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Phylogeny of Drepanosauridae (Reptilia: Diapsida)

Phil Senter [a]

[a] Division of Mathematics and Science, Lamar State College-Orange, 410 Front St., Orange, Texas, 77630, USA

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Phylogeny of Drepanosauridae (Reptilia: Diapsida)

Phil Senter
Division of Mathematics and Science, Lamar State College-Orange, 410 Front St., Orange, Texas 77630 USA

SYNOPSIS Phylogenetic analysis reveals that the Triassic diapsid family Drepanosauridae is closely related to *Coelurosauravus* and *Longisquama*. These three taxa are part of a clade for which the name Avicephala (defined as all taxa more closely related to *Coelurosauravus* and *Megalancosaurus* than to Neodiapsida) is coined. Avicephala is a sister taxon to Neodiapsida. The name Simiosauria is erected for the clade composed of all taxa more closely related to Drepanosauridae than to *Coelurosauravus* or Sauria. Simiosauria is composed of MCSNB 4751 + (*Hypuronector* + Drepanosauridae). Drepanosauridae is composed of *Drepanosaurus* + (*Dolabrosaurus* + *Megalancosaurus*). Arboreality is probably plesiomorphic for Avicephala and no convincing evidence exists that any simiosaurian was aquatic.

KEY WORDS Drepanosauridae, Simiosauria, Avicephala, Diapsida, *Coelurosauravus*, *Longisquama*, *Megalancosaurus*

Contents

Introduction **257**
Institutional Abbreviations 258
Methods **258**
Results **259**
Eosuchia 259
Avicephala 261
Coelurosauravus + *Longisquama* 261
Simiosauria 261
Hypuronector + Drepanosauridae 261
Drepanosauridae 261
Dolabrosaurus + *Megalancosaurus* 261
Neodiapsida 261
Sauria 261
Archosauromorpha 261
Prolacertiformes + Archosauriformes 262
Prolacertiformes 262
Tanystropheidae 262
Archosauriformes 262
Euparkeria + Archosauria 262
Archosauria 262
Sinosauropteryx + *Archaeopteryx* 262
Discussion **262**
Acknowledgements **264**
References **264**
Appendix 1: Character list **265**
Appendix 2: Data matrix for first phylogenetic analysis **268**

Introduction

The family Drepanosauridae consists of bizarre, arboreal diapsids from the Upper Triassic of Europe and North America. Drepanosaurids exhibit dorsoventrally deep tails, prehensile mani and pedes, elongate scapulae and anterior vertebrae with high, fused neural spines (Pinna 1984; Berman & Reisz 1992; Renesto 1994*b*; Colbert & Olsen

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2001). Drepanosauridae was erected by Berman & Reisz (1992) for the inclusion of the Italian species *Drepanosaurus unguicaudatus* and the New Mexican species *Dolabrosaurus aquatilis*. Subsequent authors have referred several more taxa to the family including: the Italian species *Megalancosaurus preonensis* (Renesto 1994*b*), the New Jersian species *Hypuronector limnaois* (Colbert & Olsen 2001), an unnamed taxon from Italy, represented by a juvenile skeleton (MCSNB 4751) that has been figured but only partially described (Renesto 2000) and an unnamed taxon from New Mexico, represented by a fully described pectoral girdle (GR 1113: Harris & Downs 2002). Dilkes (1998) provided the first phylogenetic definition (DeQueiroz & Gauthier 1992) of Drepanosauridae: 'the most recent common ancestor of *Megalancosaurus*, *Drepanosaurus* and *Dolabrosaurus* and all of its descendants'. It remains to be seen whether all of the above taxa fall within this phylogenetic bracket, since most have not yet been included in phylogenetic analyses.

Researchers disagree about the phylogenetic position of Drepanosauridae. Some authors have suggested a close relationship with Aves (Tarsitano 1991; Feduccia & Wild 1993; Feduccia 1999). This putative relationship has not yet been tested phylogenetically, since no published phylogenetic analysis includes both avian and drepanosaurid taxa. The phylogenetic analyses of Evans (1988) and Renesto (1994*b*) place *Megalancosaurus* immediately outside the clade Archosauria + Prolacertiformes. The phylogenetic analysis of Dilkes (1998) places Drepanosauridae as sister taxon to Tanystropheidae.

Here, a new phylogenetic analysis is presented in order to elucidate the relationships within Drepanosauridae and to test the various published hypotheses concerning the position of Drepanosauridae within Diapsida.

Institutional Abbreviations

AMNH = American Museum of Natural History, New York City, New York, USA.
BMNH = Natural History Museum, London, UK.
CCSR = 'Collezione del Centro Studi e Richerche' Villa Anita, Sigillo Umbro, Perugia, Italy.
GR = Ruth Hall Museum of Paleontology, Ghost Ranch Conference Center, Abiquiu, New Mexico, USA.
HMN = Museum für Naturkunde, Berlin, Germany.
JM = Jura-Museum, Eichstätt, Germany.
MBSN = Museo Brembano di Scienze Naturali, San Pellegrino, Italy.
MCSNB = Museo Civico Scienzi Naturali 'E. Caffi', Bergamo, Italy.
MCZ = Museum of Comparative Zoology, Cambridge, Massachussetts, USA.
MFSN = Museo Friulano di Storia Naturale, Udine, Italy.
MPUM = Museo Paleontologia, Università degli Studi, Milan, Italy.
NGMC = National Geological Museum of China, Beijing, China.
PIN = Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.
SAM = South African Museum, Cape Town, South Africa.
UCMP = University of California Museum of Paleontology, Berkeley, California, USA.
UMZC = University Museum of Zoology, Cambridge, UK.

Methods

A data matrix of 73 osteological characters (all binary except for one unordered, multistate character) was constructed for 19 diapsid ingroups, with the protorothyridid *Paleothyris acadiana* as an outgroup (see Appendices 1 and 2). Only one supraspecific taxon (*Coelurosauravus*) was used. The list of characters was created largely without reference to previously published character lists, so as to avoid bias of phylogenetic results toward those obtained by previous authors. For about half of the terminal taxa, character states were coded according to personal observations of specimens (Table 1). For the others, character states were coded according to descriptions in the literature (Table 1).

Terminal taxa include representatives of Aves (*Archaeopteryx*), Tanystropheidae (*Macrocnemus*, *Langobardisaurus*) and other basal Archosauromorpha (*Mesosuchus*, *Prolacerta*, *Proterosuchus*), in order to test the putative relationships between these taxa and Drepanosauridae. Representatives of other major diapsid taxa were also included to break up long branches, so as to avoid long-branch attraction (Gauthier *et al.* 1988*a*; Hendy & Penny 1989; Hillis 1996).

The analysis includes three taxa for which the cranial anatomy has been interpreted differently by different authors. These are the Permian gliding reptile *Coelurosauravus* (described most thoroughly by Evans 1987), the Triassic reptile *Longisquama insignis* (described by Sharov 1970 and Unwin *et al.* 2000) and the drepanosaurid *Megalancosaurus preonensis* (described most thoroughly by Renesto 1994*b*, 2000). Skull bones of *Coelurosauravus* have been given different identities by different authors (for a review, see Evans 1987); character state codings here follow the interpretations of Evans (1987). *L. insignis* and *M. preonensis* are said by some authors to exhibit antorbital fenestrae (Sharov 1970; Feduccia & Wild 1993; Jones *et al.* 2001) and *L. insignis* is said to exhibit a mandibular fenestra (Sharov 1970). In personal observations of the specimens, I could not confirm the presence of an antorbital fenestra in either taxon. The putative antorbital fenestrae in *L. insignis* appear to be artifacts of damage, while the relevant opening in *M. preonensis* could be an external naris. I was able to confirm that *L. insignis* lacks a mandibular fenestra, since the surangular–angular suture shows up well in the counterslab and exhibits no opening between the two bones. The ambiguity regarding the presence of an antorbital fenestra in the two taxa was dealt with as described below.

Two phylogenetic analyses were performed, using random addition sequences in branch-and-bound search mode, with PAUP 4.0b software (Swofford 2002). In the first analysis, *M. preonensis* and *L. insignis* were coded as lacking antorbital fenestrae. In the second, they were coded as exhibiting antorbital fenestrae. Bootstrap (branch-and-bound mode, 1000 replicates) and Bremer analyses were performed on the data set from each analysis, using the same software.

Extra-step analyses were also performed. The tree recovered by each phylogenetic analysis was opened in MacClade 4.0 (Maddison & Maddison 2000). The clade Simiosauria (defined below) was then moved to various positions and the change in the number of steps was recorded for each new position. Simiosauria was then placed in its original location and *Archaeopteryx* was moved to all possible positions within Avicephala (defined below) and

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Table 1 Specimens and literature consulted for construction of the phylogenetic data matrix in Appendix 2.

Taxon	Information sources
Palaeothyris acadiana	MCZ 3481, MCZ 3475, MCZ 3478, MCZ 3482, MCZ 3483, MCZ 3485, MCZ 3486, MCZ 3488, MCZ 3490, MCZ 3491, MCZ 3492
Megalancosaurus preonensis	MFSN 1769, MFSN 18443, CCSR 63115, MPUM 6008, MCSNB 7833, MBSN 25, MBSN 26
MCSNB 4751	Renesto 2000
Drepanosaurus unguicaudatus	MCSNB 5278; Pinna 1984
Dolabrosaurus aquatilis	Berman & Reisz 1992
Hypuronector limnaios	Colbert & Olsen 2001
Petrolacosaurus kansensis	CM 29904, CM 29905, KUVP 1424, KUVP 9951, KUVP 9952, KUVP 9957a, KUVP 9959, KUVP 9960, KUVP 9961, KUVP 33606, KUVP 33606a, KUVP 33607, KUVP 33608, KUVP 33609, Peabody 1952; Reisz 1981
Longisquama insignis	PIN 2584/4; T. D. Jones (unpublished photographs)
Coelurosauravus	Evans 1982, 1987
Youngina capensis	Broom 1922; Gow 1975
Gephyrosaurus bridensis	Evans 1980, 1981
Mesosuchus browni	Dilkes 1998
Prolacerta broomi	AMNH 9502, AMNH 9520, AMNH 9521, AMNH 9558, UCMP 97151; Gow 1975
Macrocnemus bassanii	Peyer 1937; Kuhn-Schnyder 1962; S. Renesto (unpublished photographs)
Langobarsidaurus pandolfi	MCSNB 2883, MCSNB 4860, Renesto 1994*a*
Ornithosuchus longidens	BMNH R 2409, BMNH R 2410 (moulds), BMNH R 3142, BMNH R 3561 (moulds), BMNH R 3916 (moulds); Walker 1964
Proterosuchus fergusi	Cruickshank 1972; Welman 1998
Euparkeria capensis	AMNH 5548, AMNH 29975 (cast of SAM 5867), UMZC T792; Ewer 1965
Archaeopteryx lithographica	BMNH 37001, UCMP V 136566 (cast of JM 2257), unnumbered cast of HMN 1880/1881 (pers. collection Ed.); Wellnhofer 1974
Sinosauropteryx prima	NGMC 54, NGMC 64; Currie & Chen 2001

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the change in the number of steps was recorded for each new position. This novel type of analysis does not elucidate phylogeny but can be used as a rough gauge for the plausibility of alternate phylogenetic hypotheses, under the assumption that the plausibility of a phylogenetic hypothesis is inversely related to the number of extra steps that it requires.

RESULTS

The first phylogenetic analysis recovered a single most-parsimonious tree of 129 steps (Fig. 1). For this tree, the consistency index (CI) = 0.574, the retention index (RI) = 0.754, the rescaled consistency index (RC) = 0.433 and the homoplasy index (HI) = 0.426. The second phylogenetic analysis recovered a single most-parsimonious tree of 131 steps, with topology identical to that of the tree recovered by the first analysis. For this tree, CI = 0.565, RI = 0.748, RC = 0.422 and HI = 0.435.

Both trees place Drepanosauridae outside Neodiapsida as a close relative of *Coelurosauravus* and *L. insignis* and not a close relative of Aves, Tanystropheidae, or Archosauromorpha (Fig. 1). Extra-step analysis on the data set from the first analysis shows that at least 6 extra steps are required to move Simiosauria to any other position in the tree and at least 16 extra steps are required to move *Archaeopteryx* to any position within Avicephala (Fig. 2).

A list of synapomorphies at each node, for the first analysis, follows. The synapomorphy list for the second analysis is identical, except for changes in the state of character 4 (presence/absence of antorbital fenestra). In the accelerated transformation (ACCTRAN) list for the second analysis, state 1 of character 4 (antorbital fenestra present) is considered to be a synapomorphy of Avicephala, which is lost in *Coelurosauravus*; in the delayed transformation (DELTRAN) list, state 1 is considered to be acquired independently in *Lonsiquama* and *Megalancosaurus*.

In the ACCTRAN mode, PAUP 4.0b assumes that for a given clade, a changed character state is a synapomorphy even if it can be confirmed in only one terminal taxon. Such dubious 'synapomorphies' are omitted in the ACCTRAN lists here.

At each node that represents a named taxon, the taxon's name and its definition are also given. Here, naming of taxa follows the rules of phylogenetic taxonomy (DeQueiroz & Gauthier 1992), e.g. (1) only clades are given taxonomic names, (2) the earliest published phylogenetic definition of a taxonomic name has priority over subsequent definitions, (3) a phylogenetic definition may be stem-based (all taxa more closely related to A than to B) or node-based (all taxa phylogenetically bracketed by A and B, i.e. A and B, their common ancestor and all of its descendants). Mere lists of included taxa are not considered valid phylogenetic definitions.

The verbal description of each synapomorphy is preceded by the number by which the character is catalogued in the character list (Appendix 1), followed in parentheses by the number representing the character state. For example, '5(1)' refers to state 1 for character 5.

Eosuchia

All taxa phylogenetically bracketed by *Coelurosauravus*, *Apsisaurus*, Younginiformes, Lepidosauria and Archosauria (Laurin 1991).

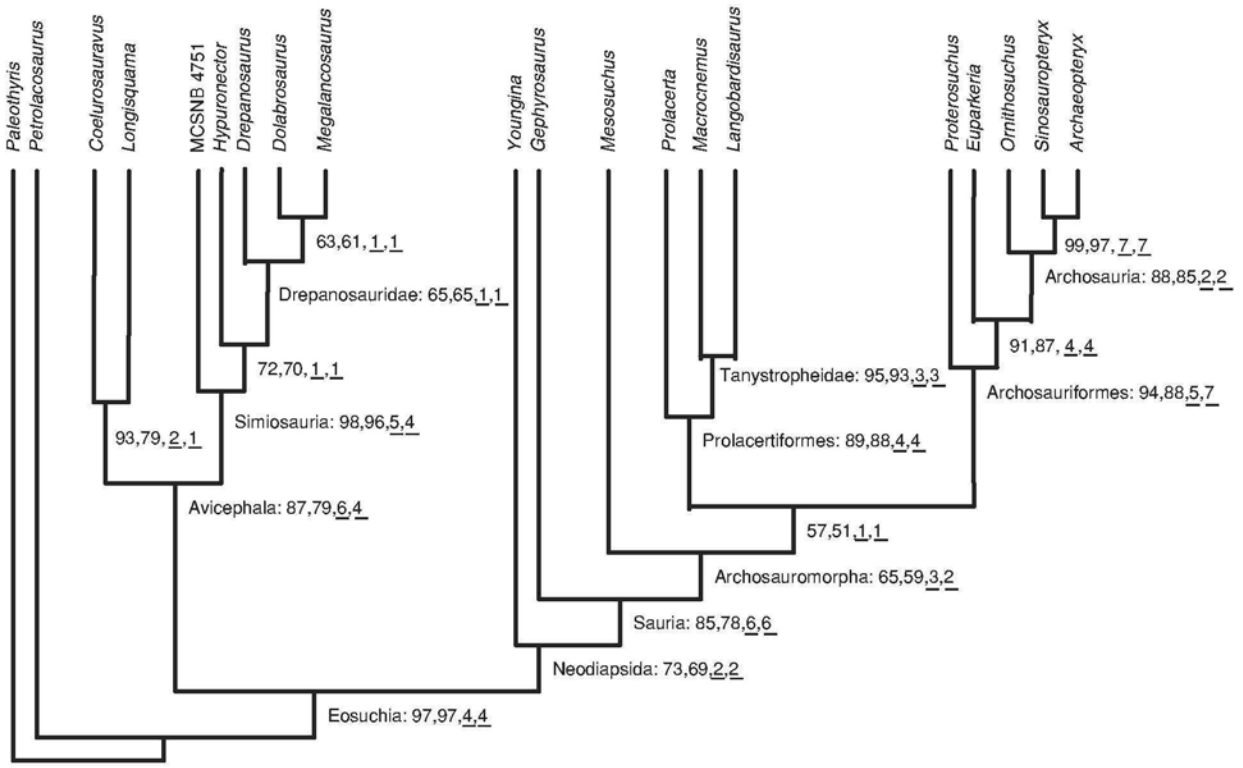

Figure 1 Results of phylogenetic, bootstrap and Bremer analyses. Numbers at each node are (left to right): bootstrap value from first analysis, bootstrap value from second analysis, Bremer value from first analysis (underlined), Bremer value from second analysis (underlined).

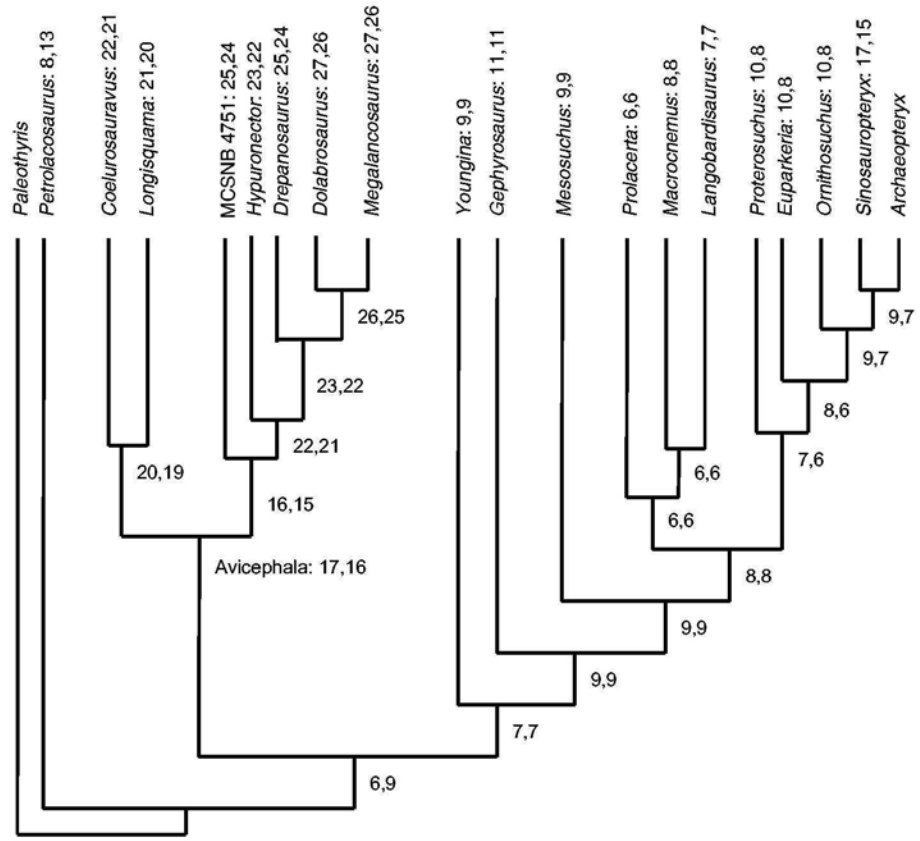

Figure 2 Results of extra step analyses, showing numbers of extra steps required to make Drepanosauroidea a sister group to given clades or terminal taxa (outside Avicephala) and number of extra steps required to make Aves a sister group to given clades or terminal taxa (Avicephala and within). At each node and terminal taxon, the number on the left is the result using the data set from the first phylogenetic analysis; the number on the right is the result using the data set from the second phylogenetic analysis.

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ACCTRAN and DELTRAN: 5(1), lacrimal excluded from external naris; 7(1), postfrontal included in supratemporal fenestra; 10(1), squamosal processes of parietals backswept; 26(1), caniniform maxillary teeth absent; 57(1), acetabulum circular; 65(1), length of pes subequal to or < femoral length.

ACCTRAN only: 6(1), lower temporal arcade incomplete.

Avicephala

New taxon, from Latin *avis*, 'bird' and Greek *kephale*, 'head': all taxa more closely related to *Coelurosauravus* and *Megalancosaurus* than to Neodiapsida.

ACCTRAN and DELTRAN: 1(1), premaxilla and dentary sharply pointed in lateral view; 17(1), craniomandibular joint suborbital; 21(1), posterior border of skull strongly inclined posteriorly; 43(1), scapula elongate; 47(1), width of distal expansion of humerus < 1/3 humeral length; 51(1), length of manus subequal to or < humeral length; 52(1), metacarpal IV not longer than metacarpal III; 68(1), metatarsal IV not longer than metatarsal III.

ACCTRAN only: 52(1), metacarpal IV not longer than metacarpal III; 55(1), iliac blade vertical; 69(1), pedal phalanx IV–1 not longer than phalanx III–1.

Coelurosauravus + *Longisquama*

ACCTRAN and DELTRAN: 22(1), parietals posteriorly upswept, forming posterodorsal crest; 23(1), parietal rim ornamented with bumps.

Simiosauria

New taxon, from Latin *simia*, 'monkey'; *saurus*, 'lizard'; named for the presence of prehensile mani, pedes and tail, which are also found in New World monkeys: all taxa more closely related to Drepanosauridae than to *Coelurosauravus* or Sauria.

ACCTRAN and DELTRAN: 31(1), anterior dorsal neural spines distally expanded and fused; 32(1), dorsal neural spines high and elongate; 35(1), mid-caudal neural spines high and elongate; 40(1), anterior hemal arches $\geq 3\times$ length of associated vertebrae; 44(1), scapula inclined anteriorly; 46(1), humeral entepicondylar foramen closed; 63(1), tibial length ≤ 0.65 femoral length; 64(1), calcaneal tuber present.

ACCTRAN only: 10(0), squamosal processes of parietals not backswept; 16(1), craniomandibular joint ventrally displaced; 33(1), number of sacrals increased to 3; 50(1), radiale and intermedium elongated.

DELTRAN only: 55(1), iliac blade vertical.

Hypuronector + Drepanosauridae

ACCTRAN and DELTRAN: 27(1), Mid-cervical vertebrae markedly longer than dorsals; 39(1), posterior trunk ribs holocephalous.

ACCTRAN only: 53(1), manual phalangeal count reduced; 66(1), pedal phalangeal count reduced.

DELTRAN only: 16(1), craniomandibular joint ventrally displaced.

Drepanosauridae

All taxa phylogenetically bracketed by *Drepanosaurus*, *Dolabrosaurus* and *Megalancosaurus* (Dilkes 1998).

ACCTRAN and DELTRAN: 37(1), terminal tail claw present; 49(1), radius extends further distally than ulna.

ACCTRAN only: 52(0), metacarpal IV longer than metacarpal III.

DELTRAN only: 50(1), radiale and intermedium elongated; 53(1), manual phalangeal count reduced; 66(1), pedal phalangeal count reduced.

Dolabrosaurus + *Megalancosaurus*

ACCTRAN and DELTRAN: 36(1), mid-caudal neural spines T-shaped.

DELTRAN only: 33(1), number of sacrals increased to 3.

Neodiapsida

All taxa phylogenetically bracketed by Younginiformes and living diapsids (Laurin 1991).

ACCTRAN and DELTRAN: 39(1), posterior trunk ribs holocephalous; 42(1), number of dorsal vertebrae decreased to ≤ 17; 48(1), pronounced olecranon process absent.

ACCTRAN only: 18(1), dorsoventral depth of surangular anteriorly $\geq 2\times$ dorsoventral depth of angular anteriorly.

DELTRAN only: 10(1), squamosal processes of parietals posteriorly backswept.

Sauria

All taxa phylogenetically bracketed by crocodilians, birds, squamates and *Sphenodon* (Gauthier *et al.* 1988*b*).

ACCTRAN and DELTRAN: 11(1), prefrontal–nasal suture diagonally oriented in dorsal view; 12(1), quadratojugal process of jugal slender and tapering; 13(1), squamosal with slender, tapering anteroventral process; 14(1), contact between palatine and ectopterygoid absent; 20(1), prominent retroarticular process present; 70(1), tarsal surface of metatarsal V faces inward, articulates with distal tarsal IV (distal tarsal V absent).

ACCTRAN only: 8(1), discrete quadratojugal ascending process present; 72(1), pedal phalanx V–2 does not extend further distally than metatarsal IV.

DELTRAN only: 6(1), lower temporal arcade incomplete.

Archosauromorpha

All taxa phylogenetically bracketed by *Prolacerta*, *Trilophosaurus* and *Hyperodapedon* (Laurin 1991).

ACCTRAN and DELTRAN: 3(1), maxilla excluded from external naris; 7(0), postfrontal not included in supratemporal fenestra; 46(1), humeral entepicondylar foramen closed.

ACCTRAN: 38(1), cervical ribs distally tapering; 47(1), width of distal expansion of humerus < 1/3 humeral length.

DELTRAN only: 8(1), discrete quadratojugal ascending process present; 72(1), pedal phalanx V–2 does not extend further distally than metatarsal IV.

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Prolacertiformes + Archosauriformes

ACCTRAN and DELTRAN: 2(1), length of skull anterior to orbit > length of skull posterior to anterior margin of orbit.

ACCTRAN only: 18(0), dorsoventral depth of surangular anteriorly < 2× dorsoventral depth of angular anteriorly; 64(1), calcaneal tuber present.

DELTRAN only: 38(1), cervical ribs distally tapering.

Prolacertiformes

New definition: all taxa more closely related to *Prolacerta* than to Archosauriformes. The name Prolacertiformes has previously been applied to this clade, but without a phylogenetic definition (Benton 1985; Evans 1988; Jalil 1997).

ACCTRAN and DELTRAN: 27(1), cervical vertebrae markedly longer than dorsals; 28(1), mid-cervical centra ≥ 3 × longer than tall; 30(1), cervical neural spines with anterior overhang; 51(1), length of manus subequal to or < humeral length; 61(1), femoral diameter distally reduced.

DELTRAN only: 47(1), width of distal expansion of humerus < 1/3 humeral length.

Tanystropheidae

All taxa phylogenetically bracketed by *Macrocnemus*, *Tanystropheus* and *Langobardisaurus* (Dilkes 1998).

ACCTRAN and DELTRAN: 1(1), premaxilla and dentary sharply pointed in lateral view; 29(1), cervical vertebrae posteriorly convex; 73(1), distal tarsal I absent.

ACCTRAN only: 64(0), calcaneal tuber absent.

Archosauriformes

New definition: all taxa phylogenetically bracketed by *Proterosuchus* and Archosauria. The name Archosauriformes has previously been applied to this clade, but without a phylogenetic definition (Gauthier *et al.* 1988*a*).

ACCTRAN and DELTRAN: 4(1), antorbital fenestra present; 6(0), lower temporal arcade complete; 9(1), pineal foramen closed; 15(1), ziphodonty present; 19(1), surangular dorsally overlaps dentary; 24(1), mandibular fenestra present.

ACCTRAN only: 53(1), manual phalangeal count reduced; 65(0), pes longer than femur.

DELTRAN only: 64(1), calcaneal tuber present.

Euparkeria + Archosauria

ACCTRAN and DELTRAN: 18(1), dorsoventral depth of surangular anteriorly ≥ 2 × dorsoventral depth of angular anteriorly; 43(1), scapula elongate; 62(1), fourth trochanter present; 68(1), metatarsal IV not longer than metatarsal III; 69(1), pedal phalanx IV–1 not longer than phalanx III–1; 73(1), distal tarsal I absent.

Archosauria

All taxa phylogenetically bracketed by Crocodylia and Aves (Gauthier 1986).

ACCTRAN and DELTRAN: 25(1), palatal teeth absent; 58(1), pubes elongate.

ACCTRAN only: 39(1), posterior trunk ribs dolichocephalous.

DELTRAN only: 47(1), width of distal expansion of humerus < 1/3 humeral length.

Sinosauropteryx + *Archaeopteryx*

ACCTRAN and DELTRAN: 33(2), number of sacrals increased to 5; 48(0), pronounced olecranon process present; 54(1), long, deep preacetabular blade present; 56(1), acetabulum open; 60(1), femoral head inturned at sub-right angle; 64(1), calcaneal tuber absent; 67(1), metatarsal I reduced to a splint; 71(1), pedal digit V vestigial.

DELTRAN only: 39(1), posterior trunk ribs dolichocephalous; 53(1), manual phalangeal count reduced; 65(0), pes longer than femur.

DISCUSSION

Other than the placement of Drepanosauridae close to *Coelurosauravus* and *Longisquama*, and the finding that Tanystropheidae is a prolacertiform taxon (contradicted in Dilkes 1998), the cladogram generally agrees with those produced by previous analyses (Benton 1985; Evans 1988; Gauthier *et al.* 1988*a*; Laurin 1991; Parrish 1993; Juul 1994; Rieppel & DeBraga 1996; Jalil 1997; Lee 1997; Wilkinson *et al.* 1997; Dilkes 1998). As each of these analyses used a different data matrix, their similar results provide independent corroboration of phylogenetic results.

High Bremer and bootstrap values at Eosuchia, Avicephala, Simiosauria, Sauria, Prolacertiformes, Tanystropheidae, Archosauriformes, *Euparkeria* + Archosauria and *Sinosauropteyx* + *Archaeopteryx* (Fig. 1) indicate high support for the recovered compositions of these taxa. Very high numbers of extra steps are required to move Simiosauria to any other position in the cladogram and to move *Archaeopteryx* into Avicephala (Fig. 2). A close relationship between Drepanosauridae and Tanystropheidae, Archosauromorpha, or Aves is therefore not supported by this analysis.

The close relationship found here between Drepanosauridae, *Coelurosauravus*, and *Longisquama* contradicts the results of three previous phylogenetic analyses (Evans 1988; Renesto 1994*b*; Dilkes 1998). Taxon and character sampling artifacts cannot be ruled out as explanations for the placement of drepanosaurids in the previous analyses, for the following reasons: (1) basal simiosaurians (MCSNB 4651, *Hypuronector*) were unknown in the literature when the three analyses were undertaken, which confined the authors to the use of highly derived simiosaurians (*Megalancosaurus* alone in Evans 1988 and Renesto 1994*b*; *Megalancosaurus* and *Drepanosaurus* in Dilkes 1998). The inclusion of derived members of a lineage without inclusion of more basal members to break up long branches, increases the danger of long branch attraction (Hendy & Penny 1989; Hillis 1996; Graybeal 1998). Long branch attraction is especially probable if a taxon exhibits a large number of convergences with unrelated taxa; this is certainly true for drepanosauroids (see below). (2) The analysis of Evans (1988) was undertaken before the posterior half of *Megalancosaurus* was known, which raises the possibility that missing data affected tree topology. (3) The analysis of Renesto (1994*b*) included

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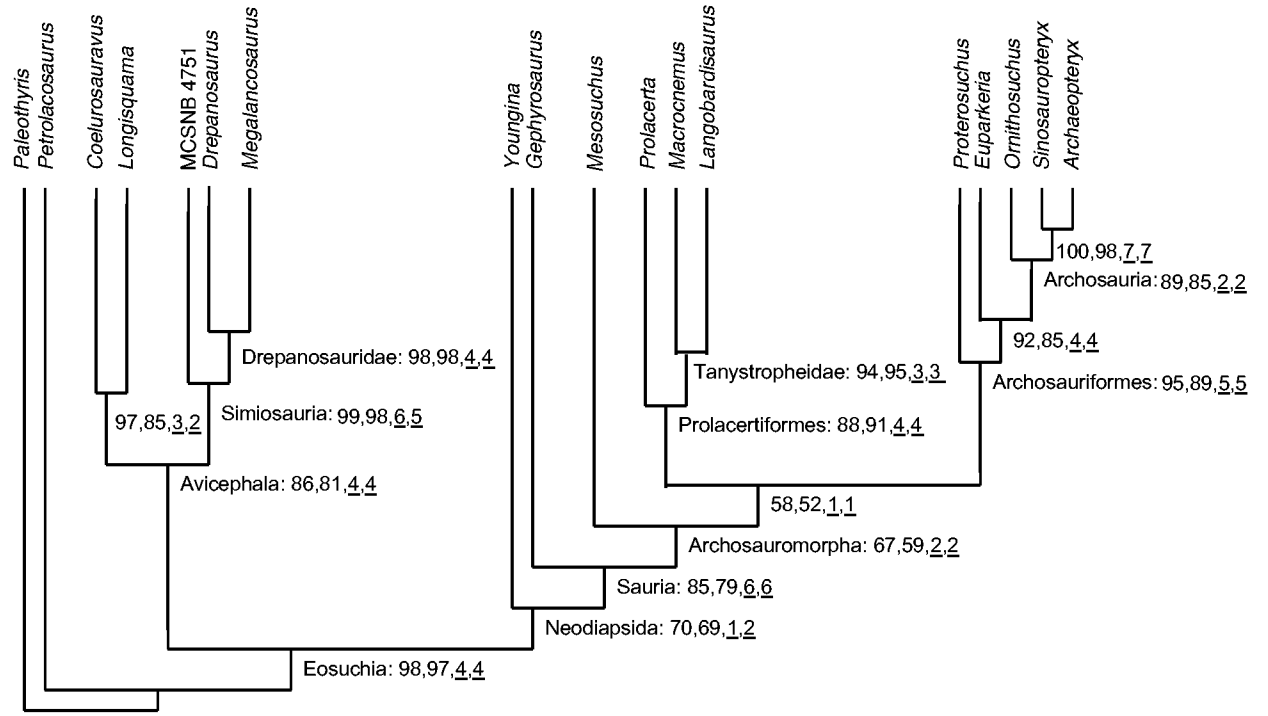

Figure 3 Results of bootstrap and Bremer analyses without *Hypuronector* and *Dolabrosaurus*. Numbers at each node correspond to their counterparts in Figure 1.

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no non-saurian taxa and, therefore, did not give *Megalancosaurus* the opportunity to fall outside Sauria. (4) The analysis of Dilkes (1998) excluded *Coelurosauravus* and, therefore, did not give drepanosaurids the opportunity to fall next to it.

Tree topology recovered here indicates that considerable convergence between avicephalan clades and neodiapsid clades has occurred. Synapomorphies of Avicephala that occur elsewhere in Diapsida include a sharply pointed snout (character 1, state 1, found also in Tanystropheidae and *Archaeopteryx*), an elongate scapular blade (character 43, state 1, found also in *Euparkeria* + Archosauria), reduction in the distal humeral width (character 47, state 1, found also in *Petrolacosaurus*, Prolacertiformes and Archosauria), shortening of the manus (character 51, state 1, found also in Prolacertiformes) and shortening of metatarsal IV (character 68, state 1, found also in *Euparkeria* + Archosauria). Synapomorphies of Simiosauria that occur elsewhere in Diapsida include closure of the humeral entepicondylar foramen (character 46, state 1, found also in Archosauromorpha) and the presence of a calcaneal tuber (character 64, state 1, found also in *Prolacerta* and Archosauriformes). Synapomorphies of *Hypuronector* + Drepanosauridae that occur elsewhere in Diapsida include the presence of cervical vertebrae that are markedly longer than the dorsals (character 27, state 1, found also in Prolacertiformes and *Archaeopteryx*) and holocephalous posterior trunk ribs (character 39, state 1, found also in Neodiapsida). A furcula (character 45, state 1) is found in both *Longisquama* and *Archaeopteryx*.

The putative antorbital fenestra in *Longisquama* and *Megalancosaurus* (Sharov 1970; Feduccia & Wild 1993; Jones *et al.* 2001) deserves special mention. Previous authors have considered the possession of an antorbital fenestra to be a synapomorphy between Aves and *Longisquama* and/or *Megalancosaurus* (Feduccia & Wild 1993; Jones *et al.* 2001). However, the results of the present analyses show that *Longisquama* and *Megalancosaurus* are not closely related to Aves or any other archosauriform. Therefore, if an antorbital fenestra is present in *Longisquama* and *Megalancosaurus*, it has been acquired independently of the avian antorbital fenestra.

Missing data can depress Bremer and boostrap values even when phylogenetic accuracy is high (Wilkinson 2003). Low Bremer and bootstrap values at nodes within Simiosauria are probably due to missing information in anatomical regions important to the reconstruction of drepanosauroid phylogeny. Regions of particular interest include cervical vertebrae (missing in *Drepanosaurus* and *Dolabrosaurus*; central morphology unknown in *Hypuronector*), manus (largely missing in *Hypuronector*, absent in *Dolabrosaurus*) and pes (largely missing in *Hypuronector* and *Dolabrosaurus*). States of characters relating to these regions are largely plesiomorphic in MCSNB 4751 and apomorphic in *Megalancosaurus* (see Appendix 1), but the distribution of missing data makes it difficult to identify the nodes within Simiosauria at which the state changes occur. Additional simiosaurian specimens are needed in order to identify these nodes and to confirm or falsify the poorly-supported topology found here within Simiosauria.

Among simiosaurians, the amount of missing data is highest in *Dolabrosaurus* and *Hypuronector*. Removal of these two taxa dramatically raises the bootstrap and Bremer values at the node *Drepanosaurus* + *Megalancosaurus* (Fig. 3). This corroborates the relative positions of those two taxa and MCSNB 4751 as found by the phylogenetic analyses that included *Dolabrosaurus* and *Hypuronector*.

As Renesto (2000) notes, the first pedal digit in some specimens of *Megalancosaurus* exhibits an unusual modification for prehension. It opposes the other digits and its second phalanx is reduced to a nub. In other specimens, the first pedal digit does not oppose the others and its second phalanx retains typical ungual morphology. Renesto (2000) mentions the possibility that the pedes of *Megalancosaurus* were sexually dimorphic. This could be confirmed if the unusual digital modification is present in approximately half the specimens in a much larger sample of *Megalancosaurus* pedes. Indeed, pedal morphology may be sexually dimorphic across Simiosauria, as the modification described above occurs in half (four out of eight) of all known simiosaurian specimens with pedes. It occurs in the one known specimen of the species represented by MCSNB 4751 (Renesto 2000), the one known specimen of *Dolabrosaurus* (for which pedal digits I–V were at first mistakenly described as digits V–I: Berman & Reisz 1992) and in two out of the four known specimens of *Megalancosaurus* that include pedes (Renesto 1994*b*). It is absent in the one known specimen of *Hypuronector* that includes pedes (Colbert & Olson 2001), the one known specimen of *Drepanosaurus* (Pinna 1984) and two out of the four specimens of *Megalancosaurus* that include pedes (Renesto & Paganoni 1995; Renesto 2000). One of these last two specimens was described as a juvenile *Drepanosaurus* (Renesto & Paganoni 1995), but its high sacral and anterior caudal neural spines and forked mid-caudal hemal spines indicate referral to *Megalancosaurus*, under which name it is currently catalogued. I have personally examined all the known specimens of *Megalancosaurus*, *Drepanosaurus* and MSCNB 4751 and can confirm the distribution of the pedal modification described above in these species; for descriptions of the pedes of the other simiosaurian species, I have relied on the literature (see Table 1). Selection for such a pedal difference between simiosaurian sexes implies that some aspect of simiosaurian behaviour differed between the sexes such that members of one sex needed a tighter pedal grip. Unfortunately, no known simiosaurian fossil is preserved 'caught in the act' of using its pedes, so the nature of this behaviour is a mystery.

The gliding surfaces of *Coelurosauravus* (Evans 1987) and the prehensile autopodia and tails of Simiosauria (Pinna 1984; Renesto 1994*b*, 2000) indicate that these are arboreal taxa. The hypothesis that *Longisquama* is also arboreal is based mainly on the dubious interpretation that its integumentary structures formed a gliding surface (Haubold & Buffetaut 1987). However, there is no evidence that contradicts the hypothesis that *Longisquama* is arboreal and *Longisquama* is phylogenetically bracketed by the arboreal taxa *Coelurosauravus* and Simiosauria. Furthermore, penultimate phalanges are elongate in all avicephalans for which penultimate phalanges are known (Pinna 1984; Evans 1987; Berman & Reisz 1982; Renesto 1994*b*, 2000; Unwin *et al.* 2000), which further suggests arboreality (Unwin *et al.* 2000). Arboreality may therefore be plesiomorphic for Avicephala.

The deep tails of *Dolabrosaurus* and *Hypuronector* have been cited as evidence of aquatic habits (Berman & Reisz 1992; Colbert & Olson 2001). However, deep tails are also present in all other simiosaurians, the prehensile tails and autopodia of which indicate arboreal habits. Also, *Hypuronector* – like all other simiosaurians in which hindlimb proportions are known – exhibits elongate stylopodia and short autopodia, whereas the reverse is typically true for aquatic diapsids (pers. obs.). The leaf-shaped tail of *Hypuronector* is, therefore, more likely to have served as a form of arboreal camouflage than as a source of aquatic propulsion.

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APPENDIX 1: CHARACTER LIST

The citation after each character refers to the first use of the character or a similar character in a numerical phylogenetic study with a published data matrix. For cases in which a character was first used in two papers in the same book, the paper occurring on lower-numbered pages is cited. Citation of Benton's (1985) landmark paper is also given for characters that were used therein. That paper did not include a numerical phylogenetic analysis or a published data matrix, but citation of it seems prudent, as subsequent authors have often used its character list as a foundation for numerical phylogenetic analyses.

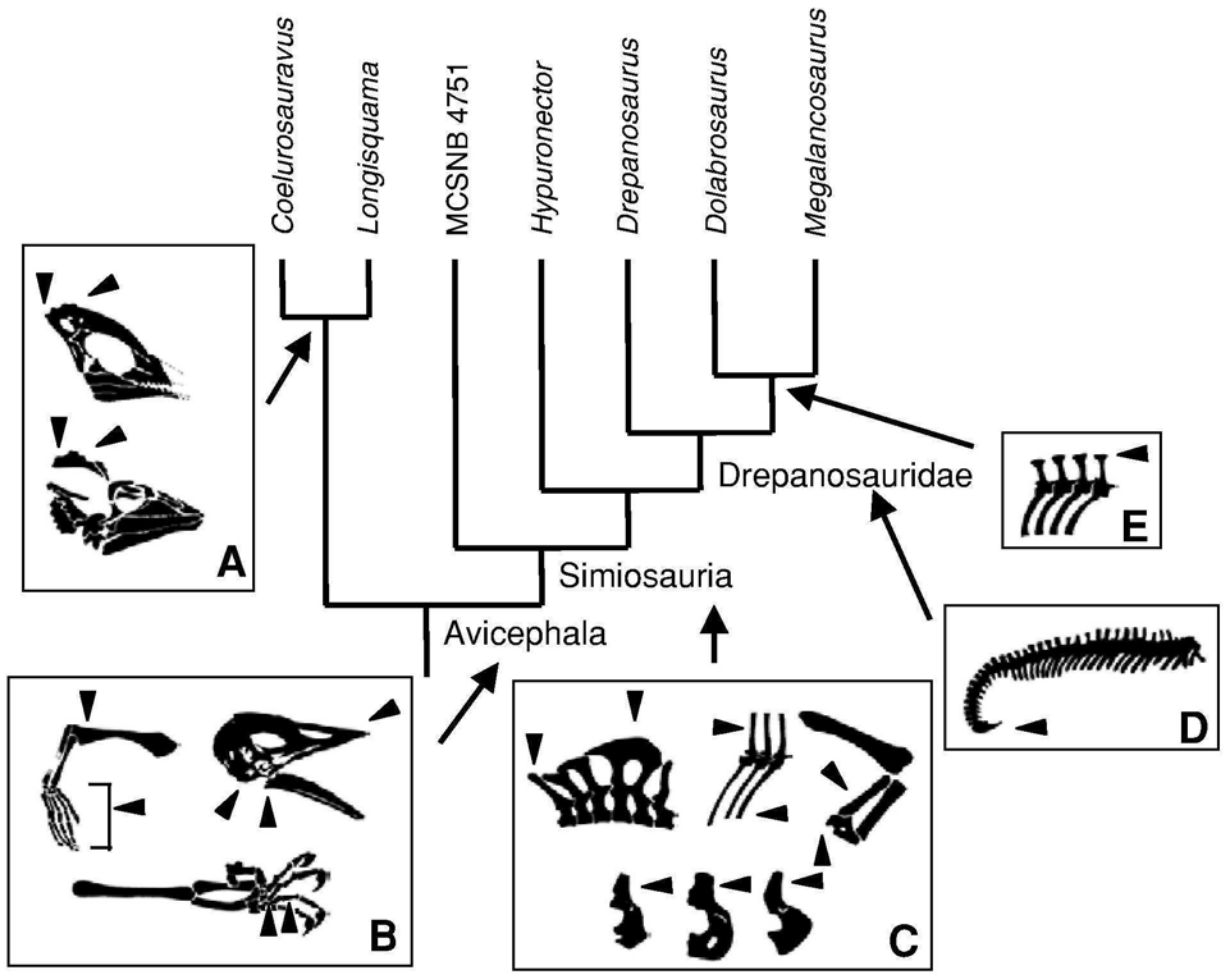

Figure 4 Select synapomorphies of Avicephala and its sub-clades. Drawings not to scale. Anterior is to the right in all cranial, axial and pelvic drawings. **A**, Skulls of *Longisquama insignis* (PIN 2584/4) and *Coelurosauravus jaekeli* (modified from Evans 1987), showing synapomorphies of *Longisquama* + *Coelurosauravus*: parietals upswept, parietal rim ornamented with bumps. **B**, Skull (MFSN 1769) and hindlimb (MBSN 26) of *Megalancosaurus preonensis*, together with forelimb of *Coelurosauravus jaekeli* (modified from Evans 1987), showing synapomorphies of Avicephala: sharply pointed snout, craniomandibular joint ventral to posterior extremity of orbit, strong posterior inclination of posterior border of skull, reduction in distal humeral width, manual length ≤ humeral length, length of metatarsal IV ≤ length of metatarsal III, length of pedal phalanx IV–1 ≤ length of pedal phalanx III–1. **C**, Anterior dorsal vertebrae of *Megalancosaurus preonensis* (modified from Renesto 1994*b*), portion of caudal series of *Hypuronector limnaios* (modified from Colbert & Olsen 2001), hindlimb of *Drepanosaurus unguicaudatus* (modifed from Pinna 1984) and pelves of (left to right) *Hypuronector limnaios* (modified from Colbert & Olsen 2001), *Drepanosaurus unguicaudatus* (modifed from Pinna 1984) and *Megalancosaurus preonensis* (MBSN 26), showing synapomorphies of Drepanosauroidea: high dorsal neural spines, distal expansions and fusion of anterior dorsal neural spines, elongate mid-caudal neural spines, anterior hemal arches ≥ 3 × longer than associated vertebrae, vertical orientation of iliac blade, tibial length ≤ 0.65 × femoral length, calcaneal tuber. **D**, Tail of *Drepanosaurus unguicaudatus* (modifed from Pinna 1984), showing a synapomorphy of Drepanosauridae: terminal caudal claw. **E**, Portion of caudal series of *Dolabrosaurus aquatilis* (Berman & Reisz 1992), showing a synapomorphy of *Dolabrosaurus* + *Megalancosaurus*: mid-caudal neural spines T-shaped.

1. Tips of premaxilla and dentary, in lateral view: (0) not sharply pointed, (1) sharply pointed (forming a strongly acute angle: Fig. 4(B)). (New character).
2. Length of skull anterior to orbit: (0) ≤ length of skull posterior to anterior margin of orbit, (1) > length of skull posterior to anterior margin of orbit (Benton 1985; Evans 1988).
3. Contact between maxilla and external naris: (0) present, (1) absent (Benton 1985; Evans 1988).
4. Antorbital fenestra: (0) absent, (1) present (Benton 1985; Gauthier *et al.* 1988*a*).
5. Contact between lacrimal and external naris: (0) present, (1) absent (Benton 1985; Gauthier *et al.* 1988*a*).
6. Lower temporal arcade: (0) complete, (1) incomplete (Benton 1985; Dilkes 1998).
7. Inclusion of postfrontal in supratemporal fenestra: (0) absent, (1) present (Benton 1985; Dilkes 1998).
8. Discrete ascending process of quadratojugal, posteriorly bordering infratemporal fenestra: (0) absent, (1) present (Gauthier *et al.* 1988*a*).
9. Pineal foramen: (0) open, (1) closed (Gauthier *et al.* 1988*a*).

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10. Squamosal processes of parietals: (0) not backswept, (1) backswept. (New character).
11. Prefrontal–nasal suture: (0) oriented parasagittally, (1) oriented diagonally in dorsal view (Laurin 1991).
12. Quadratojugal process of jugal: (0) wide and blunt, (1) slender and tapering (Laurin 1991).
13. Slender, ventrally tapering anteroventral process of squamosal: (0) absent, (1) present (Evans 1988).
14. Contact between palatine and ectopterygoid: (0) present, (1) absent. (New character).
15. Teeth: (0) not as in state 1, (1) laterally compressed, pointed, recurved and serrated (Benton 1985; Evans 1988).
16. Ventral displacement of craniomandibular joint below dorsal margin of dentary: (0) absent, (1) present (Maryanska *et al.* 2003).
17. Craniomandibular joint: (0) posterior to orbit, (1) ventral to posterior extremity of orbit (Fig. 4(B)). (New character).
18. Anterior depth of surangular: (0) $< 2\times$ that of angular, (1) $\geq 27\times$ that of angular (Gauthier 1986).
19. Dorsal overlap of dentary by surangular: (0) absent, (1) present. (New character).
20. Pronounced retroarticular process: (0) absent, (1) present (Benton 1985; Gauthier *et al.* 1988*a*).
21. Posterior border of skull: (0) not strongly inclined posteriorly, (1) strongly inclined posteriorly. (New character).
22. Posterior upsweeping of parietals, forming a posterodorsal crest: (0) absent, (1) present. (New character).
23. Ornamentation of parietal rim with pronounced bumps: (0) absent, (1) present. (New character).
24. Lateral mandibular fenestra: (0) absent, (1) present (Benton 1985; Gauthier *et al.* 1988*a*).
25. Palatal teeth: (0) present, (1) absent (Benton 1985; Gauthier *et al.* 1988*a*).
26. Caniniform teeth in maxilla: (0) present, (1) absent (Benton 1985; Gauthier *et al.* 1988*b*).
27. Mid-cervical vertebrae: (0) subequal in length to or shorter than dorsal vertebrae, (1) markedly longer than dorsals (Benton 1985; Evans 1988).
28. Length of mid-cervical centra: (0) $< 3 \times$ height, (1) $\geq 3 \times$ height. (New character).
29. Posterior face of mid-cervical centra: (0) not convex, (1) convex. (New character).
30. Anterior overhang of mid-cervical neural spines: (0) absent, (1) present. (New character).
31. Distal expansion and fusion of anterior dorsal neural spines: (0) absent, (1) present (Dilkes 1998).
32. Dorsal neural spines: (0) low, (1) high and elongate (Benton 1985; Evans 1988).
33. Number of sacral vertebrae: (0) 2, (1) 3, (2) 5 (Gauthier *et al.* 1988*a*).
34. Sacral and anterior caudal neural spines: (0) low, (1) high and elongate (Evans 1988).
35. Mid-caudal neural spines: (0) proximodistally short, (1) proximodistally elongate (height $\geq 4 \times$ anteroposterior length: Fig. 4(C). (New character).
36. Mid-caudal neural spines: (0) not T-shaped, (1) T-shaped (Dilkes 1998).
37. Terminal tail claw: (0) absent, (1) present. (New character).
38. Cervical ribs: (0) distally blunt, (1) distally tapering (Evans 1988).
39. Posterior trunk ribs: (0) dolichocephalous, (1) holocephalous (Benton 1985; Gauthier *et al.* 1988*b*).
40. Length of anterior hemal arches: (0) $< 3 \times$ length of associated vertebrae, (1) $\geq 3 \times$ length of associated vertebrae. (New character).
41. Forking and distal closure of mid-caudal hemal arches: (0) absent, (1) present. (New character).
42. Number of dorsal vertebrae: (0) ≥ 18, (1) ≤ 17. (New character).
43. Scapular blade: (0) short and broad, (1) elongate (Benton 1985; Gauthier 1986).
44. Scapular blade: (0) not inclined anteriorly, (1) anteriorly inclined (leaning forward). (New character).
45. Clavicles: (0) separate, (1) fused into a furcula (Gauthier 1986).
46. Entepicondylar foramen of humerus: (0) open, (1) closed (Benton 1985; Gauthier *et al.* 1988*a*).
47. Width of distal expansion of humerus: (0) $\geq 1/3 \times$ humeral length, (1) $< 1/3 \times$ humeral length (Benton 1985; Laurin 1991).
48. Pronounced olecranon process: (0) present, (1) absent (Benton 1985; Evans 1988).
49. Radius: (0) does not extend further distally than ulna, (1) extends further distally than ulna (Benton 1985; Evans 1988).
50. Radiale and intermedium: (0) blocklike, (1) elongate (new character).
51. Manus length: (0) > humeral length, (1) subequal to or < humeral length. (New character).
52. Metacarpal IV: (0) longer than metacarpal III, (1) not longer than metacarpal III (Evans 1988).
53. Reduction in manual phalangeal count: (0) absent, (1) present (Laurin & Reisz 1995).
54. Long, deep, preacetabular iliac blade: (0) absent, (1) present (Gauthier 1986).
55. Postacetabular iliac blade: (0) posteriorly inclined (leaning posteriorly), (1) vertical (Fig. 4(C)). (New character).
56. Acetabulum: (0) closed, (1) open (Gauthier 1986).
57. Acetabulum: (0) elongate, (1) round (Benton 1985; Gauthier *et al.* 1988*b*).
58. Pubes: (0) not elongate, (1) elongate (Evans 1988).
59. Thyroid fenestra: (0) absent, (1) present (Benton 1985; Evans 1988).
60. Femoral head: (0) not inturned at sub-right angle, (1) inturned at sub-right angle to femoral shaft (Gauthier *et al.* 1988*a*).
61. Diameter of femoral shaft: (0) constant or widening distally, (1) distally narrowed. (New character).
62. Fourth trochanter: (0) absent, (1) present (Benton 1985; Gauthier 1986).
63. Tibial length: (0) > 0.65 femoral length, (1) ≤ 0.65 femoral length. (New character).
64. Calcaneal tuber: (0) absent, (1) present (Benton 1985; Gauthier *et al.* 1988*a*).
65. Length of pes: (0) > femoral length, (1) subequal to or < femoral length. (New character).
66. Reduction in pedal phalangeal count: (0) absent, (1) present (Laurin & Reisz 1995).
67. Metatarsal I: (0) unreduced, (1) reduced to a splint (Gauthier 1986).
68. Metatarsal IV: (0) longer than metatarsal III, (1) not longer than metatarsal III. (New character).

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69. Pedal phalanx IV-1: (0) longer than pedal phalanx III-1, (1) not longer than pedal phalanx III-1. (New character).
70. Tarsal articular surface of metatarsal V: (0) faces proximally, articulates with distal tarsal V, (1) faces inward, articulates with distal tarsal IV (distal tarsal V absent) (Benton 1985; Gauthier *et al.* 1988*a*).
71. Pedal digit V: (0) functional, (1) vestigial (Benton & Clark 1988).
72. Pedal phalanx V-2: (0) extends further distally than metatarsal IV, (1) does not extend further distally than metatarsal IV. (New character).
73. Distal tarsal 1: (0) present, (1) absent (Gauthier *et al.* 1988*a*).

APPENDIX 2: DATA MATRIX FOR FIRST PHYLOGENETIC ANALYSIS

The matrix for the second phylogenetic analysis is identical to this, except that character 4 is coded '1' (antorbital fenestra present) for *Megalancosaurus preonensis* and *Longisquama insignis*.

Palaeothyris acadiana	000000-000	0000000000	0000000000	000000?00?	?000000000	0000000000	0000000000	000
Megalancosaurus preonensis	11?0????10	????011??0	1000?11111	111111??12	2011011011	1010101000	00111101-0	0-0
MCSNB 4751	?????????0	????0?1???	?00???000?	11?0100?02	0?11?11???	1?001??000	0011100???	000
Drepanosaurus unguicaudatus	??????????	??????????	??????????	11?0101?12	0011?11011	0010101010	00111101-0	0-0
Dolabrosaurus aquatilis	??????????	??????????	??????????	?11011???2	0?????????	??????????	00?1??01-0	000
Hypuronector limnaios	1?????????	????01???0	???0??1???	???1100?12	0?11?11?0?	11?010?000	001???????	???
Petrolacosaurus kansensis	1?????????	????01???0	???0??1???	???1100?12	0?11?11?0?	11?010?000	001???????	???
Longisquama insignis	???0??????	?0???010?0	1110??0??0	00????????	??101?1?00	11????????	??????????	???
Coelurosauravus	1000111?01	0?0?001000	1110?10000	000000?000	0010001000	110????000	0000100110	000
Youngina capensis	0000101001	0000000??0	0000010000	000000??10	0100000110	0000001000	0000??00?0	?0?
Gephyrosaurus bridensis	0000111?01	1111000111	0000010000	?0?000?01?	??00000???	???0001010	0000?????1	???
Mesosuchus browni	0010110101	1111000101	0000010000	?00010??10	0?0001?100	?0?0001000	00001?0001	010
Prolacerta broomi	0110110101	1111000001	0000011101	000000?110	0000011100	1000001000	1001100001	010
Macrocnemus bassanii	11?0110?0?	1???0000?1	0000?11111	000000?11?	0100011?0?	1000001000	1000100001	011
Langobardisaurus pandolfi	1??0??????	????010??1	000??11111	000000?1??	01??011100	100000??10	1000100001	0-1
Ornithosuchus longidens	0111100111	111?100??1	0001110000	001100???0	0110?1?100	?1?0001100	0101??0?1?	01?
Proterosuchus fergusi	0111100111	1111100011	0001010000	000000?110	010001?100	?0?0001000	00010?0001	010
Euparkeria capensis	0111100111	111?100111	0001010000	000000?110	0110010?0?	???0001000	0101100111	011
Archaeopteryx lithographica	110110-?11	??-1010111	0000111100	0020000100	0110111000	0-11011101	0000001111	1-1
Sinosauropteryx prima	011110-111	?11?100111	0001?10000	0020000100	0110?11000	0011011101	0100001111	1-1

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