Skull structure and evolution in tyrannosaurid dinosaurs

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Tyrannosauridae can be subdivided into two distinct subfamilies—the Albertosaurinae and the Tyrannosaurinae. Previously recognized subdivisions Aublysodontinae and Shanshanosaurinae are rejected because they are based on insufficient material and juvenile specimens. Our results are based upon a phylogenetic analysis using PAUP program (Swofford 1999) of 77 skull characters and seven genera (*Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Gorgosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*); with *Allosaurus* as outgroup. Of the 77 characters used, more than half were parsimony informative. A single most parsimonious tree was obtained with the Tree Length being 88. The analysis of cranial characters and comparison of postcranial features reveal that *Tarbosaurus bataar* is not the sister taxon of *Tyrannosaurus rex* (*contra* Holtz 2001). Their similarities are partially due to the fact that both are extremely large animals. Thus, *Tarbosaurus* should be considered a genus distinct from *Tyrannosaurus*.

Key words: Dinosauria, Theropoda, Coelurosauria, Tyrannosauridae, phylogeny, parsimonious analysis.

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Introduction

To the general public, tyrannosaurids are amongst the best known and most popular dinosaurs. Yet there have been relatively few monographic descriptions of specimens, and there is considerable disagreement about valid generic and specific names, and relationships. For example, Paul (1988) recognized 14 tyrannosaurid species in five genera (*Albertosaurus*, *Alioramus*, *Aublysodon*, *Indosuchus*, and *Tyrannosaurus*); Molnar et al. (1990) listed 12 species in at least eight genera (*Albertosaurus*, *Alectrosaurus*, *Alioramus*, *Chingkankousaurus*, *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*); Olshevsky (1995) referred to 19 species level taxa in at least 14 genera (*Albertosaurus*, *Alectrosaurus*, *Alioramus*, *Aublysodon*, *Daspletosaurus*, *Dinotyrannus*, *Gorgosaurus*, *Jenghizkhan*, *Maleevosaurus*, *Nanotyrannus*, *Shanshanosaurus*, *Stygivenator*, *Tarbosaurus*, and *Tyrannosaurus*); Holtz (2001) incorporated eleven species level taxa in at least eight genera (*Albertosaurus*, *Alectrosaurus*, *Alioramus*, *Aublysodon*, *Daspletosaurus*, *Gorgosaurus*, *Shanshanosaurus*, and *Tyrannosaurus*).

The purpose of this paper is to examine the intra-relationships of the Tyrannosauridae Osborn, 1906, a family that has been well established as coelurosaurian (Holtz 1994, 2000, 2001; Sereno 1997, 1999; Makovicky and Sues 1998). As pointed out by Holtz (2001), the relationship of tyrannosaurids to other Coelurosauria von Huene, 1914 is unclear. Because the intention of this paper was not to resolve this problem,

Allosaurus Marsh, 1877 was chosen as a theropod generalized enough to serve as the outgroup. *Siamotyrannus* Buffetaut, Suteethorn, and Tong, 1996 and *Eotyrannus* Hutt, Naish, Martill, Barker, and Newbery, 2001 (Naish et al. 2001) have both been described as primitive relatives of the Tyrannosauridae. Although the fused, dorsally convex nasals alone demonstrate the probable relationship of the latter to tyrannosaurids, we have not examined the original specimens and did not feel enough was known to meaningfully code the genera. For similar reasons, the Asian tyrannosaurid *Alectrosaurus* Gilmore, 1933 was also excluded from this analysis. The holotype material of *Alectrosaurus* does not include any cranial material (Gilmore 1933; Mader and Bradley 1989), and the skull of the better preserved Mongolian specimen (Perle 1977) has been unavailable for years.

Holtz (2001) and earlier authors recognised two subfamilies (Aublysodontinae and Tyrannosaurinae) within the Tyrannosauridae. Aublysodontinae Nopcsa, 1928 has always been a vague subfamily established on the basis of a tooth genus (*Aublysodon* Leidy, 1868). Although several skeletons have been assigned to this genus, the recent discoveries of juveniles of well-established tyrannosaurid genera (including *Albertosaurus* Osborn, 1905, *Daspletosaurus* Russell, 1970, *Gorgosaurus* Lambe, 1914, *Tarbosaurus* Maleev, 1955, and *Tyrannosaurus* Osborn, 1905) have made it increasingly obvious that *Aublysodon* is based strictly on characters that are morphologically and allometrically immature. *Aublysodon molnari* Paul, 1988 (= *Stygivenator mol-*

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nari Olshevsky, 1995) and *Albertosaurus megagracilis* Paul, 1988 (=*Dinotyrannus megagracilis* Olshevsky, 1995) are probably juveniles of *Tyrannosaurus rex* Osborn, 1905 (see Currie 2003). The Kirtland Shale aublysodontine (Lehman and Carpenter 1990) may be a juvenile *Daspletosaurus* (Holtz 2001). *Nanotyrannus* Bakker et al., 1988 was included in the Aublysodontinae by Sereno (1998), but most other authors recognize it as a tyrannosaurid that may even be congeneric with *Tyrannosaurus* (Carr 1999; Holtz 2001). *Alectrosaurus* has been placed in this subfamily because it has premaxillary teeth that lack denticles (Currie 2000), but if *Aublysodon* is congeneric with tyrannosaurine genera, then the lack of denticles cannot be used to define the subfamily Aublysodontinae. *Shanshanosaurus* Dong, 1977 has been variously assigned to its own family (Shanshanosauridae Dong, 1977), its own subfamily (Shanshanosaurinae), or to the Aublysodontinae (Paul 1988), but Currie and Dong (2001) suggested it is a tyrannosaurid that is possibly congeneric with *Tarbosaurus*. In short, there is no reason at present to assume that the Aublysodontinae exists.

This paper is based mostly on recent studies of the skull anatomy of North American tyrannosaurids (Currie 2003), and of Asian tyrannosaurids (Hurum and Sabath 2003); more detailed anatomical data are given in these two papers.

Institutional abbreviations: AMNH, American Museum of Natural History; NMC, National Museum of Canada, Ottawa; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

Phylogenetic analysis

Selection of taxa and the problem of juvenile specimens

A total of seven tyrannosaurid genera are included in this analysis. *Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Gorgosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*; with *Allosaurus* as outgroup. More than 200 original catalogued specimens of *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus*, and *Tyrannosaurus* have been studied. Whenever possible, characters were coded from adult specimens. However, examination of the only known specimens of *Alioramus remotus* Kurzanov, 1976 and *Nanotyrannus lancensis* indicate that both are clearly immature. Although some researchers (Carr 1999; Holtz 2001) believe that *Nanotyrannus* is congeneric with *Tyrannosaurus*, the high number of maxillary teeth suggests that it is distinct from *Tyrannosaurus rex* at the species or generic level (Currie 2003). Differences from other tyrannosaurids that were clearly attributable to the immaturity of *Alioramus* and *Nanotyrannus* were coded as × in the data matrix (see Appendix). For example, the maxillary fenestra of *Nanotyrannus* is relatively small and should have been coded "0"

for character 32. However, it is also evident that in *Daspletosaurus* the maxillary fenestra is small in juveniles (TMP 94.143.1) but large in adults (NMC 8506, TMP 85.64.1). Because we do not know what the maxillary fenestra of an adult *Nanotyrannus* looks like, character–32 is coded with a ×. Some characters (such as character 40) were coded as seen in the only known specimens, are different in coding from *Tarbosaurus* and/or *Tyrannosaurus*, but may ultimately prove to also be age-related and therefore invalid.

Characters

The characters used in this analysis were mostly derived from the research done by Hurum and Sabath (2003), and Currie (2003). Work by earlier researchers (especially Russell 1970; Carr 1999) provided a suitable framework for character selection, but the most relevant research is that of Holtz (1994, 2000, and especially 2001).

Holtz (2001) has done the most formal, phylogenetic analysis of the intrafamily relationships of the Tyrannosauridae, although he considered it as preliminary. In this paper, many of his characters (Holtz 2001: appendix 7.1: 2, 3, 4, 15, 42, 48, 69, 70, 72, 74, 96, 103, 106, 108, 110) have been adopted. Others (9, 12, 56, 65, 66, 104+105, 109) have been modified to accommodate the different style of presentation, and the different suites of specimens and taxa. Some of the characters used by Holtz (6, 7, 13, 42, 47, 49–55, 57, 59, 62, 63, 68, 93, 99) were incorporated into this paper, but were completely reworked or were included within character suites that bear little resemblance to his original wording.

A number of characters used by Holtz (2001) were not used in our data matrix. As this paper examines only cranial anatomy of tyrannosaurids, none of his postcranial characters were included. His characters numbered 1, 40, 41, 43, 44, 46, 58, 61, 64, 76, and 77 are considered to be allometric (either within a growth series or between taxa in which there are absolute size differences at maturity). The relative size of the prefrontals (character 5 of Holtz 2001) could not be quantified in a meaningful way, and was therefore dropped from the analysis. Prominent muscular fossae (character 10) were not recognized on the dorsal surfaces of palatines, and therefore the character was omitted pending further research. The angular is supposed to terminate posteriorly in front of the posterior surangular fenestra in *Tarbosaurus bataar* (Holtz 2001: character 73). However, this is not the case in the specimens examined by Hurum and Currie (2000). As stated above, *Aublysodon molnari* is considered as a juvenile of *Tyrannosaurus rex*, and Holtz's character 87 is probably an artefact of preservation. His character 90, hornlets on the nasal surface, was not used because it is an autapomorphy for *Alioramus*. The prootic anterior expansion and position of the trigeminal foramen were also used to characterize *Alioramus* (Holtz's characters 91, 92), but it is not clear from the specimen (PIN 3141-1) that either of these characters are real (Currie 2003). Holtz (2001) described a postorbital and lacrimal in contact with each other below the orbit in *Gorgo-*

saurus libratus, based on AMNH 5336 (Holtz 2001: character 94). This is, however, the only specimen that shows this feature. The postorbital does not show any pathological features, and the contact might be due to dorsoventral compression. Nevertheless, it is not a general character for *Gorgosaurus,* and therefore we have omitted it from the analysis. The anterior margin of the suborbital prong of the postorbital is highly variable in preservation, and using it as a character to define *Albertosaurus libratus* (Holtz 2001: character 95) cannot be confirmed at this time. Russell (1970) was the first to suggest that the premaxilla and nasal did not contact each other below the external naris in *Daspletosaurus* (Holtz 2001: character 98). However, re-examination of the holotype (NMC 8506) shows that these delicate subnarial processes are broken, but that their sutures on the maxilla clearly show that they were in contact. Furthermore, the subnarial processes are preserved in other specimens of *Daspletosaurus*, including TMP 94.143.1.

Tooth counts (Holtz 2001: characters 45, 75, 78) show no trends to indicate that they can resolve relationships in tyrannosaurids (Table 1), although they can help define individual taxa. Character 79 of Holtz (2001) was also omitted because tooth thickness is allometric and one expects small and juvenile tyrannosaurids to have ziphodont lateral teeth (Fig. 1).

Table 1. Tooth counts/alveoli in tyrannosaurids and *Allosaurus*.

	premaxillary teeth	maxillary teeth	dentary teeth
Allosaurus	5	15–16	17–18
Albertosaurus	4	14	13–15
Alioramus	4	16	18
Daspletosaurus	4	13–17	16–17
Gorgosaurus	4	13–15	15–17
Nanotyrannus	4	14	?
Tarbosaurus	4	12–13	14–15
Tyrannosaurus	4	11–12	12–14

Character 97 (interlocking premaxillae) refers to *Daspletosaurus torosus*, but only to a single individual (NMC 8506), which also has interlocking dentaries. This is probably an old individual, and the character is probably atypical for the genus. Another *Daspletosaurus torosus* specimen (TMP 2001.36.1) is almost as large (the maxillary tooth row of NMC 8506 is 530 mm long, whereas that of TMP 2001.36.1 is 525 mm in length), but does not show the same interlocking of the premaxillae. Pending further recovery of specimens, these characters are not being considered as autapomorphic for *Daspletosaurus*. Another premaxillary character (Holtz 2001: character 107) was used to distinguish *Tyrannosaurus* from other tyrannosaurids. However, the degree to which premaxillary teeth are pressed against each other is variable. A small specimen of *Daspletosaurus* (TMP 94.143.1) has teeth that are tightly packed in the premaxilla, whereas a large specimen of the same genus (NMC 8506) has widely separated premaxillary teeth. This suggests that the appression of premaxillary teeth may be ontogenetically
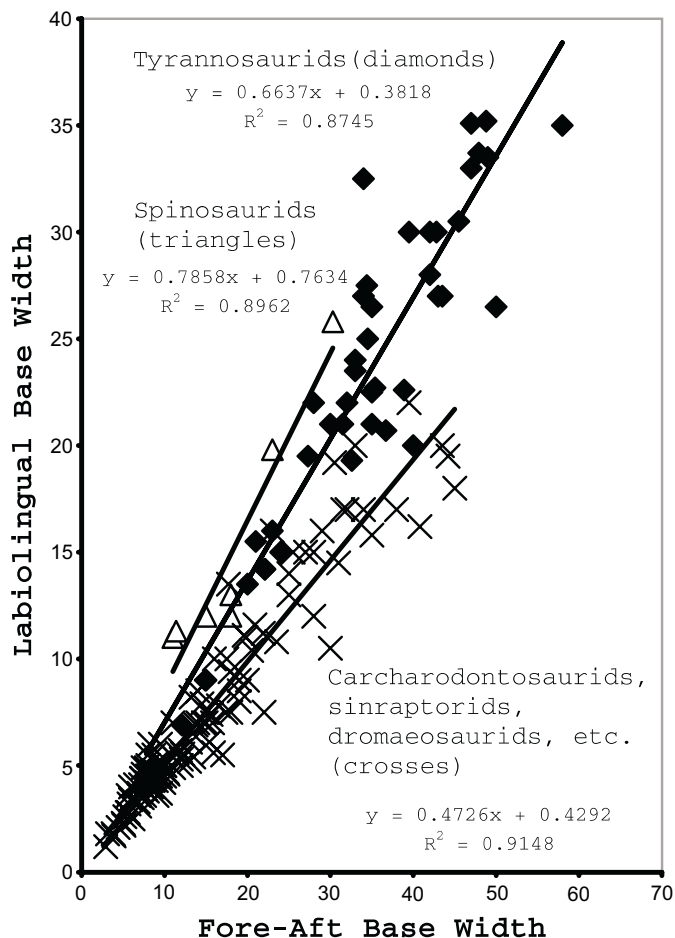

Fig. 1. Maxillary and dentary teeth of various theropods, showing the relationship between the fore-aft base length and the labiolingual base width. Graph shows that tyrannosaurids tend to have thicker teeth than most theropods other than spinosaurids. However, it also demonstrates that tooth thickness in tyrannosaurids is allometrically controlled. Small (young) tyrannosaurids have teeth that are indistinguishable in thickness from those of most other theropods.

controlled, although it may also indicate individual variation amongst an unknown number of tyrannosaurid taxa.

Finally, we did not feel confident in recognizing the distribution and/or utility of several features (Holtz 2001: characters 11, 60, 67, 71) mostly because of variation in preservation or lack of sufficient specimens.

Results

PAUP 4.0b6 (Swofford 1999) was used to produce a single, most parsimonious tree using the Exhaustive Search option. Of the 77 characters used in this analysis, 41 are parsimony informative. All of the multistate characters are unordered and given equal weight. The Tree Length is 88, the consistency index is 0.93, the homoplasy index is .07, the retention index is 0.90, and the rescaled consistency index is 0.84.

Although Aublysodontinae does not exist, there is a clear division of the Tyrannosauridae into at least two clades. The taxon Tyrannosaurinae has been in existence for a long time
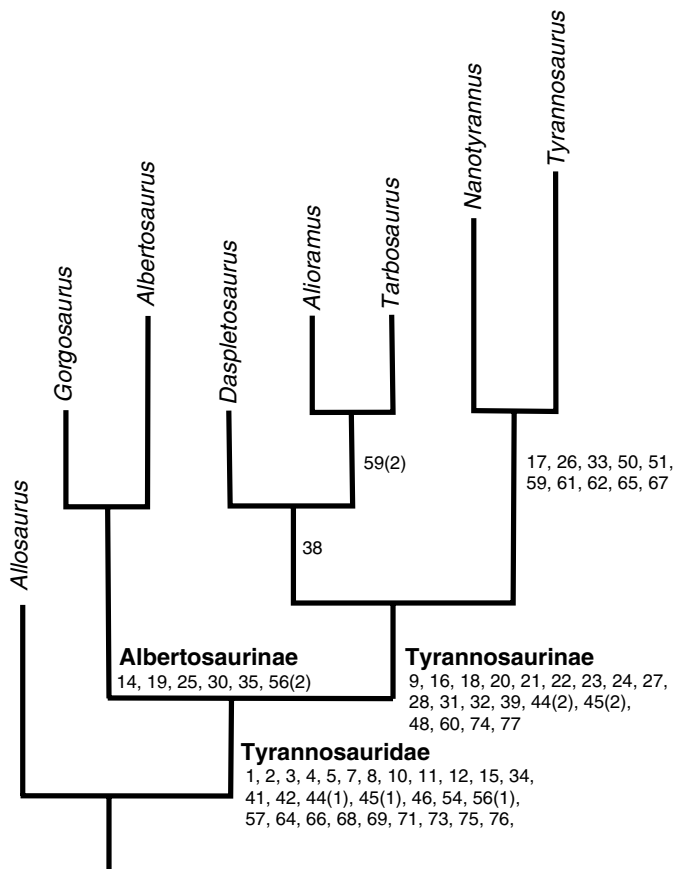
Fig. 2. Cladogram of the 77 characters and 8 taxa used in this analysis. The tree length is 88, the consistency index is 0.93, the homoplasy index is .07, the retention index is 0.90, and the rescaled consistency index is 0.84.

(Osborn 1906), but its definition and composition has been highly variable (Holtz 2001). *Albertosaurus* and *Gorgosaurus* are often considered to be congeneric (Russell 1970), but clearly represent distinct species (Currie 2003). Holtz (2001) and Currie (2003) have maintained the original generic names for the two species because there are as many or more differences between these animals as there are between tyrannosaurine genera. These taxa (*Albertosaurus sarcophagus* and *Gorgosaurus libratus*) are distinct in 6 characters from a clade composed of *Alioramus*, *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*. A new subfamily, here termed the Albertosaurinae, can be defined to include all tyrannosaurids closer to *Albertosaurus* than *Tyrannosaurus*. The Tyrannosaurinae would then include all taxa closer to *Tyrannosaurus* than *Albertosaurus*.

Tyrannosauridae are united by 30 cranial synapomorphies (1, 2, 3, 4, 5, 7, 8, 10, 11, 12, 15, 34, 41, 42, 44(1), 45(1), 46, 54, 56(1), 57, 64, 66, 68, 69, 71, 73, 75, 76 plus two of questionable use in a wider analysis: 55,70). Holtz (2001) also proposed 24 postcranial synapomorphies (16–39 in Holtz 2001: appendix 7.1) for this clade.

Albertosaurines (*Albertosaurus* + *Gorgosaurus*) are the more primitive of the two subfamilies, but are united by 6 cranial synapomorphies (14, 19, 25, 30, 35, 56(2)). Currie

(2003) also demonstrated that these were quantifiably more lightly built, longer legged, and probably faster animals than all known tyrannosaurines. *Albertosaurus* can be distinguished from *Gorgosaurus* by scoring of characters number 6, 7, 8, 40, 63.

Tyrannosaurinae (*Alioramus*, *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus)* have the following cranial synapomorphies: 9, 16, 18, 20, 21, 22, 23, 24, 27, 28, 31, 32, 39, 44(2), 45(2), 48, 60, 74, 77.

Asiatic Tyrannosaurinae (*Alioramus* and *Tarbosaurus*), informally used by Hurum and Sabath (2003), has only one synapomorphy in the skull 59(2). The current authors will undertake revisions of the postcranial skeleton of *Tarbosaurus* in the near future and describe the group formally.

Discussion

Phylogenetic analysis suggests that there are two major clades in the Tyrannosauridae, one characterized by *Albertosaurus*, and the other by *Tyrannosaurus*. Within the Tyrannosaurinae, *Daspletosaurus* shows a somewhat closer relationship to *Tarbosaurus* than *Tyrannosaurus*. Currie (in press) looked at allometry in tyrannosaurid skeletons, and observed that all genera have quantifiably longer arms than *Tarbosaurus*. This suggests that in this feature, *Tarbosaurus* is more derived than either *Daspletosaurus* or *Tyrannosaurus*. In turn, it indicates that *Tarbosaurus* is unlikely to be ancestral to either of the North American genera. Our analysis does not corroborate the close (sister taxon or congeneric) relationship between *Tyrannosaurus* and *Tarbosaurus* suggested by other workers (e.g., Paul 1988; Carr 1999; Holtz 2001).

Cranial kinesis in Tyrannosauridae

The new material (permitting detailed skull comparisons of a Mongolian *T. bataar* ZPAL MgD-I/4 with the North American *T. rex* "Stan" BHI-3033) allowed Hurum and Sabath (2003) to tentatively divide tyrannosaurines into North American and Asiatic groups on the basis of how the dorsal joints of the skull handled dorsally directed forces through the maxilla during biting (Hurum and Sabath 2003). The lack of a lacrimal process of the nasal is probably an apomorphy of Asiatic Tyrannosaurinae.

In theropods, the plesiomorphic character, presence of the nasal lacrimal process, is retained in diverse groups, (*Allosaurus*, *Carnotaurus*, *Ceratosaurus, Sinraptor*, Albertosaurinae, and *Tyrannosaurus*). The most derived lacrimal process is seen in *Tyrannosaurus* where the biting forces are directed only from the maxilla to the nasal, and from the nasal into the lacrimal. The posterodorsal end of the maxilla meeting the lacrimal is thin and laterally compressed and does not contribute to the handling of impact stress. In *Allosaurus* the main stress distribution in the skull during maximum impact is di-

rectly between the maxilla and lacrimal, but the maxilla-na-sal-lacrimal contact is also present (Rayfield et al. 2001). The primitive double skull articulation in allosaurids provides information on the plesiomorphic condition of an ancestor to both North American and Asiatic tyrannosaurines. Both articulations were present in a common ancestor and the two different articulations were improved separately. New specimens of *Daspletosaurus* (Currie 2003) show a transformation series in this respect. The lacrimal process of the nasal is present in juveniles, when there are no transverse ridges in the suture between maxilla and nasal, while the process is lost in mature animals, when the transverse ridges are developed. In *Tarbosaurus*, it is also lost in juveniles.

Observing the sutures and joints between the skull bones involved suggests that two fundamentally different mechanisms developed in tyrannosaurines for handling the stresses resulting from the powerful bite forces. *Daspletosaurus* seems to have been experimenting with both solutions, and appears to be close to the plesiomorphic condition that would have existed in the common ancestor of both *Tarbosaurus* and *Tyrannosaurus*.

Conclusions

There is no justification for maintaining the tyrannosaurid subfamilies Aublysodontinae and Shanshanosaurinae. Both were set up to include taxa that are now recognized as juvenile tyrannosaurines, and neither subfamily name has priority over Tyrannosaurinae. Nevertheless, Tyrannosauridae can be subdivided into two distinct subfamilies, here referred to as the Albertosaurinae and the Tyrannosaurinae.

The Albertosaurinae includes two monotypic genera: *Albertosaurus sarcophagus* and *Gorgosaurus libratus*. Tyrannosaurinae is presently made up of three species of *Daspletosaurus* (*D. torosus* and two undescribed species, see Currie 2003), plus *Alioramus remotus*, *Nanotyrannus lancensis*, *Tarbosaurus bataar*, and *Tyrannosaurus rex*. Until the cranial material of *Alectrosaurus olseni* can be studied in more detail, this species cannot be assigned to either subfamily.

Tarbosaurus bataar is not a direct ancestor of *Tyrannosaurus rex*. This is based on the phylogenetical analysis of cranial characters, as well as the discussed postcranial features, and differences in cranial kinesis. Similarities exist partially because both are extremely large animals. *Tarbosaurus* should be considered a genus distinct from *Tyrannosaurus*, and closer to other Asiatic tyrannosaurines.

Acknowledgements

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Appendix

Taxon character matrix

Matrix, 77 characters, 8 taxa, all characters unordered. Unknown scored as "?". Differences from other tyrannosaurids that are clearly attributable to the immaturity of *Alioramus* and *Nanotyrannus* are coded as ×.

Character states	*Allosaurus*	*Albertosaurus*	*Alioramus*	*Daspletosaurus*	*Gorgosaurus*	*Nanotyrannus*	*Tarbosaurus*	*Tyrannosaurus*
1. Articular, depression for depressor mandibulae: 0, oriented more dorsal than posterior; 1, oriented mostly posteriorly.	0	1	?	1	1	1	1	1
2. Articular, pneumatic: 0, no; 1, yes (after Harris 1998).	0	1	?	1	1	1	1	1
3. Basicranium pneumatization: 0, minimum; 1, extensive pneumatization of the basisphenoid and basioccipital.	0	1	1	1	1	1	1	1
4. Basioccipital, distance across basal tubera: 0, less than the transverse width of condyle; 1, greater than transverse width of occipital condyle (after Holtz 2000).	0	1	1	1	1	1	1	1
5. Basisphenoid, basisphenoidal recess: 0, shallow, foramina small or absent; 1, deep, foramina large (after Harris 1998, Holtz 2001: character 9).	0	1	1	1	1	1	1	1
6. Basisphenoid, foramina in basisphenoidal recess: 0, lie within same surface; 1, each foramen lies within a distinct fossa (Holtz 2001: character 96).	0	1	0	0	0	0	0	0
7. Basisphenoid, recess: 0, oriented ventrally; 1, oriented posteroventrally (after Harris, 1998).	0	1	1	1	0	1	1	1
8. Braincase, rectangle defined by positions of both basal tubera and both basipterygoid processes: 0, anteroposteriorly longer than wide; 1, mediolaterally wider than long.	0	1	1	1	0	1	1	1
9. Ectopterygoid, sinus: 0, moderate; 1, inflated (Holtz 2001: character 69).	0	0	?	1	0	1	1	1
10. Ectopterygoid, ventral pocket to ectopterygoid chambers: 0, small; 1, large.	0	1	?	1	1	1	1	1
11. Exoccipital, ventral extension: 0, notch separates basal tuber from more anteroventral extension of exoccipital-basisphenoid suture; 1, no notch.	0	1	1	1	1	1	1	1
12. Exoccipital: 0, no contact between left and right sides; 1, contact above foramen magnum (modified from Harris 1998, Holtz 2001: character 66).	0	1	1	1	1	?	1	1
13. Exoccipital-opisthotic, paroccipital process: 0, directed laterally; 1, curving ventrally, pendant.	1	0	0	0	0	0	0	0
14. Frontal, suture for postorbital: 0, little distinction between anterior and posterior parts of suture; 1, suture vertical anteriorly but is a distinct horizontal shelf posteriorly.	0	1	0	0	1	0	0	0
15. Frontal-parietal: 0, transverse dorsal suture; 1, frontals separated on midline.	0	1	1	1	1	1	1	1
16. Jugal, anterior ramus in mature specimens: 0, thin and tapering beneath the jugal pneumatic recess; 1, deep below pneumatic opening (after Carr 1999).	0	0	×	1	0	×	1	1
17. Jugal, contribution to posteroventral corner of antorbital fenestra: 0, forms the corner; 1, restricted between maxilla and lacrimal to small surface (after Holtz 2001: character 109).	?	0	?	0	0	1	0	1

Character states	*Allosaurus*	*Albertosaurus*	*Alioramus*	*Daspletosaurus*	*Gorgosaurus*	*Nanotyrannus*	*Tarbosaurus*	*Tyrannosaurus*
18. Jugal, inflection on ventral margin below postorbital process: 0, prominent but thin; 1, prominent and thick (after Carr 1999).	0	0	×	1	0	×	1	1
19. Jugal, pneumatopore: 0, axis of pneumatopore inclined at an angel of 45o to the ventral skull margin; 1, axis of relatively small pneumatopore is horizontal.	1	0	?	1	0	1	1	1
20. Jugal, postorbital process in mature specimens: 0, anteroposteriorly shorter at the base and convex laterally in all but the largest specimens; 1, anteroposteriorly broad and shallowly concave laterally.	0	0	×	1	0	×	1	1
21. Jugal, postorbital ramus: 0, tapering contact with postorbital; 1, horizontal, interlocking notch for postorbital.	0	0	?	1	0	1	1	1
22. Jugal, suborbital bar in mature specimens: 0, tall, with orbital margin at same level as ventrolateral edge of lacrimal; 1, low, with orbital margin lower than ventrolateral edge of lacrimal.	0	0	×	1	0	×	1	1
23. Lacrimal, angle between dorsal and preorbital rami in mature animals; 0, approximately perpendicular; 1, acute (after Molnar 1991).	0	0	×	1	0	×	1	1
24. Lacrimal, horn: 0, prominent, well defined apex; 1, elongate, robust ridge.	0	0	1	1	0	?	1	1
25. Lacrimal, pneumatic openings in: 0, multiple fossae; 1, set in single fossa.	1	0	?	1	0	?	1	1
26. Lacrimal, posterior end of apex (horn) in dorsal view: 0, rounded; 1, box-like.	0	0	0	0	0	?	0	1
27. Lacrimal, ventrolateral process of preorbital bar: 0, forms posterior margin of antorbital fossa as it leads into the pneumatopore in the jugal; 1, separated from the margin of the antorbital fossa ventrally by the jugal (Russell 1970).	?	0	?	1	0	1	1	1
28. Maxilla, antorbital fossa ventral margin near back of tooth row in adults: 0, coincides with lower margin of antorbital fenestra; 1, lower than ventral margin of antorbital fenestra.	1	1	×	0	1	×	0	0
29. Maxilla, interdental plates: 0, not fused; 1, fused to each other.	1	0	0	0	0	0	0	0
30. Maxilla, maxillary fenestra anterior margin in adults: 0, terminates posterior to anterior margin of antorbital fossa; 1, terminates along anterior margin of antorbital fossa (Holtz 2001: character 42).	1	0	×	1	0	×	1	1
31. Maxilla, maxillary fenestra, anteroposterior length compared to distance between anterior margins of antorbital fossa and fenestra in adults: 0, less than half; 1, more than half.	0	0	×	1	0	×	1	1
32. Maxilla, palatal shelf suture for palatine: 0, relatively shallow, tooth roots forming bulge on lateral side of dorsal surface; 1, relatively deep, thereby obscuring positions of alveoli (after Carr 1999).	0	0	?	1	0	?	1	1
33. Maxilla, palatal shelf: 0, contacts vomer for length one half or less length of tooth row; 1, contacts vomer for length greater than three quarters the length of tooth row (Holtz 2001: character 108).	0	0	?	0	0	1	0	1
34. Maxilla, posterodorsal process: 0, forms dorsomedial wall of antorbital fossa, which extends to and invades nasal; 1, forms dorsal margin of antorbital fossa, thereby preventing involvement of the nasal in the antorbital margin.	0	1	1	1	1	1	1	1
35. Maxilla, promaxillary fenestra in adults: 0, visible in lateral view; 1, obscured in lateral view by ascending ramus of maxilla (Witmer 1997).	1	0	×	1	0	×	1	1
36. Nasal, antorbital fossa: 0, lateral surface of nasal excluded from antorbital cavity: 1, lateral surface of nasal participates in antorbital fossa (after Holtz, 2000).	1	0	?	0	0	0	0	0
37. Nasal, antorbital fossa: 0, recesses absent from nasal; 1, present (after Holtz 2000).	1	0	?	0	0	0	0	0
38. Nasal, lateral finger-like lacrimal process oriented posteriorly clasps anterior end of lacrimal: 0, present; 1, absent in adults.	0	0	1	1	0	?	1	0
39. Nasal, posterior region between lacrimals: 0, expand laterally; 1, lateral margins are parallel to midline or constricted posteriorly (after Russell 1970).	0	0	?	1	0	1	1	1
40. Nasal, posterior suture shape: 0, medial projection extends as far or further posteriorly than lateral projections; 1, lateral projections extend further posteriorly than medial projections (Holtz 2001: character 48).	0	0	1	0	1	1	1	0
41. Nasal: 0, dorsally flat for most of length; 1, dorsally convex.	0	1	1	1	1	1	1	1
42. Nasal: 0, unfused; 1, fused (Holtz 2001: character 3).	0	1	1	1	1	1	1	1
43. Palatine, shape: 0, triradiate; 1, inflated trapezoid. (Holtz 2001: character 70)	0	0	?	1	0	?	1	1
44. Parietal, dorsal surface: 0, flat with ridge bordering supratemporal fossa; 1, parietals with sagittal crest; 2, sagittal crest extends forward onto back of frontals.	0	1	2	2	1	2	2	2
45. Parietal, nuchal crest: 0, as low or lower than the dorsal surface of the interorbital region; 1, tall but transversely narrow; 2, tall but broad.	0	1	2	2	1	2	2	2
46. Postorbital, dorsal surface in adults: 0, rugose (after Holtz 2001: character 56).	0	1	×	1	1	×	1	1
47. Postorbital, suborbital process: 0, not present or small; 1, well developed in mature animals(after Holtz 2001: character 57)	0	1	×	0	1	×	1	1
48. Postorbital: 0, smooth or slightly rugose posterodorsal to orbital rim; 1, low, C-shaped crest; 2, convex tablike prominence.	0	0	?	2	0	?	1	1

Character states	Allosaurus	Albertosaurus	Alioramus	Daspletosaurus	Gorgosaurus	Nanotyrannus	Tarbosaurus	Tyrannosaurus
49. Prefrontal, anterior extension compared with anterior level of dorsal exposure of the frontal: 0, extends beyond frontal; 1, approximately same anterior extent or shorter (after Carr 1999).	0	1	?	1	1	1	1	1
50. Prefrontal: 0, well developed and forming large part of mediodorsal margin preorbital bar; 1, reduced (after Gauthier, 1986).	0	0	?	0	0	?	0	1
51. Premaxilla, nasal processes: 0, slightly divergent at dorsal end; 1, tightly appressed throughout entirely length, terminate as single tip (Holtz 2001: character 106).	0	0	?	0	0	1	0	1
52. Premaxilla, tooth row arcade: 0, more anteroposteriorly than mediolaterally oriented; 1, more mediolaterally than anteroposteriorly oriented (Holtz 2001: character 2).	0	1	?	1	1	1	1	1
53. Quadrate, paraquadratic fenestra: 0, large and between Q and QJ; 1, small and enclosed in dorsal ramus of q (after Holtz 2000).	1	0	?	0	0	0	0	0
54. Quadrate, Q-QJ suture in adults: 0, unfused; 1, fused (after Holtz 2000).	0	1	×	1	1	×	1	1
55. Quadrate: 0, nonpneumatic; 1, pneumatic (Molnar, 1985).	0	1	?	1	1	1	1	1
56. Quadratojugal, dorsal flaring towards contact with squamosal: 0, virtually none; 1, moderate; 2, extensive.	0	2	?	1	2	1	1	1
57. Quadratojugal, subtemporal process: 0, tapers anteriorly; 1, squared off or double pronged anterior terminus.	0	0	?	1	0	1	1	1
58. Secondary palate: 0, absent; 1; present	0	1	?	1	1	1	1	1
59. Skull, contact amongst lacrimal, maxilla and nasal; 0, multiple anterior prongs of the anterodorsal ramus of the lacrimal clasp processes of both the maxilla and nasal; 1, lacrimal process of the nasal dominant over maxillary contact with lacrimal; 2, lacrimal process of nasal lost, maxilla-lacrimal contact dominates.	0	0	2	0	0	?	2	1
60. Skull, maxillary-nasal contact in mature specimens; 0, smooth, longitudinal groove on each; 1, interlocking transverse ridges.	0	0	×	1	0	×	1	1
61. Skull, maximum postorbital skull width: 0, less than one half premaxilla-occipital condyle length; 1, more than two-thirds premaxilla-occipital condyle length causing orbits to face forward (Holtz 2001: characters 104 and 105)	0	0	0	0	0	1	0	1
62. Skull, mediolateral width of snout at posterior end of maxillary tooth row: 0, twice or less width of nasals; 1, approximately three times width of nasals (Holtz 2001: character 103).	0	0	?	0	0	1	0	1
63. Skull, occipital region faces: 0, posteriorly; 1, posteroventrally (after Holtz 2001: character 65).	0	1	1	1	0	1	1	1
64. Skull, temporal musculature attachment area on dorsal surfaces of frontal and parietal: 0, limited; 1, extensive.	0	1	1	1	1	1	1	1
65. Splenial, anterodorsal margin; 0, abrupt step anterior to contact with supradentary; 1, smoothly tapering.	0	0	?	0	0	1	0	1
66. Splenial, splenial foramen, size: 0, small; 1, large (after Sereno et al. 1998).	0	1	?	1	1	1	1	1
67. Splenial, ventral surface; 0, low angle to the ventral margin of the dentary; 1, more than 20 degrees	0	0	?	0	0	1	0	1
68. Squamosal, recess: 0, absent; 1, present (after Holtz 2000).	0	1	?	1	1	1	1	1
69. Squamosal-quadratojugal flange constricting infratemporal fenestra: 0, absent; 1 present (Holtz 2001: character 4).	0	1	1	1	1	1	1	1
70. Supraoccipital, pronounced, strongly demarcated median ridge; 0, absent; 1, present (after Holtz 2000).	0	1	?	1	1	1	1	1
71. Supraoccipital, pair of tab-like processes on supraoccipital wedge: 0, absent; 1, present (Holtz 2001: character 8).	0	1	1	1	1	1	1	1
72. Surangular, anteroventral extension divides external mandibular fenestra by contacting angular anteriorly: 0, absent; 1, present.	1	0	?	0	0	0	0	0
73. Surangular, posterior surangular foramen: 0, small; 1, large fenestra (after Holtz 2001: character 12).	0	1	1	1	1	1	1	1
74. Surangular, shelf: 0, horizontal; 1, slightly pendant, overhangs dorsal margin of posterior surangular foramen (Holtz 2001: character 74)	0	0	?	1	0	1	1	1
75. Teeth, premaxillary tooth size: 0, subequal to lateral teeth; 1, much smaller than lateral teeth (Holtz 2001: character 15).	0	1	?	1	1	1	1	1
76. Teeth, premaxillary: 0, J-shaped in section; 1, D-shaped in basal cross section (Holtz 2001: character 14).	0	1	?	1	1	1	1	1
77. Vomer, shape of anterior end: 0, lanceolate (lateral margins parallel-sided); 1, diamond (Holtz 2001: character 110).	0	0	?	1	0	?	1	1