

tral Asia, where tyrannosaurs were spectacularly successful. In America, species of *Albertosaurus* were the first to appear and were common until they were partly displaced by species of *Tyrannosaurus*. There always seem to have been two, three, or even more tyrannosaur species living at the same time and place in western North America. Notably, the massive skulls and speed of the tyrannosaurs allowed them, and the smaller aublysodonts, to partly suppress both allosaurs and the big-brained sickle-clawed protobirds. Things were somewhat different in arid Mongolia. Here tyrannosaurs were small and not that common until near the end, when one giant *Tyrannosaurus* species became common and coexisted with the still abundant sickle-claws.

For many years the tyrannosaur family was named Deinodontidae. But because *Deinodon* itself was based on some hopelessly fragmentary remains, in 1970 Dale Russell resurrected Osborn's Tyrannosauridae. Actually, the Rules of Zoological Nomenclature favor the older name, but Tyrannosauridae has understandably become accepted. *Aublysodon* is different enough to deserve its own subfamily. A number of people are getting involved in taking a second look at tyrannosaurs. Robert Bakker has some new, interesting, and controversial ideas about them, Ken Carpenter is conducting research, and Philip Currie and I are engaged in a long-term study of the group. To arrive at a solid understanding of tyrannosaurs will take time. A lot of the genera and species are poorly defined, and many new and old specimens have to be prepared or reworked before we can figure out what is really going on.

Because they are the second largest theropod family, and particularly because more tyrannosaur species—six—are known by complete remains than in any other family, there are many tyrannosaur illustrations in this book. Besides, they are irresistible subjects. Tyrannosaurs were the final and greatest expression of big theropod evolution, and the best looking. Never before or since has the world seen anything like them.

FAMILY TYRANNOSAURIDAE Osborn, 1906

Aublysodon mirandis

A. huoyanshanensis

A. molnaris new species

Indosuchus raptorius?

Alioramus remotus

Albertosaurus? olseni

A. libratus

A. arctunguis

A. megagracilis new species

A. sarcophagus

A.? ("Nanotyrannus") lancensis

Tyrannosaurus (Daspletosaurus) torosus

T. (Tyrannosaurus) bataar

T. (T.) rex

SUBFAMILY AUBLYSODONTINAE Nopsca, 1928

These small, lightly built tyrannosaurids differ from more advanced tyrannosaurs in that the front teeth are unserrated. Their snouts are also distinctive, having low nasals and a sharp triangular profile. And their lower jaws are slender. But they were big-game hunters nonetheless—all, except perhaps for a tiny theropod from the Late Cretaceous of Mongolia whose snout Andrei Elzanowski is studying. It looks aublysodont to me, but it has conical piercing teeth for hunting insects and very small vertebrates. Another unanswered question is whether their very short forelimbs had only two fingers. Not quite enough is known about these theropods to do a skeletal restoration yet, but we can describe them as basically small, sharp-snouted tyrannosaurs with an upturned dentary tip.

GENUS AUBLYSODON Leidy, 1868

SYNONYM—*Shanshanosaurus*

AUBLYSODON MIRANDIS (Leidy, 1868)

TYPE—ANSP 9535

TIME—late Campanian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—Judith River Formation of Alberta
and Montana

NMC 343

KILOGRAMMAGE— ~80?

This species is based on an unserrated D-cross-sectioned premaxillary tooth from the Judith River. Philip Currie has some new Judith River bones that may belong to this primitive tyrannosaur.

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nosaurid; I hope more complete remains will show up and tell us more.

AUBLYSODON HUOYANSHANENSIS (Dong, 1977)

SYNONYM—*Shanshanosaurus huoyanshanensis*

TYPE—IVPP V4878

TIME—Campanian? to Maastrichtian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—*Subash Formation of China*

Type

SKULL LENGTH— ~280 mm

FEMUR LENGTH— 275 mm

KILOGRAMMAGE— ~50?

The snout and premaxillary teeth of this again fragmentary form are very like those of the American remains above and can be put in the same genus.¹⁶ Its tyrannosaurid skeletal elements prove that it was not a dromaeosaur.

AUBLYSODON MOLNARIS new species

TYPE—LACM 28741

TIME—Maastrichtian of the latest Late Cretaceous

HORIZON AND DISTRIBUTION—Hell Creek Formations of Montana

MAIN ANATOMICAL STUDY—Molnar, 1978

Type

SKULL LENGTH— ~450 mm?

KILOGRAMMAGE— ~200?

The “Jordon theropod” type snout from Montana has the same shape and front teeth as the other aublysodonts, so it most likely belongs to the same genus. This specimen’s bigger size, bigger teeth and more robust snout indicate it is a little closer to tyrannosaurs proper than the other two species are. I have named it after its describer.

SUBFAMILY TYRANNOSAURINAE (Osborn, 1906)

Allosaur-like *Indosuchus* and knobby-nosed *Alioramus* are rather odd, but the rest of the tyrannosaur genera and species are distinctly uniform. Still a few distinctive characters, including size, robustness, and features of the skull mark these genera and species. Generally, at 2500-to-10,000+ -kg *Tyrannosaurus* is

bigger, more robust (even when similar in size), bigger-toothed, deeper-jawed, and shorter-snouted than 500-to-2500-kg *Albertosaurus*. The two groups are further distinguished by the way they evolved. Big albertosaurs appear to have become increasingly more gracile, while remaining about the same size. *Tyrannosaurus* became ever larger and more robust with time. At the same time the two clades parallel one another. For example, both independently develop a bony process in the orbit, and both reduce their forelimbs with time.

Other tyrannosaur taxa have been described, but most are dubious. Philip Currie believes that some teeth and other bones suggest that a new, small gracile tyrannosaur was present in the Judith River Formation. There is also, from what I have seen of it, what appears to be a gracile late Late Cretaceous albertosaur newly found in Alabama.

GENUS *INDOSUCHUS* Huene, 1933

INDOSUCHUS RAPTORIUS Huene, 1933

TYPE—GSI K27/685

TIME—Coniacian-Santonian of the mid Late Cretaceous

HORIZON AND DISTRIBUTION—lower Lameta Group of central India

MAIN ANATOMICAL STUDIES—Huene, 1933; Chatterjee, 1978

Type

SKULL LENGTH— ~750 mm

TONNAGE— ~1?

Only well-preserved but isolated skull pieces have been found. I was skeptical about identifying them, but Sankar Chatterjee showed that they have D-cross-sectioned premaxillary teeth in the tip of the upper jaw, a tall, broad-tipped snout, a heavy dorsally convex maxilla, tyrannosaurian-type skull roof openings, and a narrowing of the skull bones above the orbits which suggests that binocular vision was already present. Because India was supposed to have been an isolated continent at this time, with its own unique fauna, there have been arguments that *Indosuchus* could not have been a tyrannosaur. But the bones say *Indosuchus* really was a small, heavily built, and very primitive tyrannosaur that in many ways was still like the advanced allosaurs it evolved from. Along with the allosaur *Indosaurus*, *Indosuchus* probably hunted the ankylosaurs and juvenile brontosaurus that shared its habitat.

GENUS *ALIORAMUS* Kurzanov, 1976

ALIORAMUS REMOTUS Kurzanov, 1976

TYPE—GI 3141/1

TIME—early Late Cretaceous

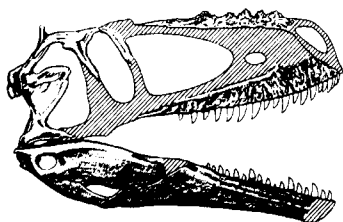
HORIZON AND DISTRIBUTION—Nogon-tsav Formation, Mongolia

Type

SKULL LENGTH— ~700 mm

TOTAL LENGTH— ~6 m?

KILOGRAMMAGE— ~700?



Alioramus remotus type GI 3141/1

This is the most recently discovered and unusual tyrannosaur. There is only one species, and since only an incomplete skull and skeleton is known, a skeletal restoration is not possible. One unusual point about this animal is the prominent, crinkly horn ridge on the nasals. However, such variation in horn morphology is just the kind expected between species, so this is not what makes this a separate genus. What is really different about *Alioramus* is the lower jaw, which is much slimmer, straighter, longer in the dentary, and less advanced than the tyrannosaurs discussed below. The upper jaw's large maxillary bone is also lightly built, with a larger preorbital depression. In these respects this is one of the least advanced tyrannosaurs.

Otherwise, what is known of this genus and species is typical tyrannosaur in design, and looks rather like a small *Albertosaurus*. The unusual nasal ridge probably supported a much more prominent and irregular nasal horn than in other tyrannosaurs, but still not as tall a one as in *Ceratosaurus*.

GENUS *ALBERTOSAURUS* Osborn, 1905

SYNONYMS—*Alectrosaurus*? *Deinodon*, *Gorgosaurus*

For a long time, *Albertosaurus* was better known as *Gorgosaurus*, but in 1970 Dale Russell decided that the first name has priority. This may not have been the best thing. The problem is that the type skull of *Albertosaurus*, which is that of *A. sarcophagus*, is so badly preserved that much work will have to be done on it and other specimens in order to determine exactly what the genus encompasses. *Albertosaurus* appears to be restricted to North America, with the apparent exception of the Mongolian *A. olseni*. Perhaps it did not favor the drier habitats of Asia. Why this would be so is not obvious since big predators are often catholic in habitat choice.

This genus is generally less advanced than *Tyrannosaurus* in having a lower, longer-snouted, shallower-jawed, lighter skull with less interbracing in the skull roof. The adult's teeth are smaller, and point more backward than in *Tyrannosaurus*. There are fewer differences in the skeleton, though *Albertosaurus* never got larger than a white rhino. In a sense the species of *Albertosaurus* can be regarded as tyrannosaurian "foxes" relative to the more robust *Tyrannosaurus* "wolves and jackals." Russell made the pertinent observation that the slender albertosaurs may have tended to hunt the more easily dispatched duckbills, leaving the formidable horned dinosaurs for stouter *Tyrannosaurus*.

The members of this genus are very similar, except for *A. lancensis*, which is more *Tyrannosaurus*-like than the others, and at the least needs its own subgenus. *A. libratus*, *A. arctunguis* and *A. megagracilis* appear to form an increasingly advanced, shorter-armed, and gracile lineage.

ALBERTOSAURUS? (*ALECTROSAURUS?*) *OLSENI* (Gilmore, 1933)

SYNONYM—*Alectrosaurus olseni*

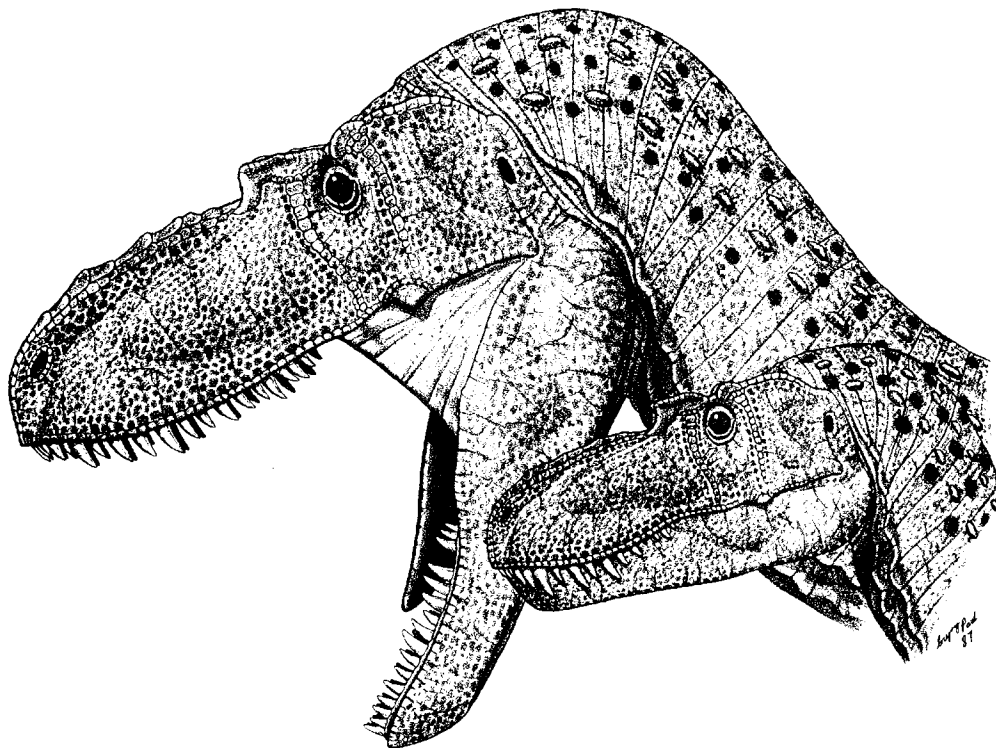
TYPE—AMNH 6554

TIME—early? Late Cretaceous

HORIZON AND DISTRIBUTION—Iren Dabasu Formation of Mongolia

	Type
SKULL LENGTH—	~600 mm
TOTAL LENGTH—	~5 m
KILOGRAMMAGE—	~500?

This poorly known species has a number of uncertainties about it. It is usually placed in its own genus because of the enormous forelimb bones found with the very incomplete type specimen. I am very skeptical about these forelimbs, however, because they look very like those of *Therizinosaurus* and segnosaurs, which are also in Mongolia. In fact, more recent finds assigned by Perle in 1977 to *A. olseni* show a typically slender tyrannosaur shoulder blade that could not support such a big arm. Perle drew a nearly complete skull reconstruction which, although too schematic to adapt for use here, is very like other albertosaurs, including the short teeth. It also lacks *Alioramus*'s peculiar nasal ridge. The hind limb is long and in most ways *Albertosaurus*-like. All in all, this looks like a small, primitive



Albertosaurus libratus adult and youngster? Or two species? Drawn to the same scale, note that the smaller individual's teeth, which are partly covered by the lips, are absolutely larger than the bigger one's. On the side of the lower jaw, the bulge of the surangular bone typical of tyrannosaurs can clearly be seen.

Asian albertosaur, primitive enough that it may be its own subgenus, or even genus, *Alectrosaurus*. It hunted the segnosaurs, protoceratopsids, and juvenile hadrosaurs in its area.

ALBERTOSAURUS LIBRATUS (Lambe, 1914)

SYNONYMS—*Gorgosaurus libratus*, *Albertosaurus sternbergi*

TYPE—NMC 2120

BEST SPECIMENS—type, TMP 85.62.1, AMNH 5458, FMNH PR308?, AMNH 5336?, USNM 12814? (juvenile?), AMNH 5664? (juvenile?), ROM 1247? (juvenile?)

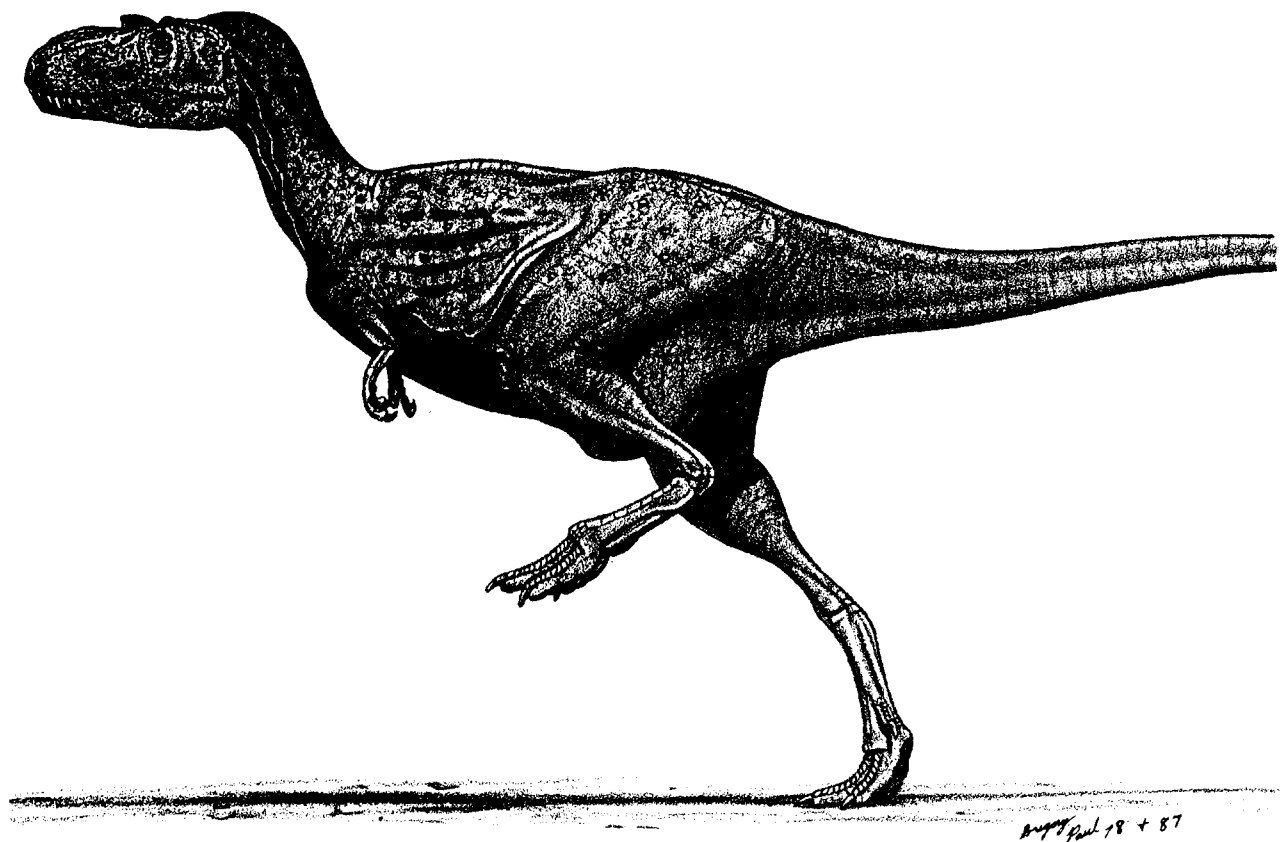
SPECIMENS ON DISPLAY AT—AMNH, FMNH, TMP, ROM, NMC, USNM

TIME—late Campanian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—Judith River Formation, western North America

MAIN ANATOMICAL STUDY—Lambe, 1917


	AMNH 5664	AMNH 5458
SKULL LENGTH—	678 mm	1040
TOTAL LENGTH—	5.8 m	8.6
FEMUR LENGTH—	700 mm	1025
HIP HEIGHT—	1.9 m	2.8
MASS—	700 kg	2.5 tonnes



This is the best known of the tyrannosaurs in terms of known remains, which include a number of fine skulls and skeletons of varying ages. Many more are being found. First discovered in the Canadian section of the Judith River (formerly Oldman) Formation in the late 1800s, Lawrence Lambe named and described the type skeleton in the WW I years. Unfortunately, he characterized it as a sluggish scavenger. Just to look at the form of the Lambe's skeleton as it was found in the ground belies this image.

It is interesting and important that two types of *A. "libratus"* heads have been found. In both the preorbital horn, which is much larger than the postorbital horn, is rather cylindrical. In the type and some others the cylinder points up and forward and forms a shorter triangle. In others the horn is more horizontal, rectangular, and longer; this second kind is seen in the FMNH skull. The suture patterns of the skull roof bones also differ, and

A running Albertosaurus libratus youngster, or an adult Albertosaurus sternbergi.



the first form has bigger, and perhaps fewer, teeth. It may be that these types represent “gracile” and “robust” forms of the sort seen in the primitive coelophysians. But the skeletons of tyrannosaurs do not show as much dual divergence as the coelophysians do, and it has not yet been shown that theropod species in general are split into two such variants. Whether the differences indicate sexes or very similar species—à la lions and tigers—is not obvious at this time. Certainly the variation in *A. libratus* is more than within *T. rex* and some other theropod species. So those specimens that may, or may not, belong to the second type have been indicated with question marks. There are more of the second type than the first, yet most of the second group seem to be juveniles.

This brings us to another point. During 1970, Dale Russell noted that the much smaller *A. sternbergi*, based on skeleton 5664, is probably a juvenile. Also observe (see pages 334-35) that its orbital horns are of the FMNH skull type. One thing Russell did not notice is that the teeth of this two-thirds-sized albertosaur are literally larger than those of the big specimen. This may mean that they are different species after all. Yet, a few skulls of differing sizes do seem to show that the teeth get smaller as they approach full size, and this supports the possibility that these skulls do represent a growth series. If so, such a dramatic tooth reduction is rare. That it can happen at all is because the teeth are continually replaced by new sets. If juveniles were abandoned by their parents at half size, their big teeth may have helped them get along in what was a very hard world. Or perhaps, like the needle-sharp teeth and claws of lion cubs, the youngsters’ big teeth allowed them to protect themselves against nonrelations that wished them harm. Possibly it was just a genetic quirk of no particular meaning.

Other possible growth changes include a moderate decrease in relative limb length, especially the extremities, with increasing size. The transverse crest atop the braincase did not become large until adulthood, and the adult’s skull was relatively bigger. There does not appear to be a consistent change in the length and depth of the snout relative to the rest of the head between different specimens.

Most *A. libratus* skulls have been flattened from side to side by the pressure of overlaying sediments, and this obscures the breadth of the back of the skull and the forward-facing of the eyes. This is shown by AMNH S336 and the new skull TMP

85.62.1. Somewhat crushed from top to bottom, they show the truly heavy build of the back of the head and the good binocular vision. Even worse is the oblique down and forward crushing a few skulls have experienced. Some artists have innocently failed to account for this, and drawn *A. libratus* with a weird, sort of pig-like snout. Like all big albertosaurs, it has smaller forelimbs than *Tyrannosaurus*. A few adult skulls show the beginnings of the kind of orbital process that becomes so well developed in later tyrannosaurs.

The adult skeleton is restored after the nearly complete New York specimen, whose skull horns are like the type's. FMNH PR308 is used to show the alternate skull form. The juvenile skeleton is one of the most complete dinosaur skeletons known, it lacks only a few tail tip vertebrae. I find this a particularly attractive dinosaur. With its big size, long limbs, long upturned skull, compact body, and long bulldog neck, it combines grace, speed, and power in an elegant hunting machine.

White-rhino-sized *Albertosaurus* was the dominant predator of the Judith River, making up about 75 percent of the big-predator fauna. The equally big *Tyrannosaurus torosus* was its main competitor, the smaller gracile albertosaur less so. The Judith River's most numerous inhabitants were rhino-sized duckbills, and they were probably the main prey of *A. libratus*. The duckbill's main defense was to run, perhaps into dense brush to try and lose the albertosaurs. However, the more powerful horned dinosaurs were by no means immune to the depredations of this tyrannosaur either.

ALBERTOSAURUS ARCTUNGUIS Parks, 1928a

TYPE—ROM 807

BEST SPECIMENS—type, TMP 81.10.1?

TIME—latest Campanian to early Maastrichtian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—Horseshoe Canyon Formation of Alberta

	Type	TMP 81.10.1
SKULL LENGTH—		970 mm
TOTAL LENGTH—	~8.6 m	~8.0
FEMUR LENGTH—	1020 mm	950
HIP HEIGHT—	2.7 m	2.5
TONNAGE—	2.5	2.0

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To be frank, I am not sure what to do with this species and the below *A. sarcophagus*, which are both from the Horseshoe Canyon Formation. This is because both species' old type remains leave a lot to be desired, and new specimens do not have enough comparable parts. This species' type, for example, is missing its head. There do appear to be two big, common tyrannosaurs in the Horseshoe Canyon. One is a robust species that may be *A. sarcophagus*, the other is gracile. The type of *A. arctunguis* is lightly built and long legged, and the same is true of the very nice new skull and partial skeleton, TMP 81.10.1 (both are missing their tails). So these may be the same gracile species. I have taken a bit of a risk and combined the two individuals to come up with a skeletal drawing that it is hoped represents *A. arctunguis*. If so then *A. arctunguis* had smaller arms and finger claws, and longer legs, than *A. libratus*. Also, the orbit is nearly cut in half by a postorbital bar like that of *Tyrannosaurus*. These characters imply that *A. arctunguis* was a direct descendant of *A. libratus*, and the direct ancestor of later *A. megagracilis*.

ALBERTOSAURUS SARCOPHAGUS Osborn, 1905

SYNONYMS—*Laelaps incrassatus*, *Dryptosaurus incrassatus*

TYPE—NMC 6500

TIME—latest Campanian to early Maastrichtian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—Horseshoe Canyon Formation of Alberta

Type

SKULL LENGTH— ~1000 mm

TONNAGE— ~2.4

As I said above, this and the other Horseshoe Canyon tyrannosaur *A. arctunguis* are real headaches. The type of this species is a partial, badly preserved skull, not enough to really tell us what kind of animal it is. Hopefully better remains will eventually help better define the species. Until then about all we can say is that it appears to be more heavily constructed than *A. arctunguis*. Just how closely related this species is to the other albertosaurs is not clear either.

ALBERTOSAURUS MEGAGRACILIS new species

TYPE AND BEST SPECIMEN—LACM 23845 (subadult?)

TIME—latest Maastrichtian of the latest Late Cretaceous

HORIZON AND DISTRIBUTION—Hell Creek Formation of Montana

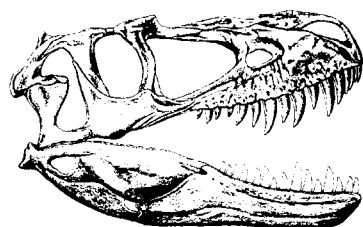
MAIN ANATOMICAL STUDY—Molnar, 1978

	Type
SKULL LENGTH—	~900 mm
TOTAL LENGTH—	~7.5 m
TONNAGE—	~1.7

In describing the one partial skeleton, Ralph Molnar tentatively assigned it to the contemporary *A. lancensis*. While looking over the remains I became convinced that they are much too big and too immature—the poorly ossified elements and moderate sized transverse crest atop the braincase suggest it was not fully grown—to belong in the much smaller species. This animal is clearly not *Tyrannosaurus* either. The next question is whether it is *A. libratus* or *A. arctunguis*. The LACM animal's extremely atrophied forelimbs, down-bent nasals, very long snout, and long hind limbs strongly indicate that it is not. A new species is therefore named, one that describes its combination of large size and gracile build. In fact, this species probably got as big as *A. libratus*. Not enough is known to allow a skeletal restoration.

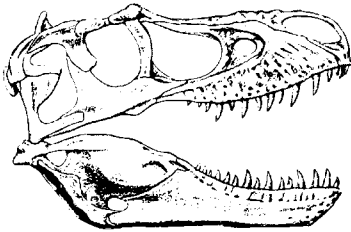
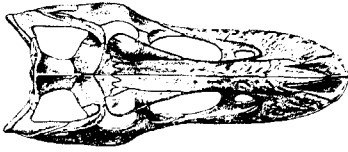
A. megagracilis is similar to and may be a direct descendant of the earlier *A. arctunguis*, which in turn may be a direct descendant of the yet earlier *A. libratus*. So these three species may represent a lineage in which size and basic design remained remarkably consistent, but the legs became increasingly long, the arms ever smaller, the snout longer, and the form overall more gracile.

Not only are the hand claws small, but their very small tubers for muscle insertion show that the arm was very weak. *A. megagracilis* is more advanced than even *Tyrannosaurus rex* in



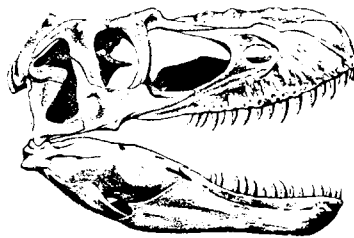
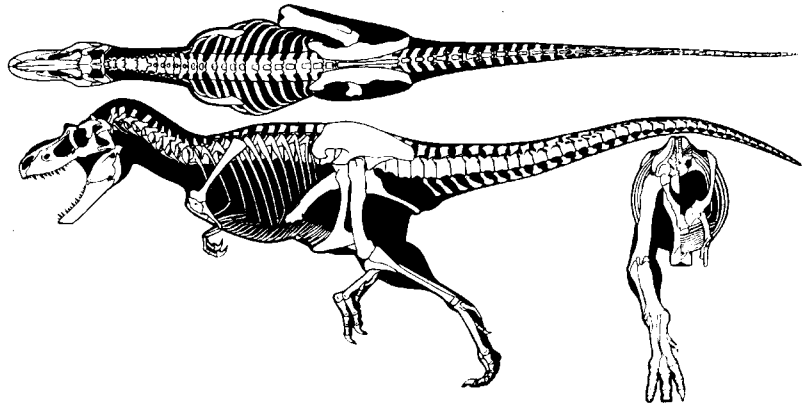
Albertosaurus libratus? AMNH
5664 juvenile



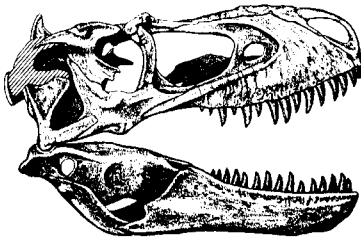


Albertosaurus libratus AMNH
5458 and TMP 85.62.1

Albertosaurus libratus AMNH
5458

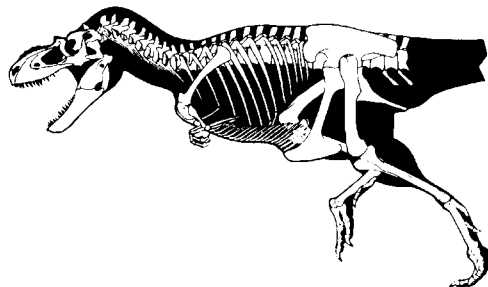


Albertosaurus libratus? FMNH
PR308



Albertosaurus arctunguis? TMP
81.10.1

Albertosaurus arctunguis ROM
807 and TMP 81.10.1



forelimb reduction, and this indicates that given a little more time albertosaurs would have abandoned them altogether.

Time it did not have, for the rarity of *A. megagracilis* relative to *T. rex* suggests that, like many other latest Cretaceous dinosaurs, it was in trouble. If so, then the big albertosaur lineage may have been doomed even if the great extinction had not taken place. This lineage's decline seems to have been due to the lessening numbers of their preferred prey, duckbills, in Maastrichtian time, not because the genus was intrinsically inferior to *Tyrannosaurus*. Aside from *T. rex*, the competitor of *A. megagracilis* was the small and equally rare *A. lancensis*.

SUBGENUS ALBERTOSAURUS ("NANOTYRANNUS") (Bakker et al., unofficial)

SYNONYM—*Albertosaurus* ("Clevelandotyrannus")

ALBERTOSAURUS? ("NANOTYRANNUS") LANCENSIS (Gilmore, 1946)

SYNONYM—*Gorgosaurus lancensis*

TYPE—CMNH 5741

TIME—latest Maastrichtian of the latest Late Cretaceous

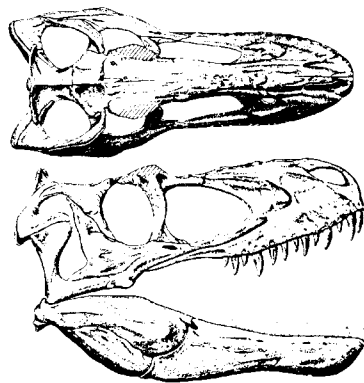
HORIZON AND DISTRIBUTION—Lance Formation of Montana

Type

SKULL LENGTH— 602 mm

TOTAL LENGTH— ~5 m

KILOGRAMMAGE— ~500



Albertosaurus ("Nanotyrannus")
lancensis type CMNH 5741

The only good specimen we have got of this one is a skull. Although small, it is not a young juvenile because of its combination of extremely good ossification, with some sutures obliterated by the bones' intergrowth, a large transverse braincase crest, and a big rugosity on the lower edge of the cheeks. Even big *Tyrannosaurus rex* skulls are no better ossified, so this individual was at least fairly close to being fully grown. *A. lancensis* was not necessarily faster than its giant relative, but this small animal could use its superior maneuverability to escape.

Note the smaller teeth of this adult tyrannosaur compared to similar-sized but big-toothed juveniles of *A. libratus*. The skull is oddly crushed, with the snout pinched narrower than it should be, and the back crushed down and backward so it is even broader than it really was. However, the truly greater breadth of the back of the skull, the more forward-facing eyes, and an advanced braincase make this the most *Tyrannosaurus*-like of the

albertosaurs, despite its small size. Indeed, the smallness, *Tyrannosaurus*-like features, and the late appearance of this animal imply that it underwent a separate evolution from the big-bodied *A. libratus*-*A. arctunguis*-*A. megagracilis* lineage. It may also be more closely related to *Tyrannosaurus* than the other albertosaurs. Robert Bakker and associates intend to give this species the new generic title "Nanotyrannus" (which replaces the aborted "Clevelandotyrannus").¹⁷ Alternately, it could be a subgenus of either *Albertosaurus* or *Tyrannosaurus*. The very long, low snout, big preorbital opening, shallow mandible, small teeth, and skull roof sutures cause me to keep it in *Albertosaurus*. An interesting and unanswered question is whether this species evolved from a big ancestor, or if they were always small like *Albertosaurus olseni*.

As with *A. megagracilis*, the rarity of this species suggests that it was in trouble. *T. rex* was a direct danger to *A. lancensis*, but was too big to be a direct rival. Its main competition came from the moderately larger *A. megagracilis*, and possibly from some of the larger, also rare sickle-claws. Certainly, small-bodied and small-toothed *A. lancensis* avoided the gigantic adult ceratopsids and duckbills in its habitat. It probably went after immature duckbills and other medium-sized herbivores such as dome-headed *Pachycephalosaurus*.

GENUS TYRANNOSAURUS Osborn, 1905

SYNONYMS—*Daspletosaurus*, *Dynamosaurus*, *Gorgosaurus*,
Tarbosaurus

Traditionally, *Tyrannosaurus* is considered to consist of only one species, *T. rex*. However, tyrannosaurs are so like one another that all the usual genera cannot be justified; they are oversplit. In particular, *Daspletosaurus* and *Tarbosaurus* share most of the key characters that characterize *T. rex*: a stocky, heavy-boned build, relatively short lower hind limbs and large arms, a short snout, smaller preorbital horns, nasal bones that are tightly constricted between the preorbital bones, deep lower jaws, and long yet stout teeth that point a little more forward than they do in *Albertosaurus*. These three species form their own clade, and the amount of variation between them is less than that seen in some well-established modern or recent genera such as *Canis* (wolves and jackals) and even our own genus *Homo*. *Daspletosaurus* and *Tarbosaurus* are, therefore, junior synon-

yms of *Tyrannosaurus*. However, *Daspletosaurus* is different enough from the other two species to warrant its own subgenus.

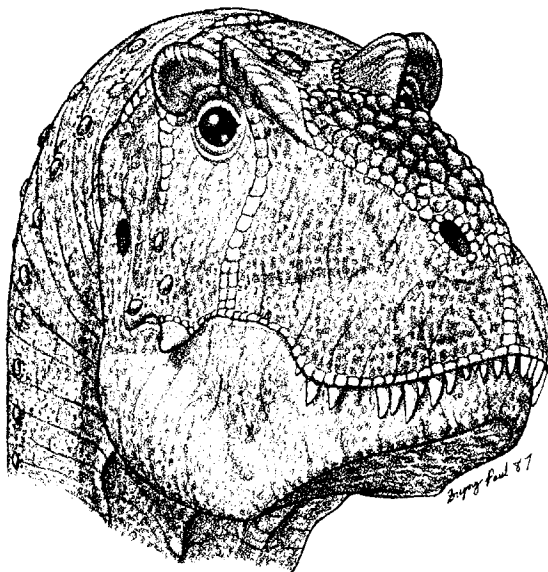
To a fair extent the *Tyrannosaurus* species are the tyrannosaur's tyrannosaurs; they have taken to an extreme the development of skull size, strength, and power. This and the larger, more forward-pointing mid-upper-jaw teeth suggest a more potent wounding ability than the albertosaur's. The stoutness of *Tyrannosaurus* relative to albertosaurs is readily apparent in the skeletal restorations. They are not as graceful, but they have a well-proportioned, majestic attractiveness of their own.

Because *Tyrannosaurus* is shorter and stockier-limbed than *Albertosaurus*, it is tempting to ascribe slower speeds to it. However, the proportional differences are not great, while the morphology is almost identical. Perhaps *Tyrannosaurus* used the power of its stouter limbs to equal the running performance of *Albertosaurus*. Or perhaps the former were better sprinters and the latter better long distance runners. The very size of *T. rex* may have made it the fastest tyrannosaur; there is no way to be certain. Stout *Tyrannosaurus* was well built for ceratopsian killing. To safely and successfully hunt ceratopsians, tyrannosaurs probably had to surprise them, or panic them into a run in which they could be approached from the rear. Otherwise the powerful horned dinosaurs may have reared like enraged bears to try and intimidate the tyrannosaurs. If that failed, a running charge was the horned dinosaur's answer, and then the tyrannosaur often did the fleeing!

Unlike *Albertosaurus*, which remained pretty much the same size and became a little more gracile over ten or so million years, *Tyrannosaurus* became much larger and stouter during this same time. *Tyrannosaurus* may have evolved from unknown tyrannosaurs, but the fact that *T. torosus* and *A. libratus* were long confused suggests that a form of *Albertosaurus* may have been its ancestor. Because *T. bataar* and *T. rex* are so similar, they must have shared a recent, common ancestor, if they were not geographic subspecies of one another.

There is more variation in this genus than in *Albertosaurus*, and the lightly built skull of *T. torosus* makes it a subgenus separate from *T. bataar* and *T. rex*. In his 1970 study, Dale Russell reported a juvenile *T. torosus*-type skeleton from the Horse-shoe Canyon Formation.

Oblique profile of a *Tyrannosaurus torosus* head. Note the good degree of binocular vision, and the bulging jaw-closing muscles on what is in effect a little frill at the back-top of the head.



SUBGENUS *TYRANNOSAURUS* (*DASPLETOSAURUS*)
(Russell, 1970)

TYRANNOSAURUS (*DASPLETOSAURUS*) *TOROSUS* (Russell, 1970)

SYNONYM—*Albertosaurus libratus*

TYPE, BEST AND DISPLAY SPECIMEN—NMC 8506

TIME—late Campanian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—Judith River Formation of Alberta

Type/AMNH 5438

SKULL LENGTH— 1107 mm

TOTAL LENGTH— 9.0 m

FEMUR LENGTH— 1000 mm

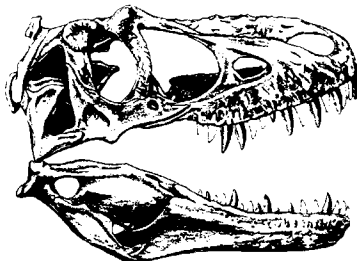
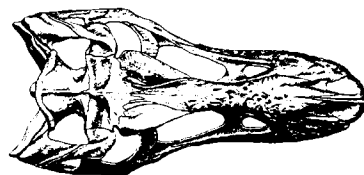
HIP HEIGHT— 2.55 m

TONNAGE— 2.3

Until recently, this species' remains were lumped in with *A. libratus* of the same formation. But even as he dug up the first good skull and skeleton in 1921, Sternberg suggested that it was a new taxa, and Dale Russell made it the type of the evocatively titled *Daspletosaurus torosus*. However, as explained above, this species belongs in *Tyrannosaurus*, of which it is the earliest. No complete skeleton is known, but Russell combined the skull and



Tyrannosaurus (Daspletosaurus)
torosus type NMC 8506 and
AMNH 5438



Tyrannosaurus (Daspletosaurus)
torosus type NMC 8506

partial skeleton of the type with the hind limbs of equal-sized AMNH 5436 and restored a few parts to make a very good restoration, one that has been modified here. Philip Currie has a hefty new preorbital horn that may come from a somewhat larger example of this species.

As well as being smaller than those of the other genus members, the skull has bigger openings and lacks the bar that nearly cuts the orbit in two. On the other hand the skull is quite big for the body. The best skull of the species, ROM 8506, is crushed from side to side and obscures the fact that *T. torosus* had a good degree of binocular vision. The moderate-sized preorbital horn is triangular; the forelimbs are the biggest known in an advanced tyrannosaur. Russell has explained that since *T. torosus* is more robust than, and one fourth as numerous as similar-sized *A. libratus*, it probably went after the relatively less common and powerful horned dinosaurs more often than the albertosaur did.

SUBGENUS *TYRANNOSAURUS* (*TYRANNOSAURUS*) (Osborn, 1906)

TYRANNOSAURUS (*TYRANNOSAURUS*) *BATAAR* Maleev, 1955

Synonyms—*Tarbosaurus bataar*, *Tarbosaurus efremovi*,
Gorgosaurus lancinator, *Gorgosaurus novojilovi*

TYPE—PIN 551-1

BEST SPECIMENS—type (skull), PIN 551-3, ZPAL MgD-1/3
(juvenile)

TIME—early to mid-Maastrichtian? of the late Late Cretaceous

HORIZON AND LOCALITY—Nemegt Formation of Mongolia

MAIN ANATOMICAL STUDY—Maleev 1974

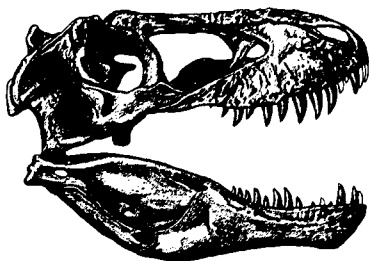
	MgD-1/3	551-3	Type
SKULL LENGTH—	745 mm	1135	~1350

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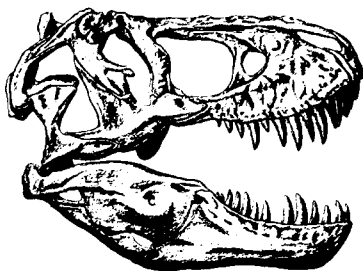
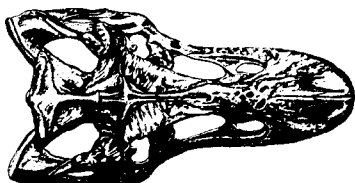
Tyrannosaurus (Tyrannosaurus)
bataar PIN 551-3



Tyrannosaurus (Tyrannosaurus)
bataar type PIN 551-1 and PIN
551-3

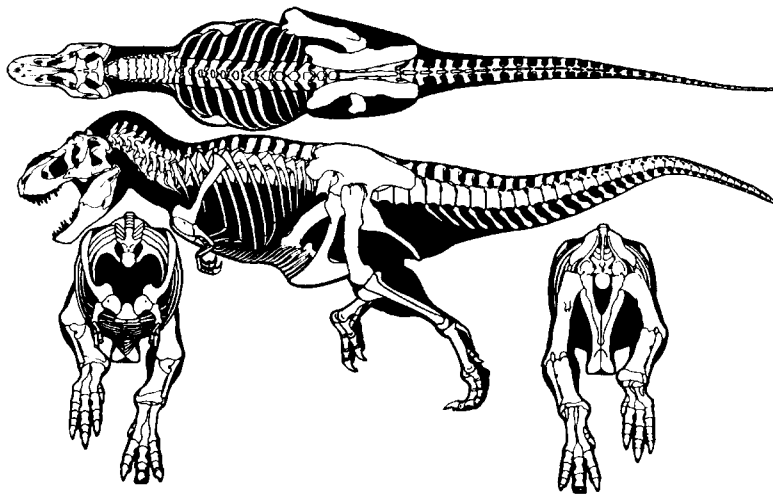


Tyrannosaurus (Tyrannosaurus)
bataar ZPAL MgD-1/3 juvenile



Tyrannosaurus (Tyrannosaurus)
rex AMNH 5027

Tyrannosaurus (Tyrannosaurus)
rex type CM 9380 and AMNH
5027



TOTAL LENGTH—	5.8 m	7.7	~10
FEMUR LENGTH—	700 mm	970	~1200
HIP HEIGHT—	1.9 m	2.4	~2.9
MASS—	760 kg	2.1 tonnes	~5

Discovered by the Soviet expedition of 1949, this taxa was at first correctly named *Tyrannosaurus bataar* by E. Maleev. But then he gave a smaller specimen the fine generic title, *Tarbosaurus*, and *T. bataar* is often sunk into the latter. But if the very big type skull had been found in North America it would have been assigned to *T. rex*: they are that alike! So much so that if they did overlap in time—the exact age of the Nemegt is hard to pin down—*T. bataar* may have even been an interbreeding, geographical subspecies of *T. rex*, much as the Eurasian brown bear and American grizzly are subspecies of *Ursus arctos*. *T. bataar*'s somewhat smaller size might be due to its living in a harsher, more arid habitat. So Maleev was right the first time in making this *Tyrannosaurus*. The Mongolian predator does have smaller teeth, a shallower snout and mandible, and somewhat different skull roof bones than *T. rex*. Also, *T. bataar*'s orbital horns, both before and behind the eye socket, appear to be the smallest among tyrannosaurs. The biggest complete *T. bataar* and *T. rex* skulls are the same length, so these individuals were about equal in size. Their skulls also share the same degree of binocular vision.

A more serious taxonomic problem is that the many good skulls and skeletons may represent more than one species.¹⁸ Maleev and Osmolska believe in two or more, Rhozhdestvensky argues for one.¹⁹ Initially, I inclined toward the former view. After all, three species of the big-cat genus *Panthera* are found in India (lion, tiger, and leopard), and there is always more than one tyrannosaur present in North American formations. That the Nemegt had only one seemed wrong. Yet, careful examination of published remains and those I saw in Warsaw leaves me pretty sure that Rhozhdestvensky is right. Whatever the specimen's size, the teeth of all the specimens are alike in size and design, the orbital horns are the same, and there just is no significant variation in morphology. One small, partial skull ("*Gorgosaurus novojilovi*," Maleev, 1955²⁰) has been restored as very long and low, quite different from the others. But the individual bones match other *T. bataar* skulls, and restored properly they form a normal skull. There have been suggestions that this specimen's foot bones are unique, but as far as I can tell they are not.

All Nemegt tyrannosaurs may therefore represent a growth

series of *T. bataar*. As the species grew up, the body became more robust, the shank and feet somewhat shorter, and the transverse braincase crest seems to have enlarged, rather like what appears to occur in *A. libratus*. Unlike the latter, *T. bataar* teeth show no dramatic alteration in size relative to the skull, but the snout did become longer as they matured.

Note that the larger skeletal restoration (see page 341) is of a fairly complete subadult skull and skeleton. Full adults were even more like *T. rex*, as shown by the big type skull. The juvenile skeleton is based on a superb individual that lacks only the tail.

Prior to the Nemegt deposition, Mongolia was too arid to support big herbivore populations large enough to feed big tyrannosaurs, so only a few big theropod teeth are known. Even the Nemegt was a dryer, more open, savanna-like habitat than were the heavily forested North American tyrannosaur environments. *T. bataar*'s prey consisted mainly of armored ankylosaurs, the big duckbill *Saurolophus*, and one or two of species of medium-sized brontosaurs. There is little doubt that 5-tonne *T. bataar* could bring down the 5-to-10-tonne brontosaurs in its neighborhood. So, although *T. rex* never met *Brontosaurus* itself, the comic books are correct in showing tyrannosaurs preying on its relative. These bulky herbivores may have provided most of *T. bataar*'s prey biomass. With the possible exception of the rare and possibly herbivorous *Deinotherium*, *T. bataar* had no competitors.

TYRANNOSAURUS (TYRANNOSAURUS) REX Osborn, 1905

SYNONYM—*Dynamosaurus imperiosus*

TYPE—CM 9380

BEST SPECIMENS—type, AMNH 5027, TMP 81.6.1

SPECIMENS ON DISPLAY AT—AMNH, CM, LACM (skull), SDSM (skull), ANSP (cast), TMP

TIME—late Maastrichtian of the latest Late Cretaceous

HORIZON AND DISTRIBUTION—Lance, Hell Creek, Scollard,

Willow Creek, Frenchman, and upper Kirtland? Formations of western North America

MAIN ANATOMICAL STUDIES—Osborn, 1906, 1912, 1916

	AMNH 5027/type	UCMP 118742
SKULL LENGTH—	1355 mm	~1750
TOTAL LENGTH—	10.6 m	~13.6
FEMUR LENGTH—	1300 mm	~1675
HIP HEIGHT—	3.4 m	~4.4
TONNAGE—	5.7	~12

This is *the* theropod. Indeed, excepting perhaps *Brontosaurus*, this is the public's favorite dinosaur, having fought King Kong for the forced favor of Fay Wray and smashed Tokyo (with inferior special effects) in the guise of Godzilla. Even the formations it is found in have fantastic names like Hell Creek and Lance. Its place as the greatest of known land predators remains secure—no other giant consists of such complete skeletons, is bigger, or as powerful. Everything said about tyrannosaur strength goes furthest with this species, and no other theropod has such a large, thickly built, powerfully muscled skull, and such large teeth for its bulk. Only *Dilophosaurus* and juvenile *A. libratus* have teeth that are nearly as large in relative measure. Sickle-clawed *Velociraptor antirrhopus* may be as formidably armed for its weight, but it is a small animal. And along with its power, *T. rex* is the fastest known animal for its size!

A number of new finds are coming onto line, including the first combination of a skull with a fairly complete skeleton, at the TMP. The skeletal restoration is after the composite New York mount. Made from the first two known skeletons, these are identical in size. 5027 provides the skull, vertebral column, rib cage, and hips; 9380 the fore and hind limbs. The 5027 skull is crushed a little, giving it a falsely dished dorsal profile and little more breadth at its back end than it really had. Since this is the most complete and best known skull, these crushed features have misled many. On the other hand, Ralph Molnar has made the back of the skull too narrow and triangular.²¹ The new skulls prove that this animal really was a very broad-cheeked animal. The rugose posterior orbital horn is larger than the reduced preorbital one, much as in *T. bataar*. The lower arm and hand are not known, but since the humerus is smaller than in other *Tyrannosaurus* species, it is likely that the arm as a whole was also. It was not until 1970 that Newman noted that the partial tail was restored with too many vertebrae. With a proper tyrannosaur tail count of thirty-seven to thirty-nine vertebrae, 5027 is thirty-four feet long, not forty-five as once claimed. Kenneth Carpenter has recently mounted a cast of this skeleton in a modern, accurate, and dynamic pose in Philadelphia. Estimates that 5027 massed close to 7 tonnes²² are reasonable if they are presumed to include fat reserves, but these estimates are not really useful because they were based on unreliable museum models, and a commercial toy made by the BMNH. Substantial growth is possible even after the skull bones start to fuse together as in 5027. I note this because

this and the other big *T. rex* specimens may or may not be subadults. This is possible because the biggest specimen is a tooth-bearing UCMP maxilla from the upper jaw that is 29 percent longer than 5027. It indicates a 12-tonne individual that could rear its head some twenty-three feet high, and could slide something the size of a whole human body down its gullet as if it were a raw oyster.²³ It is possible that this titan, known as it is from only one bone, represents a different species. If not, then 15-tonne individuals were probably fairly common, 20-tonne “record holders” were possible—though so rare that they may never be found. For comparison, most bull African elephants are 5-tonners and a fair number reach 7.5 tonnes; extremely rare are 10-tonners.

Suggestions that *T. rex* is really two species, or even two genera, have been circulating lately. Two genera is completely out of the question; at most it is a lion-versus-a-tiger kind of species separation. But the type of *Dynamosaurus imperiosus* (a wonderful name) is a front lower jaw that is hardly distinguishable from the *T. rex* type. The somewhat distorted AMNH 5027 skull may be adding to the confusion because the upper jaw’s left maxilla is too low. The right side is not so crushed and looks like other *T. rex* specimens. The hind limbs of some specimens do seem to be longer and more slender than those of the type, and they vary somewhat in the teeth. On the other hand, all the skulls are quite consistent in the preorbital horns and other skull details, more so than in *A. libratus*. So one species is most likely, perhaps one that came in “robust” and “gracile” versions, but the verdict is not in.²⁴

Of course, *T. rex* is the most illustrated of theropods, and the most famous rendition is Charles Knight’s FMNH painting of a confrontation with *Triceratops*.²⁵ The horizontal body pose is ahead of its time; on the debit side are such anatomical mistakes as the overly shallow back of the head and a small chest. Another well-known Knight *T. rex* effort²⁶ is much less satisfying, especially since the head is too small and lizard-like. Burian’s often-reproduced *T. rex*²⁷ has a badly dwarfed head and lipless teeth—it is not at all good. Neither is Rudolph Zallinger’s bloated and simplistic version in the YPM mural.²⁸ The rather uninspired commercial model put out by the BMNH is too small in the head and chest, too long-tailed, and has inappropriate plated skin.

The reason for the bulk and firepower of *T. rex* is apparent when one considers its main prey, *Triceratops*. Prior tyranno-

saurs were going after rhino-sized duckbills and ceratopsids, but by the late Maastrichtian, elephant-sized *Triceratops* was far and away the most numerous herbivore. *Triceratops* was horrendously big, fast, and agile, and it was well-armed with beak and horns. Hunging it required an equally gigantic, faster, and even more formidably armed predator. Just how formidable only became clear to me as I did the illustration of *T. rex* biting *Triceratops* in Figure 2-6 (page 35). I had to measure things out, and was appalled to find that the tyrannosaur could bite out a wound a yard long, and well over a foot deep and wide. This would have wrecked the entire upper thigh of *Triceratops*, and cut down to the femur. Some “scavenger”! It is hard to conceive of such titanic battles, with elephant-sized predators sprinting alongside a thundering herd of horned dinosaurs.

Some remains indicate that *T. rex* lived in New Mexico’s Kirtland Shale; if so, it hunted the brontosaurus there, while *Triceratops* was absent. As for competition, the smaller, more gracile and rare *Albertosaurus megagracilis* was about all, and it preferred the duckbills. *A. lancensis* was too small to be much more than its occasional prey, except when the albertosaur dared pick off a juvenile *T. rex* from under its parents’ noses!

The culmination of tyrannosaur evolution, *T. rex* was one of the very last North American dinosaurs. Nothing else combined its size, speed, and power. Since its demise we have had to make do with lions and tigers and bears, and other “little” mammalian carnivores.

MYSTERIOUS DRYPTOSAURUS

SUBORDER UNCERTAIN

FAMILY DRYPTOSAURIDAE Marsh, 1890

GENUS DRYPTOSAURUS Marsh, 1877

SYNONYM—*Laelaps*

DRYPTOSAURUS AQUILUNGIS (Cope, 1866)

SYNONYM—*Laelaps aquilungis*

TYPE—ANSP 9995

TIME—Late Maastrichtian of the late Late Cretaceous

HORIZON AND DISTRIBUTION—New Egypt Formation of New Jersey

MAIN ANATOMICAL STUDY—Cope, 1870

	Type
FEMUR LENGTH—	890 mm
TONNAGE—	~1.5?

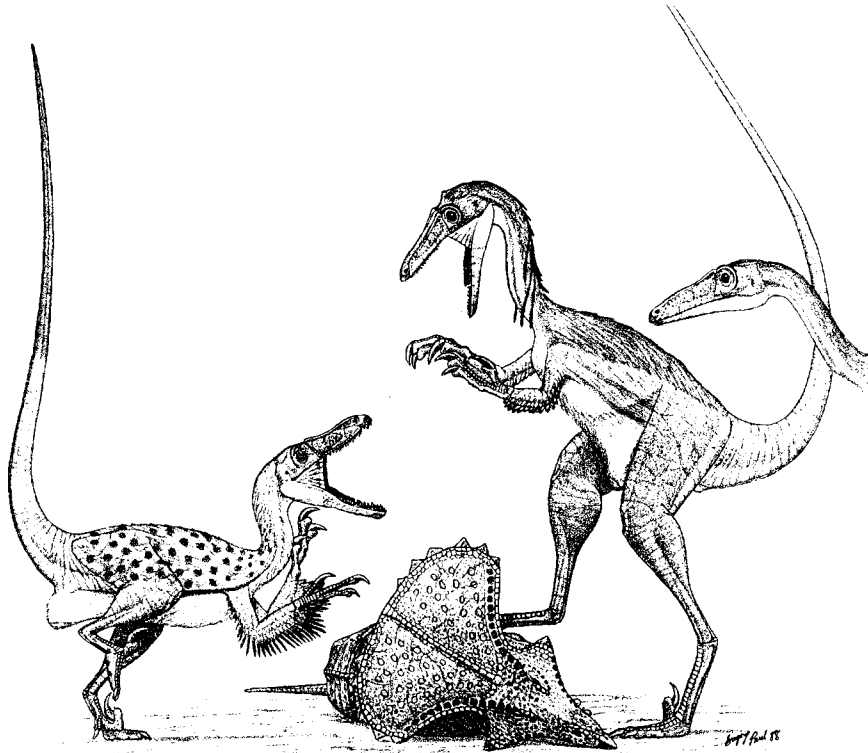
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I discuss this species here for a lack of anywhere better to do it; it is being reexamined by Kenneth Carpenter and Dale Russell. This large, gracile, aberrant, and poorly known theropod has been considered everything from a megalosaur to a tyrannosaur, to even a dromaeosaur protobird. It is none of these. The ankle is advanced and looks avetheropodian, but it is also different from other theropods, so this taxa is a unique form. A number of other theropod remains in the United States have been placed in this genus; all are dubious at best. It seems that the forelimbs are large and have very big claws, and the teeth are fairly normal blades. Duckbills were among this big animal's prey.



3
Protobirds:
Flying
and Nonflying

The members of this clade—the sister group to the allosaur-tyrannosaurs—did a fantastic and wonderful thing. They learned to fly (again, we assume that Triassic herrerasaurs and “Protoavis” are bird mimics that did not contribute to early bird evolution). Long-fingered, climbing small avetheropods of the Jurassic rather like *Compsognathus* and *Ornitholestes* may have been the beginnings of this group, which soon developed flying forms, the only known one of which is *Archaeopteryx*. What happened to the protobirds after *Archaeopteryx* is as interesting as what went on before. This is because most of the theropods closest to *Archaeopteryx* and birds lived after *Archaeopteryx*, and these Cretaceous protobirds—although nonflying—are in many important ways more birdlike than *Archaeopteryx* itself. It would seem that these were the secondarily flightless progeny of the



first flying protobirds. So, as true flying birds evolved, there may have been a parallel radiation of grounded protobirds. This is a new idea, and an unproven one. But as we shall see below, it is also logical. These long-forelimbed ground protobirds developed a number of peculiar adaptations, and seem to have displaced other theropods from the small-to-medium-predator roles. Others became herbivores, and one of the ostrich-mimics may have been gigantic.

Many features link protobirds and birds. For one example, in birds the snout is reduced. The maxilla, preorbital openings, jaw-closing muscles, and smell organs the snout contains are all reduced or lost. These things can be seen developing in protobirds; even the preorbital opening of *Velociraptor* is small compared to nonprotobird theropods. A common, but not strict, protobird trait is to have well-developed binocular vision. The way in which protobird eyes faced forward usually differed from that of tyrannosaurs (for an exception, see comments on *Dromaeosaurus*, pages 349–51). In protobirds the frontals that make

Velociraptor mongoliensis and *Troodon mongoliensis* squabble over a *Protoceratops andrewsi* carcass. The first's greater firepower matched the second's larger size.

up the skull roof above the eye sockets are triangular and broader over the back of the eye socket; this is the bird way of binocular vision. But the purpose of stereo vision was the same in tyrannosaurs, protobirds, and birds: to improve the precision of head strikes.

Notice that unlike the hips of other theropods, here the long rod is missing from the end of the ischium bone. This means that the ischial-based limb muscles again anchored along most of the bones' length, as they had in the earliest dinosaurs. This is also an avian feature, and it probably had to do with the equally birdlike initial backward-swinging of the pubis. In 1969, Dale Russell suggested that the slender, bowed outermost digit of the hand of *Troodon* could rotate backward on the wrist bones and oppose the other fingers, somewhat the way our thumb does. If correct, then this would apply to *Archaeopteryx*, dromaeosaurs, and perhaps oviraptors too, because they have similar hands.

It is remarkable how ready for avian-style flight the Jurassic avetheropods were. All they had to do was elongate their forelimbs, modify them a little, and increase their power, and they could have flown.

SUBORDER PROTOAVIA new

ARCHAEOPTERYGIANS AND DROMAEOSAURS

Many theropods have been united into new groups in this book, but the placement of *Archaeopteryx* and the sickle-clawed dromaeosaurs in the same family is by far the most radical—yet it is also one of the most necessary. It used to be thought that the good-sized, sickle-clawed, ground-dwelling dromaeosaurs and troodonts were in the same theropod family, while little-winged *Archaeopteryx* was the first bird. But as Kenneth Carpenter and I worked on these animals, we were astonished at how alike, in detail after detail, dromaeosaurs and *Archaeopteryx* were. In some ways they were almost identical. *Troodon*, in contrast, is much different when one looks below its surface. If alive today, the dromaeosaurs and *Archaeopteryx* would very probably be in one family, so I have grouped them that way here. Small *Archaeopteryx* deserves its own subfamily, much as the small aublysodonts are in a distinct subfamily from the big tyrannosaurs.

Some will object that feathered flying *Archaeopteryx* must be a bird, while the ground-dwelling dromaeosaurs, for which feathers are not known, are theropods; hence they cannot be put