Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada

PHILIP J. CURRIE

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Beautifully preserved, nearly complete theropod skeletons from Alberta (Canada) allow re-evaluation of the taxonomic status of North American tyrannosaurids. It is concluded that the most parsimonious interpretation of relationships leads to the separation of the two species of *Albertosaurus* (*sensu* Russell 1970) into *Gorgosaurus libratus* from the Campanian Dinosaur Park Formation and *Albertosaurus sarcophagus* from the upper Campanian/lower Maastrichtian Horseshoe Canyon Formation. *Albertosaurus* and *Gorgosaurus* are closely related, but can be distinguished from each other by more characters than are known to justify generic distinction within another tyrannosaurid clade that includes *Daspletosaurus*, *Tarbosaurus* and *Tyrannosaurus*. *Daspletosaurus* is known from multiple species that cover extensive geographic, ecological and temporal ranges, and it is sensible to maintain its generic distinction from *Tyrannosaurus*. All tyrannosaurid species have consistent ontogenetic trends. However, one needs to be cautious in assessing ontogenetic stage because many characters are size-dependent rather than age-dependent. There are relatively few osteological differences that can distinguish tyrannosaurid species at any age. For example, *Nanotyrannus lancensis* is probably a distinct species from *Tyrannosaurus rex* because there is no evidence of ontogenetic reduction of tooth counts in any other tyrannosaurid species. Some characters that are good for separating mature tyrannosaurids, such as differences in the sizes and shapes of maxillary fenestrae, are not useful for identifying the species of juveniles.

Key words: Dinosauria, Saurischia, Theropoda, Coelurosauria, Tyrannosauridae, Cretaceous, Alberta, skull anatomy.

Philip J. Currie [Philip.Currie@gov.ab.ca], Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, AB, T0J 0Y0 Canada.

Introduction

The earliest discoveries of tyrannosaurid theropods were generally poorly understood because of the incompleteness of the specimens recovered. Leidy (1856) described *Deinodon horridus* on the basis of isolated teeth from Montana, but even today it cannot be determined which Judithian tyrannosaurid genera they represent. The teeth of *Laelaps incrassatus* Cope, 1866 are clearly tyrannosaurid. However, the name *Laelaps* was preoccupied, and Marsh (1877) proposed the name *Dryptosaurus* as a replacement. *Aublysodon mirandus* is another tyrannosaurid established by Leidy (1868). These teeth are D-shaped in cross section, and are unquestionably tyrannosaurid premaxillary teeth. Interpreted as a gracile tyrannosaurid, at least one skeleton (Lehman and Carpenter 1990) has been referred to *Aublysodon mirandus*. Many more tyrannosaurid specimens were identified during the nineteenth century (Olshevsky 1995), but their names have not been used for Alberta tyrannosaurids.

A tyrannosaurid skull (NMC 5600) found by Joseph B. Tyrrell in 1884 near the present city of Drumheller was the first good tyrannosaurid from Alberta. Another skull (NMC 5601) was found in the same region by Thomas C. Weston in 1889. The two specimens from the Upper Campanian Horseshoe Canyon Formation were initially identified as *Laelaps incrassatus* by Cope (1892), who ignored the name *Dryptosaurus* that had been proposed by Marsh (1877). Lawrence Lambe (1903, 1904) referred the Alberta specimens to *Dryptosaurus incrassatus*. He clearly felt that *Dryptosaurus* was distinct from the somewhat older *Deinodon*. Because of the incomplete and undiagnosable nature of the type material for both *Dryptosaurus* and *Deinodon*, Osborn (1905) was justified to use the Drumheller specimens to establish a new genus and species, *Albertosaurus sarcophagus*. In the same paper he published the first description of *Tyrannosaurus rex*.

In 1914, Lambe established *Gorgosaurus libratus* for a well-preserved skeleton from today's Dinosaur Provincial Park. He followed it up in 1917 with what remains one of the best descriptions of any tyrannosaurid. Additional species of *Albertosaurus* and *Gorgosaurus* were described by Parks (1928) and Gilmore (1946). A major revision of the North American tyrannosaurids by Russell (1970) led to the synonymy of *Gorgosaurus* with *Albertosaurus*, and the establishment of a new tyrannosaurid species, *Daspletosaurus torosus*. Asian tyrannosaurid species of *Albertosaurus* and *Tyrannosaurus* were described by Maleev (1955, 1974), but are now generally referred to *Tarbosaurus bataar* (Currie 2000a).

Matthew and Brown (1922) and von Huene (1923, 1926) classified tyrannosaurids as giant coelurosaurs, but most palaeontologists regarded them as carnosaurs (Romer 1956,

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1966; Carroll 1988; Paul 1988; Molnar et al. 1990). It is now generally accepted that the original idea of coelurosaurian affinities is correct (Currie 1989; Holtz 1994, 2000, 2001).

Paul (1988) recognized two subfamilies of tyrannosaurids, the Aublysodontinae and the Tyrannosaurinae. The latter consisted of *Albertosaurus* (considered as the senior synonym of *Alectrosaurus* and *Gorgosaurus*), *Alioramus*, *Indosuchus*, and *Tyrannosaurus* (including *Daspletosaurus* and *Tarbosaurus*). Molnar et al. (1990) identified *Albertosaurus*, *Daspletosaurus*, *Nanotyrannus,* and *Tyrannosaurus* as valid North American tyrannosaurids. Olshevsky (1995) recognized *Albertosaurus*, *Aublysodon*, *Daspletosaurus*, *Gorgosaurus*, *Nanotyrannus*, and *Tyrannosaurus* as valid tyrannosaurid genera from western North America, and proposed two additional genera (*Dinotyrannus* and *Stygivenator*). Currie (2003) accepted *Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, and *Tyrannosaurus* as valid tyrannosaurid genera from western North America, and suggested that *Nanotyrannus lancensis* is distinct from *T. rex*. In a new phylogenetic analysis (Currie et al. 2003), *Albertosaurus*, and *Gorgosaurus* are linked in the subfamily Albertosaurinae, whereas *Alioramus*, *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* form a clade referred to as the Tyrannosaurinae.

In spite of the discovery of many well-preserved specimens of most tyrannosaurid genera, the taxonomy and relationships of this family have remained confusing and controversial (Russell 1970; Bakker et al. 1988; Paul 1988; Olshevsky 1995; Carr 1995, 1999). In part this relates to the fact that few tyrannosaurid specimens have been described in the kind of detail necessary to determine interrelationships. This is compounded by the fact that the ontogenetic, sexual, and individual variation of tyrannosaurid species has been until recently poorly understood. Matthew and Brown (1922) noted possible immature characters in the type specimen of *Gorgosaurus sternbergi* (AMNH 5664). Rozhdestvensky (1965) identified *Tarbosaurus efremovi*, *Gorgosaurus lancinator*, and *Gorgosaurus novojilovi* as juveniles of *Tarbosaurus bataar*, and suggested *Gorgosaurus lancensis* might be a young individual of *T. rex*. Russell (1970) discussed the ontogeny of tyrannosaurids of North America, and even reconstructed a juvenile tyrannosaurid skeleton. Carpenter (1992) showed that mature specimens of *Tarbosaurus* had deeper skulls, relatively shorter snouts, taller orbital fenestrae, more rugose postorbital bosses, relatively shorter and stouter metatarsals, and fused neurocentral sutures. Carr (1999) published the most thorough analysis of ontogenetic trends in tyrannosaurids and concluded that *Nanotyrannus lancensis* and *Maleevosaurus novojilovi* are probably immature *Tyrannosaurus*. Currie and Dong (2001) demonstrated that *Shanshanosaurus huoyanshanensis* is almost certainly a juvenile *Tarbosaurus bataar*, thereby increasing the known growth range of this species.

The size-related differences in tyrannosaurid proportions are, in most cases, independent of ontogenetic stage (Currie 2003). They cannot be used in isolation as evidence to show that small specimens are juvenile. Carr (1999) attempted to identify such differences by first analyzing the ontogenetic

differences in specimens of *Gorgosaurus*, then compared *Daspletosaurus torosus* with *T. rex*. Unfortunately, it is not always clear in his descriptions as to which are ontogenetic differences and which are taxonomically significant. Many of the described differences in proportions and shapes are undoubtedly size (but not necessarily age) dependent. This is a problem, because Carr (1999) was mostly comparing a relatively small specimen (his Stage 1) of *G. libratus* (ROM 1247) with large specimens (his Stage 4) of *Daspletosaurus* (FMNH PR308, NMC 8506) and *T. rex* (AMNH 5027). For example, the ventral margin of the angular of ROM 1247 is smoothly convex in lateral view, whereas there is a sharp inflection between the anterior process and the posterior plate in NMC 8506. No large specimen of *Gorgosaurus* is figured, nor is a small specimen of *Daspletosaurus*. However, young specimens of *G. libratus* (TMP 91.36.500) and *Daspletosaurus* sp. (TMP 94.143.1) show the first type of morphology, whereas all large tyrannosaurids (including TMP 81.10.1, *A. sarcophagus*) have a strong ventral inflection. This is also a potential problem in that *Albertosaurus* and *Gorgosaurus* were smaller at maturity than *Daspletosaurus*, *Tarbosaurus* and *Tyrannosaurus* (Currie 2003).

In recent years, the Royal Tyrrell Museum of Palaeontology has been successful in recovering tyrannosaurid skeletons from Upper Cretaceous strata in southern Alberta. Twenty-one skeletons, representing five species, have been collected, and are supplemented by several thousand isolated teeth and bones in the Tyrrell Museum collections.

One of the best specimens of *G. libratus* (TMP 91.36.500) was excavated in 1991 from the badlands of Dinosaur Provincial Park (Keiran 1999). It is an almost complete skeleton of a young adult, and in this paper forms the basis of the description of *Gorgosaurus*. The smallest known, reasonably complete skeleton is TMP 86.144.1, which in life was probably about 4.5 m long. The largest *G. libratus* skeletons (AMNH 5458, NMC 2120) are almost double that length.

Two skeletons (TMP 85.98.1, 86.205.1) of *A. sarcophagus* were collected within a few hundred meters of, and at the same level as, the site where the holotype (NMC 5600) was collected in 1884. They are not as well preserved as another specimen (TMP 81.10.1) excavated not far from where the paratype (NMC 5601) of *A. sarcophagus* was collected in 1889. A nearly complete skeleton of an immature individual of this species (TMP 86.64.1) was found less than a kilometre from the Tyrrell Museum. These specimens are supplemented by material collected from Barnum Brown's *Albertosaurus* bonebed (Currie 2000b).

The well-preserved skull of an immature *Daspletosaurus* sp. (TMP 94.143.1) provides our first glimpse of an early ontogenetic stage of this genus. It and several other specimens were collected in the Dinosaur Park Formation, whereas the holotype (NMC 8506) of *D. torosus* was recovered from the underlying Oldman Formation. It appears to represent a distinct species from the latter (Currie and Bakker in preparation). A possible third species of *Daspletosaurus* may be present in the Two Medicine Formation of Montana (Horner and Varricchio 1992).

The Tyrrell Museum has collected two skeletons of *T. rex*. TMP 81.12.1 was discovered by C. M. Sternberg in 1946 (Russell 1970) but was not excavated until almost 40 years later. The only cranial bone recovered is the left postorbital. The second specimen (TMP 81.6.1) includes a complete skull. Most other known specimens of *Tyrannosaurus* were examined by the author, and the holotype of *N. lancensis* (CMNH 7541) was studied in Cleveland. Almost thirty skulls of *Tarbosaurus bataar* were examined. Although the best specimens of *Alectrosaurus olseni* (AMNH 6554, GIN 100/50, GIN 100/51) and the only specimen of *Alioramus remotus* (PIN 3141-1) were studied, photographed and measured, they have less relevance to the taxa presently known in Alberta.

Albertosaurus, *Gorgosaurus*, *Nanotyrannus*, *Tarbosaurus* and *Tyrannosaurus* are monospecific genera represented respectively by *A. sarcophagus* Osborn 1905, *G. libratus* Lambe 1914, *N. lancensis* (Bakker et al. 1988), *Tarbosaurus bataar* Maleev 1955, and *T. rex* Osborn 1905. For the sake of brevity, the species names of these genera are not referred to in most of this paper. However, there are multiple species of *Daspletosaurus* (Horner et al. 1992; Carr and Williamson 2000), and evidence suggests that even within Dinosaur Provincial Park there are different species in the two dinosaur bearing formations. *Daspletosaurus torosus* Russell, 1970 was collected from the Oldman Formation, whereas most specimens come from high in the Dinosaur Park Formation. Until such time as the new *Daspletosaurus* specimens from Alberta, Montana and New Mexico are prepared, studied and described, they are best referred to as *Daspletosaurus* sp.

Abbreviations.—AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum of Natural History (now Natural History Museum), London; CMNH, Cleveland Museum of Natural History, Cleveland; FMNH, Field Museum of Natural History, Chicago; GIN, Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar; IVPP, Institute of Vertebrate Paleontology and Palaeoanthropology, Beijing; NMC, Canadian Museum of Nature, Ottawa; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow; ROM, Royal Ontario Museum, Toronto; SDNH, San Diego Museum of Natural History, SD; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller; UA, University of Alberta, Edmonton; USNM, United States National Museum, Smithsonian Institution, Washington; ZPAL, Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw.

Description

In the following sections, elements of *Gorgosaurus* (Figs. 1–4) will be described first. The rationale is that this is the most common (and possibly least derived) Alberta tyrannosaurid. The same elements of *Albertosaurus* are compared (Figs. 6–16), followed by those of *Daspletosaurus* (Figs. 18–36). The figures of *Gorgosaurus*, *Albertosaurus*, and *Daspletosaurus* are arranged taxonomically, rather than in the order they are referred to in the text. This is to improve the reader's chances of finding figures when leafing through the paper.

TMP 91.36.500 (Fig. 1) is a virtually complete skeleton of *Gorgosaurus libratus* that is 5.1 m in length from the premaxilla to the tip of the tail is. It was presumably a young adult. Although the neural arches are fused to the centra, the sutures are still visible. *Albertosaurus sarcophagus* is represented (Figs. 6–16) by TMP 81.10.1, which was about 8 m long at the time of death, and TMP 86.64.1, an almost complete, 6.5 m long articulated skeleton found near the Tyrrell Museum. Most of the *Daspletosaurus* specimens are large individuals. However, the best-preserved skull is that of TMP 94.143.1 (Figs. 18–36), an animal which was approximately 5.8 m long.

The skull (Fig. 2) of TMP 91.36.500 (*G. libratus*) is 640 mm long when measured between the premaxilla and the oc-

Fig. 1. Reconstruction of an immature *Gorgosaurus libratus*, based TMP 91.36.500, a complete skeleton (5.1 m long) from the Dinosaur Park Formation (Campanian, Upper Cretaceous) of Alberta, Canada.
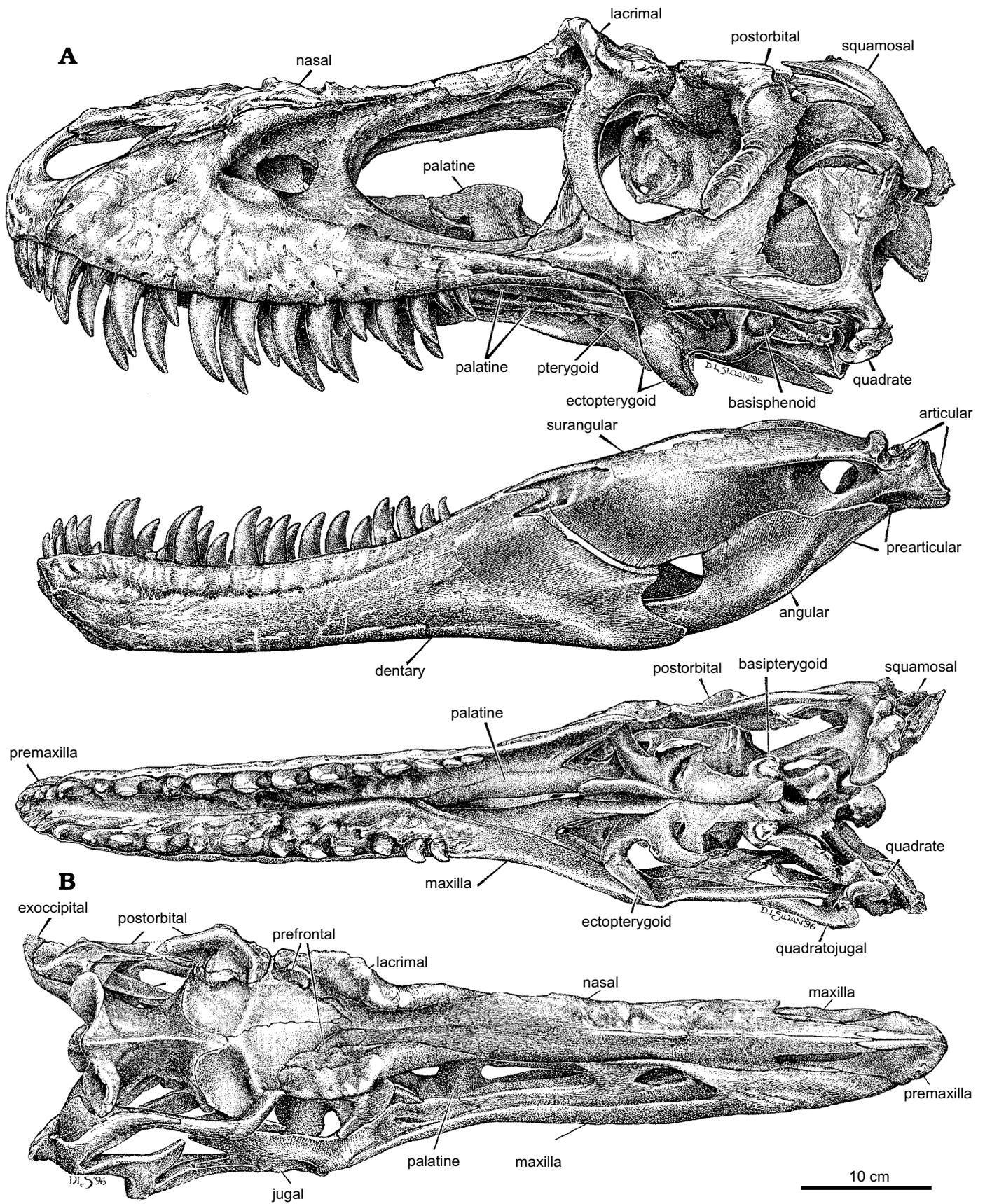
A

nasal

lacrimal

postorbital

squamosal

palatine

palatine   pterygoid

D.L.SLOAN'95

quadrate

ectopterygoid   basisphenoid

surangular

articular

prearticular

angular

dentary

postorbital   basipterygoid   squamosal

palatine

premaxilla

quadrate

B

maxilla

ectopterygoid

D.L.SLOAN'96

quadratojugal

exoccipital   postorbital   prefrontal

lacrimal

nasal

maxilla

maxilla

premaxilla

palatine   maxilla

DLS'96

jugal

10 cm

Fig. 2. *Gorgosaurus libratus* (TMP 91.36.500). Specimen drawing of skull in lateral (**A**), palatal (**B**), and dorsal (**C**) views.
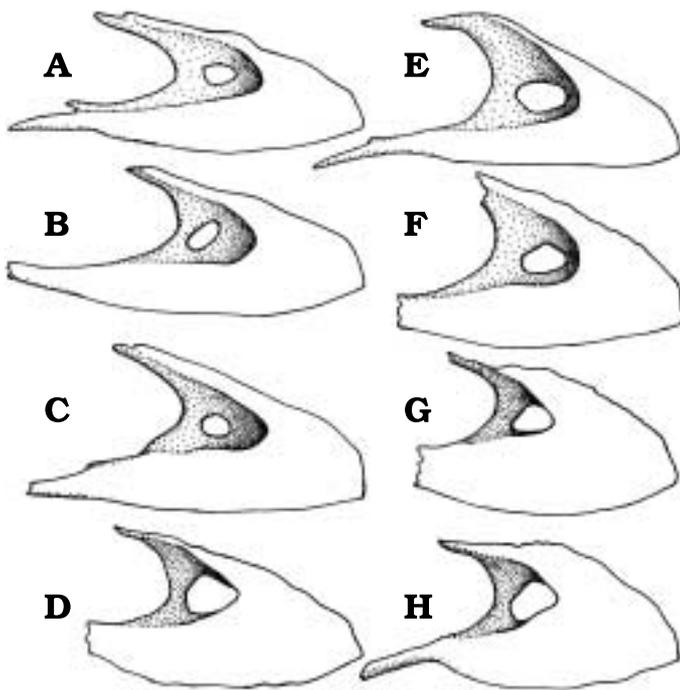
Fig. 3. Tyrannosaurid maxillae demonstrating the positions and sizes of the maxillary fenestrae. Contours show right maxillae in lateral view. Lengths of maxillary tooth rows included in brackets where known. **A**. *Gorgosaurus libratus*, juvenile (302 mm), TMP 91.36.500. **B**. *Gorgosaurus libratus*, adult (460 mm), NMC 2120. **C**. *Albertosaurus*, juvenile (335 mm), TMP 86.64.1. **D**. Mature (530 mm) *Daspletosaurus torosus*, NMC 8506. **E**. Juvenile (180 mm), probably *Tarbosaurus bataar*, IVPP V4878. **F**. Young *Tarbosaurus bataar*, GIN 100/777. **G**. Adult *Tarbosaurus bataar*, GIN 100/65. **H**. Adult (600 mm) *Tyrannosaurus rex*, LACM 23844.

cipital condyle, and 670 mm between the premaxilla and the posteroventral margin of the quadrate. The only smaller, reasonably complete skull of *G. libratus* (TMP 86.144.1) is disarticulated, but would have been 50 cm long. AMNH 5664 (the type specimen of *Gorgosaurus sternbergi*) has a slightly larger skull with a lateral length of 678 mm. Cranial fragments and a pair of nearly complete lower jaws (TMP 94.12.155) are from a smaller *G. libratus* individual whose skull would have been 364 mm long (based on a logarithmic comparison [y = 1.1068x – 0.0317, r² = 0.95] of 22 tyrannosaur skulls where both skull and jaw lengths are known).

The small skull of *Daspletosaurus* sp. (TMP 94.143.1) is about 620 mm long between the premaxilla and quadrate. Small, juvenile skulls are known for two other tyrannosaurids—that of *Nanotyrannus lancensis* (CM 7541) is 575 mm long (premaxilla to occipital condyle) and that of *Shanshanosaurus huoyanshanensis* (IVPP V4878) is an estimated 288 mm long (Currie and Dong 2001).

The skulls of smaller tyrannosaurids are relatively long and low compared to the adults. The maximum cranial width of TMP 91.36.500 is 160 mm across the postorbitals, which is half that of an adult *G. libratus* (UA 10), suggesting that the skull was relatively narrower at the back in juveniles. The equivalent width measurements in *Daspletosaurus* sp. (TMP

94.143.1) and *Nanotyrannus*, which have shorter skulls, are respectively 154 and 210 mm. These genera are clearly broader across the postorbital region of the skull at any equivalent age.

The antorbital fenestra of the small *G. libratus* (TMP 91.36.500) makes up 37% of the antorbital skull length and 62% of the preorbital height. These proportions are almost the same (38%, 63%) in an adult *G. libratus* (UA 10), which shows that there is little ontogenetic change in the length of the antorbital fenestra during growth.

Unlike allosaurids, sinraptorids and most other theropods, the tyrannosaurid antorbital fossa does not extend onto the nasal. At the level of the back of the maxillary tooth row, the ventral edge of the antorbital fossa extends more than 10 mm below the ventral border of the antorbital fenestra in *Gorgosaurus*, whereas the two margins almost coincide in *Daspletosaurus* (Fig. 16). *A. sarcophagus* (NMC 5601, TMP 81.10.1, 85.98.1) seems to have a wider, more horizontal separation between the two margins than *G. libratus*. The promaxillary slit is relatively smaller in *Daspletosaurus* (Fig. 18) and *Tyrannosaurus* (Brochu 2002) than it is in *Albertosaurus* (Russell 1970) and *Gorgosaurus*.

The maxillary fenestra is midway between the anterior margins of the antorbital fossa and antorbital fenestra (Figs. 2A, B, 3A) in *Gorgosaurus* of any age. Small tyrannosaurine specimens are similar to *Gorgosaurus* in that the maxillary fenestra is relatively small and central (Fig. 3E, F). However, mature tyrannosaurines have greatly enlarged maxillary fenestrae with anterior margins that are coincident with the anterior margins of the antorbital fossae (Fig. 3D, G, H).
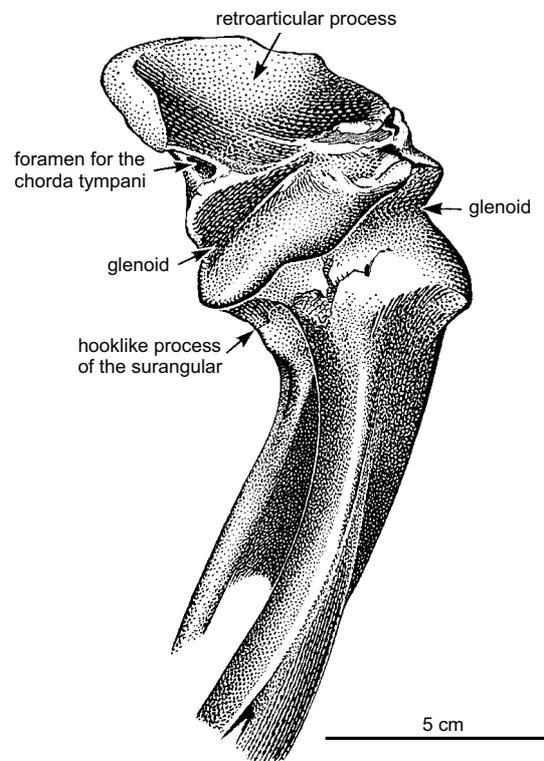

Fig. 4. *Gorgosaurus libratus* (TMP 91.36.500). Dorsal view of back of left mandible showing articular and part of surangular.
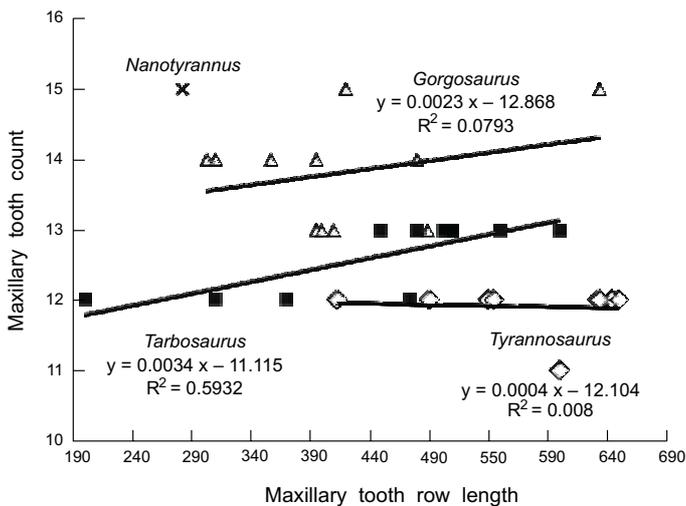
Fig. 5. Comparison of maxillary tooth counts to size in tyrannosaurids. The X-axis is the length of the maxillary tooth row, and the Y-axis represents the number of maxillary teeth. *Gorgosaurus* (triangles) and *Tarbosaurus* (solid squares) show a slight tendency to increase the number of teeth with size, whereas *Tyrannosaurus* (diamonds) shows a slight tendency to decrease the number. Known specimens of *Daspletosaurus* show an even stronger tendency to increase maxillary tooth counts with increased size, but the genus is not included here because it is highly probable that the sample includes more than one species. None of these figures are significant enough to attribute any real meaning to them, but they falsify the hypothesis that there is a tendency for tooth reduction in tyrannosaurids (Carr 1999). *Nanotyrannus* (X) is well outside the range for known specimens of *Tyrannosaurus*.

The orbits of juvenile tyrannosaurids are only slightly higher than long. Contrary to Carr (1999), this is not so much of a juvenile characteristic as it is of small size, and all theropod adults smaller than tyrannosaurid juveniles also have large, round orbits.

Premaxilla.—The pitted external surface of the premaxilla of *Gorgosaurus* is higher than long. The supranarial process only diverges slightly from the long subnarial process. The gently curving contact with the maxilla is interrupted by a slit-like subnarial foramen. The distal end of the subnarial process is separated from the maxilla by the nasal. In dromaeosaurids and ornithomimimids, the subnarial process of the premaxilla is wedged between the nasal and maxilla. The subnarial process of the *Gorgosaurus* premaxilla meets and overrides the nasal beneath the external naris as in *Daspletosaurus* (Fig. 18), *Nanotyrannus*, *Tarbosaurus* (Maleev 1974), and *Tyrannosaurus*. This may not be the case in some specimens of *Tyrannosaurus* (Brochu 2002). Russell (1970) reported that the premaxilla did not meet the nasal below the external naris in *Daspletosaurus torosus*, and used this characteristic to distinguish *Daspletosaurus* from *Albertosaurus*. However, the sutures for the premaxilla and nasal on the maxillae (NMC 8506, TMP 89.17.53, 94.172.115) demonstrate that the subnarial processes of *Daspletosaurus* met below the external naris in all specimens.

The nasal process in immature and mature specimens of *Gorgosaurus*, *Albertosaurus*, juvenile *Daspletosaurus*, and

juvenile *Tarbosaurus bataar* (GIN 100/777) are distally forked. The medial process of the fork sits in a groove on the dorsal surface of the nasal, and the distal ends of the paired premaxillae are separated from each other by the nasals. In *Nanotyrannus*, *Tyrannosaurus* (Holtz 2001, Brochu 2002), and mature specimens of *Daspletosaurus* and *Tarbosaurus*, the nasal processes are closely appressed and taper posteriorly to separate the anterior tips of the nasals. This character is gradational with the posterior tips of the nasal processes always being separated in albertosaurines and juvenile specimens of *Daspletosaurus* and *Tarbosaurus*. At least some mature *Daspletosaurus torosus* (NMC 8506) and *T. rex* specimens (BHI 3033) show a remnant of the groove in the nasal for the posterior tip of the premaxilla. The nasal processes of the premaxillae are separate distally in at least one specimen of *T. rex* (TMP 81.6.1).

In ventral view, the teeth of the paired premaxillae of *G. libratus* (TMP 91.36.500) form a semicircle that is wider than anteroposteriorly long. The premaxilla forms the anterior wall of the alveolus for the first maxillary tooth, an unusual arrangement amongst theropods.

Maxilla.—Almost half the maxillary length of *G. libratus* (TMP 91.36.500) is in front of the antorbital fenestra. One of the foramina on the external surface is relatively large and anteriorly oriented, and is connected to the subnarial foramen by a depression (Fig. 2A). As in *Albertosaurus* (Fig. 6A), *Alioramus* (Kurzanov 1976), *Daspletosaurus* (Fig. 18A), and *Tyrannosaurus* (Brochu 2002), there is a second major row of foramina that arches above the alveolar margin.

The posterior end of the maxilla bifurcates into two processes (Fig. 2A), the lower of which underlies the jugal. The medial surface of this process extends higher than the lateral surface, and the jugal sits in a shallow trough between the two. The upper process is a vertical plate that separates two processes at the front of the jugal, the outer one of which covers the lateral surface of the maxilla. The medial edge of the distal end of the maxilla reaches the ectopterygoid (Fig. 2B), although there are no conspicuous contact surfaces on either bone.

In all tyrannosaurids, the antorbital fossa forms a smooth-walled depression in the ventral margin of the posterodorsal process. Dorsally there is a laterally rugose ridge that separates the antorbital fossa and the nasal other than for a short distance posteriorly. Distally, the posterodorsal process bifurcates to embrace the margins of the anterodorsal process of the lacrimal. The lower of the two prongs contacts the lower surface of this process, whereas the shorter upper prong overlaps the lateral surface. In TMP 83.36.100 (*G. libratus*), the lacrimal extends anteriorly more than 5 cm along the medial surface of the posterodorsal process of the maxilla. The maxilla-lacrimal contacts of *A. sarcophagus* (TMP 86.64.1) and *Daspletosaurus* (Fig. 18A) are similar, although the anterior tip of the lacrimal is not separated from the maxilla by the nasal in mature specimens of *Daspletosaurus* sp. (TMP 85.62.1, 98.48.1), *Tarbosaurus* (Hurum and Sabath 2003), and some specimens of *Tyrannosaurus*.
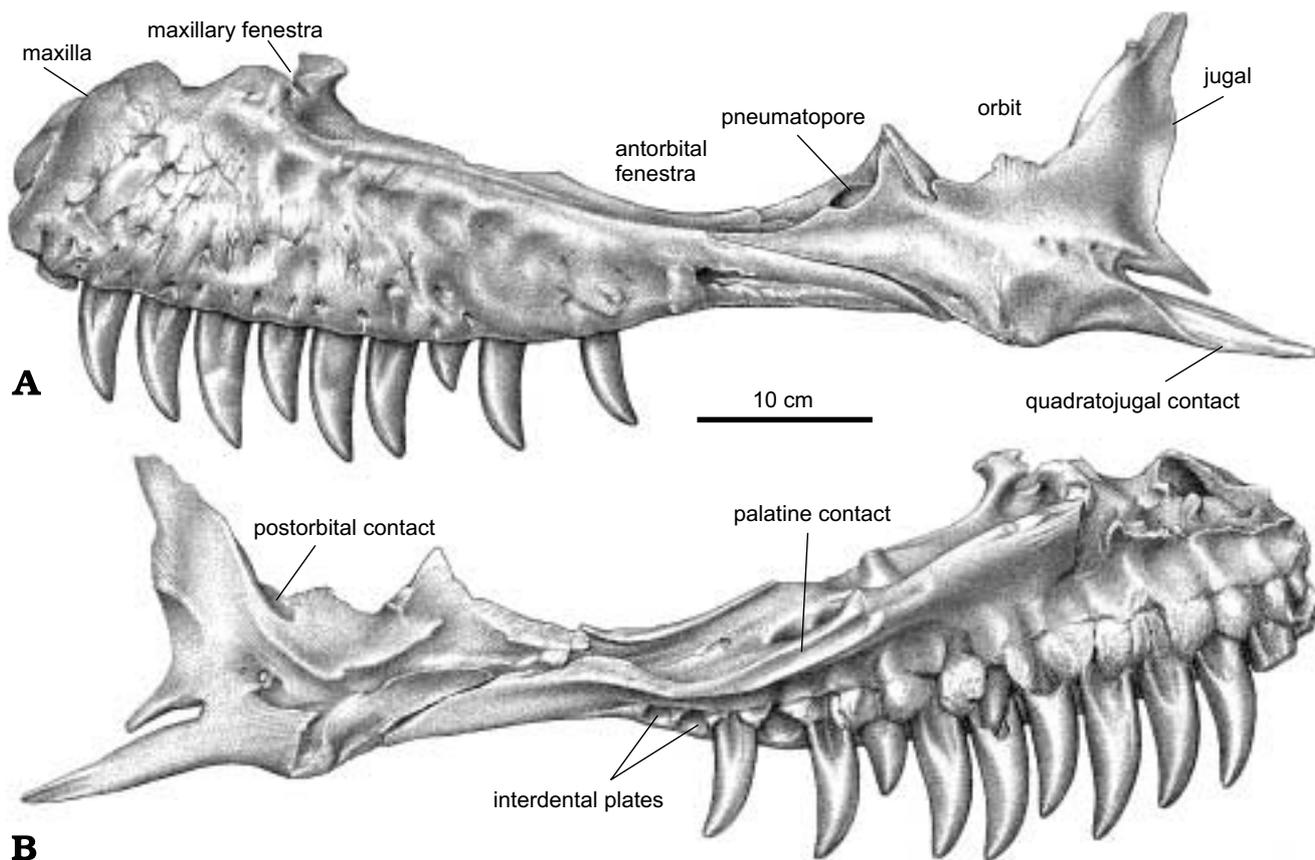
Fig. 6. *Albertosaurus sarcophagus* (TMP 81.10.1). Left maxilla and jugal in lateral (**A**) and medial (**B**) views.

The anterodorsal process on the medial side of the maxilla in tyrannosaurids protrudes only a short distance beyond the end of the bone to contact the inner surface of the premaxilla. The intermaxillary suture of *G. libratus* (TMP 85.11.3) has three prominent ridges and grooves above the first four maxillary teeth along the internal surface of the palatal shelf of the maxilla. The vomer overlapped the ventral surface at the back of this process. From a point above the fourth maxillary tooth to the level of the anterior margin of the antorbital fenestra above the eighth maxillary tooth, the internal margin of the palatal shelf is smooth and rounded to form part of the boundary of the internal naris. Behind this point there is a well-defined suture for the palatine.

The lower surface of the palatal shelf in *Gorgosaurus* has pronounced depressions that coincide with the positions of dentary teeth. The four deepest depressions are between maxillary tooth positions 2–3, 3–4, 4–5 and 5–6. These correspond to mandibular teeth 4 to 7, which are the longest teeth of the dentary. In tyrannosaurids preserved with closed jaws, the dentary teeth are found resting in these depressions. A second, less distinct set of depressions is dorsomedial to maxillary tooth positions 9 to 13 in *Gorgosaurus*, but is much shallower in *Tarbosaurus bataar* (PIN 551-1) and *T. rex* (BHI 3033, UCMP 118742). Similar depressions are much more pronounced and can be seen along the entire palatal shelf of *A. sarcophagus* (Fig. 6B, TMP 95.25.83, TMP 98.63.88, TMP 99.50.140), which seems to be an autapomorphic character.

The bottom of the maxillary fenestra in the small *G. libratus* (TMP 91.36.500) is positioned a centimetre above a line drawn between the lower margins of the external naris and the antorbital fenestra. In medial view, the maxillary fenestra opens into the maxillary antrum, which in turn is widely open medially. It is bound dorsally in TMP 83.36.100 (*G. libratus*) and other specimens by a low but conspicuous ridge to which attached a sheet of cartilage (Witmer 1997) or bone (maxillary antrum wall of Brochu 2002). This separation between the nasal passage and the maxillary antrum is osseous in many primitive theropods (Currie and Zhao 1993a). The postantral pillar is a much thinner version of the posteromedial plate of bone that encloses the maxillary antrum in *Allosaurus* (Madsen 1976), *Deinonychus* (Ostrom 1969), *Sinraptor* (Currie and Zhao 1993a) and *Troodon* (Currie 1985). There are relatively high but separate interdental plates (Fig. 6B) in all tyrannosaurids.

Nasal.—Tyrannosaurid nasals are coossified, although the suture is open anteriorly to a level behind the external nares, and can still be seen posteriorly between the lacrimals. The nasals must have coossified at a very early age in tyrannosaurids because even small nasals of *Tarbosaurus* and *T. rex* (LACM 28471) are fused to the same degree. The internasal suture of *Eotyrannus* also seems to be completely fused (Hutt et al. 2001). In *Gorgosaurus*, *Albertosaurus* (Fig. 7), and *Eotyrannus*, the nasals are broadest immediately behind the
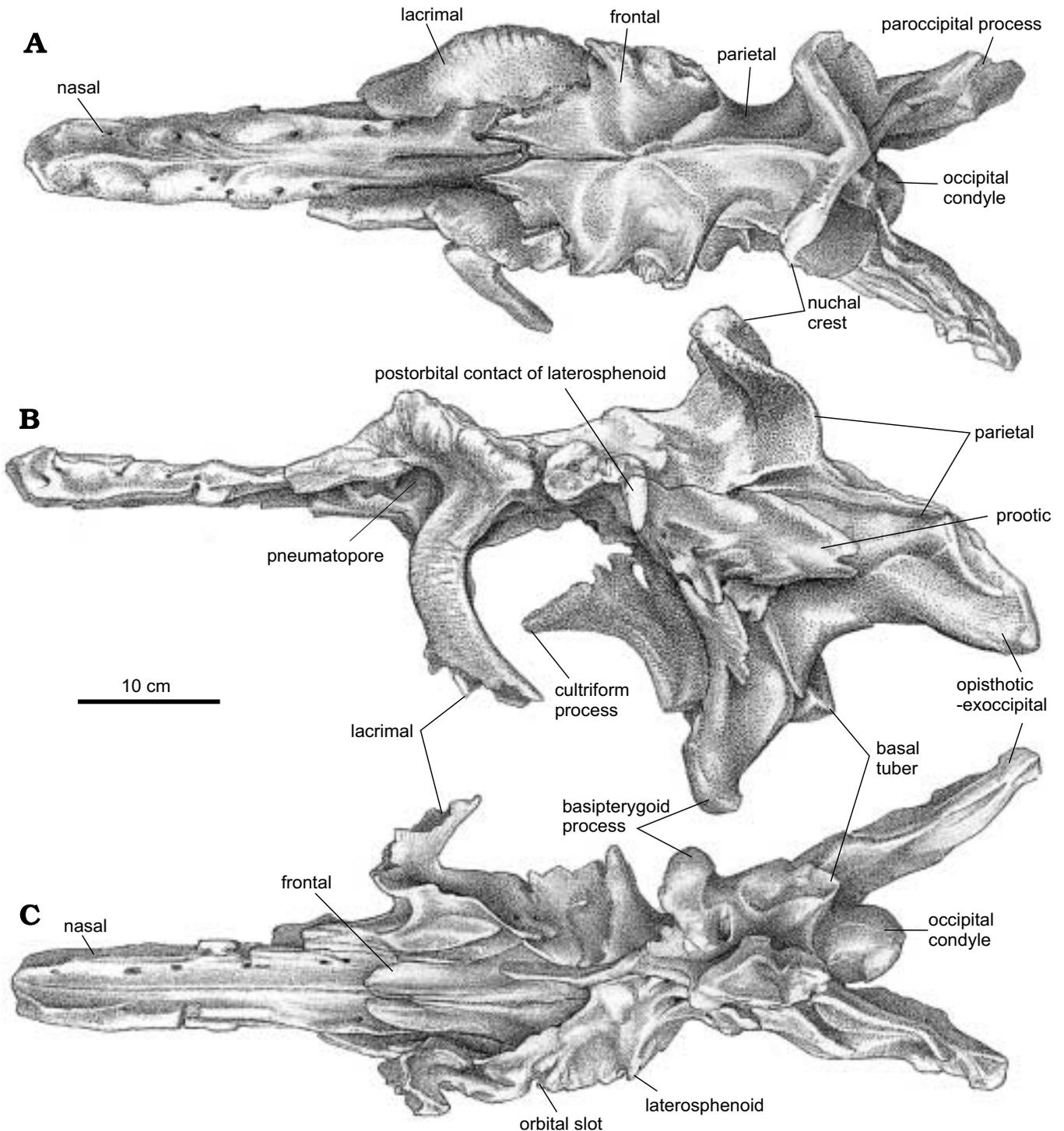
A

nasal

lacrimal

frontal

parietal

paroccipital process

occipital condyle

nuchal crest

B

postorbital contact of laterosphenoid

parietal

prootic

pneumatopore

cultriform process

opisthotic -exoccipital

10 cm

lacrimal

basal tuber

basipterygoid process

C nasal

frontal

occipital condyle

laterosphenoid

orbital slot

Fig. 7. *Albertosaurus sarcophagus* (TMP 81.10.1). Specimen drawing of top of skull in dorsal (**A**), lateral (**B**), and ventral (**C**) views.

external nares, are constricted by a third between the anterior tips of the lacrimals, and expand at the front of the prefrontals. This is similar in juveniles of *Daspletosaurus* (Fig. 18B) and *Tarbosaurus bataar* (GIN 100/66), but the nasals of mature individuals of these two genera and *Tyrannosaurus* are further constricted behind the junction of the nasal, lacrimal and maxilla. The constriction is extreme in large specimens of *T. rex* (BHI 3033) where the nasal is only one sixth its

maximum width (Holtz 2001). In cross-section, the surface of the paired nasals is dorsally convex and rugose back to the level of the lacrimals (Fig. 2A). Behind this point, the rugose surface splits and diverges to become continuous with rugosities on the anterolateral surfaces of the lacrimals, leaving a flat, smooth dorsal surface on the nasals.

Anteriorly, the nasals diverge to clasp the back ends of the premaxillae (Fig. 2C). In addition, each nasal splits anteriorly

to send a short prong to separate the posterior tips of the premaxillae as in mature specimens of *G. libratus* (TMP 94.12.602), *A. sarcophagus* (TMP 86.64.1), juvenile *Daspletosaurus* (Fig. 18B), and juvenile *Tarbosaurus bataar* (GIN 100/777). The nasal process of the premaxilla overlaps the nasal between its two anterodorsal prongs. There does not seem to be a medial prong in mature specimens of *D. torosus* (NMC 8506), *Daspletosaurus* sp. (TMP 98.48.1) or *Tarbosaurus bataar* (ZPAL MgD-I/4), or in juveniles of *T. rex* (LACM 23845, TMP 81.6.1). This is clearly not an easy character to code given ontogenetic changes and preservational distortion.

Beneath the naris, the nasal has tapering process that sits in a shallow groove on top of the maxilla. The subnarial process of the premaxilla overlaps it anteriorly. The nasal forms the dorsal boundary of the antorbital fossa for only a short distance in *G. libratus* (4 cm in TMP 91.36.500, 2 cm in TMP 83.36.100 and UA 10). There is no pneumatic invasion of the nasal such as is seen in *Allosaurus*, *Monolophosaurus*, *Sinraptor* and other carnosaurs (Currie and Zhao 1993a).

Along the entire ventrolateral margin, the nasal has a system of tongue and groove contacts for the maxilla, lacrimal and prefrontal. Most of the subnarial process has a rounded edge that sits in a groove on the dorsal surface of the maxilla. Behind the external naris, however, both the nasal and the maxilla have grooves along the edges where they are in contact. The contacts are fundamentally the same in larger, mature specimens of *Gorgosaurus* and *Albertosaurus* (Fig. 6C), and the juvenile specimen of *Daspletosaurus* (Fig. 18A). In contrast, transverse ridges break up this groove in mature tyrannosaurines (Hurum and Sabath 2003). The back of this groove is bound laterally by a fingerlike process that wraps around the anterior tip of the lacrimal. This process is absent in mature specimens of *Daspletosaurus*, *Tarbosaurus*, and some specimens of *Tyrannosaurus* (Hurum and Sabath 2003), but is found in the juvenile specimen of *Daspletosaurus* (Fig. 18A) and in several specimens of *T. rex* (TMP 81.6.1, Brochu 2002). Near the back of the nasal is a simple butt joint for the prefrontal. In lateral view, the curvature of the nasal maxillary suture is very uniform in tyrannosaurids. The margin of the nasal is concave behind the subnarial process, but becomes convex above the antorbital fenestra. Overall, the maxillary-nasal contact is an elaborate articulation that allowed some mediolateral rotation of the maxilla in albertosaurines and juvenile tyrannosaurines.

The dorsal surface of the nasal of *G. libratus* (TMP 91.36.500) is pierced by a row of about ten conspicuous foramina that pass anterodorsally from the inner surface of the bone. The most anterior foramen is at the back of the external naris, and the most posterior is level with the lacrimal "horn". Additional, more randomly distributed foramina are found throughout the sculptured region, especially at the base of the subnarial process. A similar foramen distribution is evident in *Albertosaurus* (Fig. 6A) and *Daspletosaurus* (Fig. 18B). There are fewer of these foramina in *Tarbosaurus* and *Tyrannosaurus* (Hurum and Sabath 2003).

In *Gorgosaurus*, the most posterior point of the nasal is at its posterolateral corner (Fig. 2C, NMC 2120, TMP
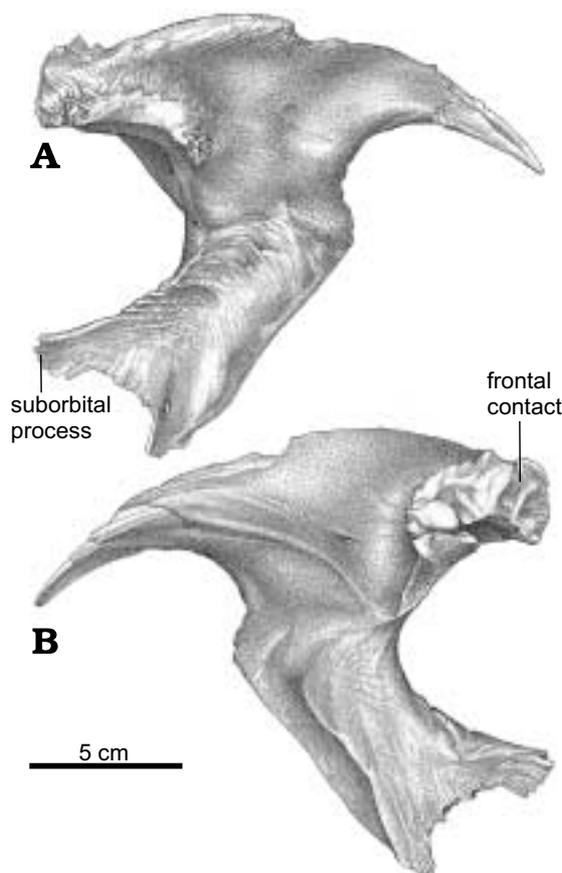

Fig. 8. *Albertosaurus sarcophagus* (TMP 81.10.1). Left postorbital in lateral (**A**) and medial (**B**) views.

94.12.602, TMP 2000.12.11, USNM 12814), which is also true for some specimens of *Daspletosaurus* sp. (Fig. 18B, TMP 98.48.1), *Nanotyrannus*, *Tarbosaurus bataar* (PIN 553-1), and *T. rex* (AMNH 5027, BHI 3033, FMNH PR2081, LACM 23845, TMP 81.6.1). In contrast, the midline process of the nasal extends as far or farther posteriorly than the posterolateral corner in *Albertosaurus* (Fig. 6A) and some specimens of *Daspletosaurus* (NMC 8506, TMP 85.62.1) and *Tyrannosaurus*. Because of the variability in *Daspletosaurus* and *Tyrannosaurus*, this character (Holtz 2001) may have questionable use in phylogenetic analyses.

In dorsal aspect the posterior margin of the nasal turns anteromedially at an acute angle from the lateral margin. This part of the nasal overlaps a long tongue-like process of the frontal. However, near the midline there is always a short but conspicuous posterior process (the medial frontal process of Carr 1999) in tyrannosaurids that along with its mate from the other nasal sits in a conspicuous midline groove in the dorsal surface of the paired frontals. In TMP 91.36.500 (*G. libratus*), this process is more than 2 cm long. A groove in the dorsal surface of the nasal separates the base of the process from the more lateral region of the nasal.

As pointed out by Russell (1970), the paired nasals expand posteriorly between the lacrimals in *Gorgosaurus* (Fig. 2C) and *Albertosaurus* (Fig. 6A). This is presumably the
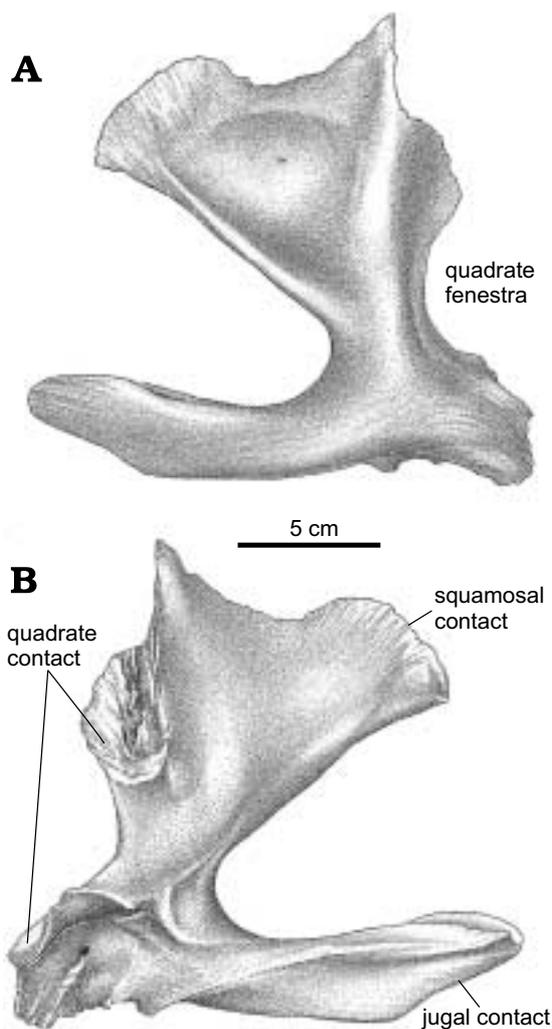
Fig. 9. *Albertosaurus sarcophagus* (TMP 81.10.1). Left quadratojugal in lateral (**A**) and medial (**B**) views.

plesiomorphic state because it is also found in carnosaurs like *Sinraptor* (Currie and Zhao 1993), and in the primitive tyrannosauroid *Eotyrannus* (Hutt et al. 2001). The nasals remain more or less the same width in this region in small specimens of *Daspletosaurus* (Fig. 18B) and *Tarbosaurus bataar* (GIN 100/66) or become narrow between the anterior tips of the prefrontals in larger specimens. The nasals also narrow posteriorly in *Tarbosaurus* and *T. rex* (LACM 23845), although it is not as conspicuous in *Nanotyrannus* (determined by the width of the nasal suture on the frontal) and juvenile specimens of *T. rex* (LACM 28471). The nature of the contact between the front of the lacrimal and the nasal is also characteristic of certain genera. Like *G. libratus* and *A. sarcophagus*, each of the nasals of several *T. rex* (BHI 3033, LACM 23845, TMP 81.6.1) have a distinct finger-like, lateral process that clasps the anterior end of the lacrimal. This is not evident in full-grown *Daspletosaurus* sp. (TMP 85.62.1, 98.48.1) and *T. rex* specimens (LACM 23844). Reduction of this process has previously been identified as an ontogenetic trend (Carr 1999).

Lacrimal.—In *Gorgosaurus* (Fig. 2A) and *Albertosaurus* (Fig. 6B), the dorsolateral margin of the lacrimal is raised into a ridge that forms a conspicuous lacrimal "horn" anterodorsal to the orbit. Ontogenetically, it is poorly developed in juvenile *G. libratus* (TMP 86.144.1), is sharp and pronounced in young adults (Fig. 2A), and becomes wider, more massive and less pronounced in large individuals (NMC 2120, TMP 94.12.602). Similar trends are evident in *A. sarcophagus* (Fig. 6B, TMP 81.10.1, 86.64.1). Juvenile *Daspletosaurus* (Fig 18A) have a low mound in the same position, but as in other tyrannosaurines this develops into an elongate, inflated ridge in adults (NMC 8506, TMP 85.62.1, 2001.36.1). MOR 590, a possible new species of *Daspletosaurus*, is intermediate in size and inflation of the lacrimal. An immature specimen of *Tarbosaurus bataar* (GIN 100/66) has pronounced lacrimal horns that are more conspicuous in lateral view than the postorbital boss. In large specimens of tyrannosaurids, the interiors of the lacrimal "horn" (in albertosaurines) and swelling (in tyrannosaurines) are hollow. The bone surrounding the sinus can be less than a few millimeters thick, and in large individuals like MOR 555 is penetrated by what appear to be small pneumatic foramina. It is unlikely that tyrannosaurs engaged in head butting (Bakker 1986, Bakker et al. 1988), even though the frontals and parietals are disproportionately thick, solid bones. Carr (1999) referred to the lack of a horn in *Tyrannosaurus* and *Tarbosaurus*, although this apparent lack is due to the inflation of the entire dorsal ramus of the lacrimal into an elongate ridge rather than a conspicuous horn. The thickness of the lacrimals in these genera and *Daspletosaurus* are comparable to the
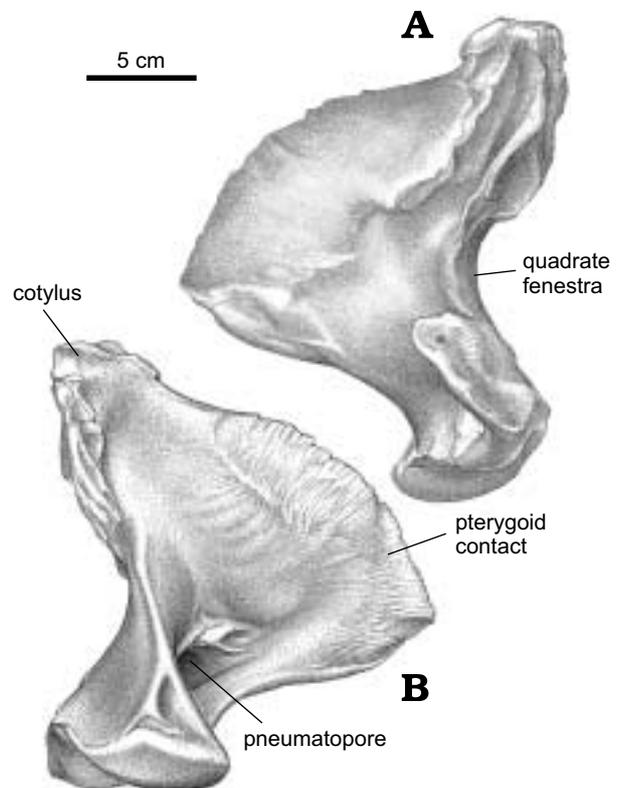

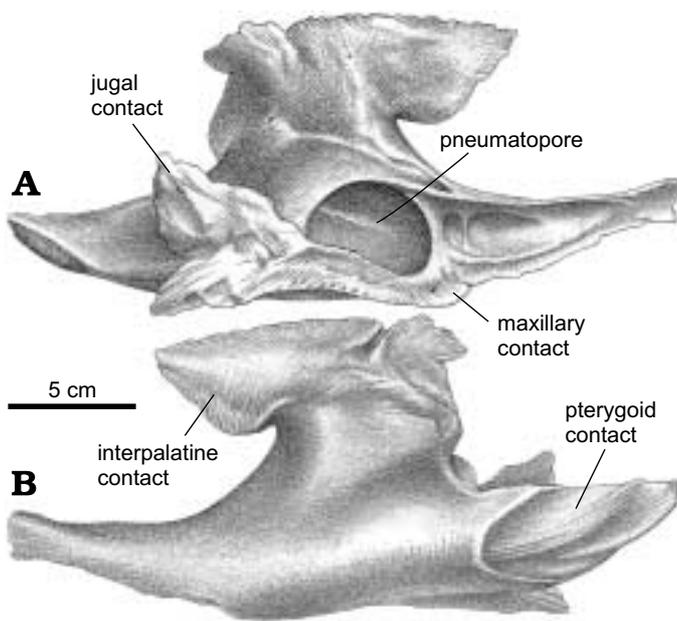Fig. 10. *Albertosaurus sarcophagus* (TMP 81.10.1). Left quadrate in lateral (**A**) and medial (**B**) views.

Fig. 11. *Albertosaurus sarcophagus* (TMP 81.10.1). Right palatine in lateral (**A**) and medial (**B**) views.

least two lacrimal ducts penetrate the medial ridge on the preorbital bar at midheight. The preorbital bar is strengthened by a vertical ridge (Fig. 19) on the medial surface, which gives it a T-shaped cross-section at midheight. Dorsally the ridge is continuous with the ventral process of the prefrontal. Ventrally the ridge twists anteriorly to wrap around the back of the anterodorsal process of the jugal. It extends beyond this region to gain lateral exposure, although it is still separated from the lateral surface of the preorbital bar by a conspicuous vertical groove (within the base of which the anterodorsal process of the jugal sits). The two laterally exposed plates diverge ventrally as the smooth-surfaced, more medial one expands anteriorly. It passes onto the inside surface of the jugal where it has a weak, squamose suture that does not contact either the maxilla or the ectopterygoid.

The lateral surface of the lacrimal passes to the outside surface of the jugal where it forms a squamose suture that is triangular in outline. In *Gorgosaurus* and *Albertosaurus*, this ventrolateral process forms the posterior margin of the antorbital fossa as it leads into the pneumatopore in the jugal. As pointed out by Russell (1970), this is not the case in *Daspletosaurus*, where the ventrolateral process does not form a conspicuous ridge. *Nanotyrannus*, *Tarbosaurus* and
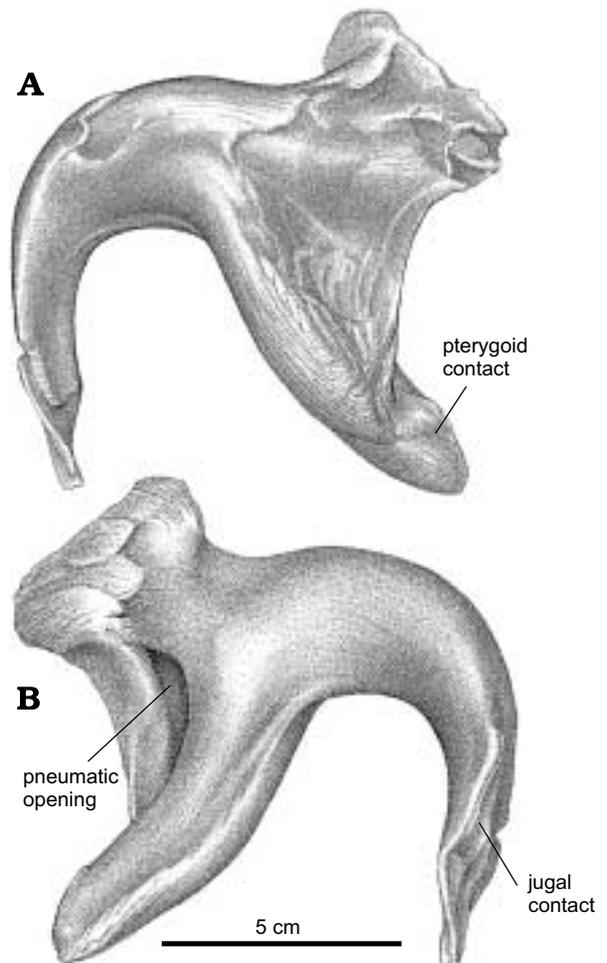
height of the horn in *Gorgosaurus*. For example, the lacrimal horn is 57 mm high in TMP 94.12.602 (a large *G. libratus*), but is 70 mm high in a slightly larger *Daspletosaurus* sp. (TMP 85.62.1).

The center of the horn is partially size dependent. In small specimens of *G. libratus* like TMP 91.36.500, it is positioned over the pneumatic fossa (Fig 2A). In larger specimens of *G. libratus* (UA 10), the center is above the front of the pneumatic fossa as in small specimens of *Daspletosaurus* (Fig. 18A) and large specimens of *Albertosaurus* (Fig. 6B).

In dorsal aspect, the lacrimal is a curved plate of bone with limited exposure (Figs. 2C, 6A, 18B). A millimeter wide slot in the small *G. libratus* (TMP 91.36.500) that gives the frontal access to the orbital rim separates the lacrimal from the postorbital. This gap closes in the largest specimens of *G. libratus* (TMP 94.12.602, UA 10) as the lacrimal contacts the postorbital.

Anteriorly, the lacrimal of *Gorgosaurus* sits in a groove on top of a long tapering process of the maxilla, and bifurcates at its contact with the maxilla and nasal. The lower process extends along the medial surface of the posterodorsal process of the maxilla, whereas the tapering upper process wraps around onto the dorsal surface of the nasal to sit in a shallow groove medial to the fingerlike process.

Posterodorsally, the tyrannosaurid lacrimal is separated from the back of the nasal and front of the frontal by the prefrontal. The crescentic prefrontal sutures on the lacrimals of an immature *A. sarcophagus* (TMP 86.144.1) extend part way down the preorbital bar. The posterior end of the lacrimal of most tyrannosaurids plugged into a concave, vertically oriented suture on the frontal.

In lateral view, the preorbital bars of tyrannosaurid lacrimals are convex anteriorly and concave posteriorly. At

Fig. 12. *Albertosaurus sarcophagus* (TMP 81.10.1). Left ectopterygoid in dorsal (**A**) and ventral (**B**) views.
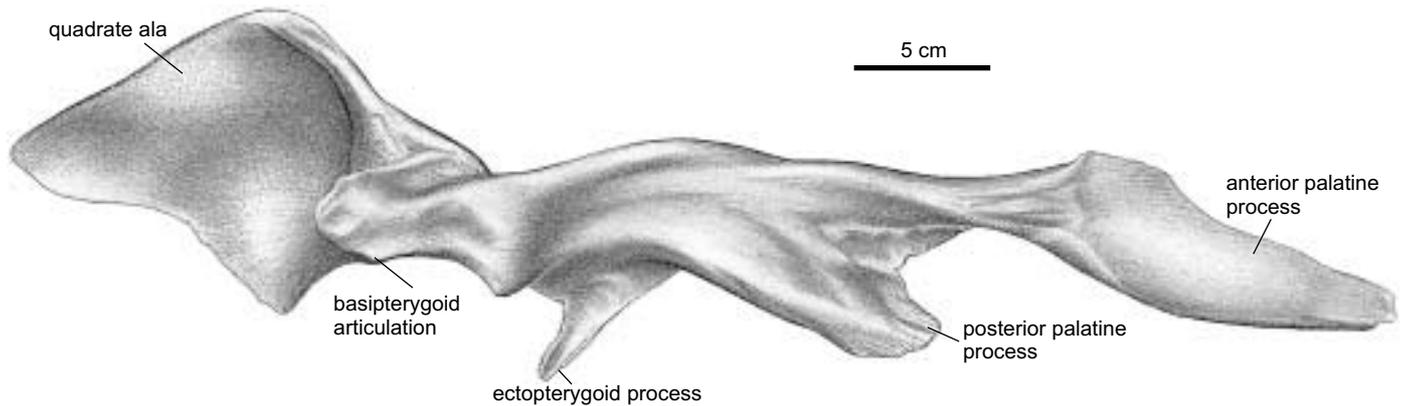
Fig. 13. *Albertosaurus sarcophagus* (TMP 81.10.1). Left pterygoid in ventromedial view.

Tyrannosaurus are like *Daspletosaurus* in this feature, so it appears to be a good character for identifying tyrannosaurines. This contact is strengthened posteriorly by a thick, fingerlike process of the jugal that extends at least 1.5 cm along the back of the lacrimal. In tyrannosaurines, the posteroventral corner of the lacrimal plugs into a socket that is supported by a small but distinct ridge on the external surface of the jugal.

In the posterodorsal corner of the antorbital fossa is found the large pneumatic opening. The triangular opening in the small *G. libratus* (TMP 91.36.500) is separated from a smaller, more anterior pneumatopore by a vertical bar of bone. Although the shapes and sizes of these openings vary considerably in different specimens, this is a characteristic arrangement in all specimens of *Gorgosaurus*. In larger specimens, the two pits are sunk into the floor of a larger depression, formed when a new vertical ridge of bone develops anteriorly (Carr 1999). The pneumatic opening of *Daspletosaurus* (TMP 85.62.1, TMP 83.30.1) is relatively small and round compared to those of *Gorgosaurus* and *Albertosaurus*. Again, this can also be attributed in part to size, and also can be correlated with ontogenetic changes in size. In juvenile *Daspletosaurus* (Fig. 18A) and *Tarbosaurus bataar* (GIN 100/66), the pneumatic openings of the lacrimals are relatively larger than they are in the adults. There are nevertheless significant differences in the pneumatization of the lacrimal in different tyrannosaurids. In *Albertosaurus* and *Gorgosaurus*, the bridge of bone separating accessory openings from the main pneumatopore is relatively short anteroposteriorly. In *Daspletosaurus*, the bridge is larger than the size of the main pneumatopore. *Tarbosaurus bataar* (GIN 100/66, GIN 107/2, PIN 551-1) does not have accessory openings.

The anterodorsal process of the lacrimal extends to about the middle of the antorbital fenestra in *Gorgosaurus* (Fig. 2A), *Albertosaurus* (5B), and juveniles of *Daspletosaurus* (Fig. 18A). Anteriorly, the upper long, slender and tapering process of the lacrimal in *Daspletosaurus* sp. (TMP 85.62.1) extends anteriorly far beyond the more ventral process to separate the maxilla and nasal for almost the entire length of the antorbital fenestra (in *Gorgosaurus* it extends less than half this distance). In consequence, the lacrimal is longer than it is tall. Furthermore, mature specimens of *Daspleto-*

saurus sp. (TMP 85.62.1, 98.48.1) lack the finger-like process on the nasal that clasps the anterior tip of the lacrimal.

Prefrontal.—The prefrontal is always exposed on the skull roof of tyrannosaurids, although the degree of exposure varies. Its presence is often not detected because it is small, sometimes is overridden by adjacent bones during postmortem distortion of the skull, and in some specimens it has fused indistinguishably to one of the adjacent bones. The prefrontal of the small *G. libratus* TMP 91.36.500 is long (61.5 mm) and narrow (12 mm). In one large *G. libratus* (UA 10), the prefrontal is distinct but seems to be fused onto the anterolateral process of the frontal, whereas in another specimen (TMP 94.12.602) it shows stronger association with the lacrimal. The anterior end of the prefrontal of *Gorgosaurus* is only slightly anterior to the anterior limit of the dorsal exposure of the frontal. The thin, tapering ventral process ends just dorsal to the lacrimal ducts. The prefrontal tends to be more elongate in *Daspletosaurus*, where it is exposed on the skull roof anterior to the anterior tip of the frontal (NMC 8506, TMP 85.62.1). It is exposed on the skull roof of *Tarbosaurus bataar* (Maleev 1974, GIN 107/2) and some specimens of *T. rex* (AMNH 5027, TMP 81.6.1).
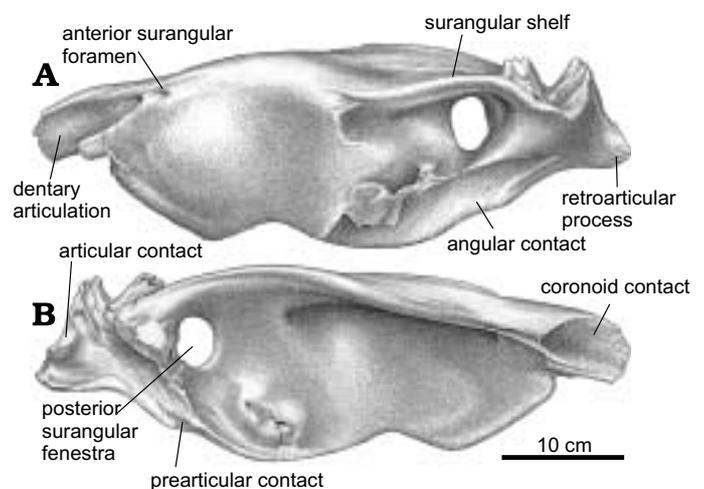

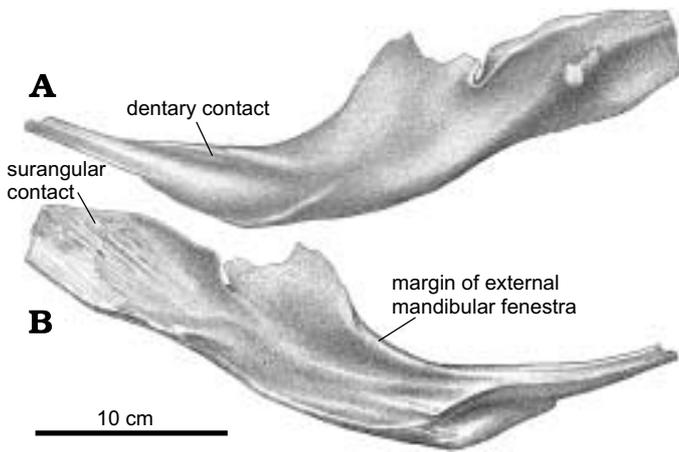Fig. 14. *Albertosaurus sarcophagus* (TMP 81.10.1). Left surangular in lateral (**A**) and medial (**B**) views.

Fig. 15. *Albertosaurus sarcophagus* (TMP 81.10.1). Left angular in lateral (**A**) and medial (**B**) views.
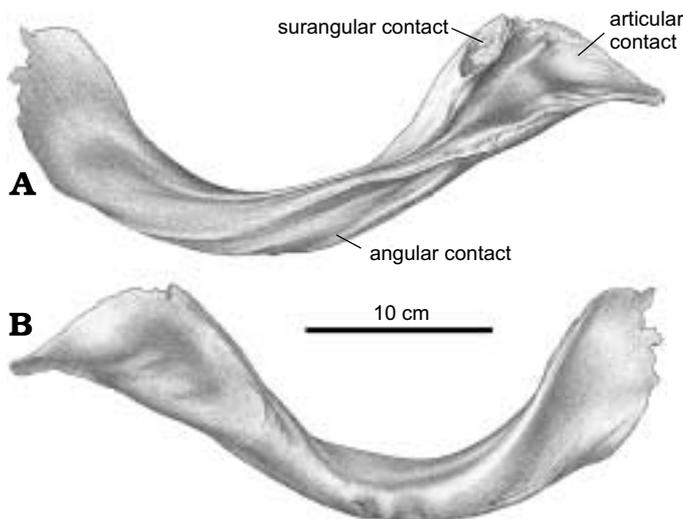

Fig. 16. *Albertosaurus sarcophagus* (TMP 81.10.1). Left prearticular in lateral (**A**) and medial (**B**) views.

Frontal.—The frontal of the immature *G. libratus* (TMP 91.36.500) appears relatively long and narrow (the width to length ratio is 0.43, compared with 0.66 in UA 10). The anterior end of the frontal is overlapped on the midline by a tapering prong of the nasal, and more laterally by a second, longer process. In *A. sarcophagus* (TMP 81.9.1, 81.10.1, 85.98.1), the nasal-frontal suture is more complex, the midline slot for the nasal expands rather than tapers and extends farther posteriorly than any of the more lateral ridges and grooves for the nasal. The prefrontal and lacrimal have more vertical contacts with the frontal in *Gorgosaurus*, the latter plugging into a socket (TMP 67.14.3, 80.16.485, 81.39.8, 82.16.181, 91.36.500) in the anterior face of the frontal as in *Daspletosaurus* (NMC 11841, TMP 80.16.924, 94.143.1). In contrast, the prefrontal seems to have more limited dorsal exposure in *A. sarcophagus* (TMP 81.9.1, 81.10.1) and the lacrimal did

not plug into a socket in the frontal, which is similar to *T. rex* (RSM 283.2, LACM 23845). However, in the AMNH braincase, there is a deep pit for the lacrimal and the prefrontal seems to have been the same as in *Daspletosaurus*. Furthermore, in an immature *T. rex* (LACM 28471), the pit is shallow posteriorly but deep medially. The anterior part of the suture with the postorbital is tall and nearly vertical, whereas posteriorly (within the boundaries of the supratemporal fossa) the postorbital overlaps a shelf on the frontal. The distinction between these two sutural surfaces is less obvious in *Daspletosaurus* and *Nanotyrannus*. As a direct consequence, the anterior margin of the supratemporal fossa tends to be more distinct in *Gorgosaurus* than it is in *Daspletosaurus* and *Nanotyrannus*.

The parietal wraps around the posterior margin of the frontal, and sends a small tapering process forward that overlaps the frontal on the midline. The dorsal margin of the frontal rises slightly to meet this process, and a foramen passes posteroventrally through the junction of the two frontals and the overlapping medial process of the fused parietals. In *Alioramus* (Kurzanov 1976), *Daspletosaurus* sp. (Fig. 20B, FMNH PR308, TMP 85.62.1), *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*, the posterior quarter of the frontals rises to take part in an elevated sagittal crest that is much more pronounced than it is in *Albertosaurus* and *Gorgosaurus*. It rises sharply above the dorsal surface of the frontal anterior to the supratemporal fossa. For example, TMP 91.36.500 (an
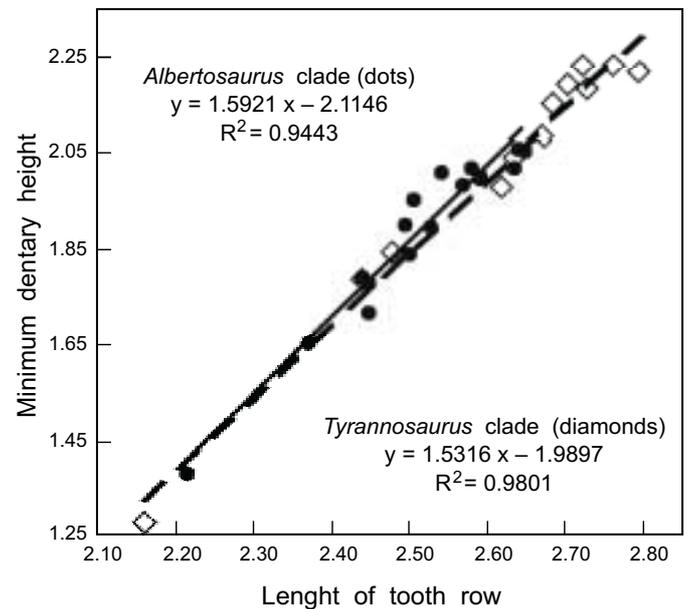

Fig. 17. Graph comparing the logarithms of the length of the dentary tooth row (X-axis) versus the minimum height of the dentary, which is close to the middle of the tooth row (Y-axis). Minimum height was used rather than maximum height because it is less susceptible to distortion during the fossilization process as this is normally the thickest part of the dentary. The *Albertosaurus* clade includes *Albertosaurus* and *Gorgosaurus*, whereas the *Tyrannosaurus* clade includes *Daspletosaurus*, *Shanshanosaurus*, *Tarbosaurus*, and *Tyrannosaurus*. The trendlines for both clades virtually coincide, showing that increased jaw depth is not characteristic of just *Tyrannosaurus*.
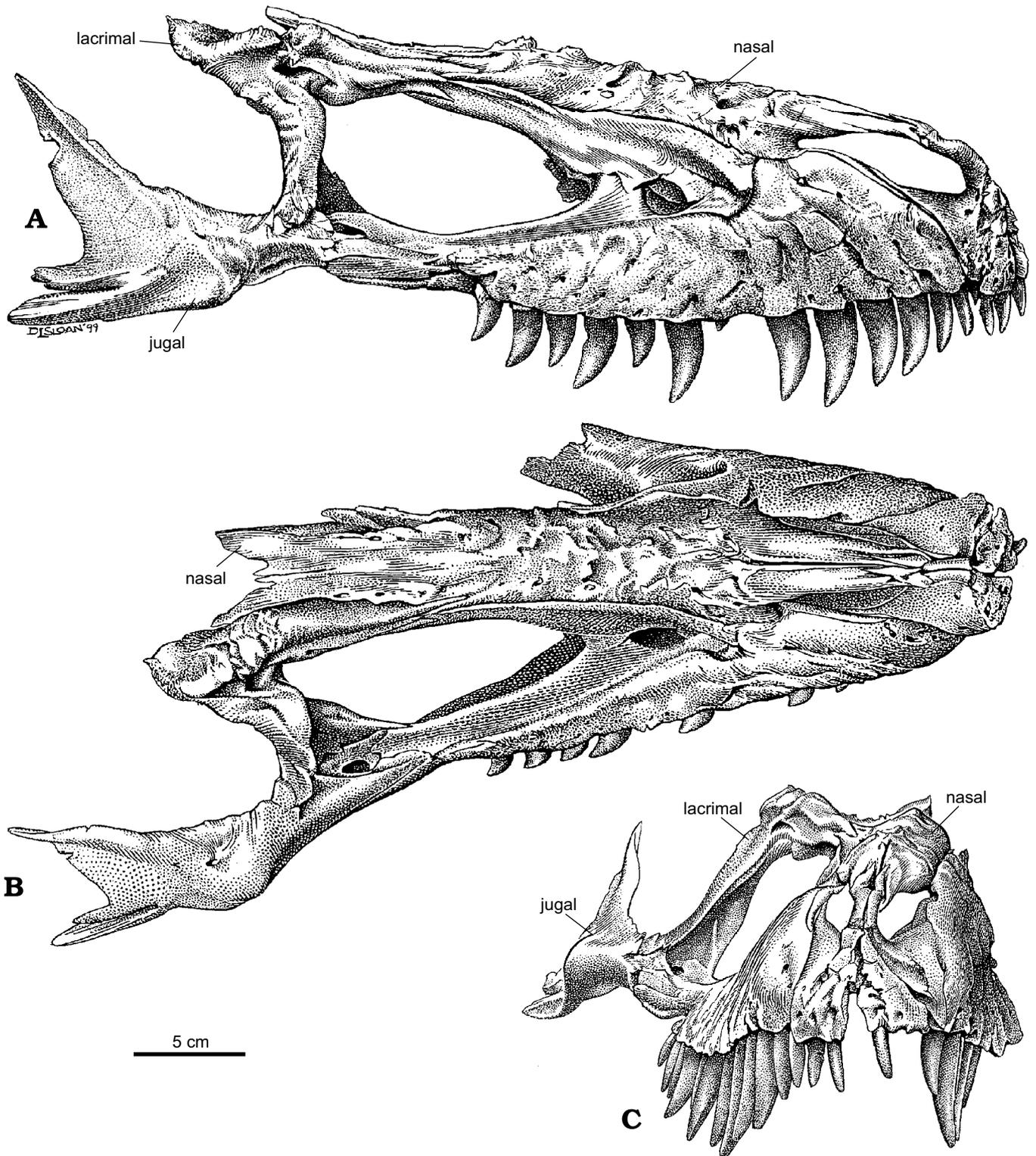
Fig. 18. *Daspletosaurus* sp. (TMP 94.143.1). Front of skull in lateral (**A**), dorsal (**B**) and anterior views.

immature *G. libratus*) represents a larger animal than TMP 94.143.1 (an immature *Daspletosaurus*) but the frontal of the latter rises more than double the height at the sagittal crest. Because of these high sagittal ridges, the foramen that is at the junction of the frontals and parietals in *G. libratus* and A.

sarcophagus is roofed over by the frontals and opens in a more anterior position in tyrannosaurines.

The frontal undergoes dramatic ontogenetic changes. Using measurements for the frontals of five tyrannosaurid species (Table 2), the coefficients of allometry were calculated

for frontal length and frontal thickness. The correlation coefficient was relatively low for length ($r^2 = 0.70$), mostly because of variable preservation. Nevertheless, comparison of the logarithms of frontal width versus length shows strong negative allometry ($k = 0.48$). On the other hand, the thickness (depth) of the bone compared to the width undergoes strong positive allometry ($k = 1.38$, $r^2 = 0.94$), probably to form a solid anchor for the jaw musculature. Frontal length is correlated with the length of the brain, which becomes relatively smaller in larger animals. The width of the skull roof increases dramatically during growth, growing outwards far beyond the orbital slots.

Parietal.—The parietal of *G. libratus* (TMP 91.36.500) has the characteristic tyrannosaurid sagittal crest, extending from the junction with the frontals to the nuchal crest. It is low anteriorly, and in lateral aspect dips posteriorly to a level below the interorbital region of the frontals. There it forms a high knife-like ridge between the supratemporal fenestrae. Posteriorly the sagittal crest rises to the level of the interorbital region of the frontals again. This arrangement is the same in all well-preserved specimens of *Gorgosaurus* and *A. sarcophagus* (TMP 81.9.1, 81.10.1), other than UA 10 where the lowest point on the sagittal crest is slightly higher than the interorbital region of the frontals. The sagittal crests on the parietals of *Daspletosaurus* sp. (Fig. 21, FMNH PR 308, NMC 11841, TMP 80.16.924, 85.62.1), *Nanotyrannus* and *Tyrannosaurus* are relatively higher than those of *Albertosaurus* and *Gorgosaurus*, mostly by virtue of the fact that the sagittal crest is much higher at the frontoparietal suture of these animals. This gives the crest of *Daspletosaurus* a more knife-like appearance, whereas the crest seems to rise higher at the nuchal crest in *Gorgosaurus* and *Albertosaurus*.

The fused parietals have an anterior process that inserts between the frontals on the midline. Frontals and parietals are elevated along their contact, and in more mature tyrannosaurid individuals (TMP 67.14.3, 81.9.1, 81.10.1) the suture is strengthened by small interdigitating processes. The parietal extends as a long tapering process along the dorsal margins of the exoccipital-opisthotic unit. Much of this process is covered by the squamosal. The parietal forms most of the characteristic tyrannosaurid nuchal crest. The nuchal crests of *Gorgosaurus* and *Albertosaurus* are significantly higher but narrower than those of equivalent sized specimens of *Daspletosaurus* (Fig. 21) or *Nanotyrannus*. This correlates with the narrower temporal fenestrae of *Gorgosaurus* and *Albertosaurus*.

Postorbital.—In large individuals of *Gorgosaurus*, *Albertosaurus*, *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*, the postorbital establishes contact with the lacrimal.

In immature *G. libratus* (TMP 91.36.500), a relatively small, rugose tuberosity rises above the lateral surface of the postorbital along the orbital margin. The size of the tuberosity is dependent on the age and size of the individual, and it is not evident in smaller specimens (TMP 86.144.1, *G. libratus*). However, regardless of size, the tuberosity is always positioned at the edge of the bone between the dorsal and poste-
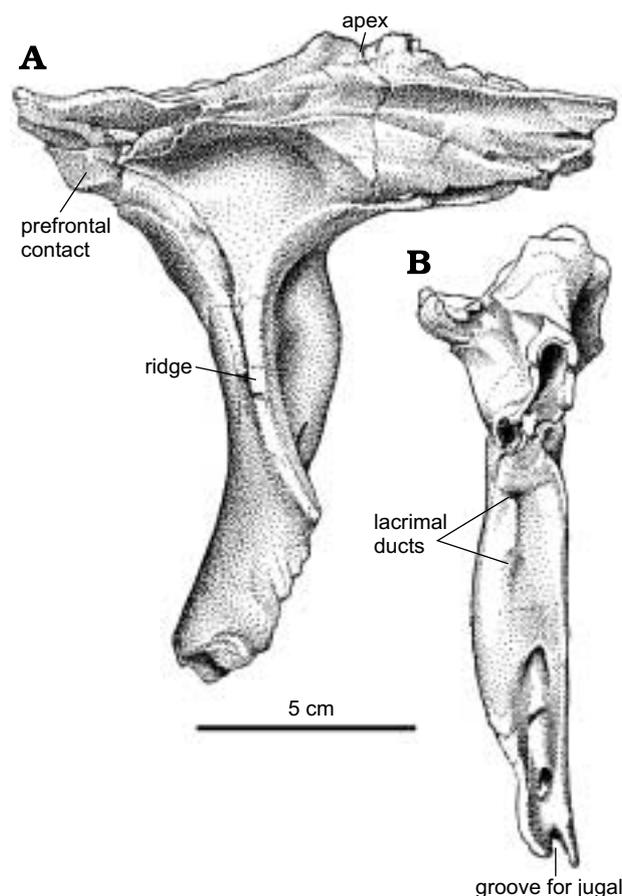

Fig. 19. *Daspletosaurus* sp. (TMP 94.143.1). Left lacrimal in medial (**A**) and anterior (**B**) views.

rior margins of the orbit. The postorbital is sculptured along the margin of the orbit anterodorsal to the tuberosity, but it is smooth along the edge of the upper temporal fenestra in *Gorgosaurus*. In large individuals of *Albertosaurus* (Fig. 8A), the rugose region extends along the entire upper edge of the postorbital anterior to the squamosal, and the tuberosity is more prominent. The size of the postorbital "horn" or rugosity varies considerably in other tyrannosaurids. This is in part ontogenetic, with larger more mature specimens having larger, more rugose tuberosities. However, there are also taxonomic differences. In both *Gorgosaurus* and *Albertosaurus*, the tuberosity is positioned immediately behind the orbital margin. In *Daspletosaurus* sp. (FMNH PR365, MOR 590, TMP 85.62.1), the postorbital "horn" is a thickened rugose ridge that runs along the anterodorsal margin of the postorbital to the middle of the postorbital bar where it curves down and forward. The rugosity therefore looks like an open "C" that faces the orbit and encloses a smooth area in the position where the tuberosity would be in albertosaurines. This is also the case in *Tyrannosaurus* and *Tarbosaurus*. The two known specimens of *Daspletosaurus torosus* (NMC 9506, TMP 2001.36.1) have a pronounced convex tuberosity in this region, as apparently does OMNH 10131 (Lehman and Carpenter 1990). The postorbitals of the
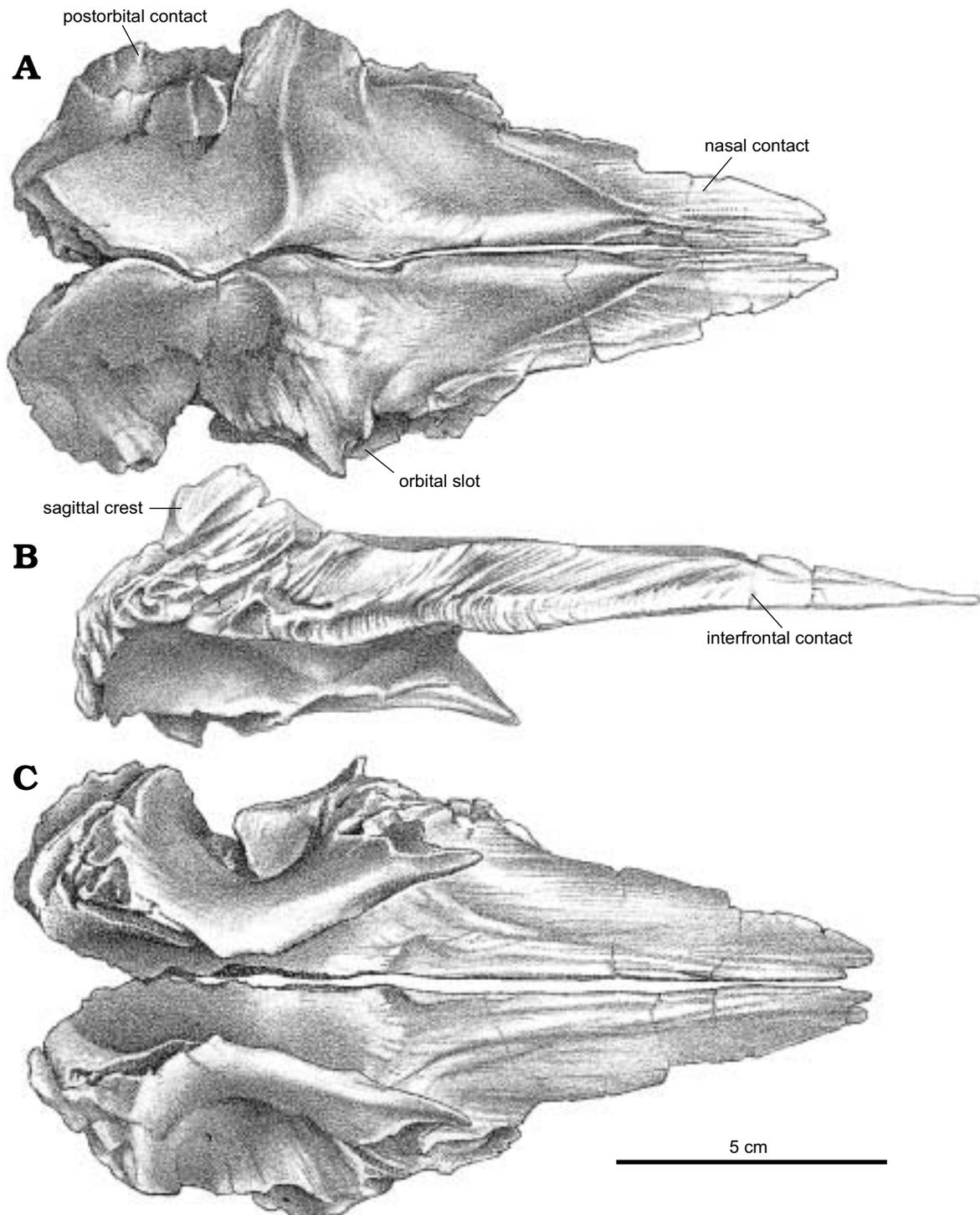
Fig. 20. *Daspletosaurus* sp. (TMP 94.143.1). Frontals in dorsal (**A**), medial (**B**, left frontal only), and ventral (**B**) views.

immature *Daspletosaurus* (Fig. 22A) and *Nanotyrannus*, on the other hand, are smoothly convex.

The intertemporal ramus curves down and back from the postorbital ramus to end in a point that is clasped dorsally and ventromedially by two processes of the squamosal. Medial to the dorsolateral margin of the intertemporal ramus, the postorbital forms the smooth, gently convex floor of the superior temporal fenestra. Anteriorly, the frontal suture of the imma-

ture *G. libratus* (TMP 91.36.500) is nearly vertical and faces anteromedially. Behind a distinct inflection, the frontal-postorbital contact becomes more or less parallel with the midline of the skull when viewed in dorsal aspect. In this region the postorbital overlaps a wide shelf on the frontal. Posteriorly the suture turns medially where the postorbital has relatively small contacts with the parietal and laterosphenoid. In larger individuals, the anterior part of the suture
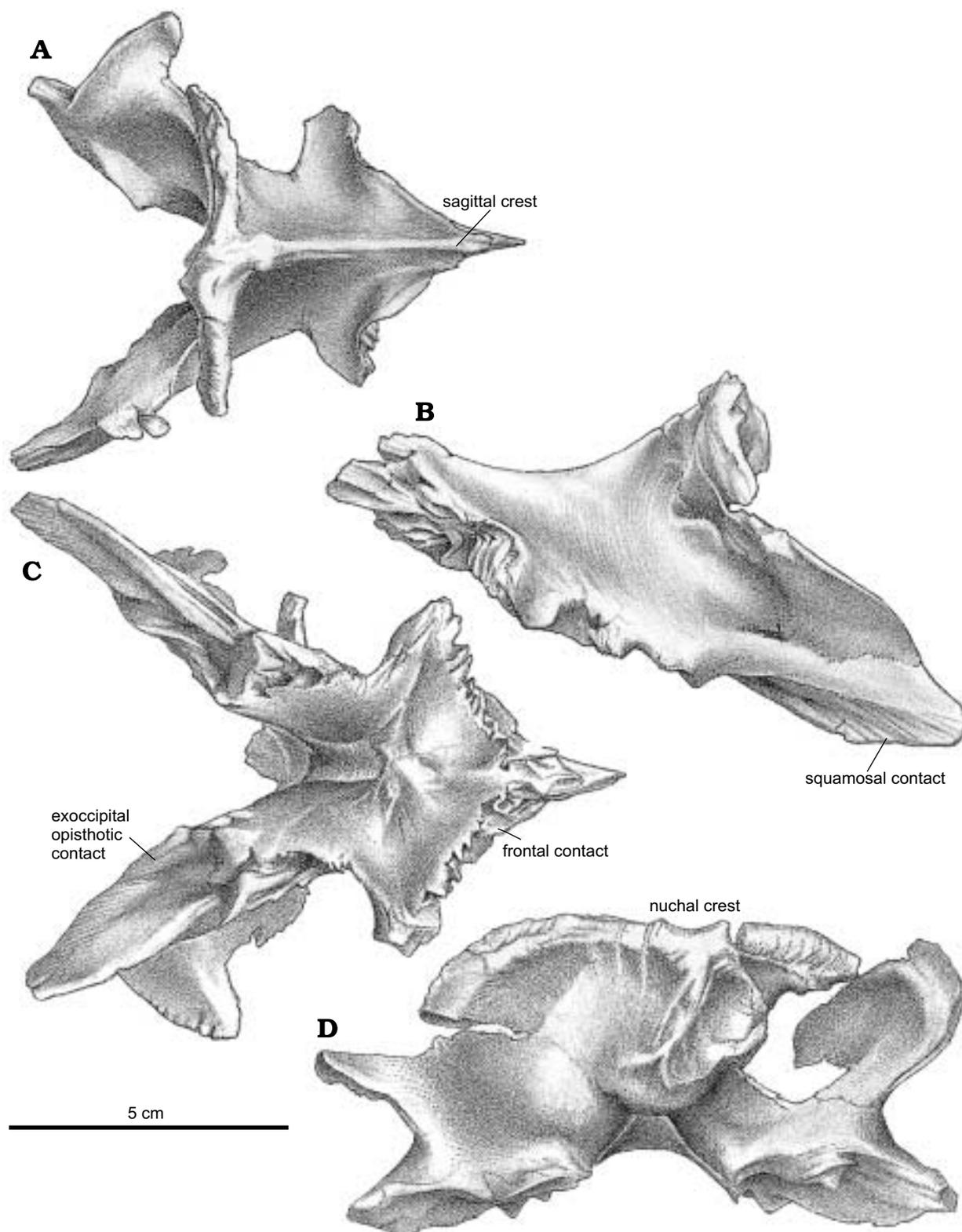
Fig. 21. *Daspletosaurus* sp. (TMP 94.143.1). Parietals in dorsal (**A**), left lateral (**B**), ventral (**C**), and posterior (**D**) aspects.

becomes deeper and more rugose than the overlapping suture behind it. The suture for the frontal, parietal and laterosphenoid is essentially the same in *Albertosaurus* (Fig. 8B) and *Daspletosaurus* (Fig. 22B).

At the top of the jugal-postorbital contact in *G. libratus* (TMP 91.36.500), the axis of the postorbital bar has a pronounced anteroventral inflection. The orbital margin is thick dorsally, but thins ventrally. The ventral end of the post-

orbital ramus of the postorbital tapers rapidly and protrudes slightly into the orbit of *G. libratus* (Fig. 2A, ROM 1247, TMP 86.144.1, USNM 12814). This seems to be an ontogenetic and size dependent character, and larger specimens of both *G. libratus* (AMNH 5336, UA 10) and *A. sarcophagus* (TMP 86.64.1, TMP 81.10.1) have more conspicuous suborbital processes. Suborbital processes are not found in *Nanotyrannus* and *Alioramus*, presumably because of their small size, nor in *Daspletosaurus* specimens of any size (Fig. 22, FMNH PR308, NMC 8506, TMP 84.60.1, TMP 85.62.1, 2001.36.1). However, they are present in all mature specimens of *Tarbosaurus* and *Tyrannosaurus*.

Jugal.—Tyrannosaurid jugals take part in the rim of the antorbital fenestra. In the immature *Gorgosaurus* (Fig. 2B), the jugal separates the maxilla and lacrimal by 17 mm on the right side, but only 4.5 mm on the left. The tapering anterior end of the jugal sits on the dorsal surface of the part of the ventral margin of the antorbital fossa formed by the maxilla. It overlaps the lateral surface of the maxilla here, but passes dorsally through a slot to the medial surface of the maxilla at the edge of the antorbital fenestra. Here it extends forward to contact the palatine. Posterior to this point, the medial surface of the jugal sits on the dorsolateral surface of the palatal shelf of the maxilla, and the top of the tapering end of the maxilla sits in a slot along the ventral margin of the jugal. The nature of the contacts is essentially the same in *Albertosaurus* (Fig. 6).

Posterior to the termination of the maxilla, the ventral margin of the jugal attains its most ventral extension (the cornual process of Carr 1999) directly beneath the orbit. The cornual rugosity is anteroposteriorly shorter but dorsoventrally deeper and thicker in *Daspletosaurus* and *Nanotyrannus* than it is in larger specimens of *Albertosaurus* and *Gorgosaurus*.

The part of the orbital margin formed by the jugal ends anteriorly in a small fingerlike process within which the lacrimal is locked in place in *Gorgosaurus* (Fig. 2A) and *Albertosaurus* (Fig. 6A). Anterior to this, the jugal has a thin, plate-like anterodorsal process that fits between the outer and inner walls of the lower end of the lacrimal (AMNH 5432). Laterally this suture extends anterodorsally to the edge of the antorbital fossa.

Tyrannosaurids all have a large pneumatopore in the posteroventral corner of the antorbital fossa. The broken surfaces of TMP 82.13.3 (*A. sarcophagus*) show that pneumatization did not extend into either the postorbital or the subtemporal processes. The pneumatopore is long but slit-like in *Gorgosaurus*, extending most of the way from the lacrimal suture to the ventral margin of the antorbital fossa. In *G. libratus* (TMP 86.144.1 and UA 10), the opening is wider ventrally than dorsally, giving a teardrop shape in anterior view. When viewed laterally, the axis of the opening is inclined at an angle of about 45 degrees from the ventral margin of the skull. In contrast, the same axes are horizontal in the relatively smaller openings of *Daspletosaurus* (Fig. 18A, B), *Nanotyrannus*, and *Tarbosaurus*. As pointed out by Carr (1999), the posterolateral margin is resorbed in larger specimens to expose more of the opening in lateral view. The
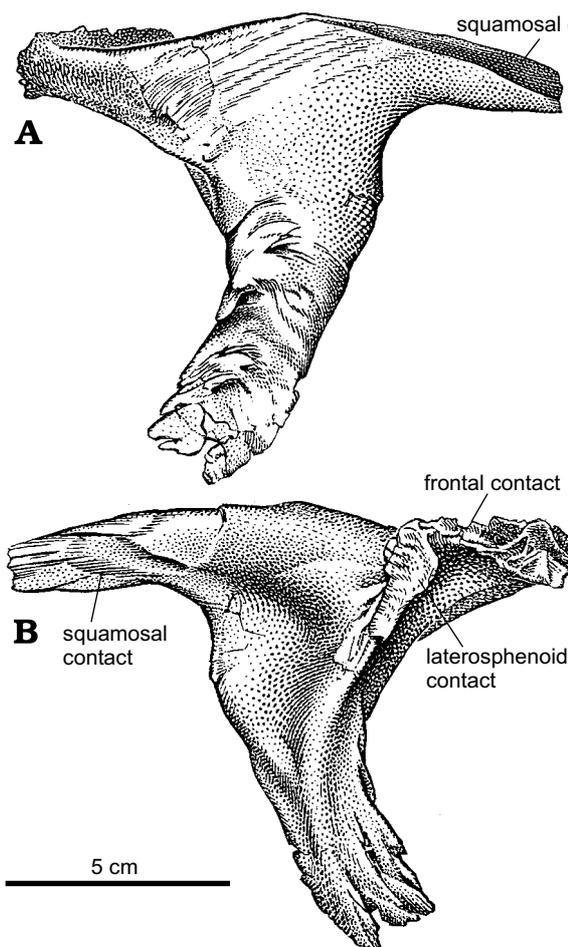

Fig. 22. *Daspletosaurus* sp. (TMP 94.143.1). Left postorbital in lateral (**A**) and medial (**B**) views.

pneumatic opening in the posteroventral corner of the antorbital fossa is rounder in outline and lower in position in *Daspletosaurus* than it is in *Albertosaurus* and *Gorgosaurus*, where it is taller and slit-like. In *Nanotyrannus* the pneumatic opening is an almost horizontal slit.

The jugals of *Albertosaurus* and *Gorgosaurus* show significant differences from that of *Daspletosaurus*. The suborbital bar is both relatively and absolutely lower in *Daspletosaurus* (74.5 mm in TMP 85.62.1 compared with 90 mm in the UA 10, which is a slightly smaller *G. libratus*), but compensates for the difference in strength by being thicker (25 mm in TMP 81.24.5 compared with 16.5 mm in TMP 81.10.1, *A. sarcophagus*). The ventral margin of the postorbital-jugal contact is higher in relation to the bottom of the orbit in even small specimens of *Daspletosaurus* than it is in either *Gorgosaurus* or *Nanotyrannus*.

The postorbital process of the jugal of the immature *G. libratus* (TMP 91.36.500) forms only the bottom of the orbital margin, and is excluded from 90 percent of the orbit by the postorbital. Carr (1999) has shown that in larger specimens of *Gorgosaurus*, the anteroventral postorbital-jugal contact is higher than the ventral orbital margin. The ventral edge of the postorbital sits on a rugose, thin shelf of bone on
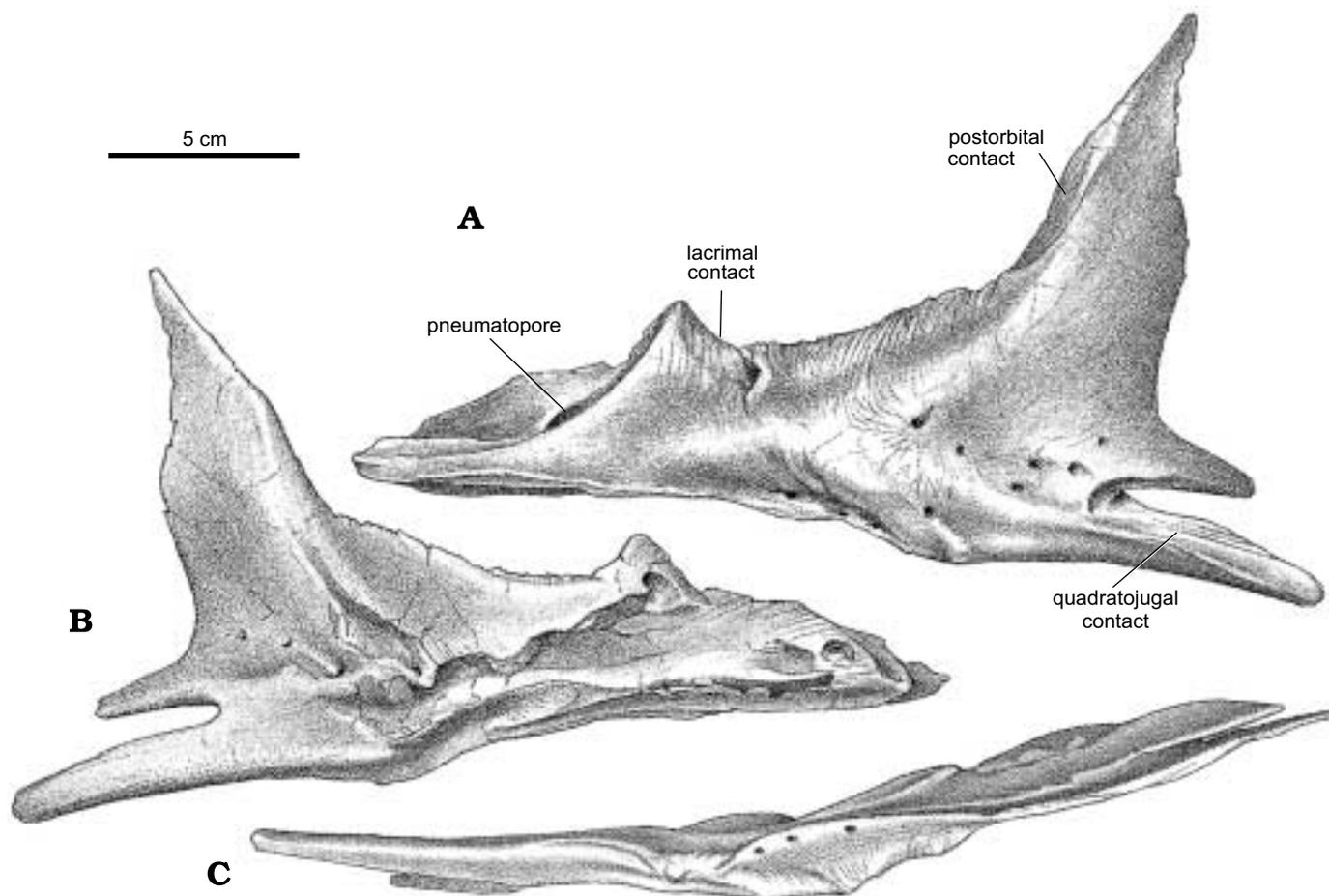
Fig. 23. *Daspletosaurus* sp. (TMP 94.143.1). Left jugal in lateral (**A**), medial (**B**), and ventral (**C**) views.

the jugal that is 12 mm long anteroposteriorly in the immature *G. libratus* (TMP 91.36.500). This shelf is not evident in TMP 86.144.1 (*G. libratus*), and appears to have been something that developed ontogenetically because it is accentuated in larger specimens of *Gorgosaurus* and *Albertosaurus*. The base of the postorbital process of *Albertosaurus* and *Gorgosaurus* is shorter anteroposteriorly and the outer surface in all but the largest specimens is generally convex in longitudinal section. Juvenile *Daspletosaurus* (Figs. 18A, 23) is similar to most albertosaurines, but larger *Daspletosaurus* have postorbital processes with much longer bases, each of which has a conspicuous lateral depression. In *Nanotyrannus* the base is broader as in *Daspletosaurus*, but lacks the outer depression, suggesting that the character is ontogenetically controlled as in *Gorgosaurus* (Carr 1999).

The elongate subtemporal process of the jugal divides into two processes, the longer ventral fork supporting the quadratojugal from below, and the dorsal fork forming the anteroventral margin of the lateral temporal fenestra. The quadratojugal laterally overlaps the jugal on the margins of the slit between the two forks, but to a much greater degree on the ventral fork. The anterior end of the quadratojugal suture tapers and thins anteriorly in most specimens of *Gorgosaurus* and *Albertosaurus*, whereas in all tyrannosaurines it

ends in a high, double-pointed recess buttressed anteriorly by a thickening on the lateral surface of the jugal (Fig. 23A).

Squamosal.—Tyrannosaurid squamosals are complex but conservative. The lateral surface of the intertemporal ramus of the squamosal is lightly sculptured above the long, slit-like articulation for the postorbital (Fig. 2A). The two branches of the intertemporal ramus both extend to the anterior margin of the lateral temporal fenestra, even though the lower one is hidden laterally by the postorbital. Isolated *G. libratus* specimens (TMP 86.144.1, TMP 92.36.82) show that the squamosal medially overlaps the posterior half of the intertemporal ramus of the postorbital. The squamosal of *Gorgosaurus* has a long tapering process that runs forward, curving somewhat downward, along the top of the anterodorsal ala of the quadratojugal. Together they almost dissect the lateral temporal fenestra. This quadratojugal process is relatively thick along its dorsal margin, and is almost completely exposed in lateral view. It is not extensively overlapped laterally as it is in *Alioramus* (Kurzanov 1976), *Daspletosaurus* sp. (Fig. 25, TMP 85.62.1) and *Tarbosaurus bataar* (GIN 107/2). Surrounded by most of the processes of the squamosal, the ventral surface is deeply concave. The juvenile specimen of *Daspletosaurus* also has a deep concavity with relatively
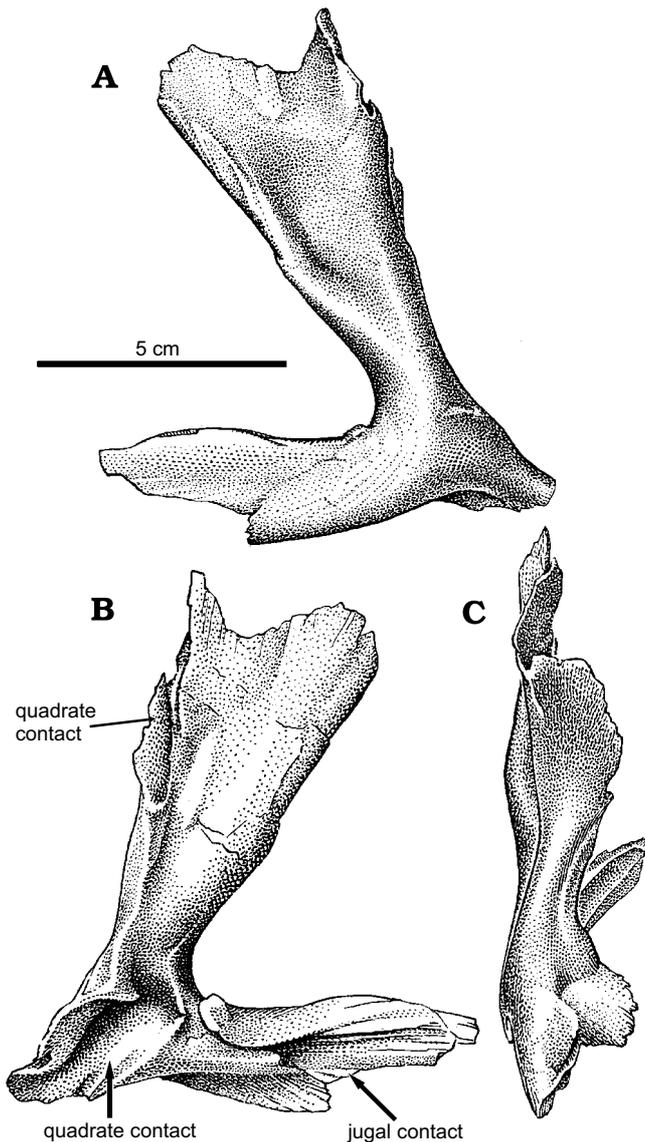
Fig. 24. *Daspletosaurus* sp. (TMP 94.143.1). Left quadratojugal in lateral (**A**), medial (**B**), and posterior (**C**) views.

poorly defined margins (Fig. 25D). In mature specimens of *Gorgosaurus*, *Albertosaurus*, and all tyrannosaurines, the concavity has a well-defined margin and extends deeply into the interior, strongly suggesting it housed an air sac.

Quadratojugal.—The quadratojugal (Fig. 2A) expands dorsally into a wing like process along its dorsal contact with the squamosal. At the back of the dorsal margin, the quadratojugal pulls away from the squamosal and contacts a ridge of the quadrate anteroventral to the quadrate cotylus. The quadratojugal thickens slightly along its sutural contact, which extends ventrally into a slot. The quadrate passes through the slot, and the quadratojugal wraps around onto the posterolateral surface of the quadrate, overlapping the quadrate extensively above the quadrate fenestra. The quadratojugal forms the lateral margin of the large quadrate fenestra, and contacts the quadrate again ventral to the opening. Medially, the quadrate suture of

G. libratus (TMP 86.144.1) and *Albertosaurus* (Fig. 9B) is concave and rugose, matching in contours the extensive sutural surface on the quadrate. The anterior process of the quadratojugal extensively overlaps the lateral surface of the lower of the two quadratojugal processes of the jugal.

The quadratojugals of *Albertosaurus* and *Gorgosaurus* are quite different from that of *Daspletosaurus* (Fig. 24, NMC 8506, TMP 85.62.1) and other tyrannosaurines, in which the dorsal contact with the squamosal is anteroposteriorly much more limited. The anterior and posterior margins of the ascending part of the quadratojugal are relatively straight in lateral view as they diverge from each other dorsally in tyrannosaurines.

Quadrate.—Tyrannosaurid quadrates (Figs. 10, 28) are relatively short in comparison with most other theropods. The quadrate has a large pneumatopore (Fig. 28C) on the ventral margin of the base of the pterygoid ala. The medial surface of the pterygoid ala has a well-defined concavity (Figs. 10B, 28B) anterodorsal to the pneumatopore that may mark the position of an air sac. It is bound anterodorsally, anteriorly and anteroventrally by the curved, squamose suture for the quadrate ala of the pterygoid. The quadrate cotylus (Fig. 28D) contacted only the squamosal. However, a small, flattened area on the medioposterior surface of the quadrate (Fig. 28B) just below the cotylar surface abutted against the opisthotic-exoccipital.

Occiput.—On the occipital surface of the immature *G. libratus* (TMP 91.36.500), the foramen magnum is less than half the diameter of the nearly circular occipital condyle. The sutures on the occiput are visible, but are better seen on TMP 86.144.1 (*G. libratus*) and 94.143.1 (*Daspletosaurus* sp.) where the bones have separated.

Supraoccipital.—The supraoccipital forms a narrow part of the dorsal margin of the foramen magnum in *G. libratus* (TMP 86.144.1, MOR 557, TMP 94.12.602), *A. sarcophagus* (TMP 81.10.1), *Daspletosaurus* (Fig. 26B) and *Tyrannosaurus* (Brochu 2002). The assumption that the exoccipitals connect across the top of the foramen magnum in tyrannosaurids (Holtz 2001) is probably incorrect for all genera. A strong midline ridge rises above the foramen magnum, and the external occipital vein exits through a depression on each side. Tyrannosaurids have a knob-like process on each side of the midline at the top of the supraoccipital. In large specimens of *G. libratus* (TMP 94.12.602), these protrude more than 3 cm from the contact with the parietal. Numerous tyrannosaurid specimens have broken supraoccipitals that reveal internal sinuses. Most of these have relatively thick walls, but in TMP 94.143.1 (*Daspletosaurus* sp.) two millimeter thick walls enclose an internal chamber that seems to be confluent with the sinuses in the paroccipital processes. The pneumaticity of a much larger *Tyrannosaurus* braincase (Brochu 2002) with 3 mm thick walls is even more impressive. The chamber is partially separated by a vertical midline ridge on the anterior wall. The pneumaticity of the supraoccipital is reminiscent of *Troodon* (Currie and Zhao, 1993B).
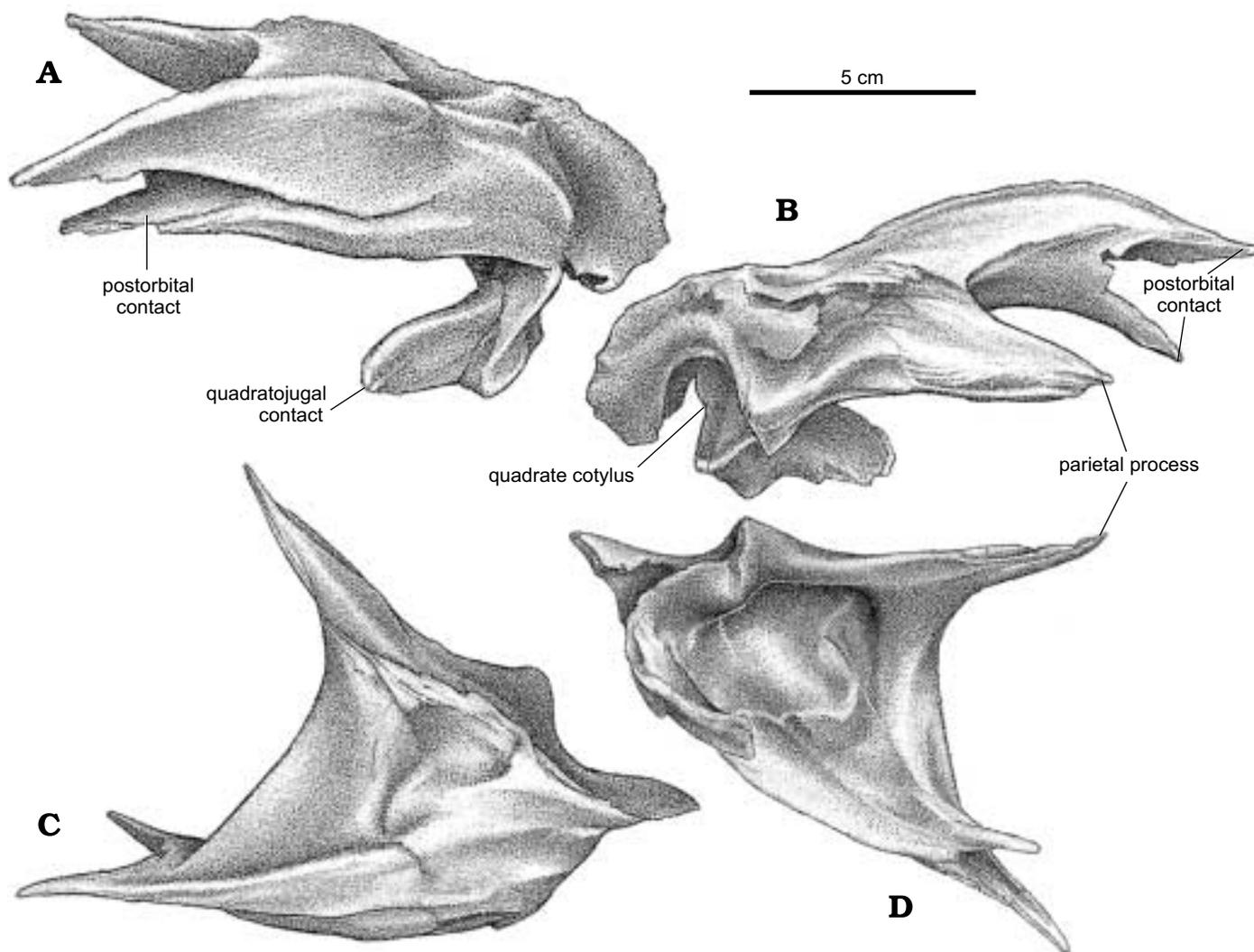
Fig. 25. *Daspletosaurus* sp. (TMP 94.143.1). Left squamosal in dorsolateral (**A**), medial (**B**), dorsal (**C**), and ventral (**D**) views.

Basioccipital.—The basioccipital narrowly separates the exoccipitals on top of the occipital condyle. The condyle in even large specimens of *Gorgosaurus* is oriented mostly posteriorly (TMP 94.12.602), but faces somewhat downward as well. Just outside of the articular surface, the neck of the *G. libratus* condyle is pierced ventrally by a single foramen, which is on the left side of TMP 86.144.1 and on the right side in TMP 91.36.500. This lack of consistency suggests that the foramen was a pneumatopore. A midline ridge supporting the condyle divides ventrally, and each resulting ridge ends at one of the basal tubera. There is a large depression lateral to each one of these ridges, which housed an air sac. Pneumatopores penetrate into the interior of the basioccipital in the dorsal region of this depression in NMC 5600 (*A. sarcophagus*), ROM 1247 (*G. libratus*), and TMP 81.10.1 (*A. sarcophagus*). This depression extends over a low ridge onto the posterior surface of the exoccipital, where one or more pneumatopores invade the interior of that bone as well. Ventrally, the basioccipital forms most of the basal tubera, which are supported anteriorly by the basisphenoid.

Anterolaterally, the metotic strut of the exoccipital-opisthotic almost reaches the ventral surface of the basal tuber. The width across the basal tubera is greater than width of the occipital condyle (25% greater in TMP 91.36.500, *G. libratus*). However, this is still relatively narrow in comparison with other tyrannosaurid genera. The height of the basioccipital below the condyle on the midline does not increase as much as the distance to the end of the basioccipital tuber with increasing age in *Albertosaurus* and *Gorgosaurus*. The ratio of basal tuber height to midline height is 1.4 in TMP 86.144.1 (*G. libratus*), 1.9 in TMP 91.36.500 (*G. libratus*), and 2.5 in TMP 81.10.1 (*A. sarcophagus*).

Exoccipital-opisthotic.—Ventrally, the metotic strut is a triangular plate of bone that contacts the basioccipital medially, but is overlapped slightly by it distally. Anterolaterally, the basisphenoid overlaps about a quarter of the metotic strut. Posteromedially, there is a shallow depression with a pneumatopore that seems to penetrate into the base of the exoccipital contribution to the occipital condyle, and another
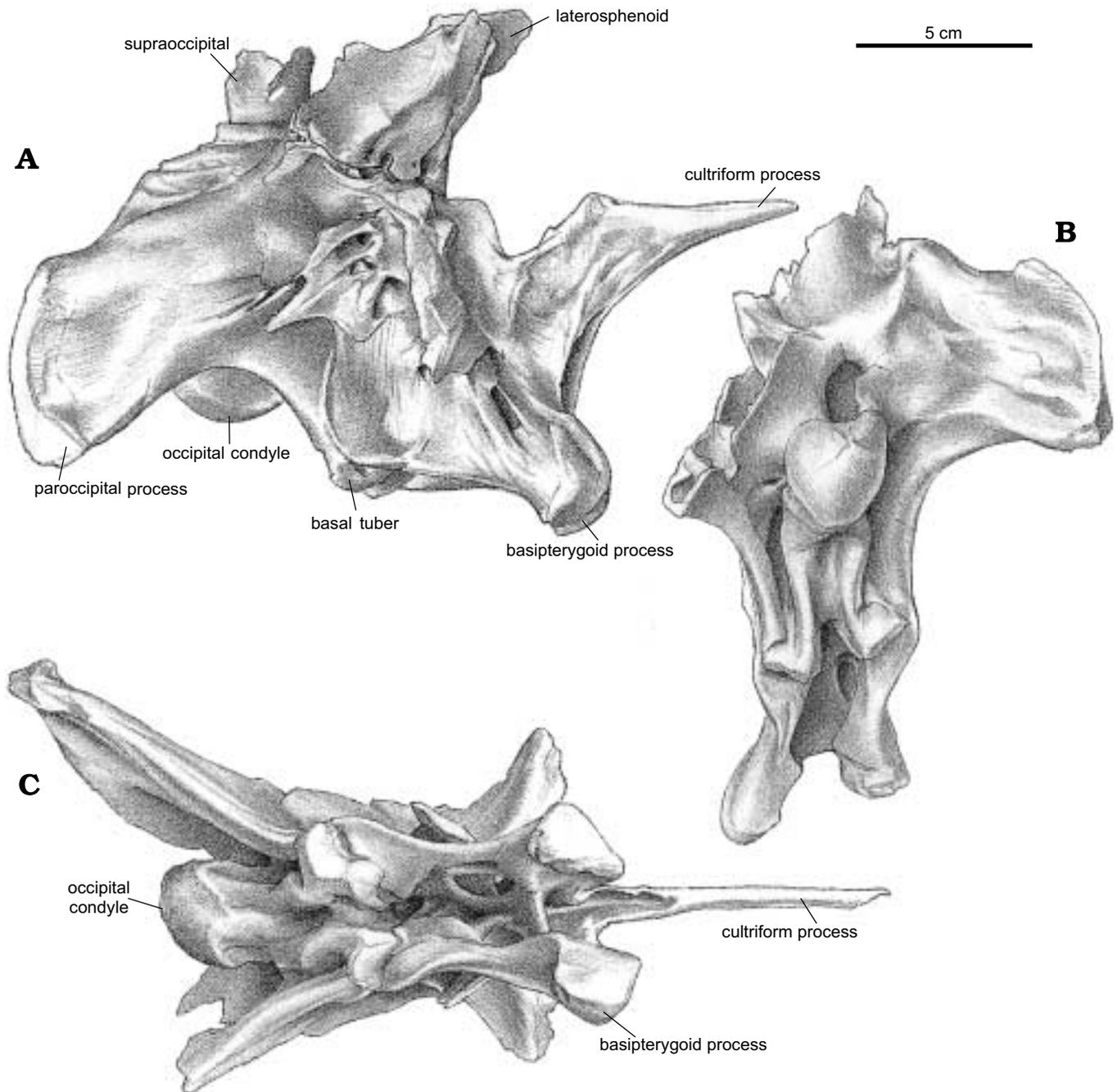
Fig. 26. *Daspletosaurus* sp. (TMP 94.143.1). Braincase in right lateral (**A**), posterior (**B**), and ventral (**C**) views.

that passes through the suture with the basisphenoid into the interior of that bone. The paroccipital process is oriented laterally, posteriorly and only slightly downward from the foramen magnum. Two foramina (Figs. 26, 27) pierce the anterolateral surface of the unit behind the fenestra ovalis. As they are not connected with any of the other foramina, it appears they might be pneumatopores that took air to the interior of the paroccipital process, making them equivalent to the posterior tympanic sinuses of troodontids and other theropods. This is particularly evident in TMP 94.143.1 (*Daspletosaurus* sp.), where the left paroccipital has been broken to ex-

pose the hollow interior (Fig. 26) that connects via tubes to the anterior tympanic recess and the hollow interior of the supraoccipital as in *Troodon* (Currie and Zhao 1993b). The exoccipital-opisthotic unit forms the dorsal, posterior and ventral edges of the fenestra ovalis, the border being completed by the prootic and the basisphenoid. Above the fenestra ovalis, the bone thickens in TMP 86.144.1 (*G. libratus*) where it encloses the back regions of the inner ear. Posterolateral to this, the anterolateral surface of the exoccipital-opisthotic is broadly overlapped by the prootic. Dorsally, the exoccipital-opisthotic has an anteroventrally

long suture with the supraoccipital-epiotic, which roofs over the inner ear. Posterolateral to this, the dorsal edge of the unit thins out along its contacts with the parietal and squamosal. Where the exoccipital-opisthotic forms the inner wall at the back of the braincase, there is a foramen for the ductus endolymphaticus behind the metotic fissure.

Basisphenoid-parasphenoid.—The cultriform process extends anteriorly just beyond the middle of the orbit, where it is a thin but solid sheet of bone. The well developed basipterygoid process inserts into the socket-like pterygoid articulation. A web of bone connects the bases of the basipterygoid processes. As in other specimens of *G. libratus* and *A. sarcophagus* (NMC 5600, ROM 1247, TMP 81.10.1, TMP 85.98.1, 86.64.1), the ventrally facing basipterygoid recess of TMP 91.36.500 (*G. libratus*) is subdivided into a large medial, anterior depression, and a pair of posterolateral pits. This is different than the broader, shallower basisphenoid recesses of *Alioramus remotus* (PIN 3141), *Daspletosaurus* sp. (FMNH PR308, NMC 8506, Fig. 26C), *Nanotyrannus*, *Tarbosaurus bataar* (PIN 553-3), and *Tyrannosaurus*, in all of which the basisphenoidal recesses are also oriented more posteroventrally. The ala basisphenoidalis (Chure and Madsen 1998) enclosed the anterior part of the air sac associated with the middle ear, and overhangs the foramen for the internal carotid.

Prootic.—The prootic in tyrannosaurids (Fig. 6B, *G. libratus* TMP 86.144.1) forms the posterior border for the opening of the trigeminal, the anterior margin of the fenestra ovalis, and completely encloses the foramina for the facial and auditory nerves. Posterolaterally the prootic extensively overlaps the anterolateral face of the opisthotic.

Laterosphenoid.—As in other theropods, the tyrannosaurid laterosphenoid forms the anterior margin of the trigeminal foramen, and there was a separate branch for the ophthalmic branch of the trigeminal. Dorsally, the postorbital process of the laterosphenoid contacted the frontoparietal suture close to where all three bones meet the postorbital (Fig. 6B). There is a shallow depression on the ventrolateral surface of the base of the postorbital process marking the contact with the epipterygoid.

Vomer.—Tyrannosaurid vomers, which are fused for most of their lengths, are distinctive in that each expands anteriorly into a relatively large, diamond-shaped plate that loosely contacts the lower surface of the palatal shelf of the maxilla. Posteriorly, the vomer splits into two vertical plates that are narrowly separated along the midline and contact the palatines and pterygoids posterolaterally in *G. libratus* (TMP 2000.12.11), *A. sarcophagus* (TMP 98.63.87), *Daspletosaurus* (Russell 1970), *Tarbosaurus bataar* (GIN 100/777, GIN 107/2), and *Tyrannosaurus* (Osborn 1912, Molnar 1991, Brochu 2002).

Palatine.—The ventral edge of the palatine is sutured to the medial edge of the palatal shelf of the maxilla for most of its length. Behind the last alveolus, this sutural surface shifts
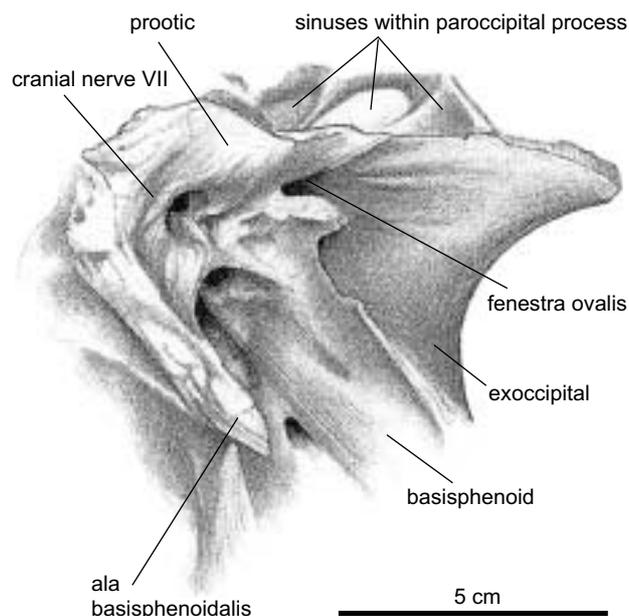

Fig. 27. *Daspletosaurus* sp. (TMP 94.143.1). Middle ear region of left side of braincase in ventrolateral view.

dorsally onto the jugal, where it becomes tall enough to contact the medial surface of the lacrimal (TMP 91.36.500 [*G. libratus*], CM 7541 [*N. lancensis*]). There is one (Fig. 11A, CM 7541) or more (Fig. 29) pneumatic openings above the maxillary suture on the lateral surface. The fenestra shows a general trend towards increasing relative size in larger individuals, and taxonomically seems to be relatively larger in *Albertosaurus*, *Gorgosaurus* and *Nanotyrannus* than it is in *Daspletosaurus*. The pneumatic space extends dorsomedially into the inflated base of the vomerine process. Anterior to the pneumatic fenestra, the lateral surface of the tapering maxillary process of the palatine has a deep concavity above the maxillary suture that also housed a pneumatic sac. The vomerine process expands dorsally (Figs. 2A, 11A) into a large, thin, almost vertical sheet of bone that covers the lateral surface of the vomerine process of the pterygoid. The palatines of *Gorgosaurus* and *Albertosaurus*, and of all tyrannosaurine juveniles are relatively flat medial to the pneumatopore. However, the base of the palatine becomes greatly inflated in large specimens of *Daspletosaurus* sp. (TMP 85.62.1), *Tarbosaurus* and *T. rex* (MOR 008, 555).

Ectopterygoid.—Tyrannosaurid ectopterygoids (Figs. 2B, 12, 32) are conservative in their features. The hook-like jugal process expands distally for its contact with the medial surface for the jugal, and just touches the maxilla anteroventrally. Dorsally the ectopterygoid develops into a broad plate that has an extensive squamose suture with the lateral surface of the pterygoid. The posterodorsal corner of this process is thickened on the ectopterygoid to form a process that plugs into a socket in the pterygoid. The more ventromedial, hooked process of the ectopterygoid protrudes below the ventral margin of the skull. The process is thick anterolaterally, and forms the margin of a prominent ventromedial pneumatopore, which is
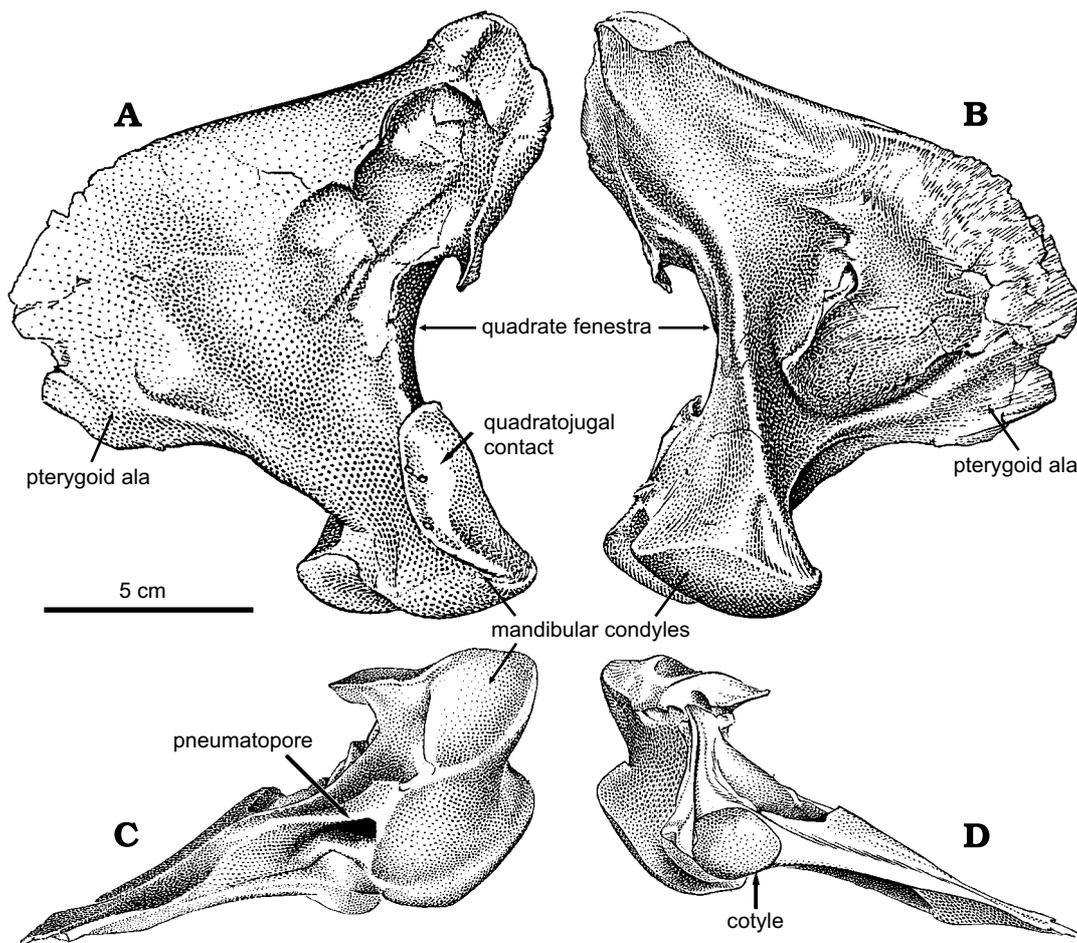
Fig. 28. *Daspletosaurus* sp. (TMP 94.143.1). Left quadrate in lateral (**A**), medial (**B**), ventral (**C**), and dorsal (**D**) views.

slit-like in *Albertosaurus* and *Gorgosaurus*. Posterior to the pneumatopore, the ectopterygoid is a thin plate of bone that is covered ventromedially by the thin, ventral process of the pterygoid. The distal end of the pterygoid wraps around onto the posterolateral face of the ventral extremity of the ectopterygoid. The ectopterygoids of tyrannosaurine juveniles are difficult to distinguish from those of albertosaurines. However, as a tyrannosaurine matured and increased in size, the base of the ectopterygoid became inflated.

Pterygoid.—The pterygoids are both well exposed in the immature *Gorgosaurus* (Fig. 2B), and extend for slightly less than half the length of the skull. As pointed out by Russell (1970), tyrannosaurid pterygoids do not contact each other on the midline, and are separated anteriorly by the paired vertical plates of the paired vomers. The pterygoids of *Gorgosaurus* and *Albertosaurus* are similar in most respects to those of *Daspletosaurus*, *Tarbosaurus* (Maleev 1974), *Nanotyrannus*, and *T. rex* (BHI 3033, Osborn 1912; Molnar 1991), except that they are somewhat more elongate between the basipterygoid articulation and the ectopterygoid process, and the anterior ramus is not as broad as in tyrannosaurines.

The anterodorsal ramus matches the shape of the dorsomedial process of the palatine, which overlaps the pterygoid

in an extensive squamose suture. The pterygoid narrows posteriorly, separates from the palatine and forms the posterior margin for an accessory opening between the two bones. In *Albertosaurus* (Fig. 13), the accessory fenestra is readily visible in ventral view, whereas in TMP 91.36.500 (*G. libratus*) it is half the size. It is also a relatively large, anteroposteriorly elongate opening in the juvenile specimen of *Daspletosaurus* (Fig. 29B), and apparently in *Nanotyrannus*. It is supposedly closed in adult specimens of *Tyrannosaurus* (Osborn 1912, Molnar 1991, Carr 1999), as a result of the anterior process of the pterygoid becoming relatively wider and because of medial expansion of the palatine. However, it never closes completely, and in BHI 3033 is still a sizeable opening. Because of overlapping bones, it may not be visible in ventral view. Posteroventral to this fenestra, there is an anteroventral projection that forms a squamose suture along the medial surface of the palatine that ends anteriorly at a thickened palatine ridge. The palatine extends far back along the lateral surface of the pterygoid, but does not contact the ectopterygoid (the contact in NMC 5600 is probably postmortem damage). The ventral border of the pterygoid is thickened below the palatine contact. There is a long fingerlike process that extends ventrally, laterally and slightly posteriorly along the posterior edge of the ventral ramus of the ectopterygoid. Be-
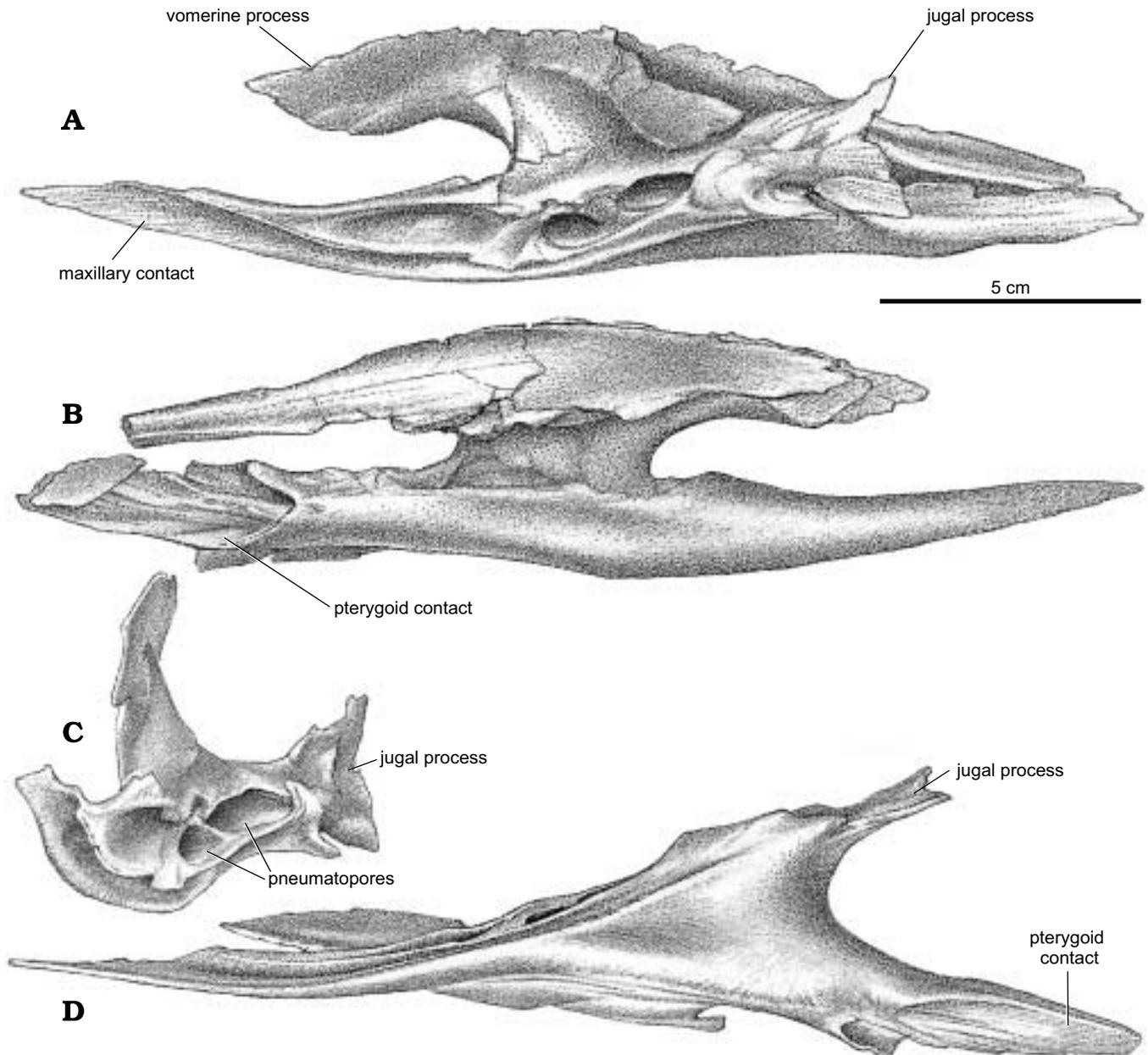
Fig. 29. *Daspletosaurus* sp. (TMP 94.143.1). Left palatine (and part of pterygoid) in lateral (**A**), medial (**B**), anterior (**C**), and ventral (**D**) views.

cause of the great posterior width of the skull, the process is relatively longer in the smaller *Nanotyrannus* skull than it is in the immature *G. libratus* (TMP 91.36.500). Near the base of the process, the pterygoid covers the ventral surface of the back of the ectopterygoid, but distally it twists around the posterior edge of the ectopterygoid to terminate on the dorsal surface. Dorsolaterally, the ectopterygoid contact extends from the base of the ventral process to plug into an antero-laterally facing socket at the base of the quadrate ala of the pterygoid. The quadrate ramus is a thin, curved, quadrilateral sheet of bone that is reinforced and strengthened by heavy ridges along the medial surface of the anterodorsal margin, and the lateral surface of the anteroventral edge. The more dorsal of these two ridges ends in a suture for the epi-

pterygoid, which also covers part of the lateral surface of the quadrate ramus of the pterygoid. Almost half of the some-what convex, lateral surface of the quadrate ala is covered by a squamose sutural contact with the quadrate.

Because the skulls of tyrannosaurines are wider behind the orbit, the quadrate process of the pterygoid is longer and more laterally oriented in tyrannosaurines.

Epipterygoid.—Epipterygoids are well preserved in two of the juvenile *Gorgosaurus*. Both are in position in TMP 91.36.500, whereas they are disarticulated in TMP 86.144.1 (*G. libratus*). Lambe (1904) described the upper part of the epipterygoid of *Albertosaurus*, which is essentially the same as an incomplete epipterygoid in *Daspletosaurus* (Fig. 31).
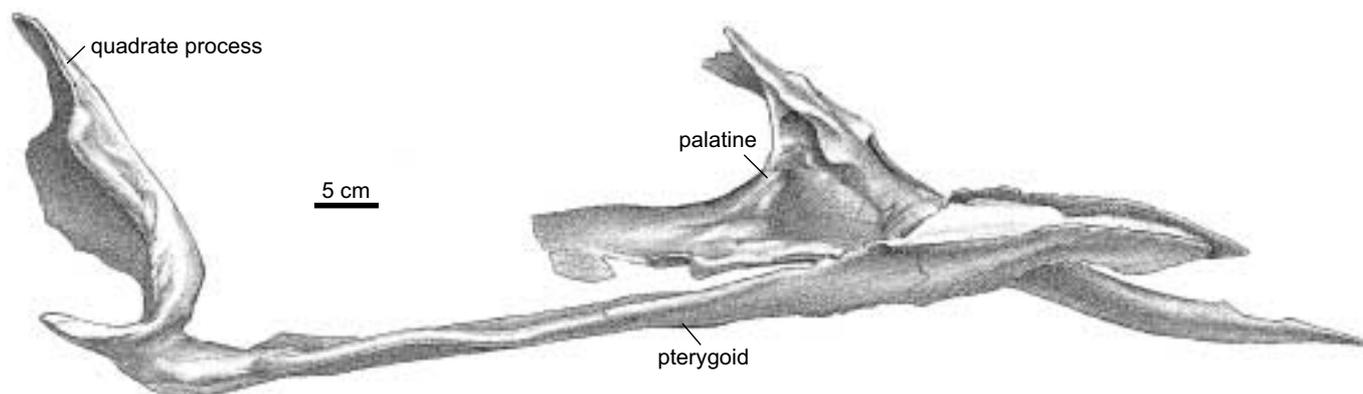
Fig. 30. *Daspletosaurus* sp. (TMP 94.143.1). Left pterygoid and palatine in ventral view.

One large *Daspletosaurus* (TMP 85.62.1) has an epipterygoid that is comparable with those reported for *Tyrannosaurus* (Osborn 1912; Molnar 1991). The epipterygoid tapers dorsally, and forks ventrally into an anterior process continuous with the anterior ridge of the quadrate process of the pterygoid, and a posterior process that extends posteriorly along the dorsal edge of the pterygoid. Both processes overlap the lateral surface of the quadrate process, although the larger, more posterior fork has a more extensive area of contact. The outer surface of the epipterygoid has a shallow concavity near its base. Dorsally, there is an anteromedially oriented facet for contact with the laterosphenoid.

Stapes.—In a large specimen of *G. libratus* (TMP 94.12.602), the preserved shaft of the stapes is 90 mm long and has a maximum shaft diameter of 2.5 mm. The stapes of *Tyrannosaurus* (Brochu 2002) is also about 2 mm in diameter.

Lower jaw

Mandible.—In the immature *G. libratus* (TMP 91.36.500), the posteriorly projecting intramandibular process of the dentary fits into a depression on the lateral surface of an anterodorsal, tongue-like process of the surangular. The external mandibular fenestra has irregular margins but is almost oval in shape. Ventrally, the anterior end of the angular slides between the dentary and splenial, separating them for a short distance where the posterior tips of the two anterior bones fit into grooves on either side of the angular. Although there appears to have been considerable sliding movement possible in the ventral part of the intramandibular joint, the complex dorsal joint between the dentary and the surangular would have only permitted the two bones a range of about 1.5 cm before they interlocked to form a pivot for any further motion. The upper part of the intramandibular joint is also stabilized by the coronoid-supradentary ossification that spans the joint. The coronoid-supradentary seems to have been capable of some limited sliding motion in a groove on the medial surface of the surangular, and is so thin that it may have been capable of some bending. The intramandibular joint of *Gorgosaurus* is typical of tyrannosaurids, although the flexi-

bility was reduced in *Tarbosaurus* (Hurum and Currie 2000) and possibly the other large tyrannosaurines. Differences in the intramandibular joints may reflect differences in feeding behavior (Hurum and Currie 2000, Hurum and Sabath 2003).

Dentary.—The lateral surface of the dentary is pierced by a dorsal row of mental foramina for innervation of the skin and lips by the inferior alveolar nerve. A row of smaller, less prominent foramina is found near the ventral margin of the lateral surface of the dentary. The interdentary symphysis is poorly defined in most tyrannosaurid jaws, and allowed some intermandibular movement. Unlike the juvenile *Daspletosaurus* sp. (Fig. 33), one large specimen of *D. torosus* (NMC 8506) has a complex, rugose symphysis, which suggests that move-
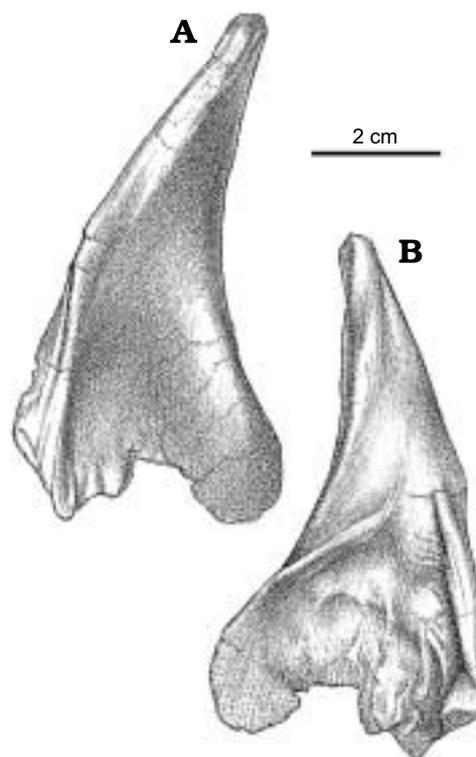

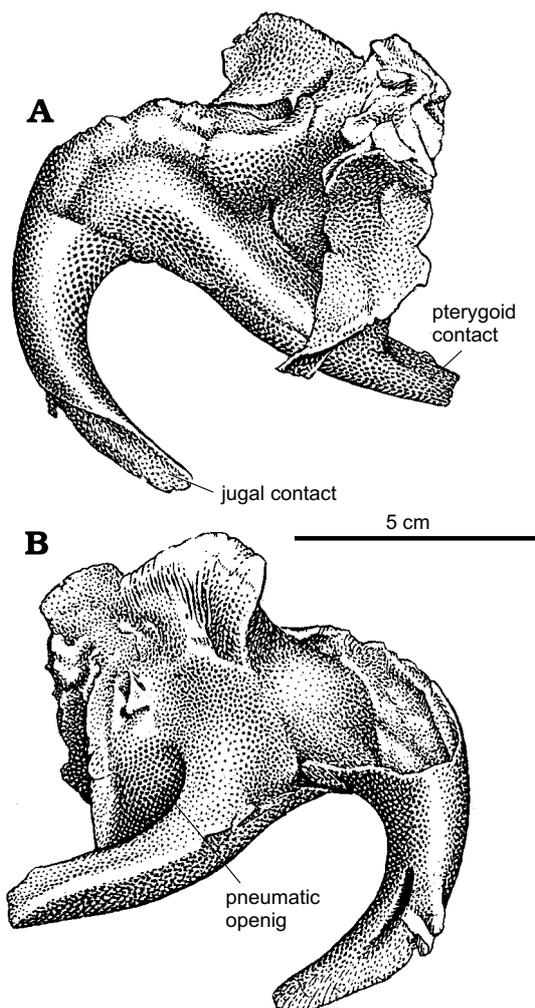Fig. 31. *Daspletosaurus* sp. (TMP 94.143.1). Left epipterygoid in lateral (**A**) and medial (**B**) views.

Fig. 32. *Daspletosaurus* sp. (TMP 94.143.1). Left ectopterygoid in dorsal (**A**) and ventral (**B**) views.

ment would not have been possible between the mandibles. This specimen also shows some coossification of the premaxillae, which is not evident in another *D. torosus* specimen (TMP 2001.36.1) that was just as large an individual. The heavy ossification of the symphysis and premaxillae of NMC 8506 may indicate a health problem.

All well-preserved tyrannosaurid dentaries have three posterior processes—the intramandibular process, a process that contacts the surangular above the external mandibular fenestra, and a process that articulates with the angular below the external mandibular fenestra (Fig. 2A). Medially, the dental shelf is thick, and ends posteromedially in a somewhat downturned process wedged between the coronoid-supradentary laterally and the splenial medially (Fig. 33B, TMP 95.5.1, *G. libratus*). In *G. libratus* (TMP 91.36.500), the most anterior dentary teeth are tiny compared to the others. The interdental plates are separate from each other in all tyrannosaurids (Fig. 33B), but are covered medially by the coronoid-supradentary.

TMP 94.12.155 is a pair of lower jaws from a small *G. libratus* (Currie and Dong 2001), with an estimated skull

length of 364 mm, which suggests that the whole animal was only about 3 m long. The dentaries are elongate (height/ length ratio of 0.10) compared to the *G. libratus* TMP 91.36.500 (ratio is 0.13) and larger specimens (for example it is 0.17 in UA 10, *G. libratus*). Mandibular proportions are ontogenetically controlled in tyrannosaurids, and become relatively deeper in larger individuals. The lowest height of the dentary in the immature *G. libratus* TMP 91.36.500 is 21% the height of the length of the dentary tooth row, and 24% higher than the tallest dentary tooth. The minimum height of the similar sized *Nanotyrannus* is also 21% of the dentary tooth row. In the smallest known *G. libratus* (TMP 94.12.155), the height of the dentary is only 14% of the dentary tooth row length, and the highest dentary tooth is actually taller than the jaw beneath it. In large specimens of *Albertosaurus* (Table 4), the height of the jaw is about 25% the length of the tooth row, and the longest tooth is half the height of the jaw. Statistically, comparison of tooth row length versus jaw height in 27 tyrannosaur jaws (Table 4) shows that the depth of the jaw increases with strong positive allometry (k= 1.43, $r^2 = 0.93$). The relationship between jaw height and tooth row length (Fig. 17) is consistent for both ontogenetic and interspecific size changes, demonstrating that relative jaw proportions cannot be used for distinguishing taxa.

Splenial.—In medial view, the posterior margin of the splenial is deeply notched where it forms the anterior margin of the internal mandibular fenestra. Posteriorly, the tapered end of the splenial sits in a triangular depression on the medial surface of the angular. The anterior mylohyoid fenestra (Fig. 34) is almost completely surrounded by the splenial, although there is a small gap in the ventral border. Compared with most theropods, it is relatively large in tyrannosaurids. The ventral margin of the splenial is thick to support an elongate ventrolaterally oriented contact with the dentary (TMP 86.144.1, *G. libratus*). Dorsal to this ridge is a groove (Fig. 34B) for the sliding contact with the angular. Ventral to the anterior mylohyoid fenestra, a second ventrally oriented butt joint for the dentary is positioned along the ventral margin. Anterior to the front margin of the Meckelian canal, the tapered end of the splenial medially overlaps the dentary. The dorsal butt joints with the dentary are elongate but poorly defined in the small specimens of *Gorgosaurus* but can be an elaborate series of anteroventrally oriented ridges and grooves in large tyrannosaurids (NMC 11594, *G. libratus*).

Coronoid-supradentary.—Forming the dorsoanterior margin of the adductor fossa, the coronoid has a concave posterior margin. Posterodorsally, it has a thin, elongate butt joint with the surangular. However, more anteriorly, the coronoid twists into a well-defined pocket on the medial surface of the anterodorsal process of the surangular (Figs. 14B, 36B). The ventral margin of the coronoid is overlapped by the posterodorsal edge of the prearticular. The coronoid extends anteriorly as the supradentary. There is no indication of a suture or line of fusion in tyrannosaurids (Fig. 35) or other theropods. The supradentary covers up the interdental plates anteriorly to at least the level of the fifth dentary tooth in the immature
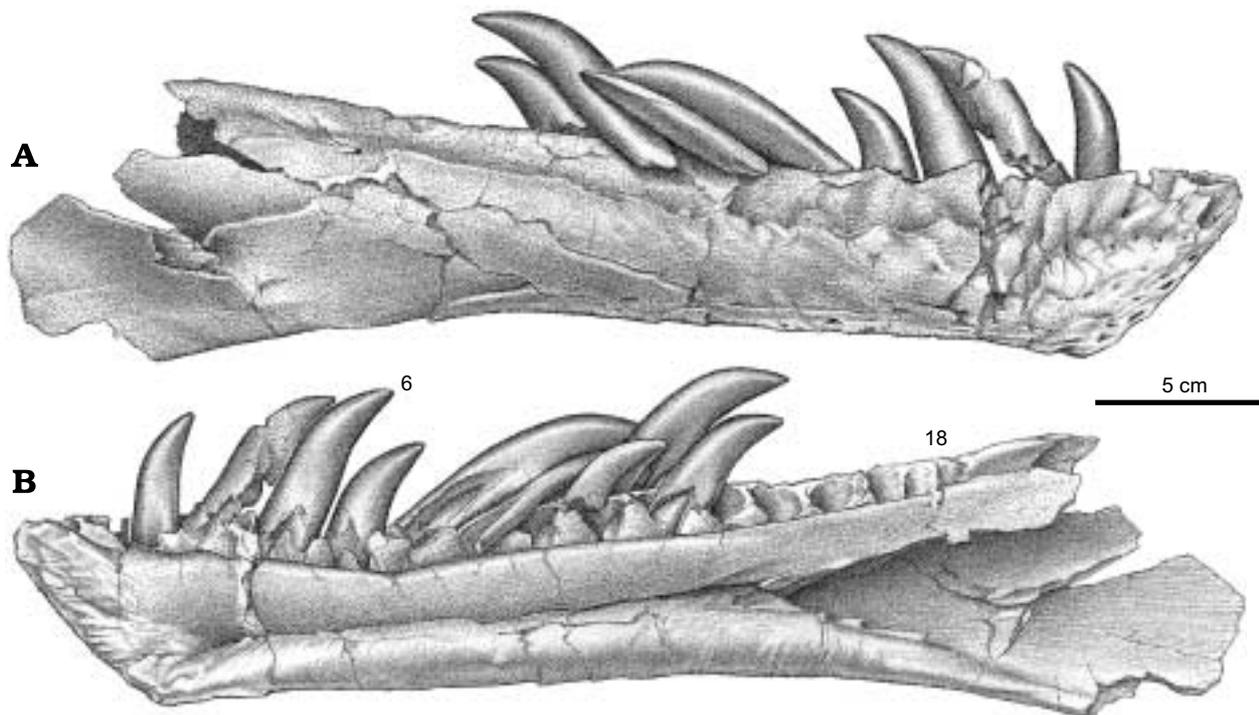
Fig. 33. *Daspletosaurus* sp. (TMP 94.143.1). Right dentary in lateral (**A**) and medial (**B**) views. Numbers represent tooth positions.

G. libratus (TMP 91.36.500), although most likely extends to the second dentary tooth as it does in NMC 5600. It is partially overlapped by the splenial behind the level of the last two dentary teeth.

Surangular.—The anterior surangular foramen opens anteriorly into a groove that is continuous anteriorly with the depression that receives the intramandibular process of the dentary. The large size of the posterior surangular fenestra is synapomorphic for tyrannosaurids (Holtz 2001). The longitudinal ridge (surangular shelf) above it becomes very wide in large tyrannosaurids, and its dorsal surface has a longitudinal concavity for the powerful M. adductor mandibulae externus. The great width of the shelf is similar to the condition seen in some other groups of large theropods, including abelisaurids and carcharodontosaurids. There is an extensive squamose suture where the angular overlaps the ventral margin of the surangular behind the external mandibular fenestra (Figs. 2, 14, 36). Behind the posterior end of the angular, the surangular forms the ventrolateral margin of the jaw. Here, it overlaps the articular, and the lateral edge of the prearticular. Posterodorsal to the posterior surangular fenestra on the medial surface there is a hook-like process (Figs. 4, 36B, 36C) that contacts the lateral surface of the prearticular and forms the posterior margin of the adductor fossa. Most of the medial surface of the surangular's contribution to the short retroarticular process is in contact with the articular. Dorsally the surangular forms half of the lateral depression of the glenoid (Fig. 4) that articulates with the lateral condyle of the quadrate.

Angular.—Tyrannosaurid angulars (Figs. 2, 15) are shallowly curved plates of bone that taper and thicken antero-

ventrally to form the posterior and ventral margins of the external mandibular fenestra. The posterior margin of the depressed articular facet for the dentary reaches the level of the posterior border of the external mandibular fenestra, but the medial depression for the splenial ends farther forward. Almost half of the length of the bone is covered laterally by the dentary. The ventral margin is strengthened by a ridge beneath the external mandibular fenestra, where the angular forms the ventral margin of the mandible. Posteriorly, the ventral edge rests in a slot on the lateral margin of the prearticular, and the dorsal margin overlaps the lateral surface of the surangular. The bone ends behind the posterior margin of the posterior
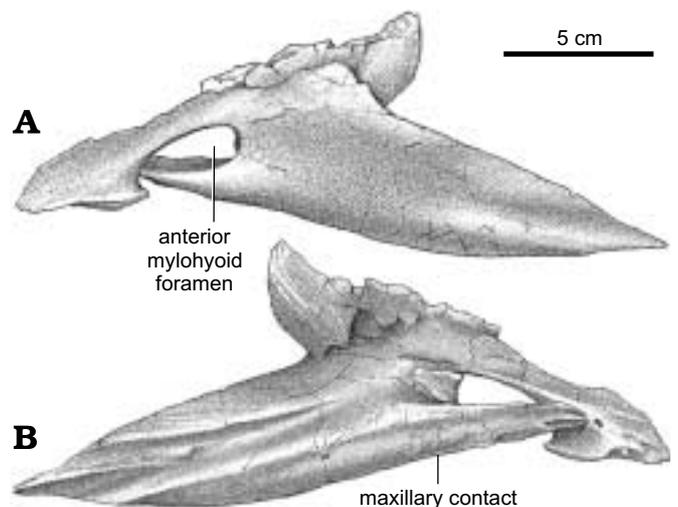

Fig. 34. *Daspletosaurus* sp. (TMP 94.143.1). Right splenial in lateral (**A**) and medial (**B**) views.

Fig. 35. *Daspletosaurus* sp. (TMP 94.143.1). Right supradentary in lingual view.

surangular fenestra in *Gorgosaurus* (Fig. 2A), behind (Fig. 36A) or beneath the fenestra in *Daspletosaurus* (Russell 1970), and behind it in *Nanotyrannus*.

Prearticular.—The elongate tyrannosaurid prearticular expands into thin, vertical plates of bone anteriorly and posteriorly (Fig. 16), but is relatively thick medially where it forms the floor of the adductor fossa and joints the angular to form the ventral margin of the jaw. The elongate but curved groove for the angular on the ventrolateral surface of the prearticular is bound dorsally by a longitudinal ridge (Fig. 16A, 86.144.1, *G. libratus*). Posteriorly, the prearticular contacts the hook-like process of the surangular behind the adductor fossa, and extensively overlaps the ventromedial surface of the articular.

Articular.—The medial glenoid and most of the interglenoid ridge for the articulation with the quadrate are found on the articular (Fig. 4). The retroarticular process is short in all tyrannosaurids, and is directed posteromedially (Fig. 2). The opening for the chorda tympani and posterior condylar artery (Fig. 4) is large, and presumably carried a diverticulum of the tympanic air sac into the hollow core of the articular (Molnar 1991). The anterior opening for the chorda tympani leaves the articular through the suture underneath the prearticular.

Teeth.—The number of teeth in tyrannosaurid jaws is consistently four in the premaxilla, but tends to vary in the maxilla and dentary. The variability in part is accounted for by our inability to clearly see the alveoli in some specimens. The small, anterior-most maxillary tooth is sometimes not preserved because this part of the maxilla is easily damaged, or it can be counted as a premaxillary tooth if the suture is not clean enough to be visible. This happens easily because of its small size, incisiform shape and position at the premaxillary-maxillary suture.

Regardless of these problems, maxillary and dentary tooth counts are still variable within any taxon. In fact they can even vary from one side of the mouth to the other. For example, TMP 94.12.602 (*G. libratus*) has 14 maxillary teeth on the right side and 15 on the left, TMP 91.36.500 (*G. libratus*) and NMC 11594 (*Daspletosaurus* sp.) have 16 dentary teeth on one side and 17 on the other, GIN 107/1 (*Tarbosaurus bataar*) has 12 and 13 alveoli in the right and left maxillae, and SDSM 12047 (*T. rex*) has 11 left and 12 right maxillary teeth (Molnar 1991). Maxillary tooth counts vary between taxa, and amongst different individuals within a genus. Most specimens of *G. libratus* have 13 or 14 maxillary teeth, but some have 15 (NMC 2270, TMP 83.36.100, 94.12.602). The same range exists in *Albertosaurus*. In *Daspletosaurus* sp., TMP 94.143.1

(Fig. 18A) has only 13 maxillary alveoli whereas all other specimens from Alberta have 15 or 16, and those from Montana have as many as 17 (MOR 590). Anatomical, geographic and stratigraphic differences, however, suggest that there are as many as three species of *Daspletosaurus*. All *Tarbosaurus bataar* specimens have either 12 or 13 maxillary teeth (GIN 107/1 has 12 in one maxilla and 13 in the other), and *T. rex* has 11 or 12 (SDSM 12047 has both counts). Dentary teeth show the same kind of variability, although there are usually one or two more alveoli in the dentary than there are in the maxilla of the same individual.

There are several synapomorphies in the premaxillary teeth of tyrannosaurids (Holtz 2001). First, they are always significantly smaller than the largest maxillary or dentary teeth (Figs. 2A, 18A, 18C). More significant for the recovery of identifiable isolated teeth, however, is the fact that they are D-shaped in cross-section (Currie et. al 1990). In tyrannosaurid premaxillary teeth, both carina are on the posterior surface of the tooth, and in most cases the maximum mediolateral width of the tooth is greater than the distance between the two carina. All premaxillary teeth in *Gorgosaurus* are serrated, in contrast with "*Aublysodon*". The holotype of "*Stygivenator molnari*" (LACM 28471), an immature specimen of *T. rex*, lacks serrations on the only premaxillary tooth preserved (Molnar 1978). The juvenile specimen of *Daspletosaurus* has no serrations on either carina, although its first incisiform maxillary tooth has denticles.

Of the fourteen maxillary teeth in the immature *G. libratus* (TMP 91.36.500), the first is incisiform and is as tall as the longest premaxillary tooth. The second maxillary tooth is transitional in size and shape, although it is no longer
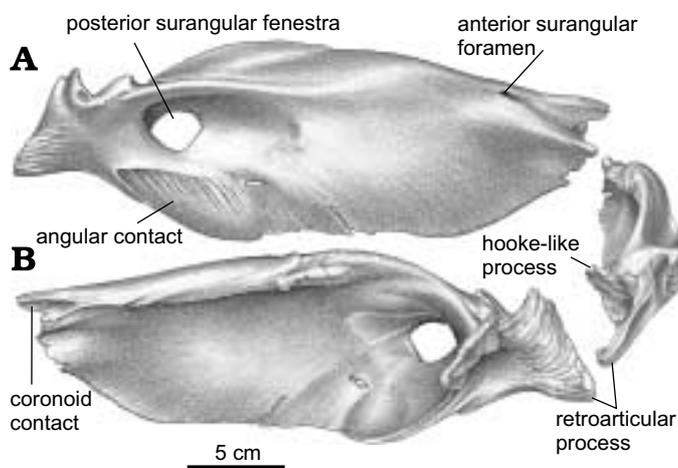

Fig. 36. *Daspletosaurus* sp. (TMP 94.143.1). Right surangular in lateral (**A**), medial (**B**), and posterior (**C**) views.

D-shaped in cross-section. By the third maxillary tooth, the anterior carina is positioned on the midline distally, but is closer to the lingual side of the tooth proximally. The posterior carina runs along the posterolabial edge of the tooth. The longest maxillary teeth are in the fourth to eighth alveoli. The last maxillary tooth is only a third of that height.

Discussion

Variability in the Tyrannosauridae

Well-preserved tyrannosaurid material from Alberta provides the greatest range of information on the tyrannosaurids of North America because it includes the most taxa and most ontogenetic stages in a relatively restricted geographic range. The influx of new tyrannosaurid specimens worldwide finally allows some resolution of taxonomic problems that have existed for many years. Although the generic and specific identification of complete adult tyrannosaurid skeletons is possible, identification of partial skeletons and juveniles is still difficult. Some specimens can be identified on the basis of only a few characters, but for most isolated bones and partial skeletons, there is enough overlapping variability to introduce some uncertainty in identification to the level of genus or species. It is most difficult to determine the identification of juveniles in which certain features do not become generically distinct until the animal is mature. For example, albertosaurine maxillary fenestrae are smaller and more posteriorly positioned than those of adult tyrannosaurines, but are very similar to those of juvenile tyrannosaurines. *Daspletosaurus* lacks a suborbital process of the postorbital bone at all stages of its life, whereas only the juveniles of other tyrannosaurid genera lack the suborbital process. Even in mature animals, individual variation can still mask the identity of a specimen. For example, albertosaurines and tyrannosaurines are generally different at the base of the postorbital process of the jugal. This region is anteroposteriorly wide at the base and externally concave in adult tyrannosaurines, but is a narrower process with a slightly convex lateral surface in most albertosaurines. However, sometimes it can look the same as a tyrannosaurine in the largest albertosaurine individuals. Furthermore, juvenile tyrannosaurines look more like albertosaurines in this region in that the external surface is flat or slightly convex. So although albertosaurines and tyrannosaurines can be identified most of the time on the basis of the postorbital process of the jugal, the identifications are not always correct. The degree of allometric (including ontogenetic), individual and interspecific variability introduces considerable uncertainty in both identifications and phylogenetic analyses. The variability is such that it is recommended that multiple characters are necessary to identify most tyrannosaurid fossils to generic level.

Cranial characters of the Tyrannosauridae

Cranial characters used by Holtz (1994, 2000, 2001), Currie et al. (2003), and others to distinguish tyrannosaurids from other theropod taxa include the dorsoventrally tall subnarial body of the premaxilla, the mediolaterally oriented premaxilla, fused nasals, the division of the lateral temporal fenestra by a squamosal-quadratojugal flange, reduced prefrontals, sagittal crest, tall nuchal crest formed by the parietals, tab-like processes on the supraoccipital, deep basisphenoidal recess with large foramina, loss of prominent muscular fossa on the dorsal surface of the palatines, fusion and expansion of the vomers into a large rhomboidal or diamond shaped plate, large posterior surangular fenestra, reduced retroarticular process, and relatively small premaxillary teeth with D-shaped cross-sections. Tyrannosauridae can be subdivided into two subfamilies on the basis of significant differences in cranial anatomy. These will be dealt with in another paper (Currie et al. 2003), but it is necessary to establish which tyrannosaurid genera are suitable for phylogenetic analysis.

All of these genera and species can be defined on the basis of characters and character suites unique within the Tyrannosauridae. As our anatomical understanding improves with all of these taxa, it may become more logical to reduce the number of genera, or alternatively to split them further.

Albertosaurus sarcophagus.—*A. sarcophagus* Osborn, 1905 is only known with certainty from the Horseshoe Canyon Formation of Alberta, Canada. There are ten skulls and skeletons known, plus a bonebed that includes at least twelve individuals of different ontogenetic stages (Currie 2000b). Russell (1970) synonymized the more ancient *Gorgosaurus* with this genus because he was unable to find any significant differences between the two forms. However, this was largely because the only cranial material of *Albertosaurus* that was available to study at that time consisted of several partial skulls that had "not been satisfactorily characterized" (Gilmore 1946). In the absence of any derived characters in the specimens available at that time, when cladistic methodology was not in widespread use in palaeontology, the synonymy of the two genera was a legitimate approach. The recovery of additional specimens has made it possible to do a more thorough comparison. *Albertosaurus* is a slightly larger animal than *Gorgosaurus*, and consequently adult specimens tend to be more robust. Compared with all other tyrannosaurids, most specimens of *Albertosaurus* have more numerous, deeper pits in the ventral surfaces of the maxillary palatal shelves to accommodate the tips of the dentary teeth. The occipital condyle is oriented more ventrally than in *Gorgosaurus*, although not to the same degree as in the tyrannosaurines. The braincase box (Bakker et al. 1988) is mediolaterally wider than anteroposteriorly long, in contrast with *Gorgosaurus* where the dimensions are the opposite. In *Albertosaurus*, the nasal-frontal suture is more complex than that of *Gorgosaurus*, and the paired midline processes of the nasals expand posteriorly (rather than taper) and extend farther backwards than the posterolateral process of the nasal. In contrast, the prefrontal seems to have very limited dorsal exposure in *Albertosaurus*, and the lacrimal did not plug into a socket in the frontal, which is more similar to *T. rex* (RSM 283.2) than *Gorgosaurus*. Finally, Carr (1999) pointed out that *Albertosaurus* differs from

other tyrannosaurids in having an angular suture between the exoccipital and basioccipital in the occipital condyle.

There are enough morphological differences to distinguish *Albertosaurus* from *Gorgosaurus*, although it is still an arbitrary decision as to whether the distinction is generic, specific or even subspecific. With the recovery of more albertosaurine specimens from New Mexico in the south to Alaska in the north, specimens are being found that have anatomical characters not seen in either of the Alberta albertosaurines. Generic distinction of *Albertosaurus* and *Gorgosaurus* gives more latitude for the assessment of relationships of these new specimens. Furthermore, there are as many anatomical differences between *Albertosaurus* and *Gorgosaurus* as there are between *Daspletosaurus*, *Tarbosaurus* and *Tyrannosaurus*. At this time, with our present state of knowledge and understanding, it is advisable to maintain generic distinction between *Albertosaurus* and *Gorgosaurus*.

Alioramus remotus.—*Alioramus remotus* Kurzanov, 1976 is known from only a single partial skull and skeleton collected from Nogon-Tsav in Mongolia. The taxonomic status of *Alioramus* is uncertain because of the incompleteness and immature nature of the specimen. Kurzanov (1976) cited certain characteristics that were supposedly different than in other tyrannosaurids. These included the presence of two conspicuous rows of foramina on the outer surface of the maxilla, and the position and contacts of the laterosphenoid. However, these are characters shared with all other tyrannosaurids. The skull is low because of the small size of the specimen, and "the greatly elongated jaws" are typical for all tyrannosaurid individuals of this size. Other characters expected in any small tyrannosaurid include the smoothness of the postorbital bone and the mediolateral compression of the teeth. The position of the maxillary fenestra falls within the range of variability for tyrannosaurines like *Tarbosaurus*. Although it has pronounced "hornlets" on the nasal, they are comparable in position and number to lower bumps in some specimens of *Daspletosaurus* and *Tarbosaurus*. The prootic is supposed to surround the trigeminal foramen, but examination of the specimen suggests that this is probably not correct. Almost certainly the anterior border of the trigeminal is formed by the laterosphenoid in the conventional way. The shape and orientation of the basisphenoid recess is very similar to these features in *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*. Skull proportions suggest that PIN 3142/1 might be an immature *Tarbosaurus*, although generic distinction is suggested by the higher number of teeth (16 or 17 maxillary, and 18 dentary teeth), and by the prominence of the osseous excrescences on the nasal bone.

Daspletosaurus.—*Daspletosaurus torosus* Russell, 1970 is known from the holotype skull and skeleton collected from the Oldman Formation of Dinosaur Park. Another specimen (TMP 2001.36.1) has been collected from the same formation some 250 kilometers southeast of Dinosaur Park on the Milk River.

The type specimen of *Daspletosaurus torosus* was collected from the Oldman Formation, which is the lower of the two terrestrial formations exposed in Dinosaur Provincial Park (Eberth et al. 2001). Additional skulls with skeletons of *Daspletosaurus* (Table 1) been recovered from the younger Dinosaur Park Formation in southern Alberta, and a skull (MOR 590) has been found in Montana. A specimen (NMC 11315) from the Horseshoe Canyon formation that was tentatively assigned to this genus (Russell 1970) is now known to be *Albertosaurus*. Based on cranial morphology (Currie and Bakker in preparation), the Dinosaur Park Formation specimens seem to represent a distinct species from *Daspletosaurus torosus*. Furthermore, MOR 590 is distinct from both in having a relatively tall, triangular lacrimal horn and seems to represent a distinct species (Horner et al. 1992). Finally, the specimen described by Lehman and Carpenter (1990) as "*Aublysodon*" may represent another undescribed species of Daspletosaurus based on differences in cranial morphology (Carr and Williamson 2000). The fact that three or more distinct forms of *Daspletosaurus* can be recognized justifies the separation of *Daspletosaurus* from *Tyrannosaurus* at the generic level. Although there has been a tendency to consider *Daspletosaurus* as a sister taxon of *Tarbosaurus* + *Tyrannosaurus*, there has been no justification to assume this is true without a full phylogenetic analysis of these animals. The analysis of Currie et al. (2003) suggests that *Tarbosaurus* is the sister taxon of *Daspletosaurus* + *Tyrannosaurus*, although the relationship is assumed on the basis of relatively few characters. Furthermore, the geographic and stratigraphic occurrences of these animals suggest the most parsimonious *a priori* interpretation is that *Daspletosaurus* and *Tyrannosaurus* are probably more closely related to each other than either is to *Tarbosaurus*.

Daspletosaurus shares many derived characters with other tyrannosaurines. It can be distinguished most easily from mature specimens of *Tarbosaurus* and *Tyrannosaurus* by its lack of a suborbital process on the postorbitals (Currie et al. 2003). Contrary to published reports (Russell 1970, Holtz 2001), the premaxilla and nasal contact each other beneath the external naris. Holtz (2001) also characterized *Daspletosaurus* as having intergrowth between the premaxillae. However, coossification of the premaxillae in *Daspletosaurus* is limited to only a single specimen (NMC 8506) of more than ten known individuals. The postorbital region of the skull is laterally expanded in *Nanotyrannus* and *Tyrannosaurus*, but like *Tarbosaurus*, *Daspletosaurus* is intermediate in the degree of expansion between these genera and albertosaurines.

Gorgosaurus libratus.—*G. libratus* Lambe, 1914 is known from more than twenty skeletons from southern Alberta. Good specimens of *Gorgosaurus* in the Museum of the Rockies and the Indianapolis Children's Museum have also been recovered from Montana, although these have not been studied closely enough to be sure that they are the same species. Russell (1970) distinguished "*Albertosaurus*" *libratus* from *A. sarcophagus* because of differences in the times when these animals lived, and because of differences in relative lengths of the dentary tooth row (compared with the fourth metatarsal), the scapulocoracoid (compared with the

Table 1. List of articulated and associated tyrannosaurid skeletons from Alberta, Canada. Abbreviations: DP, Dinosaur Park Formation; DPP, Dinosaur Provincial Park and region; HC, Horseshoe Canyon Formation; Q, quarry number; Sc, Scollard Formation; WC, Willow Creek Formation.

Species	Specimen #	Formation	Locality	Comment
Albertosaurus sarcophagus	AMNH 5218	HC	Dry Island Park	Bonebed with articulated skeletons
	AMNH 5222	HC	Red Deer River, Tolman Bridge	Scattered skull
	NMC 5600	HC	Kneehills Creek	Holotype, skull
	NMC 5601	HC	Red Deer River, Tolman Bridge	Paratype, skull
	NMC 11315	HC	Dry Island Park	Skull and skeleton
	ROM 807	HC	27or34,30,21,w4	A. arctunguis
	TMP 81.10.1	HC	Red Deer River, Tolman Bridge	Skull and skeleton
	TMP 85.98.1	HC	Kneehills Creek	Skull and skeleton
	TMP 86.64.1	HC	Drumheller	Skull and skeleton
	TMP 86.205.1	HC	Kneehills Creek	Skull and skeleton
	TMP 97.58.1	HC	Horsethief Canyon	Skull and skeleton
Daspletosaurus torosus	NMC 8506	Oldman	DPP, Q72	Holotype, skull and skeleton
	TMP 2001.36.1	Oldman	Milk River	Skull and skeleton
Daspletosaurus sp.	AMNH 5438	DP	DPP, Little Sandhill Creek	Partial skeleton
	BMNH 4863		xxxx	Partial skull
	FMNH PR308	DP	DPP, Q223	Skull and skeleton
	NMC 350	DP	DPP	Partial skeleton
	NMC 11594	DP?	Manyberries	Scattered skull
	TMP 85.62.1	DP	DPP, Q178	Skull and skeleton
	TMP 92.36.1220	DP	DPP, Q210	Skull and skeleton
	TMP 94.143.1	DP	DPP, Q215	Skull and skeleton
Gorgosaurus libratus	AMNH 5336	DP	DPP, Q106	Skull
	AMNH 5423	DP	DPP, Little Sandhill Creek	Skull and skeleton
	AMNH 5432	DP	DPP, Q90	Skull and skeleton
	AMNH 5458	DP	DPP, Little Sandhill Creek	Skull and skeleton
	AMNH 5664	DP	DPP, Q6	G. sternbergi, skull and skeleton
	FMNH PR2211	DP	DPP, Q138	Skeleton
	NMC 2120	DP	DPP, Q36	Holotype, skull and skeleton
	NMC 8782	DP	DPP	Partial skeleton
	NMC 11593	DP	DPP, Q74	Partial skeleton
	ROM 1247	DP	DPP, Q29	Skull and skeleton
	ROM 1422	DP	DPP, Q31	Scattered skull
	TMP 68.3.1	DP	White Rock Coulee	Skeleton
	TMP 73.30.1	DP	DPP	Partial skeleton
	TMP 86.144.1	DP	Sandy Point	Skull and skeleton
	TMP 91.36.500	DP	DPP, Q200	Skull and skeleton
	TMP 91.163.1	DP	Battle River	Skull and skeleton
	TMP 94.12.155	DP	DPP, Q218	Scattered skull
	TMP 94.12.602	DP	DPP, Q220	Skull and skeleton
	TMP 95.5.1	DP	DPP, Q219	Skull and skeleton
	TMP 99.33.1	DP	DPP, Q139	Skull and skeleton
	TMP 2000.12.11	DP	DPP, Q234	Scattered skull
	UA 10	DP	DPP, Q48	Skull and partial skeleton
	USNM 12814	DP	DPP, Little Sandhill Creek	Skull and skeleton
Tyrannosaurus rex	TMP 81.6.1	WC	Crowsnest Pass	Skull and skeleton
	TMP 81.12.1	Sc	Huxley	Partial skull, skeleton

femur) and the tibia plus astragalus (also compared with the femur). However, differences in relative proportions are not very reliable for taxa in which growth is allometric for most cranial and appendicular dimensions. This is confirmed by plotting tooth row versus metatarsal measurements against each other for *Albertosaurus* (four specimens) and *Gorgosaurus* (seven specimens). This particular calculation and

others done by Currie (2003) fail to show any significant differences between the regression curves of these genera.

The most detailed comparison (Bakker et al. 1988) used braincase characters to distinguish various tyrannosaurid genera, including *Albertosaurus* and *Gorgosaurus*. The basal tubera were observed to be wide and thick in *Gorgosaurus*, but reduced and thin in *Albertosaurus*, presumably reflecting a

Table 2. Measurements of tyrannosaurid frontals. (* from posterior frontoparietal suture to dorsal junction of the frontal, nasal and prefrontal; ** from midline to medial edge of slot between lacrimal and postorbital; *** on midline at front of supratemporal fossa).

Identification	Specimen #	Length*	Width**	Depth***
A. sarcophagus	81.10.1	122	75	–
	81.9.1	127	75	48
	85.98.1	101	59	–
D. torosus	NMC 8506	145	56	–
D. sp.	85.62.1	147	71	–
	91.36.403	–	31	18
	94.143.1	99	40	20
	NMC 11841	–	85	56
	SDNH 32701	128	67.5	40
G. libratus	67.14.3	119	65	36
	80.16.485	88	35	13
	81.39.8	90	48	19
	82.16.181	108	60	25
	91.36.500	96	51	–
	91.36.533	–	66	36
	92.36.76	–	57	29
	AMNH 5664	117	51	–
	ROM 1247	116	43	–
	ROM 3520	122	70	35
	UA 10	120	67	–
N. lancensis	CMNH 7541	103	46	–
Ta. bataar	GIN 107.2	–	82	–
	GIN Jap-Mong	112	60	46
	GIN PJC.2000.25	132	81	47
	GIN PJC.2000.26	81	50	18
	GIN PJC.2000.8	113	80	44
T. rex	AMNH (braincase)	150	94	55
	AMNH 5029	–	108	72
	BHI 116	68	21	6
	BHI 3033	140	117	75
	LACM 23845	139	58	36
	LACM 28471	39e	29	11.5
	MOR 008	171	116	73
	RSM 283.2	162	106	65

reduction in the size of tendonous muscle attachments. Paired pneumatic foramina in the ceiling of the basisphenoid recess are larger in *Albertosaurus* than *Gorgosaurus*, and the occipital condyle is more ventrally oriented in *Albertosaurus*.

Holtz (2001) distinguished *Albertosaurus* and *Gorgosaurus* on the basis of 14 characters, two of which he considered unique in *Gorgosaurus* amongst tyrannosaurids. These include differences in the nasal-frontal suture (his character 48), orientation of the lacrimal horn (52), presence of the suborbital process (57), orientation of the occiput (65), size of the basal tuber (67), number of foramina on the ventral surface of the palatine (71), number of incisiform maxillary teeth (78), expansion of the distal end of the scapula (82), size of deltapectoral crest (83), relative size of manual phalanx I-1 (85), position of the promaxillary fenestra (93), postorbital-lacrimal contact (94), nature of the anterior margin of the suborbital process (95), and position of the foramina in the

basisphenoidal recess (96). Although this long list should be enough to convince anyone of the distinctness of the two genera, many of the characters apply only to specific specimens. There is enough variability in anatomy in *Gorgosaurus* that any single individual is unlikely to show more than half the differences from *Albertosaurus*. Using the entire suite of character states of Bakker et al. (1988), Holtz (2001) and Currie et al. (2003), reasonably complete specimens of *Gorgosaurus* can be distinguished from *Albertosaurus*. However, it is likely that some of the characters will not code in the expected way, or will not code at all. Of the cranial characters, those associated with the braincase seem to be the most reliable for separating the two albertosaurine genera.

Nanotyrannus lancensis.—*N. lancensis* (Gilmore, 1946), originally described as *Gorgosaurus lancensis*, was proposed as a separate genus by Bakker et al. 1988. It is represented by the only known skull (CM 7541), which is less than 600 mm long, and is smaller in most dimensions than the immature *G. libratus* (TMP 91.36.500). However, the back of the skull is consistently wider in the Maastrichtian genus, with a maximum width across the postorbitals of 210 mm. *Nanotyrannus lancencis* is almost certainly an immature tyrannosaurid that is closely related to *Tyrannosaurus*, but the higher number of maxillary teeth suggest that it might be easily distinguishable from the latter genus if mature specimens were found. Carr (1999) has demonstrated that the holotype of *Nanotyrannus* is an immature individual. However, many of the characters he cites as indicators of immaturity (such as the elongate proportions of the antorbital fenestra, the length of the orbital notch, and the height of the dentary) are in fact simply a consequence of the small size of the specimen and may not have any real ontogenetic significance. The presence of immature bone grain is in itself sufficient to indicate that the specimen was a juvenile. Rozhdestvensky (1965), Carpenter (1992), Carr (1999), and others have suggested that *N. lancensis* is an immature *T. rex*. The thorough analysis done by Carr (1999) makes it clear that most of the characters used to distinguish *Nanotyrannus* from *Tyrannosaurus* (Bakker et al. 1988) are simply size-related or ontogenetic differences. However, most of the characters (on page 509) used to demonstrate that *Nanotyrannus* and *Tyrannosaurus* are synonymous are also characters of *Tarbosaurus* and *Daspletosaurus*. Dealing with the characters one at a time:

- The nasal processes of the premaxillae are tightly appressed throughout their entire length in *Tyrannosaurus*, and form a single tapering tip wedged between the nasals. However, most of the lengths of the nasal processes are not preserved in *Nanotyrannus*.
- The jugal only forms a small part of the margin of the antorbital fenestra in *Tyrannosaurus*, *Nanotyrannus*, and the other tyrannosaurines. It is variable enough that there is at least one specimen of *G. libratus* (TMP 91.36.500) in which the character can be coded differently on the left and right sides of the skull.
- The nasal makes a small but variable contribution to the antorbital fossa in all tyrannosaurids.

Table 4. Measurements of tyrannosaurid dentaries. *length of the dentary tooth row; ** minimum lateral depth of the dentary at about mid-length; *** height of longest dentary tooth crown. (check 75.11.3 right dentary, 91.36.500, 94.12.602 right dentary, 94.143.1, 99.55.170)

Identification	Specimen #	Length*	Depth**	Tooth***
G. libratus	94.12.155	164	24	25
	86.144.1	235	45	37.5
	92.36.749	275	62	–
	91.36.500	280	60	48.5
	AMNH 5423	280	52	41
	95.5.1	312	80	50.5
	99.33.1	315	69	52
	99.55.170	337	69	53
	86.49.29	347	103	–
	USNM 12814	352	–	–
	82.28.1	370	97	–
	UA 10	370	97	62
	83.36.134	390	100	58
	AMNH 3963	435	115	–
	67.9.164	445	114	57
	ROM 1246	–	79	56
A. sarcophagus	NMC 5601	320	90	53
	94.25.6	390	101	–
D. torosus	NMC 8506	455	118	60
D. sp.	FMNH PR308	430	110	–
N. lancensis	CMNH 7541	280	60	–
Ta. bataar	GIN 107.2	480	143	98
	PIN 552-2	210	54	43
	PIN 551-3	470	96	80
	PIN 551-1	551	160	84
T. rex	CM 9380	500	155	125
	AMNH 5027	530	170	130
	LACM 23844	535	153	112
	BHI 3033	580	170	140
	LACM 28471	–	37	33

Table 3. Nuchal crest of tyrannosaur parietals. Width[1], maximum width near top of crest; Width[2], minimum width on occipital view; Height[1], maximum height from top of crest to foramen magnum; Height[2], height from top of crest to top of supraoccipital.

Identification	Specimen #	Width[1]	Width[2]	Height[1]	Height[2]
A. sarcophagus	81.10.1	180	104	165	69
	85.98.1	130	–	–	–
D. sp.	FMNH PR308	240	135	145	58
	85.62.1	260	185	–	–
	94.143.1	140	94	90	35
D. torosus	NMC 8506	250	190	162	67
G. libratus	UA 10	182	160	120	30
	91.36.500	92	75	88	34
	ROM 1247	152	122	120	42
N. lancensis	CMNH 7541	150	116	90	32
Ta. bataar	Jap-Mong	177	116	118	55
	107.2	358	272	230	120
T. rex	AMNH br.	310	265	232	122
	BHI 3033	410	309	260	98
	AMNH 5029	394e	340e	255	103

– The jugal pneumatopore is transversely wide in *Nanotyrannus*, *Tarbosaurus bataar* (PIN 551-1), and *Tyrannosaurus*.
– The sagittal crest extends onto the frontal to the same degree in *Alioramus*, *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*.
– The basal tubera are short and strongly divergent in *A. sarcophagus* (NMC 5600, TMP 85.98.1), *Alioramus remotus* (PIN 3141-1) *Daspletosaurus torosus* (NMC 8506), *Nanotyrannus*, *Tarbosaurus* (Maleev 1974), and *Tyrannosaurus*. They seem more elongate and vertical in *G. libratus* (TMP 86.144.1, 94.12.602) and the juvenile specimen of *Daspletosaurus* (Fig. 26B), but this character needs to be quantified in some way.
– The lower part of the occiput is oriented to face posteroventrally in *Alioramus*, *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*.
– The subcondylar recess is shallow in *Alioramus remotus* (PIN 3141-1), *Daspletosaurus torosus* (NMC 8506), *Nanotyrannus*, *Tarbosaurus bataar* (PIN 551-1, 553-3), and *Tyrannosaurus*.
– The basisphenoid plate is deep anteroventrally but the basisphenoid recess is broader laterally than anteroventrally long in *Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Nanotyrannus*, *Tarbosaurus*, and *Tyrannosaurus*.
– The ectopterygoid is more inflated in *Daspletosaurus* and *Tarbosaurus* than it is in *Nanotyrannus*.
– The external surface of the anterior plate of the surangular is strongly convex in *Daspletosaurus* sp. (TMP 85.62.1), *Nanotyrannus*, *Tarbosaurus bataar* (GIN 100/65, 107/2), and *Tyrannosaurus*.
– The narrow snout and broad temporal region is characteristic of *Nanotyrannus* and *Tyrannosaurus*, although *Tarbosaurus* and to a lesser extent *Daspletosaurus* are intermediate between these taxa and albertosaurines.
– The jaw is no deeper in *Tyrannosaurus* and *Nanotyrannus* than it is in *Daspletosaurus* and *Tarbosaurus* (Fig. 17).

In short, almost all of the 13 characters define a broader taxonomic unit than just *Tyrannosaurus* and *Nanotyrannus*. *Nanotyrannus lancensis* is closer to *Tyrannosaurus rex* than to any other tyrannosaurid in that it is relatively broader (compared to the snout width) behind the orbit than albertosaurines. *Daspletosaurus* and *Tarbosaurus* are intermediate.

There is at least one way in which *N. lancensis* is different from *Tyrannosaurus*. The number of maxillary teeth is either 11 or 12 in *Tyrannosaurus*, whereas the holotype of *Nanotyrannus lancensis* has at least 14 (Gilmore 1946), but possibly 15 (Bakker et al. 1988) maxillary teeth. Carr (1999) speculated that the number of teeth may be reduced ontogenetically in tyrannosaurids, but the evidence for this is very weak (Currie 2003). There is no indication that any other theropod did this, and the counts always vary within one or two teeth. Given the fact that *Nanotyrannus* is difficult to distinguish from an immature *Daspletosaurus* (an animal that survived into early Maastrichtian times), and that the tooth counts are intermediate between *Daspletosaurus* and *Tyrannosaurus*, it would be

more conservative to retain *Nanotyrannus* as a distinct genus at this time. Ultimately, more specimens may resolve the problem, and tooth counts and stratigraphic position may turn out to be a valid way to distinguish *N. lancensis* from *T. rex* at the generic or species level.

Tarbosaurus bataar.—*Ta. bataar* (Maleev 1955) is a combination introduced by Rozhdestvensky 1965 (see Hurum and Sabath 2003 for details). Paul (1988), Holtz (1994, 2001), Carr (1999) and others consider *Tarbosaurus* Maleev, 1955 and *Tyrannosaurus* Osborn, 1905 to be congeneric, while some researchers (Paul 1988) even include *Daspletosaurus* Russell, 1970 within the genus *Tyrannosaurus*. At least two characters, the locking mechanism of the jaws (Hurum and Currie 2000) and the length of the arms (Holtz 2001; Currie 2003), suggest that *Tarbosaurus* is more derived than either *Daspletosaurus* or *Tyrannosaurus* and therefore could not be ancestral to either. The overall picture becomes more complicated when *Nanotyrannus* and *Alioramus* are considered, the former possibly being a sister-taxon to *Tyrannosaurus*, and the latter to *Tarbosaurus*. Holtz (2001) listed nine characters to distinguish *Tyrannosaurus* from other tyrannosaurids, including its sister taxon "*Tyrannosaurus*" *bataar*. This is the highest number of autapomorphies that he presented for any tyrannosaurid species, and argues that there is a considerable amount of difference between *T. rex* and "*Tyrannosaurus*" *bataar*. Because there are major differences between these two species, and because there are valid reasons for believing that this animal may be the sister taxon of *Daspletosaurus* + *Tyrannosaurus* (Currie et al. 2003), there is ample justification for generic distinction of *Tarbosaurus*.

Tyrannosaurus rex.—*Tyrannosaurus rex* Osborn, 1905 is now known from several well preserved specimens. Holtz (2001) listed nine autapomorphic characters for *Tyrannosaurus*, including the width of the snout at the back of the maxillary tooth row, the maximum postorbital skull width, the orientation of the orbits, the distal divergence of the nasal processes of the premaxillae, the packing of the premaxillary teeth, the length of vomerine-maxillary contact, jugal contribution to the margin of the antorbital fenestra, and the shape of the vomer. However, the distal divergence of the nasal processes of the premaxillae is variable in *Tyrannosaurus* and other tyrannosaurines, and may be in part determined by size. The length of the contact between the vomer and the maxillary palatal shelves is also probably size-related. Loosely packed premaxillary teeth are found in both *Tyrannosaurus* and some specimens of *Daspletosaurus torosus* (NMC 8506). The degree of jugal contribution to the antorbital fenestra is variable, and can even be different from one side to the other of the same skull in tyrannosaurs. Some of the remaining characters are shared with *Nanotyrannus*, although tooth counts distinguish the two animals.

Possible tyrannosaurids.—Given our current understanding of tyrannosaur variability (allometric and individual), *Dinotyrannus* Olshevsky, 1995, *Dynamosaurus* Osborn, 1905, *Jenghizkhan* Olshevsky, 1995, *Maleevosaurus* Car-

penter, 1992, and *Stygivenator* Olshevsky, 1995 all seem to be variants of either *Tarbosaurus* or *Tyrannosaurus*. It is possible that any or all of these might ultimately prove to be valid genera, shall better preserved specimens be found. Characters used to distinguish *Aublysodon* Leidy, 1868 and *Shanshanosaurus* Dong, 1977 are inconsequent in that specimens identified as these animals are almost certainly juveniles of other genera. At present, not enough is known about *Alectrosaurus* to determine whether it is an albertosaurine, a tyrannosaurine, or neither.

Acknowledgments

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