

# VARIATION AND SEXUAL DIMORPHISM IN *TYRANNOSAURUS REX*

# 8

Peter Larson

---

The science of paleontology has often been accused of being more art than science. This assessment stems from the problems encountered when dealing with the paucity and incompleteness of the fossil record. Not the least of the problems confronting paleontologists is the scarcity of specimens. To date, 46 specimens (N. L. Larson this volume) consisting of more than a few associated bones have been assigned to *Tyrannosaurus rex* Osborn (1905, 1906). Although this is a robust representation for extinct theropods, when compared with extant populations, this number seems extremely inadequate. For example, Buss (1990) reported a 1973 count of 14,309 African elephants (*Loxodonta africana*) in the 3840 km<sup>2</sup> (1483 mi<sup>2</sup>) Kabalega Falls National Park in Uganda. On its face, 46 specimens seems a paltry number from which to define a species, let alone attempt to identify males and females. Yet that is exactly what this study attempts. The use of modern taxonomic methods may be used to identify anomalous morphological characters and to remove questionable specimens from a taxon to which they have been unnaturally joined (more below). Taken even further, morphometrics, physiology, and pathology can be used to help separate and define sex morphotypes.

For this study, 34 specimens attributed to *Tyrannosaurus rex*, including specimens listed as *Tyrannosaurus* “x” and *Nanotyrannus* (considered as specimens of *T. rex* by Carr 1999), were examined. In addition, 2 specimens assigned to *Tarbosaurus bataar*, one assigned to *Gorgosaurus* and another to *Albertosaurus*, were examined as outgroups. These specimens are listed in Table 8.1.

In any population, individual variation within a species will occur. This variation is due to ontogeny, nutrition, genetic variance, pathology, and, of course, sexual dimorphism. Thus, it is imperative that these factors be excluded when examining the question: “Have researchers included specimens within the species *T. rex*, with variation beyond that expected within a living population?” Extant phylogenetic bracketing techniques (Witmer 1995) were used to evaluate the characters used in this study for the purpose of isolating those attributable to intraspecific variation.

## Introduction

Figure 8.1. (Left) *Tyrannosaurus* “x” (AMNH 5027). (Right) *Tyrannosaurus rex* (BHI 3033).

Figure 8.2. Medial view of right dentary of the type *Tyrannosaurus rex* CM 9380. Note the incisoriform first dentary tooth.

Figure 8.3. Left and right first dentary teeth of *Tyrannosaurus rex* BHI 3033. (A) Lateral view. (B) Posterior view. Note that both serrations are exposed in the posterior view, creating the typical tyrannosaurid D-shaped cross section.

## Variation

Table 8.1. *Specimens Used in the Study*

<i>Tyrannosaurus rex</i>	<i>Tyrannosaurus "x"</i>	<i>Nanotyrannus</i>	Outgroups
CM 9380	AMNH 5027	BMR P2002.4.1	<i>Tarbosaurus</i>
CM 1400	MOR 008	CMNH 7541	BHI 6236
LACM 23844	SDSM 12047	BHI 6235	ZPAL-MgD-I/4
LACM 2345	Samson	LACM 28471	<i>Gorgosaurus</i>
MOR 009			TCM2001.89.1
MOR 1128			<i>Albertosaurus</i>
MOR 1125			BHI 6234
MOR 555			
MOR 980			
FMNH PR2081			
BHI 3033			
BHI 4100			
BHI 4182			
BHI 6232			
BHI 6231			
BHI 6233			
BHI 6230			
BHI 6242			
TCM2001.90.1			
RTMP 81.12.1			
RTMP 81.6.1			
UCMP118742			
BMNH R7994			
NHM R8001			
USNM V6183			
LL.12823			

Ontogenetic variation may include aspects other than the obvious increase in size. For example, it may also include an increase in the number of alveoli, or tooth positions (e.g., *Edmontosaurus annectens*; personal observation). In certain groups (i.e., mammals), growth to adulthood may also include modification of tooth morphology, along with an increase in the number of tooth positions (Romer 1966). For many vertebrates, ontogeny also includes an increase in body size at a faster rate than for the brain, eyes, and skull (Lockley et al. this volume). Nutritional variation may manifest itself as smaller body size and smaller body mass—differences that are not generally confused with taxonomic characters. Genetic variation may be monitored by using extant populations as examples (Darwin 1868). Pathologic specimens showing evidence of disease or healed injury are relatively easily recognized, and are generally not reproducible from specimen to specimen in a form that would be noted as a taxonomic character. Finally, sexual dimorphism will be discussed in depth near the end of this chapter.

## The Case for *Tyrannosaurus* "x"

More than 25 years ago, Robert Bakker (personal communication) made the case for dividing the North American genus *Tyrannosaurus* into 2 species, *T. rex* and what he refers to as *Tyrannosaurus* "x" (Fig. 8.1). Bakker's reasoning was based on a peculiar variation in the anterior dentition of the dentary. The type of *Tyrannosaurus rex* (AMNH 973 = CM 9380) possesses a single incisiform tooth occupying the anterior position in the dentary. This tooth is morphologically reminiscent of the teeth of the premaxilla, is D shaped in cross section, and is substantially smaller than those directly posterior to it (Figs. 8.2 and 8.3). Bakker also noted that AMNH 5027 appears to possess 2 incisors in each dentary. For lack of specimens, his views were never published. Paul (1988) and Molnar (1991) have both also considered the possibility of a second species of *Tyrannosaurus*.

A quarter of a century later, there now exist at least 15 reasonably complete *Tyrannosaurus* skulls. Three of these specimens (MOR 008, SDSM 12047, and Samson) share certain characters, including the double lower incisors, with AMNH 5027 (Figs. 8.4 and 8.5). Because these "incisors" are either missing or were restored on all 4 specimens, without computed tomographic scans to look at unerupted teeth, the D-shaped morphology of these "incisors" is in question. The apparent differences seem to be best expressed by comparing the size of the second dentary tooth with that of the third, and because the teeth themselves were not always available to measure, the length of the second and third alveoli were measured and compared. The results of these measurements are found in Table 8.2.

Although all 4 skulls seem short when compared with full-grown individuals (i.e., BHI 3033 and FMNH PR2081 = BHI 2033), ontogenetic variation may be ruled out because other individuals of approximately the same skull length do not share this character. One of the specimens, Samson, has a femur (length, 129 cm) of comparable length to Stan (BHI 3033; length, 131 cm), but whose skull is less than 80% as long (104 cm). A shorter skull and variation in lower jaw dentition is unlikely to be caused by differences in nutrition. Pathology may be ruled out because of the lack of any associated manifestation of healed injury. Genetic variance also seems improbable because no modern correlates exist. A case could be made for the differences in the dentition being attributable to sexual dimorphism.

Specimen	DT2-L (mm)	DT3-L (mm)	Ratio of DT3 to DT2
<i>T. rex</i>			
CM 9380	55	54	1.0
MOR 555	52	56	1.1
MOR 980	51	51	1.0
BHI 3033	56	60	1.1
<i>T. "x"</i>			
BHI 4182	33	34	1.0
MOR 008	48	64	1.3
SDSM12047	35	55	1.6
Samson	33	54	1.6

Table 8.2. Comparison of Lengths of Second (DT2-L) and Third Dentary Tooth or Alveolus (DT3-L)

\* From the holotype.



Figure 8.4. Dorsal view of the anterior portion of the left dentary of *Tyrannosaurus rex* CM 9380 preserving small first dentary tooth DT1 and large second dentary tooth DT2.

Although there are modern examples of sexual dimorphism in the canines of some primates (Martin et al. 1994) and in the canines or incisors of walrus, elephants, bush pig, and hippopotamus (Lincoln 1994), sexual dimorphism expressed as differences in dentition in extant taxa seems to be restricted to mammals. Any dental expression of sexual dimorphism remains undocumented for crocodylians, extinct toothed birds (extant phylogenetic bracketing), or other extant reptiles.

Can the difference in the teeth be attributable to speciation? Although stratigraphic information for the 4 specimens is unavailable, there are good records available for *Tyrannosaurus rex*. BHI 2033 was collected 16 m below the K-T boundary in the Hell Creek Formation (the Hell Creek in the area, near Buffalo, SD, is approximately 150 m thick). A second indisputable specimen of *Tyrannosaurus rex* (BHI 4182) was collected nearby, from within 10 m of the base of the formation, and it represents perhaps the oldest known record of *Tyrannosaurus* from North America (Kirk Johnson, personal communication). Geographic distribution is also not a factor, because *T. rex* co-occurs with *T. "x."*



Figure 8.5. Dorsal view of the anterior portion of the left dentary of *Tyrannosaurus* "x" (Samson) preserving small alveoli for DT1 and DT2 and a large alveolus for the third dentary tooth DT3.

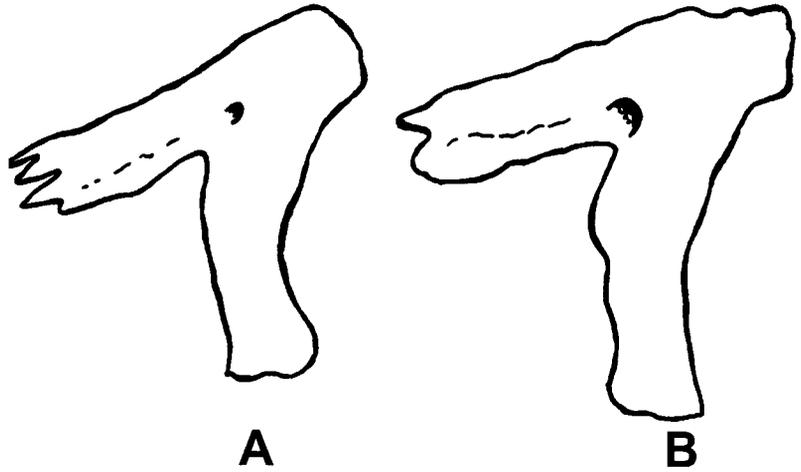
Dentary and maxillary tooth (alveoli) counts also seem to vary between the 2 "species." This is particularly evident in the dentary, with 13 or 14 for *Tyrannosaurus rex* and 14 or 15 for *T. "x."* The distribution of all of these characters, with *Tarbosaurus bataar* as an outgroup, are listed in Table 8.3.

A fourth character separating the 2 forms is the relative size of the lateral pneumatic lachrymal foramen. Specimens referable to *T. "x"* have relatively smaller lateral pneumatic lachrymal foramina than those of *Tyrannosaurus rex* (Fig. 8.6). When measured and plotted as lachrymal foramina length vs. lachrymal length (Fig. 8.7), *Tyrannosaurus "x"* clusters separately from *T. rex* (as do *Gorgosaurus* and *Nanotyrannus*). However, it should be noted that the size of the lachrymal foramina in *Allosaurus* is extremely variable, and this difference between *T. rex* and *T. "x"* may not be statistically significant, especially given the sample size (Kenneth Carpenter, personal communication).

Table 8.3. Comparison of Skull Characters

Skull Character	<i>Tyrannosaurus rex</i>	<i>Tyrannosaurus "x"</i>	<i>Tarbosaurus</i>
Lateral lachrymal pneumatic foramina	Small	Very small	Small
Maxillary tooth count	11 or 12	12	12 or 13
Dentary tooth count	13 or 14	14 or 15	15
Dentary incisor count	1	2	1
L3DT/L2DT DT3-L/DT2-L	1.0–1.1	1.3–1.6	1.2

Figure 8.6. Lateral view of the left lachrymals of (A) *Tyrannosaurus* "x" AMNH 5027 and (B) *Tyrannosaurus rex* BHI 3033. Note the larger lateral pneumatic foramen on *T. rex*.



Are these 4 cranial characters enough to erect a new species? (No significant postcranial characters were noted.) Because we are dealing with an extinct group, doing so at this time might be premature. Although it is likely that a second North American Latest Cretaceous species of *Tyrannosaurus* exists, all of the specimens in questions are in need of further preparation that will permit a more thorough comparison with the type (AMNH 973 = CM 9380) and other referred specimens. Fortunately, preparation of 2 of the specimens (SDSM 12047 and Samson) is already underway. The ultimate disposition of *Tyrannosaurus* "x" may soon be resolved.

**Is *Nanotyrannus lancensis* a Juvenile *Tyrannosaurus rex*?**

The genus *Nanotyrannus* was erected by Bakker et al. (1988) for the type specimen (CMNH 7541) of *Gorgosaurus lancensis* Gilmore (1946). This specimen (Fig. 8.8) consists of a relatively complete skull preserved with the jaws in occlusion, with very little distortion and no associated postcra-

Figure 8.7. Lachrymal length vs. lachrymal foramina length.

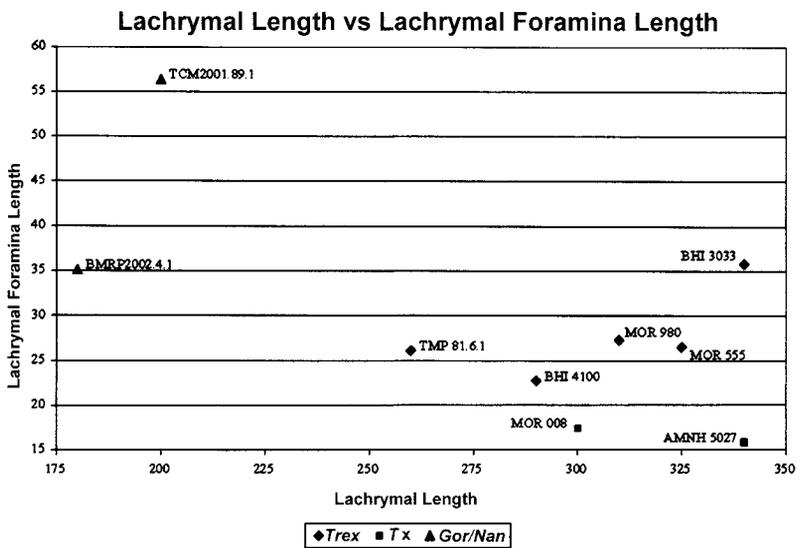




Figure 8.8. Type specimen of *Nanotyrannus lancensis* CMNH 7541.

nial material. Bakker et al. (1988) argued that certain derived characters, including the construction of the basicranium, the angle of the occipital condyle, the maxillary tooth count, the overall tooth morphology, the relative narrowness of the snout, and the expansion of the temporal region of the skull clearly separated this specimen from other tyrannosaur clades (*Gorgosaurus*, *Albertosaurus*, *Daspletosaurus*, and *Tyrannosaurus*).

Although the characters discussed by Bakker et al. (1988) clearly separated this specimen from its earlier assignment to *Gorgosaurus*, its distance from the *Tyrannosaurus* clade seemed less defined. They both “achieved the highest degree of potential stereoscopy known among large theropods,” and they agree in characters, including the orientation of the occipital condyle (Bakker et al. 1988, p. 25). They also address the question of the skull being that of a juvenile: “The sutures between the lachrymal and prefrontal have thoroughly coalesced in *Nanotyrannus*, as have the sutures between frontals and prefrontals. . . . Without question, the type of *Nanotyrannus* was fully adult and had reached the maximum size the individual would have attained if it had lived longer” (Bakker et al. 1988, p. 17).

Carpenter (1992, pp. 259, 260) disagreed with Bakker et al. (1988) when he noted that “the coalescence of cranial bones is known to be variable in dinosaurs” bringing under suspicion “its usability to ‘age’” dinosaurs. Carpenter further noted that “the oval shape of the orbit” may well

be a juvenile character. He concluded that *Nanotyrannus lancensis* could be a juvenile *T. rex*.

Carr (1999) expanded this possibility. On the basis of 17 specimens referred to *Albertosaurus libratus*, Carr erected an ontogenetic series of growth stages (1–3). From bone texture, lack of fusion, shape of the orbit, and overall skull morphology, Carr placed CMNH 7541 into his stage 1, the youngest in his ontogenetic series. Carr then declared *Nanotyrannus lancensis* to be a juvenile *Tyrannosaurus rex*. In later arguments (Carr and Williamson 2004; Carr et al. 2005), this designation was used to establish a growth series for *T. rex*, establishing a sequence of changes from the small juvenile LACM 28471, followed by the juvenile CMNH 7541 (stage 1), through subadults LACM 23845 and AMNH 5027, to the fully grown adults LACM 23844 and FMNH PR2081 (BHI 2033).

Although Carr (1999) presented a compelling and thoughtful argument, not all paleontologists agree with his assessment. Currie (2003, p. 223) pointed out that “most of the characters used to demonstrate that *Nanotyrannus* and *Tyrannosaurus* are synonymous are also characters of *Tarbosaurus* and *Daspletosaurus*.” Bakker et al. (1988; personal communication) noted the discrepancy in tooth counts—15 maxillary teeth in *Nanotyrannus* and 11 or 12 in *Tyrannosaurus rex*—and the lack of tooth reduction ontogenetically in the maxilla of any extant species. The primitive compressed nature of *Nanotyrannus* teeth (Bakker et al. 1988) as compared with the derived inflated teeth seen in *T. rex* and evidence of feeding behavior differences also argue for the uniqueness of CMNH 7541 (Larson 1999). Because the growth series argument of Carr is rooted in the assumption that *Nanotyrannus* is a juvenile *T. rex*, much of Carr’s concept of ontogenetic change and ontogenetic stages in *Tyrannosaurus rex* is in question (Jorn Hurum, personal communication). I agree with Carr and Williamson’s (2004) assessment of LACM 28471 (the so-called Jordan the-ropod) with CMNH 7541 (the type of *Nanotyrannus*), and with the designation of the subadult LACM 23845 as *Tyrannosaurus rex*. However, I disagree with the subadult designation of AMNH 5027, which groups as a full adult with *Tyrannosaurus* “x” and with *Nanotyrannus* as a juvenile *T. rex*.

An isolated left lachrymal (BHI 6235) comparable in size and morphology to CMNH 7541 was found associated with Sue (FMNH PR2081) and erroneously identified as a juvenile *T. rex* (Larson 1997). It, too, should be referred to *Nanotyrannus*. Finally, the recent discovery of a fourth specimen (BMR P2002.4.1) is clearly referable to *Nanotyrannus*. This specimen, nicknamed Jane, in addition to many uncrushed and well-preserved skull elements with a nearly complete dentition, also preserves much of the postcranial skeleton.

Although this subject is discussed in detail elsewhere (Currie 2003; Currie et al. 2003; Larson in press), a list of characters separating *Nanotyrannus* from *Tyrannosaurus* is presented in Table 8.4. For purposes of comparison as outgroups, those characters are also listed for *Tyrannosaurus* “x,” *Tarbosaurus*, *Gorgosaurus*, and *Albertosaurus*.

Table 8.4. Comparison of Tyrannosaurid Skull Characters

Skull Character	<i>Tyrannosaurus rex</i>	<i>Tyrannosaurus "x"</i>	<i>Tarbosaurus bataar</i>	<i>Tarbosaurus bataar</i> Juvenile	<i>Nanotyrannus lancensis</i>	<i>Gorgosaurus</i> sp.	<i>Albertosaurus</i> sp.
Antorbital fossa	Very deep	Deep	Deep	Deep	Very shallow	Shallow	Shallow
Ventral antorbital maxillary ridge meets jugal	No	No	No	No	Yes	Yes	Yes
Maxillary fenestra reaches rostral margin of antorbital fossa (Carr et al. 2005)	Yes	Yes	Yes	Yes	No	No	No
Maxillary fenestra reaches ventral margin of antorbital fossa (Carr et al. 2005)	Yes	Approaches	Yes	Yes	No	No	Approaches
Vomer expansion	Lateral	Lateral	Lateral	?	Dorsoventral	Dorsoventral	?
Posterior dorsal Quadratojugal notch	No	No	No	No	Yes	Yes	No
Central dorsal quadratojugal notch	No	No	No	No	Yes	Yes	No
Anterior dorsal medial notch in quadratojugal (Carr and Williamson 2004)	Yes	?	No	?	No	No	No
Lachrymal horn (cornual process)	Absent	Absent	Absent	Absent	Present	Present	Present
Lachrymal shape	Inverted L	Inverted L	Inverted L	Inverted L	T	T	T
Quadrate—squamosal articulation	Double	Double	?	?	Single	Double	Single
Cranial nerve V-2 bounded by:	Maxilla and premaxilla	Maxilla and premaxilla	Maxilla and premaxilla	Maxilla and premaxilla	Maxilla only	Maxilla only	?
Anterior maxilla fossa at cranial nerve V-2	Maxilla and premaxilla	Maxilla and premaxilla	Maxilla and premaxilla	Maxilla and premaxilla	Maxilla only	Maxilla only	?

Table 8.4 (continued).

Skull Character	<i>Tyrannosaurus rex</i>	<i>Tyrannosaurus "x"</i>	<i>Tarbosaurus bataar</i>	<i>Tarbosaurus bataar</i> Juvenile	<i>Nanotyrannus lancensis</i>	<i>Gorgosaurus</i> sp.	<i>Albertosaurus</i> sp.
Tooth cross section at base of crown	Ovate	Ovate	Compressed	Compressed	Compressed	Ovate	Compressed
Fourth maxillary tooth L/W (at base of crown)	1.76	1.23	1.68	?	2.12	1.36	?
Fourth dentary tooth L/W (at base of crown)	1.38	1.34	1.39	?	1.66	1.23	?
First maxillary tooth small and incisoform	No	No	No	No	Yes	Yes	?
D-shaped first dentary tooth	Yes	?	?	?	No	No	?
First dentary tooth reduced	Yes	Slightly	Slightly	?	Greatly	No	?
Maxillary tooth count	11–12	12–13	12–13	13	15–16	13–15	13–15
Dentary tooth count	13–14	14–15	15	?	17	15–17	13–15
Medial postorbital fossa	No	No	No	?	Yes	Yes	Yes
Foramina on lateral aspect (center) of quadratojugal	Absent	Absent	Absent	Absent	Large pneumatic	Small	Absent
Anterior squamosal pneumatic foramina	Very large	Very large	Present	?	Absent	Small	Absent
Lateral lachrymal pneumatic foramina	Small	Very small	Small	Small	Multiple, large	Large	Large
Medial lachrymal pneumatic foramina	Present, large	Present, large	Present	?	Absent	Small	Absent
Ectopterygoid pneumatic foramina bounded by thick lip (Carr et al. 2005)	Yes	Yes	Yes	?	No	No	No
Jugal pneumatic foramina	Anterolateral facing	Anterolateral facing	Anterolateral facing	Anterolateral facing	Dorsolateral facing	Anterolateral facing	?

Is it possible to recognize sexual dimorphism in *Tyrannosaurus rex*? The subject of sexual dimorphism in nonavian theropods has been examined by a number of authors over the years (e.g., Paul 1988; Colbert 1989, 1990; Raath 1990; Chinsamy 1990; Gay 2005). The subject of sexual dimorphism in *Tyrannosaurus rex* has surfaced repeatedly since Carpenter first broached the subject in 1990 (Molnar 1991; Larson and Frey 1992; Larson 1994, 1995, 2001; Horner and Lessem 1993; Carpenter and Smith 2001; Larson and Donnan 2002; Brochu 2003; Molnar 2005). These authors have also explored the possibilities of identifying, or at least separating, the sexes of various theropod species on the basis of differences in cranial ornamentation (Larson 1994; Molnar 2005), pelvic construction (Carpenter 1990; Larson 1994, 1995, 2001; Larson and Donnan 2002), erosion of the femur to liberate calcium for egg production (Chinsamy 1990), preservation of medullary bone (Schweitzer et al. 2005), differences in hemal arch (chevron) morphology (Larson and Frey 1992; Larson 1994, 1995; Erickson et al. 2005), the presence of eggs within the pelvic arc (Sato et al. 2005), and skeletal morph (i.e., gracile vs. robust morphs) (Paul 1988; Carpenter 1990; Raath 1990; Chinsamy 1990; Larson and Frey 1992; Larson 1994, 1995, 2001; Larson and Donnan 2002; Carpenter and Smith 2001).

Sexual dimorphism in extant animals is well documented. We recognize this in mammals as the presence of antlers in male cervids; longer and more massive tusks in male elephants, suids, and walrus; larger horns in male bovids; the presence of canines in male equids; and a generally larger male body size (e.g., Macdonald 1984). This sexual size dimorphism can be quite impressive, reaching as much as a 7:1 (3500 kg : 500 kg) ratio of male to female body mass in the southern elephant seal, *Mirounga leonina* (Lindenfors et al. 2002). Interestingly, for many mammals, the only obvious sexual dimorphism, excluding genitalia, is expressed in adult size, with males outweighing females (Macdonald 1984).

Many reptile groups (e.g., crocodylians; Bellairs 1970) seem to follow this mammalian pattern of sexual size dimorphism. However, it is not always the males who outweigh the females. In turtles and snakes (Fitch 1981), and even in a few mammal groups like baleen whales (Minasian et al. 1984) and hyenas (Estes 1991), sexual size dimorphism is expressed by females being larger than males. Species of invertebrates, to offer other examples, are often quite sexually size dimorphic, with the female, almost without exception, being the larger. In fact, the world record holder for the most sexually size-dimorphic animal is the blanket octopus, *Tremoctopus violaceus*, where females may outweigh males by as much as 40,000 to 1 (Norman et al. 2002).

Birds, the closest living relatives to nonavian theropods, are often quite sexually dimorphic. This dimorphism may be expressed as differences in coloration (the ostrich, *Struthio camelus*), plumage (the common peafowl, *Pavo cristatus*), keratinous structures (the rhinoceros hornbill, *Buceros rhinoceros*), fleshy head ornamentation (the common turkey, *Meleagris gallopavo*), or even inflatable fleshy structures (the greater prairie chicken, *Tympanuchus cupido*). Unfortunately, because none of these features is likely to be preserved in the fossil record, they are not much use in recognizing sexual dimorphism in extinct theropods. Sexual size dimorphism,

however, is effective in separating males from females in some bird species (Brad Livezey, personal communication). Sexual size dimorphism may also prove recognizable in nonavian theropods like *Tyrannosaurus rex*.

For many birds, sexual size dimorphism is measurable. It manifests itself as males larger than females in gulls (Ingolfsson 1969; Schnell et al. 1985; Bosch 1996), steamer ducks (Livezey and Humphrey 1984), sparrows (McGillivray and Johnston 1987), and skimmers and terns (Coulter 1986; Quinn 1990), among others. Sexual size dimorphism also occurs with females larger than males in spotted owls (Blakesley et al. 1990), ospreys (Schaadt and Bird 1993), sandpipers (Sandercock 1998), emus (Maloney and Dawson 1993), and so forth. Morphometric analysis, performed by skeletal measurements, has proven effective in separating sex when the difference in mass is over 6% (Schnell et al. 1985). It has even been possible to separate the sexes of mature individuals through morphometric examination (by using bill, wing, and tail measurements) when mass differences between the sexes was insignificant or even indiscernible (Winker et al. 1994).

Although researchers have referred to the presence of robust and gracile morphotypes, Molnar (2005) points out that to date, these morphotypes have not been adequately quantified, but rather are generally based on visual assessments. Is it possible to recognize and quantify sexual size dimorphism, and clearly classify individual *Tyrannosaurus* specimens as robust or gracile morphs? To answer this, I have taken measurements of select elements from 25 specimens of *Tyrannosaurus rex*. Measurements were also taken for 2 outgroup specimens assigned by this study to *Nanotyrannus lancensis* (CMNH 7541 and BMR P2002.4.1) and one to *Gorgosaurus* sp. (TCM2001.89.1). Even though this study considers *Tyrannosaurus* “x” to be the same genus as *T. rex* and hence should be separable in a consistent manner, 3 of these specimens (AMNH 5027, Samson, and MOR 008) also appear as outgroups. Measurements varied from element to element and consisted of lengths, widths, heights, and/or circumference, as shown in Figure 8.9; the values are found in Tables 8.5 and 8.6. Clustering on graphs is assumed to separate sexual size dimorphs. The results were then compared with a visual analysis that divided robust morphs from gracile. Some elements failed to provide significant results (e.g., dentary length vs. tooth row length). For other elements, there was simply not enough data to yield meaningful results (e.g., metatarsal II length vs. circumference, Fig. 8.11; ilium length vs. height, Fig. 8.12; and humerus length vs. circumference, Fig. 8.13), although visual examination was able to separate them, indicating that the human eye can see apparent differences (as in Fig. 8.10). Elements that provided too few data may yet prove useful for quantifiable analysis when additional specimens are discovered. Elements that were abundant, such as the femur (Fig. 8.14) and humerus (Fig. 8.13), yielded clear results, which confirmed their separation by visual inspection: robust plotted individuals look more robust.

From the results of the analysis, 2 morphs of *Tyrannosaurus* are apparent, a robust and a gracile morph. Neither geographic nor stratigraphic distribution can explain these differences. Therefore, because both crocodiles and birds show sexual size dimorphism, extant phylogenetic bracketing tells

Table 8.5. *Measurements Used in Morphometric Analysis*

<i>Specimen</i>	<i>Humerus</i>		<i>Ulna</i>		<i>Scapula</i>		<i>Iliu</i>
	L	C	L	C	L	C	L
<i>T. rex</i>							
CM 9380	350	165					
MOR 009							1160
MOR 1128							
MOR 1125			200	99		180	
MOR 555	375	162	198	106	980	185	1490
MOR 980	362	165			940	146	1397
FMNH PR 2081	390	185	220	121	1140	205	1480
BHI 3033							1550
BHI 4100					800	142	
BHI 6232							
BHI 6231	360	172					
BHI 6233							
BHI 6230	330	145	185	82			1470
BHI 6242							
TCM 2001.90.1			176	96	940	196	1275
RTMP 81.12.1							
RTMP 81.6.1	302	150					
BMNH R7994							
NHM R8001							
USNM 6183							
LL 12823							
<i>T. "x"</i>							
Samson							
<i>Nanotyrannus</i>							
BMR P2002.4.1	280	118				109	720
<i>Gorgosaurus</i>							
TCM 2001.89.1	305	130	180	74	675	120	865

Abbreviations:—C, circumference; L, length; S, sacrals; II, IV, metatarsal II, IV.

Ism		Sacrum				Metatarsal				Femur	
H	L	S-1	S-5	S-6	L II	C II	L IV	C IV	L	C	
									1200	545	
400									1260	580	
									1150	510	
565	1010	219	202	170	585	295	605	253	1275	514	
483	851				597	232	655		1232	483	
590	980	285	210	240					1340	580	
590	1060				595	280	600	247	1310	500	
									1180	527	
									1110	515	
					600	272	625	238	1190	494	
									1180	512	
490	895	240	185	204	550	267	565	263			
535	980	220	200	210					1200	560	
									1210	470	
										490	
										490	
									990	425	
									1200	467	
					610	305	635	280	1295	560	
220	500	85	64	63	510	149	513	136	720	250	
305					490	195	500	184	825	270	

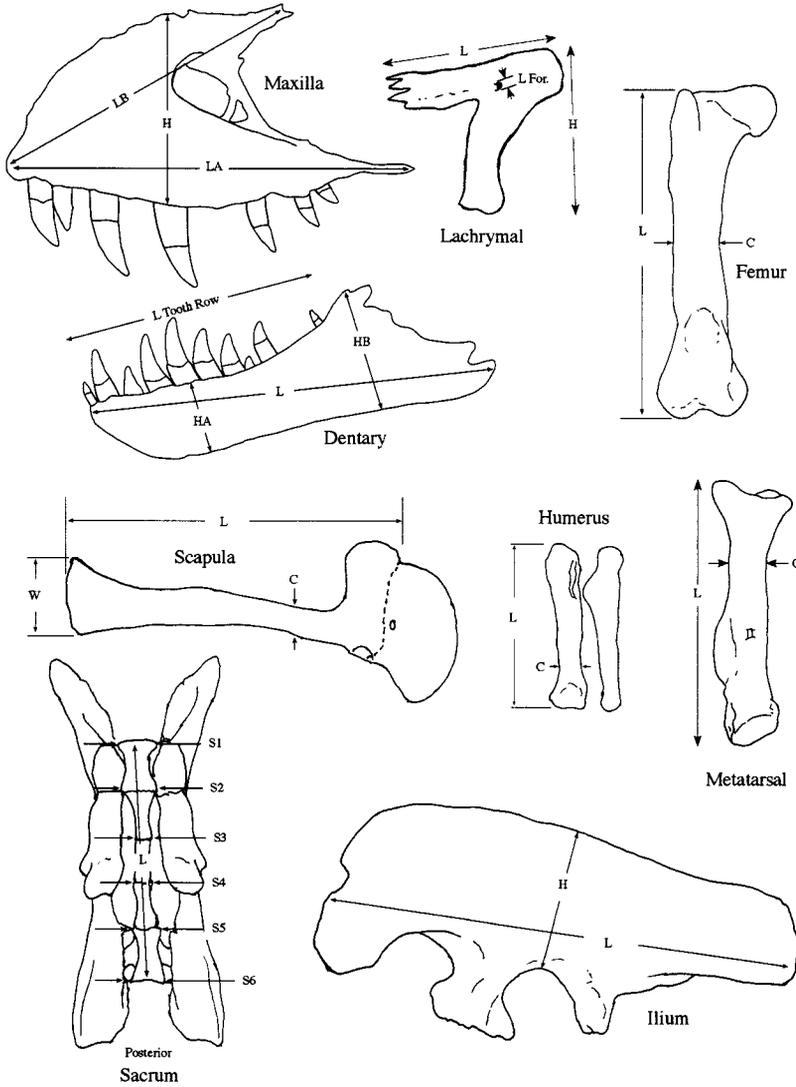
Table 8.6. *Measurements (mm) Used in Morphometric Analysis*

Specimen	Maxilla						Dentary					Lachrymal			
	H	LA	LB	LA/B	LTR	TP	L	HA	H	LTR	TP	H	L	LF	H/LF
<i>T. rex</i>															
CM 9380	380	695	620	1.12	535	12	860	180	290	510	13				
CM 1400	390	760			620	12									
LACM 23844							920	175	260	545	13				
MOR 1125	360	680	590	1.15	520	12	760	140	230	485	14				
MOR 555	395	798			620	12	990	170	310	630	13	365	325	26.5	13.8
MOR 980	340	770			560	11	900	175	280	545	13	310	310	27.3	11.4
FMNH PR2081	400	855	720	1.19	645	12	1010	200	320	620	13				
BHI 3033	395	775	650	1.19	605	11	915	175	280	570	13	340	340	35.8	9.5
BHI 4100		730					770	160		530	13	290	290	22.7	12.8
BHI 4182							910	170	270	530	14				
RTMP 81.6.1	318				540		770	143	248	530		280	260	26.1	10.7
UCMP 118742	390	810	690	1.17	625	12									
AMNH 5027	360	710	710	1	530	12	850	135	190	520	14	360	340	15.8	22.8
MOR 008	350	720			580	12	880	180	280	560	13	340	300	17.4	19.5
<i>T. "x"</i>															
Samson							870	170	270	540					
<i>Nanotyrannus</i>															
BMR P2002.4.1	160	470	385	1.22	355	15	505	69	107	318	17	163	180	35.1	4.6
CMNH 7541	150	385	309	1.25	278	15	375								
BHI 6235												120		18	6.7
<i>Gorgosaurus</i>															
TCM 2001.89.1	230	568	420	1.35	405	14	580	95	197	360	15	235	200	56.4	4.2

Note.—See Figure 8.9.

Abbreviations:—A, B refer to points in Figure 8.9. F, foramen (=lacrymal foramen); H, height; L, length; LTP, number of tooth positions; TR, tooth row.

Figure 8.9. Examples of measurement techniques used in this study.



us that the most parsimonious explanation for the presence of these 2 morphs is sexual size dimorphism. The formula developed by Anderson et al. (1985) was used to estimate the mass of the robust and gracile morphs from femur diameter. The weight estimates (Table 8.7) show a maximum weight for the gracile morphs of 4.0 metric tonnes, with a mean of 3.5 metric tonnes (6 individuals); and a maximum weight of 5.6 metric tonnes and a mean of 4.7 metric tonnes for robust morphotypes (9 individuals).

Given that the presence of 2 morphs has been established for *Tyrannosaurus rex*, can we determine the sex of the morphotypes? Carpenter (1990) suggested that, on the basis of the greater divergence of ischium (Fig. 8.17), the robust form was female. Larson and Frey (1992) agreed with Carpenter, and they further suggested that the location and morphology

## Male or Female

Figure 8.10. Anterior view of right metatarsal II of (A) *gracile* (BHI 3033) and (B) *robust* (TCM 2001.90.1) morphotypes.



of the first chevron might also be used to yield the same result. However, this method has proven unreliable (Erickson et al. 2005). Elsewhere, I (Larson 1994, 1995) have suggested that the wider pelvic arch and healed injuries of the proximal caudal vertebrae (consistent with injuries potentially inflicted by a mounting male during copulation) were restricted to robust morphotypes. I (Larson 2001; Larson and Donnan 2002) supported Carpenter's (1990) conclusion that robust individuals were female. But because of the tenuous nature of these conclusions, I have speculated that one way to positively recognize a female is to locate medullary bone within the skeleton (Larson and Donnan 2002). Medullary bone is only deposited within the medullary cavity in the long bones of female birds during ovulation, as an aid to the quick mobilization of calcium for egg

### Metatarsal II Length vs Circumference

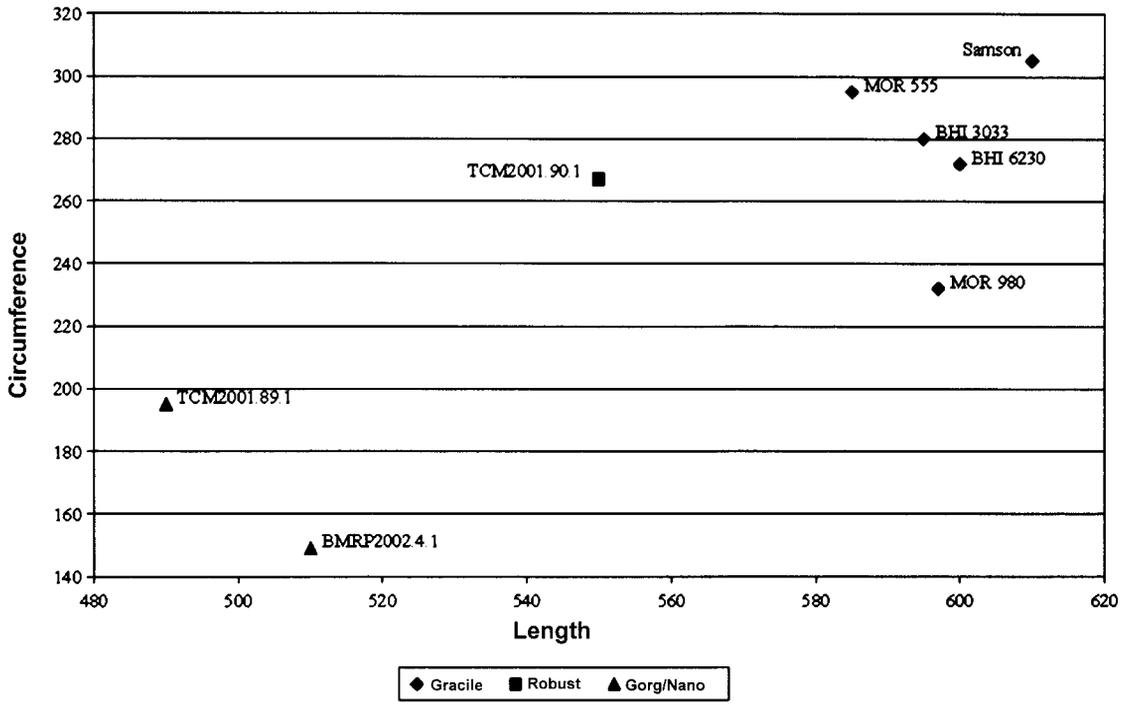


Figure 8.11. Metatarsal II length vs. circumference.

Figure 8.12. Ilium length vs. height.

### Ilium Length vs Height

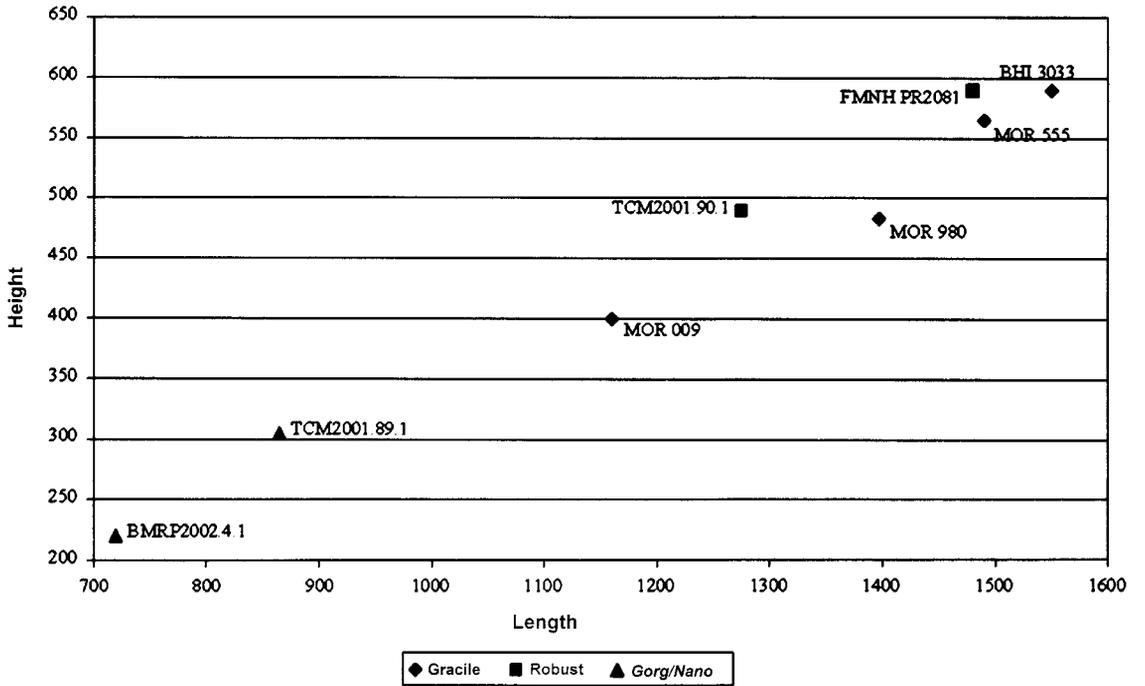




Figure 8.13. Anterior view of (A) left humerus of gracile (BHI 6230) and (B) right humerus of robust (FMNH PR2081) morphotypes.

production (Taylor 1970; Welty and Baptista 1988; Schweitzer et al. this volume). Although the absence of medullary bone is inconclusive (it is not found in males and nonovulating females), its presence unequivocally identifies a female.

Medullary bone has not been documented in ovulating female crocodylians. Although ovulating birds have medullary bone, there were no guarantees that ancestral nonavian theropods shared this character. What would be the chances of finding the fossil of an ovulating female *Tyrannosaurus rex*, preserving the medullary bone, exposing the inside of the medullary cavity, and recognizing and then verifying that the tissue is medullary bone? Unbelievably, that is exactly what Schweitzer et al. (2005, this



Figure 8.14. Anterior view of (A) left femur of gracile (BHI 3033) and (B) right femur of robust (TCM2001.90.1) morphotypes.

volume) did. Schweitzer et al. have verified the presence of medullary bone within the femur of a specimen of *Tyrannosaurus rex* by comparison with medullary bone extracted from laying chickens (*Gallus gallus*) and ostriches (*Struthio camelus*). By plotting information from the femur from which the medullary bone was found (MOR 1125), it was found that the specimen clusters with robust morphotypes (Fig. 8.18), thereby providing independent supporting evidence that the robust morphotypes are most

Table 8.7. Calculated Mass for *Tyrannosaurus* Specimens and Outgroups, *Nanotyrannus* and *Gorgosaurus*

Specimen	Type	Femur Length (mm)	Femur Circumference (mm)	Mass (kg)	Mass (tonne)	Morph
<i>T. rex</i>						
CM 9380		1200	545	4726	4.7	R
BMNH R7994			490	3535	3.5	
MOR 1128		1260	580	5601	5.6	R
MOR 1125	B-rex	1150	510	3943	3.9	R
MOR 555	Wankel rex	1275	514	4028	4.0	G
MOR 980	Peck's Rex	1232	483	3399	3.4	G
FMNH PR2081	Sue	1340	580	5601	5.6	R
BHI 3033	Stan	1310	500	3735	3.7	G
BHI 6232		1180	527	4312	4.3	R
BHI 6233		1110	515	4049	4.1	R
BHI 6230	Wyrex	1190	494	3614	3.6	G
BHI 6242	Henry	1180	512	3985	4.0	R
RTMP 81.12.1	Huxley	1200	560	5090	5.1	R
RTMP 81.6.1	Back Beauty	1210	470	3155	3.2	G
USNM V6183		990	425	2397	2.4	
LL 12823		1200	467	3100	3.1	G
<i>T. "x"</i>						
Samson	Z-rex	1295	560	5090	5.1*	R
BMR P2002.4.1	<i>Nanotyrannus</i>	720	250	563	0.6	
TCM2001.89.1	<i>Gorgosaurus</i>	825	270	695	0.7	

Abbreviations:—  
G, gracile; R, robust.  
\* Mean, 4.1.

certainly females. We may therefore assume that the gracile morphotypes are males.

## Conclusion

This study examined 34 specimens that have been assigned by various authors to *Tyrannosaurus rex*. This list also included specimens ascribed by some authors to *Nanotyrannus lancensis* but synonymized by others with *T. rex*. By use of shared and derived characters, these specimens (CMNH 7541, LACM 28471, BMR P2002.4.1, and BHI 6235) may clearly be removed from the clade, thus validating the work of Gilmore (1946) and Bakker et al. (1988). Also of contention is a group of 4 specimens (AMNH 5027, MOR 008, SDSM 12047, and Samson) that have been referred to as *Tyrannosaurus* "x." Again, by use of taxonomic characters, there is ample evidence to remove them from the species *rex*, but maintain them within the genus *Tyrannosaurus*.

By use of morphometric analysis, gracile and robust morphs are confirmed to be present within the clade *Tyrannosaurus rex*. Extant phylogenetic bracketing (comparison with living crocodiles and birds) leads us to conclude that the existence of these 2 morphs most parsimoniously repre-

## Humerus Length vs Circumference

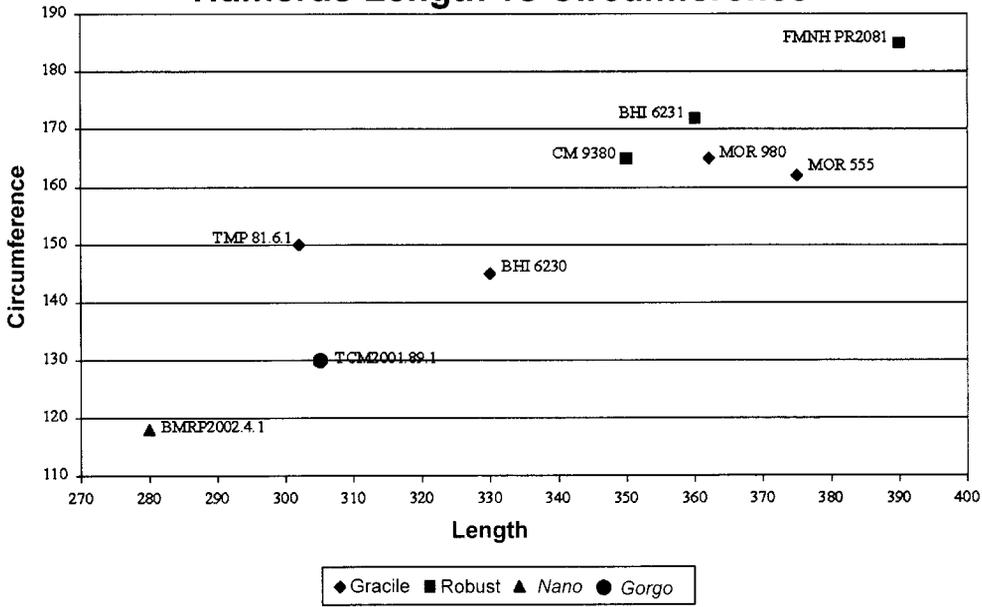
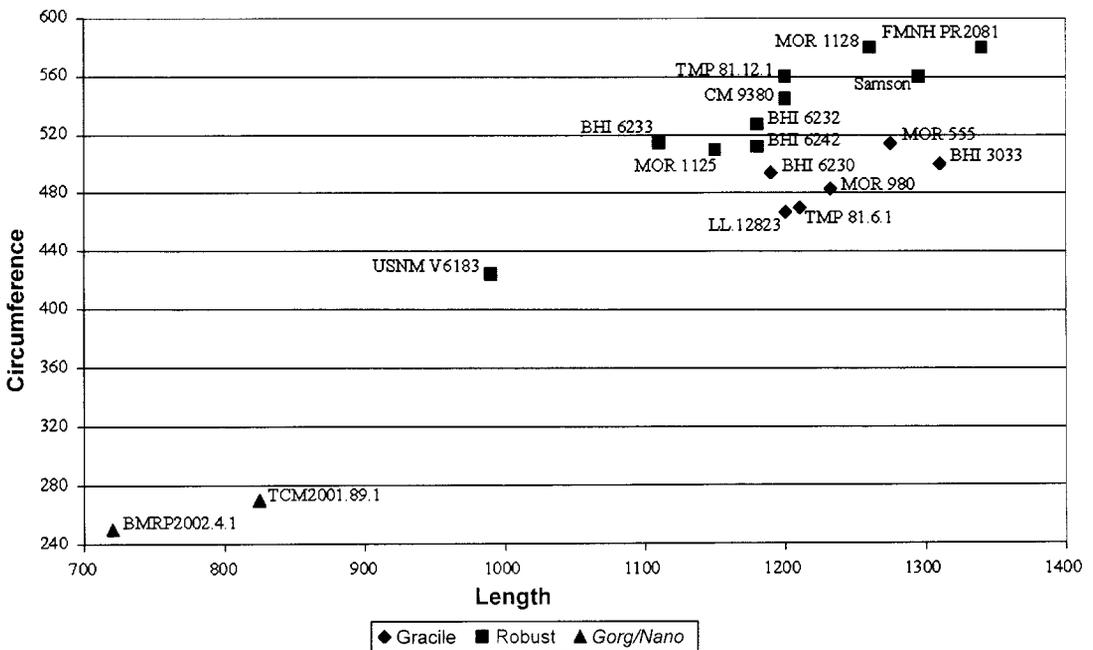


Figure 8.15. Humerus length vs. circumference.

Figure 8.16. Femur length vs. circumference.

## Femur Length vs Circumference



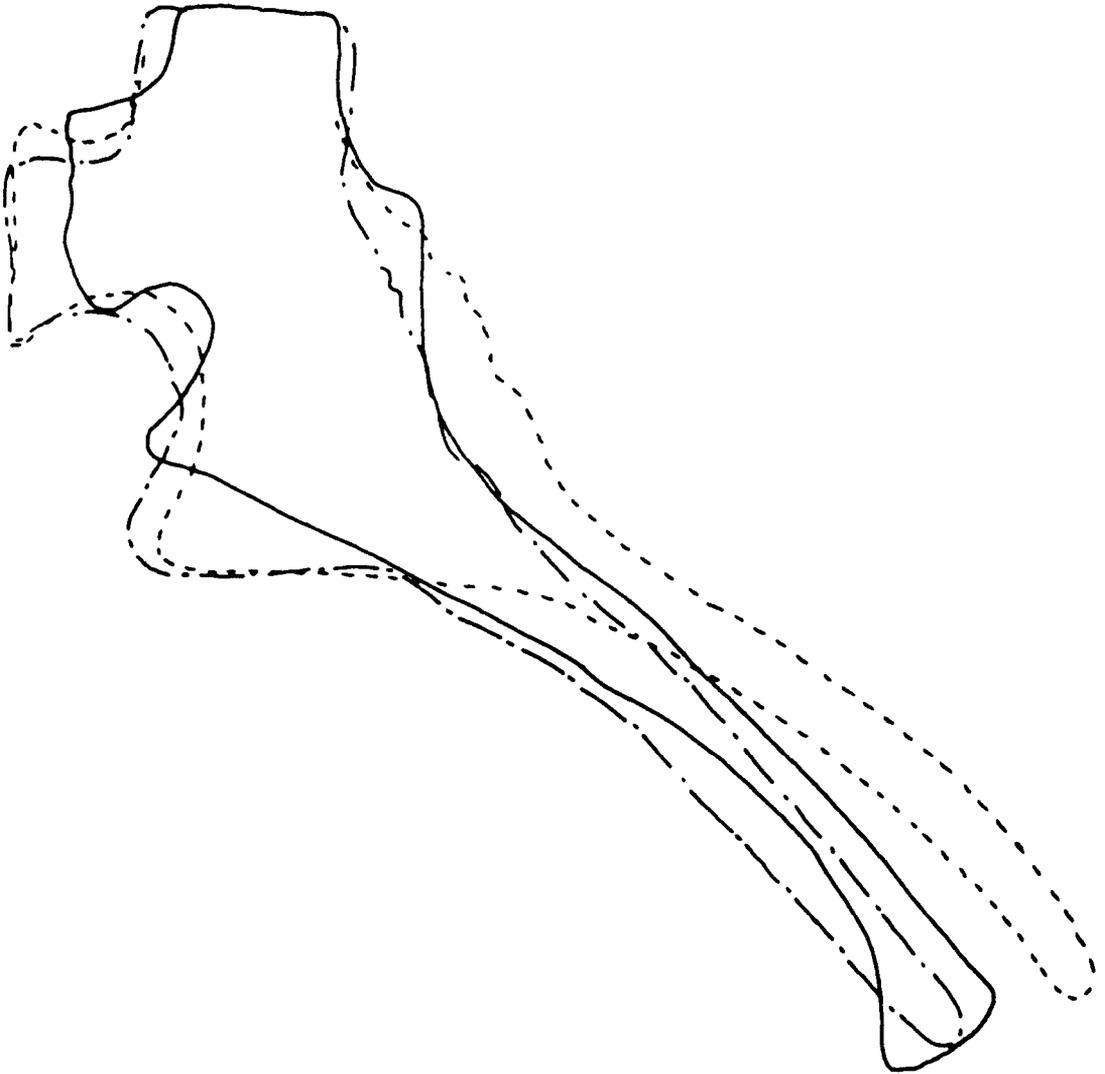


Figure 8.17. Overlay of the ischia of (A) CM 9380; (B) RTMP 81.61; and (C) AMNH 5027 (after Carpenter 1990).

sents sexual dimorphism. The discovery of medullary bone within the medullary cavity of a robust specimen of *T. rex* established MOR 1125 as female (Schweitzer et al. 2005), and therefore all other robust *T. rex* specimens are, in all probability, also female.

## Acknowledgments

I thank Larry Shaffer of Black Hills Institute for preparation of the figures and tables, and Neal Larson for some of the photography. I am extremely grateful to Phil Currie, Bill Simpson, Tim Tokaryk, Phil Fraley, Tom Williamson, Chris Morrow, Phil Manning, Kenneth Carpenter, Mike Henderson, and Scott Williams, who grabbed their tape measures and supplied missing data at a moment's notice. Conversations with Kenneth Carpenter, Ralph Molnar, Thomas Carr, Mike Henderson, Phil Currie, Jorn Hurum, Greg Erickson, Bob Bakker, and a host of others have provided insight. The

## Femur Length vs Circumference

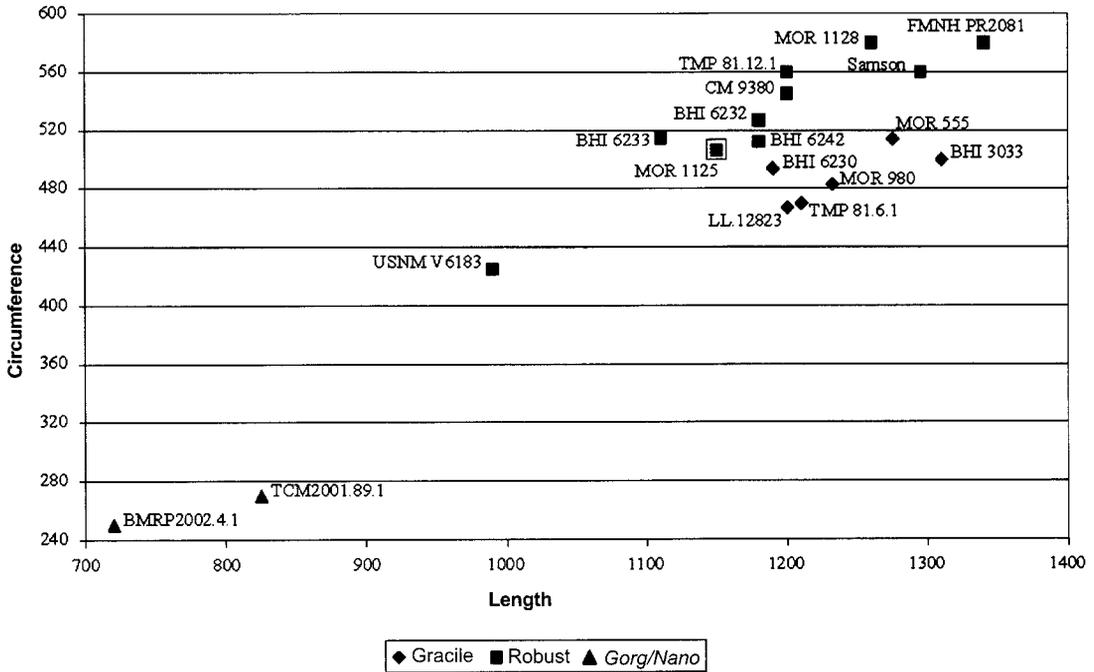


Figure 8.18. MOR 1125, a female *Tyrannosaurus rex*, clusters with other robust individuals.

compilation of data would not have been possible without the access, help, and patience provided by the curators, collection managers, and preparators at all the institutions I worked with, especially Bill Simpson, Jack Horner, Carrie Herbel, Mark Norell, Luis Chiappe, and Matt Lamanna. Last, but certainly not least, thanks to all the discoverers and collectors who saved the specimens that provided my data.

## References Cited

- Anderson, J. F., Hall-Martin, A., and Russell, D. A. 1985. Long-bone circumference and weight in mammals, birds, and dinosaurs. *Journal of the Zoological Society of London A* 207: 53–61.
- Bakker, R. T., Williams, M., and Currie, P. 1988. *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the Latest Cretaceous of Montana. *Hunteria* 1(5): 1–26.
- Bellairs, A. 1970. *The Life of Reptiles*. Universal Books, New York.
- Blakesley, J. A., Franklin, A. B., and Gutierrez, R. J. 1990. Sexual dimorphism in northern spotted owls from northwest California. *Journal of Field Ornithology* 61(3): 320–327.
- Bosch, M. 1996. Sexual size dimorphism and determination of sex in yellow-legged gulls. *Journal of Field Ornithology* 67(4): 534–541.
- Brochu, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology* Memoir 7.
- Buss, I. O. 1990. *Elephant Life: Fifteen Years of High Population Density*. Iowa University Press, Ames.
- Carpenter, K. 1990. Variations in *Tyrannosaurus rex*. P. 141–145 in Carpenter,

- K., and Currie, P. J. (eds.). *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge.
- . 1992. Tyrannosaurids (Dinosauria) of Asia and North America. P. 250–268 in Mateer, N., and Chen, P. J. *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press, Beijing.
- Carpenter, K., and Smith, M. 2001. Forelimb osteology and biomechanics of *Tyrannosaurus rex*. P. 90–116 in Tanke, D. H., and Carpenter, K. (eds.). *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington.
- Carr, T. D. 1999. Craniofacial ontogeny in tyrannosauridae (Dinosauria, Coelurosauria). *Journal of Vertebrate Paleontology* 19(3): 497–520.
- Carr, T. D., and Williamson, T. E. 2004. Diversity of Late Maastrichtian tyrannosauridae (Dinosauria: Theropoda) from western North America. *Zoological Journal of the Linnean Society* 142: 479–523.
- Carr, T. D., Williamson, T. E., and Schwimmer, D. R. 2005. A new genus of tyrannosaurid from the Late Cretaceous (Middle Campanian) Demopolis Formation of Alabama. *Journal of Vertebrate Paleontology* 25(1): 119–143.
- Chinsamy, A. 1990. Physiological implications of the bone histology of *Syntarus rhodesiensis* (Saurischia: Theropoda). *Palaeontologia Africana* 27: 77–82.
- Colbert, E. H. 1989. *The Triassic Dinosaur Coelophysis*. Museum of Northern Arizona Bulletin 57.
- . 1990. Variation in *Coelophysis bauri*. P. 81–90 in Carpenter, K., and Currie, P. J. (eds.). *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge.
- Coulter, M. C. 1986. Assertive mating and sexual dimorphism in the common tern. Savannah River Ecology Lab, South Carolina. *Wilson Bulletin* 98(1): 93–100.
- Currie, P. J. 2003. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontologica Polonica* 48(2): 191–226.
- Currie, P. J., Hurum, J. H., and Sabath, K. 2003. Skull structure and evolution in tyrannosaurid dinosaurs. *Acta Palaeontologica Polonica* 48(2): 227–234.
- Darwin, C. 1868. *The Variation of Animals and Plants under Domestication*. Vol. 1. John Murray, London.
- Erickson, G. M., Lappin, A. K., and Larson, P. L. 2005. Androgynous *rex*—the utility of chevrons for determining the sex of crocodylians and non-avian dinosaurs. *Zoology* 108: 277–286.
- Estes, R. D. 1991. *The Behavior Guide to African Mammals*. University of California Press, Berkeley.
- Fitch, H. S. 1981. *Sexual Size Differences in Reptiles*. University of Kansas Museum of Natural History Miscellaneous Publication 70.
- Gay, R. 2005. Sexual dimorphism in the Early Jurassic theropod dinosaur *Dilophosaurus* and a comparison with other related forms. P. 277–283 in Carpenter, K. (ed.). *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington.
- Gilmore, C. W. 1946. A new carnivorous dinosaur from the Lance Formation of Montana. *Smithsonian Miscellaneous Collection* 106: 1–19.
- Horner, J. R., and Lessem, D. 1993. *The Complete T. rex*. Simon & Schuster, New York.
- Ingolfsson, A. 1969. Sexual dimorphism of large gulls. *Auk* 86: 732–737.
- Larson, P. L. 1994. *Tyrannosaurus* sex. P. 139–155 in Rosenberg, G. D., and Wolberg, D. L. (eds.). *Dino Fest Proceedings*. Paleontological Society Special Publication 7.
- . 1995. To sex a *rex*. *Nature Australia* 25(2): 46–53.

- . 1997. The king's new clothes: a fresh look at *Tyrannosaurus rex*. P. 65–71 in Wolberg, D. L., Stump, E., and Rosenberg, G. D. *Dinofest International Proceedings*. Academy of Natural Sciences, Philadelphia.
- . 1999. Guess who's coming to dinner; *Tyrannosaurus* vs. *Nanotyrannus*: variance in feeding habits (abstract). *Journal of Vertebrate Paleontology*, Abstract of Papers, 58a.
- . 2001. Paleopathologies in *Tyrannosaurus rex* (in Japanese). *Dino Press* 5: 26–35.
- . In press. *The Case for Nanotyrannus*. Black Hills Institute of Geological Research.
- Larson, P. L., and Donnan, K. 2002. *Rex Appeal: The Amazing Story of Sue, the Dinosaur that Changed Science, the Law and My Life*. Invisible Cities Press, Montpelier, VT.
- Larson, P. L., and Frey, E. 1992. Sexual dimorphism in the abundant Upper Cretaceous theropod, *Tyrannosaurus rex* (abstract). *Journal of Vertebrate Paleontology*, Abstract of Papers, 38a.
- Lincoln, G. A. 1994. Teeth, horns and antlers: the weapons of sex. P. 131–159 in Short, R. V., and Balaban, E. (eds.). *The Differences between the Sexes*. Cambridge University Press, Cambridge.
- Lindenfors, P., Tullberg, B. S., and Biuw, M. 2002. Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavior, Ecology, Sociobiology* 52: 188–193.
- Livezey, B. C., and Humphrey, P. S. 1984. Sexual dimorphism in continental steamer-ducks. The Cooper Ornithological Society. *Condor* 86(3): 368–377.
- McGillivray, W. B., and Johnston, R. F. 1987. Differences in sexual size dimorphism, and body proportions between adult and subadult house sparrows in North America. 1987. *Auk* 104: 681–687.
- Macdonald, D. W. 1984. *The Encyclopedia of Mammals*. Facts on File, New York.
- Maloney, S. K., and Dawson, T. J. 1993. Sexual dimorphism in basal metabolism and body temperatures of a large bird, the emu. *Condor* (95): 1034–1037.
- Martin, L. A., Willner, L. A., and Dettling, A. 1994. The evolution of sexual size dimorphism in primates. P. 159–202, in Short, R. V., and Balaban, E. (eds.). *The Differences between the Sexes*. Cambridge University Press, Cambridge.
- Minasian, S. M., Balcomb, K. C., III, and Foster, L. 1984. *The World's Whales: The Complete Illustrated Guide*. Smithsonian Books, Washington, DC.
- Molnar, R. E. 1991. The cranial morphology of *Tyrannosaurus rex*. *Palaeontographica. Abteilung A* 217: 137–176.
- . 2005. Sexual selection and sexual dimorphism in theropods. P. 277–283 in Carpenter, K. (ed.). *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington.
- Norman, M. D., Paul, D., Finn, J., and Tregenza, T. 2002. First encounter with a live male blanket octopus: the world's most sexually size-dimorphic large animal. *New Zealand Journal of Marine and Freshwater Research* 36: 733–736.
- Osborn, H. F. 1905. *Tyrannosaurus rex* and other Cretaceous carnivorous dinosaurs. *American Museum of Natural History Bulletin* 21: 259–296.
- . 1906. *Tyrannosaurus rex*, Upper Cretaceous carnivores dinosaur (second communication). *American Museum of Natural History Bulletin* 22: 281–296.
- Paul, G. S. 1988. *Predatory Dinosaurs of the World: A Complete Illustrated Guide*. Simon & Schuster, New York.

- Quinn, J. S. 1990. Sexual size dimorphism and parental care patterns in a monomorphic and a dimorphic Larid. *Auk* 107: 260–274.
- Raath, M. A. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. P. 91–105 in Carpenter, K., and Currie, P. J. (eds.). *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge.
- Romer, A. S. 1966. *Vertebrate Paleontology*. University of Chicago Press, Chicago.
- Sandercock, B. K. 1998. Assortive mating and sexual size dimorphism in western and semipalmated sandpipers. *Auk* 115(3): 786–791.
- Sato, T., Cheng, Y., Wu, X., Zelenitsky, D. K., and Hsiao, Y. 2005. A pair of shelled eggs inside a female dinosaur. *Science* 308: 375.
- Schnell, G. D., Worthen, G. L., and Douglas, M. E. 1985. Morphometric assessment of sexual dimorphism in skeletal elements of California gulls. *Condor* 87: 484–493.
- Schweitzer, M. H., Wittmeyer, J. L., and Horner, J. R. 2005. Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. *Science* 308: 1456–1460.
- Schaadt, C. P., and Bird, D. M. 1993. Sex-specific growth in ospreys: the role of sexual size dimorphism. *Auk* 110: 900–910.
- Taylor, T. G. 1970. How an egg shell is made. *Scientific American* 222(3): 88–95.
- Welty, T. C., and Baptista, L. 1988. *The Life of Birds*. 4th ed. Saunders College Publications, Fort Worth, TX.
- Winker, K., Voelker, G. A., and Klicka, J. T. 1994. A morphometric examination of sexual dimorphism in the *Hylophilus*, *Xenops*, and an *Automolus* from southern Veracruz, Mexico. *Journal of Field Ornithology* 65(3): 307–323.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissue in fossils. P. 19–33 in Thomason, J. J. (ed.). *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge.