that all his analyses should be treated with great caution.

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CORRIGENDUM

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David W. E. Hone

Department of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK

Michael J. Benton

Department of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK

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It is regretted that in the originally published paper (Hone, D. W. E & Benton M. J. 2007) the conclusions mistakenly contained a reference to an as then unpublished supermatrix analysis. This analysis has now been published (Hone & Benton 2008) and should be referred to for full details. The authors apologise for this oversight.

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