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COMPARATIVE ASSESSMENT OF TYRANNOSAURID INTERRELATIONSHIPS

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SYNOPSIS We employ a new comparative method to four cladistic analyses of tyrannosaurid dinosaurs to identify root causes for differences between phylogenetic results. The comparative method is a three-step procedure that (1) adjusts competing hypotheses so they share equivalent taxonomic scope, (2) isolates the character data relevant to the common problem, and (3) divides relevant character data into shared and novel partitions. It is then possible to quantify the degree of similarity between character data using three indices (ancestor similarity index, character similarity index and character state similarity index).

The most parsimonious cladograms generated by the four analyses of tyrannosaurids appear fairly congruent, with two subclades present in all four analyses (*Albertosaurus* and *Gorgosaurus* versus *Daspletosaurus*, *Tarbosaurus* and *Tyrannosaurus*). A comparative examination of the underlying character data, however, highlights striking differences in character selection and significant differences in character state scores. Character selection and differences in scoring are root causes for phylogenetic incongruence. Comparative analysis reveals the existence of many data-level differences that remain largely obscured when comparison is limited to the most parsimonious cladograms.

KEY WORDS Tyrannosauridae, tyrannosaurid, comparative cladistics, taxonomic scope, character selection, data similarity indices

Contents

INTRODUCTION

Widespread use of quantitative cladistic procedures among morphology-based systematists has generated multiple partially overlapping datasets for various portions of the tree of life. Comparisons between analyses, if undertaken, are generally limited to examining the differences or similarities among most parsimonious cladograms (Sereno, 2009). Distorting the preferred cladogram from one hypothesis to another, for example, yields a quantitative measure of the additional homoplasy incurred by an opposing hypothesis.

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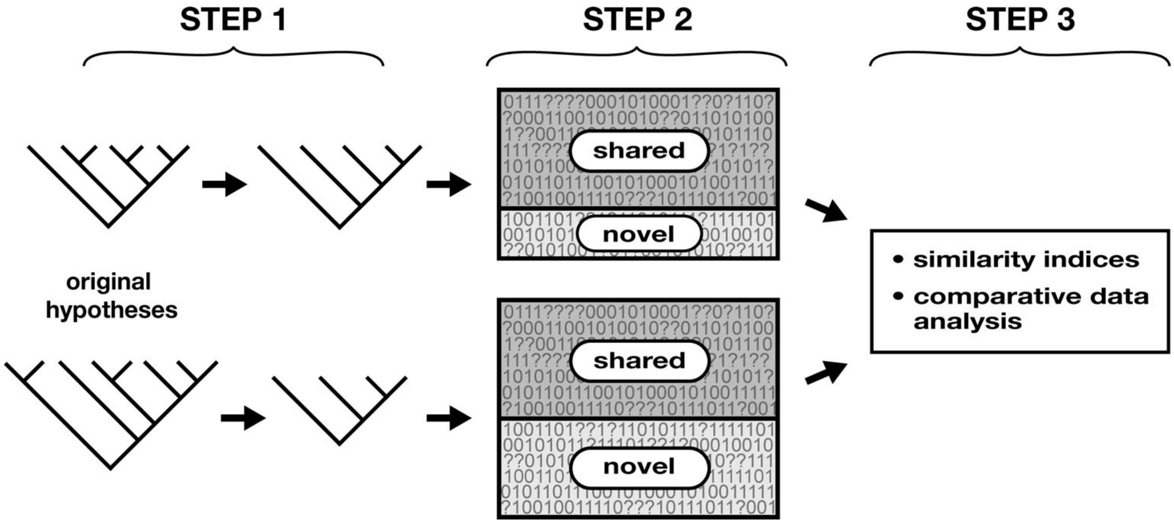


Figure 1 Graphical summary of the three principal steps in a data comparison between two hypotheses, which culminates in the calculation of data similarity indices and comparative data analysis (after Sereno 2009).

These *a posteriori* comparisons, nevertheless, are concerned with trees or cladograms – the end products of phylogenetic analysis. *A priori* comparisons involve character data, which generates most of the differences in phylogenetic results. Data-level comparisons are sometimes generated as one author critiques, character by character, the data assembled by another author for an overlapping phylogenetic problem. Character delineation, character selection and variant character state scoring loom as confounding factors in morphology-based studies (Poe & Wiens 2000; Rieppel & Kearney 2002, 2007; Sereno 2007, 2009). Character critiques can be selective or global in coverage; they can involve character revision, rejection or addition; they often cite character state scores for particular terminal taxa as erroneous.

They do not, however, yield quantitative, normalised comparisons comparable to those generated by *a posteriori* analysis (e.g. consistency index, tree length, decay index). Quantification of results is inhibited foremost by differences in terminal taxa, or what can be called the 'taxonomic scope' of an analysis (Sereno 2009). Some analyses use suprageneric taxa whereas others use species; some are broad scale whereas others consider relationships within a particular subclade. Thus, we are left to ponder how a particular pair of studies differs at the level of character data. How many characters are shared between any two analyses? Are scoring differences significant? Are assumptions about ancestral conditions the same?

Here we employ new methods in comparative cladistics (Sereno 2009; Fig. 1) to pinpoint fundamental differences between four hypotheses for tyrannosaurid dinosaurs that overlap in taxonomic scope (Holtz 2001; Currie *et al.* 2003; Holtz *et al.* 2004; Carr *et al.* 2005; Table 1). These competing analyses represent a relatively simple case study and include all analyses that have considered relationships among the best known species of tyrannosaurids. Few comparisons have ever been made between these studies. One of these studies (Holtz *et al.* 2004) includes a much broader range of non-tyrannosaurid taxa and characters; another (Carr *et al.* 2005) is limited to character data that can be observed in a new taxon under description. Results from these analyses concur regarding some species and conflict regarding others.

Effective comparison of morphology-based phylogenetic hypotheses requires the isolation and measurement of similarity (or difference) in character data between

Table 1 Phylogenetic definitions for Tyrannosauroidea and subgroups used in this paper.

Taxon	Phylogenetic definition	Definitional type
Tyrannosauroidea Osborn, 1906	The most inclusive clade containing *Tyrannosaurus rex* Osborn, 1905 but not *Ornithomimus edmontonicus* Sternberg, 1933, *Troodon formosus* Leidy, 1856, *Velociraptor mongoliensis* Osborn, 1924.	Stem
Tyrannosauridae Osborn, 1906	The least inclusive clade containing *Tyrannosaurus rex* Osborn, 1905, *Gorgosaurus libratus* Lambe, 1914, *Albertosaurus sarcophagus* Osborn, 1905.	Node
Tyrannosaurinae Osborn, 1906	The most inclusive clade containing *Tyrannosaurus rex* Osborn, 1905 but not *Gorgosaurus libratus* Lambe, 1914, *Albertosaurus sarcophagus* Osborn, 1905.	Stem

Phylogenetic definitions are available at: http://www.taxonsearch.org.
For background see Sereno (2005*b*) and Sereno *et al.* (2005).

Table 2 Profile of phylogenetic analyses that consider relationships within Tyrannosauridae.

Authors		Matrix				Character documentation				
No.	Analysis	Printed	e-Archived	No. ingroups	No. characters	Character listed	Character states listed	Original author citeds	Character description	Character figured (%)
1	Holtz 2001	+	—	12	111	+	+	—	—	0
2	Currie *et al.* 2003	+	—	7	77	+	+	+	—	0
3	Holtz *et al.* 2004	—	+	75	638	+	+	—	—	~5
4	Carr *et al.* 2005	—	+	7	31	+	+	—	—	~5

competing hypotheses. Our aim is, thus, to make a quantitative comparison between these studies that simultaneously evaluates similarity in ancestral (or outgroup) assumptions, character selection and character state scoring.

MATERIALS AND METHODS

Case study: Tyrannosauridae

We chose tyrannosaurid dinosaurs as a case study among many possibilities because many of the same species were used in four recent cladistic analyses (Holtz 2001; Currie *et al*. 2003; Holtz *et al.* 2004; Carr *et al.* 2005), which simplified the comparisons. These analyses vary considerably in taxonomic scope; Holtz *et al.* (2004), for example, included many other non-tyrannosaurid ingroups. Two of the studies have the same first author, which may well have enhanced overlap of character data. This case study encountered many of the usual hurdles in comparing morphological character data between competing hypotheses (Sereno 2007). The comparison that is the focus of this study, nevertheless, is limited to six species and less than 100 characters.

Tyrannosaurids are large-bodied theropod dinosaurs that are limited in time to the Late Cretaceous and in geography to Asia and North America (Holtz 2004). The clade is founded on *Tyrannosaurus rex*, a well-known species that thrived in North America just prior to the end-Cretaceous extinction. *Tarbosaurus bataar*, long thought to be most closely related to *T. rex*, and several other slightly older and generally slightly smaller-bodied species from North America (*Albertosaurus sarcophaghus, Daspletosaurus torosus, Gorgosaurus libratus*) complete the roster of species known from multiple articulated skeletons.

Tyrannosaurid taxa considered

Suprageneric taxa

The taxa Tyrannosauroidea, Tyrannosauridae and Tyrannosaurinae have been used and defined phylogenetically in various ways, and this historical usage has been logged, reviewed and posted on-line (Sereno 2005*a*, *b*; Sereno *et al.* 2005). We use 'Tyrannosauridae' to include all of the most familiar large-bodied species from Asia and North America (Table 1).

Genera

This paper is limited to relationships within Tyrannosauridae, the shared taxonomic scope of the four analyses under comparison. Six monotypic genera are present in nearly all of the four analyses and include *Gorgosaurus libratus*, *Albertosaurus sarcophagus*, *Alioramus remotus*, *Daspletosaurus torosus*, *Tarbosaurus bataar* and *Tyrannosaurus rex*.

Some authors (Holtz 2001; Carr *et al.* 2005) have regarded *Gorgosaurus* and *Tarbosaurus* as junior synonyms of *Albertosaurus* and *Tyrannosaurus*, respectively. Their generic distinction, however, seems warranted as long as some phylogenetic analyses fail to unite *Gorgosaurus* and *Albertosaurus* as closest relatives (Holtz 2001) and others insert genera between *Tarbosaurus* and *Tyrannosaurus* (Currie *et al.* 2003). We use *Gorgosaurus libratus* and *Tarbosaurus bataar* (or the genus alone) for these reasons.

The newly described tyrannosauroids *Dilong* (Xu *et al.* 2004), *Guanlong* (Xu *et al.* 2006), *Aviatyrannis* (Rauhut 2003*a*), *Eotyrannus* (Hutt *et al.* 2001) and *Appalachiosaurus* (Carr *et al.* 2005) lie outside Tyrannosauridae and were not considered in most of the analyses we compared. Several other poorly known genera, such as *Nanotyrannus* (Bakker *et al.* 1988; Carr 1999), *Alectrosaurus* (Mader & Bradley 1989; Currie 2000), *Stokesosaurus* (Chure & Madsen 1998; Foster & Chure 2000), *Dryptosaurus* (Carpenter *et al.* 1997) and *Bagaraatan* (Osmólska 1996; Holtz *et al.* 2004), are excluded for similar reasons.

Analyses compared

The four analyses here considered vary in outgroup assumptions, number of ingroups and characters, and character documentation (Table 2; Fig. 2A–D). Major topological differences between the four analyses include the placement of *Alioramus, Daspletosaurus* and *Tarbosaurus*, such that a strict consensus tree collapses all but *Albertosaurus* + *Gorgosaurus* (Fig. 2E). Holtz (2001) regarded *Alioramus* as a basal tyrannosauroid positioned outside Tyrannosauridae (as here defined). In a subsequent analysis, Holtz *et al.* (2004) regarded its position within Tyrannosauridae as equally parsimonious. *Daspletosaurus* has been positioned outside a clade composed of *Tarbosaurus* and *Tyrannosaurus* (Holtz 2001; Holtz *et al.* 2004) or outside a clade composed of *Alioramus* and *Tarbosaurus* (Currie *et al.* 2003). Finally, *Tarbosaurus* and *Tyrannosaurus* are regarded either as the closest of

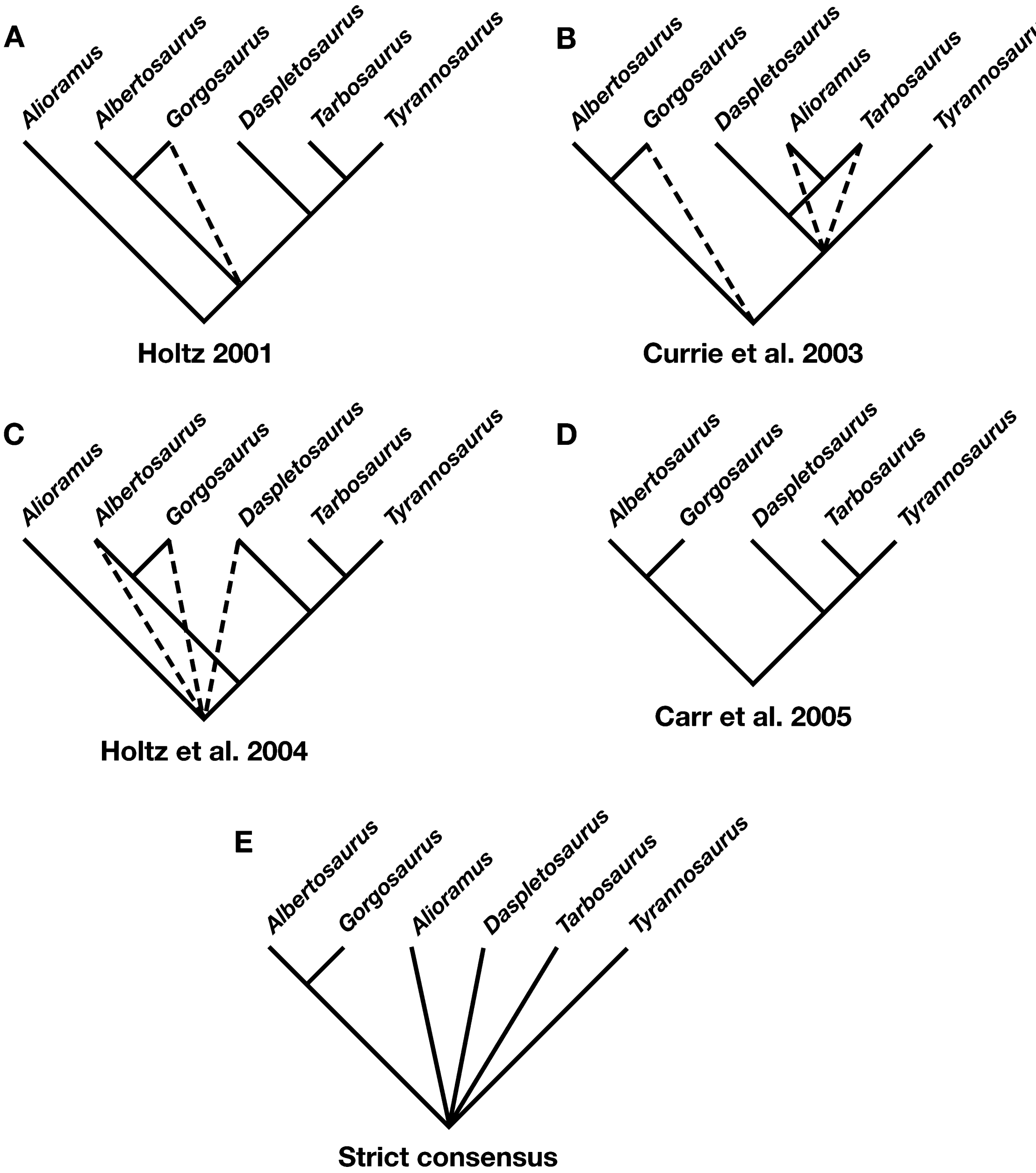


Figure 2 Cladograms (strict consensus) from analyses of Tyrannosauridae after reduction in terminal taxa. Dashed lines indicate collapse of structure with the addition of 2 steps. **A**, Holtz (2001) showing genera rather than species. **B**, Currie *et al.* (2003). **C**, Holtz *et al.* (2004) with *Alectrosaurus* removed and two equally parsimonious positions for *Alioramus* shown (dashed lines). **D**, Carr *et al.* (2005) with *Tyrannosaurus bataar* and *Albertosaurus libratus* referred to the genera *Tarbosaurus* and *Gorgosaurus*, respectively. **E**, Strict consensus tree for the hypotheses shown in A–D.

relatives and/or congeneric (Holtz 2001; Holtz *et al.* 2004; Carr *et al.* 2005) or as more distantly related (Currie *et al.* 2003).

Comparative method

Comparative cladistics

In morphology-based cladistics, character delineation, selection, coding and scoring tend to influence phylogenetic results more strongly than assumptions or options during phylogenetic analysis. Labeled the 'bête noire' of morphology-based cladistics, these *a priori* operations have generated a fierce critique and repeated calls for greater care, introspection and 'explicitness' (Pogue & Mickevich 1990; Stevens 1991; Patterson & Johnson 1997; Poe & Wiens 2000; Rieppel & Kearney 2002, 2007; Jenner 2004).

The aim of comparative cladistics is to lift the veil on these *a priori* operations by outlining simple standards to reduce unnecessary variation in character data and by providing the means to quantify the characterisation and comparison of character data (Sereno 2007, 2009). Taming the bête noire requires an understanding of the symbolic structure of character data and the ability to measure the magnitude of problems such as character selection and scoring.

The concept of 'taxonomic scope' is at the heart of data comparison (Sereno 2009). The taxonomic scope of a phylogenetic hypothesis is its potential synapomorphy space, as determined by its lower and upper boundaries – the most proximate outgroup taxon (lower) and the inclusiveness of ingroup taxa (upper). Because most hypotheses to be compared differ in taxonomic scope, the portion of one hypothesis that overlaps another – 'the shared taxonomic scope' of one hypothesis relative to another – must be ascertained to normalise data comparison. The character data that remains informative for the overlapping or shared portion of the hypotheses to be compared is termed the 'relevant' character data. Relevant character data can be compared in detail to determine how many characters are shared and how many have no counterpart in an opposing hypothesis. Shared character data, in turn, can be examined to determine similarity or differences in character states scores.

Data comparison, thus, is a three-step procedure (Fig. 1) that establishes shared taxonomic scope (step 1), isolates and then partitions relevant character data (step 2) and measures similarity between data sets by pinpointing their differences (step 3).

Data similarity indices

'Data similarity indices' measure the degree of similarity of (1) the character states of the comparable common ancestor (ancestor similarity index or ASI), (2) the characters used in respective analyses (character similarity index or CSI) and (3) the character states for shared data scored in comparable ingroup taxa (character state similarity index or CSSI) (Sereno 2009).

ASI is a measure of the proportion of similar character states in shared character data for the comparable common ancestor between two analyses:

$$\mathrm{ASI} = \frac{\mathrm{tcs} - (\mathrm{csc} + 0.5\,(\mathrm{csd}))}{\mathrm{tcs}}$$

where: tcs = total number of character states
csc = number of character state conflicts (e.g. 0 versus 1)
csd = number of character state disparities (e.g. 0 versus ?)

An ASI of 1.0 indicates identical character states in the comparable common ancestor for all characters that are shared between two analyses.

CSI is a measure of the proportion of shared character data between two analyses:

$$\mathrm{CSI} = \frac{\mathrm{sc}}{\mathrm{tc}}$$

where: sc = number of shared characters between two datasets
tc = total number of characters between two datasets

A CSI of 1.0 indicates complete overlap of character data between two analyses, an improbable circumstance with morphological data. As the proportion of shared data decreases relative to the pooled (or total) number of unique characters across two analyses, the CSI decreases from 1.0. The CSI, thus, is a measure of character selection.

CSSI is a measure of the proportion of shared character states in shared character data as scored in two opposing analyses:

$$\mathrm{CSSI} = \frac{\mathrm{tcs} - (\mathrm{csc} + 0.5\,(\mathrm{csd}))}{\mathrm{tcs}}$$

where: tcs = total number of character states
csc = number of character state conflicts (e.g. 0 versus 1)
csd = number of character state disparities (e.g. 0 versus ?)

A CSSI of 1.0 indicates total overlap of character state scores for the same characters between two analyses, an improbable circumstance with morphological data. The CSSI is expected to be significantly different from 1.0, when available material for sampled taxa is poorly known or described. It should approach 1.0 as observational variation is addressed. Character state scores for the same character may differ between analyses in two fundamental ways, other mitigating circumstances aside; states may show *disparity* in resolution differ in their *resolution* (e.g. ? versus 1) or may be scored in *conflict* (e.g. 0 versus 1). The penalty in the former case is 0.5 and in the latter case 1.0. For binary characters, an unknown character state (?) in the former case is operationally equivalent to polymorphism (0, 1), which differs from a single state score (0 or 1) by one-half (50%) (Sereno 2009).

COMPARATIVE ANALYSIS

Shared taxonomic scope

The first step in the comparative analysis is to define the boundaries of the phylogenetic problem under comparison. The boundaries, or *taxonomic scope*, of the problem is determined by specifying outgroup and ingroup terminal taxa. In this case, we are interested in the interrelationships between six monotypic tyrannosaurid genera (*Alioramus remotus, Gorgosaurus libratus, Albertosaurus sarcophagus, Daspletosaurus torosus*, *Tarbosaurus bataar, Tyrannosaurus rex*). We assume tyrannosaurid monophyly and are interested in character data that is informative within this clade. All six taxa are used in three of the analyses (Holtz 2001; Currie *et al.* 2003; Holtz *et al.* 2004; Fig. 2A–C); *Alioramus remotus* was not included in the fourth analysis (Carr *et al.* 2005; Fig. 2D), and character data was purposely limited to that which could be scored in a new taxon under study (*Appalachiosaurus*).

Because the taxonomic scope of the problem we have identified is the interrelationships between six monotypic tyrannosaurid genera (their generic names serving as proxy), some of the characters in the four analyses will be excluded as uninformative. That is, they are informative only when additional ingroups are present that extend beyond the taxonomic scope of interest. This is particularly true for Holtz *et al.* (2004), an analysis that included a broad array of non-tyrannosaurid ingroups.

Isolating relevant character data

We isolated relevant character data for our comparison by reanalysing the data with restrictions on ingroup and outgroup

Table 3 Original number of ingroups and characters are reduced to isolate comparable data in four analyses of Tyrannosauridae (see Table 4).

Authors		Ingroups		Characters		Indices	
No.	Analysis	Original	Reduced	Original	Reduced	CI	RI
1	Holtz 2001	14	6	111	42	0.83	0.76
2	Currie *et al.* 2003	7	6	77	34	0.93	0.90
3	Holtz *et al.* 2004	75	6	638	48	0.35	0.72
4	Carr *et al.* 2005	7	5	31	19	0.54	0.59

CI, consistency index; RI, retention index

taxa, using branch-and-bound and heuristic search options in PAUP* 4.0 (Swofford 2002).

Holtz 2001

The character data that is relevant (informative) to the problem circumscribed above can be isolated by removing all ingroup terminal taxa except the six cited tyrannosaurids and culling uninformative character data. Besides the six species of interest, an additional eight terminal taxa were scored. All of these are poorly known; one (*Siamotyrannus*) is probably not a tyrannosauroid (Rauhut 2003*b*; Brusatte & Sereno 2008); a second (*Shanshanosaurus*) is probably an immature specimen of *Tarbosaurus bataar* (Currie & Dong 2001); two more are undescribed ('Kirtland aublysodontine', 'Two Medicine tyrannosaurine'); the status of *Nanotyrannus* and *Maleevosaurus* remain controversial (Carr 1999; Currie 2000, 2003); and the final two are either known from very fragmentary material (*Aublysodon*) or are poorly described (*Alectrosaurus*; Currie 2000, 2003).

Of the 111 characters listed, Holtz acknowledged that only 87 are informative for the original set of taxa. When the ingroup was limited to the six identified tyrannosaurids, the number of informative characters dropped to either 43 (Ornithomimosauria or Maniraptora as outgroup) or 42 (all-zero outgroup), depending on the outgroups used. These 42 characters were informative for relationships among tyrannosaurids (Table 3).

Currie et al. *2003*

The relevant (informative) character data for the problem we circumscribed is easy to isolate, because the original ingroup taxa include only one taxon beyond the set of six species we have selected. If that additional taxon, *Nanotyrannus*, joins the cladogram between any of the six ingroup taxa selected, it would only subdivide rather than expand the synapomorphy space circumscribed by the six ingroup taxa. In that case, it could be left in the analysis as a unique ingroup taxon (Sereno 2009). *Nanotyrannus*, however, is shown as sister-taxon to *Tyrannosaurus rex* (Currie *et al.* 2003; Fig. 2B), which creates a node that lies outside the taxonomic scope of the problem under study. *Nanotyrannus*, in other words, must be removed.

Of the 77 characters listed by Currie *et al.* (2003), only 41 were informative as mentioned by the authors. The analysis was re-run without *Nanotyrannus* to check for additional characters that owed their informative status to the presence of this additional ingroup. Seven additional characters were uninformative when *Nanotyrannus* was removed, which reduced the relevant character data from 41 to 34 characters (see Table 3).

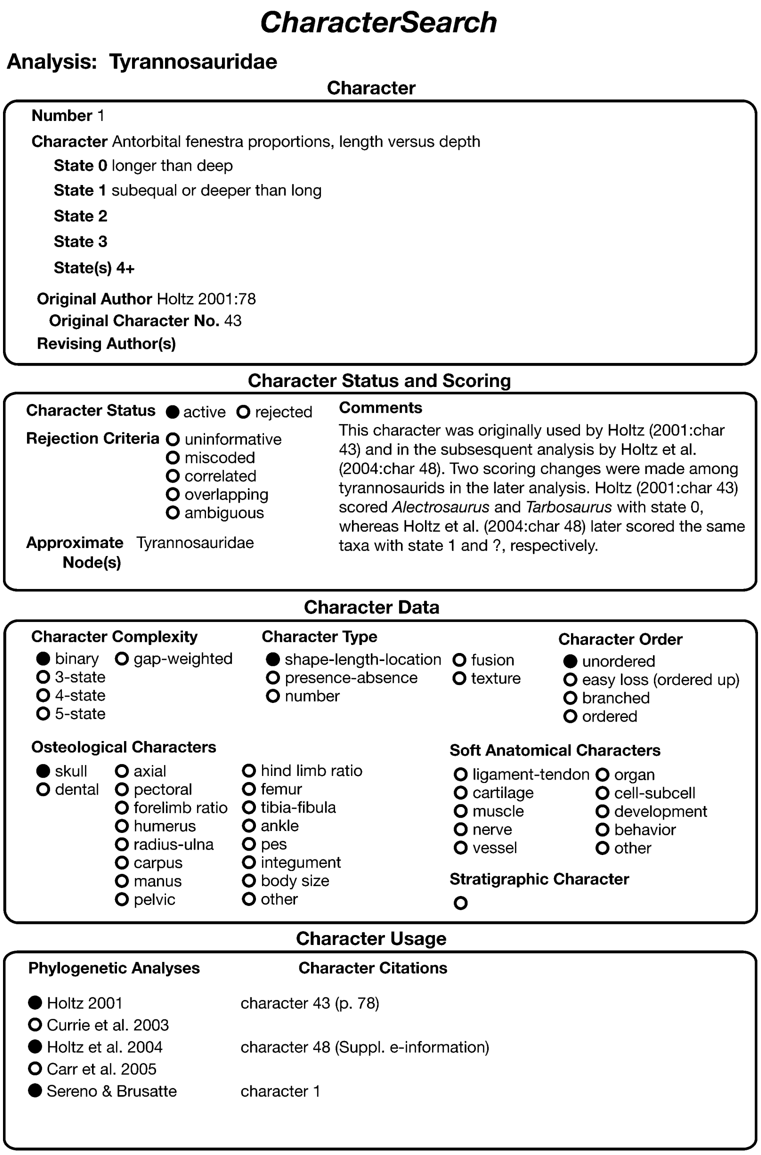
Holtz et al. *2004*

Holtz *et al.* (2004) considered tyrannosaurid interrelationships in the context of an analysis of basal tetanuran theropods, in which tyrannosaurids comprised a small portion of the 75 ingroup taxa. A total of 638 characters were scored with Herrerasauridae as the outgroup. Holtz *et al.* (2004) reported obtaining 2,544 most-parsimonious trees (MPTs) with a length of 2,444 steps (Consistency Index (CI) = 0.35; Retention Index (RI) = 0.72; Holtz *et al.* 2004: 94, fig. 4.20). It was not possible, however, to obtain their strict consensus cladogram from their matrix (available online: www.ucpress.edu/books/pages/2601001/2601001. supplement.html). A re-run of the data (with 61 of the 136 multistate characters ordered as indicated) yielded substantially less resolution, as might be expected given the inclusion of very incomplete taxa. Tree length was actually somewhat shorter than reported (2,436 steps or less), and 27 out of the 638 characters were uninformative. Herrerasauridae was the outgroup in the available matrix (rather than Sauropodomorpha as shown on their cladogram).

A strict consensus tree differed markedly from that given by Holtz *et al.* (2004: fig. 4.20):

(1) 'Ceratosauria' is paraphyletic (Coelophysoidea and Abelisauridae are successive stems, as found elsewhere; Carrano *et al.* 2002; Sereno *et al.* 2004).
(2) Tetanurae is an unresolved polytomy comprising Spinosauroidea and 13 genera, including many that were shown by Holtz *et al.* to lie within Coelurosauria (*Compsognathus, Sinosauropteryx, Nedcolbertia, Scipionyx, Proceratosaurus, Ornitholestes, Nqwebasaurus*).
(3) Neither Avetheropoda ('Carnosauria' + Coelurosauria) nor 'Carnosauria' are resolved (shown as labelled nodes on their cladogram).

For the purposes of this paper, however, we were concerned only with character data relevant to Tyrannosauridae. There were 12 tyrannosauroid genera in the analysis, six of which were the focus of this study. We re-analysed the data with ingroups limited to these six genera and with remaining tyrannosauroids and Ornithomiminae as outgroups. There were 78 informative characters and 141 minimum-length trees of 319 steps. The number of characters could be further reduced by excluding those that varied only among the outgroups. Using Holtz *et al.*'s terminal taxon



CharacterSearch

Analysis: Tyrannosauridae

Character

Number 1
Character Antorbital fenestra proportions, length versus depth
State 0 longer than deep
State 1 subequal or deeper than long
State 2
State 3
State(s) 4+
Original Author Holtz 2001:78
Original Character No. 43
Revising Author(s)

Character Status and Scoring

Character Status ● active ○ rejected
Rejection Criteria ○ uninformative ○ miscoded ○ correlated ○ overlapping ○ ambiguous
Approximate Node(s) Tyrannosauridae

Comments
This character was originally used by Holtz (2001:char 43) and in the subsequent analysis by Holtz et al. (2004:char 48). Two scoring changes were made among tyrannosaurids in the later analysis. Holtz (2001:char 43) scored *Alectrosaurus* and *Tarbosaurus* with state 0, whereas Holtz et al. (2004:char 48) later scored the same taxa with state 1 and ?, respectively.

Character Data

Character Complexity
● binary ○ gap-weighted
○ 3-state
○ 4-state
○ 5-state

Character Type
● shape-length-location ○ fusion
○ presence-absence ○ texture
○ number

Character Order
● unordered
○ easy loss (ordered up)
○ branched
○ ordered

Osteological Characters
● skull ○ dental
○ axial ○ pectoral ○ forelimb ratio ○ humerus ○ radius-ulna ○ carpus ○ manus ○ pelvic
○ hind limb ratio ○ femur ○ tibia-fibula ○ ankle ○ pes ○ integument ○ body size ○ other

Soft Anatomical Characters
○ ligament-tendon ○ cartilage ○ muscle ○ nerve ○ vessel
○ organ ○ cell-subcell ○ development ○ behavior ○ other

Stratigraphic Character
○

Character Usage

Phylogenetic Analyses	**Character Citations**
● Holtz 2001	character 43 (p. 78)
○ Currie et al. 2003	
● Holtz et al. 2004	character 48 (Suppl. e-information)
○ Carr et al. 2005	
● Sereno & Brusatte	character 1

Figure 3 The first of 85 character records in the file 'Tyrannosauridae' in the database *CharacterSearch* used for data characterisation (Sereno 2009). This simple database facilitates the logging of relevant character information, generates simple output files and figures (see Fig. 4) and can be rendered web-accessible for flexible data exploration.

Ornithomiminae as the sole outgroup, we obtained the same tyrannosaurid tree with 48 characters (17 of which are ordered). These 48 characters comprised the relevant data for comparison (Table 3).

Carr et al. *2005*

Five out of the six tyrannosaurid genera we chose were included among ingroup taxa (no data was presented for *Alioramus*). Three additional fragmentary taxa were included (*Shanshanosaurus, Dryptosaurus, Appalachiosaurus*), although only the latter two were included on the cladogram. Carr *et al.* (2005) scored 31 characters and used 12 outgroups (some quite remote from Tyrannosauroidea). They presented an outgroup constraint tree and reported a single minimum-length tree of 102 steps. One fragmentary taxon (*Shanshanosaurus*, possibly a juvenile individual of *Tarbosaurus bataar*) must be removed to obtain a tree consistent with that figured by Carr *et al.* (2005: fig. 21). Only 25 out of 31 characters were informative. Re-analysis of the data with ingroup taxa restricted to those of interest (Fig. 2D) left 19 informative characters (Table 3).

Data compilation

Character search

To organise and analyse the relevant character data that we isolated, we used a prototype of a database application called *CharacterSearch* (Sereno 2004, 2009). Slated for on-line access, *CharacterSearch* facilitates the compilation of character 'records', which include fields for the character and its character states (Fig. 3), as well as information used during data characterisation (such as character structure, type, authorship, anatomical location and use among competing analyses; Fig. 4). This application facilitates rapid location of character statements, sorting in innumerable ways and tracking of character data across analyses.

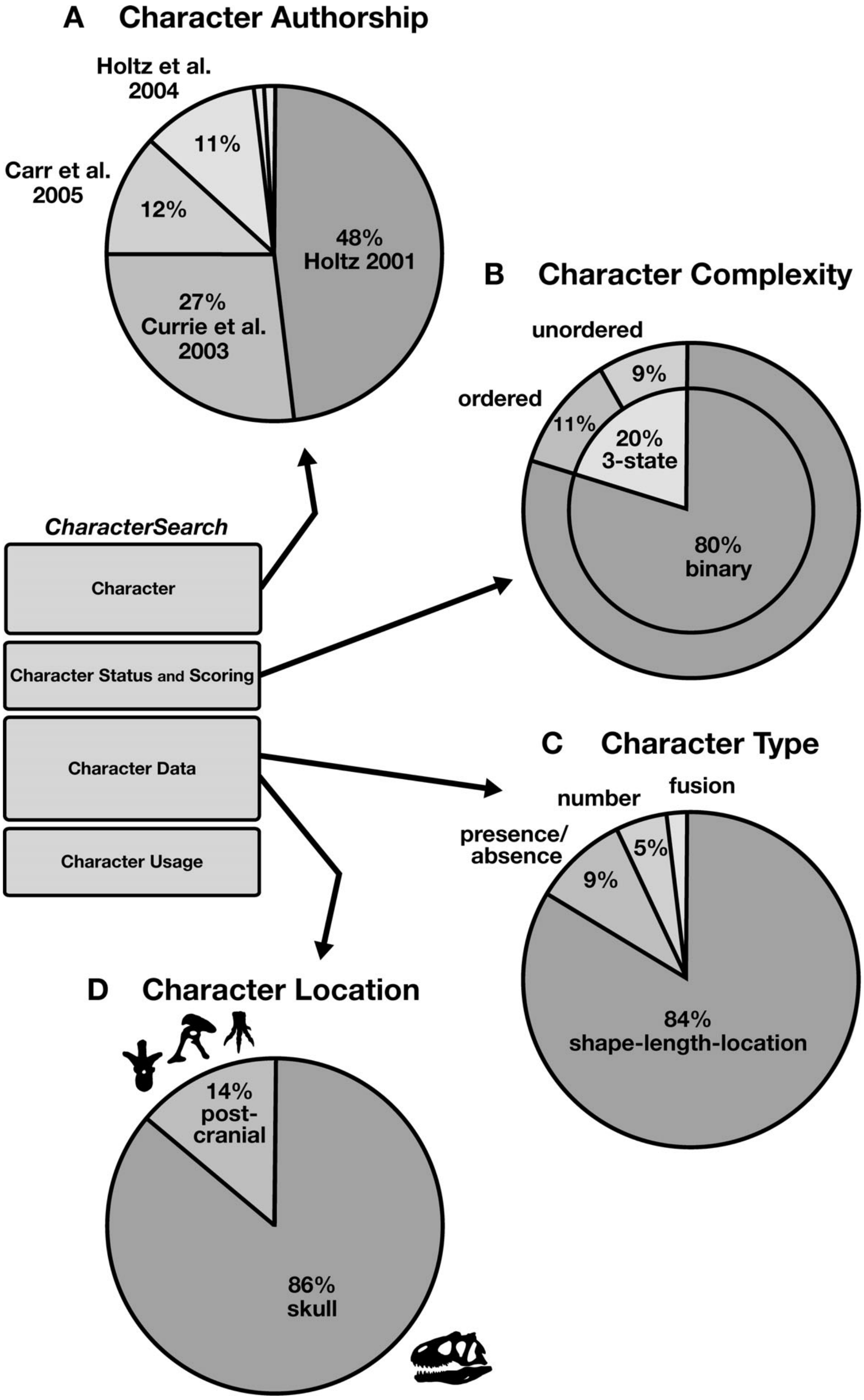


Figure 4 Pie charts summarising aspects of the 85 character statements that compose the relevant data in the comparative analysis (see Appendix). **A**, character authorship. **B**, character complexity. **C**, character type. **D**, character location.

Data characterisation

Characters

There are 85 unique characters among the four analyses that are informative for determining the interrelationships of the six tyrannosaurids (see Appendix). A pie chart showing the original authorship of character data shows the contribution each analysis made to the total pool of unique characters (Fig. 4A). Approximately half of the character data (48%) was used in the first analysis of tyrannosaurid relationships (Holtz 2001). Original authorship for the remaining character data is split among the other three analyses. Earlier studies that focused on higher-level relationships of theropods rather than the relationships of tyrannosaurids in particular (Gauthier 1986; Harris 1998) each contributed one character (1%).

Table 4 Informative characters in four analyses for evaluating phylogenetic relationships between *Alioramus, Gorgosaurus*, *Albertosaurus*, *Daspletosaurus*, *Tarbosaurus* and *Tyrannosaurus*.

		States/ordering (number, %)			
Analysis	Characters	2	≥3	Order	Characters
Holtz 2001	42	26 (62%)	16 (38%)	13 (81%)	12^{λ}, $\underline{23}^{*}$, $\underline{30}^{*}$, $\underline{40}^{\lambda}$, 41^{λ}, **42**, 43^{*}, $\underline{44}^{*}$, 45, $\underline{47}^{\lambda}$, 49^{*}, 50^{λ}, **51**, 52, 53^{λ}, **54**, 55^{*}, 56^{λ}, 57^{λ}, 60^{*}, $\underline{61}$, $\underline{62}^{*}$, 63^{λ}, 64^{*}, 65^{λ}, 66^{λ}, 67^{*}, 68, **69**, 70^{λ}, 71^{*}, 72^{*}, 74^{λ}, 75^{*}, 79^{*}, 80^{*}, 81^{*}, 82^{*}, 83^{*}, $\underline{84}^{*}$, $\underline{85}^{*}$, 86^{*}
Currie *et al.* 2003	34	29 (85%)	5 (15%)	0	7, 8, **9**, 14, 16, 18, 19, 20, 21, 22, **23**, **24**, 25^{*}, 27, 28^{*}, **30**, 31^{λ}, 32, 35^{*}, 38^{*}, 39^{λ}, 40^{λ}, 43^{λ}, 44, 45^{λ}, 47^{λ}, 48, 56, 57, 59, 60, 63^{λ}, 74^{λ}, 77
Holtz *et al.* 2004	48	31 (65%)	17 (35%)	15 (88%)	$\underline{32}^{*}$, 38^{*}, $\underline{39}^{\lambda}$, 42^{λ}, 43, 48^{*}, 53^{*}, $\underline{55}^{\lambda}$, 56^{λ}, 66^{*}, **69**, 70, 71^{λ}, 72^{λ}, **74**, $\underline{75}^{*}$, $\underline{86}$, $\underline{87}^{*}$, 101^{λ}, 104, 108^{λ}, 109^{*}, 114^{*}, 126, 132, 141^{λ}, $\underline{146}$, $\underline{147}^{*}$, $\underline{\mathbf{152}}$, $\underline{153}^{*}$, 157^{λ}, 158^{*}, 159^{*}, 190^{*}, 202^{λ}, 203^{λ}, 219, 224^{*}, $\underline{228}^{\lambda}$, $\underline{249}$, 309^{*}, 386^{*}, $\underline{457}^{*}$, 485^{*}, 489, $\underline{513}^{*}$, $\underline{534}^{*}$, 621
Carr *et al.* 2005	19	10 (53%)	9 (47%)	0	**1**, 2^{λ}, **5**, **6**, 7^{λ}, 8, 9, 10^{λ}, 11, 12, 14, 15, **16**, 17, 18, 19, 29^{*}, 30^{λ}, 31

Ordered characters are underlined.

Symbols: *, shared by two analyses; $^{\lambda}$, shared by three analyses; **bold**, shared by four analyses. Note that the character listed above as 386 in Holtz *et al.* (2004) seems to have been inadvertently scored in their matrix as character 385.

A pie chart for character structure shows that most (80%) are binary (Fig. 4B). The remaining 3-state characters (20%) are roughly evenly split between ordered and unordered. A few of the characters were multistate as published but binary when re-analysed with pruned ingroup taxa.

Shape-length-location characters dominate character type (84%; Fig. 4C), and cranial characters (86%) are far more common than postcranial characters (14%) (Fig. 4D). The paucity of postcranial features most probably reflects a longstanding bias among systematists favouring the skull as well as the rarity of articulated skeletons.

Missing data

Five of the six shared taxa (*Tyrannosaurus*, *Tarbosaurus*, *Daspletosaurus*, *Albertosaurus*, *Gorgosaurus*) are positively coded for all phylogenetically informative characters in the studies of Holtz (2001), Currie *et al.* (2003), and Holtz *et al.* (2004). Substantial missing data, by contrast, is present for *Alioramus*. In the analysis of Currie *et al.* (2003), this taxon is positively coded for only 10 of the 34 relevant characters (71% missing data). In the analysis of Holtz *et al.* (2004), *Alioramus* is positively coded for 29 of the 50 informative characters (42% missing data).

This large amount of missing data is partially responsible for the instability of *Alioramus* in the analysis of Holtz *et al.* (2004), where it is positioned either as a basal tyrannosaurid or sister-group to *Tarbosaurus* + *Tyrannosaurus*. Ironically, *Alioramus* is more stable in the analysis of Currie *et al.* (2003), which includes substantially more missing data. In either case, *Alioramus* has little effect on the relationships between the other five ingroup taxa. When *Alioramus* is removed, the relative relationships of the other five taxa remain unchanged in both analyses.

Data comparison

As outlined above, we re-analysed the data in the four analyses to isolate the informative partition for the interrelationships between six species of the genera *Alioramus, Gorgosaurus, Albertosaurus, Daspletosaurus, Tarbosaurus* and *Tyrannosaurus*. The reduction of taxa and characters from the original analysis is indicated in Table 3, with results shown in Figure 2A–D. Specific characters in support of these cladograms are listed as originally numbered in Table 4.

Comparable common ancestor

The four analyses employ different outgroups. Holtz (2001) used an all-zero outgroup, although he claimed it was based on the basal coelurosaurs *Scipionyx*, *Coelurus* and *Ornitholestes*. Currie *et al.* (2003) used the basal tetanuran *Allosaurus*, while Carr *et al.* (2005) used a suite of theropods tied to a constraint tree. Holtz *et al.* (2004) used *Herrerasaurus*, although his ingroup included a number of taxa closer to tyrannosaurids such as *Allosaurus*. It is unclear how different outgroup assumptions affect the polarisation of character data in opposing hypotheses. How different is the comparable common ancestor for shared character data?

An exact comparison between two hypotheses necessitates the isolation of the comparable common ancestor, which includes the character states for characters used by both hypotheses. An ancestor similarity index can be calculated, which measures the proportion of shared character states for shared characters. In the four hypotheses under comparison, this is most easily accomplished between Holtz (2001) and Currie *et al.* (2003), the former employing an all-zero outgroup and the later using *Allosaurus*.

In the original dataset of 77 characters (Currie *et al.* 2003), 13 characters for *Allosaurus* are scored with a character state other than 0: two are scored as unknown (?) and 11

Table 5 Character state variation in 22 characters across the four analyses considering tyrannosaurid interrelationships.

		Taxa (character state scores)					
Character number		*Ali*	*Gor*	*Alb*	*Das*	*Tar*	*Tyr*
1	h43					0	
	H48					1	
2	h40	?			1		
	H39	0			2		
4	h42				0		
	C30, H43				1		
11	C38				1		
	H66				0		
12	h48	?				0	0
	H56	0				1	1
	C40	1				1	0
15	h60	0		0			0
	H109	1		1			1
21	h51, H69, c6				0		
	C24				1		
23	h53, H71		1		1		
	c7		0,1		0,1		
24	C23				1		
	h54, H74, c5				0		
33	h56, H101	0					
	C46	?					
34	h57		0				
	H108, C47		1				
42	h61	1					
	H86	0					
44	h63, H157				0		
	C45				1		
45	h64	0					
	H158	1					
52	H153			1	1		
	c13			0	0,1		
55	h70, H171				0		
	C43				1		
61	h65, H202				0		
	C63				1		
62	C70	?	1	1	1		
	H159	0	0	0	0		
63	h66, H203	0					
	C12	1					
69	h74	0				1	
	C74	?				1	
	H230	0				0	
73	h79	0					
	H263	?					
74	h80				1	1	1
	H309				0	0	0

These 22 characters exhibit character state disparity (unresolved versus a resolved state), character state conflict (conflicting resolved states) or both. Character numbers in the first column correspond to those in the character list (see Appendix). Character numbers in the second column correspond to those in the original analyses (letter designation indicates author, see key below). Character states listed under the six tyrannosaurid genera (taxon abbreviations below) correspond to character states in the character list (See Appendix). Several characters listed above exhibit character state mismatch between analyses (where equivalent states were assigned different character state numbers); these have been renumbered following the character list (See Appendix). Abbreviations: c, Carr *et al.* 2005; C, Currie *et al.* 2003; h, Holtz 2001; H, Holtz *et al.* 2004; *Ali*, *Alioramus*; *Gor*, *Gorgosaurus*; *Alb*, *Albertosaurus*; *Das*, *Daspletosaurus*; *Tar*, *Tarbosaurus*; *Tyr*, *Tyrannosaurus*.

are scored as derived (1). However, only 10 of the 77 characters are shared between these two hypotheses (Tables 5, 6), three of which (characters 25, 30, 35) are assigned different character states. These represent positive character state differences (0 versus 1) referred to as character state 'conflict' (Sereno 2009). The ancestor similarity index (ASI) is 0.70 (seven identical states out of 10 compared: see Materials and Methods, above). This indicates a 30% difference in character state scores for the ancestral condition, a proportion that is cause for concern. In this case, however, re-analysis of the data in Currie *et al.* (2003) with an all-zero ancestor in place of *Allosaurus* does not alter the most parsimonious cladogram. There exists, nevertheless, significant variation in the ancestral condition for shared characters between these two competing hypotheses.

Character selection

We tabulated all informative characters used by the four analyses to evaluate relationships among the six tyrannosaurids considered. There are 85 such characters (see Appendix), although no single analysis has more than about half of these (Table 4). The remarkable outcome of this tabulation is that there are only four informative characters shared by all four analyses for the taxa of concern (Table 4, character numbers in bold). Furthermore, less than half of the characters are shared by at least three of the four analyses and many characters are only used in a single analysis. Character selection, thus, is likely to play a major role in generating differences in phylogenetic results.

A few characters were rendered uninformative by their particular character state scores in a given analysis and, thus, are not listed in Table 4. The size of the posterior surangular foramen, for example, was used by all four analyses but is informative only in three; the uniform coding of this character among ingroup tyrannosaurids by Currie *et al.* (2003) rendered it uninformative. The focus here on informative characters is appropriate, as only they carry phylogenetic information relevant to ingroup relationships.

Table 6 Calculation of shared character index (CSI) between analyses.

Analyses compared	No. raw shared characters	Shared relevant characters	No. shared relevant characters	Total no. relevant characters	CSI
h vs C	15	3, 4, 13, 21, 24, 34, 49, 55, 61, 74	10	66	0.15
h vs H	40	1–5, 13, 14, 20–22, 24, 27, 34, 36, 37, 42–45, 49, 55, 56, 61, 63, 66, 68, 70, 74, 76, 78, 81–83	33	57	0.58
h vs c	8	2, 4, 20–22, 24, 49, 70	8	53	0.15
C vs H	19	2, 4, 9, 11–13, 19, 21, 24, 34, 49, 55, 61	13	69	0.19
C vs c	6	4, 7, 21, 24, 49	5	48	0.10
H vs c	9	2, 4, 20–22, 24, 49, 70	8	59	0.14

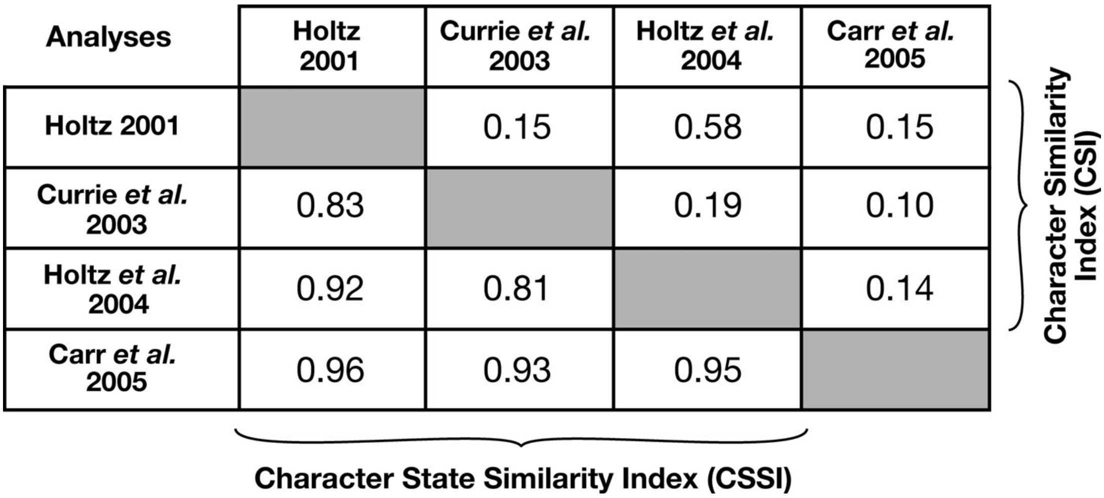
The CSI is the number of shared relevant characters divided by the total number of relevant characters in a comparison between two analyses. Shared relevant characters are numbered as in the Appendix. Abbreviations: c, Carr *et al.* 2005; C, Currie *et al.* 2003; h, Holtz 2001; H, Holtz *et al.* 2004.

To quantify character selection, we use the character similarity index (CSI: see Materials and Methods, above), or the number of shared informative characters divided by the pooled number of informative characters in a comparison between two analyses. This index ranges from 1.0, when the same characters are used by two analyses, to a fraction of unity, when the characters selected overlap to a lesser degree. The tabulation of this index for the six possible pairwise comparisons of the four analyses is given Table 6 and Figure 5 (upper right cells).

The results show remarkable disparity in character selection between analyses. The greatest similarity in character data is between the two analyses with Holtz as first author, the latter of which (Holtz *et al.* 2004) may have included a version of the data in the former (Holtz 2001). Yet even here, character similarity falls short of 60%, a remarkable finding. The other pairwise comparisons show very low character similarity ranging from 14–19% (CSI = 0.14–0.19) (Figure 5, upper right cells). Some disparity is to be expected: Currie *et al.* (2003) only used cranial characters, while Carr *et al.* (2005) only used characters that could be scored in the new tyrannosaurid *Appalachiosaurus*. Most of the composite list of informative characters, nevertheless, are cranial (86%), and *Appalachiosaurus* preserves many parts of the skull. Thus, the amount of character dissimilarity must be reflective of the early stage of analysis of tyrannosaurid relationships, when insufficient attention has been paid to available character data. The disparate nature of the character data in these analyses is invisible when comparisons are limited to the phylogenetic trees each dataset generates.

Character state scoring

Another source for conflicting results is differential in character state scores for characters used by more than a single analysis. We tabulated all such character state discrepancies across all four analyses for all informative characters (Table 5). The remarkable outcome of this tabulation is that there are 22 characters that show a total of 35 variant character state scores from one analysis to another. Most of these discrepancies (80%) involve character state



Analyses	Holtz 2001	Currie *et al.* 2003	Holtz *et al.* 2004	Carr *et al.* 2005
Holtz 2001		0.15	0.58	0.15
Currie *et al.* 2003	0.83		0.19	0.10
Holtz *et al.* 2004	0.92	0.81		0.14
Carr *et al.* 2005	0.96	0.93	0.95	

Figure 5 Pairwise comparison betweem four analyses measuring character selection and character state choice. Character Similarity Index (CSI: upper right cells) measures the percentage of shared character data between two analyses (see Table 6). Character State Similarity Index (CSSI: lower left cells) measures scoring differences (character state disparity, conflict) in shared character data between two analyses (see Table 7). Comparisons are limited to those characters that are informative for the common phylogenetic problem (see Table 4).

Table 7 Calculation of shared character state index (CSSI) between analyses.

Analyses compared	Shared informative characters	Shared informative character states	Character state conflict	Character state disparity	Character state similarity sum	CSSI
h vs C	10	60	9	3	49.5	0.83
h vs H	33	198	15	3	181.5	0.92
h vs c	8	48	0	2	47.0	0.96
C vs H	13	78	13	3	63.5	0.81
C vs c	5	30	2	0	28.0	0.93
H vs c	8	48	1	3	45.5	0.95

The shared character state index is the total number of identical character states minus the sum of the number of character state conflicts plus 0.5 times the number of disparate character states divided by the total number of shared informative character states (character state disparity and conflict are listed individually in Table 5).

Abbreviations: c, Carr *et al.* 2005; C, Currie *et al.* 2003; h, Holtz 2001; H, Holtz *et al.* 2004.

conflict (e.g. 1 versus 0) rather than character state disparity (20%).

To quantify similarity in character states, we use the character state similarity index (CSSI: see Materials and Methods, above), or the sum of the number of identical character states (plus 0.5 times the number of ? versus positive state pairings) divided by the total number of shared character states. This index ranges from 1.0, when the same characters in two analyses have exactly the same character states, to a fraction of unity, when character state choice overlaps to a lesser degree. The tabulation of this index for the six possible pairwise comparisons of the four analyses is given in Table 7 and Figure 5 (lower left cells).

The results show significant disparity in character state scores between analyses, varying from 0.81 to 0.96. Analyses that share the greatest number of character states (and thus are more effectively compared) include 198 character states for Holtz (2001) versus Holtz *et al.* (2004) and 78 character states for Currie *et al.* (2003) versus Holtz *et al.* (2004) (Table 7, lines 2 and 4). In the former pair of analyses with Holtz as first author, 8% of the character states (CSSI = 0.92) for the same characters in the same taxa are scored with a different state. This significant discrepancy in character state scoring may contribute to differing results but, unless isolated, would go unnoticed. In the latter comparison involving Currie *et al.* (2003) and Holtz *et al.* (2004), the shared character state index is 0.81, suggesting that 19% of the character state scores for the same characters in the same taxa differ in some significant manner. This is an unsettling amount of scoring differences between studies.

We swapped conflictive character state scores between analyses as one way to test the significance of these scoring differences. We, thus, re-analysed the data in Currie *et al.* (2003) using character state scores from Holtz *et al.* (2004) for states that differed between the analyses (Fig. 6A). We then performed a reciprocal procedure for the analysis of Holtz *et al.* (2004), substituting the conflictive character state scores from Currie *et al.* (2003) (Fig. 6B). This is a relatively weak test, as the original datasets yielded results that were similar in many regards.

Re-analysis of Currie *et al.* (2003) with swapped states failed to resolve the unique *Tyrannosaurus* + (*Daspletosaurus* + *Tarbosaurus*) topology in the original analysis (Fig. 6A) but instead linked *Tyrannosaurus* and *Tarbosaurus* as recovered by Holtz *et al.* (2004). Four characters that were not informative in the original analysis (characters

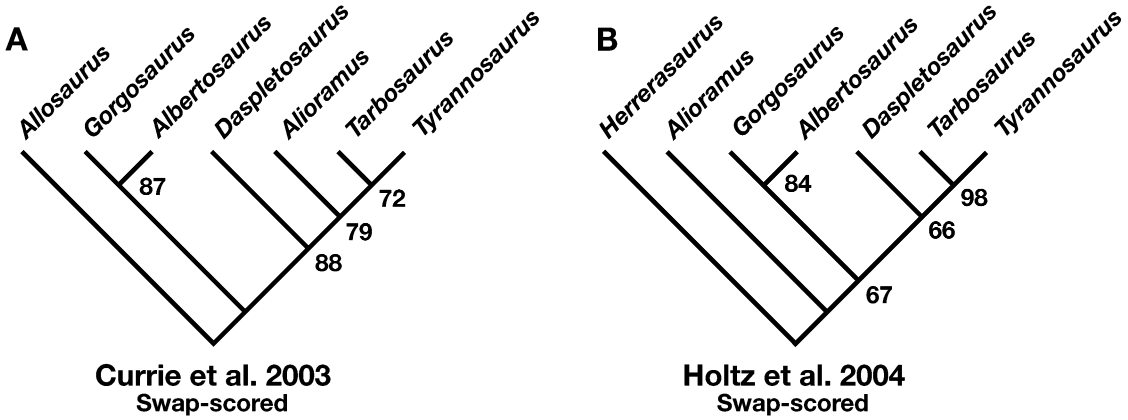


Figure 6 Re-analysis of relevant character data in a pair of opposing analyses after swapping discordant character state scores. **A**, minimum-length tree from re-analysis of Currie *et al.* (2003) after swapping in conflictive character state scores from Holtz *et al.* (2004). **B**, minimum-length tree from re-analysis of Holtz *et al.* (2004) after swapping in conflictive character state scores from Currie *et al.* (2003).

12, 36, 70, 73) are informative when using the character state scores in Holtz *et al.* (2004). These eight informative characters are shared between the analyses, two of which (characters 23, 70) are unequivocal synapomorphies uniting *Tarbosaurus* and *Tyrannosaurus*. When the same procedure is applied to the analysis of Holtz *et al.* (2004), tree topology does not change from the original analysis (Fig. 6B); *Tarbosaurus* and *Tyrannosaurus* are still recovered as sister-taxa with *Daspletosaurus* their sister-taxon. However, the character state scores adopted from Currie *et al.* (2003) alter the distribution of four characters (56, 74, 159, 202) that were previously synapomorphies uniting *Tarbosaurus* and *Tyrannosaurus*.

Conclusions

Cladistic analysis of morphological data has greatly increased knowledge of dinosaur phylogeny over the past 20 years. When overlapping phylogenetic analyses differ, nevertheless, there is usually little understanding of the root causes underlying different results. In discussing the current state of metazoan phylogenetics, Jenner (2004: 296) lamented 'the myriad hidden details in which published. . .cladistic analyses differ from each other prevent at this time any straightforward conclusion about the relative merit of the different cladogram topologies generated by these studies.' In what might be called 'Jenner's paradox', years of diligent logging and quantitative analysis of character data has somehow left us in a situation where we are unable to effectively evaluate different results.

In the case study we present, marked discrepancies in the ancestral condition, character selection and character state scoring play significant roles in generating the observed differences in phylogenic results. Differential character selection is strong and renders incomparable much of the original character data. For the data partition that is shared between any two hypotheses, differences in character state scores is significant and has important phylogenetic effects. Variation in one of every four character states for shared characters in Currie *et al.* (2003) and Holtz *et al.* (2004) is a startling revelation. Molecular sequence data has its own distinctive roster of comparative limitations. Yet, imagine a readily-aligned gene for a species that is being sequenced in parallel in two labs. The results show a 30% divergence in base pairs that is due simply to differences of opinion, error, or some unknown combination of the two. Would the method go unchallenged?

The first step in any solution to 'Jenner's paradox' – i.e. the increasing disparity in character selection and scoring between ever larger morphology-based cladistic analyses – is more rigorous comparison of alternative datasets. As the sheer number of characters and analyses expand, we need efficient methods for isolating and measuring key differences in character data between analyses. Once these differences are laid bare, the path to greater consensus is clear: (1) reduce character variation at the outset by adopting minimal standards for morphological characters (Sereno 2007); (2) cite and defend the exclusion of any relevant character data used in competing analyses; (3) cite and defend the adoption of character state scores that are at variance with those in competing analyses.

The comparative results for tyrannosaurid analyses that show marked variation in character selection and scoring should give morphologists pause. Until the comparative methods employed here are facilitated by appropriate software, their application will probably be limited (Sereno 2009). Most competing cladistic analyses will continue to be compared by *a posteriori* assessment of nodal support, and the scale of the discrepancies in the underlying data will remain largely unappreciated. Isolating, measuring and resolving marked variation in character selection, coding and scoring, nevertheless, constitutes the frontier for future research on tyrannosaurid interrelationships and for morphology-based phylogenetics in general.

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APPENDIX: CHARACTER LIST

Eighty-five character statements are listed below that were used in the four analyses being compared (Holtz 2001; Currie *et al.* 2003; Holtz *et al.* 2004; Carr *et al.* 2005). The list is limited to character statements from those analyses that are informative for relationships between the six tyrannosaurids being considered (*Alioramus remotus, Gorgosaurus libratus, Albertosaurus sarcophagus, Daspletosaurus torosus*, *Tarbosaurus bataar, Tyrannosaurus rex*). The original author for each character statement is indicated in parentheses.

For uniformity and clarity, many of the characters statements were edited to conform to character standards, in which the most general locator is positioned first, variables are identified and variable qualifiers are removed from character states (Sereno 2007). Character statements 2 and 22, which we list as formulated, mix absence with transformational character states. Our purpose in this appendix is to compile all of the relevant characters used in these analyses. We do not necessarily endorse all of these characters nor consider the list exhaustive for the problem under consideration.

Cranial

1. Antorbital fenestra proportions, length versus depth: longer than deep (0); subequal or deeper than long (1). (Holtz 2001)
2. Maxilla, flange enclosing anterior corner of the antorbital fossa, strength: absent (0); rudimentary crest (1); flange (2). (modified from Holtz 2001)
3. Maxillary fenestra, size relative to the eyeball-bearing portion of orbit: less than 50% (0); approximately 66% (1). (Holtz 2001)
4. Maxillary fenestra, anteroposterior location: separated from (0), or approaches (1), anterior margin of antorbital fossa. (Holtz 2001)
5. Maxilla, form of alveolar margin: straight (0); slightly convex (1); strongly convex (1). (Holtz 2001)
6. Maxilla, tooth count: 18 (0); 14–17 (1); 13 or fewer (2). (Holtz 2001; modified by Holtz *et al.* 2004)

7. Maxilla, ventral margin of antorbital fossa: present (0); absent (1). (Currie *et al.* 2003)
8. Maxilla, depth of palatal shelf for palatine: shallow (tooth roots forming bulge) (0); deep (obscuring alveoli) (1). (Currie *et al.* 2003)
9. Maxilla, promaxillary fenestra, exposure in lateral view: obscured (by ascending ramus of maxilla) (0); exposed (1). (Currie *et al.* 2003)
10. Maxillary–nasal suture, form: smooth groove (0); interlocking transverse ridges (1). (Currie *et al.* 2003)
11. Nasal posterolateral lacrimal process: present (0); absent (1). (Currie *et al.* 2003)
12. Nasal posterior suture, length of lateral process relative to medial process: subequal (0); longer (1). (Holtz 2001)
13. Nasal, width over snout: expanding posteriorly (0); pinched to a narrower width (1). (Holtz 2001)
14. Nasal antorbital fossa: present (0); absent (1). (modified from Holtz 2001)
15. Lacrimal–nasal–maxilla contact, form: multiple anterior lacrimal prongs (0); lacrimal process dominant (1); nasal lacrimal process lost (2). (Currie *et al.* 2003)
16. Lacrimal, border of antorbital fossa: present (0); absent (1). (Currie *et al.* 2003)
17. Lacrimal, position of accessory recess: proximal (0); distal (1). (Carr *et al.* 2005)
18. Lacrimal, size of pneumatic recess: small (0); large (1). (Carr *et al.* 2005)
19. Lacrimal, pneumatic openings: single (0); multiple (1). (Currie *et al.* 2003)
20. Lacrimal anterior ramus, form: low (0); swollen (1). (Holtz 2001)
21. Lacrimal cornual process, form: subtriangular, prominent (0); rounded ridge (1). (Currie *et al.* 2003)
22. Lacrimal cornual process, orientation: absent (0); dorsal (1); anterodorsal (2). (Holtz 2001)
23. Lacrimal cornual process, position relative to ventral ramus: dorsal (0); anterior (1). (Holtz 2001; modified by Carr *et al.* 2005)
24. Lacrimal rami, divergence angle: 75–90° (0); approximately 45–60° (1). (modified from Holtz 2001)
25. Jugal, depth of anterior ramus below pneumatic opening: tapering (0); deep (1). (Currie *et al.* 2003)
26. Jugal, thickness of inflection on ventral margin below postorbital process: thin (0); thick (1). (Currie *et al.* 2003)
27. Jugal antorbital fossa: present (0); absent (1). (modified from Holtz 2001)
28. Jugal pneumatopore, axis: inclined at 45° (0); horizontal (1). (Currie *et al.* 2003)
29. Jugal postorbital process, form: narrow, laterally convex (0); broad, laterally concave. (Currie *et al.* 2003)
30. Jugal–postorbital suture, form: scarf joint (0); horizontal, interlocking notch (1). (Currie *et al.* 2003)
31. Jugal, orbital margin, location relative to the ventral edge of the lacrimal: even with (0); ventral (1). (modified from Currie *et al.* 2003)
32. Postorbital, posterior tip of squamosal process, location relative to the laterotemporal fenestra: posteriormost end (0); along mid-section (1). (modified from Carr *et al.* 2005)
33. Postorbital, dorsal surface, texture: smooth (0); rugose (1). (modified from Holtz 2001)
34. Postorbital, suborbital flange: absent or small (0); prominently developed (1). (modified from Holtz 2001)
35. Postorbital ventral ramus, orientation of principal axis: subvertical (0); sloping anteroventrally (1). (Holtz *et al.* 2004)
36. Postorbital, form of orbital rim: rounded (0); tab-shaped (1); C-shaped. (Currie *et al.* 2003)
37. Squamosal–quadratojugal suture, position: level with (0), or elevated dorsal to (1), the postorbital–jugal suture. (modified from Holtz 2001)
38. Quadratojugal, distal flaring of dorsal process: absent (0); moderate (1); extensive (2). (Currie *et al.* 2003)
39. Quadratojugal, tip of anterior process, location relative to the laterotemporal fenestra: ventral (0); anterior (1). (Holtz *et al.* 2004)
40. Quadratojugal, anterior process, shape: anteriorly tapered (0); squared or double-pronged (1). (Currie *et al.* 2003)
41. Frontal–postorbital suture, form: undifferentiated (0); subdivided into vertical and horizontal (posterior) parts (1). (Currie *et al.* 2003)
42. Frontal shape: triangular (0); posterior end expanded (1); rectangular base, small anterior triangle (2). (Holtz 2001)
43. Frontal, extent of supratemporal fossa: posterior rim of fossa (0); broad area of fossa on dorsal aspect (1); broader area with median sagittal crest. (modified from Holtz 2001)
44. Parietal nuchal crest, height relative to 50% width: less (0); more (1). (Holtz 2001)
45. Parietal nuchal crest, thickness and texture: thin, smooth (0); thick, rugose (1). (Holtz 2001)
46. Parietal sagittal crest length: parietal (0); parietal and posterior aspect of frontal (1). (Currie *et al.* 2003)
47. Quadrate condyle, position relative to occipital condyle: approximately aligned (0); completely anterior (1); completely posterior (2). (Holtz *et al.* 2004)
48. Ectopterygoid with ventral pocket to chambers: present (0); greatly reduced (1). (modified from Holtz 2001)
49. Ectopterygoid sinus, form: hollows bone without swelling (0); inflates bone (1). (modified from Holtz 2001)
50. Ectopterygoid, length of jugal process: short (0); wide (1). (Carr *et al.* 2005)
51. Ectopterygoid, position of pneumatic recess: restricted to posterior aspect (0); extends anteriorly (1). (Carr *et al.* 2005)
52. Ectopterygoid, number of pneumatic foramina: 1 (0); 2 (1). (Holtz *et al.* 2004)
53. Ectopterygoid, pneumatic foramen rim: flat (0); rounded (1). (Carr *et al.* 2005)
54. Ectopterygoid, posterior surface of jugal process: imperforate (0); perforate (1). (Carr *et al.* 2005)
55. Palatine form: triradiate (no jugal process) (0); tetraradiate, inflated (1). (Holtz 2001)
56. Palatine lateral foramina, number: 1 (0); 2 or more (1). (Holtz 2001)
57. Palatine, length of the dorsal process: short (0); long (1). (Carr *et al.* 2005)
58. Palatine, height of the dorsal process: tall (0); short (1). (Carr *et al.* 2005)
59. Palatine foramen (dorsal aspect of palatine recess), size: small (0); large (1). (Holtz *et al.* 2004)

60. Vomer anterior end, form: lanceolate (0); diamond (1). (Currie *et al.* 2003)
61. Occiput, facing orientation: posteriorly (0); posteroventrally (1). (Holtz 2001)
62. Supraoccipital, pronounced median ridge: absent (0); present (1). (Currie *et al.* 2003)
63. Supraoccipital, contribution to foramen magnum: enters dorsal margin (0); excluded (exoccipitals contact) (1). (Holtz 2001)
64. Basisphenoid recess, orientation of central axis: vertical (0); posteroventral (1). (Harris 1998)
65. Basal tubera and basipterygoid processes, position: anteroposteriorly (0), or transversely (1), broader. (Currie *et al.* 2003)
66. Basal tubera size: subequal to (0), or significantly smaller than (1), basipterygoid processes. (Holtz 2001)
67. Dentary, tooth-bearing ramus, relative relation of dorsal and ventral margins: subparallel (0); posteriorly divergent (1). (Holtz *et al.* 2004)
68. Dentary, depth of posterior end: 150% (0), or greater than 200% (1), of the depth at the symphysis. (Holtz 2001)
69. Surangular shelf, orientation: horizontal (0); pendant (1). (Holtz 2001)
70. Surangular, posterior foramen, size: foramen (0); enlarged fenestra (1). (Gauthier 1986)
71. Retroarticular process, shape (posterodorsal view): longer than broad (0); broader than long (1). (Holtz *et al.* 2004)
72. Dentary tooth count: 16 or more (0); 15 or fewer (1). (Holtz 2001)
73. Crown form, lateral teeth: ziphodont (0); incrassate (1). (Holtz 2001)

Postcranial

74. Mid cervical centrum, length relative to diameter of anterior face: 200% (0); less than 50% (1). (Holtz 2001)
75. Cervical neural spines, height relative to the vertical diameter of the centrum: less (0); more (1). (Holtz 2001)
76. Scapular blade, distal end, width relative to midshaft: subequal (0); approximately twice (1). (Holtz 2001)
77. Humerus, deltopectoral crest, size: large (0); reduced (1). (Holtz 2001)
78. Metacarpal 2–metacarpal 1 length ratio: 2–1.8 (0); 1.8–1.6 (1); 1.6 or less (2). (Holtz 2001 as modified by Holtz *et al.* 2004)
79. Manual digit I phalanx 1, length relative to metacarpal 2: longer (0); subequal (1); shorter (2). (Holtz 2001)
80. Manual ungual shape (lateral view): trenchant (0); straight (1). (Holtz *et al.* 2004)
81. Manual unguals, form of distal end: tapered to a point (0); blunt-ended (1). (Holtz 2001)
82. Ilium, length relative to femur: shorter (0); subequal (1); longer (2). (Holtz 2001)
83. Pubic foot, length: approximately 33% (0), 50% (1), or 66% (2) maximum length of pubis. (Holtz 2001)
84. Femur, scar on shaft (caudifemoralis longus), location: posterior (0); posteromedial (1). (Holtz *et al.* 2004)
85. Metatarsal 3, form of shaft (anterior view); straight (0); sigmoid (1). (Holtz *et al.* 2004)