
Supplementary information

***Nanotyrannus* and *Tyrannosaurus* coexisted
at the close of the Cretaceous**

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Supplementary Information 1

for the manuscript: *Nanotyrannus* and *T. rex* coexisted at the close of the Cretaceous

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SI.1.1. Table of Specimens studied firsthand or via shared data (excluding literature-only references). We examined isolated tyrannosauroid teeth for this study but do not list those specimens individually here.

Specimen	Taxonomic Assignment	Mode of Study	Remarks
NCSM 40000	<i>Nanotyrannus lancensis</i>	Firsthand observation and new microCT data acquired by the authors	
CMNH 7541	<i>Nanotyrannus lancensis</i>	Firsthand observation and new microCT data acquired by the authors	Holotype specimen.
KUVP 156375	<i>Nanotyrannus lancensis</i>	Firsthand observation	
BMRP 2002.4.1	<i>Nanotyrannus lethaeus</i>	Firsthand observation and new microCT data acquired by the authors	Holotype specimen of new taxon. Currently under monographic description by Carr et al. (in prep).
BMRP 2006.4.4	<i>Nanotyrannus</i> sp.	Firsthand observation	We cautiously do not refer BMRP 2006.4.4 to a species given its incompleteness. Humerus appears closer to <i>N. lancensis</i> than <i>N. lethaeus</i> , but overlapping elements indicate this individual was larger than any individual of these taxa, and differences exist between manual unguals of NCSM 40000 and BMRP 2006.4.4, precluding confident referral. Additionally problematic is that the humerus of BMRP 2002.4.1 is heavily crushed, thus at present, we cannot be certain that perceived differences are not taphonomic.
AMNH FARB 2438	? <i>Dryptosaurus aquilunguis</i>	Firsthand observation	Metatarsal IV from the quarry that yielded the holotype of <i>Dryptosaurus aquilunguis</i> . Has been considered to pertain to the same individual ¹ , but it's morphology is not consistent with other tyrannosaurians and we are not certain that it is referable. We conservatively exclude it from our consideration of <i>Dryptosaurus</i> .
AMNH FARB 5027	<i>Tyrannosaurus rex</i>	Firsthand observation	
AMNH FARB 5050	Eutyranosauria indet.	Firsthand observation	Small, fragmentary dentary from Hell Creek Formation. Lacks autapomorphies permitting any confident referral.

AMNH FARB 5117	<i>Tyrannosaurus rex</i>	Firsthand observation	
AMNH FARB 5336	? <i>Gorgosaurus libratus</i>	Firsthand observation	
AMNH FARB 5346	<i>Daspletosaurus sp.</i>	Firsthand observation	
AMNH FARB 5438	<i>Daspletosaurus sp.</i>	Firsthand observation	
AMNH FARB 5428	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
AMNH FARB 5477	<i>Daspletosaurus horneri</i>	Firsthand observation	
AMNH FARB 5664	<i>Gorgosaurus sp.</i>	Firsthand observation	Former holotype of <i>Gorgosaurus sternbergi</i> . Under evaluation by Napoli et al.
AMNH FARB 6554	<i>Alectrosaurus olseni</i>	Firsthand observation	Holotype specimen.
AMNH FARB 11040	<i>Dryptosaurus aquilunguis</i>	Firsthand observation	Cast of ANSP 9995 (holotype)
BTs230910-LEZ1(A)	Eutyranosauria indet.	Firsthand observation	Uncataloged IP-MAS specimen under study by Zanno et al.
BTS23-SGL-70	Eutyranosauria indet.	Firsthand observation	Uncataloged IP-MAS specimen under study by Zanno et al.
BYU 8210-9396	<i>Teratophoneus curriei</i>	Firsthand observation	Holotype individual of <i>Teratophoneus curriei</i> , repositied under multiple specimen numbers.
BYU 8210-9397	<i>Teratophoneus curriei</i>	Firsthand observation	Holotype individual of <i>Teratophoneus curriei</i> , repositied under multiple specimen numbers.
BYU 8210-9402	<i>Teratophoneus curriei</i>	Firsthand observation	Holotype individual of <i>Teratophoneus curriei</i> , repositied under multiple specimen numbers.
BYU 826-9401	<i>Teratophoneus curriei</i>	Firsthand observation	Holotype individual of <i>Teratophoneus curriei</i> , repositied under multiple specimen numbers.
BYU 13719	<i>Teratophoneus curriei</i>	Firsthand observation	Holotype individual of <i>Teratophoneus curriei</i> , repositied under multiple specimen numbers.
BYU 9400	<i>Teratophoneus curriei</i>	Firsthand observation	Holotype individual of <i>Teratophoneus curriei</i> , repositied under multiple specimen numbers.
CM 1400	<i>Tyrannosaurus rex</i>	Firsthand observation	

CM 9380	<i>Tyrannosaurus rex</i>	Firsthand observation	Holotype specimen.
CM 9401	<i>Tyrannosaurus sp.</i>	Firsthand observation	Isolated lacrimal of uncertain stratigraphic provenance. Morphologically referable to <i>Tyrannosaurus</i> , potentially representing a Campanian occurrence of the genus.
CMN 2120	<i>Gorgosaurus libratus</i>	Firsthand observation	Holotype specimen.
CMN 5600	<i>Albertosaurus sarcophagus</i>	Firsthand observation	Holotype specimen.
CMN 5601	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
CMN 8506	<i>Daspletosaurus torosus</i>	Firsthand observation	Holotype specimen.
FMNH PR 2081	<i>Tyrannosaurus rex</i>	Firsthand observation	
FMNH PR 2211	<i>Gorgosaurus libratus</i>	Firsthand observation	
HRC 8438	Eutyranosauria indet.	Firsthand observation	Previously referred to <i>Nanotyrannus</i> . Currently being described by Napoli and Zanno.
KUVP 155809	<i>Tyrannosaurus rex</i>	Firsthand observation	
LACM 23845	<i>Tyrannosaurus rex</i>	Firsthand observation and new CT data acquired by the authors	Former holotype of “ <i>Dinotyrannus megagracilis</i> ”. Juvenile approximately the same size as holotype of <i>N. lethaeus</i> , but apomorphically identifiable as <i>T. rex</i> .
LACM 28471	Eutyranosauria indet.	Firsthand observation and new CT data acquired by the authors	
LACM 150167	<i>Tyrannosaurus rex</i>	Firsthand observation and new CT data acquired by the authors	
MNA V12400	? <i>Bistahieversor sealeyi</i>	Firsthand observation	Referred by Carr and Williamson ² to <i>Bistahieversor sealeyi</i> , as a putative juvenile individual. We regard this assignment as tentative.
MOR 002	Albertosaurinae indet.	Firsthand observation	Has been considered <i>T. rex</i> , but these isolated humeri bear greater resemblance to <i>Gorgosaurus</i> and <i>Albertosaurus</i> . Heavily worn, likely precluding any chance of confident referral.
MOR 008	<i>Tyrannosaurus rex</i>	Firsthand observation	
MOR 009	<i>Tyrannosaurus rex</i>	Firsthand observation	

MOR 395	<i>?Gorgosaurus libratus</i>	Firsthand observation	
MOR 553	<i>Daspletosaurus horneri</i>	Firsthand observation	
MOR 590	<i>Daspletosaurus horneri</i>	Firsthand observation	Holotype specimen.
MOR 657	<i>Daspletosaurus sp.</i>	Firsthand observation	Specimen includes two left maxillae, so certainly represents multiple individuals.
MOR 980	<i>Tyrannosaurus rex</i>	Firsthand observation	
MOR 1125	<i>Tyrannosaurus rex</i>	Firsthand observation	
MOR 1128	<i>Tyrannosaurus rex</i>	Firsthand observation	
MOR 1130	<i>Daspletosaurus ?horneri</i>	Firsthand observation	Paratype specimen of <i>Daspletosaurus horneri</i> . Firsthand study leads us to doubt the taxonomic assignment of this animal, which we will explore in a forthcoming contribution. Following our agreement with MOR curatorial staff, this project will begin following publication of a long-form description that is already underway by Carr et al. (in prep).
MPC-D 100/50	<i>Khankhuuluu mongoliensis</i>	Photographs provided by C. Tsogtbaatar and S. Finch.	
MPC-D 100/51	<i>Khankhuuluu mongoliensis</i>	Photographs provided by C. Tsogtbaatar.	
MPC-D 100/60	<i>Tarbosaurus bataar</i>	Firsthand observation	
MPC-D 100/65	<i>Tarbosaurus bataar</i>	Firsthand observation	
MPC-D 100/66	<i>Tarbosaurus bataar</i>	Firsthand observation	
MPC-D 100/1844	<i>Alioramus altai</i>	Firsthand observation and CT data provided by E. Gold.	
MPC-D 107/2	<i>Tarbosaurus bataar</i>	Firsthand observation	
MPC-D 107/3	<i>Tarbosaurus bataar</i>	Firsthand observation	
MPC-D 107/7	<i>Tarbosaurus bataar</i>	Firsthand observation	
MSM P4754	<i>Suskityrannus hazelae</i>	Studied from CT data and casts provided by S Nesbitt. Histology studied firsthand.	Holotype specimen.
NHMUK PV R 4860	<i>Proceratosaurus bradleyi</i>	Studied from CT data provided by O Rauhut.	Holotype specimen.

NMMNH P27469	<i>Bistahieversor sealeyi</i>	Firsthand observation	Holotype specimen.
ROM 807	<i>Albertosaurus sarcophagus</i>	Studied 3D photogrammetric models.	
TMP 1967.15.17	<i>Gorgosaurus sp.</i>	Firsthand observation	
TMP 1981.6.1	<i>Tyrannosaurus rex</i>	Firsthand observation	
TMP 1981.10.001	<i>Albertosaurus sp. nov.</i>	Firsthand observation	Under description by Powers et al.
TMP 1982.16.374	Albertosaurinae indet.	Firsthand observation	
TMP 1985.11.3	Albertosaurinae gen. et sp. nov.	Firsthand observation	Under description by Powers et al.
TMP 1985.98.001	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 1986.64.001	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 1991.01.001	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 1991.36.500	<i>Gorgosaurus libratus</i>	Firsthand observation	
TMP 1991.163.1	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
TMP 1992.36.81	Albertosaurinae indet.	Firsthand observation	
TMP 1993.12.27	Eutyranosauria indet.	Firsthand observation	Isolated quadratojugal with quadratojugal foramen.
TMP 1993.36.539	<i>Gorgosaurus libratus</i>	Firsthand observation	
TMP 1994.12.155	<i>Gorgosaurus sp.</i>	Firsthand observation	
TMP 1994.12.602	Albertosaurinae gen. et sp. nov.	Firsthand observation	Under description by Powers et al.
TMP 1994.143.1	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
TMP 1995.25.83	<i>Gorgosaurus libratus</i>	Firsthand observation	
TMP 1995.5.1	Albertosaurinae gen. et sp. nov.	Firsthand observation	Under description by Powers et al.
TMP 1996.12.161	<i>Gorgosaurus sp.</i>	Firsthand observation	
TMP 1996.12.404	? <i>Daspletosaurus sp.</i>	Firsthand observation	
TMP 1997.12.17	Eutyranosauria indet.	Firsthand observation	
TMP 1997.12.223	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
TMP 1997.36.0428	Tyrannosauridae indet.	Firsthand observation	

TMP 1999.33.1	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
TMP 1999.050.0021	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 1999.050.15	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 1999.50.240	Albertosaurinae indet.	Firsthand observation	
TMP 1999.50.33	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 2001.36.1	<i>Daspletosaurus torosus</i>	Firsthand observation	We consider this specimen to represent <i>Daspletosaurus torosus</i> , but note that some authors consider this to be <i>D. wilsoni</i> ³ and that the <i>Daspletosaurus</i> hypodigm is currently under reevaluation by Coppock et al.
TMP 2001.45.53	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 2003.045.0073	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 2004.56.57	<i>Albertosaurus sarcophagus</i>	Firsthand observation	
TMP 2009.12.14	<i>Gorgosaurus libratus</i>	Firsthand observation	
TMP 2013.18.11	<i>Daspletosaurus sp.</i>	Firsthand observation	
TMP 2016.14.1	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
SDSM 12047	<i>Tyrannosaurus rex</i>	Firsthand observation	
TCMI 2001.89.1	Albertosaurinae gen. et sp. nov.	Firsthand observation	Under description by Napoli et al.
TCMI 2001.90.1	<i>Tyrannosaurus rex</i>	Firsthand observation	
TCMI 2003.66.1	<i>Tyrannosaurus rex</i>	Firsthand observation	
UALVP 10	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
UALVP 49500	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
UALVP 52981	Albertosaurinae gen. et sp. nov.	Firsthand observation	Under description by Powers et al.
UALVP 56630	<i>Gorgosaurus libratus</i>	Firsthand observation	
UALVP 57870	Tyrannosauridae indet.	Firsthand observation	
UALVP 59184	Tyrannosauridae indet.	Firsthand observation	
UALVP 60836	Tyrannosauridae indet.	Firsthand observation	

UALVP 61560	<i>Gorgosaurus sp.</i>	Firsthand observation	Under evaluation by Napoli et al.
UALVP 61993	<i>Gorgosaurus sp.</i>	Firsthand observation	
UMNH VP 11000	<i>Tyrannosaurus rex</i>	Firsthand observation	
UMNH VP 16690	<i>?Teratophoneus curriei</i>	Firsthand observation	Our phylogenetic results yield equivocal support for the taxonomic affinities of this specimen, and re-evaluation of it represents a goal of future work.
UMNH VP 16691	<i>Teratophoneus curriei</i>	Firsthand observation	
UMNH VP 20200	<i>Lythronax argestes</i>	Firsthand observation	Holotype specimen.
USNM PAL 12814	<i>Gorgosaurus sp.</i>	Photographs provided by MT Carrano.	Under evaluation by Napoli et al.
USNM PAL 555000	<i>Tyrannosaurus rex</i>	Studied from 3D surface scans made prior to mounting for display.	
UWBM 99000	<i>Tyrannosaurus rex</i>	Firsthand observation, supplemented by 3D surface scans made prior to exhibition.	
UWBM 84009	Eutyranosauria indet.	Firsthand observation	

SI.1.2. Table of. Specimens Coded in Phylogenetic Matrix.

Operational Taxonomic Unit	Specimen(s)	Source of Coding	Notes
<i>Majungasaurus crenatissimus</i>	FMNH PR 2100, FMNH PR 2008, FMNH PR 2278, MNHN.MAJ 1, UA 8716, UA 8717, UA 8678, FMNH PR 2423, FMNH PR 2424, UA 9077, UA Bv-532, FMNH PR 2426, FMNH PR 2427, UA 9038, FMNH PR 2429, UA 9042, UA 9039, FMNH PR 2430, FMNH PR 2431, FMNH PR 2432, FMNH PR 2434, FMNH PR 2836, UA 9860	Study of publicly available microCT datasets; Sampson and Witmer ⁴ , Smith ⁵ , O'Connor ⁶ , Carrano ⁷ , Burch and Carrano ⁸ , Burch ⁹	
<i>Monolophosaurus jiangi</i>	IVPP V84019	Zhao and Currie ¹⁰ , Brusatte et al. ¹¹	
<i>Dubreuillosaurus valesdunensis</i>	MNHN 1998-13	Allain ^{12,13}	
<i>Sinraptor dongi</i>	IVPP V10600	Currie and Zhao ¹⁴	
<i>Allosaurus fragilis</i>	USNM 4734 (primary reference specimen), supplemented by description and figures derived from numerous Cleveland-Lloyd	Gilmore ¹⁶ , Madsen ¹⁵ , Loewen and Chure ¹⁷	

	Dinosaur Quarry specimens, described by Madsen ¹⁵ .		
<i>Allosaurus jimadseni</i>	DINO 11541, MOR 693	Firsthand observation; Loewen and Chure ¹⁷	
<i>Acrocanthosaurus atokensis</i>	NCSM 14345	Firsthand observation; Currie and Carpenter ¹⁸ , Eddy and Clarke ¹⁹	
<i>Zuolong salleei</i>	IVPP V15912	Choiniere et al. ²⁰ , Choiniere ²¹	
<i>Compsognathus longipes</i>	B.S.P. A.S. I 563, MNHN CNJ 79	Ostrom ²² , Gishlick and Gauthier ²³ , Peyer ²⁴	
<i>Guanlong wucaii</i>	IVPP V14531, IVPP V14532	Photographs shared by J.M. Clark; Xu et al. ²⁵ , Choiniere ²¹	
<i>Kileskus aristotocus</i>	ZIN PH 5/117, ZIN PH 6/117, ZIN PH 7/117, IZN PH 8/117, ZIN PH 9/117, ZIN PH 10/117, ZIN PH 11/117, IZN PH 12/117, ZIN PH 13/117, ZIN PH 92/117, ZIN PH 91/117, ZIN PH 100/117, ZIN PH 83/117, ZIN PH 84/117	Averianov et al. ^{26,27}	
<i>Proceratosaurus bradleyi</i>	NHM R 4860	Study of microCT dataset; Rahut et al. ²⁸	
<i>Sinotyrannus kazuoensis</i>	KZV-001	Ji et al. ²⁹	
<i>Yutyrannus huali</i>	ZCDM V5000, ZCDM V5001, ELDM V1001	Xu et al. ³⁰	
<i>Dilong paradoxus</i>	IVPP V14243, IVPP V11579	Photographs shared by P.J. Makovicky; Xu et al. ³¹ , Porfiri et al. ³² , Kundrát et al. ³³	
<i>Juratyran langhami</i>	OUMNH J.3311	Benson ³⁴ , Brusatte and Benson ³⁵	
<i>Stokesosaurus clevelandi</i>	UMNH VP 7473	Brusatte and Benson ³⁵	
<i>Eotyrannus lengi</i>	IWCMS 1997.550	Naish and Cau ³⁶	
<i>Suskityrannus hazelae</i>	MSM P4754, MS P6178	Firsthand study of casts, study of microCT dataset; Nesbitt et al. ³⁷	
<i>Xiongguanlong baimoensis</i>	FRDC-GS JB16-2-1	Photographs shared by PJ Makovicky; Li et al. ³⁸	
<i>Timurlengia euotica</i>	ZIN PH 1146/16, ZIN PH 2330/16, ZIN PH 676/16, ZIN PH 2296/16, ZIN PH 15/16, ZIN PH 1239/16, ZIN PH 2350/16, ZIN PH 1035/16, ZIN PH 1034/16, ZIN PH 1033/16, ZIN PH 1039/16, ZIN PH 693/16, ZIN PH 756/16, ZIN PH 733/16, ZIN	Averianov and Sues ³⁹ , Brusatte et al. ⁴⁰	We note that materials currently referred to this taxon may represent several taxa, given that they were not found in association; we tentatively retain it as a single OTU to capture the greatest character information for “mid-grade” tyrannosauroids

	PH 737/16, ZIN PH 734/16, ZIN PH 671/16, USNM 538131, CCMGE 432/12457, ZIN PH 120/16, ZIN PH 507/16, ZIN PH 619/16, USNM 538181, ZIN PH 124/16, USNM 538167		from the mid-Cretaceous of Asia without creating multiple data-deficient OTUs, following Brusatte et al. ⁴⁰
<i>Alectrosaurus olseni</i>	AMNH FARB 6554	Firsthand observation; Carr ⁴¹	
<i>Khankhuuluu mongoliensis</i>	MPC-D 100/50; MPC-D 100/51	Voris et al. ⁴²	
<i>Moros intrepidus</i>	NCSM 33392	Firsthand observation; Zanno et al. ⁴³	
<i>Jinbeisaurus wangi</i>	SMG V0003	Wu et al. ⁴⁴	
<i>Nanotyrannus lancensis</i>	CMNH 7541, NCSM 40000, KUVLP 156375	Firsthand observation and study of novel microCT datasets generated for CMNH 7451 and NCSM 40000; Witmer and Ridgely ^{45,46}	Each specimen coded as a separate OTU to facilitate a phylogenetic test of species monophyly, and to accommodate the possibility that some specimens were juvenile <i>Tyrannosaurus rex</i> .
<i>Nanotyrannus lethaeus</i>	BMRP 2002.4.1	Firsthand observation	
<i>Nanotyrannus sp.</i>	BMRP 2006.4.4	Firsthand observation	Due to incompleteness of this specimen, and possible deformation to overlapping parts of BMRP 2002.4.1, we do not feel comfortable referring this specimen to the species level.
<i>Dryptosaurus aquilunguis</i>	ANSP 9995, AMNH FARB 11040, NHM OR50100	Studied from microCT scans of casts held at NHMUK (which preserve detail now lost due to pyrite degradation of the holotype specimen ¹), and firsthand observation of AMNH FARB 11040; Brusatte et al. ¹	
<i>Appalachiosaurus montgomeriensis</i>	RMM 6670	Carr et al. ⁴⁷	
<i>Thanatotheristes degrootorum</i>	TMP 2010.5.1	Firsthand observation; Voris et al. ⁴⁸	
<i>Daspletosaurus torosus</i>	CMN 8506, TMP 2001.36.1	Firsthand observation; Coppock et al. ⁴⁹ , Paulina Carabajal ⁵⁰ , Russell ⁵¹	
<i>Daspletosaurus wilsoni</i>	BDM 107	Warshaw and Fowler ³	
<i>Daspletosaurus horneri</i>	MOR 590, MOR 1130, MOR 553, AMNH FARB 5477	Firsthand observation; Carr et al. ⁵²	
UALVP 52981	UALVP 52981	Firsthand observation	
TCMI 2001.81.1	TCMI 2001.81.1	Firsthand observation	

<i>Gorgosaurus sp. nov.</i>	UALVP 10, ROM 1247, TMP 1999.33.1, TMP 2016.14.1, UALVP 49500	Firsthand observation; Currie ⁵³ , Voris et al. ^{54,55}	Following Napoli et al. ⁵⁶ , we recognize two distinct morphotypes within the hypodigm traditionally encompassed by <i>Gorgosaurus libratus</i> , which are largely separated stratigraphically. We are currently evaluating these animals to determine whether <i>Gorgosaurus libratus</i> should be split, and which specimens represent each potential subsidiary taxon. At present, we include these specimens as a separate OTU to be conservative in our concept of <i>G. libratus</i> .
<i>Gorgosaurus libratus</i>	CMN 2120, TMP 1991.35.500, TMP 2009.12.14	Firsthand observation; Currie ⁵³ , Voris et al. ^{54,55,57}	
<i>Albertosaurus sarcophagus</i>	CMN 5600, CMN 5601, ROM 807, TMP 1986.64.1	Firsthand observation; Carr ⁵⁸ , Currie ^{53,59}	
<i>Albertosaurus sp. nov.</i>	TMP 1981.10.1	Firsthand observation; Currie ⁵³	New species under description by Powers et al.
<i>Qianzhousaurus sinensis</i>	GM F10004	Photographs shared by S.L. Brusatte; Lü et al. ⁶⁰ , Foster et al. ⁶¹	
<i>Alioramus altai</i>	MPC-D 100/1844	Study of microCT data; Bever et al. ⁶² , Brusatte et al. ^{63,64} , Gold and Norell ⁶⁵	
<i>Bistahieversor sealeyi</i>	NMMNH P-27469	Firsthand observation; Carr and Williamson ²	
<i>Dynamoterror dynastes</i>	UMNH VP 28348	McDonald et al. ⁶⁶	Excluded from analyses <i>a priori</i> due to wildcard behavior.
<i>Teratophoneus curriei</i>	BYU 8120/9396, BYU 8120/9397, BYU 826/9402, BYU 9398, BYU 13719	Firsthand observation; Carr et al. ⁶⁷	
UMNH VP 16690	UMNH VP 16690	Firsthand observation; Loewen et al. ⁶⁸	
<i>Lythronax argestes</i>	UMNH VP 20200	Firsthand observation; Loewen et al. ⁶⁸	
<i>Asiatyrannus xui</i>	ZMNH M30360	Zheng et al. ⁶⁹	
<i>Nanuqsaurus hoglundi</i>	DMNH 21461	Fiorillo and Tykoski ⁷⁰	Excluded from analyses <i>a priori</i> due to wildcard behavior.
<i>Zhuchengtyrannus magnus</i>	ZCDM V0031	Hone et al. ⁷¹	
<i>Tarbosaurus bataar</i>	MPC-D 100/60, ZPaL MgD-I/4	Firsthand observation; Hurum and Sabath ⁷² , Tsuihiji et al. ⁷³	

<i>Tyrannosaurus mcraeensis</i>	NMMNH P-3698	Dalman et al. ⁷⁴	
<i>Tyrannosaurus rex</i>	CM 9380, AMNH FARB 5027, AMNH FARB 5117, FMNH PR 2081, LACM 23845, LACM 150167, MOR 980, MOR 1125, USNM PAL 555000, UWBM 99000	Firsthand observation; Osborn ^{75,76} , Molnar ⁷⁷ , Brochu ⁷⁸ , Witmer and Ridgely ⁴⁵	

SI.1.3. Differential Diagnosis of *Nanotyrannus*.

Nanotyrannus can be distinguished from *Tyrannosaurus* by an abundance of traits, including smaller maximum body size, absolutely larger forelimb elements, higher maxillary and dentary tooth count; apically blunted premaxillary crowns lacking serrations; presence of lacrimal cornual process; absence of postorbital cornual process; presence of quadratojugal pneumatic recess; abducens nerve that nearly intersects the pituitary fossa (presence of a sinus cavernosus); presence of an ascending diverticulum of the rostral tympanic recess; strong condylotuberal crests; extension of the subsellar sinus into the cultriform process; strap-like proatlantal arches; fewer caudal vertebrae (n=35); and a larger humerus and hand relative to femoral length. Characters shared between *Nanotyrannus* and *Tyrannosaurus* are, contra Carr⁷⁹ and following authors, widely distributed among derived tyrannosauroids. Therefore, they do not provide positive evidence of species synonymy or a sister-taxon relationship as was concluded by Currie⁵³. Currie⁵³ reviewed these characters in detail, and we refer the reader to his discussion. We add to his discussion, however, that the “appressed” nasal processes of the premaxillae of *Tyrannosaurus* are not autapomorphic; contra Carr⁷⁹ and Carr and Williamson⁸⁰. Recently, Voris et al.⁴² suggested that *Nanotyrannus* and *Tyrannosaurus* are united to the exclusion of all other tyrannosauroids by the absence of a prefrontonasal process of the frontal. However, absence of this feature in *Alioramus altai* (MPC-D 100/1844) means that this is not an exclusive synapomorphy; furthermore, we have identified it in at least one specimen of *Tyrannosaurus* (AMNH FARB 5117), and the feature actually seems to be *present* in CMNH 7541, though damage to the skull roof makes this somewhat equivocal. The condition in NCSM 40000 cannot currently be assessed. Regardless of the condition in CMNH 7541, this character does not provide evidence of synonymy with *Tyrannosaurus*.

SI.1.4. Extended description of NCSM 40000.

NCSM 40000 deserves, and will soon receive, a monographic osteological description. This endeavor is beyond the scope of the current manuscript. Instead, we provide an expanded description herein, capturing essential morphological details of the new specimen specifically and comparative anatomy of *N. lancensis* in general. We also focus on distinguishing *Nanotyrannus* (as typified by NCSM 40000) from other eutyrranosaurians, specifically *Tyrannosaurus*.

SI.1.4.i. General comments.

NCSM 40000 is a complete skeleton. Portions of the postcranial skeleton are visible in ventral, cranial, and right lateral views. The skeleton is fully articulated, with minor separations between vertebrae of the

cranial and mid-caudal series. Moderate predepositional damage on the skeleton is concentrated on the skull and pectoral girdle. The ventral aspects of presacral vertebrae 10–12, the right pelvic girdle and hind limb, including the acetabulum, ischiadic peduncle, proximal ischium, femoral midshaft, distal tibia, and proximal metatarsus, were fractured by heavy equipment during excavation by the discovery team and have been maximally reconstructed by the NCMS preparation staff. The specimen was separated into multiple jackets when collected. The left pes and most of the tail were jacketed separately from the remainder of the skeleton, which was collected in a single jacket. The tail itself was collected in five portions. The first and second caudals remain in the main body block. Caudal vertebrae 3–21 are in a separate jacket. Caudal vertebrae 22–26 were preserved underneath (stratigraphic bottom) of the ceratopsian pes. Caudal vertebrae 27–33 were collected in a single jacket. The distalmost two caudal vertebrae were collected directly from the quarry. Photographic documentation of the specimen in situ was used to determine that no caudals are missing from the sequence, and the 35 caudal count is complete.

The entire skeleton of NCSM 40000 was surface scanned with lidar before NCSM acquisition. Once accessioned at NCSM, the skull, right forelimb, portions of the left forelimb, and the distalmost two caudal vertebrae of NCSM 40000 were prepared separately, 3D surface scanned with structured light scanning, microCT scanned, and scanned with high-energy, monochromatic x-ray CT (synchrotron radiation).

SI.1.4.ii. Skull.

The **premaxillae** bear four straight, chisel-shaped, unserrated teeth (Extended Data 3), in contrast to *Tyrannosaurus* and all ontogenetic stages of *Tarbosaurus*. The presence of serrated premaxillary teeth has been considered an ontogenetically variable trait in tyrannosaurids, but distribution does not currently support this hypothesis. Young specimens of *Gorgosaurus libratus* (e.g., FMNH PR 2211) and *Tarbosaurus bataar* (Tsuihiji et al. 2011) have serrated premaxillary teeth, as does the juvenile holotype of *Raptorex kriegsteini*⁸¹. In contrast, unserrated premaxillary teeth are known from mid-Cretaceous deposits and attributed to several non-eutyrannosaurian tyrannosauroids such as *Moros intrepidus*^{43,82}, *Xiongguanlong baimoensis*³⁸, and *Timurlengia euotica*³⁹, some of which are documented histologically to represent animals of significant age, approaching somatic maturity (e.g., *Moros*⁴³). Premaxillary crowns also bear a pronounced median vertical ridge, like tyrannosauroid teeth from mid-Cretaceous formations^{43,37,43,82}, but unlike *Tyrannosaurus*.

Tyrannosauroids generally have a well-developed subnarial foramen near the ventral extremity of the premaxilla-maxilla contact; this feature is absent in NCSM 40000 and the holotype specimens of *N. lancensis* and *N. lethaeus* (Figs. 1–2; Extended Data 1–3). The absence of an externally visible subnarial foramen is considered here a putative autapomorphy of the genus *Nanotyrannus*, as it is unknown among other tyrannosauroids. The anatomically lateral surface of the subnarial process of the premaxilla faces dorsally in NCSM 40000, as in most tyrannosaurids except *Tyrannosaurus rex* and *Daspletosaurus torosus*, in which it faces slightly dorsomedially, and *N. lethaeus* in which it faces dorsolaterally. This trait appears to be allometric, as it is also seen in the large-bodied basal tyrannosauroid *Yutyrannus huali*³⁰ and is not seen in the smaller holotype of *N. lancensis*.

The **maxilla** is long and low. The subcutaneous surface of the maxilla lacks the deep fossae exhibited by *Albertosaurus*, *Tyrannosaurus*, *Tarbosaurus*, and *Zhuchengtyrannus*. The maxillary flange that characterizes eutyranosaurians is represented only by a subtle convexity, rather than a pronounced convex lamina that invades the nasal in lateral view (Figs. 1-2). Alioramini and *Daspletosaurus torosus* also lack a maxillary flange. A well-developed maxillary flange is present in small juveniles of *Gorgosaurus libratus* and retained in large-bodied specimens, suggesting the trait is ontogenetically invariant. A maxillary flange is present, yet weak in *N. lethaeus*. The promaxillary fenestra is exposed in lateral view, unlike *Tyrannosaurus*, and is bounded ventrally by a ridge, as opposed to a step as in *N. lethaeus* and most tyrannosaurids. The pila interfenestralis is vertical, rather than rostradorsally inclined as in some albertosaurines, *Lythronax*, *Tarbosaurus*, and *Tyrannosaurus*. The maxillary fenestra is small compared to that of tyrannosaurids. As in many tyrannosauroids, yet in contrast to *Daspletosaurus* and *Alioramus*, the maxillary fenestra takes the form of a rostradorsally oriented trapezoid, but in contrast to most other tyrannosauroids the usual long axis (rostradorsal-caudoventral) is about as long as the short (rostrventral-caudodorsal) axis. Only *Bistahieversor* has a similarly proportioned maxillary fenestra to *N. lancensis*. *N. lethaeus* and tyrannosaurids generally have a rostrocaudally elongate maxillary fenestra. The maxillary fenestra does elongate with positive allometry in tyrannosaurid ontogeny, but even the smallest juvenile *Gorgosaurus* spp. specimens have maxillary fenestrae that are proportionally similar to adult conspecifics. The antorbital fossa reaches the nasal suture, a tyrannosauroid symplesiomorphy that is secondarily evolved in *Tarbosaurus* and *Tyrannosaurus*. There are 16 and 17 **teeth** in the left and right maxillae, respectively (asymmetrical count), a number only seen otherwise in *Daspletosaurus* and *Alioramus*⁶⁴. This tooth count is greater than the 15 preserved in the *N. lancensis* holotype specimen (CMNH 7541), yet comparable to the 16 in *N. lethaeus*. This count is far from the 11–12 maxillary teeth in all known *Tyrannosaurus rex* individuals, and greater than the maxillary dental count in tyrannosaurids except *Alioramus* and *Daspletosaurus*, which have greater or comparable tooth counts. The maxilla attributed to *Timurlengia euotica* also has a similarly high tooth count³⁹. Whereas maxillary tooth counts are variable in many reptiles, with the exception of distantly-related noasaurid ceratosaurs^{83,84}, ontogenetic loss of maxillary tooth positions is not documented in crocodylians or other theropods^{85,86}; prior assertions of this pattern in crocodylians⁷⁹ were made in error⁸⁶. As in many tyrannosauroids but in contrast to *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*, the first maxillary tooth is small and “premaxillariform”. In general form, maxillary teeth are ziphodont, unlike the incrassate teeth of most tyrannosaurids, especially *Tyrannosaurus*.

The **nasal** is parallel-sided and contralateral nasals are fused. The caudolateral processes of the nasal are large and well developed. The apomorphic caudomedial processes that characterize tyrannosaurids are present only as nascent tabs. These processes are elongate in most tyrannosaurids and in *Albertosaurus* and *Daspletosaurus* are longer than the caudolateral processes. Prior work has claimed that “tightly appressed” nasal processes of the premaxillae is an exclusive synapomorphy of *Nanotyrannus* and *Tyrannosaurus*^{79,80}. However, divergent nasal processes in albertosaurines arise from the apomorphic origin of a median interpremaxillary process of the nasal that is absent in all other eutyranosaurians. Thus, this similarity between is, instead, a symplesiomorphy. The contralateral nasals are fused, and slightly ornamented but not heavily rugose, and superficially textured by midline tubercles extending from a subtle midline ridge. *Gorgosaurus* and *Albertosaurus* also show a tendency for rugosities to develop along the midline, but the rugosities of NCSM 40000 do not form a nasal “blade” as in *Gorgosaurus* and

*Albertosaurus*⁵⁴, nor do they form prominent midline conical hornlets along the dorsal midline as in alioramins^{60,61,63,64}. In other tyrannosaurids, the nasal rugosities do not develop in a clear pattern.

The **lacrimal** has a rostradorsal process that interlocks with the nasal, as in most eutyranosaurians, but in contrast to *Daspletosaurus*, *Alioramus*, and *Tarbosaurus*. The lacrimal bears a cornual process, which is developed as a convex ridge without a discrete apex, centered rostral to the preorbital bar. It lacks a dorsolateral shelf and is not inflated by the large lacrimal pneumatic recess. *Tyrannosaurus* entirely lacks a lacrimal cornual process. The **jugal** exhibits a shallow, unexpanded maxillary ramus, unlike tyrannosaurids, and a horizontal pneumatic recess ostium, as in *Bistahieversor* and *Alioramus* but distinct from *Tyrannosaurus* and other tyrannosaurids. The pneumatic recess is partially obscured in lateral view by the subcutaneous lamina of the jugal. The jugal of NCSM 40000 also lacks a lateral fossa on the postorbital process, which is present in most *Tyrannosaurus*, *Tarbosaurus*, *Daspletosaurus*, and *Bistahieversor*. The orbital margin of the jugal is relatively wide and weakly concave, in contrast to the narrow and strongly concave orbital margin of the jugal (U-shaped) of *Tyrannosaurus* and other large tyrannosaurids. The **postorbital** is textured along the orbital margin but lacks any indication of a cornual process, which develops early in tyrannosaurid ontogeny and present and taxonomically informative even in very young tyrannosaurid individuals^{54,55}. Instead, it has rugose striations along the orbital margin. The squamosal ramus of the postorbital lacks the notch present in albertosaurines, but like albertosaurines (*Gorgosaurus* and *Albertosaurus*) and in contrast to *Daspletosaurus* the dorsal squamosal articular facet extends rostral to the infratemporal fossa. *N. lethaeus* has a distinct prong on the postorbital that braced the medial aspect of the squamosal, absent in *N. lancensis*. The ventral ramus of the postorbital lacks the suborbital flange present in tyrannosaurids. The orbital surface of the postorbital forms a distinct fossa, rather than the flat to convex surface of *Tyrannosaurus*. The **frontal** bears a short prefrontolacrimal process, unlike albertosaurines, and a flat “forehead” region, unlike *Tyrannosaurus* and many tyrannosaurines. It is typical of derived tyrannosauroids in having medially extensive supratemporal fossae, and it is overlain by the **parietal**, which forms a thin, blade-like frontoparietal peak, rather than a broad tuber as in *Tyrannosaurus*, most tyrannosaurines, and some albertosaurines. The dorsal midline of the parietal bears a thin sagittal crest, and the parietal is transversely expanded caudally into a tall nuchal crest lacking the parasagittal fossae present on *T. rex* (AMNH FARB 5117; LACM 150167; UWBM 99000) and *Albertosaurus*.

The **squamosal** and **quadratojugal** form a long flange that constricts the infratemporal fenestra to about half its rostrocaudal length, as in *Xiongguanlong*, but in contrast to earlier-diverging tyrannosauroids (which have an unconstricted fenestra) or tyrannosaurids (in which the fenestra is nearly divided). The quadratojugal process of the squamosal is straight, as in *Asiatyrannus*, yet unlike most tyrannosaurids. The quadratojugal lacks the *Tyrannosaurus* autapomorphy of a notch at its rostradorsal extent. The quadratojugal has a pneumatic recess invading its lateral surface (Extended Data 1). Outside of the genus *Nanotyrannus*, pneumatic invasion of the quadratojugal is currently evident in MOR 1130 (the paratype of *Daspletosaurus horneri*) and one isolated quadratojugal from the Dinosaur Park Formation (TMP 1993.12.27), typically considered *Gorgosaurus libratus* but lacking character data facilitating a species-level referral. Several *Gorgosaurus* specimens also have a foramen in this region, but they are smaller and are not obviously pneumatic in origin. This recess is absent in all examined specimens of *Tyrannosaurus rex*, and there is currently no evidence to suggest its presence is ontogenetically variable. Just lateral to the enlarged quadrate foramen, the quadratojugal forms a distinct fossa absent in

Tyrannosaurus. This fossa is more strongly developed in *N. lethaeus*, where it is bounded laterally by a thin blade-like ridge (as in *Alioramus*), unlike the rounded pillar of *N. lancensis*. The **quadrate** condyles are approximately in line with the occipital condyle, in contrast to the condition in most tyrannosaurids, but similar to *Daspletosaurus*.

The **vomer** has a deep ventral keel (which is currently considered an autapomorphy of *Daspletosaurus* spp.⁵² but appears to have a wider distribution) and is rostrally lanceolate rather than diamond-shaped as in *Daspletosaurus*, *Tyrannosaurus rex*, and *Tarbosaurus bataar*. The **palatine** has a tall vomeropterygoid neck, which expands dorsally into a shallow but elongate vomeropterygoid process unlike the tall process of *Tyrannosaurus* and most albertosaurines, and both rostral and caudal pneumatic recesses. The caudal (=primary) palatine recess is small, and the rostral recess extends rostrally into a diminutive pneumatic chamber, which is otherwise unknown in tyrannosaurids and here considered a putative autapomorphy of *Nanotyrannus lancensis*. *N. lethaeus* bears a shallow fossa in this region as opposed to a deep pocket. The jugal process is not inflated, unlike tyrannosaurids. The caudal extent of the joint surface for the maxilla of NCSM 40000 extends onto the ventral surface of the palatine, as in *Nanotyrannus lethaeus*, *Daspletosaurus*, and *Alioramus*, but in contrast to *Gorgosaurus*, *Albertosaurus*, and *Tyrannosaurus rex*. *Nanotyrannus lethaeus* bears an articular surface for the jugal with a lateral eminence at its rostroventral corner that forms a “jugal brace,” distinct from the “maxillary brace” described for *Alioramus*⁶⁴. The **ectopterygoid** is not inflated and does not bear a ridge caudal to the ostium of its pneumatic recess, unlike *Daspletosaurus*, *Qianzhousaurus*, and *Tyrannosaurus rex*.

The **braincase** of *N. lancensis* is only preserved in articulated specimens, where it is difficult to visualize in gross inspection; it is unknown for *N. lethaeus*. On NCSM 40000, it is largely unexposed. The **supraoccipital** exhibits two prongs bordering a midline groove. Diagnostic characters of the braincase of *N. lancensis* that can be verified (Extended Data 3) are the absence of ventral flanges of the paroccipital processes (visible on NCSM 40000), a shallow paracondylar pocket, and a widely exposed otic recess—all present in tyrannosaurids^{45,46}—and a deep subcondylar recess of the basioccipital, distinct from the apomorphically shallow condition of *Tyrannosaurus*. The basipterygoid processes are slightly rostral to the basal tubera, as in most tyrannosaurids, yet unlike *Tyrannosaurus*, and the cultriform process is rostrocaudally long with an extensive subsellar recess⁴⁶, unlike *Tyrannosaurus*. CMNH 7541 and *Alioramus* plesiomorphically share the presence of a sinus cavernosus, in which the abducens nerve passes through the pituitary fossa, but in all other tyrannosaurids, the abducens passes lateral to the pituitary fossa⁶².

NCSM 40000 has a rounded rostral margin of the **dentary**, unlike *N. lethaeus*, *Tyrannosaurus*, *Thanatotheristes*, and *Daspletosaurus*. The dentary lacks a chin and in *N. lethaeus* the symphysis is ridged unlike albertosaurines, *Daspletosaurus*, and *Tyrannosaurus*. The joint surface for the **splenial** on *N. lethaeus* is smooth and the Meckelian fossa is dorsoventrally taller than the medial surface ventral to it, unlike *Tyrannosaurus*. *Nanotyrannus* has 16–18 **dentary teeth**, similar to or lower than the counts in *Daspletosaurus* and *Alioramus*, yet greater than most tyrannosaurids, and much greater than the 12–13 of *Tyrannosaurus*. NCSM 40000 bears an asymmetrical tooth count in the dentary as it does in the maxilla: 17 dentary teeth in the left mandible and 18 in the right mandible. In NCSM 40000, the first two dentary alveoli are distinctly smaller than the rest, but in *T. rex* and *N. lethaeus* only the first alveolus is small (Extended Data 1). This character is highly variable among tyrannosaurids, but perinatal remains indicate that the character is established prenatally⁸⁷ and thus likely to be taxonomically informative. The rostral

mylohyoid foramen of the splenial in NCSM 40000 is over 3x longer than tall, as in *Alioramus* and *D. wilsoni*, yet unlike other tyrannosaurids. The surangular of NCSM 40000 has a prominent, laterally directed shelf that abuts (but does not overhang) an enlarged surangular foramen. The surangular shelf is oriented rostrocaudally, not rostrorodorsally as in *Bistahieversor* and UMNH VP 16690.

SI.1.4.iii. Axial column.

NCSM 40000 preserves an articulated, presumably complete **axial column**; however, portions are currently obscured by soft tissue preservation in the surrounding sediment, including the dorsal and lateral aspects of most cervical vertebrae and the dorsal series. Twenty presacral (**p**) and thirty-five caudal (**c**) vertebrae are exposed, including portions of all cervicals.

A pair of chevron-shaped, unfused proatlantal arches is preserved. Individual proatlantal arches are simple and straplike, unlike the triradiate arches of *T. rex* (FMNH PR 2081⁷⁸) and confirm that the latter are proatlantal arches. A complete **atlas/axis** (p1/p2) complex is preserved for NCSM 40000 and was prepared separately. The atlantal intercentrum and neural arches are unfused. The atlantal pleurocentrum is fused to the axial intercentrum. Likewise, the axial intercentrum and pleurocentrum are fused to each other and the axial neural arch. The intercentrum/pleurocentrum suture on the right side remains open (visible); however, the neurocentral suture appears to have begun closing at its cranialmost extent. The axis is highly pneumatic with diverticular invasion in four discrete regions. Paired, triple, or single external pleurocoels pierce the lateral centrum, the base of the tabular neural spine in ventral view, the neural arch just caudal to the prezygopophyses, and the ventral margin of the intrapostzygapophyseal lamina. Three individual pleurocoels puncture the right lateral surface of the axial centrum, but only one or two puncture the left side (siderite nodules partially obscure this area). They are housed in a gently depressed region, as in *T. rex*⁷⁸, and in contrast to the confluent condition of *A. altai*⁶⁴. In contrast, it is the left side of the neural arch that exhibits enhanced external evidence of pneumaticity. Although paired pleurocoels pierce the base of the neural spine just caudal to the prezygopophyses, the left pleurocoel is larger. Moreover, a pleurocoel is only present on the left side of the ventral intrapostzygapophyseal lamina and caudal aspect of the neural spine just dorsal to the site of the interspinous ligament attachment. The contralateral regions bear no external pleurocoels. Two distinct pleurocoels are present in *T. rex* and TCM 2001.81.1 “*Gorgosaurus*”, in contrast to *X. baimoensis*, *Bistahieversor*, *Qianzhousaurus*, and *N. lethaeus*, which bear only one axial pleurocoel on each side (the plesiomorphic condition). The axial neural spine is sheet-like (relatively straight with minor undulations); whereas in *N. lethaeus* it bears a distinctly crenulated appearance. The axis lacks the ventral ridge or funnel-like supradiapophyseal fossae observed in *Tyrannosaurus*. Atlantal ribs (r1) extend to the caudalmost margin of the axial centrum. Axial ribs (r2) are present and unfused. They are double-headed and straplike. There are ten weakly opisthocoelous, roughly equidimensional cervical centra.

Aside from some visibility in ventral view of the cervical and cervico-dorsal centra, much of the presacral vertebral column is currently obscured. Presacral neural arches p3–6 bear epipophyses. Epipophyses are moderately developed (unlike the extensive epipophyses of *Tyrannosaurus* and tyrannosaurids except *Alioramus*). Ventrally, cervical centra are flattened, with weak ventral ridges on p7–9 and a strong keel on p10–14. Centra p8–10 possess hypapophyses in contrast to *T. rex*, which reportedly bears hypapophyses on p3–5 and p14–16⁷⁸. Centra p2 through at least p7 bear lateral pleurocoels. The possibility of a

pleurocoel cannot be assessed on centrum p8, but one is absent on p9. There is a cranially projecting spur on rib ten just distal to the tuberculum. Most cervical ribs appear pneumatic; shafts are flattened and ventrally imbricated—at least four overlap in one lateral to a single cervical centrum. Exposed **dorsals** are pneumatic. The **sacrum** is largely obscured by articulated ilia. An estimated five sacral vertebrae with fused neural spines are present. In *N. lethaeus* the fifth sacral hyposphene is distinct from *Tyrannosaurus* in that it comprises two parallel sheets, rather than a single midline structure.

The **caudal** series of NCSM 40000 is complete, articulated, and completely exposed (Fig. 2). It comprises 35 vertebrae; the first 14 (40%) possess caudal ribs. This compares well with *Tarbosaurus* (MPC-D 100/60), which preserves 41 caudal vertebrae (41% bearing caudal ribs, n=17). Complete tails are unknown for *Tyrannosaurus*; however, FMNH PR 2081 preserves 35, 17 of which bear caudal ribs. Given an approximately similar extent of the M. caudofemoralis, a minimum estimate for *Tyrannosaurus* would be 42–43 vertebrae, within the 40–45 estimate given by Brochu⁷⁸. Caudal vertebrae 5–8 exhibit singular, ovate pneumatopores excising the ventral surface of prezygadiapophyseal laminae, and C11–14 display a pitted texture on the neural arch ventral to the caudal ribs. Caudal vertebrae are generally apneumatic in derived tyrannosauroids, but some specimens of *Tyrannosaurus* and “*Gorgosaurus*” (TCMI 2001.81.1) display pneumatization of the caudal vertebrae. *N. lethaeus* does not have pneumatic caudal vertebrae. Transverse processes of the proximal caudal vertebrae are expanded caudally, not craniocaudally as in *Tyrannosaurus* and *Tarbosaurus*. Mid- to distal caudal vertebrae are elongate relative to *Tyrannosaurus*, bearing pronounced lateral ridges and a pinched ventral profile with contralateral longitudinal depressions. Haemal arches transition rapidly in the proximal tail to an L-shape morphology with a flat ventral margin. This is in contrast to the vertically elongate haemal arches on the proximal tail and the deeply curved haemal arches of the mid-series of *T. rex* (FMNH PR 2081), and suggests a more lightly built, less muscular tail in *Nanotyrannus*.

SI.1.4.iv. Pectoral girdle.

The **scapular** blade is robust, with subparallel margins throughout most of its length. It is not strongly constricted, in contrast to *Tyrannosaurus*. The dorsal scapular margin appears to grade gently from the shaft to the acromion in contrast to BMRP 2002.4.1 and BMPR 2006.4.4; however, this area is shattered and remains unreconstructed in NCSM 40000. The glenoid is caudoventrally offset, with subequal scapula and coracoid contributions. It is uniquely configured, lapping broadly onto the lateral surface of the scapula and entirely restricted to the ventral aspect of the coracoid as in *Suskityrannus* and *Khankhuuluu* (Extended Data 1). This contrasts with the ventral orientation of the glenoid on *Tyrannosaurus* and other tyrannosaurids⁸⁸. A **coracoid** biceps tubercle is weak to absent. Instead, the region is depressed and slightly roughened. The **furcula** preserves epicleidea with tab-like terminals with a caudoventral strut as in *Daspletosaurus* (TMP 2001.36.1). It forms a narrow U-shape, as in TCMI 2001.81.1 and *Gorgosaurus*, in contrast to most *Tyrannosaurus* individuals and *Daspletosaurus*.

SI.1.4.v. Forelimb.

Among later-branching tyrannosauroids, the forelimb of NCSM 40000 (Extended Data 2) is large (relative to body size) and robust, with well-defined, complex articular surfaces. The **humerus** is long relative to the femur, unlike albertosaurines and tyrannosaurines, and is further distinguished from

Tyrannosaurus in having a strongly bowed and “twisted” shaft. The humerus also possesses a broad distal end and a flattened, ventrolaterally sloping humeral head, autapomorphic for *N. lancensis*, and possibly the genus *Nanotyrannus* (see below). The latter trait renders a medially offset apex to the proximal humeral profile in caudal view and ventrally displaces the external tuberosity relative to its internal counterpart, in contrast to tyrannosaurids, which exhibit a relatively symmetrical and proximally domed humeral head and subhorizontal internal and external tuberosities, but similar to TCM 2001.81.1. The external tuberosity of NCSM 40000 is proximally concave instead of broadly convex as in *Daspletosaurus* and *T. rex*. The deltopectoral crest is enlarged and medially recurved.

Differential crushing of the proximal humerus between *N. lancensis* (NCSM 40000), *N. lethaeus* (BMRP 2002.4.1), and BMRP 2006.4.4 prevents us from confidently ascribing BMRP 2006.4.4 to *N. lancensis* despite the fact that the humerus of this specimen is most similar to NCSM 40000. We also take a conservative approach by not adding conditions observed to the species-level diagnoses for these taxa. Specifically, the proximal humerus of *N. lancensis* (NCSM 40000) and BMRP 2006.4.4 are slightly crushed proximodistally, which has the effect of enhancing the flattened appearance of the humeral head, whereas this region in *N. lethaeus* (BMRP 2002.4.1) is crushed craniocaudally, somewhat distorting the humeral head into a more dome-like appearance. Similar crushing artifacts distort the medial recurvature of the deltopectoral crest (less recurved in *N. lethaeus* (BMRP 2002.4.1)).

The distal humerus of NCSM 40000 comprises five well-formed condyles and a deep extensor fossa bounded by thickened and bulbous ectepicondylar and supraradiocondylar ridges and a sharp entepicondylar ridge, a morphology unique to *Nanotyrannus* (Extended Data 2). An ectepicondylar ridge is absent in tyrannosaurines. The condition of the supraradiocondylar and entepicondylar ridge mirrors that observed in BMRP 2006.4.4, making it tempting to refer BMRP 2006.4.4 to *N. lancensis*. However, we have concerns that these features could vary with the relative robusticity of the forelimb as a function of skeletal maturity. Given that BMRP 2002.4.1 represents a skeletally immature individual and lacks some of these features, whereas BMRP 2006.4.4 and NCSM 40000 are individuals that already entered the asymptotic growth phase at death, we have opted to take a conservative approach and we are not including these humeral differences in the species-level diagnoses of *N. lancensis* and *N. lethaeus*. We, therefore, consider it imprudent to refer BMRP 2006.4.4 to *N. lancensis* based on shared humeral morphology with NCSM 40000.

A well-formed, subspherical condyle projects distally between the ulnar condyle and a proximomedially projecting, prong-shaped entepicondyle. The ectepicondyle is craniocaudally expanded, broadly extending onto the caudal aspect. These traits combine to form a complex articular surface comprising three bulbous condyles (cranial-facing ulnar and radial condyles and a distally projecting accessory condyle) bracketed by two elongate articular surfaces that craniocaudally wrap the distal humerus. Similar problems with crushing impact the interpretation of the distal humerus morphology between BMRP 2002.4.1 and BMRP 2006.4.4, amplifying perceived differences. The distal humerus of BMRP 2002.4.1 is slightly mediolaterally compressed such that the ulnar condyle is off-axis, whereas that of BMRP 2006.4.4 is craniocaudally crushed.

Articular complexity of the humerus of NCSM 40000 is mirrored in the proximal **antebrachium**. The **ulna** is elongate with a convex distal end that differs from *Tyrannosaurus*. Its proximal articular surface is

enlarged and fully envelopes the proximal radius medially. Its craniomedial margin is kinked to face proximomedially. The same morphology is evident on the lateralmost margin of the proximal radius. Articulated, they form a triple-faceted, transversely expanded, shelf-like proximal articular surface, braced by a broad and craniocaudally compressed olecranon in contrast to the mediolaterally compressed proximal aspect of the ulna in ROM 807, TMP 1986.64.01. The **wrist** comprises four carpals—unfused distal I and II, radiale, and intermedium (Fig. 6; Extended Data 2).

The manus shares discrete similarities with albertosaurines. The medial distal condyle of **MCI** is distinctly subtriangular and reduced, in contrast to tyrannosaurids. The proximolateral surface of MCI is concave, bounded medially and laterally by ridges as in *Gorgosaurus* (TMP.1991.36.05), and in contrast to tyrannosaurines. **DCII** rests confluent against the proximal aspect of **MCII**, forming a high-angle articular surface. The dorsal margin of MCII at the point of contact with DCII is disrupted by a narrow groove, as in *Albertosaurus* (ROM 807), in contrast to the broad notch of *Tyrannosaurus*, *Daspletosaurus*, and *Gorgosaurus*. The lateral margin of the proximal end of MCII is bicondylar, bearing a hypertrophied caudolateral shelf as in *Albertosaurus* (ROM 807) confluent with the proximal articular surface of DCII that buttresses a similarly hypertrophied medial projection of the ulna. Together, they form a unique articular surface for wrist folding. In this way, part of the proximal articular surface of MCII may have contacted the antebrachium during wrist flexion, which is, to our knowledge, unique in coelurosaurians.

MCIII is sigmoid, with a subtriangular, robust proximal half and a tapering distal aspect terminating in articulation with a rudimentary, amorphic manual PIII-1 (Fig. 6; Extended Data 2). Tyrannosaurids are generally stated to possess only two digits, but the well-preserved articulated manus of *Gorgosaurus libratus* (TMP 1991.36.05) also has a free rudimentary III-1, and in *Tyrannosaurus rex* (MOR 980), this element appears to be fused to the distal end of MCIII. In NCSM 40000, only the lateralmost rim of the proximal end of MCIII articulates with the carpals or antebrachium. Otherwise, MCIII appears genuinely splint-like, despite being robust proximally.

The manus of *Nanotyrannus* is characterized by distinctly long autopodial elements, most notably an elongate phalanx (P)I-1 (nearly twice the absolute dimensions of one of the largest known *T. rex* individuals, such as FMNH PR 2081 and MOR 980). PI-1 of NCSM 40000 is long (over 20% femur length; compare 19% in *Dryptosaurus*, ~15% in *Daspletosaurus*, 10-12% in *Gorgosaurus*, and 5-10% in *Tyrannosaurus*, *Tarbosaurus*, and *Albertosaurus*), medially bowed, and distally canted medially, such that the distal condyles are rotated approximately 15 degrees relative to the proximal cotyle. A similar condition is seen in all tyrannosaurids with known forelimbs but is weakest in *Tyrannosaurus rex*, where shaft torsion is sometimes absent (e.g., FMNH PR 2081). The distal condyles of PII-1 are distinctly reduced in height and displaced ventrally, a feature present on isolated tyrannosauroid manual PII-Is from the Bayanshiree Formation (e.g., BTS23-SGL-70) and *Albertosaurus* (ROM 807). in contrast to these taxa, the shaft of this element in NCSM 40000 exhibits a “pinched and peaked” morphology composed of an extensor fossa emarginated by a bulbous rim with a proximolateral tubercle. It is most similar to TCMI 2001.81. PII-3 is similar in length to PI-2 yet markedly straightened; the flexor tubercle is offset proximally by a deep groove. The manus of NCSM 40000 is functionally didactyl and retains a vestigial PIII-1 as in *Tyrannosaurus* (MOR 980), but unlike *Tyrannosaurus* PIII-1 of *N. lancensis* is unfused, a trait also present in *Gorgosaurus libratus* (TMP 1991.36.500). The second manual ungual (PII-3) is distinctly flattened relative to the first (PI-2), which is deeply recurved.

SI.1.4.vi. Pelvic girdle.

The **ilium** of NCSM 40000 is long (~107% femoral length) and low, and the dorsal margin is relatively straight (Fig. 2). The preacetabular blade is cranially extensive, with a distinctly straightened ventral profile and an expanded medial wall of the cuppedicus fossa. It has a sharply hooked preacetabular wing that reaches the ventral extent of the pubic peduncle as in albertosaurines (TCMI 2001.81.1), yet unlike tyrannosaurines, although the full extent of hook recurvature cannot be assessed due to damage. As in all tyrannosauroids, the ilium bears a well-defined proximodistal ridge, which in *Nanotyrannus* is vertical to slightly rostr dorsally oriented, craniocaudally thin, and does not reach the striated attachment surface of the iliofibularis muscle. The caudodorsal aspect of the postacetabular blade is gently curved, in contrast to the subrectangular profile of *Tyrannosaurus* (FMNH PR 2081). The pubic peduncle is not dorsally constricted as in *Tyrannosaurus* (FMNH PR 2081; USNM 555000); however, a distinct step defining the cranioventral extent of the acetabular hood is present. The **pubis** is notably elongate, being nearly 90% the length of the ilium in NCSM 40000, much greater than the 78% pubis to ilium length ratio of *T. rex*⁷⁸. The pubic shaft is straight in *N. lancensis* and most tyrannosaurids yet cranially concave in *N. lethaeus*, *Albertosaurus*, and *Tyrannosaurus*. The pubic boot is moderately sized (~62% pubis length), compared to ~75% in *T. rex*⁷⁸. It is subtriangular in lateral view, lacking the dorsally concave cranial and caudal projections and the dorsally upturned caudal aspect of *T. rex* (FMNH PR 2081) and UALVP 52981. Only a section of the proximal ischium, including a portion of the subtriangular obturator process, is exposed.

SI.1.4.vii. Hindlimb.

The hind limbs of NCSM 40000 are relatively elongate for an eutyrranosaurian, particularly for an individual in the asymptotic growth phase. The **femur** is greater in length than the ilium (~107%), compared to *T. rex*, in which the femur is only 90% the length of the ilium. The femur of NCSM 40000 smoothly arcs along its long axis. Mediolateral crushing and shearing of the proximal and distal portions, respectively, obscure the strength of bowing and the precise morphology. As a result, it is not clear if NCSM 40000 shares the distinctive femoral profile of characterizing UMNH VP 16690 and MNA V. 12400 (described as juvenile “*Teratophoneus*” and “*Bistahieversor*,” respectively) formed by the combination of a straightened proximal portion, long, low fourth trochanter, and strongly arched shaft. The lesser trochanter has a strongly developed proximodistal ridge, unlike *Tyrannosaurus*. The trochanteric crest is rugose and bulbous, as in tyrannosaurids generally, and the accessory trochanter forms a prominent flange. The principal nutrient foramen pierces the shaft medial to the axis of the lesser trochanter, as in other tyrannosauroids⁴³. The fourth trochanter is parallel to the femoral shaft, and does not form a prominent peak in *N. lethaeus*, a trait shared with *Moros* and UMNH VP 16690. Unlike *Tyrannosaurus*, the scar for adductor femoris 1 is not displaced to the caudomedial extremity of the femoral shaft. Unlike tyrannosaurines, the femur retains a fossa on the medial surface distally. The crista tibiofibularis is proportionally enormous, raised from the lateral condyle by a pedicle, and caudomedially concave (shared with *Tyrannosaurus* and *Bistahieversor*). The proximal tibia is depressed with a dorsally projecting cnemial crest and lateral condyle, confluent with an accessory condyle, and an elongate, subtriangular fibular crest. The distal half of the fibular shaft is deeply grooved medially as in *D. horneri* and UMNHVP 16690, in contrast to the flat condition of *Tyrannosaurus* and many tyrannosaurids.

Complete, articulated **tarsi**, **metatarsi**, and **pes** are preserved, including two distal tarsals. The metatarsus of NCSM 40000, and *Nanotyrannus* generally, is notably elongate (Extended Data 2, 8). The metatarsus displays the typical tyrannosauroid arctometatarsalian condition of a caudally exposed MTIII shaft proximally. Proximally, MTIII articulates along the caudal margin of MTIV, bows medially, with a distal terminus resting along the point of contact between MTII and MTIII. Medial and lateral convexities on the shaft of metatarsal III are relatively symmetrical. Metatarsal III and some pedal phalanges of NCSM 40000 are distinctive in exhibiting distal condyles that are uniquely canted toward the flexor surface, resulting in a “droopy” appearance (distal condyles are reoriented flexor to an axis drawn across the dorsal aspect of the elements.) The distal condyle of MTIV is craniocaudally elongate relative to *Tyrannosaurus* (longer in *N. lethaeus*, *Moros*, and *Gorgosaurus* than in *N. lancensis*).

SI.1.5. Table of Measurements (NCSM 40000). Measurements were taken from 3D renders with Blender v3.0-4.4. Asterisk indicates estimate.

Element	Measurement (mm)	Element	Measurement (mm)
Skull craniocaudal length	~713	Phalanx II-2, maximum proximodistal length	103.2
Skull, caudal half, craniocaudal length	469.7	Phalanx II-3, maximum proximodistal length (linear)	121
Skull, cranial half, craniocaudal length	490.1	Phalanx II-3, maximum proximodistal length (arc)	147
Skull, maximum dorsoventral height	~176.2	Phalanx III-1, maximum proximodistal length	12.7
Skull, maximum mediolateral width	~273.4	Ilium, maximum craniocaudal length	673.5
Scapula, blade length (from glenoid)	405*	Ilium, preacetabular process, maximum craniocaudal length	275
Scapula, minimum blade height	44.8	Ilium, postacetabular process, maximum craniocaudal length	304.4
Scapula, height of acromion process	65.5	Ilium, dorsoventral height at acetabulum	210
Humerus, maximum proximodistal length	279.4	Pubis, proximodistal length	660*
Humerus, maximum proximal mediolateral width	69.3	Pubis, boot, craniocaudal length	407
Humerus, maximum distal mediolateral width	76.1	Femur, proximodistal length	717
Humerus, length head to deltopectoral crest distalmost extent	144.2	Femur, maximum proximodistal length	717
Humerus, minimum shaft circumference	115	Femur, maximum distal mediolateral width	140*
Ulna, maximum proximodistal length	214.4	Femur, minimum shaft circumference	235
Radius, maximum proximodistal length	174.1	Tibia, proximodistal length	820
Metacarpal I, maximum proximodistal length	66.6	Fibula, proximodistal length	760*
Metacarpal II, maximum proximodistal length	112.1	Metatarsal I, proximodistal length	83.5+
Metacarpal III, maximum proximodistal length	68.1	Metatarsal II, proximodistal length	497.5
Phalanx I-1, maximum proximodistal length	156.5	Metatarsal III, proximodistal length	559.8
Phalanx I-2, maximum proximodistal length (linear)	121.8	Metatarsal IV, proximodistal length	504.4
Phalanx I-2, maximum proximodistal length (arc)	150	Metatarsal V, proximodistal length	173.6
Phalanx II-1, maximum proximodistal length	64.6		

SI.1.6. Table of CGM Circumferences and Body Mass Estimates.

Specimen	Element	Preserved LAG #	Radius (mm)	Circumference (mm)	Notes	Body Mass (kg) DME
NCSM 40000	Femur	n/a	n/a	n/a	Neonatal mass	0.07
NCSM 40000	Femur	1	25.424	159.74	-	221.04
NCSM 40000	Femur	2	26.97	169.46	-	263.90
NCSM 40000	Femur	3	28.459	178.81	-	310.04
NCSM 40000	Femur	4	29.598	185.97	-	348.79
NCSM 40000	Femur	5	31.215	196.13	-	409.14
NCSM 40000	Femur	6	33.017	207.45	-	484.15
NCSM 40000	Femur	7	34.302	215.53	-	542.95
NCSM 40000	Femur	8	35.476	222.90	-	600.57
NCSM 40000	Femur	9	36.197	227.43	-	637.94
NCSM 40000	Femur	10	36.906	231.89	EFS	676.21
NCSM 40000	Femur	11	37.127	233.28	EFS	688.44
NCSM 40000	Femur	12	37.226	233.90	EFS	693.95
NCSM 40000	Femur	13	37.4	235.00	EFS; LAG and Periosteal Circumference	703.78
BMRP 2002.4.1	Femur	n/a	n/a	n/a	Neonatal mass	0.08
BMRP 2002.4.1	Femur	n/a	22.24	139.74	Endosteal Circumference	n/a
BMRP 2002.4.1	Femur	1	23.973	150.63	-	206.51
BMRP 2002.4.1	Femur	2	29.323	184.24	-	359.65
BMRP 2002.4.1	Femur	3	31.835	200.03	-	451.01
BMRP 2002.4.1	Femur	4	34.91	219.35	-	581.39
BMRP 2002.4.1	Femur	5	36.51	229.40	-	657.76
BMRP 2002.4.1	Femur	6	38.372	241.10	-	754.33
BMRP 2002.4.1	Femur	7	39.534	248.40	-	818.93
BMRP 2002.4.1	Femur	n/a	39.79	250.00	Periosteal Circumference	833.54
BMRP 2006.4.4	Femur	n/a	n/a	n/a	Neonatal mass	0.08
BMRP 2006.4.4	Femur	n/a	23.816	149.64	Endosteal Circumference	
BMRP 2006.4.4	Femur	1	27.688	173.97	-	307.08
BMRP 2006.4.4	Femur	2	30.088	189.05	-	386.08
BMRP 2006.4.4	Femur	3	33.665	211.52	-	526.06
BMRP 2006.4.4	Femur	4	35.421	222.56	-	605.13
BMRP 2006.4.4	Femur	5	37.476	235.47	-	706.81
BMRP 2006.4.4	Femur	6	38.626	242.69	-	768.16

BMRP 2006.4.4	Femur	7	39.56	248.56	-	820.41
BMRP 2006.4.4	Femur	8	40.093	251.91	-	851.21
BMRP 2006.4.4	Femur	9	40.554	254.81	-	878.44
BMRP 2006.4.4	Femur	10	40.77	256.13	-	891.08
BMRP 2006.4.4	Femur	11	40.903	257.00	LAG and Periosteal Circumference	899.41
FMNH PR 2081	Femur	n/a	n/a	n/a	Neonatal mass	0.22
FMNH PR 2081	Femur	n/a	47.2	296.57	Endosteal Circumference	n/a
FMNH PR 2081	Femur	1	59.691	375.05	-	2547.07
FMNH PR 2081	Femur	2	65.161	409.42	-	3242.72
FMNH PR 2081	Femur	3	68.811	432.35	-	3767.88
FMNH PR 2081	Femur	4	71.422	448.76	-	4174.85
FMNH PR 2081	Femur	5	76.378	479.90	-	5022.06
FMNH PR 2081	Femur	6	80.609	506.48	-	5825.96
FMNH PR 2081	Femur	7	83.288	523.31	-	6374.87
FMNH PR 2081	Femur	8	85.893	539.68	-	6939.16
FMNH PR 2081	Femur	9	87.46	549.53	-	7293.41
FMNH PR 2081	Femur	10	88.687	557.24	-	7578.68
FMNH PR 2081	Femur	11	89.543	562.62	-	7781.84
FMNH PR 2081	Femur	12	90.11	566.18	-	7918.30
FMNH PR 2081	Femur	13	90.43	568.19	EFS	7995.99
FMNH PR 2081	Femur	14	90.477	568.48	EFS	8007.44
FMNH PR 2081	Femur	15	90.667	569.68	EFS	8053.83
FMNH PR 2081	Femur	16	90.721	570.02	EFS	8067.05
FMNH PR 2081	Femur	17	90.856	570.87	EFS	8100.15
FMNH PR 2081	Femur	18	90.919	571.26	EFS	8115.63
FMNH PR 2081	Femur	19	91.055	572.12	EFS	8149.11
FMNH PR 2081	Femur	20	91.101	572.40	EFS	8160.45
FMNH PR 2081	Femur	n/a	91.35	574.00	Periosteal Circumference	8223.25
TCMI 2003.66.1	Femur	n/a	n/a	n/a	Neonatal mass	0.20
TCMI 2003.66.1	Femur	1	66.28	416.44	-	3398.10
TCMI 2003.66.1	Femur	2	70.10	440.44	-	3965.14
TCMI 2003.66.1	Femur	3	72.52	455.69	-	4354.81
TCMI 2003.66.1	Femur	4	75.22	472.65	-	4816.01
TCMI 2003.66.1	Femur	5	77.32	485.81	-	5194.29
TCMI 2003.66.1	Femur	6	79.45	499.22	-	5598.73
TCMI 2003.66.1	Femur	7	81.92	514.71	-	6090.42
TCMI 2003.66.1	Femur	8	83.64	525.53	-	6449.53

TCMI 2003.66.1	Femur	9	84.50	530.94	-	6634.03
TCMI 2003.66.1	Femur	10	84.80	532.79	-	6697.79
TCMI 2003.66.1	Femur	11	85.05	534.38	-	6753.19
TCMI 2003.66.1	Femur	n/a	85.15	535	Periosteal Circumference	n/a

SI.1.7. Modeling Growth.

SI.1.7.i. Sample.

We directly examined 11 osteohistological sections from the hind limb of eight tyrannosauroid specimens from the Maastrichtian Hell Creek and Lance Formations. We produced new ground osteohistological sections from NCSM 40000 (right femur and right tibia) and TCMI 2003.66.1 (left femur). Existing osteohistological sections were loaned to the NCMS and examined firsthand for FMNH PR 2081 (femur), BMRP 2006.4.4 (left femur, left tibia), and BMRP 2002.4.1 (femur, right tibia). Specimens examined are accessioned at the North Carolina Museum of Natural Sciences, Raleigh, North Carolina (NCSM), Museum of the Rockies, Bozeman, Montana (MOR), Field Museum of Natural History, Chicago, Illinois (FMNH PR), Burpee Museum of Natural History, Rockford, Illinois (BMRP), Southwestern Adventist University Historical Research (HRC), Burke Museum (UWBM), and The Children’s Museum of Indianapolis (TCMI).

SI.1.7.ii. Methods.

New osteohistological sections.

Before sampling, specimens were molded and digitized via photogrammetry (Abound v.3.0.1) and/or structured light scanning (Artec Spider 2 processed with Artec Pro 19). We sampled femora through the mid-diaphysis—the region that preserves the longest growth record. Sampled bone sections were embedded in a clear epoxy resin (EPO-TEK 301) and cut along the transversal plane with a Buehler IsoMet 1000 Precision Saw. Specimens were then polished on one side with a Buehler MetaServ 250 Grinder Polisher or by hand using a series of abrasive paper disks with decreasing grit sizes (400–1200). Polished blocks were mounted on frosted glass or plexiglass slides with epoxy and ground to the desired thickness ($\approx 100\text{--}80\text{ }\mu\text{m}$). Thin sections were observed and photographed with a Nikon Eclipse Ci POL microscope equipped with a polarizer, lambda filter, and a Nikon DS-Fi2 digital camera and a Keyence VHX-7000 Digital Microscope with a plane polarizing filter and a custom-built lambda filter.

Approach and Terminology.

Our osteohistological examination reveals complexity in the skeletal growth record of tyrannosauroids as recorded by cyclical growth markers (CGMs). Among CGMs, we observe singular, well-developed lines of arrested growth (LAGs) demarking annual growth cycles. However, we also observe double, triple, and quadruple “stacked” LAGs and closely spaced CGM “clusters,” features we denote here as “CGM

complexes.” CGM complexes are widely reported within compact cortices of theropod limb bones (e.g., Cullen et al.⁸⁹), but to date, there are no uniformly adopted terminological definitions, which is a hindrance. Some authors define CGMs as circumferentially complete bone growth markers (BGMs) that reflect seasonal or annual periodicity, and LAGs, as CGMs representing circumferentially complete annual boundaries (e.g. Woodward et al.⁹⁰). However, in practice, it can be difficult to unambiguously determine which CGMs are best interpreted as LAGs (annual boundaries) in fossils, and often a single growth cessation event appears to be marked by multiple CGMs.

Here, we follow Woodward et al.⁹⁰ in defining LAGs as CGMs marking annual growth boundaries. We establish the term “stacked LAGs” as multiple LAG complexes separated by avascular tissue, yet still representing a single annual boundary. Stacked LAGs that remain distinct are termed “parallel stacked LAGs” (Extended Data 7). They may instead merge and split across the cortex, variably appearing as single and multiple LAGs, which we term “braided stacked LAGs” (Extended Data 7). Because it is not currently possible to determine which CGM in a stacked LAG represents the start or end of a growth boundary, and it is typically not realistic to count these as individual CGMs in CGM counts, we prefer to use the term LAG instead of CGM for these multiple markers. By these definitions, stacked LAGs are equivalent to the “double” or “doublet LAGs” of Lee and O’Connor⁹¹ (fig 3).

We define “CGM clusters” as closely spaced CGMs separated by the deposition of woven- or parallel-fibred bone incised by vessels (Extended Data 7) that together, but not individually, represent the boundary/ies of an annual growth cycle. CGM clusters may also be “braided” or “parallel,” typically mirroring relative cortical expansion rates that vary due to shape change during growth. They may contain combinations of single LAGs, stacked LAGs, and non-LAG CGMs, but are most reasonably interpreted as a package of CGMs representing an annual growth cessation. CGM clusters are variably termed by existing authors. Our usage would be consistent with the use of “annulus” in Lee and O’Connor⁹¹ (fig 3). Cullen et al.⁸⁹ use the term “clustered double/multiple growth mark sets” to refer solely to braided CGMs, but did not differentiate them based on the presence of vascularity. They otherwise consider all non-braiding LAGs to represent individual annual growth boundaries. In addition to CGM complexes, we also observe a spectrum of individual CGM types in our sample, including poorly developed (diffuse) CGMs or circumferentially incomplete CGMs (transitioning from dark hypermineralized lines to dense highly-organized bands of tissue with high birefringences across the circumference) that may instead represent non-cyclical growth markers or even cortical drift lines (CDLs, *sensu* Woodward et al.⁹⁰).

The spectrum of CGMs represented in our sample, sometimes observed within a single osteohistological section, introduces subjectivity to the interpretation of growth cycles. Here, we interpret stacked and braided LAGs, and one CGM within a CGM cluster, as marking the reinitiation/cessation of growth and therefore bounding one annual growth cycle. Because of the difficulty in parsing individual LAGs within stacked and braided LAGs, we treat them as a single CGM in our CGM counts and descriptions. Although we interpret both braided and parallel CGM clusters as representing one growth cessation/initiation event, we count parallel CGM clusters as multiple CGMs because individual CGMs within these clusters are typically distinguishable at the figured scale and do not merge.

CGM circumferences are necessary data for modeling growth. Deriving the most appropriate CGM circumferences to bound annual skeletal growth is complicated by the presence of CGM complexes. For

stacked LAGs, we mark the growth cycle at the mean circumference. However, in cases of CGM clusters, we do not see a justification for assuming that an annual growth cycle will *uniformly* initiate/terminate at the first or last CGM (thereby marking that CGM as a LAG). For this reason, we prefer a case-by-case approach based on direct examination of the tissue. In Extended Data 5 and 6, we indicate our preferred demarcation for the beginning and end of growth cycles. These determinations are based on examination of the intervening tissue matrix types (woven matrix was deemed to mark the initiation of a growth cycle) and the strength of preserved CGMs (the strongest CGM in a cluster was determined to represent the termination of a growth cycle, and therefore a LAG).

Interpreting Annual Growth Cycles.

NCSM 40000—We examined a complete transverse cortical section taken from the midshaft of the right femur of NCSM 40000. The compact cortex transitions from predominant plexiform vascularization to predominantly circumferential, reticular, and longitudinal vascularization, with increasing longitudinal and decreasing circumferential canals toward the periosteum. Fiber matrix transitions from more woven (isotropic) to more anisotropic centrifugally in the mid-cortex. Subperiosteally, the matrix becomes sublamellar (highly organized parallel-fibered), osteocyte lacunae flatten, and vascularity progressively decreases, concomitant with early formation of an EFS, indicative of extremely reduced growth and effective skeletal maturity⁹². We emphasize that the femoral cortex of NCSM 40000 is observed to grow faster caudally, and in this region there is less tissue compaction between all CGMs (including those that represent the incipient EFS surrounding much of the craniolateral to craniomedial cortex). Thus an EFS has not yet fully developed in the caudal region of the femur. Secondary remodeling, although dense in some areas, is limited to the inner half of the preserved cortex, aside from large bands of remodeling along the craniolateral and caudolateral aspects. Multiple generations of endosteal lamellar bone are present. These features, combined, confirm that NCSM 40000 had entered the asymptotic growth phase at death.

The femur of NCSM 40000 preserves a minimum of 25 visible CGMs, some of which are difficult to visualize in the subperiosteal tissue because of taphonomic staining and slight wear at the periostealmost circumference. We have been conservative in our approach to growth cycles and CGM count, counting bands only as CGMs when pronounced and well-defined, circumferentially around the section. We discretize these into 13 complete and one incomplete annual growth cycles (at least 14 years of growth) based on tissue deposition rates, as interpreted through bone fiber organization, osteocyte lacunae morphology, and vascular patterns. Determining an accurate CGM count within the periostealmost cortex is challenging due to the tissue density, taphonomic staining, and degradation of the periosteal surface. In the caudomedial area, four CGMs are evident in the periostealmost 1 mm of the cortex (only two of which are pronounced and counted as LAGs). Whereas, in other regions (for example, the craniolateral and craniomedial aspects) up to nine distinct CGMs are visible in the periostealmost 1 mm. Based on the circumferential variability in the distinctness of these CGMs, we have chosen a conservative approach, only considering CGMs represented by dark, hypermineralized, and distinct bands that circle the entire circumference as LAGs, and therefore only interpreting only one complete and one partial growth cycle in the periostealmost 1 mm of the femur of NCSM 40000 our age counts, so as not to over interpret the growth asymptote. Due to strong cortical drift, almost half of the growth record is preserved only within the cranial aspect of the section. These innermost GCMs form a tight circumference; thus, we suggest that

most of the early growth record of NCSM 40000 remains preserved. Given that the preserved number of CGMs is much higher than the growth cycles we interpret, any bias in our interpretations would underestimate growth cycles in NCSM 40000. A more stringent 1:1 interpretation of CGMs to growth cycle count, as employed in other studies of tyrannosauroid growth (e.g., Woodward et al.⁹³), would yield an age at death for NCSM 40000 of at or greater than 26 years, only strengthening the argument for a growth trajectory in NCSM 40000 distinct from that of FMNH PR 2081.

To confirm the skeletal maturity of NCSM 40000 independently in a second appendicular element, we transversely sectioned an anterior fragment of the right tibia. The tibial cortex is primarily composed of fibrolamellar bone with well-developed CGMs. The matrix becomes increasingly organized toward the periosteum. The preserved portion of the compact cortex exhibits circumferential, reticular, and longitudinal vascularization as in the femur, although portions display plexiform vascularization. Twelve growth cycles are evident in the preserved portion (ten complete and two incomplete), four comprising an EFS. However, this section does not preserve the entire endosteal to periosteal cortex, and it is unclear how many additional growth cycles would be evident in a complete section. Subperiosteally, vascularity decreases, and as in the femur, LAGs become separated by only one or two circumferential rows of predominantly longitudinal canals in the EFS. The matrix transitions rapidly to more organized parallel-fibered tissue endosteal to the EFS by one CGM. The preserved EFS retains sporadic reticular vascularization in addition to simple longitudinal vessels.

Regarding the circumferentially incomplete development of an EFS in NCSM 40000, we note that an EFS would not be expected to develop simultaneously and uniformly across the entire femoral circumference, nor between the femur and tibia, due to interelemental variation in growth cessation across the skeleton, a known trait of theropod dinosaurs⁸⁹. Tissue deposition rates are not homogeneous in limb bones; instead, they are a mechanism for and reflection of shape change during growth. Prolonged asymptotic growth, as is observed in FMNH PR 2081 (8+ years in the asymptotic growth stage), is likely necessary for a well-developed EFS to characterize the entire femoral circumference. Moreover, although the EFS of specific taxa is avascular and lamellar-fibered, in others, especially some avian and non-avian dinosaurs, EFS tissue may only show progressively reduced vascularity and/or parallel-fibered matrix^{94,95}. For example, this is observed in *T. rex* (MOR 1152) (Woodward et al.⁹⁰, fig. 1c), *Confuciusornis* (Andrade et al.⁹⁶, fig. 2Ef), and in NCSM 40000.

Finally, Woodward et al.⁹³ also observed the development of an EFS-like structure in a restricted femur region in BMRP 2006.4.4 (caudal aspect). They considered this tissue an annulus as opposed to a localized development of an EFS. In support of this interpretation, Woodward et al.⁹³ noted the presence of additional woven bone deposited centripetally to this annulus. We have examined this section and confirm the presence of woven bone deposited periosteally to the compact tissue of BMRP 2006.4.4. No such fast-growing tissue is observed centripetal to the EFS on the femoral section of NCSM 40000 that would cast doubt on an EFS interpretation.

BMRP 2002.4.1—A histological description of the femur of BMRP 2002.4.1 was published by Woodward et al.⁹³. We reevaluated CGM count in the femoral section of BMRP 2004.4.1 Fe1-3 by direct examination. We observe 13 CGMs (10 LAGs) representing eight years of growth (six complete and two partial growth cycles [endosteal- and periostealmost are incompletely preserved]). We consider LAG

clusters to represent a single growth cessation event (season) and count them as a single annual boundary. Three such pairings are observed. Woodward et al. (2020) also interpreted 13 CGMs in the femur of BMRP 2002.4.1 and 10 in the tibia, but interpreted this as 13 preserved growth cycles, significantly more than we interpret from our examination of the section. Longrich and Saitta⁹⁷ used the published CGM counts and circumferences from BMRP 2002.4.1 from Woodward et al.⁹³ (2020). Cullen et al.⁸⁹ did not report CGM data for BMRP 2002.4.1.

BMRP 2006.4.4—A histological description of the femur of BMRP 2006.4.4 was published by Woodward et al.⁹³. BMRP 2006.4.4 is represented by complete transverse sections of the left femur (midshaft) and left tibia (proximal to midshaft). We reevaluated CGM count in both sections by direct examination. In the femur, we observe a maximum of 17 CGMs (13 LAGs) representing 12 growth cycles (ten full and two partial years of growth [endosteal- and periostealmost growth cycles are incompletely preserved]). In the tibia, we observe a maximum of 18 circumferentially complete CGMs (13-14 LAGs) representing thirteen years of growth (eleven full and two partial growth cycles [endosteal- and periostealmost growth cycles are incompletely preserved]).

The number of growth cycles interpreted from the hind limb elements of BMRP 2006.4.4 in the literature varies. Woodward et al.⁹³ recognized 15 CGMs in the femur and 13-18 in the tibia, interpreting an age at death of at least 15 years. Cullen et al.⁸⁹ reported seven CGMs for the femur and nine in the tibia (estimating a minimum age at death of only seven years), noting that their lower count is at least partially a reflection of a different approach to what they interpret as “double” or “multiple growth marks” or growth marks that split or merge. However, because the slides were inaccessible at the time of the investigation, CGM tracings by Cullen et al.⁸⁹ were conducted using high-resolution images, which undoubtedly affected the visibility of the microstructure. Longrich and Saitta⁹⁷ did not provide interpretations of CGM counts in BMRP 2006.4.4, instead using the published CGM counts and circumferences from Cullen et al.⁸⁹.

FMNH PR 2081—We reevaluated CGM count in the cored partial femoral section of FMNH PR 2081⁸⁹ by direct examination. Our CGM count agrees with Cullen et al.⁸⁹ in recognizing the presence of 12 visible CGMs between the endosteum and EFS on FMNH PR 2081; however, we interpret fewer CGMs within the EFS itself. We interpret the annual growth cycles within the cortex of FMNH PR 2081 as beginning with a more disorganized band of bone, consisting of a woven matrix with plump osteocyte lacunae and a higher frequency of larger longitudinal and circumferential vascular canals, organized into circumferential rings (indicative of rapid growth). The size and abundance of longitudinal vascular canals decrease centrifugally until the end of the annual growth cycle (next CGM). CGMs in the cortex are bordered by anisotropic lamellar bone matrix observable under cross-polarized light with lambda filtration. We used the same pattern to discern the number of CGMs within the EFS of FMNH PR 2081. The presence of a highly vascularized band marks the initiation of growth cycles preserved within the EFS. Darkly mineralized circumferential vascular canals mimic CGMs by creating a dark band; however, mineralized circumferential vascular canals throughout the cortex of FMNH PR 2081 are connected by longitudinal canals, allowing them to be confidently differentiated from CGMs. It is this pattern that we rely on to differentiate vascular artifacts from CGMs within the tight banding of the EFS in FMNH PR 2081—if longitudinal canals pierce a band, we do not interpret this as a CGM. Vascularity becomes progressively reduced within the EFS until it is sparse, and bands of vascularization are weakly developed. The

innermost half of the EFS maintains vascular density similar to the preceding tissue. In contrast, vascularity decreases substantially in the outer half of the EFS, but the EFS is not avascular. Tissue matrix is a combination of parallel-fibered to lamellar. Increasing organization of the tissue occurs transitionally rather than abruptly, with patchy regions of increased fiber-matrix organization deposited centripetally in the EFS, and patchy regions of parallel-fibered tissue extending into the EFS. Although the EFS does bear some regions of lamellar matrix, these are highly localized. CGMs in the EFS are paired, and as growth slows, they become more compact and regular. CGMs in the EFS are bordered by anisotropic lamellar bone matrix observable under cross-polarized light with lambda filtration. Our data suggest that eight CGMs (four pairs) are preserved within the EFS of FMNH PR 2081, which is slightly less than the 11 reported by Cullen et al.⁸⁹ and subsequently adopted by Longrich and Saitta⁹⁷, for a total CGM count in the femur of FMNH PR 2081 of 20.

TCMI 2003.66.1—We observe 12 CGMs representing a minimum of 12 growth cycles and an additional two incomplete non-cyclical growth marks (possible CDLs). The periosteal-most three CGMs comprise an EFS. The cortex of TCM 2003.66.1 is heavily remodeled across at least the endosteal-most two-thirds, obscuring at least half of the growth record in this section. The matrix appears relatively homogeneously parallel-fibered in the visible region, although more organized bands of tissue are observed bracketing CGMs. The compact cortex exhibits predominantly plexiform vascularization, with some reticular canals toward the periosteal surface. This pattern transitions abruptly to longitudinal vascularization in the EFS itself.

SI.5.b.iv CGM circumference calculations: Previous models of tyrannosaur growth use CGM data compiled from different skeletal elements⁹⁷⁻⁹⁹. This is problematic because intraskeletal variability in growth markers is documented across the archosaur skeleton^{89,100}. We control for variability in interelemental growth by constraining our sample to the cranialmost transect available for mid-diaphyseal sections of femora only. Femora preserve the least remodeled growth record in most dinosaur clades, including large theropods⁸⁹ and hadrosaurids¹⁰¹.

Ideally, CGM circumferences would be measured by tracing CGMs around complete cortical sections. However, full circumferential sections could not be traced for our key taxonomic comparisons, the *Tyrannosaurus rex* specimens FMNH PR 2081 and TCM 2003.66.1, nor for BMRP 2002.4.1. FMNH PR 2081 is represented solely by an endosteal-periosteal core, and extensive remodeling and taphonomic crushing obscure the majority of the cortex of TCM 2003.66.1. The transverse section of BMRP 2002.4.1 was made from a femoral fragment. To avoid introducing bias into our growth models between *Tyrannosaurus* and *Nanotyrannus*, we adopted a standardized approach we could apply consistently to all sections: we estimated CGM circumferences by measuring CGM distance along a location-standardized transect through the cranial cortex. We then used Ramanujan's¹⁰² formula:

$$(1) C = \pi \left[3(a + b) \sqrt{(a + 3b)(3a + b)} \right]$$

where C is the circumference, a is the major axis, and b is the minor axis, to calculate intracortical CGM circumferences.

NCSM 40000: NCSM 40000 is represented by a complete femoral transverse section and a partial tibial section. We measured the femur's circumference at the point of sectioning (235 mm femoral circumference), excluding breaks, to calculate a “retrodeformed” section periosteal circumference (only slight adjustments were necessary). We retrodeformed the femoral cross-section for CGM tracings by realigning the circumference in Photoshop (26.0.0). We calculated the radius of this circumference, approximated as a circle (37.4 mm), and measured 90° from the periosteal margin.

BMRP 2002.4.1: BMRP 2002.4.1 is represented by a partial femoral and complete tibial section; thus, the periosteal femoral circumference must be estimated. However, neither BMRP 2006.4.4 nor NCSM 40000 provides good comparisons. The femur of BMRP 2002.4.1 is incomplete in length, so we cannot use relative femoral length to estimate femoral circumference. Similarly, the tibia of BMRP 2006.4.4 is incomplete in length, and the exposed tibia of NCSM 40000 is incomplete in circumference. We therefore took several approaches to approximate a femoral circumference for CGM calculations. First, we measured the perimeters of the two existing osteohistological sections of the femur of BMRP 2002.4.1 to get a minimum preserved circumference of 196 mm. Next, we measured the length of the tibia of BMRP 2002.4.1 (854 mm) in Blender ver.4.3 and compared this to the tibia length of NCSM 40000 (782 mm). The tibia of BMRP 2002.4.1 is 9.2% larger than NCSM 40000. Considering similar proportions in the femur results in an estimated minimum femoral circumference of 257 mm and a maximum radius of 40.84 mm for BMRP 2002.4.1. Finally, we compared the relative circumference of the tibiae of BMRP 2002.4.1 (238 mm) and 2006.4.4 (256 mm). The tibia of BMRP 2002.4.1 is 93% of the circumference of BMRP 2006.4.4. Applying this proportion to the femur results in a circumference estimate for BMRP 2002.4.1 of 239 mm. We consider this a minimum because the osteohistological section of BMRP 2006.4.4 was taken through the fibular crest. So, this difference is expected to be inflated by the proximal position of the BMRP 2006.4.4 section relative to that of 2002.4.1. In sum, our estimates produce a potential range of 239 - 257 mm for the femur of BMRP 2002.4.1, with the accurate circumference likely to fall at the upper end of this range, so we use the measurement of 250 mm (max radius 39.79 mm) in our resulting calculations.

BMRP 2006.4.4: BMRP 2006.4.4 is represented by complete transverse sections of the left femur (midshaft) and left tibia (proximal to midshaft). We measured the entire periosteal circumference of the femur from the osteohistological section (257 mm), then calculated the radius of the entire periosteal circumference approximated as a circle (40.903 mm). Cullen et al.⁸⁹ report a maximum CGM circumference (not periosteal circumference) for the femur of BMRP 2006.4.4 of 234.8 mm. This estimate most closely approximates our estimate for the circumference of CGM 5, rather than the periostealmost CGM we observed (CGM #10 = 257 mm).

FMNH PR 2081: FMNH PR 2081 is represented by an incomplete femoral transverse section produced by coring⁸⁹. This section is too fragmentary to apply the same methodology for BMRP 2002.4.1. Therefore, we generated CGM circumference data by using the maximum radius from the periosteal circumference (outermost LAG) reported in Cullen et al.⁸⁹ to estimate periosteal circumference (574.00 mm) and a maximum radius (91.35 mm).

TCMI 2003.66.1: TCMI 2003.66.1 is represented by a complete femoral transverse section. We measured the entire periosteal circumference of the femur from the osteohistological section (535 mm), then calculated the radius of the entire periosteal circumference approximated as a circle (85.15 mm).

All specimens: Once periosteal circumferences and maximum radii were derived, we measured centripetally along the anteriormost transect, capturing the longest growth record to calculate the radius of each CGM determined to represent the termination of an annual growth cycle, and used these measurements to calculate circumferences.

Body Mass Estimates.

Estimating body masses from stylopodial element circumference derived from CGM data requires an extant-scaling approach. We used the limb-scaling equation for bipeds in the MASSTIMATE package¹⁰³ (version 1.3) in R version 4.4.3¹⁰⁴ to calculate body masses at each CGM denoted as an annual growth boundary, applying Developmental Mass Extrapolation (DME)¹⁰⁵ adjustments:

$$\begin{aligned}\log BM_{\text{adult}} &= 2.754 \times \log(C_{\text{femur adult}}) - 0.683 \\ \text{Percent of Adult Size} &= (C_{\text{femur developing}}^3 / C_{\text{femur adult}}^3) \times 100 \\ BM_{\text{developing}} &= (C_{\text{femur developing}}^3 / C_{\text{femur adult}}^3) * BM_{\text{adult}}\end{aligned}$$

Developmental Mass Extrapolation assumes that body mass scales isometrically with linear skeletal measurements¹⁰⁵. This assumption has not been rigorously evaluated in extant taxa as an appropriate scaling methodology to account for potential bias in estimating the mass of skeletally immature growth stages¹⁰⁶, but is commonly employed as an ontogenetic correction. FMNH PR 2081, TCMI 2003.66.1, and NCSM 40000 represent skeletally mature individuals. Therefore, we derived skeletally mature (“adult”) body mass from the maximum femoral circumference measured directly from each individual. BMRP 2006.4.1 is not skeletally mature; however, there are no skeletally mature specimens referable to *Nanotyrannus lethaeus* to derive “adult” mass. The species referral of BMRP 2006.4.4 is unclear, but the animal was already larger than NCMS 40000 at death, so we used the maximum periosteal circumference of BMRP 2002.4.1 and 2006.4.4 for this purpose. We used the default correction factor (2) and the “phycor” estimation equation for cQE (a phylogenetically corrected relationship).

Neonatal Mass—We adopted the commonly applied approach to estimating neonatal mass^{89,91} derived from the approach of Grady et al.¹⁰⁷:

$$\begin{aligned}\text{Egg mass} &= 0.05 \times (\text{adult mass})^{0.46} \\ \text{Neonatal mass} &= \text{egg mass} * 0.7\end{aligned}$$

Applying DME to estimate neonatal femoral circumference from neonatal mass following Cullen et al.⁸⁹:

$$\text{Neonatal mass} = \text{adult mass} * (\text{neonatal femoral circum} / \text{adult femur circum})^3$$

These masses are held constant in our nonlinear models, but are used as a starting point for the mixed-model approach and ultimately retrocalculated.

SI.1.8. Table Summarizing Growth Model Results. Supported models ($<10 \Delta_i(\text{AICc})$) in **bold**. Best-fit model marked with asterisk (*). NLME models with biologically plausible neonatal mass retrocalculations denoted by double arrow ($\ddagger$). Best-fit model after ad hoc pruning of unrealistic neonatal mass retrocalculations following Lee and O'Connor⁸⁸ marked with a double asterisk (**).

Nonlinear Fixed-Effect Model Results							
Taxon	Specimen Number	Model	AICc	$\Delta_i(\text{AICc})$	Neonatal Mass (kg)	Age at Death (yrs)	Age at Death (yrs) (Weighted Model Average)
Nanotyrannus	NCSM 40000, BMRP 2002.4.1, BMRP 2006.4.4	Monomolecular	363.6075770	0.52	0.077	15.21972	22.25631
		Von Bertalanffy	363.2724981	0.19	0.077	17.83014	
		Gompertz	363.1685893	0.08	0.077	20.97340	
		Logistic*	363.0855017*	0.00	0.077	35.82280*	
		Extreme	363.68555532	0.60	0.077	53.43980	
		Innominate	3.660122e+02	2.93	0.077	72.08958	
Nanotyrannus lancensis	NCSM 40000	Monomolecular	1.296417e+02	39.57	0.07	16.10626	60.68516
		Von Bertalanffy	1.239184e+02	33.85	0.07	19.28997	
		Gompertz	121.014846879	30.94	0.07	23.11693	
		Logistic	111.475515555	21.41	0.07	40.21973	
		Extreme	90.9275619	0.86	0.07	56.79123	
		Innominate*	90.0699867*	0.00	0.07	68.46169*	
Nanotyrannus lethaeus	BMRP 2002.4.1	Monomolecular*	59.0471139	0.00	0.08	8.231173*	9.965562
		Von Bertalanffy	61.6263211	2.58	0.08	9.874291	
		Gompertz	63.0620445	4.01	0.08	11.834550	
		Logistic	66.61613986	7.57	0.08	20.739874	
		Extreme	70.373065931	11.33	0.08	30.718519	
		Innominate	74.263183748	15.22	0.08	38.775873	
Nanotyrannus sp.	BMRP 2006.4.4	Monomolecular	104.44689634	22.16	0.08	12.91115	27.58886
		Von Bertalanffy	96.60876335	14.32	0.08	14.95447	
		Gompertz	92.4587639	10.17	0.08	17.41089	
		Logistic*	82.2887357	0.00	0.08	29.40050*	
		Extreme	92.183980	9.90	0.08	43.40019	
		Innominate	104.949213250	22.66	0.08	55.95912	
Tyrannosaurus	FMNH PR 2081, TCM1 2003.66.1	Monomolecular	444.10404347	18.41	0.21	23.37774	38.50494
		Von Bertalanffy	437.5865756	11.89	0.21	26.85530	
		Gompertz	434.9673153	9.27	0.21	31.45137	
		Logistic	429.1380800	3.44	0.21	56.27551	
		Extreme*	425.69334586	0.00	0.21	87.94803*	

		Innominate	4.316968e+02	6.00	0.21	118.74375	
Tyrannosaurus	FMNH PR 2081	Monomolecular	2.913403e+02	64.66	0.22	22.44576	66.92430
		Von Bertalanffy	2.792323e+02	52.56	0.22	25.24401	
		Gompertz	272.88988489	46.21	0.22	29.00662	
		Logistic	251.3225920	24.65	0.22	48.59914	
		Extreme*	226.6757669	0.00	0.22	70.78881*	
		Innominate	2.569165e+02	30.24	0.22	89.45177	
Tyrannosaurus	TCMI 2003.66.1	Monomolecular	131.95034359	14.80	0.20	15.17582	69.40981
		Von Bertalanffy	129.66352740	12.51	0.20	18.74035	
		Gompertz	128.57759713	11.42	0.20	23.26662	
		Logistic	125.3727420	8.22	0.20	47.40775	
		Extreme	120.4185414	3.26	0.20	77.19431	
		Innominate*	117.1545657	0.00	0.20	101.35348*	
Nonlinear Mixed-Effect Model Results							
Taxon	Specimen Number	Model	AICc	$\Delta_i(\text{AICc})$	Neonatal Mass (kg)	Age at Death (yrs)	Age at Death (yrs) (Weighted Model Average)
Nanotyrannus	NCSM 40000, BMRP 2002.4.1, BMRP 2006.4.4	Monomolecular	268.423251461198	5.25	n/a	n/a	n/a
		Von Bertalanffy	263.962789996163	0.79	n/a	n/a	
		Gompertz*	263.17065505887	0	n/a	n/a	
		Logistic	265.821943102049	2.65	n/a	n/a	
		Extreme	276.327977353228	13.16	n/a	n/a	
		Innominate	289.491994912589	26.32	n/a	n/a	
Nanotyrannus lancensis	NCSM 40000 (all-species model)	Monomolecular†	n/a	n/a	0.128	15.13817	17.60522
		Von Bertalanffy†**	n/a	n/a	5.08	17.43198**	
		Gompertz*	n/a	n/a	20.8	17.629710*	
		Logistic	n/a	n/a	42	18.60724	
		Extreme	n/a	n/a	44.2	20.76802	
		Innominate	n/a	n/a	38.3	23.49756	
Nanotyrannus lancensis	NCSM 40000 (one-species model)	Monomolecular†**	116.40318	19.74164	0.13	15.08717**	21.69294
		Von Bertalanffy	113.34113	16.67959	5.12	17.37467	
		Gompertz	111.66961	15.00806	20.8	17.60848	
		Logistic	106.32874	9.66719	42.1	18.62348	

		Extreme*	96.66155	0	46.5	20.76044*	
		Innominate	97.94711	1.28557	43.3	23.51967	
Nanotyrannus lethaeus	BMRP 2002.4.1 (all-species model)	Monomolecular†	n/a	n/a	0.107	12.13633	14.45132
		Von Bertalanffy†**	n/a	n/a	1.84	13.78099**	
		Gompertz*	n/a	n/a	9.04	14.48114*	
		Logistic	n/a	n/a	19.4	16.64295	
		Extreme	n/a	n/a	28.7	19.19125	
		Innominate	n/a	n/a	26.1	22.03248	
Nanotyrannus lethaeus	BMRP 2002.4.1 (one-species model)	Monomolecular†*	75.7504744	0	0.211	7.239757*	8.19501
		Von Bertalanffy†	77.19735653	1.45	0.784	8.69240	
		Gompertz†	78.15032761	2.40	3.86	9.47115	
		Logistic	80.94125009	5.19	13.3	11.19692	
		Extreme	84.33922587	8.58	17.9	13.56253	
		Innominate	86.72208658	10.97	17.8	15.99994	
Nanotyrannus sp.	BMRP 2006.4.4 (all-species model)	Monomolecular†	n/a	n/a	0.101	7.16886	9.38234
		Von Bertalanffy†**	n/a	n/a	1.01	8.64747**	
		Gompertz*	n/a	n/a	5.77	9.41474*	
		Logistic	n/a	n/a	14.5	11.69978	
		Extreme	n/a	n/a	23.5	14.18319	
		Innominate	n/a	n/a	27.2	16.82378	
Nanotyrannus sp.	BMRP 2006.4.4 (one-species model)	Monomolecular†	104.99986	6.28651	0.776	11.91169	16.60649
		Von Bertalanffy†	102.25853	3.54518	1.22	13.74090	
		Gompertz†**	101.00956	2.29621	3.06	15.04131**	
		Logistic*	98.71334	0	16.4	17.112668*	
		Extreme	101.47298	2.75964	28.3	19.19075	
		Innominate	109.10979	10.3964 4	35.7	21.94260	
Tyrannosaurus	FMNH PR 2081, TCM I 2003.66.1	Monomolecular	382.6836756256 35	18.80	n/a	n/a	n/a
		Von Bertalanffy	377.0290641057 45	13.15	n/a	n/a	
		Gompertz	374.1806596756 72	10.30	n/a	n/a	
		Logistic	366.9430404897 52	3.06	n/a	n/a	
		Extreme*	363.8797173949 17	0	n/a	n/a	
		Innominate	379.5701340551 69	15.69	n/a	n/a	
Tyrannosaurus	FMNH PR 2081 (all-species model)	Monomolecular†	n/a	n/a	0.212	21.53974	34.95465
		Von Bertalanffy†**	n/a	n/a	1.31	24.28949**	

		Gompertz	n/a	n/a	12.3	26.34318	
		Logistic	n/a	n/a	80.9	30.56448	
		Extreme*	n/a	n/a	122	35.96675*	
		Innominate	n/a	n/a	115	42.23911	
Tyrannosaurus	FMNH PR 2081 (one-species model)	Monomolecular†	257.60840	18.30314	0.211	21.42253	35.00899
		Von Bertalanffy***	252.17443	12.86917	1.18	24.19216**	
		Gompertz	249.47118	10.16591	11.5	26.26173	
		Logistic	242.55300	3.24774	78.9	30.53159	
		Extreme*	239.30526	0	120	35.95038*	
		Innominate	251.74959	12.44433	114	42.21727	
Tyrannosaurus	TCMI 2003.66.1 (all-species model)	Monomolecular†	n/a	n/a	0.213	14.14256	28.35998
		Von Bertalanffy***	n/a	n/a	2.01	17.62028**	
		Gompertz	n/a	n/a	19	19.84976	
		Logistic	n/a	n/a	127	23.91255	
		Extreme*	n/a	n/a	210	29.38370*	
		Innominate	n/a	n/a	200	36.505867	
Tyrannosaurus	TCMI 2003.66.1 (one-species model)	Monomolecular†	135.51143	4.58332	0.213	14.16483	28.57842
		Von Bertalanffy***	134.37254	3.44442	2.02	17.54946**	
		Gompertz	133.83872	2.91060	18.9	19.77430	
		Logistic	132.46248	1.53437	127	23.88995	
		Extreme*	130.92812	0	209	29.37880*	
		Innominate	131.21734	0.28922	201	36.50413	
Tyrannosaurus	NCSM 40000, BMRP 2002.4.1, BMRP 2006.4.4, FMNH PR 2081, TCMI 2003.66.1 (all specimens as Tyrannosaurus model)	Monomolecular†	unable to generate	-	-	-	-
		Von Bertalanffy***	unable to generate	-	-	-	-
		Gompertz	703.12740	25.65608	n/a	n/a	n/a
		Logistic	687.19022	9.71890	n/a	n/a	n/a
		Extreme*	677.47132	0	n/a	n/a	n/a
		Innominate	698.13895	20.66763	n/a	n/a	n/a

SL1.9. Table of Geologic Age Data used for branch scaling and FBD.

Age Reference	Taxon	Formation	Member/Informal Division/Locality	Min Age	Max Age	Mean/Most Likely
Allain ¹³	<i>Dubreuillosaurus valesdunensis</i>	Calcaire de Caen Formation		165.30	168.20	166.75
Conrad ¹⁰⁸	<i>Compsognathus longipes</i>	Solnhofen Formation		143.10	149.20	146.15

Zhao and Currie ¹⁰	<i>Monolophosaurus jiangi</i>	Wucaiwan Formation	Junggar Basin	161.50	174.70	168.10
Xu et al. ¹⁰⁹	<i>Sinraptor dongi</i>	Shishugou Formation		160.40	162.20	161.30
Rogers et al. ¹¹⁰	<i>Majungasaurus crenatissimus</i>	Maevarano Formation		66.00	72.20	69.10
Nydam and Cifelli ¹¹¹	<i>Acrocanthosaurus atokensis</i>	Antlers Formation		100.50	121.40	110.95
Xu et al. ¹⁰⁹	<i>Zuolong salleei</i>	Shishugou Formation		160.40	162.20	161.30
Chure and Loewen ¹⁷	<i>Allosaurus jimmadseni</i>	Morrison Formation	Salt Wash Member	152.77	157.32	155.05
Galli et al. ¹¹² ; Kowallis et al. ¹¹³ 2007	<i>Allosaurus fragilis</i>	Morrison Formation	Brushy Basin Member	149.43	152.77	151.10
Galli et al. ¹¹² ; Kowallis et al. ¹¹³	<i>Stokesosaurus clevelandi</i>	Morrison Formation	Brushy Basin Member	149.43	152.77	151.10
Ramezani et al. ¹¹⁴	<i>Gorgosaurus sp. nov.</i>	Dinosaur Park		74.44	76.47	75.46
Ramezani et al. ¹¹⁴	<i>Gorgosaurus libratus</i>	Dinosaur Park		74.44	76.47	75.46
Ramezani et al. ¹¹⁴ ; Rogers et al. ¹¹⁵	TCMI 2001.81.1	Two Medicine formation		74.40	82.40	77.72
Brusatte & Benson ³⁵	<i>Juratyrant langhami</i>	Kimmeridge Clay Formation		148.00	152.00	150.00
Naish and Cau ³⁶ ; Naish et al. ¹¹⁶	<i>Eotyrannus lengi</i>	Wessex Formation	L11 Grange Chine Black Band	121.40	125.77	123.59
Gallagher ¹¹⁷	<i>Dryptosaurus aquilunguis</i>	New Egypt Formation		66.00	69.00	67.50
Carr et al. ⁴⁷	<i>Appalachiosaurus montgomeriensis</i>	Dermopolis Formation		76.50	78.50	77.50
Tucker et al. ¹¹⁸	<i>Moros intrepidus</i>	Cedar Mountain Formation	upper Mussentuchit Member	99.41	99.43	99.42
Cilliers et al. ¹¹⁹	<i>Suskityrannus hazelae</i>	Moreno Hill Formation	lower member	88.60	90.90	89.75
Voris et al. ⁴⁸ ; Fowler ¹²⁰	<i>Thanatotheristes degrootorum</i>	Foremost Formation	Taber Coal Zone & Herronton Sandstone	79.52	80.17	79.85
Carr et al. ⁵²	<i>Daspletosaurus horneri</i>	Two Medicine Formation	upper member	74.38	75.03	74.71
Warshaw and Fowler ³	<i>Daspletosaurus wilsoni</i>	Judith River Formation		75.64	77.00	76.32
Ramezani et al. ¹¹⁴	UALVP_52981	Oldman Formation	UALVP 52981 was found slightly below the Field Station Bentonite	76.71	76.73	76.72
Ramezani et al. ¹¹⁴	<i>Daspletosaurus torosus</i>	Oldman Formation		74.29	76.72	76.72
Eberth and Kamo ¹²¹	<i>Albertosaurus sarcophagus</i>	Horseshoe Canyon	Horsethief, Morrin, and lowermost Tolman	69.60	72.20	70.90
Eberth and Kamo ¹²¹	<i>Albertosaurus sp. nov.</i>	Horseshoe Canyon	Tolman Member	69.60	70.90	70.25
Dalman et al. ¹²²	<i>Dynamoterror dynastes</i>	Menefee Formation	Allison Member	80.00	83.50	81.75

Fowler ¹²⁰	<i>Bistahieversor sealeyi</i>	Kirtland Formation	Hunter Wash Member	74.57	75.17	74.87
Beveridge et al. ¹²³	<i>Lythronax argestes</i>	Wahweap Formation	Reynolds Point Member	81.48	81.50	81.49
Loewen et al. ⁶⁸ ; Ramezani et al. ¹¹⁴	<i>Teratophoneus curriei</i>	Kaiparowits Formation	upper middle member, The Blues	75.36	76.00	75.68
Loewen et al. ⁶⁸ ; Ramezani et al. ¹¹⁴	UMNH_VP_16690	Kaiparowits Formation	lower middle member, Horse Mountain	76.00	76.63	76.31
Fiorillo and Tykoski ⁷⁰ ; Fowler ¹²⁰	<i>Nanuqsaurus hoglundi</i>	Prince Creek Formation		69.99	70.01	70.00
Dalman et al. ⁷⁴	<i>Tyrannosaurus mcraeensis</i>	Hall Lake Formation	43 m above base of the Hall Lake Formation	70.90	72.70	71.80
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	CMNH_7541	Hell Creek Formation		66.00	67.00	66.50
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	NCSM_40000	Hell Creek Formation	lower member	66.00	67.00	66.50
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	KUVP_156375	Hell Creek Formation		66.00	67.00	66.50
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	BMRP_2006.4.4	Hell Creek Formation		66.00	67.00	66.50
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	BMRP_2002.4.1	Hell Creek Formation	upper member	66.00	67.00	66.50
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	FMNH_PR_2081	Hell Creek Formation		66.00	67.00	66.50
Fowler ¹²⁰ ; Roberts et al. ¹²⁴	<i>Tyrannosaurus rex</i>	Hell Creek Formation		66.00	67.00	66.50
Zhang et al. ¹²⁵	<i>Zhuchengtyrannus magnus</i>	Xingezhuang Formation		81.00	83.00	82.00
youngest following Tanabe et al. ¹²⁶ , oldest set at Maastrichtian boundary	<i>Alioramus altai</i>	Nemegt Formation		66.70	72.20	69.45
youngest following Tanabe et al. ¹²⁶ , oldest set at Maastrichtian boundary	<i>Tarbosaurus bataar</i>	Nemegt Formation		66.70	72.20	69.45
Xu et al. ¹⁰⁹	<i>Guanlong wucaii</i>	Shishugou Formation		159.70	160.40	160.05
Zheng et al. ⁶⁹	<i>Asiatyrannus xui</i>	Nanxiong Formation		66.00	72.20	69.10
Zheng et al. ⁶⁹	<i>Qianzhousaurus sinensis</i>	Nanxiong Formation		66.00	72.20	69.10
Brusatte et al. ⁴⁰	<i>Timurlengia euotica</i>	Bissekty Formation	middle - upper Turonian	90.00	92.00	91.00
Suarez et al. ¹²⁷	<i>Xiongguanlong baimoensis</i>	Xiagou Formation	White Ghost Castle field area, Yujingzi Basin	115.00	123.00	119.00
Chang et al. ¹²⁸	<i>Yutyrannus huali</i>	Yixian Formation		122.10	129.70	125.90
Chang et al. ¹²⁸	<i>Dilong paradoxus</i>	Yixian Formation	lower sand beds	122.10	129.70	125.90
Chang et al. ¹²⁸ ; Zhang et al. ¹²⁵	<i>Sinotyrannus kazuoensis</i>	Jiufotang Formation	lower part	121.27	122.10	121.69

Averianov and Sues ¹²⁹	<i>Alectrosaurus olseni</i>	Iren Dabasu Formation		83.60	85.70	84.65
Wu et al. ⁴⁴	<i>Junbeisaurus wangi</i>	Huiquanpu Formation	upper	66.00	100.50	83.25
Rauhut et al. ²⁸	<i>Proceratosaurus bradleyi</i>	Great Oolite Group		165.30	168.20	166.75
Averianov et al. ^{27,130}	<i>Kileskus aristotocus</i>	Itat Formation		165.30	168.20	166.75
Voris et al. ⁴²	<i>Khankhuuluu mongoliensis</i>	Bayanshiree Formation	upper	83.6	93.9	88.75

SI.1.10. Phylogenetic Protocol and Analyses.

SI.1.10.i. Matrix Building.

Resolving the phylogenetic positions of *Nanotyrannus lancensis* and *N. lethaeus* presents a difficult problem. Current studies of tyrannosauroid systematics overwhelmingly use one of two ingroup matrices. One of these is a descendant of that originally published in 2010 by Carr and Williamson², which has been iteratively expanded and revised^{52,131,132}. We began with a recent version of this matrix⁵² as modified by Zanno et al. in the description of *Moros intrepidus*⁴³ and, for brevity, refer to it as C17. The tyrannosauroid-specific characters in this dataset were also integrated into the Theropod Working Group (TWiG) matrix¹³³, a broader coelurosaur matrix comprising over 800 characters. Given that *Nanotyrannus lancensis* is indisputably a tyrannosauroid, we did not use the TWiG matrix for our analyses and instead focused on ingroup matrices. An alternative matrix was presented by Loewen et al.⁶⁸, L13 for brevity. The L13 phylogeny differs from C17 in several respects: most significantly, it recovers alioramin tyrannosauroids as outside of Tyrannosauridae, the genus *Daspletosaurus* as paraphyletic (also suggested by the recent description of *Daspletosaurus wilsoni*³), and the tyrannosaurids *Lythronax argestes*, *Teratophoneus curriei*, and *Bistahieversor sealeyi* as more closely related to *Tyrannosaurus rex* than is *Daspletosaurus*. Although these differences do create fundamental discordance between topologies, it is worth noting that most of these differences equate to the movement of taxa one or two steps from their position in the other matrix. The most significant discordance is the position of *Bistahieversor sealeyi*, which is recovered as the outgroup to Tyrannosauridae by C17 and its ancestors, not deeply nested within Tyrannosauridae as in L13.

Brusatte and Carr¹³² extensively reviewed L13 and integrated many of its characters into their matrix (which are retained in its derivative, C17) but discarded others they considered to be overly correlated with general skull proportions, along with invariant or autapomorphic characters. We do not necessarily agree with this assessment; however, given that the proportions of the skull of *Nanotyrannus* differ significantly from those of many derived tyrannosauroids and that skull proportions are highly ontogenetically variable in amniotes generally, we considered this aspect of L13 as potentially problematic for our study. Perhaps more relevant, C17 is used in the most recent tyrannosaur systematics because it incorporates much data from its antecedents and L13^{3,37,43,48,55,134-137}. Despite its presumed benefits, we find C17 unsuitable to test our question in its published state. We scrutinized the character matrix and found that many characters were defined in problematic ways—for example, “absence coding” (*sensu* Simões et al.¹³⁸), in which “absence” is incorporated into a multistate transformation series.

Although this can be defensible, contingent coding (*sensu* Brazeau¹³⁹; viz., coding presence and absence of a trait as its own character and any subsequent variations of that trait as subsidiary characters that are inapplicable if the trait is absent) is preferable given the recent proliferation of analytical approaches to accommodating inapplicable character data. It has also been demonstrated that contingent coding performs better under Bayesian analytical protocols, further incentivizing our conversion of many C17 characters to a contingent coding scheme.

Far more problematic is that C17 was built under a set of operational assumptions regarding tyrannosauroid ontogeny and variation that are contradicted by our study. Carr⁷⁹ was the first to formally synonymize *Nanotyrannus* with *Tyrannosaurus*; he has maintained this taxonomic opinion in subsequent papers and used principles arising from Carr⁷⁹ in interpreting the anatomy and taxonomy of other tyrannosauroids, including *Bistahieversor*², *Alioramus altai*⁶⁴, and *Daspletosaurus*⁵². Our detailed review of the C17 character list found that many characters articulated by other authors in favor of a distinct *Nanotyrannus* have not been included in any form, presumably because they were considered to represent ontogenetic variation with no phylogenetic significance. We consider this approach problematic in two respects. First, *Nanotyrannus* differs from *Tyrannosaurus rex* adults in many other characters that *are* included in C17; under a consistent approach to character selection, we fail to understand why these characters would not also be discarded on the basis of being ontogenetically variable. Second, many of the excluded characters distinguishing *Nanotyrannus* from *Tyrannosaurus* are shared with other tyrannosauroids, such as *Gorgosaurus libratus*⁸⁸, and therefore cannot be ascribed to ontogenetic variation alone.

Additionally, and most concerning for our study, several characters in C17 explicitly address the condition in juveniles compared to adults within one operational taxonomic unit, presumably based on ontogenetic changes then hypothesized to occur in *T. rex*. No criteria are given for determining which animals are “juveniles” or “adults,” which makes these characters challenging to score, and some characters relate to ontogenetic transformations that are invalidated by our study (e.g., proposed loss or gain of a quadratojugal foramen during ontogeny). Finally, some characters are seemingly constructed under the presumption that *Nanotyrannus* was an immature *T. rex*, and attempt to circumvent ontogenetic variation via character construction. For instance, C17:261 breaks the number of maxillary teeth into two states: “13 or more” or “less than 13 in the largest adult specimens”. Not only is it unlikely that tyrannosauroids lost teeth as they grew⁸⁶, but even if tooth count *was* ontogenetically variable, this character is constructed in a way that obscures most of the variation in tyrannosauroid tooth count (which varies between 11 and 18 maxillary teeth) to accommodate proposed ontogenetic transformations *a priori*. It is unclear if a taxon known only from an immature specimen can logically be coded for this character or in the matrix as a whole.

For comparability with prior work, we initially scored *N. lancensis* and *N. lethaeus* in C17; all *Nanotyrannus* specimens formed a polytomy, placed as sister to Eutyranosauria (results not shown). However, following our reasoning above, we chose to re-evaluate morphological transformations within tyrannosauroid evolution and generate a phylogenetic character list and matrix *de novo* to conduct a robust test of the phylogenetic placement of *Nanotyrannus*. To do so, we studied over 119 tyrannosauroid specimens firsthand and captured three-dimensional morphological data.

We began by critically evaluating each character in C17 for possible inclusion in our matrix based on first-hand observations across our specimen sample. Characters prescribing contentious ontogenetic transformations or for which we could not replicate the range of published scorings were discarded. We retained 149 defensible and informative characters in their original form (33.79% of the new matrix). A further 140 (31.75%) of our characters were based upon characters in C17, but reconceptualized and subsequently heavily modified. These included cases in which we could not replicate prior scorings (but could understand what morphology was being described in the prior character), we split up characters to permit contingent coding, re-arranged states to correct ordered morphoclines (in which intermediate states were at the end of a transformation series), we added or combined states to capture the range of variation we observed or to fill logically unscorable gaps, or in which we fixed characters that were improperly constructed. We also added 152 new characters (34.47% of new matrix) based on our observations. These additions include a suite of new characters that can now be recognized due to the complete preservation and unique anatomy of the forelimb of *Nanotyrannus*, as well as many unique observations and characters drawn from anatomical descriptions that have not yet been incorporated into a phylogenetic matrix. We re-scored all taxa, integrating previously published scorings only when we could not evaluate scorings firsthand or from the published literature (first-hand versus scoring from the literature noted in Supplementary Information 1.2). Due to the significant alterations to matrix construction and numerous differences of taxonomic opinion between us and the authors of C17 we did not attempt to record all cases in which our scoring of a taxon differed from that of C17. We consider our phylogenetic matrix the first in a “lineage” of new matrices, because we intend to iteratively revise and refine it as we continue researching a multitude of new tyrannosauroid specimens, focusing on different regions of the tyrannosauroid phylogeny. We also expect the matrix to be improved by different core groups of workers under distinct sets of operational and philosophical criteria.

SI.1.10.ii. Outgroup Selection.

We have also altered the outgroup selection strategy of C17. The original matrix used several outgroups to polarize character state transformations. These include *Allosaurus* (a non-coelurosaur), *Compsognathus* (an early diverging coelurosaur), and composite OTUs of Maniraptora and Ornithomimosauria. However, this outgrouping strategy has several drawbacks. Composite OTUs conflate the character data across multiple species and are generally discouraged, but in this case, they are particularly problematic. Ornithomimosauria and Maniraptora are diverse clades with significant ingroup morphological diversity. This is particularly true in Maniraptora, which includes therizinosaurs, oviraptorosaurs, dromaeosaurids, troodontids, and birds, at minimum. Both groups also notably lack a significant fossil record of early-diverging forms, causing their early history (the part of their evolution most informative for character polarization within tyrannosauroids) to be poorly understood. Character data are most readily available for highly derived species that lived in the Late Cretaceous. Proceratosauridae emerged by the Bathonian, indicating that the origin of Tyrannosauroidea occurred by the Middle Jurassic at the latest, 80 million years before the best fossil material of most maniraptorans. Furthermore, all of these outgroups except *Allosaurus* appear to form a clade exclusive of Tyrannosauroidea within Coelurosauria (Maniraptoromorpha and/or Neocoelurosauria, which have different definitions but currently include the same array of taxa), meaning that they need not represent the plesiomorphic condition for Tyrannosauroidea.

We follow the recommendations of Carrano et al.¹⁴⁰ in employing an alternative outgroup strategy focused on sampling early-diverging members of theropod clades positioned stemward of Tyrannosauroida within the broader clade Averostra. We selectively include those taxa that are early diverging within their clades, known from reasonably complete skeletal material, and/or are either comprehensively described or accessible to us for firsthand study. Our selected outgroups include *Majungasaurus crenatissimus* (known from many exquisite specimens, including a fully digitized skull), *Monolophosaurus jiangi* (of uncertain affinity but considered either a basal tetanuran or a basal carnosaur), *Dubreuillosaurus valesdunensis* (an intermediate megalosaur), *Sinraptor dongi* (a metriacanthosaur, part of an early-diverging carnosaur lineage), and *Acrocanthosaurus atokensis* (a large-bodied allosauroid). Furthermore, we include the small-bodied coelurosaurian *Zuolong saleeii*, which has been recovered in several analyses as the earliest diverging coelurosaur currently known as an additional outgroup. We retain both *Compsognathus longipes* and *Allosaurus fragilis* as outgroups.

Two small theropods from the Morrison Formation, *Coelurus fragilis*, and *Tanycolagreus topwilsoni*, have been recovered as early diverging tyrannosauroids in prior analyses. However, ongoing study of the former taxon¹⁴¹ suggests a more crownward placement for these taxa. Therefore, we do not include them herein.

SI.1.10.iii. Inapplicable Character Treatment.

Recently, several authors have proposed general analytical solutions for the longstanding problem of the handling of inapplicable data in phylogenetic analysis. The classic “tail absent, red, or blue” problem first articulated by Maddison¹⁴² has received significant discussion in the literature, which we will not reiterate here. However, we consider the problem introduced by the most accepted method for dealing with this method—contingent, or reductive, coding—to be a significant one. The most-used phylogenetic algorithms will apply some state for each character to each internal node, and therefore, a node where a primary character is absent will nevertheless have an optimization for the secondary character, which logically does not apply. To use the example of Goloboff et al.¹⁴³, the algorithm may optimize a node such that a tail is absent, but the absent tail is blue—clearly, a biologically meaningless optimization.

Analytically, this is a concern only for our analyses using maximum parsimony because the Fitch algorithm uses “down-pass” and “up-pass” phases to optimize ancestral states, whereas phylogenetic tree reconstruction using Bayesian inference relies on Felsenstein optimizations (“down-pass” only). Matrices comprising an unmodified contingent coding scheme are demonstrated to perform as well using Bayesian inference as matrices correcting for inapplicable characters resulting from contingent coding when analyzed in a maximum parsimony framework¹⁴⁴. For this reason, we only apply contingent coding corrections to our matrices intended for parsimony analyses. Below, we describe our approach to modifying the matrix to appropriately handle contingent coding in a maximum parsimony framework.

Two authors have recently published accessible approaches to deal with this problem. Brazeau et al.¹⁴⁵ introduced a strategy in which separate up- and down-passes penalize topologies in which a character becomes applicable multiple times¹⁴⁵. This method is implemented in R via the package “TreeSearch” and, because each character is optimized separately, does not require any information about which characters are subordinate to which other characters. However, more recent work has criticized this

approach and presented an alternative solution, in which complexes of superordinate and subordinate characters are combined into step-matrices and analyzed as ‘x-transformations’. This method is implemented in TNT v1.6. The x-transformation approach requires that superordinate and subordinate characters be explicitly linked *a priori*, and appears more methodologically robust¹⁴³. While x-transformations do appear superior, they introduce a difficult limitation in how many characters and states may relate to a superordinate character. We therefore attempted to use both approaches in our work; however, we found that analyses in R using “TreeSearch” failed to arrive at well-resolved topologies even after running for many hours. Given both the faster speed and superior reasoning behind x-transformations, we made several changes to our matrix to meet the comparatively stringent requirements of that method, and did not pursue the former approach further. The decisions were as follows:

1. In our original matrix, the presence of a maxillary fenestra was denoted by a character (Character 13) with seven subordinate characters, exceeding the permitted number of subordinate character states. Only two taxa (*Majungasaurus crenatissimus* and *Monolophosaurus jiangi*) lack a maxillary fenestra, and because both were constrained as outgroups we did not treat characters describing the maxillary fenestra as subordinate to Character 13.
2. We scored our matrix treating two characters as dependent upon the presence of both a caudolateral and a caudomedial process of the nasal. X-transformations do not permit a character to depend upon two characters that are equal in hierarchy. However, the only taxon to lack these processes is *Majungasaurus crenatissimus*, so we did not convert these characters to an x-transformation.
3. Our original matrix treated the presence of a lacrimal cornual process as superordinate to four other characters, two of which had three states. This creates a 37-state space, exceeding the 32-state limit of TNT. To resolve this, we combined states 1 and 2 of character 69 (describing increasing degrees of lacrimal rugosity), bringing the number of unique states to 25, and treating lacrimal rugosity as a simple presence-absence character.
4. Our original matrix recognized an intermediate state in the presence or absence of a postorbital cornual process, in which it was present only as a rugose strip of bone. Superordinate characters under x-transformations must have only two states (absent or present). We redefined this character complex, with a primary superordinate character describing the presence of postorbital ornamentation, a subordinate character describing whether that ornamentation forms a cornual process, and four following characters subordinate to the postorbital cornual process that describe its morphology and position.
5. The character relating height of the caudal palatine recess to the height of the rostral palatine recess was considered only as contingent upon the presence of the rostral pneumatic recess, because there are no taxa in our dataset in which a rostral palatine recess is present but a caudal palatine recess is absent.
6. Character 124 (expansion of quadratojugal-squamosal flange) is a 4-state ordered morphocline, for which states 2 and 3 allow coding of the two subsequent characters. X-transformations require the superordinate character to be a simple absence/presence character, so we were unable to implement it here - though we note that all taxa within our area of interest have state 2 or 3, so this is unlikely to affect the position of *Nanotyrannus* in our analysis.

7. Character 352 (number of phalanges in digit III) was only confidently scored as “-” in *Tyrannosaurus rex*, rendering it unnecessary to convert character 351 to fit an x-transformation scoring scheme.

SI.1.10.iv. Analytical Protocol

We employed maximum parsimony optimality and maximum likelihood methods (Bayesian inference, with and without total-evidence dating) to explore the evolutionary relationships of tyrannosauroids.

Maximum Parsimony

We employed both equal-weights and implied-weights parsimony, running multiple iterations of the latter to explore the effect of different concavity constant (K) values, which ranged from 6 to 24. Implied weights allow the phylogenetic analyses to down-weight heavily homoplastic characters, and typically outperform equal-weights parsimony¹⁴⁶⁻¹⁴⁸. Prior work has suggested $K=12$ to be an optimal value^{147,149}, and this is the parsimony topology we present in the main text; we note, however, that we generally found limited discordance between parsimony tree topologies even under varying settings. In all parsimony analyses, *Nanuqsaurus hoglundi* and *Dynamoterror dynastes*, which are known from only very fragmentary material^{66,70}, acted as wildcards and were pruned from our analyses *a priori*. Clade support was calculated as the relative Bremer support¹⁵⁰, facilitating comparison between equal- and implied-weights parsimony, in which more common absolute Bremer supports are difficult to interpret. Relative Bremer support describes the relative amount of character evidence supporting and contradicting a node¹⁵¹. For all analyses, multistate characters that contained apparent morphoclines were treated as ordered, adding steps for transitions between nonadjacent character states: this included 48 total characters: 3, 4, 12, 14, 25, 34, 36, 58, 63, 67, 83, 90, 93, 103, 111, 120, 124, 129, 157, 160, 161, 163, 165, 175, 190, 219, 220, 221, 238, 247, 251, 253, 254, 266, 281, 283, 287, 298, 326, 336, 338, 351, 352, 354, 365, 395, 404, and 436.

Analysis under equal weights yielded 100 most parsimonious trees (MPTs) with a score of 1490. Analysis under $K = 24$ yielded 75 MPTs with a score of 33.32779. Analysis under $K = 12$ yielded 15 MPTs with a score of 59.87241. Analysis under $K = 6$ yielded 15 MPTs with a score of 97.44051.

Our parsimony analyses yielded broadly concordant results, consistently placing *Nanotyrannus* outside of Tyrannosauridae and consistently placing BMRP 2002.4.1 outside of a clade containing all other *Nanotyrannus* individuals we scored, providing strong evidence in support of the taxonomic distinction of *Nanotyrannus lethaeus* (known only from BMRP 2002.4.1 at present) and *Nanotyrannus lancensis*. Trees obtained under equal weights and $K = 24$ were identical, except that the latter parameter prevented *Moros intrepidus* from exhibiting wildcard behavior and instead placed it within Nanotyrannidae. Trees obtained under $K = 12$ and $K = 6$ differed primarily in the placement of *Lythronax argestes*. Under equal weights and $K = 24$, this taxon was placed in a clade with UMNH VP 16690, *Bistahieversor sealeyi*, and *Jinbeisaurus wangi*, a clade recovered as the earliest-diverging group of albertosaurines. Under $K = 12$ and $K = 6$, *Lythronax* instead is the outgroup of a clade comprising *Zhuchengtyrannus magnus*, *Tarbosaurus bataar*, and *Tyrannosaurus*. The only topological difference between $K = 12$ and $K = 6$ is

that in the latter, *Teratophoneus* is the sister taxon to an undescribed albertosaurine UALVP 52981, rather than an outgroup to UALVP 52981, *Gorgosaurus*, and *Albertosaurus* as in all other topologies.

Maximum Likelihood

We implemented phylogenetic analyses using Bayesian inference in MrBayes ver. 3.2.7a¹⁵² variably deploying two data partitioning schemes with and without a clock model of geochronological metadata for a total of four protocols: Protocol 0 (default): (part_N) Protocol 1 (part_Y1); Protocol 2 (part_Y2); and Protocol 3 (Part_Y2_FBD, favored partition with tip-dating). For Partition Scheme 1 (Par_Y1), we created character sets following standard skeletal divisions (skull (“cranial”), vertebral column (“axial”), pectoral girdle and forelimb (“arm”), and pelvic girdle and hindlimb (“leg”) resulting in a minimum of 36 and maximum of 287 characters per partition across four partitions. For Partition Scheme 2 (Par_Y2), we sought to link character complexes with evidence for integration. We, therefore, created character sets recapitulating the skull element modules identified by geometric morphometric data in Felice et al.¹⁵³: premaxilla, maxilla, nasal (“rostrum”); quadrate, jugal, quadratojugal (“suspens”); parietal, frontal, postorbital, lacrimal, prefrontal, squamosal (“skull roof”); supraoccipital, basioccipital, and other braincase elements (“braincase”). We then divided the remaining characters into “palate,” “mandible,” “teeth,” “axial,” “arm,” and “leg” charsets, for a total of 10 partitions. Partitions were unlinked to allow independent character evolution between morphological modules^{149,154}.

We used the Mkv Model with an ascertainment bias correction for the unobservability of invariant characters (functionally excludes autapomorphies in the data matrix) and lognormal character rate variation, shown to be favored over gamma rate distributions for discrete morphological data with slow evolvability¹⁵⁵ (Harrison and Larsson 2014). We executed 500 million generations, with four runs and four chains, with three swaps per cycle and a 25% burn-in sampling every 1000 generations. We used split frequency rather than likelihood trends to assess stationarity, terminating analyses when split frequency values descended below a threshold of 0.01.

We mirrored the same additive character designations as in parsimony analyses. However, MrBayes has a limit on the number of six states for additive characters. This only affected two characters in our matrix (tooth counts). To accommodate, we rescored states for characters 281 and 283, combining states 5-7 for character 281 (state 5 now equal to or greater than 16 teeth) and 5-9 for character 283 (state 5 now equal to or greater than 17 teeth). These coding changes affected *Majungasaurus* (281), *Monolophosaurus* (283), *Allosaurus fragilis* (281), *Allosaurus jimadseni* (283), *Proceratosaurus* (283), *Compsognathus* (281 & 283), *Proceratosaurus* (281), *Kileskus* (281), NCSM 40000 (281), *Timurlengia* (281), *Alioramus altai* (281 & 283), and *Daspletosaurus horneri* (281). To maintain consistency with analyses using maximum parsimony, we enforced the same topological constraints and excluded two OTUs a priori: *Dynamoterror*, *Nanuqsaurus*.

Our final analyses (Protocol 4) modeled tyrannosauroid evolution and divergence ages using the fossilized bird-death (FBD) process with diversified sampling and otherwise unaltered model choice, parameters, and priors, employing only our favored partitioning scheme (part_Y2). Nexus files with MrBayes blocks and log files for all protocols are included as Supplementary Information 11–14.

Studies have emphasized the potential value of including autapomorphies for model-based inference (e.g., Matzke and Irmis¹⁵⁶), a position with which we agree. However, we question whether, in practice, tyrannosauroid autapomorphies derived from existing published diagnoses can be appropriately sourced for this purpose in their current form. We are wary of introducing additional biases into rate estimations via uneven sampling of autapomorphies from inconsistently constructed diagnoses that span a century in the rapidly changing landscape of tyrannosauroid taxonomy. The inclusion of autapomorphies is only shown to have a substantial effect in tip-dated analyses of characters with clock-like behavior¹⁵⁶, and even in these circumstances, effects are limited to mean rate parameters, with little demonstrable impact on topology. Thus, we do not expect impacts on our main conclusions from the variable-only sampling strategy we employ here. To assess model sensitivity (particularly topological effects), we instead rely on multiple protocols (as described above), including tip-dated and non-tip-dated analyses.

SI.1.10.v. Additional Discussion of Phylogenetic Results

Proponents of a valid *Nanotyrannus* have typically inferred an albertosaurine affinity for the genus; however, *Nanotyrannus* lacks albertosaurine synapomorphies such as a median interpremaxillary process of the nasal, a nasal “blade”, long caudomedial processes of the nasal, long prefrontolacrimal processes of the frontal, a dorsoventrally tall vomeropterygoid process of the palatine, and a distinct notch in the postorbital ramus of the squamosal. Other authors have floated affinities with alioramins. *Nanotyrannus* lacks alioramin synapomorphies such as a laterally directed jugal hornlet, an elongated ventral postorbital process of the squamosal, an acuminate caudal margin of the choana, and a proximally restricted lateral malleolus of the tibia; however, both alioramins and *N. lancensis* lack a maxillary flange, and the two taxa do share features of the braincase such as a long, low cultriform process and presence of a sinus cavernosus. The sinus cavernosus and absence of a maxillary flange are seen in more basal theropods, and optimize in our analysis as symplesiomorphies; we predict that they are unknown in more basal tyrannosauroids due to missing data. *Nanotyrannus* and *Alioramus* do appear to uniquely share a communication between the rostral and caudal palatine recesses, which our analysis infers to be homoplastic and may relate to generally increased pneumaticity in the skull in both clades.

SI.1.11. Note on *Stygivenator*

A small, fragmentary theropod skull from the Hell Creek Formation (LACM 28471), known as the “Jordan theropod”, was first reported in 1978 by Molnar¹⁵⁷, who considered it to represent a dromaeosaurid. The specimen was first recognized as tyrannosauroid by Paul¹⁵⁸, who placed it in the genus “*Aublysodon*” and named it after its initial describer as “*Aublysodon*” *molnaris*. “*Aublysodon*” is a tooth taxon, based on a single lectotype specimen (ANSP 9535) that is now lost⁸⁰. The specimen was redescribed by Molnar and Carpenter¹⁵⁹ who referred it to the species *Aublysodon mirandus*” under the assumption that the mesialmost preserved tooth in the maxilla was a premaxillary tooth. “*Aublysodon*” was diagnosed as an unserrated, chisel-shaped premaxillary tooth—we now recognize that these features are common to “mid-grade” tyrannosauroids and plesiomorphically retained by *Nanotyrannus*^{38,43,82}, and as such *Aublysodon* is a *nomen dubium* regardless of whether the lectotype is located, or if casts of the lectotype were proposed as a neotype. Olshevsky¹⁶⁰ considered the “premaxillary” tooth of LACM 28471 to be significantly narrower in lateral view than the lectotype of “*Aublysodon mirandus*”, and transferred it to a new genus, creating the new combination *Stygivenator molnari*. Following Carr and Williamson⁸⁰,

this taxon has generally been considered to be a junior synonym of *Tyrannosaurus rex* based on a very young specimen. Longrich and Saitta⁹⁷ recently proposed that NCSM 40000 was diagnostically distinct from *Nanotyrannus lancensis* and may instead represent *Stygivenator*. Longrich and Saitta⁹⁷ did not study NCSM 40000, nor to our knowledge examine the specimen firsthand, instead apparently basing their referral on photographs of the specimen published in a popular magazine. This proposal was recently repeated by Paul¹⁶¹, who referred NCSM 40000 to *Stygivenator sp.*

We have studied LACM 28471 firsthand, and based upon our observations we consider it undiagnostic and recommend treating “*Stygivenator molnari*” as a *nomen dubium*. The mesialmost tooth is not a premaxillary tooth; instead, we agree with Carr and Williamson⁸⁰ that it represents a “premaxillariform” maxillary tooth, which is common to derived tyrannosauroids (present in *Nanotyrannus* and most albertosaurines, and inferred in alioramins⁶⁴). The “hooked” dentary of LACM 28471 with an “elevated” first three dentary teeth described in various terms by Olshevsky¹⁶⁰ and Longrich and Saitta⁹⁷ is not a natural feature, as it is not present on the contralateral (right) dentary; we are as of yet unsure whether it represents taphonomic alteration or pathology (CT data will be required to assess the condition), but in either case it is not a valid autapomorphy. Additionally, it is important to note that Longrich and Saitta⁹⁷ proposed that NCSM 40000 represented “*Stygivenator*” because they interpreted it as differing from BMRP 2002.4.1, which they treated as an exemplar of *Nanotyrannus lancensis*—however, our data support BMRP 2002.4.1 as the distinct taxon. LACM 28471 may preserve one *Nanotyrannus* autapomorphy—a small or absent subnarial foramen. However, damage to the rostral region of the maxilla precludes confidence in this assessment. If LACM 28471 is proven to be referable to *Nanotyrannus*, its comparatively narrower rostral end of the antorbital fenestra (which does compare favorably to NCSM 40000) may suggest referral to *Nanotyrannus lancensis*. LACM 28471 further differs from BMRP 2002.4.1 in having a relatively long facet for the caudomedial process of the nasal on the frontal, suggesting that the caudomedial process was not reduced to a subtle tab as in BMRP 2002.4.1. Ongoing study of tomographic datasets of NCSM 40000 will determine whether *Nanotyrannus lancensis* had relatively longer caudomedial processes of the nasal than *Nanotyrannus lethaeus*. However, LACM 28471 does compare more favorably with BMRP 2002.4.1 in that the first dentary tooth is distinctly smaller than the other teeth, with the second intermediate in size. We note that there are potentially phylogenetically important characteristics of the dentition preserved on LACM 28471 that may permit some level of taxonomic referral; however, current evidence does not support “*Stygivenator molnari*” as a valid species and only equivocally supports referral of LACM 28471 to *Nanotyrannus*, and based upon materials currently available it is more likely that LACM 28471 pertains to *Nanotyrannus lancensis* than to *Nanotyrannus lethaeus*, so “*Stygivenator molnari*” is not a senior synonym of *Nanotyrannus lethaeus*. The genus name *Nanotyrannus* was established in 1988¹⁶², prior to “*Stygivenator*” in 1995¹⁶⁰, so even if future study confirms the absence of a subnarial foramen in LACM 28471, *Nanotyrannus* remains the oldest available name for the genus; the original combination *Gorgosaurus lancensis* was erected in 1946¹⁶³, so *lancensis* would retain priority over “*molnaris/molnari*”.

SI.1.12. Phylogenetic Character List

1. Premaxilla, deep foramen or fossa in the base of the nasal process, within the rostroventral corner of the narial fossa, presence, lateral view: Absent (0); Present (1).
2. Premaxilla, main body, dorsoventral height, lateral view: Less than or equal to rostrocaudal length (0); Greater than rostrocaudal length (1).

3. Premaxilla, subnarial process, orientation, lateral view: Mostly laterally (widely visible in lateral view) (0); Dorsolaterally (1); Dorsally (mostly hidden in lateral view) (2); Dorsomedially (3).
4. Premaxilla, orientation of tooth row, ventral view: Strongly parasagittal (0); First two teeth oriented mediolaterally, but 3rd and 4th teeth oriented parasagittally (1); Entire toothrow oriented mediolaterally and all teeth visible in rostral view (2).
5. Premaxilla, narial fossa ventral to bony naris, form, lateral view: Shallowly excavated (0); Deeply excavated, rostral margin invaginated as a deep groove (1).
6. Premaxilla, body, rostral margin, shape, lateral view: Slopes caudodorsally (0); Vertical (1).
7. Premaxilla, nasal process, rostral margin, shape, lateral view: Smoothly curved (0); With a distinct inflection point between a more vertical rostral region and a more horizontal caudal region (1).
8. Premaxilla, palatal process, dorsoventral position, medial view: Immediately above interdental plates (0); Separated from interdental plates by deep lingual surface of premaxilla (1).
9. Premaxilla, palatal process, dorsal flange, presence, medial view: Absent (0); Present (1).
10. Premaxilla and maxilla, subnarial foramen, presence as a clearly-defined concavity along the contact surface of the two bones: Absent (0); Present (1).
11. Maxilla, promaxillary fenestra, dorsoventral position, lateral view: At approximately midheight of antorbital fossa (0); Extreme rostroventral corner of antorbital fossa (1).
12. Maxilla, antorbital fossa, promaxillary recess, promaxillary fossa, ventral demarcation: Flush with antorbital fossa ventrally (0); Bounded by a step (1); Strongly bounded ventrally by a pronounced ridge, which dorsally demarcates a concave depression within the rostroventral corner of the antorbital fossa (2).
13. Maxilla, maxillary fenestra, presence, lateral view: Absent (0); Present (1).
14. Maxilla, pila promaxillaris, rostrocaudal exposure, lateral view: Widely exposed (0); Narrowly exposed (1); Obscured by rostral margin of antorbital fossa (2).
15. Maxilla, length of pila interfenestralis relative to length of preantorbital antorbital fossa: Greater than 20% (0); Less than 20% (1).
16. Maxilla, pila interfenestralis, orientation, lateral view: Vertical (0); Inclined strongly rostradorsally (1).
17. Maxilla, maxillary fenestra, dorsoventral position, lateral view: Dorsal to ventral margin of antorbital fossa (0); Abuts ventral margin of antorbital fossa (1).
18. Maxilla, maxillary fenestra, form, lateral view: Elliptical (0); Quadrangular (1).
19. Maxilla, maxillary fenestra, rostrocaudal axis, orientation, lateral view: Horizontal (0); Inclined approximately 30 degrees from horizontal (1).
20. Maxilla, maxillary fenestra, proportions, lateral view: Longer than tall (0); Taller than long (1).
21. Maxilla, maxillary fenestra, dorsoventral position within maxillary antrum, medial view: Does not abut dorsal border of maxillary antrum in medial view (0); Abuts dorsal border of maxillary antrum in medial view (1).
22. Maxilla, maxillary fenestra, caudal margin, shape, lateral view: Rounded (0); V-shaped (1).
23. Maxilla, accessory depression caudodorsal to promaxillary fenestra, presence, lateral view: Absent (0); Present (1).
24. Maxilla, antorbital fossa, rostradorsal depression, presence, lateral view: Absent (0); Present (1).
25. Maxilla, accessory depression dorsal to pila interfenestralis, presence, lateral view: Absent (0); Present as a pneumatic depression (1); Present and pierces the bone forming an accessory fenestra (2).
26. Maxilla, antorbital fossa, contact with nasal, lateral view: Antorbital fossa reaches nasal suture (0); Antorbital fossa does not reach nasal suture (1).

27. Maxilla, rostral ramus, presence, lateral view: Absent (0); Present due to rostrrodorsal 'step' in rostrrodorsal margin of maxilla (1).
28. Maxilla, ventral margin of the rostral region of the bone, profile, lateral view: Straight (0); Convex (1).
29. Maxilla, antorbital fossa, trend of dorsoventral height along horizontal ramus below the internal antorbital fenestra, lateral view: Uniform (0); Decreases as it extends caudally (1).
30. Maxilla, main body, subcutaneous flange, presence, lateral view: Absent (0); Present (1).
31. Maxilla, subcutaneous surface texture, form, lateral view: Random foramina and shallow grooves and ridges (0); Deep, prominent, dorsoventrally trending grooves and ridges (1).
32. Maxilla, subcutaneous surface texture, coarse rugosity rostral to antorbital fossa, presence: Absent (0); Present (1).
33. Maxilla, subcutaneous surface texture, fossae, lateral view: Deep fossae absent (0); Deep fossae present (1).
34. Maxilla, main body, depth covered by antorbital fossa under midpoint of antorbital fenestra: Covers more than 65% of main body (0); Covers between 50-60% of main body (1); Covers less than 45% of main body (2).
35. Maxilla, antorbital fossa, rostral half of ventral margin, distinct ventral rim: Absent (0); Present (1).
36. Maxilla, form of contact with nasal, lateral view: Smooth (0); Weakly scalloped (1); Deeply scalloped with interlocking transverse ridges on both bones (2).
37. Maxilla, maxillary flange, presence: Absent (0); Present (1).
38. Maxilla, maxillary flange, size: Small, represented only as a subtle convexity (0); Large, present as a well-defined dorsal flange (1).
39. Maxilla, joint surface for the palatine, rostral half, form, medial view: Planar (0); Groove or slot (1).
40. Maxilla, joint surface for the palatine, rostral half, dorsal roof, presence: Absent (0); Present (1).
41. Maxilla, joint surface for the palatine, rostral half, form of dorsally roofing lamina: Smooth (0); Rugose, due to dorsolateral expansion of the palatine (1).
42. Maxilla, palatine joint surface, rostral "buttress", presence: Absent (0); Present (1).
43. Maxilla, joint surface for the palatine, dorsoventral height, medial view: Shallow, does not conceal the tooth root bulges from view (0); Tall, conceals tooth root bulges from view (1).
44. Maxilla, joint surface for the palatine, caudal half, form: Dorsoventrally planar (0); Palatine is overlapped dorsally by maxilla (1).
45. Maxilla, pila postantralis, rostrocaudal thickness: Rostrocaudally thin, essentially forming only the caudal wall of the maxillary antrum (0); Rostrocaudally thick, forming a stout strut that is excavated by the antrum (1).
46. Maxilla, palatal shelf, form, medial view: Straight (0); Sigmoid (1).
47. Maxilla, palatal process, ventral surface, dental pits, presence: Absent (0); Present (1).
48. Nasal, fusion, presence: Absent, nasals are separate (0); Present, nasals are fused into a single midline element (1).
49. Nasal, median interpremaxillary process, presence: Absent (0); Present (1).
50. Nasal, premaxillary process, ventral shelf underlying nasal process of premaxilla, presence: Absent (0); Present (1).
51. Nasal, ventral surface, shape: Flat (0); Concave (vaulted) rostrally, gradually flattening caudally (1); Concave (vaulted) rostrally, and strongly concave until flattening abruptly caudally (2).
52. Nasal, midline crest on dorsal surface, presence: Absent (0); Present (1).

53. Nasal, external texture of mid-section of bone: Smooth to slightly rugose (0); Pronounced rugosities and associated vascular foramina (1).
54. Nasal, external surface, midline ridge: Absent (0); Present (1).
55. Nasal, external surface, midline ridge, rostral expansion into a nasal 'blade' Absent (0); Present (1).
56. Nasal, external surface, midline tubercles, presence: Absent (0); Present (1).
57. Nasal, external surface, midline tubercles, size: Small, distinct but small excrescences (0); Large, prominent midline hornlets (1).
58. Nasal, shape, dorsal view: Expands in width caudally (0); Relatively constant width along the length of the bone, due to subparallel lateral sides (1); Tapers in width caudally (2).
59. Nasal, external pneumatic recess, presence: Absent (0); Present (1).
60. Nasal, notch for rostradorsal process of lacrimal, presence: Absent (0); Present (1).
61. Nasal, caudolateral process, presence: Absent (0); Present (1).
62. Nasal, caudomedial process, presence: Absent (0); Present (1).
63. Nasal, caudomedial process, length: Rudimentary tab, much shorter than caudolateral process (0); Short prong, developed as a discrete prong that caudally invades the frontal but does not reach the caudal extent of the caudolateral process (1); Long prong, developed as a discrete prong that ends at the caudal level of the caudolateral process (2); Extremely long prong, extends further caudally than the caudolateral process (3).
64. Nasal, accessory caudomedial process, presence: Absent (0); Present (1).
65. Nasal, thin, low, and laterally projecting crest at the corner where the lateral and dorsal surfaces meet, presence: Absent (0); Present (1).
66. Lacrimal, cornual process, presence: Absent (0); Present (1).
67. Lacrimal, cornual process, shape of dorsal margin, lateral view: Rounded convexity, lacking a discrete apex (0); Broad triangular process with a discrete apex (1); Narrow, subconical process with a discrete apex (2).
68. Lacrimal, cornual process, position of highest point, lateral view: Distinctly rostral to the ventral ramus of the lacrimal (0); Dorsal to the ventral ramus of the lacrimal (1).
69. Lacrimal, cornual process, surface texture: Smooth or subtly rugose (0); Highly rugose, with prominent vertical striations (1).
70. Lacrimal, cornual process, inflation: Absent, cornual process is not inflated (0); Present, cornual process is inflated such that it appears swollen (1).
71. Lacrimal, dorsolateral shelf, presence: Absent (0); Present (1).
72. Lacrimal, caudolateral projection, presence: Absent (0); Present (1).
73. Lacrimal, primary pneumatic recess, presence: Absent (0); Present (1).
74. Lacrimal, primary pneumatic recess, dorsoventral height of ostium: Greater than 1/3 the height of rostral ramus (0); Less than 1/3 the height of the rostral ramus (1).
75. Lacrimal, primary pneumatic recess, rostral extent, lateral view: Far rostral to the rostral margin of the ventral ramus (0); Level with or caudal to the rostral margin of the ventral ramus (1).
76. Lacrimal, ventral ramus, transition between antorbital fossa and the subcutaneous surface, form: Surfaces are continuous with each other (0); Fossa is deeply inset, forming a ridge along the subcutaneous surface (1).
77. Lacrimal, accessory external openings on the rostral ramus, presence: Absent (0); Present (1).
78. Lacrimal, accessory external openings on the rostral ramus, position: Proximal to primary pneumatic recess (0); Distal to primary pneumatic recess (1).

79. Lacrimal, rostral ramus, cross sectional shape: Mediolaterally flattened (0); Rounded (1).
80. Lacrimal, medial pneumatic recess, presence: Absent (0); Present (1).
81. Lacrimal, medial pneumatic recess, form: Thin, ovoid slot (0); Wide fenestra (1).
82. Lacrimal, medial pneumatic recess, orientation: Faces rostrally (0); Faces medially (1).
83. Lacrimal, supraorbital process, proportions: Elongate, rostrocaudally longer than dorsoventrally tall (0); Roughly square shaped, dorsoventral height equal to twice rostrocaudal length (1); Dorsoventrally massive, dorsoventral height more than twice rostrocaudal length (2).
84. Lacrimal, rostroventral ala, length along jugal contact, lateral view: Extends for greater than 60% of contact (0); Extends for less than 60% of contact (1).
85. Lacrimal, supraorbital process, frontal joint surface, form: Flat, planar (0); Interdigitate (1).
86. Jugal, maxillary ramus, depth: Shallow, not expanded relative to suborbital portion of the bone (0); Deep, expanded relative to suborbital portion of the bone (1).
87. Jugal, pneumatic recess, presence: Absent (0); Present (1).
88. Jugal, jugal pneumatic recess, ostium, long axis orientation, lateral view: Approximately horizontal (0); Inclined at approximately 45 degrees relative to the ventral skull margin (1).
89. Jugal, pneumatic recess, ostium, exposure in lateral view: Pneumatic recess ostium is visible in lateral view (0); Pneumatic recess ostium is obscured in lateral view by a dorsally expanded lateral lamina of the jugal (1).
90. Jugal, lacrimal contact, angle of caudal half of contact: Horizontal (0); Low angle (1); Steep angle (2).
91. Jugal, postorbital process, lateral fossa, presence: Absent (0); Present (1).
92. Jugal, postorbital process, lateral fossa, depth: Shallow (0); Deep (1).
93. Jugal, articulation with postorbital, form of ventral extremity of suture: Tapering scarf joint (0); Shallow interlocking notch for postorbital (1); Deep interlocking notch for postorbital, defined by a flange rostral to the notch on the jugal (2).
94. Jugal, postorbital process, joint surface for postorbital, lateral joint surface, presence, lateral view: Absent (0); Present, postorbital wraps onto lateral surface of postorbital process of jugal (1).
95. Jugal, postorbital process, medial shelf, presence, lateral view: Absent (0); Present (1).
96. Jugal, postorbital process, extent of medial shelf of postorbital process, lateral view: Limited, occupies less than 50% of the rostrocaudal length of the process (0); Extensive, occupies approximately 50-75% of the rostrocaudal length of the process (1).
97. Jugal, postorbital process, orientation relative to ventral margin of jugal, lateral view: Approximately perpendicular (0); Strongly caudodorsal (1).
98. Jugal, ventral flange, presence: Absent (0); Present (1).
99. Jugal, lateral surface, texture: Smooth (0); Rugose (1).
100. Jugal, lateral surface, textured region, form: Bulbous eminence (0); Distinct laterally directed hornlet (1).
101. Jugal, dorsal quadratojugal process, orientation: Caudal (0); Caudodorsal (1).
102. Jugal, quadratojugal joint surface, rostral extent, rugose knob bracing rostral end of quadratojugal: Absent (0); Present (1).
103. Jugal, quadratojugal joint surface, shape of rostral margin: Acuminate (0); Blunted (1); Squared-off (2).

104. Jugal, quadratojugal joint surface, rostral extent: Terminates caudal to the rostral to the rostral margin of the infratemporal fenestra (0); Terminates at or rostral to the rostral margin of the infratemporal fenestra (1).

105. Jugal, quadratojugal joint surface, ventral margin, separation from ventral margin of jugal: Quadratojugal joint surface is fully separated from the ventral margin of the jugal (0); Quadratojugal joint surface is rostrally separated from ventral margin but breaches the ventral margin caudally (1); Quadratojugal joint surface reaches the ventral margin of the jugal along most of its length (2).

106. Jugal, quadratojugal joint surface, ventral margin, form: Continuous (0); Interrupted by a distinct inflection point separating a more horizontal rostral region from a more vertical caudal region (1).

107. Jugal, orbital margin, shape: Weakly concave (0); U-shaped (1).

108. Jugal, raised rim on lateral surface, paralleling the margin of the antorbital fossa, presence: Absent (0); Present (1).

109. Postorbital, ornamentation, presence: Absent (0); Present (1).

110. Postorbital, cornual process, presence: Absent (0); Present (1).

111. Postorbital, cornual process, form: Located at the orbital margin (0); Extends far past the orbital margin but does not exceed the rostrocaudal midpoint of the bone (1); Extends 50% or more of the rostrocaudal length of the body of the postorbital (2).

112. Postorbital, cornual process, dorsoventral position: Separated from dorsal margin of postorbital by a smooth, convex region (0); Reaches or extends past dorsal margin of postorbital (1).

113. Postorbital, cornual process, division: Absent, forms a single structure (0); Present, divided by a wide depression into two distinct structures (1).

114. Postorbital, cornual process, smooth 'curled' tongue-like surface and caudal groove, presence: Absent (0); Present (1).

115. Postorbital, squamosal ramus, concave notch for squamosal, lateral view: Absent (0); Present (1).

116. Postorbital, rostral limit of dorsal squamosal facet: Caudal or level to the rostral margin of the infratemporal fenestra (0); Rostral to the rostral margin of the infratemporal fenestra (1).

117. Postorbital, subocular process, presence: Absent (0); Present (1).

118. Postorbital, subocular process, size: Small, ventral ramus tongue-shaped (0); Large, forming a distinct flange (1).

119. Postorbital, subocular process, position: At ventral end of ventral process (0); Separated from ventral tip of ventral process by a notch (1).

120. Postorbital, rostral process, shape: Slender and elongate (0); Intermediate (1); Short and massive (2).

121. Postorbital, jugal process, craniocaudal width: Approximately the same width as the ventral ramus of the lacrimal at midheight (0); Much wider than the width of the ventral ramus of the lacrimal at midheight (1).

122. Postorbital, orbital surface, form: Flat or convex (0); Distinct concave fossa (1).

123. Postorbital, squamosal ramus, caudodorsal prong, presence: Absent (0); Present (1).

124. Quadratojugal and squamosal, constriction of infratemporal fossa: Absent, rostral margin of both bones are approximately vertical (0); Present, convex kink along the rostral margin of the two bones (1); Present, dorsal region of quadratojugal expanded to form a quadratojugal-squamosal flange, constricting the infratemporal fenestra (2); Present and extreme, quadratojugal-squamosal flange expanded to greater than twice the minimum rostrocaudal length of the quadratojugal shaft (3).

125. Squamosal, quadratojugal process, shape of dorsal margin: Straight (0); Arched dorsally (1).

126. Squamosal, quadratojugal process, tip, shape: Acuminate (0); Blunt (1).
127. Squamosal, caudal process, length of long axis compared to the long axis of the quadratojugal process, lateral view: Long, approximately 1/3-1/2 (0); Short, approximately 1/6 (1).
128. Squamosal, postorbital processes, rostral extent of dorsal process relative to ventral process: Dorsal process extends farther rostrally (0); Ventral process extends as far or farther rostrally (1).
129. Squamosal, postorbital facet, level of caudal termination: Terminates rostral to the caudal margin of the infratemporal fossa (0); Terminates at the level of the caudal margin of the infratemporal fossa (1); Terminates caudal to the caudal margin of the infratemporal fossa (2).
130. Squamosal, pneumaticity, presence: Absent (0); Present (1).
131. Squamosal, pneumaticity, form: Developed as a fossa in the roof of the squamosal (0); Developed as a distinct pneumatic chamber with undercut edges (1).
132. Quadratojugal, dorsal process, ridge along rostral margin of lateral surface, presence: Absent (0); Present (1).
133. Quadratojugal, dorsal process, ridge along rostral margin of lateral surface, extent: Subtle, fading in strength dorsally (0); Robust, extending to the dorsal margin of the bone (1).
134. Quadratojugal, dorsal process, rostral margin, notch, presence: Absent (0); Present (1).
135. Quadratojugal, dorsal jugal facet, caudal extent: Dorsal jugal facet is far removed from the caudoventral corner of the infratemporal fossa, separated by greater than the minimum length of the quadratojugal shaft (0); Dorsal jugal facet closely approaches caudoventral corner of infratemporal fossa, separated by less than minimum rostrocaudal length of the quadratojugal shaft (1).
136. Quadratojugal, fossa lateral to quadrate foramen, presence: Absent (0); Present (1).
137. Quadratojugal, ridge lateral to fossa lateral to quadrate foramen, mediolateral thickness: Medirolaterally wide, forming a rounded pillar (0); Medirolaterally narrow, forming a thin blade-like ridge (1).
138. Quadratojugal, ventral quadrate process, presence: Absent (0); Present (1).
139. Quadratojugal, ventral quadrate process, length and orientation: Short, oriented mostly laterally (0); Long, wrapping onto the caudal surface of the quadrate condyles (1).
140. Quadratojugal, shaft, pneumatic foramen, presence: Absent (0); Present (1).
141. Quadratojugal, dorsal margin, shape: Deep concavity, separated from rostralmost extent by a deep step (0); Straight margin, separated from rostralmost extent by a small step (1).
142. Quadratojugal, infratemporal fossa, caudoventral corner, shape: Rounded (0); Squared-off (1).
143. Quadrate and quadratojugal, quadrate foramen, position: Formed entirely within quadrate (0); Formed between the quadrate and the quadratojugal (1).
144. Quadrate, quadrate foramen, size, caudal view: Small, long axis approximately 10% of the dorsoventral height of the quadrate shaft (0); Large, long axis greater than 20% of the dorsoventral height of the quadrate shaft (1).
145. Quadrate, quadrate foramen, position of ventral edge, caudal view: Separated from the ventral margin of the quadrate by more than twice the dorsoventral height of the quadrate condyles (0); Separated from the ventral margin of the quadrate by less than twice the dorsoventral height of the quadrate condyles (1).
146. Quadrate, juncture of pterygoid ala and condyles, ventral pneumatic recess, presence, rostral view: Absent (0); Present (1).
147. Quadrate, ventral pneumatic recess, medial lamina, development, medial view: Strongly developed (0); Weakly developed, causing ventral pneumatic recess to be widely visible in medial view (1).

148. Quadrate, medial surface of pterygoid ala, medial pneumatic recess, presence, medial view: Absent (0); Present (1).
149. Quadrate, shaft, caudomedial surface, large pneumatic foramen, presence, caudal view: Absent (0); Present (1).
150. Quadrate, quadrate condyles, position relative to occipital condyle when skull is in articulation, lateral view: Approximately aligned (0); Completely caudal (1).
151. Quadrate, pterygoid ala, medial surface, fossa, presence, medial view: Absent (0); Present (1).
152. Quadrate, pterygoid ala, medial fossa, distinct dorsal rim, presence, medial view: Absent (0); Present (1).
153. Quadrate, pterygoid ala, medial fossa, distinct ventral rim, presence, medial view: Absent (0); Present (1).
154. Quadrate, medial condyle, ligament attachment, presence, medial view: Absent (0); Present (1).
155. Quadrate, medial condyle, ligament attachment, position, medial view: Rostral to medial margin of quadrate shaft (0); Caudal to medial margin of quadrate shaft (1).
156. Prefrontal, exposure, dorsal view: Widely exposed along orbital margin, forming much of the orbital rim and usually separating or nearly separating the frontal and lacrimal (0); Reduced, not exposed along the orbital rim and allows for wide contact between frontal and lacrimal (1).
157. Frontal, rostrocaudal length of exposed portion on skull roof relative to exposed width at midpoint, dorsal view: Greater than 2.5 (0); Between 2.5 and 2.0 (1); Less than 2.0 (2).
158. Frontal, prefrontolacrimal process, presence, dorsal view: Absent (0); Present (1).
159. Frontal, prefrontonasal process, presence, dorsal view: Absent (0); Present (1).
160. Frontal, prefrontolacrimal process, length, dorsal view: Short, terminates caudal to the rostral extent of the prefrontonasal process (0); Long, terminates level with the rostral extent of the prefrontonasal process (1); Very long, terminates rostral to the rostral extent of the prefrontonasal process (2).
161. Frontal, supratemporal fossa, rostrocaudal length compared to overall length of exposed portion of frontal on skull roof, dorsal view: Less than 30% (0); 30%-50% (1); 50%-60% (2); Greater than 60% (3).
162. Frontal, supratemporal fossa, medial extension, dorsal view: Fossa restricted to caudolateral corner of the frontal (0); Fossae meet opposing counterpart on the midline (1).
163. Frontal, postorbital joint surface, form, lateral view: Dorsoventrally shallow and undifferentiated (0); Dorsoventrally shallow and differentiated into a vertical region rostrally and a horizontal region caudally (1); Dorsoventrally deep, approximately twice as long as deep, and subtly differentiated into vertical and horizontal regions (2).
164. Frontal, contribution to orbital rim, dorsal and lateral views: Extensive (0); Restricted to a narrow orbital slot (1).
165. Frontal, slope of dorsal surface, rostral to supratemporal fossa: Convex, bones extend dorsomedially to the interfrontal suture (0); Flat (1); Concave, bones extend ventromedially to the interfrontal suture (2).
166. Parietal, frontoparietal suture, form: Extends mediolaterally (0); Parietal overlies frontal to form a frontoparietal peak (1).
167. Parietal, frontoparietal peak, form, dorsal view: Narrow, bladelikey (0); Expanded mediolaterally into a broad tuber (1).
168. Parietal, apposition of supratemporal fossae, presence, dorsal view: Absent (0); Present (1).

169. Parietal, apposition of supratemporal fossae, extent, dorsal view: Present caudally, but fossae are separated cranially (forming a caudally restricted sagittal crest) (0); Present across the length of the parietal (forming an extensive sagittal crest) (1).

170. Parietal, sagittal crest, ventral extent, lateral view: Fully dorsal to dorsal margin of interorbital region (0); Strongly concave and dips below the dorsal margin of the interorbital region (1).

171. Parietal, nuchal crest, dorsoventral depth, lateral view: Weakly developed, does not exceed the dorsal level of the interorbital region (0); Strongly developed, projects higher than the dorsal level of the interorbital region (1).

172. Parietal, nuchal crest, caudal surface, parasagittal fossae, presence, caudal view: Absent (0); Present (1).

173. Braincase, basicranium (rectangle defined by positions of basal tubera and basiptyergoid processes), shape, ventral view: Rostrocaudally longer than mediolaterally wide (0); Mediolaterally wider than rostrocaudally long (1).

174. Braincase, ossified sphenethmoid and mesethmoid, lateral and frontal views: Absent (0); Present (1).

175. Supraoccipital, contribution to dorsal rim of foramen magnum: Forms entire rim (0); Makes limited contribution to rim via triangular ventral process (1); Completely excluded from rim (2).

176. Supraoccipital, dorsal margin, form, caudal view: Smoothly convex and undivided (0); Divided into two processes ("forked") (1).

177. Supraoccipital, form, caudal view: Pronounced midline crest with a deep fossa on each side or flat plate that abuts the caudal surface of the parietal (0); Flat and expands dorsally into caudally projecting tubercles or tabs (1).

178. Supraoccipital, pneumaticity, presence: Absent (0); Present (1).

179. Supraoccipital, caudal surface, midline ridge, presence, caudal view: Absent (0); Present (1).

180. Otoccipital, paroccipital process, ventral flange at distal end, caudal and lateral views: Absent (0); Present (1).

181. Otoccipital, paroccipital process, caudal surface dorsolateral to foramen magnum, deep fossa, presence, caudal view: Absent (0); Present (1).

182. Otoccipital, crista tuberalis, extent, caudal view: Limited, mediolateral width across opposing cristae less than one-half the dorsoventral depth of the braincase from the dorsal tip of the supraoccipital to the ventral tip of the basal tubera (0); Extensive, width greater than one-half the braincase depth (1).

183. Otoccipital, paracondylar pocket, depth, caudal view: Shallow (0); Deep (1).

184. Otoccipital, otic recess, enclosure, lateral view: Not enclosed by a superficial lamina of the prootic, and as a result having a large external opening (0); Recess enclosed by the superficial lamina of the prootic (1).

185. Otoccipital, caudal tympanic recess, presence, lateral view: Absent (0); Present (1).

186. Basioccipital, basal tubera, notch between opposing tubera, shape, caudal view: Poorly defined concavity (0); Distinct parabolic notch (1).

187. Basioccipital, basal tubera, notch between opposing tubera, width, caudal view: Wider than basal tuber (0); Narrower than basal tuber (1).

188. Basioccipital, basal tubera, lateral splaying, caudal view: Absent, medial margin of tuber is medial to lateral margin of occipital condyle (0); Present, basal tubera are placed fully lateral to the occipital condyle (1).

189. Basioccipital, subcondylar recess, depth, caudal view: Shallow (0); Deep (1).

190. Parabasisphenoid, basisphenoid recess, closure and orientation of central axis, caudal and lateral views: Ventral, basiptyergoid processes are far rostral to the basal tubera (0); Caudovernal, basiptyergoid processes are only slightly rostral to the basal tubera (1); Closed and caudovernal, basiptyergoid processes are located ventral to the basal tubera (2).
191. Parabasisphenoid, basisphenoid recess, rostral wall, inflation, ventral view Absent (0); Present (1).
192. Parabasisphenoid, parasphenoid rostrum, shape, lateral view: Rostrocaudally long, ventral margin is a smooth concave arch (0); Dorsoventrally tall, ventral margin is nearly vertical caudally, nearly horizontal rostrally, and has a distinct inflection point (1).
193. Parabasisphenoid, subsellar recess, extent within parasphenoid rostrum, ventral view: Invades much of parasphenoid rostrum (0); Restricted to proximal base of the parasphenoid rostrum (1).
194. Parabasisphenoid, sinus cavernosus, presence: Absent (abducens canal runs lateral to pituitary fossa) (0); Present (abducens canal enters pituitary fossa) (1).
195. Prootic, dorsal tympanic recess, presence, lateral view: Absent (0); Present (1).
196. Prootic, prootic fossa, presence, lateral view: Absent (0); Present (1).
197. Prootic, rostral tympanic recess, dorsal diverticulum, presence: Absent (0); Present (1).
198. Prootic, endocranial surface, number of trigeminal foramina, medial view: One (Gasserian ganglion was within the prootic) (0); Two (Gasserian ganglion was within the endocranial cavity) (1).
199. Laterosphenoid, antotic crest, presence, lateral view: Absent (0); Present (1).
200. Laterosphenoid, epiptyergoid fossa, presence, lateral view: Absent (0); Present (1).
201. Laterosphenoid, lateral crest, presence, lateral view: Absent (0); Present (1).
202. Laterosphenoid, lateral crest, caudal extent, lateral view: Does not reach prootic (0); Reaches prootic (1).
203. Laterosphenoid, lateral crest, caudal extent, expansion into a tubercle, lateral view: Absent (0); Present (1).
204. Laterosphenoid, canal for rostral middle cerebral vein, presence: Absent (0); Present (1).
205. Endocast, midbrain flexure, condition: Prominent (0); Reduced (1).
206. Endocast, midbrain peak, presence: Absent (0); Present (1).
207. Endocast, cochlear duct, length: Short (0); Long (1).
208. Vomer, rostral end, shape, ventral view: Lanceolate (0); Expanded into a diamond (1).
209. Vomer, ventral keel, presence, lateral and ventral views: Absent (0); Present (1).
210. Vomer, ventral keel, depth, lateral view: Low ridge (0); Deep flange (1).
211. Palatine, vomeropterygoid process, length relative to minimum rostrocaudal length of vomeropterygoid neck, lateral view: Greater than twice as long (0); Less than twice as long (1).
212. Palatine, caudal margin of choana, shape, lateral view: Rounded (0); Acuminate (1).
213. Palatine, vomeropterygoid neck, orientation: Long axis inclined rostradorsally (0); Long axis vertical (1).
214. Palatine, vomeropterygoid process, trend of dorsal and ventral margins, lateral view: Parallel (0); Oblique, resulting in an acuminate rostral tip of the process (1).
215. Palatine, vomeropterygoid process, dorsoventral extent of vomeropterygoid process relative to combined vomeropterygoid neck and process, lateral view: Vomeropterygoid process height is less than half combined height of vomeropterygoid neck and process (0); Vomeropterygoid process height is greater than half combined height of vomeropterygoid neck and process (1).
216. Palatine, caudal (=primary) pneumatic recess, presence, lateral view: Absent (0); Present (1).
217. Palatine, rostral pneumatic recess, presence, lateral view: Absent (0); Present (1).

218. Palatine, rostral pneumatic recess, development, lateral view: Developed as a pneumatic fossa (0); Pierces bone to form a distinct pneumatic chamber (1).

219. Palatine, caudal recess, caudal margin, position, lateral view: Extends far caudal to caudal margin of vomeropterygoid process neck (0); Level with caudal margin of vomeropterygoid process neck (1); Ends far rostral to caudal margin of vomeropterygoid process neck (2).

220. Palatine, caudal recess, location of rostral margin, lateral view: Caudal to rostral margin of vomeropterygoid process neck (0); Level with rostral margin of vomeropterygoid process neck (1); Far rostral to rostral margin of vomeropterygoid process neck (2).

221. Palatine, caudal recess, dorsoventral height relative to rostral recess, lateral view: Caudal recess is shorter than rostral recess (0); Caudal recess is equal in height to rostral recess (1); Caudal recess is taller than rostral recess (2).

222. Palatine, jugal process, location of contact surface for lacrimal, lateral view: Caudal ("distal"), separated from caudal recess by wide margin (0); Rostral ("proximal"), closely approaches margin of caudal recess (1).

223. Palatine, jugal process, inflation, presence: Absent (0); Present (1).

224. Palatine, maxillary process, shape, lateral or medial view: Curves smoothly rostradorsally throughout its full length (0); Shifts orientation mid-length, rostralmost extent is subhorizontal with jugal process (1).

225. Palatine, caudal extent of maxillary joint surface, position, lateral view: Maxillary joint surface continues on ventral surface of jugal-lacrimal process (e.g., palatine overlies maxilla at caudalmost extent of joint surface) (0); Maxillary joint surface passes on lateral surface of the jugal-lacrimal process (e.g., palatine and maxilla have an approximately planar suture at the caudalmost extent of the joint surface) (1).

226. Palatine, rostroventral corner, maxillary "brace", presence: Absent (0); Present (1).

227. Palatine, jugal buttress, presence, lateral view: Absent (0); Present (1).

228. Ectopterygoid, body and pterygoid process, inflation, presence: Absent (0); Present (1).

229. Ectopterygoid, jugal process, external pneumatic foramina leading into jugal recess, presence, caudal view: Absent (0); Present (1).

230. Ectopterygoid, jugal process, inflation, presence: Absent (0); Present (1).

231. Ectopterygoid, pneumatic ostium, shape, ventral view: Thin ovoid slot (0); Round or subtriangular (1).

232. Ectopterygoid, pneumatic ostium, size, ventral view: Small, medial extent is less than half the distance between the lateral extent of the opening and the joint surface for the pterygoid (0); Large, medial extent is more than half the distance between the lateral extent of the opening and the joint surface for the pterygoid (1).

233. Ectopterygoid, ridge caudal to pneumatic ostium, presence, ventral view: Absent (0); Present (1).

234. Mandible, external mandibular fenestra, dorsoventral depth relative to the depth of the mandible at the midpoint of the fenestra, lateral view: Greater than 25% (0); Less than 25% (1).

235. Mandible, glenoid, dorsoventral position relative to level of alveolar margin of dentary, lateral view: Ventral or level (0); Dorsal (1).

236. Dentary, transition point, rostrocaudal position, lateral view: Alveolus 3 or more mesial (0); Alveolus 4 or more distal (1).

237. Dentary, rostral margin, shape, lateral view: Rounded (0); Straight (1).

238. Dentary, symphysis, texture, medial view: Smooth (0); Ridged but not rugose (1); Both ridges and rugosities present (2).
239. Dentary, chin, presence, medial view: Absent (0); Present (1).
240. Dentary, splenial joint surface, texture, medial view: Smooth (0); Rugose (1).
241. Dentary, medial aspect of dentary ventral to Meckelian fossa, height relative to Meckelian fossa, medial view: Markedly shorter (0); Subequal (1).
242. Dentary, mesial alveoli, size in comparison to mid-dentary teeth, dorsal view: Approximately the same size (0); First alveolus substantially smaller (1); First two alveoli substantially smaller (2).
243. Dentary, primary neurovascular foramina, arrangement, lateral view: Distinct foramina or set into a shallow groove caudally (0); Set into a deep and sharp groove across the middle and caudal regions of the dentary (1).
244. Dentary, alveolar margin, shape, lateral view: Straight (0); Concave (1).
245. Dentary, caudal half, lateral surface, form, lateral view: Flat or convex (0); Concave (1).
246. Dentary, Meckelian groove, form, medial view: Dorsoventrally deep and shallowly inset into medial surface of the bone (0); Dorsoventrally shallow and deeply inset into bone, groove appears as a thin, sharp structure (1).
247. Dentary, orientation of rostral margin relative to the dorsal margin of the bone, lateral view: Majority of rostral margin approaches 90 degree angle to dorsal margin (0); Dorsalmost part of rostral margin perpendicular to dorsal margin, but inclined at approximately a 45 degree angle ventrally (1); Majority of rostral margin is 45 degrees or less to dorsal margin (2).
248. Dentary, rugose knob ventral or caudoventral to Meckelian foramen, presence, medial view: Absent (0); Present (1).
249. Surangular, caudal surangular foramen, presence, lateral view: Absent (0); Present (1).
250. Surangular, caudal surangular foramen, size: Small foramen (0); Large fenestra, approximately 30% depth of caudal end of surangular (1).
251. Surangular, surangular shelf, orientation relative to the long axis of the mandible, lateral view: Rostrodorsal (0); Straight rostrocaudally (1); Rostroventral (2).
252. Surangular, surangular shelf, form, lateral view: Straight (0); Distinctly arched (1).
253. Surangular, surangular shelf, dorsoventral thickness, lateral view: Surangular shelf is a low ridge (0); Surangular shelf is present as a distinct shelf that is dorsoventrally thin (1); Surangular shelf is present as a distinct shelf that is dorsoventrally thick (2).
254. Surangular, surangular shelf, position, lateral view: Placed far dorsal to caudal surangular foramen (0); Abuts caudal surangular foramen but does not overhang it such that the shelf obscures the dorsal margin of the foramen (1); Abuts and overhangs caudal surangular foramen, obscuring the dorsal margin of the foramen in lateral view (2).
255. Surangular, caudal surangular foramen, pneumatic pocket caudodorsal to foramen, presence, lateral view: Absent (0); Present (1).
256. Surangular, caudal surangular foramen, pneumatic pocket, depth, lateral view: Shallow (0); Deeply excavated (1).
257. Surangular, muscle attachment surface dorsal to the surangular shelf, form, lateral view: Concave (0); Convex (1).
258. Surangular, rostral ligament pit, presence, lateral view: Absent (0); Present (1).
259. Surangular, caudal ligament pit, presence, lateral view: Absent (0); Present (1).

260. Surangular, rostrocaudal length of rostral flange (region rostral to rostral margin of the external mandibular fenestra), lateral view: Less than 30% of length of surangular (0); Greater than 30% of length of surangular (1).
261. Angular, ventral margin, form, lateral view Smoothly convex (0); Rostral region “flexed” relative to caudal region, such that there is a discrete step between them (1).
262. Articular, mediolateral width of jaw muscle attachment site, dorsal and caudal views: Less than width of glenoid (0); Greater than or equal to width of glenoid (1).
263. Articular, glenoid and retroarticular process, position, dorsal view: Separated by a non-articular region of the bone (0); Directly adjacent to one another (1).
264. Splenial, rostral mylohyoid foramen, form, medial view: Present as a small foramen (0); Present as a large fenestra (1).
265. Splenial, rostral mylohyoid foramen, height, medial view: Dorsal margin of mylohyoid foramen is ventral to the level of the dorsal margin of the rostral process of splenial (0); Dorsal margin of mylohyoid foramen is dorsal to the level of the dorsal margin of the rostral process of splenial (1).
266. Splenial, rostral mylohyoid foramen, shape, ratio of long axis length to short axis length: Less than 2.0 (0); Between 2.0 and 3.0 (1); Greater than 3.0 (2).
267. Splenial, rostral mylohyoid foramen, ventral margin, closure, medial view: Ventral margin is fully closed (0); Ventral margin of open due to a hiatus in the ventral border of the splenial (1); Ventral margin is fully closed (2).
268. Prearticular, medial shelf, presence, medial and dorsal views: Absent (0); Present (1).
269. Preaticular, neurovascular groove, position, medial view: Approximately centered at midshaft (0); Rostrodorsally displaced, such that the rostradorsal margin of the groove is at the rostradorsal margin of the prearticular shaft in medial view (1).
270. Preaticular, caudoventral margin, form, medial view: Does not wrap medially around the caudal margin of the angular (0); Wraps medially, developing a slot to receive caudal margin of the angular (1).
271. Inter coronoid, shape, medial view: Straight (0); Crescentic (1).
272. Dentition, premaxillary dentition, tooth count: Five (0); Four (1).
273. Dentition, premaxillary dentition, 'D-shaped' premaxillary teeth, presence: Absent, mesial carina is offset mesial to distal carina on all teeth (teeth ziphodont) (0); Present, mesial carina is rotted distally on some premaxillary teeth (1).
274. Dentition, premaxillary dentition, 'D-shaped' premaxillary teeth, number: Mesial premaxillary teeth are D-shaped, but distal teeth are ziphodont (0); All premaxillary teeth are D-shaped (1).
275. Dentition, premaxillary dentition, fourth tooth crown, apicobasal height relative to largest maxillary crown: Subequal (0); Approximately half as high (1).
276. Dentition, premaxillary dentition, median vertical ridge on lingual surface: Absent (0); Present (1).
277. Dentition, premaxillary dentition, lingual ridge, apicobasal groove, presence: Absent (0); Present (1).
278. Dentition, premaxillary dentition, mesial premaxillary teeth, serrations, presence: Absent from majority of crown (0); Present on majority of crown (1).
279. Dentition, premaxillary dentition, shape of crown, lingual view: Squared, chisel-shaped (0); Acuminate, distinctly pointed (1).
280. Dentition, premaxillary dentition, crown, shape, mesial and distal views: Recurved (0); Straight (1).
281. Dentition, maxillary dentition, maxillary tooth count: 11 (0); 12 (1); 13 (2); 14 (3); 15 (4); 16 (5); 17 (6); 18 or greater (7).

282. Dentition, maxillary dentition, incisiform first maxillary tooth, presence: Absent (0); Present (1).
283. Dentition, dentary dentition, dentary tooth count: 12 (0); 13 (1); 14 (2); 15 (3); 16 (4); 17 (5); 18 (6); 19 (7); 20 (8); 21 (9).
284. Dentition, lateral dentition, mesial and distal carina, position: Carinae centered on opposite sides of a lens-shaped crown (0); Asymmetrical, mesial carina shifted lingually and distal carina shifted labially (1).
285. Dentition, lateral dentition, mesial carina, denticles, presence: Absent (0); Present (1).
286. Dentition, lateral dentition, mesial carina, denticles, size relative to distal denticles: Approximately the same size (0); Significantly smaller (1).
287. Dentition, lateral dentition, form: Ziphodont, labiolingual width of base less than 60% of mesiodistal length (0); Incrassate, width greater than 60% of length (1); Incrassate, width nearly equal to length (2).
288. Axis and postaxial cervicals, maximum craniocaudal length of centrum compared to dorsoventral height of caudal centrum face: Longer than caudal centrum face (0); Shorter than or equal to caudal centrum face (1).
289. Axis, pleurocoel, position: Near midheight of centrum (0); Dorsally located, directly underneath neurocentral suture and directly posterior to diapophysis (1).
290. Axis, pleurocoel, number: One (0); Two (1).
291. Axis, pleurocoel, surrounding fossa, extent: Limited to margins of pleurocoel (0); Extensive, occupies most of lateral surface of centrum (1).
292. Axis, ventral surface, ridge, presence: Absent (0); Present (1).
293. Axis, neural spine, pneumatic foramen and fossa on each side of cranial ridge: Absent (0); Present (1).
294. Axis, neural spine, dorsal region of cranial surface, texture: Generally smooth or with subtle texture (0); Highly rugose, with series of grooves, ridges, and eminences (1).
295. Axis, neural spine, "crown" region, midline projection, presence: Absent (0); Present (1).
296. Axis, neural spine, form: Sheet-like (0); Low eminence (1).
297. Axis, deep and funnel-like supradiapophyseal fossa, presence: Absent (0); Present (1).
298. Axis and cranial-middle cervicals, epipophysis, caudal extent: Flush with caudal extent of postzygapophyses (0); Extend slightly caudal to postzygapophyses (1); Extend far caudal to postzygapophyses (2).
299. Axis and cranial-middle cervicals, epipophysis, form: Small, pyramidal mound (0); Large, rugose flange (1).
300. Cervical vertebrae, middle-caudal cervicals, neural spine, shape, dorsal view: Long rectangle, much longer craniocaudally than wide transversely (0); Short rectangle, base is essentially square-shaped due to nearly equal craniocaudal and transverse dimensions (1).
301. Cervical vertebrae, middle-caudal cervicals, neural spine, height: Shorter than caudal centrum face (0); Taller than caudal centrum face (1).
302. Cervical vertebrae, cranial-middle cervicals, caudal centrodiapophyseal lamina, presence: Absent (0); Present (1).
303. Cervical vertebrae, cranial-middle cervicals, caudal centrodiapophyseal laminae, form: Weak ridge (0); Thick, laterally offset lamina demarcating a deep infrapostzygapophyseal fossa (1).

304. Cervical vertebrae, cranial-middle cervicals, caudal centrodiapophyseal laminae, orientation: Projects caudoventrally, infrapostzygapophyseal fossa located primarily caudal to lamina (0); Nearly horizontal, fossa located primarily dorsal to lamina (1).
305. Cervical vertebrae, cranial cervicals, ventral surface, anterior region, hypapophysis, presence: Absent (0); Present (1).
306. Caudal cervical and cranial dorsal vertebrae, ventral surface, hypapophysis, presence: Absent (0); Present (1).
307. Cervical vertebrae, prezygapophysis in middle cervicals, position: Slightly overhang centrum laterally (0); Strongly overhang centrum laterally, entire prezygapophyseal facet is placed lateral to centrum (1).
308. Cervical ribs, pneumaticity, presence: Absent (0); Present (1).
309. Cervical and dorsal vertebrae, rugose ligament attachment scars in pre- and post-spinal fossae, presence: Absent or weakly developed (0); Present (1).
310. Cervical and dorsal vertebrae, rugose ligament attachment scars in pre- and post-spinal fossae, size: Strongly developed as prominent, rectangular flanges that extend outside of the fossae and are visible in posterior view, but on the dorsal vertebrae only (0); Prominent in dorsals and cervicals (1).
311. Dorsal vertebrae, pneumaticity, presence of pneumatic foramina on lateral centrum surface: Absent (0); Present (1).
312. Dorsal vertebrae, pneumaticity, extent, lateral view: Limited to cranial dorsals (0); Present throughout dorsal column (1).
313. Dorsal vertebrae, neural spine, level of caudal termination: At approximately the same level as the caudal centrum face (0); Far caudal to the caudal centrum face (1).
314. Dorsal vertebrae, middle-caudal dorsals, craniocaudal length compared to dorsoventral height of caudal centrum face: Greater than dorsoventral height of the caudal centrum face (0); Less than or equal to dorsoventral height of the caudal centrum face (1).
315. Dorsal vertebrae, middle-caudal dorsals, postzygapophysis, position: At same level as prezygapophysis (0); Elevated dorsally above prezygapophysis (1).
316. Dorsal vertebrae, middle-caudal dorsals, form of cranial and caudal centrodiapophyseal laminae, contact: Make contact on ventral surface of transverse process, demarcating a triangular infradiapophyseal fossa (0); Do not make contact but roughly parallel to each other, infraprezygapophyseal and infradiapophyseal fossae merged into a single fossa (1).
317. Dorsal ribs, pneumaticity, presence: Absent (0); Present (1).
318. Sacral vertebrae, pleurocoels on lateral surfaces of centra, presence: Absent (0); Present (1).
319. Sacral vertebrae, neural spines, fusion, presence: Absent, spines unfused (0); Present, spines fused (1).
320. Sacral vertebrae, neural spines, fenestrae between fused neural spines, presence: Absent (0); Present (1).
321. Sacral ribs, position: Span two sacrals (0); Limited to a single sacral (1).
322. Sacral ribs, position of rib attachments for central ribs on individual sacrals: Span centrum and neural arch (0); Limited to neural arch only (1).
323. Sacral vertebra five, position of ventral margin of caudal articular face: At same level as ventral margin of cranial articular face (0); Positioned ventral to ventral margin of cranial articular face (1).
324. Sacral vertebra five, hyposphene, presence: Absent (0); Present (1).

325. Sacral vertebra five, hyposphene, form: Present as a single midline structure (0); Comprised of two parallel-sided sheets (1).
326. Caudal vertebrae, proximal caudals, shape of transverse process: Rectangular, with parallel cranial and caudal sides (0); Distal end is expanded caudally, but not cranially (1); Distal end is expanded both caudally and cranially (2).
327. Caudal vertebrae, proximal caudals, two laminae linking prezygapophysis and transverse process, between which is a deep, triangular fossa, presence: Absent (0); Present (1).
328. Caudal vertebrae, proximal caudals, pneumatic foramen inferior to prezygapophysis: Absent (0); Present (1).
329. Caudal vertebrae, most distal caudal with a transverse process: Caudal 15 or more proximal (0); Caudal 16 or more distal (1).
330. Scapula, glenoid fossa, extension of articular surface onto lateral surface: Absent (0); Present (1).
331. Scapula, angle between caudal margin of glenoid and dorsal margin of blade: Greater than 90 degrees (0); Approximately 90 degrees (1).
332. Scapula, acromion, dorsoventral depth: Less than 3 times minimum dorsoventral depth of blade (0); Greater than 3 times minimum dorsoventral depth of blade (1).
333. Furcula, angle between long axes of epicledial processes: Less than 90 degrees (furcula is a narrow U shape) (0); Greater than 90 degrees (furcula is a broad U shape) (1).
334. Furcula, epicledial processes, flange at distal end, presence: Absent (0); Present (1).
335. Furcula, hypocledium, presence: Absent (0); Present (1).
336. Humerus, length relative to femur: Greater than 45% femur length (0); Between 33% and 45% femur length (1); Less than 33% femur length (2).
337. Humerus, rotation along shaft, orientation of long axis of proximal end relative to that of distal end: Distal end is distinctly canted relative to the proximal end (0); Approximately parallel, shaft rotation absent (1).
338. Humerus, external tuberosity, form of proximolateral surface: Concave, creating appearance of a saddle-shaped region between the apex of the external tuberosity and the humeral head (0); Straight, and resultantly slightly offset from humeral head (1); Convex, smoothly confluent with the humeral head (2).
339. Humerus, humeral head, form: Broadly convex (0); Lateral aspect flattened, forming a medially-positioned apex (1).
340. Humerus, humeral head, craniocaudal expansion: Expanded caudally to overhang caudal aspect of the proximal humerus (0); Expanded cranially and caudally, overhanging both cranial and caudal aspects of the proximal humerus (1).
341. Humerus, entepicondylar ridge, presence: Absent (0); Present (1).
342. Humerus, supraradiocondylar ridge, presence: Absent (0); Present (1).
343. Humerus, ectepicondylar ridge, presence: Absent (0); Present (1).
344. Humerus, entepicondyle, presence: Absent (0); Present (1).
345. Humerus, entepicondyle, orientation: Projects proximally (0); Projects laterally (1).
346. Ulna, length relative to femur: Greater than 25% femoral length (0); Less than 25% femoral length (1).
347. Radius and ulna, proximal articular facets, distal expansion onto lateral/medial aspects of radius/ulna: Absent (0); Present (1).
348. Ulna, distal end, craniomedial process: Absent (0); Present (1).
349. Ulna, distal end, shape: Convex (0); Straight (1).

350. Carpus, distal carpal 1, mediolateral width relative to metacarpal I proximal end, extensor view: Longer than proximal end of metacarpal I (0); Shorter than proximal end of metacarpal I (1).
351. Manus, number of digits: Four (0); Three (1); Two (2).
352. Manus, digit III, number of phalanges: Four (0); Three (1); Two (2); One (3).
353. Manus, metacarpal I, distal articular surface, symmetry: Approximately symmetrical, medial and lateral condyles are approximately the same size (0); Highly asymmetrical, lateral condyle is much smaller than the medial condyle (1).
354. Manus, metacarpal II, length relative to femur length: Greater than 17% femur length (0); Between 11% and 17% femur length (1); Less than 11% femur length (2).
355. Manus, metacarpal II, midshaft width relative to metacarpal I: Narrower than metacarpal I (0); Wider than metacarpal I (1).
356. Manus, metacarpal II, hypertrophied flexor projection of proximal medial condyle, presence: Absent (0); Present (1).
357. Manus, metacarpal II, proximal articular surface, orientation: Flat (0); Slopes distomedially (1).
358. Manus, metacarpal II, proximal articular surface, shape: Concave (0); Flat, with a narrow groove (1).
359. Manus, metacarpal III, proximal articular surface, presence: Absent, metacarpal III is highly reduced (0); Present (1).
360. Manus, phalanx I-1, length relative to femur length: Greater than 15% of femur length (0); Less than 15% of femur length (1).
361. Manus, phalanx I-1, shaft torsion, presence: Absent (0); Present (1).
362. Manus, phalanx II-1, length relative to femur length: Greater than 10% of femur length (0); Less than 10% of femur length (1).
363. Manus, phalanx II-1, extensor pit, proximal margin, demarcation by a "peak": Absent (0); Present (1).
364. Manus, phalanx II-1, flexor displacement of distal condyles: Absent (0); Present (1).
365. Manus, ungual phalanges, recurvature: All unguals strongly recurved (0); Ungual phalanx I is highly recurved but ungual phalanx II is flattened (1); All ungual phalanges are flattened (2).
366. Ilium, length relative to femur length: Ilium is shorter than femur (0); Ilium is longer than femur (1).
367. Ilium, supraacetabular ridge, presence: Absent (0); Present (1).
368. Ilium, supraacetabular ridge, robustness: Craniocaudal width of the ridge is greater than 10% of dorsoventral height of ilium over acetabulum (0); Craniocaudal width of the ridge is less than 10% of dorsoventral height of ilium over acetabulum (1).
369. Ilium, supraacetabular ridge, dorsal extent: Extends to the iliotibialis origin scar (0); Does not extend to iliotibialis origin scar (1).
370. Ilium, supraacetabular ridge, orientation: Oriented vertically or slightly cranially (0); Oriented caudodorsally (1).
371. Ilium, preacetabular process, preacetabular hook, presence: Absent (0); Present (1).
372. Ilium, preacetabular process, ventral level: Reaches the ventral level of the tip of the ischiadic peduncle (0); Terminates dorsal to the ventral level of the tip of the ischiadic peduncle (1).
373. Ilium, preacetabular process, angle of ventral margin: Oriented cranioventrally from its origin, demarcating a narrow notch between the preacetabular process and the pubic peduncle (0); Arches craniodorsally, demarcating a wide notch between the preacetabular process and the pubic peduncle (1).

374. Ilium, preacetabular process, craniodorsal notch, presence: Absent (0); Present (1).
375. Ilium, dorsal margin, shape: Smoothly convex or flat across entire length (0); Convex anteriorly and straightens out posteriorly (1).
376. Ilium, aspect ratio: Craniocaudal length is more than 3 times greater than dorsoventral height over acetabulum (0); Craniocaudal length is less than 3 times greater than dorsoventral height over acetabulum (1).
377. Ilium, dorsal margin over ischiadic peduncle, shape: Flat (0); With a concave step (1).
378. Ilium, postacetabular process, profile: Tapering along its length (0); Tongue-like, with an expanded caudodorsal region (1).
379. Ilium, postacetabular process, posterior margin, shape: Smoothly convex (0); Blunt, subrectangular (1).
380. Ilium, dorsal margin, position relative to sacral neural spines: Separated by a gap (0); Lies against sacral neural spines and opposing iliac blades may make contact above neural spines in some individuals (1).
381. Ilium, ischiadic peduncle, antitrochanter, demarcation from supraacetabular hood: Absent, the structures are smoothly confluent (0); Present, the structures are demarcated by a groove (1).
382. Ilium, supraacetabular crest, extent on pubic peduncle: Extensive, extends along most or all of the edge of the peduncle (0); Limited, discretely offset from acetabular edge of pubic peduncle (1).
383. Ilium, supraacetabular crest, size: Small, does not conceal the craniodorsal corner of the acetabulum in lateral view (0); Large, massive hood-like supraacetabular crest conceals rostradorsal corner of the acetabulum in lateral view (1).
384. Ilium, pubic peduncle, joint surface, orientation: Parallel to long axis of ilium (0); Angled distinctly craniodorsally relative to the long axis of the ilium (1).
385. Ilium, brevis fossa, medial wall, exposure in lateral view: Absent, medial wall is hidden in lateral view (0); Present, medial wall is exposed in lateral view (1).
386. Pubis, shaft, shape: Straight (0); Cranially concave (1).
387. Pubis, pubic boot, length relative to pubic shaft: Less than 50% pubic shaft length (0); Greater than 50% pubic shaft length (1).
388. Pubis, pubic boot, cranial process, length relative to caudal process: Less than 60% length of caudal process (0); Greater than 60% length of caudal process (1).
389. Pubis, pubic boot, cranial process, dorsal recurvature: Absent (0); Present (1).
390. Pubis, pubic boot, caudal process, dorsal recurvature: Absent (0); Present (1).
391. Pubis, caudal process, dorsal margin, cranial half, shape in lateral view: Straight (0); Convex (1).
392. Pubis, obturator flange, presence: Absent (0); Present (1).
393. Pubis, pubic tubercle, presence: Absent (0); Present (1).
394. Pubis, pubic tubercle, form: Present as a convexity (0); Present as a rugose flange (1).
395. Pubis, pubic tubercle, dorsoventral position: Located fully ventral to obturator notch (0); Located approximately at the level of the obturator notch (1); Located fully dorsal to obturator notch (2).
396. Ischium, ischiadic tubercle, presence: Absent (0); Present (1).
397. Ischium, ischiadic tubercle, form: Convex bulge (0); Rugose flange (1).
398. Ischium, ischiadic boot, presence: Absent (0); Present (1).
399. Ischium, ischiadic shaft, midshaft craniocaudal diameter relative to pubic midshaft craniocaudal diameter: Greater than 50% (0); Less than 50% (1).
400. Ischium, shaft, curvature: Absent, shaft straight (0); Present, shaft is cranially concave (1).

401. Femur, shaft bowing, degree: Shaft not strongly bowed (0); Shaft strongly bowed, such that the caudal margin of the femoral shaft extends cranial to the cranial margin of the femoral head (1).
402. Femur, fourth trochanter, caudal profile: Parallel to femoral shaft (0); Peaked (1).
403. Femur, adductor femoris 1 scar, presence: Absent (0); Present (1).
404. Femur, adductor femoris 1 scar, position: Central (0); Medial (1); Caudomedial extremity of shaft (2).
405. Femur, lesser trochanter, dorsal extent: Terminates further distally than the greater trochanter (0); Terminates at approximately the level of the greater trochanter (1).
406. Femur, lesser trochanter, caudal proximodistal ridge, development: Weakly developed, giving lesser trochanter a convex or D-shaped profile in proximal view (0); Strongly developed, giving lesser trochanter a distinctly pointed lateral margin in proximal view (1).
407. Femur, accessory trochanter, form: Present as a distinct flange off the lesser trochanter (0); Reduced to a subtle convexity on the cranial margin of the lesser trochanter (1).
408. Femur, primary nutrient foramen, position: Distinctly lateral to the long axis of the lesser trochanter (0); Aligned with or medial to the long axis of the lesser trochanter (1).
409. Femur, proximal margin, form: Approximately straight (0); Concave, due to a greater trochanter that is elevated substantially relative to the lateral portion of the proximal surface of the head (1).
410. Femur, distal end, medial fossa: Absent (0); Present (1).
411. Femur, distal end, medial fossa, development: Demarcated by a ridge on the cranial side only (0); Demarcated by ridges on both the cranial and the caudal sides (1).
412. Femur, mesiodistal crest, form: Single structure (0); Bifurcates distally to enclose fossa on the medial surface of the medial condyle (1).
413. Femur, mesiodistal crest, caudal division, orientation: Trends inferiorly paralleling craniomedial margin of femur (0); Trends caudally to terminate on the caudal aspect of the medial condyle (1).
414. Femur, extensor groove, form in distal view: Broad concavity (0); Deep U-shaped cleft (1).
415. Femur, crista tibiofibularis, form: Projects straight caudally (0); Medially inflected, such that the medial surface of the tibiofibular crest is concave (1).
416. Tibia, lateral proximal condyle, cranial process, presence: Absent (0); Present (1).
417. Tibia, cnemial crest, proximal extent: Cnemial crest extends farther proximally than condyles (0); Cnemial crest and condyles extend to the same approximate level proximally (1).
418. Tibia, lateral malleolus, lateral extent: Extends laterally by less than 60% width of adjacent tibial shaft (0); Extends laterally by more than 60% width of adjacent tibial shaft (1).
419. Tibia, lateral malleolus, proximodistal position: Extends to approximately the same proximodistal level as the medial malleolus (0); Extends significantly farther distally than the medial malleolus (1).
420. Fibula, iliofibularis tubercle, form: Single crest (0); Large, rugose and formed by two crests separated by a depressed fossa ("bipartite" condition) (1).
421. Fibula, medial fossa, shape: Ovoid (0); Subtriangular (1).
422. Fibula, distal half of shaft, medial groove: Absent, surface may be slightly concave but no pronounced groove is present (0); Present, surface is markedly concave due to a pronounced distal groove (1).
423. Astragalus, ascending process, mediolateral width of base: Half or less width of bone (0); Greater than half width of bone (1).
424. Astragalus, ascending process, cranial surface, fossa, form: Shallow concavity that covers most of the ventral region of the ascending process (0); Deep, triangular or ovoid fossa immediately above

midpoint of condyles, set within a broad fossa that covers most of the ventral region of the ascending process (1).

425. Metatarsus, arctometatarsus, presence: Absent, metatarsal III proximal end is exposed in cranial view (0); Present, metatarsal III is wedge-shaped and the proximal end is concealed cranially by contact of metatarsal II and metatarsal IV (1).

426. Metatarsus, metatarsal II, articular scar for metatarsal III, form: Small, entirely bounded within the cranial and caudal margins of the proximal shaft of metatarsal II in lateral view (0); Large, expands beyond cranial and caudal margins of proximal shaft of metatarsal II in lateral view, which distorts the profile of the bone (1).

427. Metatarsus, metatarsal III, distal shaft, lateral expansion, presence: Absent; lateral margin is convex or straight but there is no concavity between the shaft and distal condyles that demarcates a distinct lateral expansion (0); Present; lateral margin is convex and forms a distinct lateral expansion that is ventrally demarcated from the distal condyles by a concave lateral margin (1).

428. Metatarsus, metatarsal III, extensor fossa, medial extent: Limited to the lateral half of the distal end of metatarsal III due to extremely shallow medial development of fossa (0); Extensor fossa is well-defined across distal end of metatarsal III (1).

429. Metatarsus, metatarsal III, extensor fossa, distal margin, shape, cranial (extensor) view: Flat (0); Deeply arched, such that the extensor pit is chevron-shaped and peaks at about the mediolateral midpoint of the distal condyle (1).

430. Metatarsus, metatarsal III, distal condyle, cranial extent in medial view: Does not extend past the cranial margin of the shaft (0); Extends past the cranial margin of the shaft (1).

431. Metatarsus, metatarsal III, distal condyle, lateral margin of articular surface: Completely caps the condyle (0); Obliquely oriented and consequently incompletely caps the condyle (1).

432. Metatarsus, metatarsal III, distal condyle, position: In line with cranial margin of shaft (0); Displaced caudally due to bowed distal half of shaft (1).

433. Metatarsus, metatarsal III, distal articular surface, caudal (flexor) extent: Wraps far proximally onto the caudal (flexor) surface of metatarsal III (0); Restricted to distal end of metatarsal III, leaving a raised, subtriangular, nonarticular platform proximal to the articular surface (1).

434. Metatarsus, metatarsal IV, proximal half of shaft, medial fossa cranial (extensor) to facet for metatarsal III, presence: Absent (0); Present (1).

435. Metatarsus, metatarsal IV, length: Approximately equal in length to metatarsal II, distal condyles are approximately level with each other in articulation (0); Metatarsal IV is elongated relative to metatarsal II, with its distal condyle nearly level with that of metatarsal III and distinctly distal to that of metatarsal II (1).

436. Metatarsus, metatarsal IV, distal condyle, shape: Craniocaudally elongate, ratio of craniocaudal length to mediolateral width is greater than 1.4 (0); Intermediate, ratio of craniocaudal length to mediolateral width is between 1.2 and 1.4 (1); Craniocaudally short, ratio of craniocaudal length to mediolateral width is less than 1.2 (2).

437. Metatarsus, metatarsal IV, gastrocnemius pars lateralis insertion scar, morphology: Dorsoventrally long and narrow (0); Wide oval rugosity that covers more than half the shaft (1).

438. Pes, phalanx I-1, notch in plantar margin of proximal articular surface, presence: Absent (0); Present (1).

439. Pes, phalanx III-1, length relative to midshaft width: Greater than 3 times as long as wide (0); Less than 3 times as long as wide (1).

440. Pes, phalanx III-1, distal margin, shape, cranial (extensor) view: Deeply concave (0); Approximately flat (1).
441. Pes, phalanx IV-1, medial margin, shape in proximal view: Strongly convex (0); Approximately flat (1).

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