Is there any Consensus on Basal Archosaur Phylogeny?

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Is there any consensus on basal archosaur phylogeny?

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SUMMARY

Studies of basal archosaur phylogeny since 1975 were reviewed to assess directly opposing views on the (dis)agreement reached as a result of adopting cladistic methodology. The transition to modern numerical cladistic analyses has been long, including two principal stages: with listing of derived characters as node support eventually replaced by explicit data and methodology presentation. All four existing explicit numerical studies are reanalysed, and a semi-strict reduced cladistic consensus is constructed for them and compared with earlier 'cladistic' studies where data was not presented. The two principal steps to modern numerical analyses have been accompanied by an increase in the agreement between separate hypotheses, and there exists substantial current consensus on the resolution of many pre-cladistically vague relationships. However, Bremer support values calculated for the four numerical studies indicate that the strength of hypothesised clades is generally low to minimal. Because a previous review (Charig 1993) included many non-cladistic studies, using its failure to find consensus as a basis for broader criticisms of cladistic methods is considered unjustified. However, some of Charig's (1993) criticisms of current practises are endorsed. Reproducibility of results, greater methodological awareness, and more rigorous assessment of hypothesis robustness are identified as additional issues requiring consideration in future studies.

1. INTRODUCTION

As with other groups, phylogenetic relationships within archosaurs (loosely conceived of as crocodiles, birds, dinosaurs, pterosaurs and their nearest relatives), increasingly have been investigated using cladistic methods. Recently, Charig (1993) reviewed the literature and concluded that 'the recent analyses have told us nothing that we did not know 35 years ago' i.e. before the adoption of cladistic methods, and he used his pessimistic conclusion to launch a more general attack on cladistic methods. Charig's (1993) conclusions are in stark contrast to the 'radical new consensus' on archosaur phylogeny that Benton (1984*a*) proclaimed had been arrived at through newly adopted cladistic methods. Here we evaluate these opposing views, consider the impact of cladistic methods, and assess whether there is any current cladistic consensus in basal archosaur phylogeny and any advance over pre-cladistic understanding (or lack thereof). We follow Juul (1994) in using the traditional meaning of Archosauria rather than the crown-group concept of Gauthier (1986). Archosaurians, in the sense of Gauthier, are referred to here as 'crown-group archosaurs'.

2. BACKGROUND

Charig (1993) listed some 29 publications since 1975 that he considered included 'significant phylogenetic analyses of the Triassic Archosauria'. For a subset of 18 of these studies (published between 1979 and 1993), he compared published cladograms, or cladograms he produced from published phylogenetic trees or sketches, with the intention of constructing a consensus tree. The extent of disagreement he encountered made it 'virtually impossible to draw up any sort of consensus tree' (Charig 1993), and led him to conclude that the discovery of additional material, the numerous phylogenetic studies, and the adoption of cladistic methods have provided no new insight into basal archosaur phylogeny over the conventional views of the 1950s (figure 1).

Summary comments on the recent studies of archosaur phylogeny listed by Charig (1993) are provided in table 1. Many of these studies are not cladistic. Some (Cruickshank 1979; Chatterjee 1982; Cruickshank & Benton 1985) are based exclusively on archosaur ankle types, and represent unconvincing and unjustified assessments of a single multistate character (Gauthier 1988). Another group of studies (see, for example, Bonaparte 1975*a*; Norman 1984; Benton 1984*c*; Sereno 1984) present assessments of relationships within rather than between main basal archosaur lineages. A total of four studies (Benton 1984*d*, 1986; Bonaparte 1984; Parrish 1984) include no phylogenetic analyses or conclusions. Thus, many of the studies listed by Charig (1993) can neither be considered cladistic nor to involve major phylogenetic analyses of basal archosaurs of any other kind.

Adoption of cladistic methods by students of archosaurs has clearly been a slow and gradual process. The earliest 'cladistic' studies employed cladograms rather than phylogenetic sketches and emphasised the importance of derived characters, so that cladograms were accompanied by lists of synapomorphies taken as

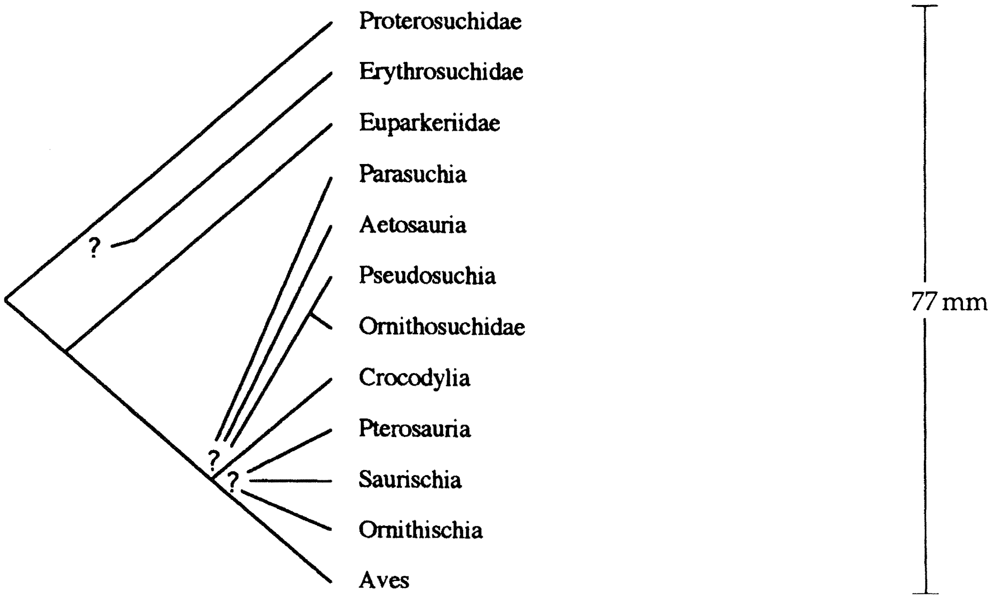

Figure 1. Tree considered by Charig (1993: figure 15) to represent conventional view of basal archosaur phylogeny in the 1950s.

supporting nodes. However, cladogram–hypothesis choice was not explicit, incongruence was either ignored or the subject of extremely limited discussion, and data matrices, if ever assembled as such, were not published. There have been just four recognizably modern cladistic analyses of basal archosaur phylogeny, with published data matrices and explicit criteria of hypothesis choice.

3. MATERIALS AND METHODS

We compared and sought a consensus among all modern cladistic studies of basal archosaur phylogeny involving numerical analyses of published data (Sereno & Arcucci 1990; Sereno 1991; Parrish 1993; Juul 1994), and then compared this consensus to relationships posited by the main cladistic studies of basal archosaur phylogeny in which nodes were supported by lists of synapomorphies without any rigorous numerical analyses (Benton 1985; Gauthier 1986; Benton & Clark 1988: table 1 indicates other references that these three summarise or that stem from them). Included in our comparisons, is the recent numerical study by Juul (1994) that was not considered by Charig (1993). Excluded from consideration are the studies by Gardiner (1982, 1993) which attempt to place fossil taxa within a phylogenetic framework constructed for recent groups, and propose the radical (and largely unaccepted) view that archosaurs, as considered here, are not monophyletic. Also excluded is the numerical study of Gauthier *et al.* (1988), where the crown-group archosaurs were represented by just two terminal taxa. Conclusions from (and assumptions of) the latter study are represented by Gauthier's (1986) cladogram. Comparisons were complicated by differences in the nomenclature adopted by different workers for their terminal taxa, and in some cases by differences in the composition of terminal taxa. A summary of these differences is presented in table 2, and the fundamental cladograms of which a consensus is sought, with a standardized nomenclature for terminal taxa, are illustrated in figures 2 and 3.

We used the reduced cladistic consensus (RCC) method (Wilkinson 1994) because of its sensitivity to common cladistic structure in fundamental trees. Because the studies we compared include different terminal taxa, we employed a semi-strict RCC method (Wilkinson 1994, 1995), which allows taxa that are not present in all the fundamental trees to be included in the consensus tree, provided that their relationships are not contradicted by any fundamental trees. Taxa that were included in only a single fundamental tree, and which therefore could not be the subject of disagreement between trees, are indicated in the consensus by dashed lines. Where fundamental trees include polytomies, we interpreted these as soft. Where a single 'higher' terminal taxon in one fundamental tree is equivalent to a collection of distinct terminal taxa in another fundamental tree, the single taxon was interpreted as a soft polytomy of the distinct taxa.

Bremer support, the difference in tree length between the shortest trees including a clade and those not including it (Källersjö *et al.* 1992), gives one measure of the strength of phylogenetic hypotheses (Bremer 1988). We used the topological constraints option in PAUP 3.1.1 (Swofford 1993) to determine Bremer support for all clades unambiguously supported by the parsimonious interpretation of each of the four basal archosaur data sets that have been published to date.

4. RESULTS

The semi-strict RCC tree of the four fundamental trees based on numerical analyses (figure 2) is shown in figure 4. There is impressive agreement regarding the sequence of the most basal branchings in the archosaur tree, and also not inconsiderable agreement within the crown group (i.e. above node 1). The main area of disagreement between the existing numerical cladistic studies is the resolution of the crocodile branch of the main crown-group dichotomy, particularly in the positions of the Ornithosuchidae and some of the taxa grouped together pre-cladistically as rauisuchians (*Prestosuchus*, *Ticinosuchus*, *Saurosuchus*), which because of their variable placements are excluded from the consensus. While there is a lack of consensus on the precise position of the Ornithosuchidae, the results of all the numerical cladistic analyses are consistent with the hypothesis that they are more closely related to suchians and parasuchians than to dinosaurians.

Table 1. *Studies considered by Charig (1993) to include significant phylogenetic analyses of the Triassic Archosauria*

(* denotes study selected for more detailed consideration by Charig.)

study	comments
Bonaparte (1975*a*)	A systematic review of Ornithosuchidae, with a brief discussion of relationships to other basal archosaurs summarized in a phylogenetic sketch.
Bonaparte (1975*b*)	Phylogenetic sketches and discussions of morphology.
Cruickshank (1979)*	Basal archosaur phylogenetic tree based almost exclusively on interpretation of ankle types.
Bonaparte (1982)	Basal archosaur phylogenetic chart, and some description/discussion of characters.
Chatterjee (1982)*	Basal archosaur phylogenetic tree based on interpretation of ankle types.
Gardiner (1982)*	Tetrapod cladogram with lists of synapomorphies supporting nodes.
Benton (1984*b*)*	Diapsid cladogram with lists of synapomorphies supporting nodes. No discussion of incongruence. Results are a summary of Benton (1985).
Benton (1984*c*)	Lists of synapomorphies supporting dinosaur monophyla. No cladogram. Unsupported statement that Ornithosuchidae is the sister group of Dinosauria.
Benton (1984*d*)	Discussion of rauisuchian biology.
Bonaparte (1984)	Discussion of rauisuchid morphology and locomotion.
Gauthier (1984)*	Diapsid cladograms with detailed discussions of synapomorphies supporting nodes, and of incongruent evidence. Basal archosaur part summarised in Gauthier (1986).
Norman (1984)	Ornithischian cladogram with lists of synapomorphies supporting nodes.
Padian (1984)*	Discussion of affinities of pterosaurs and *Scleromochlus* within the context of Gauthier's (1984) phylogenetic hypothesis.
Parrish (1984)	Discussion and listing of archosaur locomotor grades.
Paul (1984*a*)*	Basal archosaur cladogram with similarities supporting nodes. Presented as a tentative outline of work in progress.
Paul (1984*b*)	Cladogram within dinosaurs, with lists of supporting synapomorphies.
Sereno (1984)	Ornithischian cladogram with summary lists of synapomorphies supporting nodes.
Benton (1985)*	Diapsid cladograms with lists of synapomorphies supporting nodes. Some discussion of incongruence and weight of evidence. Expanded version of phylogenetic part of Benton's (1984*b*) study.
Cruickshank & Benton (1985)*	Basal archosaur phylogenetic sketch based on interpretation of ankle types.
Gauthier & Padian (1985)*	Basal archosaur cladogram based on Gauthier (1984).
Benton (1986)	Listing of characters of rauisuchids, and discussion of some further characters.
Gauthier (1986)*	Basal archosaur phylogeny with lists of synapomorphies supporting nodes and some discussion of incongruence and weight of evidence. Presented to place a numerical phylogenetic analysis of a saurischian data matrix in context.
Benton (1988)*	Cladogram of dinosaurs and nearest outgroups, with lists of synapomorphies supporting nodes. Summary of previously published studies.
Benton & Clark (1988)*	Basal archosaur cladogram based ostensibly on a numerical analysis. Data matrix not published, and cladogram is not most parsimonious tree, so that hypothesis selection criterion is unclear. Lists of synapomorphies supporting nodes with limited discussion of incongruence.
Novas (1989)*	Numerical analysis of published matrix of only tibiotarsal data for 'crocodile-reversed archosaurs'.
Benton (1990)*	Basal archosaur cladogram with lists of synapomorphies from previously published studies.
Sereno & Arcucci (1990)*	Basal archosaur cladogram based on numerical analysis of published data matrix.
Sereno (1991)*	Basal archosaur cladogram based on numerical analysis of published data matrix.

Table 2. *Correlation of varying terminal taxa employed in seven basal archosaur studies, and standardisations applied here in figures* 2, 3, *and* 4

(Correlation does not imply equivalence because comparable terminal taxa may represent different ranks. Assumptions made about taxon composition where not originally specified are as follows: 1 here assumed to represent the pre-cladistic (see, for example, Chatterjee 1985) grouping of all poposaurids, rauisuchids, and prestosuchids; 2 assumed to be in the sense of Sereno (1991); and 3 assumed to be in the sense of Gauthier (1986).)

Standardisations applied here	Benton (1984*b*, 1985)	Gauthier (1986)	Benton & Clark (1988)	Sereno & Arcucci (1990)	Sereno (1991)	Parrish (1993)		Juul (1994)
						matrix	cladogram	
Proterosuchidae	*Proterosuchus*	Proterosuchidae	Proterosuchidae	Proterosuchidae	*Proterosuchus*	*Proterosuchus*		*Proterosuchus*
Erythrosuchidae	*Erythrosuchus*	Erythrosuchidae	Erythrosuchidae	Erythrosuchidae	Erythrosuchidae	*Ervthrosuchus*	Erythrosuchia	Erythrosuchidae
Proterochampsidae		Proterochampsidae	Proterochampsidae	Proterochampsidae	Proterochampsidae	*Chanaresuchus*	Proterochampsidae	Proterochampsidae
Euparkeria	*Euparkeria*	*Euparkeria*	*Euparkeria*	*Euparkeria*	*Euparkeria*	*Euparkeria*		*Euparkeria*
Pterosauria	Pterosauria	Pterosauria		Pterosauria	Pterosauria		Ornithodira (3)	Pterosauria
Lagosuchus	Later archosaurs	*Lagosuchus*	*Lagosuchus*	*Lagosuchus* + Dinosauria	Dinosauromorpha	*Lagosuchus*		Lagosuchus
Dinosauria		Dinosauria	Dinosauria			*Plateosaurus*		Ornithischia Sauropodomorpha *Herrerasaurus* Ceratosauria + Tetanurae
Ornithosuchidae		Ornithosuchidae	Ornithosuchidae	Ornithosuchidae	*Ornithosuchus* *Riojasuchus*	 *Riojasuchus*	Ornithosuchidae	Ornithosuchidae
Parasuchia		Parasuchia	Phytosauridae	Parasuchia	Parasuchia	*Rutiodon*	Parasuchia	Parasuchia
Crocodylomorpha		Crocodylomorpha	*Crocodylia* *Protosuchus* *Terrestrisuchus*	Suchia (2)	Suchia	*Alligator* *Pseudhesperosuch*	Crocodylomorpha	Crocodylomorpha
Aetosauria		Aetosauria	Stagonolepididae			*Desmatosuchus*	Aetosauria	Stagonolepidae
Gracilisuchus			*Gracilisuchus*			*Gracilisuchus*		*Gracilisuchus*
Postosuchus		Rauisuchia (1)	*Postosuchus*			*Postosuchus*	Poposauridae	*Postosuchus*
Rauisuchus *Fasolasuchus* Kupferzell rauisuchid *Lotosaurus*						*Rauisuchus* *Fasolasuchus* Kupferzell rauisuchid *Lotosaurus*		
Saurosuchus			*Saurosuchus*			*Saurosuchus* San Juan Sauro	*Saurosuchus*	Prestosuchidae
Ticinosuchus			*Ticinosuchus*			*Ticinosuchus*		
Prestosuchus						*Prestosuchus* PAPresto	*Prestosuchus*	
Doswelia			*Doswellia*					
Scleromochlus					*Scleromochlus*			
Lewisuchus						*Lewisuchus*		
T. dabanensis						*Turfanosuchus dabanensis*		

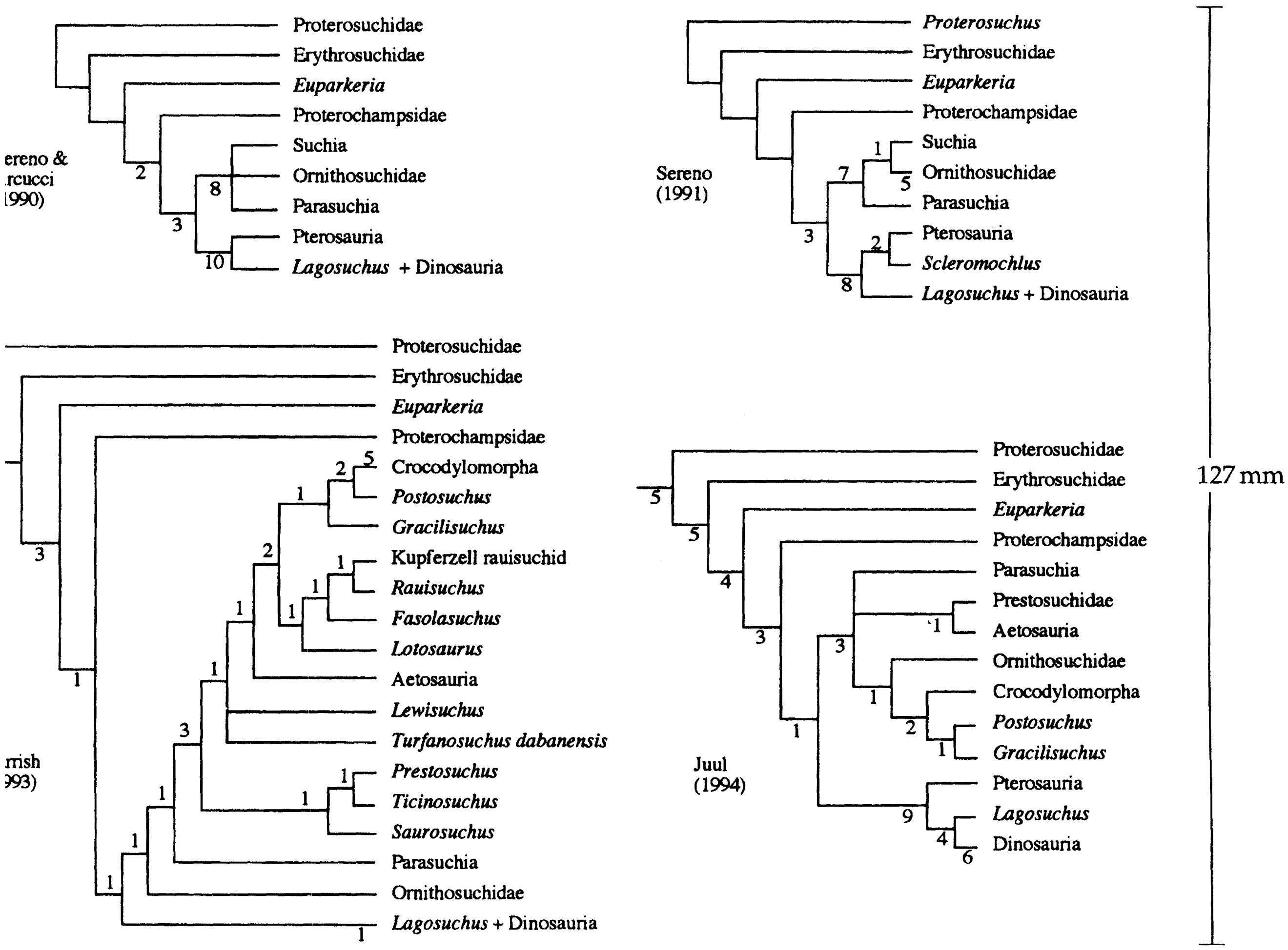

Figure 2. Cladograms of basal archosaur relationships based on explicit numerical cladistic analyses. Certain terminal taxa have been standardised from original publication following table 2. Non-archosaurian outgroup taxa have been omitted from Juul's hypothesis. While Erythrosuchidae and *Proterosuchus* were coded as a single terminal taxon in the data matrix of Sereno and Arcucci (1990), and omitted in that of Sereno (1991), their position is discussed and depicted in the hypothesised topologies. Numbers represent Bremer support for corresponding clades.

There is less consensus when earlier non-numerical 'cladistic' studies (figure 3) are also considered (there could not be more), but there are still many points of agreement. The relative positions of the Proterosuchidae, Erythrosuchidae and Proterochampsidae outside the crown-group clade are consistent across all studies, and there is consensus that parasuchians, aetosaurs, and 'rauisuchians' are part of the crocodile line clade within the crown group, and on the holophyly of *Lagosuchus* + the Dinosauria (including birds). The additional consensus that emerges from the numerical cladistic studies are thus: (i) that pterosaurs are the sister group to dinosauromorph crown-group archosaurs; (ii) that ornithosuchids belong to the crocodile, rather than bird, branch of the main crown-group dichotomy; and (iii) that *Euparkeria* lies outside the crown group. These points of agreement demonstrate a greatly increased consensus on basal archosaur relationships over what Charig (1993) considered to be the conventional views of the 1950s (figure 1).

Bremer support values for the clades found in the numerical analyses are indicated in figure 2. It is noteworthy that a large number of clades in both of the most comprehensive numerical analyses, those of Parrish (1993) and Juul (1994), are lost in trees requiring only a single extra step, indicating only weak support for these phylogenetic hypotheses.

5. DISCUSSION

Charig (1993) attempted to support his pessimistic view of the (lack of) progress in archosaur phylogeny by seeking to demonstrate a lack of consensus among the many studies published over approximately the past 20 years. We consider Charig's (1993) assessment to be flawed because it did not discriminate between the very different kinds of studies that have been done at different points on the temporal trajectory leading to modern cladistic analyses. Certainly, given that many of the studies he considered are not cladistic, the lack of agreement among them cannot legitimately be attributed to cladistic methods! Contrary to Charig (1993), our analyses show that two stages in the adoption of cladistic methods, the listing of characters supporting nodes in cladograms, and the use of explicit numerical phylogenetic analyses of published data, have both been accompanied by an increased consensus in the resolution of basal archosaur phylogeny.

Charig (1993) stated that 'it would be misleading and unscientific to claim that any one of the recent

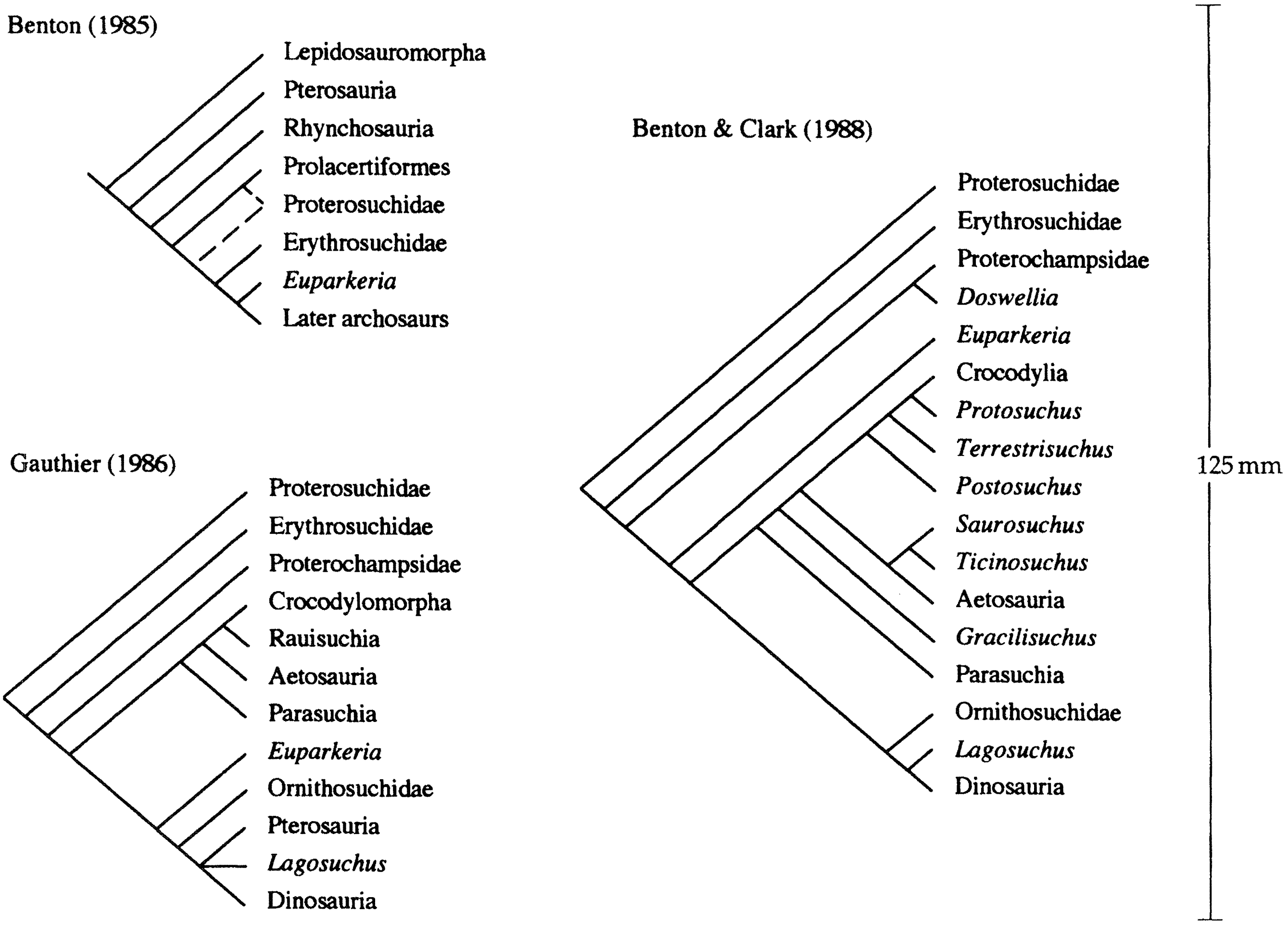

Figure 3. Cladograms of basal archosaur relationships from cladistic studies, but where numerical analyses were not done or presented. Certain terminal taxa have been standardised following table 2. Some non-archosaurian diapsids are omitted from Benton's hypothesis.

cladograms tells us what we want to know'. Although none of the cladograms based on numerical studies is compelling (see below), the consensus of these studies (see figure 4) does provide a reasonable working hypothesis. More importantly, because these studies are explicit and present their data, they provide a foundation upon which to build. Despite our differing interpretation on the consensus on basal archosaur phylogeny, we share some of Charig's concerns over current practises.

Charig (1993) deplores the establishment of new higher taxa on the basis of each new (but probably ephemeral) phylogenetic hypothesis. We agree that a more 'hands-off' approach to taxonomy is sensible while the understanding of the relationships and composition of certain higher taxa is in a state of flux. The newly erected taxa Dromaeosuchia (Juul 1994), and Rauisuchiformes and Paracrocodylomorpha (Parrish 1993), for example, are based on hypothesised clades with minimum possible (+1) Bremer support. Readiness to propose new names for poorly supported hypotheses runs counter to the desire for stability in classification.

We endorse Charig's (1993) criticisms of the discarding of conflicting evidence without discussion, and of unclear character state definitions. There appears to be a widespread misconception that derived character states must be unique to a clade to provide evidence for that clade. This has led to the dismissal of characters that show any indication of homoplasy, and Charig (1993) himself repeatedly criticises evidence cited by other authors in support of hypothesised relationships because the derived character states also occur elsewhere, and therefore cannot be synapomorphies. It should be stressed that globally homoplastic characters can be locally informative (see, for example, Farris & Kluge 1985), and should not be discarded on the basis of their global homoplasy alone.

In addition to the points raised by Charig (1993), we recognize further issues that need to be addressed by future studies. A specific problem arises with the recent conclusion (Long & Murray 1995) that *Postosuchus*, frequently used as a terminal taxon in recent archosaur phylogenies to represent the Poposauridae, was originally based on a blend of three taxa possibly referrable to two separate families (Poposauridae and Rauisuchidae in the sense of Long & Murray 1995). This adds to the uncertainty that we have identified surrounding the position of various 'rauisuchians' (as pre-cladistically conceived) among the crocodile-line crown-group archosaurs.

Despite finding considerable agreement between the existing numerical cladistic studies, we have recognized a number of limitations within some of those studies

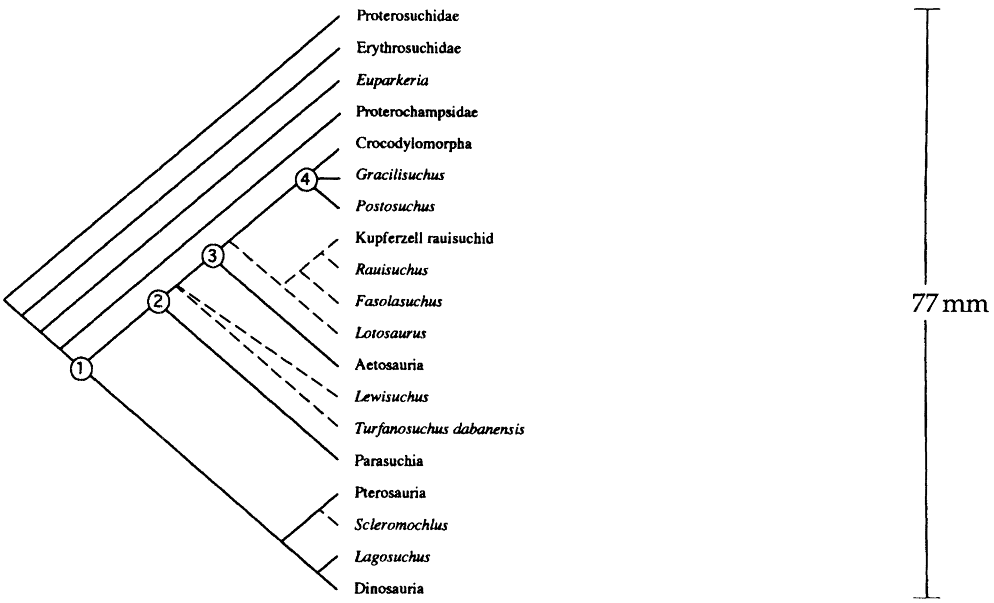

Figure 4. Semi-strict reduced cladistic consensus of the four existing numerical cladisitc analyses of basal archosaurs (figure 2). Dotted lines indicate taxa included in only a single analysis. Possible positions of pruned taxa are: Ornithosuchidae – between nodes 1 and 2 (Sereno & Arcucci 1990; Parrish 1993), between 2 and 3 (Sereno & Arcucci 1990; Sereno 1991), as sister group to Parasuchia (Sereno & Arcucci 1990), or between 3 and 4 (Juul 1994); *Saurosuchus* + *Ticinosuchus* + *Prestosuchus* – between 2 and 3 (Parrish 1993), or sister group to Aetosauria (Juul 1994).

through reanalysis of published data. Any preferred phylogenetic hypothesis needs to be reproducable from the published numerical data. Discrepancies between most parsimonious tree statistics as presented by Parrish (1993) and those recovered from reanalysis of his published data, and contradictions between his data matrix and his text and figures (some of which are considered by Juul 1994; Gower 1996; and Gower & Wilkinson 1997) all limit the confidence that can be invested in the published hypothesis.

Assessing the robustness of a preferred hypothesis is increasingly recognised as an important area in phylogenetic inference. Basal archosaur phylogeny has thus far been the subject of restricted investigations of sub-optimal trees by Parrish (1993) and Juul (1994), who both investigated how many additional steps were required to support some competing hypotheses. Our calculation of Bremer support values (figure 2) indicate that the previous lack, or limited use of investigations of support have obscured the frailty of some of the existing hypotheses. While Parrish (1993) recognized that Sereno's (1991) contrasting resolution of the Suchia-Ornithosuchidae-Parasuchia trichotomy based on his own data set required only a single additional step, he did not demonstrate that other important topologies he hypothesised were similarly based on minimal Bremer support. With Juul's (1994) data, clades with minimal support include the newly erected Dromaeosuchia, and none of the clades within his Crurotarsi have higher Bremer support than +2. Bremer support for Sereno's (1991) important resolution of the Suchia-Ornithosuchidae-Parasuchia trichotomy is also minimal. Considerations of hypothesis robustness are also useful in removing the focus from constructing and asserting a single phylogenetic result, to assessing data quality and identifying, rather than obscuring areas in particular need of future research.

We believe that there is every reason for estimates of basal archosaur phylogeny to continue to advance, particularly if explicit analyses are accompanied by greater methodological awareness, more rigorous character formulation, a greater emphasis on testing and evaluating phylogenetic hypotheses inferred from the data, and an improvement in the knowledge of basal archosaur morphology, and hope that this paper will be some contribution to that end.

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