Phylogeny of Allosauroidea (Dinosauria: Theropoda): Comparative analysis and resolution

Stephen L. Brusatte & Paul C. Sereno

To cite this article: Stephen L. Brusatte & Paul C. Sereno (2008) Phylogeny of Allosauroidea (Dinosauria: Theropoda): Comparative analysis and resolution, Journal of Systematic Palaeontology, 6:2, 155-182, DOI: 10.1017/S1477201907002404

To link to this article: https://doi.org/10.1017/S1477201907002404

Published online: 09 Mar 2010.
PHYLOGENY OF ALLOSAUROIDEA  
(DINOSAURIA: THEROPODA):  
COMPARATIVE ANALYSIS AND  
RESOLUTION

Stephen L. Brusatte†  
University of Chicago, Department of the Geophysical Sciences, 5734 S. Ellis Avenue, Chicago, Illinois 60637, USA

Paul C. Sereno  
University of Chicago, Department of Organismal Biology and Anatomy, 1027 E. 57th Street, Chicago, Illinois 60637, USA

SYNOPSIS  Allosauroida, a clade of large-bodied theropod dinosaurs that ranged from the Middle Jurassic until the Late Cretaceous, has been the subject of extensive phylogenetic study. However, despite the publication of 12 cladistic analyses little phylogenetic consensus has emerged, frustrating attempts to use these dinosaurs to study character evolution, biogeography and the quality of the fossil record. Here we analyse a core subset of allosauroids using cladistic methodology and several comparative methods. After reviewing previous studies and their points of disagreement, we present a new cladistic analysis that integrates data from these studies with new characters. This analysis finds strong support for placing Sinraptor as a basal allosauroid, Neovenator as a basal member of Carcharodontosauridae and Acrocanthosaurus as a more derived member of Carcharodontosauridae, rather than the sister taxon of Allosaurus as sometimes advocated. The current dataset is compared in detail to those of previous studies to determine the degree of overlap and the basis for differing topologies. These comparisons show that scoring differences, character choice and taxonomic sampling all play a major role in generating incongruence. Finally, the recovered most parsimonious topology is used to assess character evolution, stratigraphical congruence and biogeography. This topology shows a strong overall match with the stratigraphical record and is much more congruent with stratigraphy than any alternative topology. The biogeographical history of core allosauroids is found to be congruent with the breakup sequence of Pangaea, but more complete assessment is hampered by sampling biases.

KEY WORDS  vertebrate palaeontology, evolution, cladistics, stratigraphy, palaeobiogeography, Mesozoic

Contents

Introduction  156
Institutional abbreviations  157
Allosauroid monophyly  158
Recent cladistic analyses  158
New cladistic analysis  160
Materials and methods  160
Ingroup selection  160
Outgroup selection  160
Character choice  161
New characters  161
Missing data  161
Results  161
Tree support measures  162
Alternative topologies  164

†Current address: Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK.
E-mail address: brusatte@uchicago.edu

Published online 09 Mar 2010
INTRODUCTION

The large-bodied Late Jurassic theropod *Allosaurus* (Fig. 1) is among the best-studied dinosaur genera, represented by hundreds of specimens that have formed the basis for a wide range of research. In recent years *Allosaurus* has featured prominently in studies of palaeopathology (Hanna 2002), taphonomy and palaeoecology (Gates 2005), intraspecific variation (Chure & Madsen 1996; Smith 1998; Smith et al. 1999; Smith & Lisak 2001), growth and ontogeny (Rauhut & Fechner 2005; Bybee et al. 2006), biomechanics (Rayfield et al. 2001; Rayfield 2005), and biogeography (Perez-Moreno et al. 1999; Sereno 1999b). Over the past decade numerous phylogenetic studies have also clarified the higher-level position of *Allosaurus* among theropods. Although once allied with *Tyrannosaurus* and other large theropods (within ‘Camosauria’), *Allosaurus* is now routinely recovered as a basal tetanuran, closely related to *Sinraptor*, *Carcharodontosaurus* and *Giganotosaurus* (e.g. Holz 1994, 2000; Sereno et al. 1996; Rauhut 2003; Holz et al. 2004). These taxa, along with *Acrocanthosaurus*, *Neovenator* and several new genera, comprise Allosauroidea (Table 1). Defined as a stem-based taxon, Allosauroidea comprises the most inclusive clade containing *Allosaurus fragilis* but not *Passer domesticus*.

Although Allosauroidea is confidently placed near the base of Tetanurae, the ingroup relationships of this clade remain contentious and unresolved. While more attention has been devoted to the phylogeny of allosauroids than to nearly any other archosaur clade (12 cladistic analyses), little phylogenetic consensus has emerged (Sereno et al. 1996; Harris 1998; Forster 1999; Azuma & Currie 2000; Currie & Carpenter 2000; Holz 2000; Allain 2002; Coria & Currie 2002; Rauhut 2003; Holz et al. 2004; Novas et al. 2005; Coria & Currie 2006). *Acrocanthosaurus* and *Neovenator* are alternatively recovered as either sister taxa to *Allosaurus* or as more closely related to *Carcharodontosaurus*, and *Sinraptor* is positioned either as the basal-most allosauroid or as the sister taxon to carcharodontosaurs. Understanding and resolving these conflicts is critical, as allosauroids are a diverse, long-lived and geographically widespread group...
PHYLOGENY OF ALLOSAUROIDEA (DINOSAURIA: THEROPODA)

Figure 1  Skeletal reconstruction of the Late Jurassic theropod Allosaurus fragilis, the best known member of Allosauroidea and one of the most common dinosaur discoveries in Upper Jurassic fossil deposits (from Sereno 1999a). Scale bar = 1 m.

well-suited for studies of character acquisition, biogeography, distribution, and the quality of the fossil record. Unfortunately, reasons for these different topologies are not immediately obvious, and are not discussed in detail in any of the published analyses. This underscores a much larger problem in the study of dinosaur phylogeny: although certain clades are subjected to a great deal of phylogenetic study, there is often little attempt to record shared data and critically compare alternative analyses.

Here, we aim to analyse allosauroid phylogeny and evolutionary history using cladistic methodology and several comparative methods. First, we review previous studies and assess the current points of disagreement and consensus in allosauroid phylogeny. Next, we present a new cladistic analysis that integrates data from previous studies and adds several new characters, resulting in the most expansive data-set applied to this clade. Many of these new characters, as well as revision of published characters, stem from the discovery of several new taxa (Eocarcharia, Mapusaurus, Tyrannotitan), description of new specimens (Carcharodontosaurus: Brusatte & Sereno 2005, 2007), and the reanalysis of described material (Neovenator: Brusatte et al., unpublished results) which allow for new character scores and the discovery of new synapomorphies. Then, we extensively compare our data to those in previous studies, evaluate the degree of overlap and attempt to identify the source for different topologies. Finally, we use our recovered topology to assess character evolution, stratigraphic congruence and biogeography.

INSTITUTIONAL ABBREVIATIONS

| BMNH = The Natural History Museum, London, England |
| IVPP = Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China |
| MIWG = Dinosaur Isle (Museum of Isle of Wight Geology), Sandown, England |
| MNN = Musée National du Niger, Niamey, République du Niger |
| MUCPv-CH = Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén, Argentina |

Table 1  A list of allosauroid terminal taxa used in this analysis, their geographical locations and their temporal ranges.

<table>
<thead>
<tr>
<th>Terminal taxon</th>
<th>Original description</th>
<th>Location</th>
<th>Stratigraphical age</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrocanthosaurus</td>
<td>Stovall &amp; Langston 1950</td>
<td>North America</td>
<td>Early Cretaceous (Aptian-Albian)</td>
<td>1</td>
</tr>
<tr>
<td>Allosaurus</td>
<td>Marsh 1877</td>
<td>North America, Europe (Portugal)</td>
<td>Late Jurassic (Kimmeridgian-Tithonian)</td>
<td>3</td>
</tr>
<tr>
<td>Carcharodontosaurus</td>
<td>Depéret &amp; Savornin 1927</td>
<td>Africa (Morocco, Niger, Egypt, Tunisia, Algeria)</td>
<td>Early Cretaceous (Aptian, Albian-Cenomanian)</td>
<td>2</td>
</tr>
<tr>
<td>Gigantosaurus</td>
<td>Coria &amp; Salgado 1995</td>
<td>South America (Argentina)</td>
<td>Early Cretaceous (Aptian-Albian)</td>
<td>1</td>
</tr>
<tr>
<td>Eocarcharia</td>
<td>Sereno &amp; Brusatte 2007</td>
<td>Africa (Niger)</td>
<td>Early Cretaceous (Albian-Cenomanian or ?Turonian)</td>
<td>1</td>
</tr>
<tr>
<td>Mapusaurus</td>
<td>Coria &amp; Currie 2006</td>
<td>South America (Argentina)</td>
<td>Early Cretaceous (Aptian-Albian)</td>
<td>1</td>
</tr>
<tr>
<td>Neovenator</td>
<td>Hutt et al. 1996</td>
<td>Europe (England)</td>
<td>Early Cretaceous (Barremian)</td>
<td>1</td>
</tr>
<tr>
<td>Sinraptor</td>
<td>Currie &amp; Zhao 1993</td>
<td>Asia (China)</td>
<td>Middle-Late Jurassic (Cenomanian-Oxfordian)</td>
<td>2</td>
</tr>
<tr>
<td>Tyrannotitan</td>
<td>Novas et al. 2005</td>
<td>South America (Argentina)</td>
<td>Early Cretaceous (Aptian)</td>
<td>1</td>
</tr>
</tbody>
</table>

Source: data taken from Weishampel et al. 2004 and original descriptions.
ALLOSAUROID MONOPHYLY

Allosauroidea is employed here as a stem-based taxon that encompasses all dinosaurs closer to Allosaurus than to birds. The monophyly of such a taxon has been demonstrated by nearly every large-scale study of theropod phylogeny, which find support for a grouping of Allosaurus, Sinraptor and carcharodontosaurids to the exclusion of spinosaurids, Afrovenator, Torvosaurus and other ‘megalosaur-grade’ taxa (Sereno et al. 1996; Holtz 2000; Holtz et al. 2004; see Rauhut 2003) for a somewhat different topology). Supporting synapomorphies include nasal participation in the antorbital fossa, invaginated recesses within the lacrimal, a dorsal boss on the postorbital, a large articular flange on the quadrate for the quadratejugal, strongly ventrally deflected paroccipital processes and a notch between the paroccipital processes and the basal tubera. Other synapomorphies listed in the studies cited above are less secure in the light of recent discoveries and re-analysis.

Table 2  Description of 12 recent allosauroid cladistic analyses, along with a quantification of data shared with the current study.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Allosauroid taxa</th>
<th>Characters</th>
<th>Informative characters</th>
<th>Shared characters</th>
<th>Used characters</th>
<th>Scoring differences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sereno et al. 1996</td>
<td>5</td>
<td>61</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Harris 1998</td>
<td>9</td>
<td>145</td>
<td>20</td>
<td>32</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>Forster 1999</td>
<td>4</td>
<td>99</td>
<td>25</td>
<td>21</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>Holtz 2000</td>
<td>7</td>
<td>386</td>
<td>52</td>
<td>42</td>
<td>22</td>
<td>29</td>
</tr>
<tr>
<td>Currie &amp; Carpenter 2000</td>
<td>5</td>
<td>110</td>
<td>35</td>
<td>34</td>
<td>21</td>
<td>19</td>
</tr>
<tr>
<td>Azuma &amp; Currie 2000</td>
<td>6</td>
<td>110</td>
<td>17</td>
<td>21</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Allain 2002</td>
<td>5</td>
<td>45</td>
<td>13</td>
<td>12</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Coria &amp; Currie 2002</td>
<td>5</td>
<td>15</td>
<td>12</td>
<td>8</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Rauhut 2003</td>
<td>5</td>
<td>224</td>
<td>9</td>
<td>23</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Holtz et al. 2004</td>
<td>6</td>
<td>638</td>
<td>88</td>
<td>61</td>
<td>42</td>
<td>33</td>
</tr>
<tr>
<td>Novas et al. 2005</td>
<td>6</td>
<td>106</td>
<td>48</td>
<td>37</td>
<td>26</td>
<td>18</td>
</tr>
<tr>
<td>Coria &amp; Currie 2006</td>
<td>6</td>
<td>110</td>
<td>46</td>
<td>35</td>
<td>22</td>
<td>20</td>
</tr>
</tbody>
</table>

Informative characters include those characters informative at the level of Allosauroidea (reduced to a common set of taxa shared with the present analysis: Allosaurus, Acrocanthosaurus, Carcharodontosaurus, Gigantosaurus, Sinraptor and Neovenator).

Shared characters refer to the number of characters in the current analysis also used by the previous analyses in question.

Used characters refer to the number of informative characters in the previous analyses used in the current analysis.

Scoring differences only include those differences that involve positive codings; a change to or from a missing datum (?) is not included.

RECENT CLADISTIC ANALYSES

Twelve published studies have analysed allosauroid interrelationships, although each considers relationships well beyond Allosauroidea. Topologies recovered by these studies are shown in Fig. 2, with only the allosauroid terminal taxa shown. Basic descriptive statistics for each study are provided in Table 2, including the number of informative characters applicable to Allosauroidea. A strict consensus tree of these studies lacks any structure (Fig. 2L), and clearly demonstrates that there is little agreement regarding allosauroid inter-relationships.

All analyses recovered a monophyletic Allosauroidea, with the exception of Forster (1999), who found allosaurids as a paraphyletic grade relative to Tyranosaurus, the representative coelurosaur in the analysis. In the other studies, Allosauroidea usually includes three family-level taxa: Sinraptoridae, Allosauridae and Carcharodontosauridae. Phylogenetic definitions of these taxa are provided in the Phylogenetic Taxonomy section below.

The inter-relationships of Sinraptoridae are not considered by most studies. Although Sinraptor and Yangchuanosaurus are often referred to this taxon, the species Sinraptor dongi is the best described and most often coded, either as a species or as a representative of the family.
Several analyses (e.g., Sereno et al. 1996; Currie & Carpenter 2000; Rauhut 2003; Holtz et al. 2004; Coria & Currie 2006) recovered a polytomy of Sinraptor, Allosauridae, and Carcharodontosauridae (and sometimes other taxa). Forster (1999) placed Sinraptor as the sister taxon to a novel Allosaurus + Tyrannosaurus clade, but no other studies found a grouping of Allosauridae and Sinraptor to the exclusion of other allosauroids. Some studies (Allain 2002; Coria & Currie 2002) placed Sinraptor as the sister group to Carcharodontosauridae. Re-analysis of the data presented by Novas et al. (2005) also supports this pairing, although the published cladogram shows a different topology. Finally, other studies (Harris 1998; Holtz 2000) recovered Sinraptor as the basalmost allosauroid, a position concordant with stratigraphy.

Carcharodontosauridae includes Carcharodontosaurus and Giganotosaurus, as well as several taxa described recently. Of these new discoveries, only the South American Tyrannotitan and Mapusaurus have appeared in previously-published analyses (Novas et al. 2005 and Coria & Currie 2006, respectively). Only Forster (1999) failed to recover a monophyletic grouping of Carcharodontosaurus and Giganotosaurus, positioning them instead as successive outgroups to a clade of Sinraptor, Allosaurus and...
**NEW CLADISTIC ANALYSIS**

A new phylogeny of Allosauroida is presented here, based on a matrix of characters culled from previous phylogenetic analyses, as well as several new characters. Details on taxon selection, outgroups, character choice and missing data are presented below, and the character list (Appendix 1) and data matrix (Appendix 2) are included at the end of this paper, while a supertree summary is included in the Supplementary Information (Supplementary Appendix 1 available online at: http://www.journals.cup.org/abstract_S1477201907002404).

**Materials and methods**

Nine ingroup taxa and four outgroups were scored for 99 morphological characters. The data matrix was created in MacClade 4.06 (Maddison & Maddison 2003) and analysed using PAUP* v.4.0b10 (Swofford 2000). A branch-and-bound search generated a single most-parsimonious tree (MPT), which is discussed in the Results, below. The robustness of individual clades was assessed using two tree-support measures: the bootstrap (1000 replicates) and Bremer support (decay indices).

**Ingroup selection**

The nine selected ingroup taxa include: *Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Giganotosaurus*, *Mapusaurus*, *Neovenator*, *Sinraptor* and *Tyrannotitan*. These comprise the best known and previously-analysed allosaroids, based on a number of higher-level analyses of theropod phylogeny (Sereno et al. 1996; Sereno 1999a; Holtz 2000; Rauhut 2003; Holtz 2004; Coria & Currie 2006). Although Sinraptoridae is often coded as a single terminal taxon in other analyses, several problems have been identified with the use of higher-level terminal taxa in phylogenetic studies (Bininda-Emonds et al. 1998). Thus, we have elected to code the genus *Sinraptor* as a representative for sinraptorids, based on our examination of original material (IVPP 10600) and its well-documented morphology (Gao et al. 1992; Currie & Zhao 1993). We exclude *Yangchuanosaurus*, as although one of us (P.C.S.) has examined some of the material first-hand, published descriptions are incomplete (e.g. Dong et al. 1978, 1983) and this taxon appears to be extremely similar to *Sinraptor* in overall morphology (Rauhut 2003). We also exclude *Saurophaganax*, as its generic status is controversial (Smith 1998), the known material is fragmentary and poorly-preserved (Chure 1995, 2000) and this taxon appears to be extremely similar to *Allosaurus* in overall morphology (S.I.L.B., pers. obs.).

*Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Giganotosaurus*, *Mapusaurus* and *Sinraptor* were scored on the basis of first-hand observations, as well as published reports. *Mapusaurus* and *Tyrannotitan* were scored on the basis of published reports. A full list of scoring sources is provided in Appendix 3.

**Outgroup selection**

Based on several higher-level analyses of theropod phylogeny (Sereno 1999a; Holtz 2000; Rauhut 2003; Holtz et al. 2004), four outgroups (*Herrerasaurus*, *Coelophysis*,
**Phylogeny of Allosauroida (Dinosauria: Theropoda)**

---

*Torvosaurus, Compsognathidae* were chosen to determine character polarity. These taxa are well-known representatives of Herrerasauridae, Coelophysidae, Spinosauridae and basal coelurosaurians, respectively, which represent important, successively more closely related, outgroups to Allosauroida. Furthermore, these particular outgroups were selected to represent the presumed ancestral condition of Theropoda, Neotheropoda, Tetanurae and Coelurosauria, respectively. Choosing a taxon to represent the primitive coelurosaur bauplan is not trivial, as many basal coelurosaur groups (tyrannosauroids, ornithomimids, alvarezsaurids) are significantly derived and often possess a highly autapomorphic morphology. Although one recent analysis (Hwang *et al.* 2004) recovered compsognathids as more derived than tyrannosauroids and ornithomimids, we feel that Compsognathidae best encompasses primitive coelurosaur morphology. While the use of higher-level terminal taxa can be problematic, Compsognathidae is demonstrably monophyletic (Hwang *et al.* 2004) and codings based on several taxa (*Compsognathus, Sinosauropteryx, Huaxiagnathus,* and *Mirischia*) compensate for fragmentary specimens and incomplete illustrations and descriptions. In addition, there are no demonstrable polymorphisms for the characters in this analysis. In the future, several recently-discovered basal tyrannosauroids (Hutt *et al.* 2001; Xu *et al.* 2004, 2006) may provide a more accurate basal coelurosaur outgroup free from compensating fragmentary specimens and incomplete illustrations and descriptions. In addition, many of these taxa are still poorly understood.

Selecting a basal tetanuran outgroup is also difficult, as *Afrovenator* and *Dubreuillosaurus, Torvosaurus* and spinosaurids are exceedingly incomplete and/or only briefly described in the literature. Although it can be scored for only 51 of our characters (52%), *Torvosaurus* was employed as an outgroup over other spinosaurids that remain relatively less well documented.

*Herrerasaurus* was scored on the basis of our own observations, while *Coelophysis, Torvosaurus* and Compsognathidae were primarily scored from published descriptions and figures, as well as from casts.

**Character choice**

Taxa were scored for 99 morphological characters, 21 of which are new to this study. Other characters were culled from the literature and every published character that was informative for allosauroid phylogeny was considered. Although an attempt was made to use all previous character data that remained informative, some characters were dismissed if they: (1) were poorly defined or could not be sufficiently quantified, (2) exhibited overlapping variation that could not be separated in ingroup and outgroup taxa, (3) were redundant with other characters, or (4) were only informative at the level of Allosauroida due to scoring mistakes (see Supplementary Appendix 3). Original authorship of all characters is shown after the character in Appendix 1. Polarity was determined by reference to the outgroups, whose relationships were constrained on the basis of published analyses of theropod phylogeny (Sereno *et al.* 1996; 1999a; Holtz 2000; Holtz *et al.* 2004). Most of the characters are binary, although five are multistate, all of which were left unordered. These characters include 59 (60%) cranial characters, 16 (16%) axial characters and 24 (24%) appendicular characters.

**Table 3** Missing data in allosauroid terminal taxa.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>%</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrocanthosaurus</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Allosaurus</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Carcrophosaurus</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Giganotosaurus</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Eocarcharia</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Mapusaurus</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Neovenator</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Sinraptor</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Tyrannotitan</td>
<td>9</td>
<td>9</td>
</tr>
</tbody>
</table>

Missing data is listed as the percentage of missing data and the rank for each terminal relative to others (most complete ranked highest).

**New characters**

The 21 new characters (10 cranial, 2 axial, 9 appendicular), comprise 21% of the dataset. The primitive and derived states of most of these characters are illustrated (Figs 3 & 4).

Four new characters (50–53) concern the dentary and came to light during the description of a partial dentary of *Carcharodontosaurus* (Brusatte & Sereno 2005, 2007). Derived states include a distinct ventral dentary flange ("dentary chin"), a principal row of neurovascular foramina that curves ventrally as it extends posteriorly, external texturing and a marked angle between opposing dentaries at the symphysis, each of which is scored for several carcharodontosaurs. In addition, two new characters concern the gastralia: a medial gastral element that expands distally into a club-shaped prominence (74) and multiple sets of fused medial elements (75). Re-examination of allosauroid tibiae revealed two additional derived states shared by some carcharodontosaurs: an elongated and expanded medial malleolus (90) and a distally expanded lateral malleolus (91). Finally, the recently-described *Mapusaurus* shares with *Acrocanthosaurus* metacarpals with greatly expanded proximal articular surfaces (99).

**Missing data**

Missing data range from 0% (Allosaurus) to 80% (Tyranosaurus) (Table 3). *Sinraptor* and *Acrocanthosaurus* both have less than 10% missing data, while *Eocarcharia* and *Mapusaurus* have more than 50%. The total missing data in this 9 × 99 matrix is 35%. Missing data is not concentrated in any one anatomical region, as some taxa are known from little skull material (e.g. *Tyranosaurus*), whereas others are represented by few postcranial elements (e.g. *Carcharodontosaurus, Eocarcharia*). Although large amounts of missing data can substantially increase the number of most parsimonious trees (MPTs), taxa with large amounts of missing data are here included for completeness (Kearney & Clark 2003), as no terminal taxa fulfill Wilkinson’s (1995) criteria for safe taxonomic reduction.

**Results**

With outgroups constrained, the analysis yielded a single MPT with a tree length (TL) of 171 steps, a consistency index (CI) of 0.61 and a retention index (RI) of 0.70 (Fig. 5). *Sinraptor* is recovered as the most basal allosauroid taxon, with *Allosaurus* and Carcharodontosaurus being
successively more derived. Every terminal taxon in the analysis, with the exception of *Sinraptor* and *Allosaurus*, belongs to Carcharodontosauridae by definition (see Phylogenetic Taxonomy, below). Within Carcharodontosauridae, *Neovenator* is recovered as the most basal member of the group, followed successively by *Tyrannotitan*, a clade comprised of *Acrocanthosaurus* and *Eocarcharia*, a clade comprised of *Giganotosaurus* and *Mapusaurus*, and *Carcharodontosaurus*. A list of synapomorphies, as optimised under accelerated (ACCTRAN) and derived (DELTRAN) transformation assumptions, is presented in Appendix 1, “Supplementary data” available on Cambridge Journals Online: http://www.journals.cup.org/abstract_S1477201907002404.

Tree support measures
Robustness was assessed using bootstrap (1000 replicates) and Bremer support (decay) indices (Fig. 5). Both methods were chosen to give a more complete description of

---

**Figure 3**  Illustration of cladistic characters new to this study. 1: Maxillae of *Sinraptor* (a), *Allosaurus* (b) and *Carcharodontosaurus* (c) in medial view; 2: Dentaries of *Allosaurus* (a) and *Carcharodontosaurus* (b) in left lateral view; 3: Dentaries of *Allosaurus* (a) and *Carcharodontosaurus* (b) in dorsal view; 4: Premaxillae of *Allosaurus* (a) and *Neovenator* (b) in left lateral view; 5: Squamosals of *Sinraptor* (a) and *Allosaurus* (b) in left lateral view; 6: Gastralia of a generalised theropod (a) and *Carcharodontosaurus* (b) in dorsal view. Images 1a and 5a were modified from Currie & Zhao 1993; 1b, 2a, 4a and 5b from Madsen 1976; 4b from Hutt 1999; 6b from Stromer 1934. Numbers refer to the character number in Appendix 1, while the numbers in parentheses refer to character states. Scale bars = 5 cm. No scale bars for 6a, b.
Figure 4  Illustration of cladistic characters new to this study. 1: Ilium of Allosaurus (a) and Mapusaurus (b) in left lateral view; 2: Ischium of Sinraptor (a) in left lateral view and Allosaurus (b) in medial view; 3: Femur of Allosaurus (a) and Carcharodontosaurus (b) in anterior view; 4: Tibiae of Sinraptor (a) and Acrocanthosaurus (b) in anterior view; 5: Metacarpals 2 of Allosaurus (a, c) and Acrocanthosaurus (b, d) in lateral (a, b) and proximal (c, d) views. 1a, 3a, 5a, 5c modified from Madsen 1976; 1b from Coria & Currie 2006; 2a, 4a from Currie & Zhao 1993; 3b from Stromer 1931; 4b from Stovall & Langston 1950; 5b, 5d from Currie & Carpenter 2000. Numbers refer to the character number in Appendix 1, while the numbers in parentheses refer to character states. Scale bars = 5 cm. No scale bars for 3b and 4b.

Clade robustness, as problems have been identified with each method (Kitching et al. 1998). All ingroup nodes except for the Giganotosaurus + Mapusaurus node have a Bremer support value greater than 1 — that is, they still appear in the strict consensus of all trees up to one step longer than the MPT. The highest decay indices are exhibited by Carcharodontosauridae node, which collapse 5 steps out from the MPT. All other nodes have decay indices of 2. Not surprisingly, high bootstrap values are also seen at the Carcharodontosaurus + Giganotosaurus node (91%), Tyrannosaurus + derived carcharodontosauroids node (80%), Carcharodontosauridae node (90%) and Allosaurus + Carcharodontosauridae node (84%).
Figure 5  Single most parsimonious cladogram recovered by the current analysis (99 characters in 9 ingroup and 4 outgroup taxa). Tree length (TL = 171, consistency index (CI) = 0.61, retention index (RI) = 0.70. Numbers next to clades denote bootstrap support value/Bremer support value.

Alternative topologies
Constraining tree topology in PAUP* allows for the examination of alternative topologies, as well as the cost required to assume these topologies. An *Acrocanthosaurus + Allosaurus* grouping to the exclusion of carcharodontosaurids, as hypothesised by many studies (e.g. Currie & Carpenter 2000; Allain 2002; Coria & Currie 2002, 2006; Novas et al. 2005) requires an additional 27 steps, or 16% of the length of the MPT. A sister group relationship between *Allosaurus* and *Neovenator*, as found by Holtz (2000), requires an additional 5 steps. Placing *Sinraptor* as the sister group to carcharodontosaurids requires 8 additional steps.

Taxon removal
Although ingroup taxa with high amounts of missing data were not deleted from the initial analysis, several fragmentary terminal taxa were excluded to observe any effect on tree topology (Fig. 6). Deletion of *Eocarcharia* (69% missing data) and *Tyrannotitan* (80% missing data) did not affect tree topology. However, deletion of *Neovenator* (44%) results in four MPTs, the strict consensus of which collapses *Allosaurus, Fukuiraptor, Monolophosaurus* and *Carcharodontosaurus* into a polytomy more derived than *Sinraptor*. Other than the creation of this polytomy, tree topology does not change. However, it must be noted that all characters were selected to be informative among the nine original ingroups, without reference to *Monolophosaurus* and *Fukuiraptor* during the character selection process. Since basal tetanuran characters and ingroups are not included in the present analysis, and due to high amounts of missing data (due to fragmentary specimens and/or brief literature descriptions), these placements should be regarded as tentative. What is significant is that inclusion of these two potentially basal allosaurids does not change the relative topology of the nine original terminal taxa.

Figure 6  Cladogram recovered by re-running the current analysis after the deletion of *Neovenator*.

**Additional taxa**
Although *Fukuiraptor* and *Monolophosaurus* are not recovered as allosaurids in all higher-level analyses of theropod phylogeny (see above), they were scored to examine any effects they may have on tree topology (Appendix 2). When *Fukuiraptor* and *Monolophosaurus* are included in the analysis 5 MPTs result (TL = 180, CI = 0.58, RI = 0.69), the strict consensus of which collapses *Allosaurus, Fukuiraptor, Monolophosaurus* and *Carcharodontosaurus* into a polytomy more derived than *Sinraptor*. Other than the creation of this polytomy, tree topology does not change. However, it must be noted that all characters were selected to be informative among the nine original ingroups, without reference to *Monolophosaurus* and *Fukuiraptor* during the character selection process. Since basal tetanuran characters and ingroups are not included in the present analysis, and due to high amounts of missing data (due to fragmentary specimens and/or brief literature descriptions), these placements should be regarded as tentative. What is significant is that inclusion of these two potentially basal allosaurids does not change the relative topology of the nine original terminal taxa.
COMPARATIVE CLADISTICS

The new cladistic analysis presented herein is the thirteenth such study to examine allosauroid interrelationships. As described above, previous studies have produced numerous different topologies, due largely to the widely varying positions of Sinraptor, Acrocanthosaurus and Neovenator. This problem is not unique to Allosauridea, as the widespread use of cladistics over the past two decades has produced copious alternative phylogenetic hypotheses for many clades. Unfortunately, in the dinosaur literature, little attempt has been made to enumerate carefully the similarities and differences between studies, or to examine critically why alternative analyses produce differing results. Often, differing topologies are noted and compared, but little effort is expended to determine the root causes underlying different results. As Allosauridea is a relatively small clade that has received much phylogenetic attention, it is well suited for a more thorough examination of cladogram incongruence.

We compare our results with those of Currie & Carpenter (2000), Allain (2002) and Novas et al. (2005). These analyses were chosen because their topologies differ most substantially from that of the current analysis. Other analyses (e.g. Sereno et al. 1996; Harris 1998; Rauhut 2003; Holtz et al. 2004) largely agree with the current study, whereas those of Forster (1999) and Azuma & Currie (2000) contain too few allosauroid taxa for extensive comparison. The 15-character analysis of Coria & Currie (2002) also produces a very different topology, but most of their characters are utilised by Novas et al. (2005). In addition, the analysis of Coria & Currie (2006) uses the character list and data matrix of Currie & Carpenter (2000) and, thus, is not considered separately. Although it is not fully critiqued, the analysis of Holtz (2000) is briefly discussed at the end of this section. In the following discussion, character numbers in parentheses refer to those in the original dataset under discussion, unless otherwise noted.

Currie & Carpenter 2000

When condensed into a set of shared taxa, the topology presented here agrees with that of Currie & Carpenter (Fig. 2) in only one aspect: the sister-group relationship between Carcharodontosaurus and Giganotosaurus. Whereas Acrocanthosaurus is recovered as a carcharodontosaurid here, Currie & Carpenter (2000) place it as the sister taxon to Allosaurus (albeit with a low bootstrap support of 37% and a Bremer support of 1). Furthermore, Sinraptor, Carcharodontosauridae and their Allosauridae form a polytomy. In the current analysis, Sinraptor falls out as the most basal allosauroid. Since the relationships of Sinraptor are unresolved in Currie & Carpenter's (2000) study, here we focus on the position of Acrocanthosaurus, whose sister-group relationship with Allosaurus is supported by nine synapomorphies in their analysis. These are discussed individually below.

Antorbital Openings: Acrocanthosaurus and Allosaurus were united by the possession of a promaxillary and maxillary fenestra (character 3). However, Giganotosaurus was incorrectly scored as possessing only a promaxillary fenestra. The holotype maxilla (MUCP-v-CH-1) has both a large, laterally-facing maxillary fenestra and a smaller, slit-shaped promaxillary fenestra.

Basal Tubera: Acrocanthosaurus and Allosaurus were scored as having basiocciptals that do not participate in the basal tubera (character 24). This character has a long history in studies of theropod phylogeny and was used in the analyses of Sereno et al. (1996), Harris (1998), Forster (1999), Azuma & Currie (2000), Holtz (2000), Allain (2002) and Novas et al. (2005). However, rampant scoring differences exist among these studies, especially concerning Sinraptor and Acrocanthosaurus. Rauhut (2003:55) heavily modified the wording of this character and his more explicit language was followed by Holtz et al. (2004) and this study. The character employed in this study (character 46 herein) only scores Allosaurus and Sinraptor as possessing the derived state (a basal tubera subdivided into a medial part entirely formed by the basioccipital and a lateral part formed by the basisphenoid). Acrocanthosaurus and Carcharodontosaurus are scored for the primitive state.

Paroccipital Processes: Currie & Carpenter (2000: character 26) scored Acrocanthosaurus and Allosaurus as possessing downturned paroccipital processes, the distal ends of which are located below the foramen magnum. Carcharodontosaurus, Giganotosaurus and Sinraptor are scored for moderately-downturned processes. This character has also been used by several authors, but analysis of new material of Carcharodontosaurus (Fig. 7C;
Acrocanthosaurus and Allosaurus were scored for a pneumatised internal carotid artery opening (character 29), a character state also seen in many coelurosaurians. While this character has also been used in many previous analyses, examination of ingroup and outgroup braincase material reveals only slight differences among taxa. We feel that this character is too variable and poorly defined to score accurately.

Haemal Arches: Currie & Carpenter (2000: character 64) scored Acrocanthosaurus and Allosaurus for haemal arches with paired anterior and posterior processes at their base. Carcharodontosaurus was scored for the primitive state, whereas Giganotosaurus and Sinraptor were scored '?'. As unequivocal haemal arches are not known for Carcharodontosaurus, this taxon must be scored '?'. Although still synapomorphic for Allosaurus and Acrocanthosaurus, missing data now render this character ambiguous.

Scapulocoracoid Notch: Acrocanthosaurus and Allosaurus were scored for the presence of a distinct notch between the scapular acromion process and the coracoid, while Carcharodontosaurus, Giganotosaurus and Sinraptor were scored '?' (character 68). Re-examination of the holotype (MUCP-v-CH-1) and published figures (Calvo 1999: fig. 14) confirm that Giganotosaurus also possesses this notch and re-examination of the holotype and published figures (IVPP 10600; Currie & Zhao 1993: fig. 20, Gao 1992: fig. 4) indicate that Sinraptor does not. With these changed scores, this character is now diagnostic of a more inclusive clade.

Metacarpal 4 and Mandibular Fenestra: While Acrocanthosaurus and Allosaurus are united to the exclusion of Sinraptor by the loss of metacarpal 4 (character 79) and a reduced external mandibular fenestra (character 38), missing data in Carcharodontosaurus and Giganotosaurus render these synapomorphies ambiguous.

Cranial Nerve V: Acrocanthosaurus and Allosaurus were scored for a fully separated trigeminal nerve foramen, while Sinraptor and Carcharodontosaurus were scored for an incipiently-divided foramen (character 28); Giganotosaurus was scored '?', but Coria & Currie (2002) later described an undivided trigeminal foramen in this taxon. The score for Acrocanthosaurus was based on the NCSM 14345 (P.J. Currie, pers. comm.), but the holotype braincase (OMNH 10146) shows a single, undivided foramen (Frazzetta & Rowe 2005: figs 1, 2). Similar variation is seen in Carcharodontosaurus: C. saharicus (SGM-Din 1) characterised by a single foramen and C. iguidensis (Brusatte & Sereno 2005, 2007) possesses an incipiently divided foramen (Figs 7A & B). In view of this variation, we do not consider this character to be informative and reject it here.

This brief discussion of characters makes it clear that many scoring differences exist between Currie & Carpenter’s (2000) analysis and our study. In fact, among the 34 characters shared between the two analyses, there are 30 scoring differences (see Supplementary data Appendix 2). Nineteen of these differences involve positive scores (i.e. involve more than simply a change to or from a missing datum). To observe the effect of these scoring differences, we rescored Currie & Carpenter’s (2000) matrix to include the 30 scores favoured by our analysis. Analysing this matrix in PAUP* produced a single MPT of length 235 (CI = 0.61, RI = 0.58), compared to two MPTs of length 224 in the original study. This tree (Fig. 8A) places Acrocanthosaurus as the sister taxon to a Carcharodontosaurus + Giganotosaurus clade, a placement found in our analysis but not in the original study of Currie & Carpenter (2000). This suggests that scoring differences are a major source of incongruence between the topology of Currie & Carpenter (2000) and that presented here.

In addition, the present analysis and that of Currie & Carpenter (2000) differ greatly in the number and use of informative characters. Currie & Carpenter (2000) include 35 characters informative at the level of Allosauroidea, whereas the present analysis uses 99 characters. In the present analysis, 34 of the 99 characters (34%) were also used by Currie & Carpenter (2000). Furthermore, the present analysis includes only 21 of the 35 informative characters used by Currie & Carpenter (2000).
Currie & Carpenter (2000), or about 60% of their data (for a list of rejected characters, see Supplementary data Appendix 3). Four of these rejected characters are synapomorphies of *Allosaurus + Acrocanthosaurus* in the analysis of Currie & Carpenter (2000); these characters (numbers 26, 28, 29 and 64 in the original study) are discussed above. Of the remaining rejected characters, two unite all allosauroids to the exclusion of *Sinraptor* (30, 95); two unite *Acrocanthosaurus, Allosaurus* and *Sinraptor* (62, 100); one unites *Acrocanthosaurus* and *Sinraptor* (16); two unite *Giganotosaurus* and *Carcharodontosaurus* (23, 42); and the others are ambiguous due to missing data (27, 46, 85). Finally, the analysis of Currie & Carpenter (2000) does not include several characters linking *Acrocanthosaurus, Carcharodontosaurus* and *Giganotosaurus* that are used in this analysis.

The present analysis and that of Currie & Carpenter (2000) also differ in the number of allosauroid terminal taxa. The current study employs nine terminals, whereas Currie & Carpenter (2000) use five (*Acrocanthosaurus, Allosaurus, Carcharodontosaurus, Giganotosaurus, Sinraptor*). To examine the effect of differential taxonomic sampling, *Neovenator* was scored for the 110 characters of Currie & Carpenter (2000) and the matrix (without any scoring changes from the original) was run using PAUP* (see Supplementary data Appendix 4). Due to their incompleteness, *Eocarcharia* and *Tyrannosaurus* were not included. Two MPTs of 230 steps resulted, the strict consensus of which places *Neovenator* as the sister taxon to *Acrocanthosaurus* (Fig. 9A). The relative positions of the other five taxa do not change. Thus, taxonomic sampling is not a major source of incongruence between the two analyses.

In summary, while taxonomic sampling is not likely to be an important source of topological incongruence between the current analysis and that of Currie & Carpenter (2000), scoring differences and character choice are critical.

Finally, Coria & Currie (2006) utilise the character list and data matrix of Currie & Carpenter (2000), to which they added *Mapusaurus* and changed 10 scores for *Giganotosaurus*, five for *Allosaurus*, two for *Sinraptoridae* and two for *Carcharodontosaurus*. This analysis recovers *Mapusaurus* as the sister taxon to *Giganotosaurus* and agrees with the earlier analysis of Currie & Carpenter (2000) in all other aspects of allosauroid phylogeny. The current analysis also recovers *Giganotosaurus* and *Mapusaurus* as sister taxa.

### Allain 2002

The topology presented here also agrees with that of Allain (2002) only in the sister-group relationship between *Carcharodontosaurus* and *Giganotosaurus*. Allain (2002) finds *Acrocanthosaurus* and *Allosaurus* as sister taxa and *Sinraptor* as the immediate outgroup to *Carcharodontosauridae* (a node supported by relatively low bootstrap and Bremer support values of 46% and 1, respectively). In contrast, the current analysis finds *Sinraptor* as the most basal allosauroid and *Acrocanthosaurus* as a carcharodontosaurid.

Four synapomorphies linked *Acrocanthosaurus* and *Allosaurus* in Allain’s (2002) study, including the aforementioned problematic characters concerning the basal tubera (character 15), paroccipital processes (32) and external mandibular fenestra (44). These two taxa were also united by a keyhole-shaped infratemporal fenestra (character 41). However, *Carcharodontosaurus* and *Giganotosaurus* were scored for the primitive state, even though the pertinent circumtemporal bones are not known. This character is rendered ambiguous when these taxa are scored correctly.

Two synapomorphies united *Sinraptor* and carcharodontosaurids in Allain’s (2002) study: a posteroventrally-sloping occiput (character 43) and a reversal to a non-pneumatised opening for the internal carotid (character 23). While we agree that the first synapomorphy is valid, problems with the second character are discussed above; this character is too variable and poorly defined to score accurately.

Among the 12 characters shared between the two analyses, seven scoring differences exist, two of which involve positive scores (see Supplementary Appendix 2). Rerunning Allain’s (2002) dataset with the scores favoured by the current analysis results in 52 MPTs of length 86, compared to three MPTs of length 83 in the original analysis. The strict consensus of these trees (Fig. 8B) shows little resolution, with only the *Carcharodontosaurus + Giganotosaurus* sister group remaining. *Sinraptor, Acrocanthosaurus* and *Allosaurus* fall into a polytomy with *Carcharodontosauridae* at the base of Allosauroidia. This suggests that scoring differences are a source of incongruence between our topology and that of Allain (2002).

Allain’s (2002) analysis also differs considerably in the number, distribution and use of informative characters. Allain (2002) includes only cranial characters, 13 of which...
are informative at the level of Allosauroidea. In the present analysis, 12 of the 99 characters (12%) are also used by Allain (2002). Furthermore, the present analysis includes only eight of the 13 informative characters used by Allain (2002) (62%; see Supplementary data Appendix 3). Two of these rejected characters are synapomorphies of Allosaurus + Acrocanthosaurus (characters 23, 32) and are discussed above. One is a synapomorphy of Carcharodontosaurs and Giganotosaurus (42), one links Allosaurus and Sinraptor (20), while one unites Allosaurus, Sinraptor and Acrocanthosaurus (6). In addition, Allain (2002) does not include several characters, many of which are postcranial, that unite Acrocanthosaurus with carcharodontosauroids and place Sinraptor as basal in the present study.

Allain (2002) includes only five allosauroid terminal taxa, excluding Neovenator, as well as Eocarcharia, Mapusaurus and Tyrannotitan, which were not known at the time of his analysis. When Neovenator was scored for Allain's (2002) 45-character dataset and the matrix rerun in PAUP* (see Supplementary data Appendix 4), 52 MPTs of length 84 resulted. The strict consensus recovers little structure, as only the Carcharodontosaurus + Giganotosaurus sister grouping is recovered and all other allosauroids fall into a polytomy, which also includes several non-allosauroid taxa (Fig. 9B). Therefore, taxonomic sampling is also a source of incongruence between the current study and Allain's (2002).

In summary, scoring differences, character choice and taxonomic sampling may all play a role in the incongruence between our analysis and that of Allain (2002).

Novas et al. 2005

The topology of Novas et al. (2005) is very similar to that found by Allain (2002) and differs substantially from that recovered here. Like Currie & Carpenter (2000) and Allain (2002), Novas et al. (2005) find support for an Acrocanthosaurus + Allosaurus sister group relationship (but with a low bootstrap support of 41% and Bremer support of 1). In addition, although the cladogram reported by Novas et al. (2005: fig. 3) shows Sinraptor as basal to all other allosauroid taxa, re-analysis of their data positions Sinraptor as the closest outgroup to Carcharodontosauroids. As the tree statistics are identical in the published and re-analysed tree, it is assumed that the published tree was mistakenly included.

Novas et al. (2005) find 11 synapomorphies linking Acrocanthosaurus and Allosaurus. Of these, characters concerning accessory antorbital openings (character 1), the tritigermal foramen (19), the external mandibular fenestra (21), scapulocoracoid notch (44), metacarpal 4 (51), basil tubera (78), paracapsit processes (79) and internal carotid artery (80) are discussed as problematic above. Three additional characters are discussed below.

Internal Mandibular Fenestra: Novas et al. (2005: character 22) scored Acrocanthosaurus and Allosaurus as possessing a splenial that is notched to form the anterior margin of the internal antorbital fenestra. Sinraptor is scored for the primitive state, while Carcharodontosaurus, Giganotosaurus and Tyrannotitan are scored '?'. However, published figures suggest that the splenial of Sinraptor is notched for the internal mandibular fenestra (Currie & Zhao 1993: fig. 11). With this corrected score, all allosauroids with known splenials are scored for the derived state.

Haemal Arch Shape: Acrocanthosaurus and Allosaurus were scored for L-shaped haemal arches on the distal caudal vertebrae (character 41), whereas Giganotosaurus was scored as lacking an L-shape and Carcharodontosaurus, Sinraptor and Tyrannotitan were scored '?'. However, as far as we are aware, no chevrons are known for Giganotosaurus beyond the mid caudal vertebrae. Even if the distal chevrons of Giganotosaurus are not L-shaped, however, this is best interpreted as a reversal, as several allosauroid outgroups (Torvosaurus, compogspholidae) possess L-shaped chevrons, which have been interpreted by many authors (e.g. Sereno et al. 1996) as diagnostic of Neotetanurae.

Basipterygoid Processes: Novas et al. (2005: character 20) scored Acrocanthosaurus and Allosaurus as possessing long basipterygoid processes, whereas Sinraptor was scored for the primitive condition (short processes) and all allosauroids were scored '?'. This character has been used in many studies of theropod phylogeny, but rampant scoring disagreement persists. We could not sufficiently quantify this character, so it is rejected in the present analysis.

Sinraptor was united with Carcharodontosauroidae based on eight synapomorphies. Three of these (characters 17, 92, 93), dealing with the posterovertrally-sloping occiput, are here considered redundant. However, as discussed above, a posterovertrally-sloping occiput is accepted as a valid synapomorphy of Sinraptor and carcharodontosauroids. In addition, several braincase characters (91, 94), originally identified by Coria & Currie (2002) and included by Novas et al. (2005), are also accepted as valid here. Three additional synapomorphies deserve comment.

Postorbital Flange: Novas et al. (2005: character nine) scored Carcharodontosaurus, Giganotosaurus and Sinraptor as possessing a suborbital flange on the postorbital. Allosaurus and Acrocanthosaurus were scored for the (primitive) lack of this flange and Tyrannotitan was scored '?'. However, published figures (Currie & Zhao 1993: fig. 8) and observation of the holotype (IVPP 10600) clearly show that Sinraptor does not possess a suborbital flange similar in morphology to the pronounced processes of Carcharodontosaurus and Giganotosaurus. Rather, Sinraptor is characterised by a slight rugosity on the anterior edge of the ventral ramus of the postorbital. Furthermore, personal observation of the holotype (OMNH 10146) reveals that Acrocanthosaurus is characterised by such a flange, although it is broken (Fig. 7D). Thus, the suborbital flange appears to be a synapomorphy of Acrocanthosaurus, Carcharodontosaurus and Giganotosaurus and is optimised as diagnostic of this carcharodontosaurid subgroup in the present analysis.

Axial Intercentrum: Giganotosaurus and Sinraptor were scored for a dorsally-tilted ventral margin of the axial intercentrum (character 28), whereas Acrocanthosaurus and Allosaurus were scored for the primitive parallel-trending intercentrum and Carcharodontosaurus and
**Tyrannotitan** were scored ‘?’. While we agree that *Acrocanthosaurus* (and also *Neovenator*) should be scored for the primitive state, new material of *Allosaurus* (Chure 2000), along with careful examination of published figures (Madsen 1976: plate 11), suggests that this taxon should also be scored for the derived state. As a result, this character is now diagnostic of a much more inclusive clade.

**Supraoccipital Expansion:** Novas et al. (2005: character 97) scored *Carcharodontosaurus*, *Giganotosaurus* and *Sinraptor* for a derived supraoccipital with a dorsal expansion that is at least two times the width of the foramen magnum. *Allosaurus* and *Acrocanthosaurus* were scored for the primitive state and *Tyrannotitan* scored ‘?’. Measurements of allosaurid braincases, as well as interpretation of published figures (Madsen 1976: fig. 13; Currie & Zhao 1993: figs 3, 7; Coria & Currie 2002: fig. 5), indicates that no allosaurs possess a supraoccipital expansion more than twice the width of the foramen magnum. In addition, no significant differences in supraoccipital morphology were found. Thus, this character is discarded in the present analysis.

Finally, Novas et al. (2005) list several characters diagnostic of their Carcharodontosauridae, which includes *Carcharodontosaurus*, *Giganotosaurus* and *Tyrannotitan*, but not *Acrocanthosaurus*. Of these characters, a dentary with a squared-off anterior end (25), postaxial cervicals with two pleurocoels (32) and pleurocoels throughout the dorsal vertebral column (34) are also found in *Acrocanthosaurus*.

Among the 37 characters shared between the current analysis and that of Novas et al. (2005), 29 scoring differences exist, 18 involving positive scores (see Supplementary data Appendix 2). Rerunning the dataset of Novas et al. (2005) with the scores favoured by the present analysis results in one MPT of 235 steps (CI = 0.55, RI = 0.62), compared to one MPT of length 227 in the original analysis. This tree (Fig. 8C) is remarkably different from that of the original analysis: *Acrocanthosaurus* and *Allosaurus* are no longer sister taxa and *Giganotosaurus* and *Tyrannotitan* comprise a clade exclusive of *Carcharodontosaurus*. This suggests that scoring differences are a source of incongruence between our topology and that of Novas et al. (2005), especially concerning the placement of *Acrocanthosaurus*.

The present analysis and that of Novas et al. (2005) also differ in the number and distribution of informative characters. Novas et al. (2005) use 48 informative characters, 26 of which are also utilised in the present analysis (34%; see Supplementary data Appendix 3). Overall, 37 of the 99 characters (37%) used in the present analysis also appear in the character list of Novas et al. (2005). As outlined above, six of these characters are synapomorphies of *Acrocanthosaurus* and *Allosaurus* (20, 22, 36, 41, 79, 80), while three link *Sinraptor* and carcharodontosaurids (17, 92, 97). In addition, Novas et al. (2005) did not utilise several characters that unite *Acrocanthosaurus* with carcharodontosaurids and place *Sinraptor* as basal in the present study.

The analysis of Novas et al. (2005) includes six allosaurid terminal taxa. They introduced *Tyrannotitan* as a new basal carcharodontosaurid but did not include *Neovenator*, another taxon with a potentially similar position among allosaurs. When *Neovenator* is added, their analysis yields a single MPT of 230 steps (Fig. 9C, Supplementary data Appendix 4). *Neovenator* is recovered as the sister taxon to *Acrocanthosaurus*, and the relative positions of the other allosaurid taxa remain unchanged. In summary, scoring differences and character choice are sources of incongruence between the present analysis and that of Novas et al. (2005), but taxonomic sampling probably does not explain topological differences.

**Holtz 2000**

The analysis of Holtz (2000) agrees with the present study in most aspects, the lone exception being the sister group relationship between *Allosaurus* and *Neovenator*. Holtz (2000) presents three unambiguous synapomorphies supporting this grouping: five premaxillary teeth (character 3), moderately elongated distal caudal prezygapophyses that extend more than one half but less than one times the length of the centrum (character 199) and a reversal to a broad distal scapula expansion (character 212). We agree that five premaxillary teeth uniquely characterise these two taxa. However, new illustrations of *Neovenator* (Hutt 1999) and re-examination of the holotype (MIWG 6348/BMNH R1001) clearly show elongated distal caudal prezygapophyses. Furthermore, measurement of allosaurid scapulae reveals no quantifiable pattern in distal scapular expansion width.

**DISCUSSION AND IMPLICATIONS**

**Current consensus in allosaurid phylogeny**

Allosaurs have been the subject of many phylogenetic analyses. Consensus, however, has been slow to emerge, as cladistic analyses continue to disagree on the position of *Sinraptor*, *Acrocanthosaurus* and *Neovenator*. The only consistent node among various studies has been the grouping of derived carcharodontosaurids (*Carcharodontosaurus* and *Giganotosaurus*), which is found in nearly every published analysis. The discovery of new taxa (Hutt et al. 1996; Novas et al. 2005; Coria & Currie 2006; Sereno & Brusatte 2008) and the publication of three detailed theropod phylogenies (Holtz 2000; Rauhut 2003; Holtz et al. 2004) have done little to resolve problematic areas of allosaurid phylogeny. Frus-tratingly, despite an average publication rate of over one new allosaurid phylogenetic study per year, only cursory discussion has been devoted to similarities and differences between analyses. As a result, problematic characters have endured in the literature and coding differences have proliferated.

Based on the new analysis and comparisons with previously-published studies, the current state of allosaurid phylogeny can be assessed. The analysis presented here, which consists of 99 characters scored across nine ingroup taxa, integrates previously-published characters with several new characters. Some published characters were rejected, but the reasons for this have been noted (Supplementary data Appendix 3). In addition, the new analysis also includes several newly described taxa (*Eocarcharia*, *Mapusaurus*, *Tyrannotitan*) and data from newly-available material.
The recovered most parsimonious cladogram (Fig. 5) places Sinraptor as a basal allosauroid, a position supported by robust Bremer support (5) and bootstrap (84%) measures for the less inclusive Allosaurus + Carcharodontosauridae node. This conflicts with several previous studies that place Sinraptor as the sister taxon to Carcharodontosauridae. In two such analyses (Allain 2002; Novas et al. 2005), several braincase characters provided key support for uniting these two taxa. Although most of these characters are included in the present analysis, many other characters from other skeletal regions unite Allosaurus and Carcharodontosauridae to the exclusion of Sinraptor (19 characters under ACCTRAN, 20 under DELTRAN, 14 unambiguous). Many of these characters are not included in the analyses of Allain (2002) and Novas et al. (2005). Two non-braincase characters linking Sinraptor and carcharodontosaurids in the latter study are rejected here because of what we regard as errors in character state scores. Due to this character support, as well as the high tree support measures discussed above and problems with characters from other analyses, the basal position of Sinraptor appears to be well supported by the present dataset.

The present analysis places Acrocanthosaurus within Carcharodontosauridae, a position robustly supported by numerous characters and relatively high Bremer support and bootstrap values (Fig. 5). An additional 27 steps are required to reposition Acrocanthosaurus as the sister taxon to Allosaurus, as is advocated by many alternative studies. Five characters in the current study do unite Acrocanthosaurus and Allosaurus (30, 48, 55, 56, 58), but these are ambiguous due to missing data in carcharodontosaurids. Although the analyses of Currie & Carpenter (2000), Allain (2002) and Novas et al. (2005) each unite Acrocanthosaurus and Allosaurus, nearly every supporting synapomorphy appears problematic and bootstrap and Bremer support values supporting this grouping are weak (Fig. 2). Furthermore, when incongruent scores are changed to those favoured in the present analysis, the Acrocanthosaurus + Allosaurus grouping found in all three alternative studies collapses. Thus, the carcharodontosaur affinity of Acrocanthosaurus is considered strongly supported by the present analysis, whereas an Acrocanthosaurus + Allosaurus sister relationship is highly uns parsimonious and supported by few data.

The interrelationships within Carcharodontosauridae are less secure, as several taxa are based on fragmentary material. The position of Neovenator as closer to Carcharodontosaurus than to Allosaurus is considered robust, however, due to several synapomorphies (29 under ACCTRAN, 11 under DELTRAN, 10 unambiguous) and high tree support values (Bremer support = 5, bootstrap = 90%). Although Holtz (2000) recovered Neovenator and Allosaurus as sister taxa, our review of the character evidence leaves only one supporting character. The sister group relationship between Carcharodontosaurus and the Giganotosaurus + Mapusaurus clade also appears to be robust, as it is supported here by high tree support values (Bremer support = 2, bootstrap = 91%) and numerous synapomorphies (18 under ACCTRAN, 16 under DELTRAN, 13 unambiguous), and has been recovered in most previous analyses. Future work may find support for a clade of endemic South American carcharodontosaurids, with the poorly-known Tyrannotitan repositioned closer to Giganotosaurus than to Carcharodontosaurus and more basal carcharodontosaurids. This is currently less parsimoni ous with the present dataset, but abundant missing data in Tyrannotitan renders its placement somewhat problematic. Indeed, when conflicting scores in the analysis of Novas et al. (2005) are changed to those favoured by the current analysis, movement of Tyrannotitan from a basal carcharodontosaurid position to a sister-group relationship with Giganotosaurus seems secure.

Finally, the number of previously published characters rejected in the current analysis may appear alarming (see Supplementary data Appendix 3). However, each of the 12 published analyses considers allosauroids along with several non-allosauroid taxa and many employ vastly different outgroups. Although some characters are found to be informative in the original analyses, comparison with allosauroid outgroups often reveals extreme variation, rendering polarity determination difficult and suggesting that the character may have little phylogenetic utility. Furthermore, in our experience large-scale theropod phylogenetic analyses are especially prone to incorrect scores and redundant characters (for example, scores for characters 555–578 for Carcharodontosaurus seem to be accidentally shifted one space in the analysis of Holtz et al. 2004), which may artificially inflate the number of characters informative at a single node, such as Allosauroida. Regardless, every character that was informative at the level of Allosauroida in each of the 12 analyses was carefully considered for this study.

Character evolution in Allosauroida

Several characters of particular note are discussed below. A complete list of synapomorphies for each allosauroid clade is provided in Supplementary data Appendix 1. Carcharodontosaurus and Giganotosaurus are united by several synapomorphies, most of which are cranial. Many of these synapomorphies involve bone texture, fusion and the highly apomorphic morphology of the braincase. Carcharodontosauridae, by contrast, is diagnosed by both cranial and postcranial synapomorphies. More exclusive clades within Carcharodontosauridae are united by characters related to vertebral pneumatism, which is prone to individual (Chure & Madsen 1996) and ontogenetic (Rauhut & Fechner 2005) variation. While this may be problematic, copious additional synapomorphies also unite clades within Carcharodontosauridae. Furthermore, although Currie & Carpenter (2000) dismiss several synapomorphies of Acrocanthosaurus and Carcharodontosaurus as size-related, many of these are seen in the much smaller Eocarcharia (Sereno & Brusatte 2008), and are not seen in other large-bodied theropods such as spinosaurids. Although Currie & Carpenter (2000) are correct in asserting that Acrocanthosaurus lacks many derived characters seen in Carcharodontosaurus and Giganotosaurus, including heavily-sculptured cranial bones and the highly-derived braincase, these characters are here interpreted as synapomorphies of the derived Carcharodontosaurinae. Their absence in Acrocanthosaurus does not contradict its placement as closer to Carcharodontosaurus than to Allosaurus.

The phylogenetic analysis presented here is highly homoplastic and, consequently, many putative synapomorphies are rejected as non-homologous among taxa. Foremost among these are the many braincase characters that unite Sinraptor, Carcharodontosaurus and Giganotosaurus to the exclusion of Acrocanthosaurus and Allosaurus. Based
on the recovered topology, it is most parsimonious to conclude that these characters evolved independently in *Sinraptor* and Carcharodontosaurinae. Similarly, five premaxillary teeth may have alternatively evolved in the common ancestor of *Allosaurus* and Carcharodontosauridae and been lost in all carcharodontosaurids more derived than *Neovenator*, or they may have arisen independently in *Allosaurus* and *Neovenator*.

**Status of controversial taxa**

Several theropod taxa not included in this analysis have been recovered as allosauroids in previous higher-level analyses of theropod phylogeny. The current study cannot adequately test the phylogenetic relationships of these taxa, as this would require the inclusion of a diverse array of non-allosauroid terminal taxa. However, some of these taxa are briefly discussed below, along with character support for their inclusion in Allosauroidea.

*Abelisauridae*

Some authors (Novas 1997; Sampson et al. 1998) have noted numerous similarities between carcharodontosaurids and the Cretaceous abelisaurid theropods. Although most studies place abelisaurids as basal theropods closely related to *Ceratosaurus*, Forster (1999) positioned abelisaurids among basal tetanurans, and thus more closely related to allosauroids than to other primitive theropods. Carcharodontosaurids share with abelisaurids several cranial similarities, including a postorbital–lacrimal contact excluding the frontal from the orbital rim, a suborbital flange on the postorbital, an anteroventrally-orientated ventral process of the postorbital, fused frontal–parietal sutures and heavily textured cranial bones. However, abelisaurids lack many other tetanuran and allosauroid synapomorphies, while character states in basal members of both clades (Rugops: Sereno et al. 2004; Eocarcharia: Sereno & Brusatte 2008) suggest that most of the features shared between carcharodontosaurids and abelisaurids evolved independently. Thus, an allosaurid (or tetanuran) placement for abelisaurids is highly unparsimonious and the similarities between these two clades are best interpreted as convergences.

*Monolophosaurus*

Some analyses (e.g. Sereno et al. 1996; Holtz 2000; Currie & Carpenter 2000; Novas et al. 2005) have positioned the Chinese *Monolophosaurus* nested within the stem-based Allosauroida, whereas others have placed it in an unresolved polytomy with many disparate taxa (Harris 1998; Rauhut 2003). *Monolophosaurus* shares with *Allosaurus* and *Neovenator* a square-shaped premaxillary body and a maxilla with a vertical articulation for the premaxilla. These characters, however, appear to have a broader distribution among basal tetanurans. Like all scorable allosauroids other than *Sinraptor*, the infratemporal fenestra of *Monolophosaurus* is constricted by an inflection from the squamosal. In addition, *Monolophosaurus* possesses a highly pneumatic jugal, rugose nasals as well as nasals and lacrimals with raised crests, like many allosauroids. However, these latter features are difficult to compare topologically and thus homologise with allosauroids due to the highly autapomorphic cranial crest of *Monolophosaurus*. Although *Monolophosaurus* is positioned as more derived than *Sinraptor* when included in the present analysis, many aspects of its morphology suggest that its affinities lie elsewhere (Brusatte et al. unpublished results).

*Cryolophosaurus*

Sereno et al. (1996) recovered the Early Jurassic Antarctic genus *Cryolophosaurus* as an allosauroid based on an examination of the skull. Most other analyses have not included this highly incomplete taxon. A recent analysis based on the complete skeleton, discussed only in an abstract (Smith et al. 2005), placed *Cryolophosaurus* as a basal tetanuran. As this taxon is currently under study by N. D. Smith et al., it will not be discussed further here.

*Siamotyrannus*

Originally described as a basal tyrannosaurid (Buffetaut et al. 1996), *Siamotyrannus* was recovered as an allosauroid by Rauhut (2003) and Holtz et al. (2004). *Siamotyrannus* possesses an expanded anterior projection of the pubic boot like many allosauroids except *Sinraptor*. Furthermore, the ischia of *Acrocanthosaurus* and *Siamotyrannus* are marked by a distinct muscle attachment scar on the posterior surface. Thus, *Siamotyrannus* may be a carcharodontosaurid, but a careful re-examination of the fragmentary type material is needed before the phylogenetic relationships of this taxon can be assessed critically.

*Lourinhanosaurus*

Described as an allosauroid by Mateus (1998), *Lourinhanosaurus* has been included in only one cladistic analysis (Holtz et al. 2004), which corroborates this placement. Like *Allosaurus*, *Sinraptor* and *Siamotyrannus*, *Lourinhanosaurus* is characterised by an ilium with a straight anterior margin (character 77). However, recently it has been suggested that this taxon may be a spinosauroid (Allain 2005).

*Megaraptor*

The bizarre but fragmentary Late Cretaceous *Megaraptor* was described by Novas (1998) as a large dromaeosaurid, largely due to its sickle-like second pedal ungual. The discovery of additional specimens (Lamanna et al. 2004; Calvo et al. 2004) revealed this claw to be a manual element, thus erasing any significant support for dromaeosaurid affinities. Calvo et al. (2004) noted that *Megaraptor* resembled carcharodontosaurids in several vertebral features and Lamanna et al. (2004) briefly discussed a cladistic analysis that recovered this taxon as the basal-most allosauroid, but a list of characters and codings was not presented. In the present analysis, *Megaraptor* shares with many carcharodontosaurids pleurocoels in anterior caudal vertebrae and a strongly hooked coracoid. However, as with *Monolophosaurus*, the phylogenetic relationships of *Megaraptor* can only be tested within the context of a larger analysis of basal tetanurans.

*Fukuiraptor*

This large theropod from the Albian of Japan has been included in the cladistic analyses of Azuma & Currie (2000) and Holtz et al. (2004), which recover it as an allosauroid. In the present character list, *Fukuiraptor* shares with all scorable allosauroids, other than *Sinraptor*, a pronounced medial epicondyle of the femur (character 85) and a strongly hooked posteroverentral process of the coracoid (character 95). Like
Monolophosaurus, Fukuiraptor is recovered as more derived than Sinraptor when included in the present analysis, but must be analysed by a larger study before its relationships can be confidently assessed.

**Phylogenetic taxonomy**

Defining clades by reference to tree topology rather than lists of characters or included taxa has become commonplace among archosauromorph systematists (de Queiroz & Gauthier 1990, 1992; Sereno 1998). Although allosauroid phylogenetic taxonomy has generated much less debate and controversy than that of other theropod clades, alternative definitions exist for all allosauroid taxa. With the help of the new database TaxonSearch (Sereno et al. 2005), we briefly review the history of allosauroid phylogenetic taxonomy and provide a clear set of definitions for all taxa. This proposed taxonomy, based largely on the previous work of Sereno (2005), aims to provide stability of membership and preserve priority of definition and original intent where possible. A more complete discussion of allosauroid taxonomy and a list of all proposed definitions can be found in the TaxonSearch file ‘Stem Archosaurus’ (Sereno 2005; Sereno et al. 2005). Names used here are applied to the clades shown in Fig. 5.

**Allosauroida**

This superfamilly-level taxon, attributed to Marsh (1878) who coined the term Allosauridae, was first explicitly utilised by Currie & Zhao (1993). They included the family-level Allosauridae and Sinraptoridae and excluded other basal tetanurans, such as ‘megalosaurs’ and Monolophosaurus. Padian & Hutchinson (1997) provided the first definition of Allosauroida: Allosaurus and Sinraptor and all descendants of their most recent common ancestor. Independently, Sereno (1998) defined Allosauroida as a stem-based clade encompassing all neotetanurans closer to Allosaurus than to Neornithes. A similar stem-based definition, however, was coined for the clade Carnosauria (Padian & Hutchinson 1997; Padian et al. 1999; Holtz et al. 2004). These node and stem-based definitions may differ in content, as some basal tetanurans that fall outside the Sinraptor + Allosaurus node would be considered allosaurids in the taxonomy of Sereno (1998, 2005), but non-allosaurian carnosaurs in the system of Padian and others. While basal tetanuran phylogeny is still unresolved, some analyses (Holtz 2000; Rauhut 2003; Holtz et al. 2004) suggest that taxa such as Monolophosaurus and Fukuiraptor may occupy this problematic zone. We advise against the continued use of Carnosauria, due to its long history as a ‘wastebasket’ taxon for a phylogenetically disparate array of large theropods (tyranosaurids, abelisaurids, allosauroids). Given the current state of flux of basal tetanuran phylogeny, we favour a stem-based definition for Allosauroida that may eventually absorb several poorly-known taxa, if new information suggests they lie closer to Allosaurus than to birds. Thus, the preferred definition of Allosauroida is: the most inclusive clade containing Allosaurus fragilis Marsh, 1877, but not Passer domesticus Linnaeus, 1758.

In the future, as the relationships of Monolophosaurus, Fukuiraptor, Lourinhanosaurus and spinosaurids become clearer, it may be useful to name a node-based taxonomy to encompass Allosauridae and Carcharodontosauridae (and probably Sinraptoridae) to the exclusion of more basal allosaurids. This node would be equivalent to Allosauroida as defined by Padian & Hutchinson (1997), Padian et al. (1999) and Holtz et al. (2004) and essentially encompasses the nine ingroup taxa in the current analysis. However, until the relationships of basal tetanurans and basal allosaurids are better resolved, we choose not to name such a node here.

**Allosauridae**

Coined by Marsh (1878). Allosauridae was originally defined as a stem-based clade encompassing theropods closer to Allosaurus than to Sinraptor (Padian & Hutchinson 1997). Independently, Sereno (1998) used a similar definition but added Carcharodontosauridae, Monolophosaurus, Cryolophosaurus and, eventually, the neornithine Passer (Sereno 2005) as external specifiers to better limit potential included taxa in the event that Allosauridea is not monophyletic. Sereno’s (2005) definition is followed here: the most inclusive clade containing Allosaurus fragilis Marsh, 1877, but not Sinraptor dongi Currie & Zhao, 1993, Carcharodontosaurus saharicus Depéret & Savornin, 1927, or Passer domesticus Linnaeus, 1758.

**Sinraptoridae**

This clade name was first used by Currie & Zhao (1993), first defined by Padian & Hutchinson (1997) as a stem-based taxon and revised by Sereno (1998, 2005), who added several external specifiers. Sereno’s (2005) definition is followed here: the most inclusive clade containing Sinraptor dongi Currie & Zhao, 1993, but not Allosaurus fragilis Marsh, 1877, Carcharodontosaurus saharicus Depéret & Savornin, 1927, or Passer domesticus Linnaeus, 1758.

**Carcharodontosauridae**

Coined by Stromer (1931) and first defined by Sereno (1998) as a stem-based taxon, we follow Sereno’s (2005) revised definition here: the most inclusive clade containing Carcharodontosaurus saharicus Depéret & Savornin, 1927, but not Sinraptor dongi Currie & Zhao, 1993, Allosaurus fragilis Marsh, 1877, or Passer domesticus Linnaeus, 1758.

**Carcharodontosaurinae n. tax.**

The discovery of new genera (Eocarcharia, Tyrannotitan) and the corroboration of the carcharodontosaurid affinities of Neovenator have greatly expanded the membership of Carcharodontosauridae. Ingroup relationships within the clade are problematic due to large amounts of missing data, but the close relationship between Carcharodontosaurus, Giganotosaurus and Mapusaurus is highly supported by robust tree support measures, enumerated by several synapomorphies and corroborated by nearly every published cladistic analysis. As an increase in fossil collecting in Africa and South America make it probable that close relatives of these genera will be discovered, we elect to use Carcharodontosaurinae to refer to the very derived, large-bodied carcharodontosaurids. This clade is here defined as: the least inclusive clade containing Carcharodontosaurus saharicus Depéret & Savornin, 1927 and Giganotosaurus carolinii Coria & Salgado, 1995.

**Giganotosaurini n.tax.**

In their description of Mapusaurus, Coria & Currie (2006) named the new taxon Giganotosaurini to refer to those carcharodontosaurids closer to Giganotosaurus and
Mapusaurus than to Carcharodontosaurus. We feel, however, that the subfamily-level taxon Carcharodontosaurinae, which has long been available as a co-ordinate taxon of Carcharodontosauridae Stromer, 1931, is most useful and appropriate to encompass the clade of highly derived, large-bodied carcharodontosaurids including Carcharodontosaurus. Giganotosaurinae would then be included within another taxon (Carcharodontosauridae) with an identical Linnaean suffix. To preserve the traditional hierarchy of Linnaean suffixes, we therefore erect Giganotosaurini to replace Giganotosaurinae, as defined by Coria & Currie (2006). Giganotosaurini is here defined as: the most inclusive clade containing Giganotosaurus carolinii Coria & Salgado, 1995, but not Carcharodontosaurus saharicus Depéret & Savornin, 1927. In this way, Giganotosaurini includes the carcharodontosaurines most closely related to Giganotosaurus among carcharodontosaurids. In this classification scheme, it would be possible to erect a subfamily-level taxon for those taxa close to Acrocanthosaurus and a tribe-level taxon for those taxa more closely related to Carcharodontosaurus than to Giganotosaurus, should the requisite specimens be discovered.

Stratigraphical congruence

Cladistic hypotheses imply a relative temporal ordering of branching events in a clade’s history (Fig. 10). Ideally, since there is one true history of life, this hierarchically-arranged ordering should be congruent with the linear stratigraphical succession of the clade’s fossil record. In recent years, workers have devised several metrics to quantify the congruence between a specific phylogenetic hypothesis and the known fossil record of the clade in question. These metrics fall into two categories: (1) gap metrics, which measure sampling gaps inferred by a specific phylogenetic hypothesis (Relative Completeness Index (RCI): Benton & Storrs 1994;
Gap Excess Ratio (GER): Wills 1999; modified Manhattan Stratigraphic Measure (MSM*): Siddall 1998, Pol & Norell 2001; Retention Index of the Stratigraphic Character (RI5): Fisher 1992; Clyde & Fisher 1997; Finarelli & Clyde 2002) and (2) consistency metrics, which compare the rank order of cladistic branching with the first appearance of terminal taxa in the fossil record (Spearman Rank Correlation (SRC): Gauthier et al. 1988; Norell & Novacek 1992; Stratigraphic Consistency Index (SCI): Huelsenbeck 1994; for a review, see Wagner & Sidor 2000). Although these metrics are all designed to measure the fit of stratigraphy to a cladogram, considerable debate persists over the potential biases and relevant uses of each. In particular, simulation studies have clearly shown that these metrics are often sensitive to tree size, tree shape, sampling intensity and the stratigraphical ages of terminal taxa (Norell & Novacek 1992; Siddall 1996, 1997; Hitchin & Benton 1997; Wills 1999; Pol & Norell 2001; Pol et al. 2004).

Although potential problems exist with every stratigraphical metric yet devised, some metrics are more robust than others (Pol et al. 2004) and can be useful for measuring both the stratigraphical fit of a specific phylogenetic hypothesis, as well as the relative stratigraphical fits of alternative hypotheses for the same clade. In these cases, knowledge of stratigraphical congruence can build or weaken confidence in a specific hypothesis and help choose between competing hypotheses, respectively. This is especially true for allosauroid clades, a clade described by several competing phylogenetic hypotheses. Along with the character data discussed above, the relative stratigraphical fits of alternative hypotheses can be used as a measure of comparison. Choosing which metric(s) to use is difficult, but three in particular are well-suited for an extinct group of terrestrial vertebrates known almost entirely from ‘point occurrences’ in the fossil record. These metrics include the SCI (Huelsenbeck 1994), the GER (Wills 1999) and the MSM* (Siddall 1998; Pol & Norell 2001). Complete definitions of each of these metrics can be found in the literature, as well as discussion of potential biases (see Pol et al. 2004 for an overview).

A list of these metrics compiled for the current study and several alternative hypotheses is presented in Table 4. For all comparisons, the current study is pruned to a common set of taxa (five shared taxa for comparisons with the analyses of Allain (2002), Coria & Currie (2002) and Novas et al. (2005), and six shared taxa for comparisons with Holtz (2000)), thus eliminating all potential biases except for those relating to tree shape.

With its full set of nine allosauroid terminal taxa, the present analysis is characterized by high values for all three metrics. For the MSM*, the current analysis is stratigraphically congruent at the p = 0.002 level — that is, less than 0.2% of the time would a stratigraphical fit that is better than the observed fit be expected from randomised data. Thus, the current analysis is considered to be largely congruent with stratigraphy. Although the SRC, which plots clade rank against age rank (Gauthier et al. 1988), has fallen widely out of use due to its biases, this metric is well-suited to the largely pectinate tree topology found by the current analysis. Plotting clade rank against age rank (based on earliest known occurrence) for individual clades, with the Acrocanthosaurus + Eocarcharia node collapsed following Norell & Novacek (1992), gives an SRC of 0.91. This correlation is significant at the p < 0.0009 level and, in fact, all deviation from a perfect SRC (SRC = 1.0) is due solely to the statistical problem of identical ages for several terminal taxa. This indicates that the known fossil record, coupled with the present phylogeny, is a good representation of allosauroid history.

When pruned to a common set of taxa and compared to several alternative phylogenies, the current analysis is consistently more congruent with stratigraphy than any competing published analysis. The large discrepancy between the current analysis and the alternatives is readily shown by the MSM*, which, simulations have shown, is least sensitive to stratigraphical resolution in which the taxon first appeared, based on the timescale of Gradstein et al. (2004). Due to impression in fossil dating, Acrocanthosaurus, Carcharodontosaurus, Giganotosaurus and Mapusaurus were treated as temporally equivalent. For pruned stratocladistic analyses, stratigraphical character states not coded for any of the shared taxa were deleted.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>SCI</th>
<th>GER</th>
<th>MSM*</th>
<th>p</th>
<th>RI5</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Full analysis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>This analysis</td>
<td>1.00</td>
<td>1.00</td>
<td>0.76</td>
<td>0.002</td>
<td>1.00</td>
<td>5</td>
</tr>
<tr>
<td><strong>Pruned to 5 shared taxa</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>This analysis</td>
<td>1.00</td>
<td>1.00</td>
<td>0.73</td>
<td>0.05</td>
<td>0.71</td>
<td>2</td>
</tr>
<tr>
<td>Alternative 1</td>
<td>0.75</td>
<td>0.55</td>
<td>0.36</td>
<td>0.80</td>
<td>0.43</td>
<td>4</td>
</tr>
<tr>
<td>Alternative 2</td>
<td>0.75</td>
<td>0.66</td>
<td>0.36</td>
<td>0.43</td>
<td>0.53</td>
<td>3</td>
</tr>
<tr>
<td><strong>Pruned to 6 shared taxa</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>This analysis</td>
<td>1.00</td>
<td>1.00</td>
<td>0.75</td>
<td>0.007</td>
<td>0.75</td>
<td>3</td>
</tr>
<tr>
<td>Holtz 2000</td>
<td>0.80</td>
<td>0.84</td>
<td>0.51</td>
<td>0.05</td>
<td>0.67</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 4 Comparison of stratigraphical consistency metrics for the current analysis (ingroup phylogeny only) and several alternative studies.

Alternative 1 refers to the topology found in the analyses of Allain (2002) and Coria & Currie (2002), while Alternative 2 refers to the topology presented in Novas et al. (2005). Note that the topology presented by Novas et al. (2005) was not found in a re-analysis of their dataset.

Abbreviations: SCI, Stratigraphic Consistency Index (Huelsenbeck 1994); GER, Gap Excess Ratio (Wills 1999); MSM*, modified Manhattan Stratigraphic Measure (Siddall 1998, Pol & Norell 2001); p, significance of the MSM* metric, describing the expected frequency of a better stratigraphical fit than that observed; RI5, Retention Index of the Stratigraphic Character (Fisher 1992, Clyde & Fisher 1997); SD, Stratigraphic Debt, as calculated by a stratocladistic analysis (Fisher 1992) with five coded stratigraphical intervals (see Supplementary data Appendix 5).

Each taxon was treated as a ‘point occurrence’ for the GER and MSM, with absolute dates taken as the midpoint of the stage (or stages, depending on stratigraphical resolution) in which the taxon first appeared, based on the timescale of Gradstein et al. (2004). Due to impression in fossil dating, Acrocanthosaurus, Carcharodontosaurus, Giganotosaurus and Mapusaurus were treated as temporally equivalent. For pruned stratocladistic analyses, stratigraphical character states not coded for any of the shared taxa were deleted.

1. Acrocanthosaurus, Allosaurus, Carcharodontosaurus, Giganotosaurus, Sinraptor
1. the above plus Neovenator.
Tyronnotitan was not included in the calculation of the comparative metrics for the pruned analyses, as its position in the present analysis is considered unstable.
phylogenetic relationships. The results of the biogeographical study have shown that Allosauroids have figured prominently in discussions of palaeogeography for a long time (Fisher 1992; Clyde & Fisher 1997; Fox et al. 1999; Bodenbender & Fisher 2001). Stratocladistics has been criticised from many angles (Adrain & Westrop 2001; Sumrall & Brochu 2003) and has only been applied to one published dinosaur dataset, an analysis of sauropod phylogeny (Wilson 2005). Although we have serious philosophical and practical reservations concerning stratocladistics, we believe that it can be valuable as a heuristic tool to identify robust and problematic areas of a phylogenetic reconstruction (Angielczyk & Fox 2006). We are also interested in empirically testing the effect of using stratocladistic analysis on a dataset of dinosaur phylogeny. For this analysis of allosauroids, we used MacClade to score a stratigraphical character, which was divided into five states (see Supplementary data Appendix 5). Admittedly, selection of these states is somewhat arbitrary, but they were conservatively selected so as to minimise gaps and imprecision in fossil dating, following the guidelines set out by proponents of stratocladistics (e.g. Clyde & Fisher 1997; Bodenbender & Fisher 2001). When added to the current analysis and several alternative datasets, in no case did this stratigraphical character alter the most parsimonious topology. However, the retention index of this character (RI3), as well as the number of implied interval crossings by non-preserved lineages (stratigraphic debt, SD), differs for each of the alternative analyses (Table 4). As the congruence metrics discussed above, the present phylogeny consistently is characterized by a higher RI3 and less stratigraphic debt than any published alternative.

**Palaeobiogeography**

Allosauroids have figured prominently in discussions of Mesozoic palaeobiogeography because they comprise a long-lived and diverse group that originated when Pangaea was largely coherent and evolved during its fragmentation (Harris 1998; Perez-Moreno et al. 1999; Sereno 1999a, b; Upchurch et al. 2002). These studies can be divided into two general approaches. The first, or traditional approach, is to combine palaeogeographical data with knowledge of the age, distribution and relationships of the taxa under study (as well as other co-existing taxa). The finished hypothesis is what might be viewed as a "most probable scenario" (Sereno 1997). For allosauroids, these scenarios have identified a clade of southern allosauroids, the derived carcharodontosaurids Carcharodontosaurus and Giganotosaurus, which may well have radiated largely after the isolation of Gondwana during the Cretaceous (Sereno et al. 1996; Harris 1998; Perez-Moreno et al. 1999; Sereno 1999b).

The second approach is quantitative and attempts to determine palaeogeographical signal independently from phylogenetic relationships. The results of the biogeographical analysis are then compared with palaeogeographical information. These analyses can involve parsimony analysis of endemism (e.g. Le Loeuff 1991), a method now largely abandoned, or a variety of manipulations involving area cladograms based on taxon cladograms such as component analysis (Platnick & Nelson 1981), Brooks Parsimony Analysis (Brooks & McLennan 1991; Brooks et al. 2001) and three-area statements (Nelson & Ladiges 1991). These methods, which are usually applied to extant taxa with better-resolved distributions, are applied one of these methods, three-area analysis (Nelson & Ladiges 1991), to analyse allosauroid biogeography. This method was selected because it is straightforward to implement, can be applied to a single clade and emphasises information from cladogram topology — the primary phylogenetic pattern — while minimising problems due to widespread taxa. A matrix of three-area statements was generated on the basis of our most parsimonious cladogram (see Supplementary Appendix 6). When analysed using PAUP*, this matrix produces a single MPT (TL = 30, CI = 0.90, RI = 0.89; Fig. 11), which places North America, Europe and Asia as successive outgroups to a sister-grouping of Africa and South America. Two nodes show strong bootstrap (1000 replicates) and Bremer support values (Fig. 11).

Notably, the topology recovered by three-area analysis matches the most common version of the breakup sequence of Pangaea (Rubinowitz & LaBrecque 1979; Smith et al. 1994; Scotese 2004), in which Asia becomes isolated first, followed successively by North America and then by South America plus Africa. The position of Europe during the breakup is often viewed as equivocal, as much of the European landmass was intermittently exposed as a series of islands during much of the Jurassic and Cretaceous (Smith et al. 1994). Congruence between allosauroid phylogeny and Pangaea fragmentation has been noted by previous authors, but based on smaller phylogenetic datasets and a literal reading of phylogeny (the "first approach" reviewed above: Harris 1998; Sereno 1999a, b). It is significant that a more rigorous cladistic
biogeographical method applied to a larger cladistic dataset recovered the same pattern in this analysis.

However, while the biogeographical analysis may appear to indicate that allosauroids diversified in a vicariant pattern as Pangaea split, this conclusion is premature. Currently, this seemingly congruent pattern must be tempered by acknowledging that the basal areas on the cladogram are occupied by the oldest (and lone) Jurassic taxa in the analysis. The basal position of northern areas may well be an artifact of sampling the oldest and most primitive taxa. Whereas it is clear that there was an array of Jurassic tetanurans of some kind on southern continents as early as the Middle Jurassic, these remain poorly documented (e.g. Maganuco et al. 2007).

In addition, it is surprising that the basal theropods Ceratosaurus, Torvosaurus and Allosaurus – long known only from western North America – have all been discovered in recent years in coeval Late Jurassic deposits in Portugal (Mateus et al. 2006). Finally, we note that the isolation of Africa as part of a larger Gondwanan landmass for much of the Cretaceous remains a hypothesis challenged by many taxa that suggest at least intermittent connection to Europe (Gheerbrant & Rage 2006). Thus, more complete fossil sampling and larger phylogenetic analyses that take into account a broader array of potential allosauroids and other basal tetanurans are needed to more confidently assess the biogeographical history of allosauroids and the hypothesis that they evolved and diversified in concert with the fragmentation of Pangaea.

CONCLUSIONS

A new analysis of allosauroid theropods based on 99 characters scored across nine ingroup taxa (Fig. 5) yielded results that include the following: (1) Sinraptor is positioned as the most basal allosauroid of the taxa considered, followed successively by Allosaurus and Carcharodontosauridae; (2) Neovenator is recovered as a basal carcharodontosaurid rather than as a sister taxon to Allosaurus; (3) Acanthosaurus is strongly supported as a carcharodontosaurid closer to the Gondwanan genera Carcharodontosaurus and Giganotosaurus than to Allosaurus; (4) alternative topologies in the literature are based on important differences in taxonomic sampling, included characters and scoring differences among shared characters; (5) the topology recovered by the current analysis shows a strong overall match with the stratigraphic record and is much more congruent with stratigraphy than any alternative study; (6) the biogeographical history of allosauroids is congruent with the breakup sequence of Pangaea, but requires further testing to more confidently assess this. Resolution of conflict among competing phylogenetic analyses will only come with increased attention and comparison at the level of character data and specimens. It is hoped that future studies of archosaur phylogeny pay close attention to specific differences with alternative studies, in order to gain a more complete understanding of why cladistic hypotheses continue to disagree even after years of study.

ACKNOWLEDGEMENTS

This paper is a modified version of a senior undergraduate honours project submitted by S.L.B. to the Department of the Geophysical Sciences at the University of Chicago, and advised by P.C.S. and M. Webster. We thank D. Chure and an anonymous reviewer for critical comments that improved the manuscript, and M. Webster, M. LaBarbera and L. Heuney for their critical reviews of the thesis. For access to specimens in their care, we thank S. Chapman and A. Milner (BMNH), R. Coria (MACN), M. Munt and S. Hutt (MIWG), R. Cifelli, N. Czapelewski and J. Person (OMNH), and Zhao Xijin and Xu Xing (IVPP). We thank C. Abraczinskas for advice on the figures and final execution of Fig. 1. This work benefited from discussions with S. Hutt (who graciously provided us with a copy of his MPhil dissertation), R. Benson, P. Currie, T. Holtz, T. Carr, J. Franzosa, M. LaBarbera, L. Heuney and M. Kearney. This project was supported by two Howard Hughes Institute Undergraduate Education Initiative Grants at the University of Chicago (to S.L.B.), grants from the Jurassic Foundation and the Palaeontographical Society (to S.L.B. and R. Benson), a travel grant from the University of Chicago Behrens Fund (to S.L.B.) and the National Science Foundation (to P.C.S.).

REFERENCES


Britt, B. B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, late Jurassic), Colorado, with emphasis on the osteology of Torvosaurus tanneri. Brigham Young University, Geology Studies 37: 1–72.


implications for allosauroid phylogeny. *Journal of Vertebrate Paleontology* 25(3): 40A.


Hwang, S. H., Norell, M. A., Ji, Q. & Gao, K. 2004. A large compo-


Walen, A. & Antunes, M. T. 2006. The large theropod fauna of the Lourinha Formation (Portugal) and its similarity to that of the Morrison Formation. New Mexico Museum of Natural History and Science, Bulletin 86.


APPENDIX 1: CHARACTER LIST AND DESCRIPTIONS

Characters and character states are listed below along with the citation for their first use in the cladistic literature. Several of the characters that involve the presence or absence of a feature, as well as its variation (characters 6–8, 10, 12, 13, 25–28, 47) are better coded as independent characters (Sereno 2007) but were left as single characters here for ease of comparison to character data in previous studies.

1. External naris, long axis length: less than 50% anteroposterior diameter of the orbit (0); more than 50% anteroposterior diameter of the orbit (1). (Modified from Holtz et al. 2004:51).
2. Premaxilla, number of teeth: three or four (0); five (1). (Harris 1998:47).
3. Premaxilla, main body, proportions: anteroposteriorly longer than dorsoventrally deep (0); approximately as long as deep (1); deeper than long (2). (Modified from Holtz 2000:5).
4. Premaxilla, ventral portion of anterior margin, inclination: vertical (0); inclined slightly posterodorsally (1). (New).
5. Maxilla, antorbital fenestra, ventral margin, position of the medial rim: lower than lateral rim (0); level with lateral rim (1). (Modified from Holtz et al. 2004:36).
6. Maxilla, promaxillary fenestra, lateral exposure: absent, no fenestra (0); fully exposed (1); present, obscured by the lateral lamina of the ascending ramus (2). (Modified from Harris 1998:2).
7. Maxilla, pro-maxillary fenestra, orientation: absent or laterally facing (0); anteriorly facing (1). (Holtz et al. 2004:38).
8. Maxilla, maxillary fenestra, position relative to the anterior corner of the antorbital fossa: absent or anterior margin terminates posterior to the anterior margin of the antorbital fossa (0); terminates along the anterior margin of the antorbital fossa (1). (Holtz et al. 2004:43).
9. Maxilla, pneumatic excavation on the medial lamina of the ascending ramus: absent (0); present (1). (Harris 1998:2).
10. Maxilla, promaxillary recess, form of medial wall: recess absent or small (0); solid (1); fenestrated, open medially (2). (Modified from Allain 2002:5).
11. Maxilla, articular surface with the premaxilla, inclination in lateral view: angled strongly posterodorsally (0); subvertical (1). (New).
12. Maxilla, lateral lamina of ascending ramus, form: absent or present as a slightly overhanging crest (0); present as a large shelf overlapping the anterior part of the antorbital fossa (1). (Holtz et al. 2004:39).
13. Maxilla, external sculpturing, extent: absent or present and restricted to the anterior and lateral margins above the tooth row (0); present and extensively covering the main body of the maxilla (1). (Forster 1999:11).
14. Maxilla, posterior interdental plates: separate (0); fully co-ossified (1). (Forster 1999:3).
15. Maxilla, posterior interdental plates, dorsoventral depth: less (0); or more (1) than twice anteroposterior width. (New).
16. Nasal, dorsal surface, form: low texture (0); heavily rugose (1). (Forster 1999:11).
17. Nasal, shape in dorsal view: expanding posteriorly, so that the lateral margins diverge (0); parallel-sided throughout its length (1). (Modified from Rauhut 2003:21).
18. Nasal, lateral margin, form: flat (0); offset with a small lateral crest (1). (Modified from Rauhut 2003:22).
19. Nasal, shape of the posterior suture: medial projection less (0); or more (1) than twice anteroposterior width. (New).
20. Lacrimal, dorsal surface, form: unpronounced, level with or only slightly raised above skull roof (0); rugose, with a raised crest or a pronounced horn (1). (Harris 1998:11).
21. Lacrimal, posterior surface, form: smoothly concave (0); marked by a prominent projecting suborbital flange (1). (Currie & Carpenter 2000:19).
22. Postorbital, ventral process, orientation: subvertical (0); angled anteroventrally (1). (Holtz et al. 2004:104).
23. Postorbital, suborbital flange on ventral process, form: absent or indistinct (0); present as a discrete projection on the ventral ramus (1). (Sereno et al. 1996:49).
24. Postorbital, ventral tip of the ventral process, extent: nearly as ventral as the ventral-most margin of orbit and clearly ventral to the squamosal–quadrijugal contact (0); well dorsal to the ventral-most margin of the orbit and at approximately the same level as the squamosal–quadrijugal contact (1). (Harris 1998:7).
25. Postorbital, dorsal surface, form: smooth (0); convex rugosity (1); anteriorly-projecting rugosity (2). (Holtz 2000:52).
26. Postorbital, dorsal boss, size: absent or only slightly overhanging orbit (0); bulbous swelling extensively overhanging orbit (1). (New).
27. Jugal, antorbital fossa, form: absent or developed as a slight, narrow depression (0); present and developed as a large, extensive depression (1). (Modified from Holtz et al. 2004:116).
28. Jugal, pneumatisation: absent or shallow (0); extensive, invaginated recess externally (1). (Modified from Harris 1998:12).
29. Squamosal, ventral (=precotylotid) process, flange into lateral temporal fenestra: absent (0); present (1). (Holtz 2000:57).
30. Squamosal, ventral (=precotylotid) process, length relative to the posterior (=postcotylotid) process in lateral view: longer (0); subequal (1). (New).
31. Prefrontal: present as a distinct element (0); absent, lost or co-ossified with the lacrimal or frontal and not visibly distinct (1). (New).
32. Frontal, supratemporal fossa, exposure in dorsal view: broadly exposed on frontal (0); mostly hidden, restricted by overhanging frontoparietal shelf (1). (Modified from Coria & Currie 2002:1).
33. Frontal, anteromedial corner of the supratemporal fossa, form: open dorsally (0); roofed over by a frontoparietal shelf (1). (Forster 1999:33).
34. Frontal, interfrontal suture: open (0); co-ossified (1). (Holtz 2000:41).
35. Frontal, suture with parietal: open (0); co-ossified (1). (Forster 1999:38).
36. Frontal, contribution to the orbital rim: present (0); absent, excluded by lacrimal–postorbital contact (1). (Sereno et al. 1996:48).
37. Parietal, nuchal plate, orientation with respect to frontal–parietal–postorbital suture: not parallel (0); parallel (1). (Modified from Coria & Currie 2002:10).
38. Parietal, posteriorly-placed knob-like dorsal projection, form: absent or very low (0); pronounced (1). (Modified from Rauhut 2003:42).
39. Braincase, basal tubera, transverse width relative to that of the occipital condyle: greater (0); less (1). (Holtz 2000:97).
40. Braincase, occipital condyle, shape: subspherical (0); dorsoventrally compressed (1). (Coria & Currie 2002:15).
41. Braincase, neck of occipital condyle, paired pneumatic openings that join in midline: absent (0); present (1). (Modified from Coria & Currie 2002:6).
42. Braincase, angle between the axis of the occipital condyle and the transverse plane of the basal tubera: approximately 90 degrees (0); less than 75 degrees (1). (Modified from Forster 1999:43).
43. Braincase, ossification of the interorbital septum: absent (0); present (1). (Modified from Coria & Currie 2002:4).
44. Braincase, trigeminal (nerve V) foramen, location relative to nuchal crest: anterior or ventral (0); posterior (1). (Coria & Currie 2002:2).
45. Braincase, supratemporal fenestrae, orientation: dorsal (0); anterolateral (1). (Coria & Currie 2002:9).
46. Braincase, basal tubera, composition: formed equally by the basioccipital and basisphenoid and not subdivided (0); subdivided by a lateral longitudinal groove into a medial part entirely formed by the basioccipital and a lateral part entirely formed by the basisphenoid (1). (Sereno et al. 1996:44).
47. Palatine, pneumatic recess, form: absent or small foramen (0); large fossa with one or more foramina (1). (Harris 1998:33).
48. Lower jaw, external mandibular fenestra, size: large (0); small (1). (Harris 1998:38).
49. Dentary, anterior end, shape: rounded (0); squared and expanded (1). (Sereno et al. 1996:50).
50. Dentary, anteroventral margin, form: smooth, convex (0); marked by a projecting flange, forming a ‘dentary chin’ (1). (New).
51. Dentary, posterior end of principal neurovascular foramina row, location: parallels the tooth row (0); curves ventrally as it extends posteriorly (1). (New).
52. Dentary, external surface, texture: smooth (0); rugose, marked by pronounced lineations and ridges (1). (New).
53. Dentary, symphysis, angle in dorsal view: low, acute angle, tooth row forms V-shaped convergence (0); high, obtuse angle, tooth row forms U-shaped convergence (1). (New).
54. Dentary, orientation of dorsal and ventral margins of the tooth-bearing section: subparallel (0); caudally divergent (1). (Holtz et al. 2004:219).
55. Dentary, posterior end, form: strongly forked (0); slightly forked or straight (1). (Rauhut 2003:77).
56. Surangular, dorsosentral depth over the external mandibular fenestra: less (0) or more than (1) half the depth of the mandible. (Sereno et al. 1996:47).
57. Surangular, anterior ramus, depth relative to the depth of the surangular and angular under the lateral temporal fenestra: less (0) or more than (1) 50%. (Forster 1999:8).
58. Articular, retroarticular process, form: long, narrow and rod-like (0); broadened, with a posterior groove (1). (Holtz et al. 2004:249).
59. Maxillary and dentary teeth in centre of tooth rows, profile of posterior margin (away from the tip): concave (0); straight, crown recurvature absent (1). (Modified from Holtz et al. 2004:265).
60. Axis, ventral margin of the axial intercentrum, orientation relative to the ventral margin of the axial centrum: approximately parallel (0); angled strongly dorsally (1). (Harris 1998:50).
61. Axis, ventral keel: present (0); absent (1). (Harris 1998:51).
62. Cervicals, posterior articular face of mid cervical centra, width: approximately as broad as tall (0); at least 20% broader than tall (1). (Sereno et al. 1996:53).
63. Cervicals, anterior articular face of mid cervical centra, orientation relative to posterior face: elevated (0); approximately at same level (1). (Sereno et al. 1996:54).
64. Cervicals, interior structure of centrum, pneumaticity: apneumatic or camerate (simple) (0); camellate (complex) (1). (Harris 1998:62).
65. Cervicals, pleurocoels on postaxial cervicals, form: absent or single opening (0); multiple openings within in a single fossa (1). (Harris 1998:61).
66. Cervicals, location of the zygapophyses relative to the midline: over centrum (0); displaced lateral to centrum (1). (Modified from Holtz 2000:155).
67. Dorsals, pleurocoels, distribution: absent or restricted to the anterior dorsals (0); present on all dorsals (1). (Harris 1998:66).
68. Dorsals, posterior centra, anteroposterior length: approximately equal to or longer than dorsoventral depth (0); shorter than deep (1). (Holtz et al. 2004:337).
69. Dorsals, neural spines, height relative to centrum: less than twice centrum height (0); more than twice centrum height (1). (Holtz 2000:167).
70. Dorsals, centrum, shape relative to mid section height: subcylindrical, the dorsoventral thickness of the centrum section greater than 60% the height of the cranial face (0); hourglass-shaped, the dorsoventral thickness less than 60% of the height of the cranial face (1). (Holtz 2000:175).
71. Sacrals, pleurocoels: absent (0); present (1). (Holtz 1998:70).
72. Caudals, rudimentary pleurocoels: absent (or as shallow fossa) (0); present (1). (Sereno et al. 1996:55).
73. Caudals, distal caudal prezygapophyses, length: more than 40% overlap of the preceding vertebral body (0); less than 40% overlap of the preceding vertebral body (1). (Holtz 2000:199).
74. Gastralia, distal end of medial element, shape: tapered (0); club-shaped prominence (1). (New).
75. Gastralia, number of sets of fused medial elements: zero or one (0); greater than one (1). (New).
76. Ilium, posterior margin or postacetabular process, profile: gently convex or posteriorly tapering (0); straight along its entire margin (1). (New).
77. Ilium, anterior margin of preacetabular process, profile: gently convex (0); straight (1). (New).
78. Ilium, pubic peduncle, position relative to the preacetabular process: anterior margin located posterior to the anterior margin of the preacetabular process (0); anterior margin located even with the anterior margin of the preacetabular process (1). (New).
79. Pubis, pubic boot, anterior expansion: absent or weakly developed (0); expanded (1). (Harris 1998:13).
80. Pubis, public boot, size relative to pubic length: less than 50% (0); 50-60% (1); greater than 60% (2). (Sereno et al. 1996:51).
81. Ischium, distal end, form: confluent with shaft or only slightly expanded (0); strongly expanded into distinct boot, with anterior and posterior projections (1). (Harris 1998:119).
82. Ischium, posteriorly-directed flange on iliac peduncle: absent (0); present (1). (New).
83. Femur, orientation of central axis of head to shaft in anterior view: approximately perpendicular (0); angled dorsally, resulting in an obtuse angle between the head and the shaft (1). (Harris 1998:121).
84. Femur, lateral distal condyle, form: bulbous (0); cone-shaped (1). (New).
85. Femur, medial epicondyle (=mediodistal crest), length: poorly developed or short (0); pronounced, extending 30% or more up the length of the femoral shaft (1). (Holtz et al. 2004:574).
86. Femur, fourth trochanter, form: robust or completely absent (0); present but reduced to a weak crest (1). (Harris 1998:126).
87. Femur, extensor groove on distal end, form: deep and narrow (0); shallow and broad (1). (Harris 1998:127).
88. Femur, ridge for cruciate ligaments in flexor groove, form: absent or indistinct (0); present and robust (1). (Harris 1998:128).
89. Tibia, lateral condyle separation from remainder of proximal end in proximal view: bulging from the main surface of the tibia (0); conspicuous narrowing between the body of the condyle and the main body of the tibia (1). (Modified from Azuma & Currie 2000:108).
90. Tibia, medial malleolus, medial expansion: only slightly expanded medially (0); expanded 9% or more the length of the tibia (1). (New).
91. Tibia, lateral malleolus, distal extension relative to medial malleolus: even with or extends slightly distally (0); extent beyond the medial malleolus 7% or more of the length of the tibia (1). (New).
92. Fibula, length relative to femur: greater than 70% (0); less than 70% (1). (New).
93. Astragius, height of ascending process relative to tibial length: less than 1/6 (0); between 1/6 and 1/4 (or greater than 1/4 in Compsognathidae) (1). (Harris 1998:135).
94. Scapulocoracoid, notch between scapular acromion process and coracoid: absent (0); present (1). (Currie & Carpenter 2000:68).
95. Coracoid, posteroventral process, length relative to the width of the glenoid: shorter (0); longer, process strongly hooked (1). (Sereno et al. 1996:28).
96. Scapula, acromion process, size: prominent (0); reduced or absent (1). (Holtz 2000:213).
97. Scapula, blade, length relative to minimum neck width: more than 7.5 (0); less than 7.5 (1). (Forster 1999:63).
98. Metacarpal 4: present (0); absent (1). (Sereno & Novas 1993).
99. Metacarpals, proximal articular ends, transverse width: less than minimum transverse shaft width (0); two times or more than minimum transverse shaft width (1). (New).

**APPENDIX 2: Data Matrix**

**OUTGROUPS**

**Herrerasaurus**

**Cololophyris**

**Tyrannotitan**

**Neovenator**

**Compsognathidae**

**INGROUP**

**Acrocanthosaurus**

**Maiasaura**

**Giganotosaurus**

**Eocarcharia**

**Gigantosaurus**

**APPENDIX 3 Scoring Sources**

**Herrerasaurus**: PVSJ 407 (original material and cast); Novas 1993; Sereno 1993; Sereno & Novas 1993.

**Cololophyris**: Colbert 1989; Rowe 1989; Bristowe & Raath 2004; Tykoski & Rowe 2004.

**Torvosaurus**: UUVP cast material; Galton & Jensen 1979; Britt 1991.


**Acrocanthosaurus**: OMNH 10146, OMNH 10147, NCSM 14345 (original material); Stovall & Langston 1950; Harris 1998; Currie & Carpenter 2000; Fransozia & Rowe 2005.

**Allosaurus**: UUVP/UMNH VP original and cast material (numerous specimen numbers, skull and forelimbs); Madsen 1976; Chure 2000, 2001.

**Carcharodontosaurus**: C. saharicus: SGM-Din 1 (neotype skull), SGM-Din 3, 4, 5 (cervical vertebrae), numerous UCR uncataloged elements; C. iguidensis: MNNG IUG 2 (holotype maxilla), MNNG IUG 3 (braincase), MNNG IUG 4 (lacrimal), MNNG IUG 5 (dentary), MNNG IUG 6, 7, 8, 9, 10 (isolated teeth) (original material); Storimer 1931, 1934; Rauhut 1995; Sereno et al. 1996; Larsson 2001; Brusatte & Sereno 2005, 2007.

**Eocarcharia**: MNN GAD 3, 4, 5, 6 (postorbital), MNN GAD 7, 8, 9 (maxillae), MNN GAD 10, 11 (frontal and prefrontal); MNN GAD 12, 13, 14 (teeth) (original material); Brusatte & Sereno 2006; Sereno & Brusatte 2008.

**Giganotosaurus**: MUCPv-CH1 (original material); Coria & Salgado 1995; Calvo 1999; Calvo & Coria 2000; Coria & Currie 2002.

**Maiasaura**: Coria & Currie 2006.

**Neovenator**: MUG 5470, 6348, 5470; BMNH R1001 (original material); Hutt et al. 1996; Hutt 1999 (unpublished thesis); Naish et al. 2001.

**Sinraptor**: IVPP 10600 (original material); Gao 1992; Currie & Zhao 1993.